agronomy

Review

A Review of the Soil Seedbank from a Weed Scientists Perspective

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Abstract: Despite efforts to eliminate weeds, they continue to thrive. Weed persistence is reliant upon the soil seedbank. Knowledge of the soil seedbank is continually expanding, but with the rising threat of herbicide-resistant weeds in agriculture, weed scientists have, in the past, focused their management tactics to more short-term solutions that tackle the aboveground problems, rather than long-term solutions. This article summarized the soil seedbank dynamics of weed seeds and derives management options, from a North American weed scientists' perspective, that (i) favor the depletion of the seedbank, (ii) favor the germination of the seedbank, and (iii) reduce the possibilities of seed produced by the seedlings that germinated to return the soil. These options can potentially deter herbicide resistance and are successful in the short term for reducing field weed infestations, but are likely to take many years to affect recruitment to the weed seedbank, including recruitment of weed species with a high risk for resistance. The natural longevity of the seedbank suggests that alternative or additional weed management tactics are required to reduce the store of weed seeds in the active seedbank.

Keywords: management; weed biology; weed ecology

1. Introduction

Despite efforts to eliminate weeds, typically, they continue to thrive and weed persistence is reliant upon the soil seedbank [1]. Soil seedbanks serve as pools of genetic material that enable a range of responses to environmental conditions and buffer populations against temporary adverse environmental conditions [2]. Many weed communities are regulated by the soil seedbank [1]. Therefore, an understanding of soil seedbank dynamics is critical to the development of more efficient weed management systems [1,3]. Forcella et al. [4] postulated that, in order to reduce the chemical herbicide load to the environment, without affecting crop yield, an intimate understanding of weed ecology is necessary, including seedbank density, seed dormancy, seedling emergence, and environmental variables that regulate these factors is necessary.

The literature characterizing the soil seedbank is extensive and is continually expanding. Studies range from the spatial distribution of seeds, through simulated germination, to evolutionary consequences. While studies focus on enhancing the soil seedbank in natural systems, the weed soil seedbank, from an agronomist or weed scientist's perspective, generally focuses on the reduction of weed seeds from best management practices (BMPs) being implemented on the aboveground population [5].

The response of the weed soil seedbank to BMPs, such as weed free fields at planting, scout fields regularly, use multiple effective modes of action for weed control, use cultural and mechanical management practices when appropriate, manage weed seed at harvest, and prevent a buildup of weeds on field margins. Additionally, the economics associated with weed control is generally poorly understood by growers and academics alike. In spite of the widespread adoption of genetically modified (GM) herbicide resistant crops and the evolution of herbicide resistant (HR) weed biotypes, GM cropping systems have had only minimal effects on weed species communities [6–10]. Even though little is known about how the weed soil seedbank responds to BMPs, only limited shifts in weed composition have been reported [11,12]. There has been a call to action by researchers to evaluate the weed soil seedbank, but current research has indirectly focused on this issue by evaluating seed production via weed seed shatter and retention [13–19]. Herbicide-resistance simulation models have clearly demonstrated that the risk of resistance is proportional to the size of the soil seedbank [20,21].

2. Herbicide Resistant Weeds

Currently worldwide, there are 499 unique cases of resistance, 164 of which are found in the United States [22]. The rise in HR weeds and transgenic crop use has led to an oversimplification of weed management tactics. Growers can now apply a single active ingredient (ai) at higher rates and at multiple times in a growing season without concern to the crop [23]. Thus, the number of effective herbicide site of actions (SOAs) has declined, therefore the ecological implications, such as population shifts and the continuing evolution of HR weeds, has increased.

Even with the evolution of herbicide resistance, herbicides will continue to play an important role in weed management tactics in agriculture. Generally, weed management has not changed in more than a century [5,24,25]. However, the intensity of herbicide use has increased over the past 25 years, with a greater rate in non-genetically modified crops than in genetically modified (GM) crops; although the toxicity of herbicides used has not increased [26]. The use rate of herbicides is projected to increase further with new GM crops, along with the selection pressure for new cases of HR weeds [27,28]. For example, the introduction of new (GM) crop technologies (plant growth regulator (PGR) and HPPD-inhibitor tolerance would increase selection pressures of weed resistance to HPPD-inhibiting and PGR-inhibiting herbicides, which has been linked to metabolic resistance [29–31]. This type of resistance can potentially confer cross-resistance to other SOA groups. Recent work on metabolic resistance may change the field of crop protection, since herbicide SOA tank mixes and rotations, the foundational practices for diversifying weed management tactics, are much less effective in cases of metabolic resistance [32]. Thus, theoretically, alternation between HPPD-inhibiting and PGR-inhibiting herbicides may be selecting for the same detoxifying cytochrome p450 monooxygenase in weed populations; therefore, Integrated Weed Management (IWM) has become more important than ever [33].

3. Seedbank Dynamics

There are two general types of a seedbank: Transient and persistent [34]. A transient seedbank is defined as one in which seeds do not live until the second germination season following maturation, whereas seeds in a persistent seedbank live until the second or subsequent germination season [35]. Weed scientists, as a whole, are more interested in the persistent than transient seedbank. Weed species that form persistent seedbanks are a concern for future weed management. The persistence of viable seeds in the soil seedbank depends on a wide range of interacting factors, such as production practices and environmental conditions [21,36]. Factors include germination cues, seed dormancy, seed size, physiological age, predation, microbial decay, environmental conditions, burial depth, burial duration, and tillage [37–42]. Reducing the number of germinable seeds will decrease the number of individuals that will be subjected to weed management operations, which would influence HR development, and the number of escapes that could replenish the soil seedbank [42].

Longevity of seeds in the soil is the most determinant factor for the success of future generations. The persistence and viability of some weed species after long burial periods is well documented [43,44]. For example, morninngglories (*Ipomoea* spp.), can persist in the soil seedbank for at least 39 years [45]. In the absence of seed return, some weed species like common cocklebur

(*Xanthium strumarium* L.), *Sisybrium orientale* L., prickly sida (*Sida spinosa* L.), spurges (*Euphorbia* spp.), waterhemp (*Amaranthus tuberculatus*), and redroot pigweed (*Amaranthus retroflexus* L.) will approach exhaustion by 3 to 4 years [46–48]. However, the majority of weed species lose seed viability after relatively short periods of burial. This is true particularly for small-sized seeds such as Palmer amaranth (*Amaranthus palmeri*) or waterhemp [43,49–52]. The literature, however, seems to vary considerably on this, ranging from 1 to 40 years [36,45,51,53–57]. Studies have indicated that the seedbank can be reduced by at least 90% within four years if little to no seed is returned to the soil [58,59]. Furthermore, Burnside et al. [60], reported that when weed seed return was prevented, soil weed seedbank declined by 95% over a 5-year study period (20 seed to 1 seed 454 g^{-1} soil). However, one year without weed control following 5 years without any weed seeds returning to the soil seedbank was sufficient to replenish the weed seedbank population at two of five locations. This illustrates that, in order to maintain low soil seedbank levels, an effective weed management program must be utilized. In order to accomplish this level of decline appropriate weed management tactics must be employed for the target weed species that minimize seed return.

Consequently, weed seedbanks can replenish quickly. Furthermore, Williams and Harvey [61] conducted a field experiment with wild-proso millet (*Panicum miliaceum* L.) between 1988 and 1993 to determine the seed number that could be returned to the soil without further increasing the seedbank population. Simulated seed rain treatments included 0, 3, 6, 12, 24, and 48% of the initial seedbank (15,300 seed m^{-2}) returned each fall. By 1993 >90% of the original wild-proso millet seedbank population had been depleted for all treatments. It was estimated that 68% of the seedbank and 77% of the seed rain was lost each year. These studies and others indicate the same outcome of increased seedbanks when weed populations are not controlled. While growers already use some level of BMPs, minimizing weed escapes from setting seed should be a priority.

4. Management Implications

For a weed management program to be successful, a weed species biology and ecology must be understood [4,62]. Ideally, weed management decisions should focus on managing weed populations over time instead of minimizing the yield effect of weeds in a single growing season [63]. The seedbank can be managed by (1) increasing seed mortality, (2) manipulating seed germination or emergence, (3) removing aboveground weeds, or (4) reducing seed production. Objectives for long-term seedbank management include maintaining the seedbank at some level that requires similar annual weed management inputs or initiating practices that promote a decline in soil seedbank density [64]. A decline in soil seedbank density would require a weed seed production below the seedbank replacement value. Additional research in this area would be valuable for sustainable weed management practices and could help save producers money as well as reduce the pesticide load in the environment. Herbicide resistant weeds, however, hinder this process because allowing any seed return could lead to control failures and increased selection pressure on effective postemergence herbicides. Managing weed populations by focusing on reducing the soil seedbank number will likely add additional input costs for producers. Future research must show that the investment of managing the soil seedbank will eventually provide an economic return, such as a reduction in future weed control costs, due to a reduced soil seedbank, or crop yield increases. Jones and Medd [63] compared a population management strategy to a static economic threshold management strategy using a model with a 20-year time horizon. They reported that the economic benefits from a population management strategy was greater and the final seedbank numbers lower than that of the economic threshold strategy. Weed management strategies incorporating BMPs to reduce the risk of herbicide-resistant weeds should be multifaceted and include cultural, mechanical, and chemical control options that will prevent an influx of seeds into the soil seedbank.

4.1. Mechanical Weed Management

Soil cultivation alters the soil physical properties, often exposing seeds to conditions favorable for germination and therefore seedbank reduction, as long as the weeds are controlled [65,66]. Tillage system and type of tillage can influence the specific composition and/or density of the soil seedbank [65,67–72]. Species diversity is also greater for no-till, minimum till, low input, and organic production systems compared to conventional tillage [72,73]. Many studies report, higher seedbank/weed populations associated with no-till and generally decline as tillage intensity increases [67,68,72,73]. However, other studies report that weed seedbank densities in no-till systems are significantly less compared to conventional till [66,70]. Similarly, Popay et al. [74] reported that, over a seven-year period, 24,000 fewer weeds emerged in no-till plots compared to deep cultivated plots.

The largest quantities of seed are typically found in the top 10 cm of the soil profile [67,69,70]. Typically, the extent and depth of seed distribution in the soil profile is directly related to the amount of soil disturbance [71], which can be influenced by the type of cultivation implement and tillage system [67,69–71]. However, this is not always the case [75]. Furthermore, small seeds are more likely to become buried than large weed seeds. Whether buried seeds contribute to soil seedbank persistence and weed population regeneration depends on the depth from which the seeds can germinate [42]. The importance of soil tillage has been mentioned as a primary tool for the depletion of seedbank persistence. Various studies [71,73] reported that conservation or no-till systems, where seed density is the greatest in the top 5 cm of soil, resulted in reductions of weed populations and seedbank depletion. However, accumulation of seeds on soil surface in reduced-tillage cropping systems could increase seed mortality due to increased seed predation [76]. Intensive soil cultivation, such as moldboard plowing, that turns the soil up to 20 cm, has a more uniform distribution of seed in the soil profile. Lack of soil disturbance via tillage could also encourage higher predator populations, as it enhances the number, diversity, and/or activity of seed-consumption [77,78].

An alternative mechanical weed management tactic that influences the soil seedbank is harvest weed seed control (HWSC) that targets escaped weed seeds at grain harvest. There are six main types of HWSC: 1. Chaff carts, 2. Bale-direct systems, 3. Mill systems (e.x. Integrated Harrington Seed Destructor (iHSD)), 4. Narrow windrow burning, 5. Chaff lining, and 6. Chaff tramlining [14]. The efficacy of HWSC on dominant weed species has been tested in some form across the US, Europe, and Australia with success. In the US, the potential for processing soybean (*Glycine max* Merr.) chaff sufficiently with the iHSD to target the seeds of the major weed species of soybean production systems has been established. This testing examined 12 weed species, broadleaves and grasses with seed sizes ranging from 0.5 to 7.6 mm [79]. The impact mill demonstrated high weed seed destruction efficacy (>99%) for 11 of the 12 weed species. Furthermore, a 3-year large scale field trial examined the impact of combinations of herbicide programs and HWSC tactics on Palmer amaranth density in soybean. Overall, an effective herbicide program coupled with HWSC reduced the number of Palmer amaranth plants over time. Narrow-windrow burning appears to be more effective than the chaff cart treatment and similar to standard tillage practices [80]. These studies demonstrated that the most effective way to control dominant weed species is through the use of multiple, effective management practices, which include a robust herbicide program with multiple sites of action and non-herbicidal management practices. The limitation with the current methods of HSWC is that they are used only in grain crops. This limitation can be partly overcome by crop rotations where non-grain crops are in production. This illustrates further that integrated weed control methods must be employed for successful long-term weed management.

4.2. Cultural Weed Management

An ecologically based weed management program promotes cultural practices that enhance the natural loss of weed seeds in the soil, decreases weed establishment, and reduces seed production by individual plants. Categories of cultural practices include crop rotation design, crop sequencing, no-till, crop residue management, and competitive crop canopies [81].

4.2.1. Crop Rotation.

Crop rotation has long been recognized as one of the most fundament and effective weed management tools [82–84]. Crop rotations of winter and summer annual crops can benefit weed management [85]. Planting and harvest date differences among crops in a rotation provide opportunities to prevent weed establishment or seed production. Growing crops with different life cycles in a rotation favors the natural loss of weed seeds across time by preventing seed return [81]. In addition, growing crops with diverse characteristics disrupts weed life cycles and prevents any single weed from becoming adapted to a cropping system. Simple rotations of crops with different characteristics, however, may not be sufficient to provide weed control benefits [83]. For instance, weed density has been shown to increase in rotations consisting of one cool-season crop followed by one warm-season crop [83,86]. In addition, the sequence of a given set of crops in rotation can play an important role in managing weed populations [87].

Strategic crop rotations can be a cultural weed management tactic that reduces the requirement for direct control methods such as cultivation and herbicides [82]. Anderson [85] showed that rotations can be designed to balance the frequency of seed production with seedbank decline of annual weeds. Crop rotation designs that included a two-year interval, where seed production of the target weed is prevented, greatly reduced weed populations. The most beneficial rotation sequences for weed management included four different crops in sequences of two cool-season crops followed by two warm season crops [86]. Therefore, eliminating seed production of cool-season weeds during the two-year warm-season crop cycle, populations of the cool-season weed will be reduced significantly by year three when a cool-season crop is grown [81]. The basis for this rotation sequence to work is related to the rapid loss of viable seed in the seedbank during the first two years after seed rain [82,85]. If the same crop was grown in consecutive years, however, the benefit of the rotation design on weed density was reduced considerably. Anderson [85] concluded that crop rotation designs that utilize balanced life-cycle intervals reduce weed density, allows producers to use alternative weed management strategies, improve herbicide efficacy, and minimize herbicide resistance. Within a life-cycle category, such as warm-season crops, diversifying crops with different planting dates (e.x. corn (*Zea mays* L.) to sunflower (*Helianthus annus* L.)) enhances the benefit of rotations comprised of two-year intervals of cool- and warm-season crops [81,83]. Diverse three to four-year crop rotations where reduced inputs were applied have been shown to provide similar weed suppression compared to conventionally managed two-year rotations because of increased stress and mortality factors [88,89]. There is evidence in the literature to support the benefit of having cereal crops in a rotation plan [81,90–92]. Doucet et al. [90] reported that within herbicide treated plots weed densities were higher following corn and lower when a cereal crop was included in the rotation. Likewise, Schreiber [92] showed that in non-treated areas in no-till plots a soybean to wheat (*Triticum aestivum* L.) to corn rotation was able to eliminate giant foxtail (*Seteria faberi* Herrm.) from the area. Crop stacking is another rotation approach that can reduce weed seedbank densities [82]. Their study showed that crop stacking in rotations was able to reduce the total number of weed seeds. They concluded that stacked rotations result in stronger weed competition because each switch to a different crop type can change which weed performs better. Higher stacking numbers allow the effects of a certain crop to have time to accumulate and keep overall weed populations lower.

While cultivation and crop rotation have an impact on the species composition and density of the seedbank, it is difficult to generalize how species will respond because most studies have many factors (tillage, level of herbicide use, crop rotation, location, etc.) that are interacting to influence seedbank dynamics. For instance, Légère and Samson [93] reported that species dominance in various cropping systems was mostly explained by interactions among weed management intensity, tillage, and crop rotation. Some studies suggest that crop rotation may be more important than tillage in determining seedbank density and/or composition [65,67,94,95]. Still yet, Derksen et al. [95] concluded that location and year were more important than tillage in determining weed community shifts.

4.2.2. Crop Sequences.

Crop sequences determine the time and type of tillage operations and herbicide use [65]. Crop management systems (rotation and tillage) have been shown to be the most important variable influencing weed density [96,97]. Several studies indicate that weed seed survival across time is reduced by no-till systems and rotations that include cool-season crops [98,99]. Herbicides used in a cropping sequence can shift the weed seedbank in favor of species less susceptible to the applied herbicides [67]. These factors contribute to how a crop rotation sequence will influence species composition and seedbank dynamics. The complexity of the interaction between location, crop rotation, herbicide use patterns and selection, tillage methods, weather patterns, and weed species dynamics, indicates crop management practices need to be developed for major weed species in a given geographic area. Review of the literature indicates that no single agronomic input (crop rotation, herbicide program, tillage system, etc.) can provide long-term weed control. All available tools must be organized into a sound systems approach in order to achieve long-term weed management.

4.2.3. Intercropping.

Research has shown that the use of cover crops, a stale seedbed, soil amendments, and the return of residues to the soil may compensate for any negative effect of tillage [100,101], and rotational tillage systems with cover crops or manure may reach higher levels of organic matter than no-till systems [102]. However, there seems to be a movement away from tillage and towards the use of high biomass cover crop residue to control weeds in organic systems. Weed suppression in no-till systems using cover crop biomass only became possible with the introduction of the roller-crimper [103]. The use of cereal rye (*Secale cereale* L.) forms the basis for this strategy in soybean, specifically, with mechanical termination and the use of a roller-crimper. Greater than 8000 kg ha^{-1} has been determined to be the threshold for annual weed suppression, with challenges posed by early-emerging annual weeds, high seedbank densities of weeds (over 10,000 seeds m^{-2}), and perennial species [103]. While adoption of cover crops is increasing, there is still grower resistance to implementation. In a survey of US grower's perceptions on herbicide resistance management, growers have suggested that cover crops can present challenges, and there are few available profitable crops to rotate with cash crops [104], even though diversity in crop rotations is recognized as an effective herbicide resistance management tactic [5]. Another seed suppression method is the use of stale seedbeds, which creates an additional lapse between seedbed preparation and seeding germination [105]. The first weed flush can therefore be easily controlled.

4.2.4. Additional Factors.

Additional cultural weed management tactics, such as planting date and irrigation can increase the number of germinable weed seed present in the soil seedbank. Temperatures typically increase, for spring sown crops, throughout the growing season, thus as planting date increases so does temperature. Germination of weed seed and time of emergence are greatly affected by temperature [106]. The effects of temperature on seed germination of nine *Amaranthus* species were examined under varying temperature regimens [106]. All species reached 50% germination within 3 to 8 days at 20 °C, germination increased for Palmer amaranth only at higher temperatures. Furthermore, fluctuations in seasonal temperature can affect primary or secondary dormancy of seeds that might influence their germination rate, ultimately reducing the soil seedbank [107]. An irrigation event following a tillage application/treatment can influence germination of weed seeds. This coupled with a timely herbicide application can effectively control weed species and deplete the seedbank [108,109].

4.3. Chemical Weed Management

Soil weed seed densities can also influence the effectiveness of preemergence and postemergence weed control tactics [110–112]. It has been shown that the interaction between initial weed seedling density, postemergence herbicide, and mechanical weed control provides a positive linear relationship between initial seedling density and density of surviving seedlings [113]. Furthermore, the development of effective management strategies that reduce weed fecundity, will be aided by species-level information that identify tactics most appropriate for a given weed spectrum. Research has demonstrated that herbicides applied at early flower or pod set can reduce potential seedbank replenishment [114–119]. Additionally, seed weight reduction, seed viability, and seedling recruitment can affect the presence of plant species in the following season [118]. As seedbanks are composed of a few dominant weed species [67], weed management strategies should be customized to those particular species. This illustrates the importance of managing weed seed return for effective weed management.

Additionally, some weeds are capable of setting viable seeds within 30 days after emergence during late summer and early fall [120,121]. Post-harvest weed control is especially important when combatting HR weeds. Problem fields should be identified and receive top priority for preventing seed return to the soil seedbank. Fields should then be regularly scouted for emerged weeds and additional control tactics applied prior to seed set. This will require close inspection of weed species to determine when they are flowering. Once weed species are observed in a flowering state, a weed control operation should be implemented. Depending on weather conditions following harvest, weed control tactics may need to be implemented approximately every 3 to 4 weeks until a killing frost has occurred. Plant back restrictions for specific crops should be checked on the herbicide label as well. If HR weeds are an issue, a BMP tactic such as mowing, tillage, cover crops, crop rotation, or herbicide application should be employed

5. Economic Constraints

The economic implications from the loss of effective herbicide modes of action are staggering. Corn, soybean, cotton (*Gossypium hirsutum* L.), and rice (*Oryza sativa* L.) contribute roughly $130 billion in total revenues [122]. It has been estimated that it costs an additional $40, $52, and $74 per hectare for corn, soybean, and cotton, respectively, to control HR weeds [123]. Growers and crop consultants are primarily concerned with controlling HR weeds and the associated cost [120,121]. Other important factors included return profit, time constraints, and application timing. In addition, by the time resistance is recognized, weeds have grown out of the stage of effective control with other post-emergence herbicides [124]. Furthermore, grower budgets are typically tight in the fall and spending additional money on weed control when no crops are in the field is difficult, but by identifying fields in need of post-harvest weed management and by implementing field preparation in a timely, well-spaced manner can go a long way in reducing future weed numbers in fields. However, the cost to bring a new herbicide to market is estimated to be $286 million [104]. Thus, most agro-chemical companies research dollars are not invested to develop new herbicide modes of action but rather are using old herbicides in new ways by engineering HR traits in GM crops. Furthermore, socio-economic conditions determine the feasibility of control measures.

6. Conclusions

Recommendations that promote BMPs to delay herbicide resistance are successful in the short term for reducing field weed infestations while maintaining robust crop yield potential, but are likely to take many years to affect recruitment from the weed seedbank, especially with continual inputs into the seedbank, including recruitment of weed species with a high risk for resistance. The natural longevity of the seedbank suggests that alternative or additional weed management tactics are required to reduce the store of weed seeds in the active seedbank. Management strategies need to be developed that are targeted towards reducing the number of weed species on a species-by-species basis, considering the geography and cropping system.

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