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Weed dynamics and conservation agriculture principles: A review

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ABSTRACT

Conservation agriculture (CA) is based on minimum soil disturbance, permanent soil cover, and crop rotation; it is promoted as a sustainable alternative to systems involving conventional tillage. Adoption of CA changes weed dynamics and communities and therefore necessitates adjusting weed control methods. The objectives of this review are to summarize literature concerning CA principles and their interactive effects on weed life cycles and community composition, briefly review CA-appropriate cultural practices for additional weed control, and identify areas where further research is needed. No-till systems accumulate seeds near the soil surface where they are more likely to germinate but are also exposed to greater mortality risks through weather variability and predation. Assuming no seed input into the system, germinable seedbanks under no-till decrease more rapidly than under conventional tillage. Reducing tillage may shift weed communities from annual dicots to grassy annuals and perennials. Surface residues lower average soil temperatures and may delay emergence of both crops and weeds. Germination and growth of small-seeded annuals will suffer from restricted light availability, physical growth barriers and potential allelopathic effects from surface residue. Crop rotation affects weeds via allelopathy and altered timing of both crop management and resource demands. Rotations should incorporate crops sown in varied seasons (e.g., autumn and spring), annuals and perennials, different herbicides, and/or various crop families. Literature indicates implementing no-till without crop rotation can result in severe weed problems; greater rotational crop diversity results in easier weed management. Additional cultural practices for CA include: (i) selecting highly competitive varieties; (ii) altering planting dates; (iii) preventing weed seed recruitment; (iv) adjusting planting arrangement, densities, and fertilizer placement; and (v) microbial bio-controls. Further research is needed concerning: (i) the interactive effects of tillage and surface residue on weeds; (ii) the use of models and/or meta-analyses to predict weed responses, and to identify intervention points in CA; and (iii) the weed-suppressive potential of longer (4+ years) rotations.

Contents

Abbreviations: CA, conservation agriculture; NT, no-tillzero-tillage; CT, conventional tillage; NT+Res, no-till with surface residue retained; CT+Res, conventional tillage with residue incorporated; US, United States.

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1. Introduction

Conservation agriculture (CA) in its simplest form includes minimum soil disturbance, permanent soil cover, and crop rotation (Hobbs, 2007). Although benefits are context specific, CA has been identified as an effective tool for sustainably increasing yields in many parts of the world (Hobbs et al., 2008; Pittelkow et al., 2015). Producers adopting CA will face several managerial changes, and weed control is perceived as one of the most challenging (Derksen et al., 2002; Wall, 2007; Giller et al., 2009; Farooq et al., 2011). Weed pressure and crop yield are inversely related; weed management is therefore crucial to achieving the potential yield gains offered by CA systems. Under CA weed control via tillage is no longer an option, and weed communities and growth dynamics will change compared to under conventional tillage systems; the methods of weed control under CA will likewise need to be adjusted. Information on what CA adopters should expect and effective tactics for controlling weeds in CA systems are needed.

There are very few studies that systematically examine both the direct and interactive effects of the three CA principles on weed dynamics (Chauhan et al., 2012; Giller et al., 2009; Farooq et al., 2011). These types of studies are needed so that weed control can be included in cost-benefit analyses concerning the adoption of each practice (e.g. Beuchelt et al., 2015) and be incorporated into analytical models of weed dynamics. However, there is a substantial body of literature concerning the use of each principle outside the context of CA. Here we review the literature to summarize current knowledge and to identify knowledge gaps. Additionally, this information can be used to provide guidance for CA practitioners during the adoption and sustained use of CA principles, whether the adoption is partial or complete.

We have organized this review using an ecologically-based framework for weed management. A basic representation of stocks and flows in an annual weed's lifecycle (Fig. 1) corresponds to four possible areas of intervention:

(1) Inducing dormancy and enhancing natural loss of viable weed seeds in and on the soil.
(2) Manipulating weed seedling establishment.
(3) Minimizing seed production by established plants.
(4) Preventing seed dispersal and recruitment.

Biennial and perennial weed lifecycles will differ from Fig. 1, but the basic stock and flow framework still applies. We examine

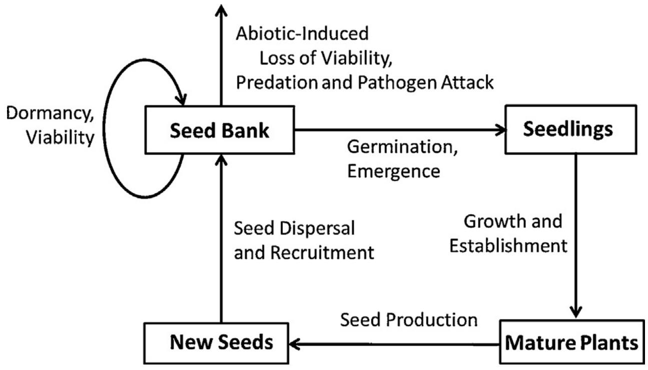

Fig. 1. Simplified conceptual representation of transitions among annual weed states.

literature concerning the effect of each CA principle on the transitions between weed states, as well as how each principle may affect the weed community as a whole. We then summarize the literature that looks at interactions between CA practices. We present a brief overview of practices that may offer additional weed control for CA practitioners. Based on the reviewed literature we provide recommendations for CA weed control during both the transition to and continued use of CA principles. Finally, we identify areas that would benefit from further research. We consider only agronomic cash crop rotations grown in spatial monoculture; practices such as intercropping and cover cropping are not considered in this review.

It should be noted that the effect of weeds need not be considered negative in all cases. They can contribute ground cover, nutrient stabilization, pest predator habitat, nutritious food sources, and do not necessarily reduce yield. However, even small weed populations can leave a lasting legacy of infestations; when considering long-term management tolerable weed levels are quite low.

2. Tillage practice

Minimum soil disturbance includes a range of tillage regimes and its exact definition is usually context specific. For the purposes of this review we refer to any practice where the entire soil surface is disturbed at least once during the growing season as conventional tillage (CT). Differentiation is made between zero soil disturbance (no-till; NT) and minimum or reduced tillage when applicable.

2.1. Effect of tillage practices on the weed seedbank

2.1.1. Size of weed seedbank

The effect of tillage on the size of the weed seedbank depends on many factors (Mohler, 1993). As a result, empirical studies produce contradicting outcomes, with studies showing tillage has no effect on (Bàrberi et al., 2001), reduces (Clements et al., 1996; Murphy et al., 2006), or increases (Ball, 1992; Moyer et al., 1994; Dorado et al., 1999; Cardina et al., 2002; Sosnoskie et al., 2006) weed seedbank densities. Several studies show that the weed seedbank response to tillage depends on the weed species (Moyer et al., 1994; Buhler et al., 1996; Farooq et al., 2011), and Mohler (1993) noted that weed response to tillage involves a complex interaction between factors such as weather, duration of experiment, and long-term field history. The initial state and distribution of the weed seedbank also strongly influences study results, but can be time-consuming and difficult to measure and are therefore rarely reported (Mohler, 2001d).

2.1.2. Vertical distribution of weed seeds

The vertical distribution of seeds will dictate which seeds produce potentially crop-competitive weeds. The effect of tillage on the distribution of seeds in the soil profile is simpler than the effect on seed bank size; regardless of soil type, tillage redistributes seeds throughout the soil profile. In NT soils, seeds infiltrate the soil via very slow processes (cracks, fauna, freeze-dry cycles), resulting in an accumulation of weed seeds (60–90%) in the top 5 cm of the soil (Yenish et al., 1992; Hoffman et al., 1998; Bàrberi et al., 2001). Common tillage regimes have generalized patterns of seed distributions (Ball, 1992; Mohler, 1993; Dorado et al., 1999;Fig. 2). Tillage-induced changes in seed distribution therefore indirectly affect germination (Section 2.1.3.1) and seedling establishment (Section 2.2).

2.1.3. Germination of weed seeds

Tilled soils offer better germination environments for most seeds both physically and chemically, as the soils are more aerated, warmer, and experience larger temperature fluctuations (Mohler, 2001a). Tillage itself provides germination stimulus for weeds requiring light flashes, scarification, fluctuating temperatures, ambient (rather than elevated) CO_2 concentrations, and/or higher nitrate concentrations to break dormancy (Benech-Arnold et al., 2000).

Regardless of the tillage regime, in non-moisture limiting conditions germination stimulus is generally higher near the soil surface (light-rich with diurnal temperature fluctuations) and decreases with depth (dark with buffered temperature changes). Because NT seedbanks are concentrated in the top layer of the soil (Fig. 2a) a higher proportion of NT seedbanks will germinate compared with CT seedbanks (Gallandt et al., 2004).

2.1.4. Predation of weed seeds

Insects, rodents, and birds can consume a significant amount of weed seed in agricultural landscapes both before and after dispersal from the parent plant, and therefore represent a potentially valuable tool for reducing seedbank size (Harrison et al., 2003; Anderson, 2005; Jacob et al., 2006; Chauhan et al., 2010). Seed predation appears to be limited by the amount of accessible seed (Westerman et al., 2006) and seed burial decreases availability to predators (Hume et al., 1991). In theory, surface accumulation of seeds under NT (Fig. 2a) would increase predator access to seeds and therefore could increase their removal rates. Lack of soil disturbance via tillage could also encourage higher predator populations.

Studies have reported increased number, diversity, or activity of seed-consuming fauna in NT fields as compared to conventionally managed fields (Brust and House, 1988; Cléments et al., 1994; Trichard et al., 2014; Blubaugh and Kaplan, 2015). Other studies have found no difference (Cardina et al., 1996; Cromar et al., 1999), but both of these studies were conducted in plots less than 0.3 ha in size which may not have been large enough to detect differences due to the mobility of predators (Menalled et al., 2006). The reported increases in numbers of predators may be due to both increased habitat (Díaz, 1991; Kromp, 1999; Cunningham et al., 2004; Baraibar et al., 2009) or decreased tillage-induced mortality (Thorbek and Bilde, 2004; Shearin et al., 2007). Overall, adoption of NT may encourage seed losses via predation by both increasing the proportion of seed available to predators and by minimizing mortality and/or forced relocation of granivores.

2.1.5. Viability of weed seeds

Tillage-induced changes in seed distribution (Fig. 2) will also have implications for seed viability. Burial increases seed survival (Froud-Williams et al., 1984; Mohler and Galford, 1997), while seeds on or close to the soil surface can lose viability due to desiccation and harsh weather (Moyer et al., 1994; Anderson, 2005). Therefore, depending on the extremity of the environment, the accumulation of seeds on un-tilled soil surfaces may increase the proportion of un-viable weed seeds in the seedbank.

2.2. Effect of tillage practice on the growth and establishment of germinated weeds

Tillage reduces resistance to root and seedling penetration, which affects the growth and establishment of germinated weed seeds (Ensminger, 1994; Verhulst et al., 2010). The reduced resistance in tilled soils translates to a higher probability of a germinated seed succesfully emerging (Mohler, 1993; Mohler and Galford, 1997; Grundy et al., 2003). Tilled soils also allow seedlings to emerge from deeper in the soil compared to un-tilled soils (Froud-Williams et al., 1984; Buhler and Mester, 1991; Mohler and Galford, 1997; Chhokar et al., 2007; Franke et al., 2007). In addition to seedling emergence, seedling establishment is affected by tillage. If located directly on the surface of un-tilled soils, the radicle of

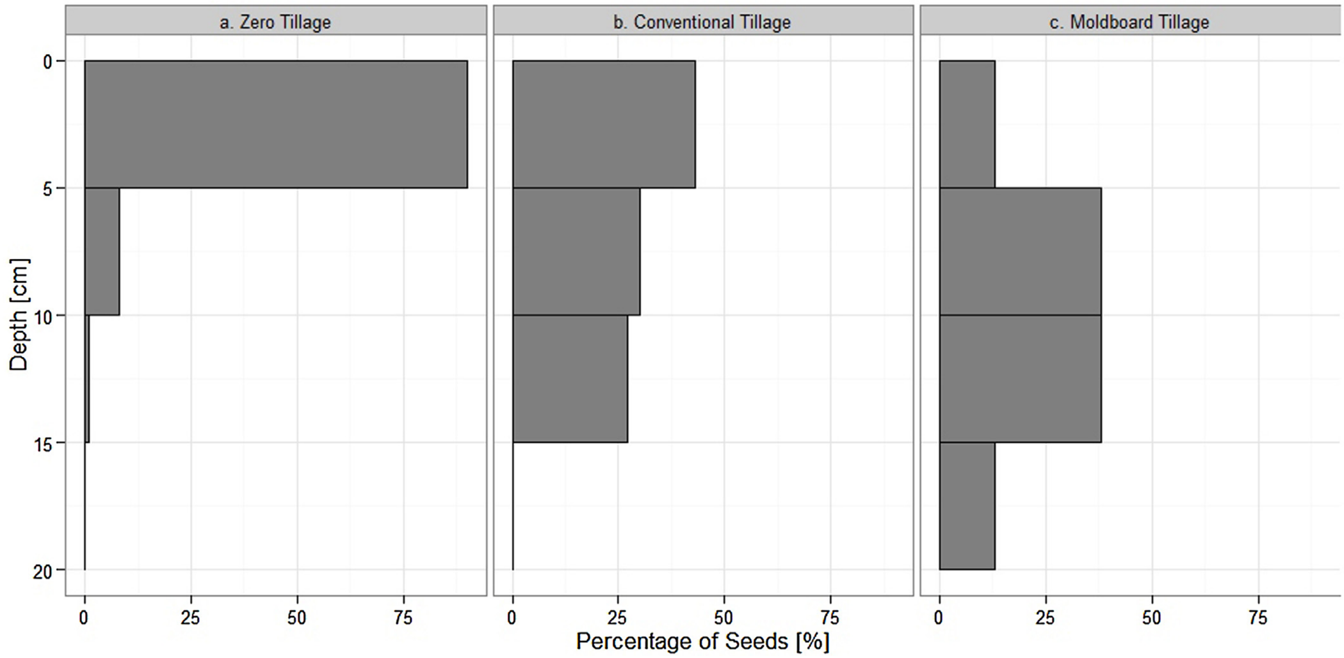

Fig. 2. Theoretical seed distribution in year one following seed rain in (a) zero tillage systems[1], (b) conventional tillage[2] to a depth of 15 cm, (c) moldboard tillage[3] to a depth of 20 cm.[1] based on equations from Mohler (1993) assuming a 0.4 rate of decline in seed density; [2]average values from equations representing rotary tillage from Mohler (1993) and reported values from chisel plowing from Ball (1992); [3]based on equations from Mohler (1993) and results from Dorado et al. (1999).

germinated weed seeds may have difficultly penetrating NT soil surfaces, resulting in lethal germination (Mohler, 2001d).

Models can help elucidate how these observations translate on a cropping systems level. Mohler (1993) constructed an analytical model to explore how seed characteristics (dormancy, emergence vigor, and surface-survival) influenced seedling emergence under different tillage systems. Assuming a seed rain in year zero followed by tillage, he found that for most plausible seed characteristics the number of emerged seedlings in the first year of NT was higher than all other tillage systems. However, with the assumption of no new seed input in year two, in following years the model predicted that tilled soils would almost always have more emerged seedlings compared to NT soils starting in year two. Additionally, again assuming no seedbank replenishment, over time the NT systems exhausted germinable seedbanks more quickly (Fig. 3).

Completely eliminating weed seed production and recruitment is unrealistic, but this model conceptually demonstrates how, if seed input is controlled, NT conditions will quickly reduce the germinable weed seedbank stock (Fig. 1). Many field-based experiments have produced results in accordance with the model's predictions (see references within Mohler, 2001d; Gallandt et al., 2004; Anderson, 2005; Mwale, 2009; Pittelkow et al., 2012). However, there are studies that show persistent weed problems in NT compared to CT even after several years (Anderson et al., 1998; Menalled et al., 2001), re-emphasizing that other management factors are important as well. Nonetheless, if carefully managed, the germination and emergence of a high proportion of the weed seed bank during the first year of NT can be used as an opportunity for long-term weed control (Egley and Williams, 1990; Buhler et al., 1997).

2.3. *Effect of tillage practice on production, dispersal, and recruitment of weed seed*

Tillage is a mechanical method of weed control that can kill live weeds before they reproduce, thus preventing seed production; it is a useful tool for controlling established weed populations. In select NT systems there is still the opportunity for weed control via mechanical soil disturbance, an example being the reshaping of permanently raised beds (see Govaerts et al., 2007). However in general, once a weed is established in NT fields, options for termination before seed-set are limited to herbicides, hand weeding, or relying on field traffic (planting, fertilizing, harvesting, etc.). The soil structure and environment from which a weed seedling emerges may affect its seed production; however the effect is likely inconsequential. In one study Clements et al. (1996) found seed production of common lambsquarters (*Chenopodium album* L.) on a per plant basis was the same across four tillage systems. The number of weeds is likely a more important metric compared to the number of seeds produced per weed. In NT systems, preventing weed establishment may therefore be more crucial in preventing weed seed production than in tilled systems.

Seed dispersal and recruitment may be affected by tillage practice. Field traffic and machinery operations such as tillage provide opportunities to introduce or spread weed seeds (Schippers et al., 1993; Buhler et al., 1997). One study showed cultivation following harvest significantly increased weed seed dispersal (Heijting et al., 2009), and another found the weed seeds travelled 2–3 m in the direction of tillage, while in un-tilled soils the distance was negligible (Barroso et al., 2006). Reducing tillage can therefore reduce the spread of weed seed both within and across fields.

2.4. *Effect of tillage practice on the weed community*

Weed control involves the management of weed communities—therefore changes in weed community composition and diversity are important to identify. Crop management strongly influences weed communities and a change in tillage is expected to have a pronounced effect on the weed community.

2.4.1. *Composition and diversity of weed species*

Changing tillage regimes changes the disturbance frequency of the farm field, which results in a shift in weed species (Pollard and Cussans, 1981; Buhler et al., 1994; Clements et al., 1994; Swanton

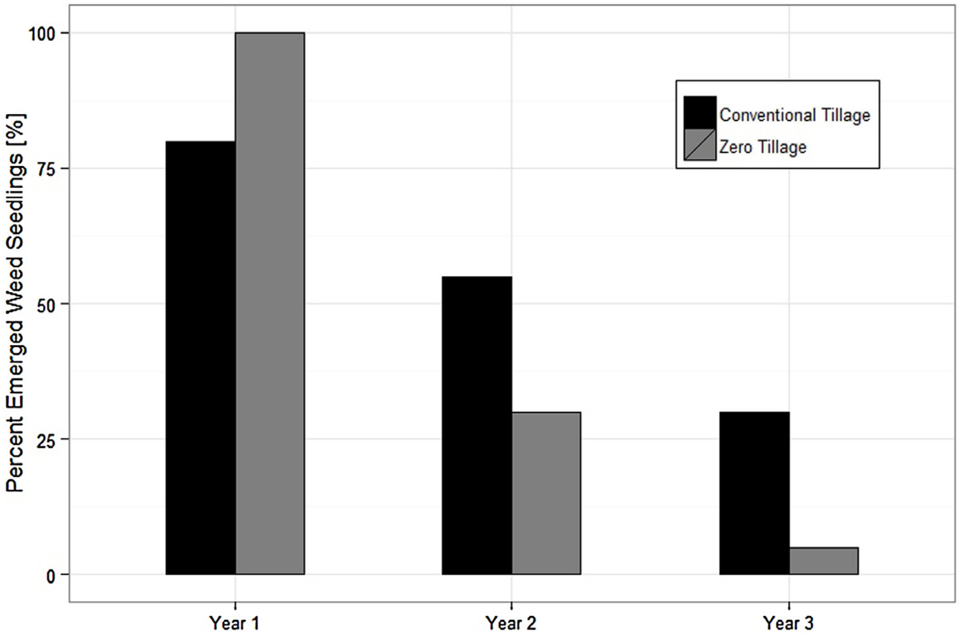

Fig. 3. Theoretical effect of tillage on number of emerged weed seedlings (expressed as a percentage of highest number of emerged weeds observed) over time assuming zero seed rain, adapted from Anderson (2005).

et al., 1999; Erenstein and Laxmi, 2008; Boscutti et al., 2015). Because NT fields mimic pasture or roadside conditions, weeds may spread more easily from these environments (Froud-Williams et al., 1981; Tuesca et al., 2001). As NT can favor certain granivore species over others, the associated shift in preferred seed consumption may contribute to altered seedbank composition (Brust and House, 1988). Volunteer crops may become an issue in NT systems (Derksen et al., 1993), although this depends heavily on the crop rotation (Derksen et al., 1994).

While there is consensus that the weed species composition will shift in response to changes in tillage, whether the diversity of the weed community increases is less clear. Ecologically, highly disturbed environments will tend to be simpler than more stable ones. Compared to tilled soils, higher weed species diversity has been observed in NT seedbanks (Cardina et al., 2002; Sosnoskie et al., 2006) emerged weed communities (Derksen et al., 1993; Menalled et al., 2001) or both (Murphy et al., 2006). Studies that report no increase in diversity with NT all found either crop rotation or weather had a larger effect on weed species diversity. While tillage will contribute to community shifts, the weed species present will be an expression of both management and the environment, which in many cases may be simply the weather (Stevenson et al., 1997; Legere et al., 2005; Plaza et al., 2011; Boscutti et al., 2015).

2.4.2. *Perennial vs. annual weeds*

The common assumption that NT systems favor perennial weeds may be true in some cases but is by no means universal. Ecological succession theory suggests perennials will come to dominate undisturbed systems. Indeed high disturbance environments such as CT systems have been shown to favor annual broadleaves, while lower disturbance NT systems favor perennial weeds and species that can successfully germinate on the soil surface such as annual grasses (Hume et al., 1991; Moyer et al., 1994; Bàrberi et al., 2001; Menalled et al., 2001; Tuesca et al., 2001; Taa et al., 2004). However in a literature review Moyer et al. (1994) found there are certain weeds (both annual and perennial) that thrive in NT systems and others which are suppressed. This may be because NT systems still experience periodic disturbance via field activities and depending on the timing, activities that damage or remove above ground material (e.g. harvest) can effectively kill perennials (Mohler, 2001b). In another review, researchers found no consistent trend in long-term tillage studies regarding increases in perennial weeds, and concluded that changes in weed management often associated with crop rotation plays a large role in dictating weed communities (Swanton et al., 1993). Reduced tillage may amplify the selection of weed species whose lifecycles and resource demands complement those of the agronomic crop, regardless of annual or perennial classification (Chancellor, 1985; Dorado et al., 1999). Indeed there are reports where changing to NT in rotations including two or more crops did not result in an increase in perennial weeds (Derksen et al., 1993; Blackshaw et al., 2001; Tuesca et al., 2001). This emphasizes the importance of crop rotation in weed management, especially in reduced tillage systems (Section 4).

3. Crop residues

Crop residue may be kept in the field in either CT or NT systems (CT + Res and NT + Res, respectively). In CT + Res the residue is incorporated into the soil, with the depth and extent of mixing depending upon type of tillage. Although incorporated residue may affect weeds via altered nutrient dynamics, the effects will be highly dependent on the type of tillage used, the carbon to nitrogen ratio of the residue, the type of soil, and the environment (Liebman and Mohler, 2001). It is therefore difficult to extract useful generalities. Consequently, in this review we focus on the effects of surface residues on weeds regardless of tillage regime.

3.1. *Effect of crop residues on the weed seedbank*

3.1.1. *Germination of weed seeds*

Surface residues can affect seed germination via physical and chemical changes in the seed environment. The two main physical effects include a reduction in light and soil surface insulation. Insulation of the soil surface has implications for both soil temperature and moisture. Even under heavy crop residue loads, most seeds on the soil surface receive sufficient light to trigger germination (Teasdale and Mohler, 1993). As such, decreased weed seed germination due to insufficient light-availability is likely not a major advantage of residue retention.

Surface residue decreases the daily maximum soil temperature but has little effect on the daily minimum (Teasdale and Mohler, 1993) resulting in two changes: cooler average soil temperatures and less drastic fluctuations. Most agronomic crops and many weeds require soil temperatures above a certain threshold in order to germinate—lower average soil temperatures would therefore delay germination of both. This delayed germination and resulting shorter growing season of the crop can reduce yield, and it is emphasized that residue amounts should optimize yield rather than weed control (Wicks et al., 1994). Some weed species' germination is enhanced by larger temperature fluctuations (Liebman and Mohler, 2001); the buffered soil temperature could therefore reduce germination rates in addition to causing later germination.

Surface residue conserves soil moisture (Teasdale and Mohler, 1993; Bussière and Cellier, 1994)—how this affects germination rates depends on the environment. In water-limited environments residue may promote weed seed germination while in wetter conditions it may have little effect (Teasdale and Mohler, 1993; Wicks et al., 1994; Vidal and Bauman, 1996). This is exemplified by studies where residue was less effective in suppressing weeds in drier sites or years (Buhler et al., 1996; Mashingaidze et al., 2012; Ngwira et al., 2014).

Surface residues change the chemical environment of the weed seed via allelopathy. Allelopathy is the phenomenon in which a plant produces biochemicals that affect the growth of either itself or other organisms. Allelopathic compounds can be released by live plants or when residues decompose. Allelopathic effects from crop residue tend to have more pronounced effects on small seeds (Putnam and DeFrank, 1983; Liebman and Davis, 2000). This may be due to several factors but in general results in preferential suppression of weed growth compared to that of large-seeded crops (Liebman and Mohler, 2001). Greenhouse studies have shown allelopathic compounds can significantly reduce seed germination and may hamper seedling growth (Barnes and Putnam, 1986; Prati and Bossdorf, 2004). Although identification of allelopathic activity in the laboratory does not always translate to the field and it is difficult to isolate allelopathic effects of residue from associated bio-physical changes (Weston, 2000), in some situations it appears allelopathy reduces weed emergence on a field-scale (Einhellig and Rasmussen, 1989; Narwal, 2000; Mamolos and Kalburtji, 2001). Rye (Barnes and Putnam, 1986), barley (Overland, 1966), wheat (Steinsiek et al., 1982), rice (Olofsdotter, 2001), sorghum (Einhellig and Rasmussen, 1989), alfalfa (Hedge and Miller, 1990), sunflower (Khanh et al., 2005), as well as oat and several clover residues (Liebman and Mohler, 2001) exhibit allelopathic suppression of weed seed germination and emergence. Wheat and rice residue have been identified as exhibiting genetically controlled allelopathy which could be exploited for weed control (Wu et al., 2001; Khanh et al., 2007). Some studies have shown surface residue is more suppressive than incorporated residue in suppressing plant growth (Roth et al., 2000). Allelopathic control of weeds depends on environmental conditions and can last for a short duration (Kimber, 1973; Cochran et al., 1977). Therefore, although it can be effective, using crop residue as allelopathic weed control should be part of a larger weed management plan.

3.1.2. Weed seed predation, pathogen attack, and viability

Surface residue may indirectly encourage seed predation by providing foraging and nesting habitat for predators, but may also restrict their mobility. Studies have shown residue effects on predation rates depend on the type of residue, surrounding landscapes, and the type of native predator populations (Bommarco, 1998; Cromar et al., 1999; Liebman, 2001). Some studies report extended season ground cover is correlated with increased predation (Gallandt et al., 2005; Heggenstaller et al., 2006) while others have found no effect (Harrison et al., 2003; Jacob et al., 2006; Chauhan et al., 2010). Modeling studies predict that increasing vegetative cover throughout the season will decrease over-winter seed survival, which will lead to significantly lower weed populations (Davis et al., 2009). The plethora of external factors may explain the lack of consensus among studies.

Residue on the soil surface provides an insulated soil-atmosphere boundary that will decrease evaporative losses and maintain humidity. In moisture-limited environments this will protect seeds from desiccation. In environments with sufficient moisture, residue could promote higher rates of seed decay. The increased micro-flora activity and biomass under residue (Doran, 1980; Govaerts et al., 2007; Yang et al., 2013) would seem to encourage higher rates of seed losses under residue due to decay (Derksen et al., 1996; Kennedy and Kremer, 1996; Chee-Sanford et al., 2006). This hypothesis has had little field testing, but one study found no difference in percent seed decay in exposed versus residue protected soil (Gallandt et al., 2004), indicating the effects may be more complicated and could involve nutrient status and seed coat characteristics (Davis, 2009).

3.2. Effect of crop residues on the growth and establishment of germinated weed seeds

Crop residues provide physical barriers that can prevent both light penetration and seedling emergence. The reduction in available light under surface residue has significant effects on seedling growth; as germinated seeds search for light they exhaust energy reserves and become etiolated, weak, and more susceptible to certain types of herbicide damage (Crutchfield et al., 1986). Light filtered through dead biomass does not change in quality, only intensity (Teasdale and Mohler, 1993). While 100% ground cover does not necessarily correspond to 100% light interception, it provides a useful proxy for estimating how much residue is needed to inhibit seedling growth. The amount varies by crop, with small grain crops requiring less (2–8 Mg ha^{-1}) and large grains more (6–17 Mg ha^{-1}; Greb, 1967; Teasdale et al., 1991; Wicks et al., 1994). For example, in a wheat-maize rotation study Crutchfield et al. (1986) found that at least 3.4 Mg wheat straw ha^{-1} was needed in order to significantly reduce weed biomass, while in a monoculture maize system in Zimbabwe Ngwira et al. (2014) found 6 Mg of maize stover ha^{-1} was needed. In general, a linear increase in biomass results in an exponential decay in the percentage of germinated seeds that successfully emerge, although the exact relationship depends heavily on residue characteristics (Teasdale and Mohler, 2009; Ngwira et al., 2014). Often CA systems strive to leave at least 30% of the ground covered; while this amount of residue may provide soil quality benefits it may not significantly reduce weed germination and emergence (Teasdale et al., 1991; Vidal and Bauman, 1996; Liebman and Mohler, 2001). A low light environment will have a more profound effect on small-seeded annual weeds and crops, as they are initially more dependent on light compared to perennials and large-seeded species (Crutchfield et al., 1986; Mohler, 1996).

Although crop residue can intercept herbicide, this does not necessarily translate to reduced weed control (Wicks et al., 1994; Derksen et al., 1995; Chauhan, 2013; Ngwira et al., 2014). Studies have shown that the weed suppression provided by surface residue more than compensates for reduced herbicide contact with weeds (Crutchfield et al., 1986; Derksen et al., 1995; Teasdale et al., 2003).

3.3. Effect of crop residues on production, dispersal, and recruitment of weed seed

Crop residues can indirectly reduce weed seed production by limiting weed growth (via light interception, physical barriers, and allelopathy)—smaller weed plants result in lower weed seed production, as the two have a strong linear relationship (Wilson et al., 1995; Franke et al., 2007). Residue may also trap wind-dispersed weed seeds, leading to higher recruitment of these weeds in systems that retain surface residue as compared to systems that leave the ground bare for large parts of the season (Derksen et al., 1993; Moyer et al., 1994; Tuesca et al., 2001).

4. Crop rotation

Crop rotations are arguably the most effective way to control weeds. Every crop applies a unique set of biotic and abiotic constraints on the weed community; this will promote the growth of some weeds while inhibiting that of others. In this way, any given crop can be thought of as filter, only allowing certain weeds to pass through its management regime (Booth and Swanton, 2002). Rotating crops will rotate selection pressures, preventing one weed from being repeatedly successful, and thus preventing its establishment. Rotations alter selection pressures via three main mechanisms including (i) altering managements (e.g., timing of field activities, herbicides), (ii) varying patterns of resource competition, and (iii) allelopathy. Not all rotations utilize all three—which mechanisms a rotation is employing should be considered when looking at the effects of a particular rotation on weed dynamics.

4.1. Effect of crop rotation on the weed seedbank

4.1.1. Size of the weed seedbank

Crop rotation interacts with other practices, particularly tillage, when considering seedbank size (Section 5). Rotating crops with dissimilar planting dates appears to be key in reducing the size of the seedbank, presumably because it changes the timing of field activities. Studies looking at rotations that include varied planting dates show decreased weed seed densities while rotations with identical planting dates do not (see references within Liebman and Dyck, 1993; Dorado et al., 1999; Bàrberi et al., 2001).

4.1.2. Germination of weed seeds

Every crop is associated with a distinct set of management practices that creates both spatial and temporal variability in nutrient, water, and light availability. Variability of these resources will affect where and when the soil is favorable for seed germination. For example, in a water-limited environment a spring-irrigated crop will promote spring weed seed germination, while a fall-irrigated crop will promote fall weed germination.

Crops with different growing seasons or growth patterns also alter the light environment of the soil. Unlike dead residue, live plants change the quality of light that reaches the soil surface. The quality of canopy-filtered light can inhibit germination of several weed species (Fenner, 1980; Silvertown, 1980), probably due to the pioneering nature of weeds. One advantage of including a perennial phase in a rotation is a result of this inhibition; weed seed germination and therefore weed production is minimized while seed mortality via predation and loss of viability continues undisturbed.

Incorporation of allelopathic crops in a rotation can also reduce weed seed germination. In a study done in the mid-western US, researchers compared the maize phase of a two- (maize–soybean) and three-year (maize–soybean–wheat) rotation (Schreiber, 1992). Although the weed seedbank size did not differ between the rotations, regardless of tillage the maize in the three-year rotation had had lower weed densities compared to the maize-soybean rotation, meaning less of the seedbank germinated. The researchers attributed this to the allelopathic effects of wheat, although it is confounded with the effect of including a winter crop. Allelopathic effects of crop residues are discussed in more detail in Section 3.1.

4.1.3. Predation of weed seeds

There is scant literature concerning how rates of seed predation differ between crops, much less between crop rotations (Menalled et al., 2006). There is evidence that utilizing phenologically dissimilar crops increases predation pressure, and that seasonality of seed predation follows the crop cycle (Heggenstaller et al., 2009; Westerman et al., 2011). Additionally, certain crops seem to encourage predation of distinct weed seeds (Honek et al., 2003; Menalled et al., 2006; O'Rourke et al., 2006). These studies suggest rotating crops with varied growing seasons could increase the diversity of seeds consumed.

4.2. Effect of crop rotation on establishment, seed set, and seed dispersal of germinated weed seeds

Prevention of weed seed-set is perhaps one of the most powerful mechanisms of weed control offered by rotations. Weeds can be successful in reproducing when they mimic the crop life cycle (Liebman and Dyck, 1993; Moyer et al., 1994; Derksen et al., 2002). Weed growth that is poorly synchronized with the crop presents unique opportunities for weed control; weeds growing in the absence of a crop may be terminated using non-selective herbicide, and weeds in their vegetative stage during harvest are terminated before they set seed. Changing crops allows control of weeds with different emergence seasons, preventing a particular type of weed from repeatedly completing its life cycle.

4.3. Effect of crop rotation on the composition and diversity of weed species

A study done in France surveyed weeds in over 500 agricultural fields and found that the crop sowing date was an effective predictor of the weed community (Gunton et al., 2011). This is supported by studies that show rotations incorporating varied growing seasons alter weed community composition (Chancellor, 1985; Ball, 1992; Cardina et al., 2002). This indicates rotations that include crops with dissimilar sowing dates can be expected to change the weed communities. Many studies also show an increase in weed diversity under these conditions (Liebman and Dyck, 1993; Stevenson et al., 1997; Anderson et al., 1998; Dorado et al., 1999; Sosnoskie et al., 2006). Monocultures often lead to weed simplification with only a few dominant weeds (Moyer et al., 1994; Anderson et al., 1998; Blackshaw et al., 2001; Cardina et al., 2002), potentially simplifying the choice of herbicide but potentially increasing selection pressure for herbicide resistant weeds.

5. Interactions between CA principles

5.1. Tillage practice interactions with crop residues

It has been shown that NT combined with residue removal leads to a severe degradation in soil quality (Verhulst et al., 2009), but there are few studies that look at the behavior of weeds in these systems. Often, studies concerning tillage do not include a NT treatment with residue removal or a CT treatment with surface residue, so the interactions between NT and surface residue are unclear. In one study Anderson (1999) used a sweep plow that tilled to a depth of 5–8 cm but left 90% of the residue on the surface. He found that sweep-plowed fields had weed densities 35–50% higher than NT fields, but the study did not include a CT treatment so the weed suppression of residue wasn't estimated. Another study done in Zimbabwe compared CT, NT, and NT + Res, and found similar weed biomass in CT and NT + Res, while NT without surface residue had nearly double the weed biomass (Ngwira et al., 2014). The latter study indicates in some NT situations residue provides significant weed control, but more research is needed to elucidate exact mechanisms. There is evidence NT + Res promotes seed predation, increasing predatory seed loss by two (Brust and House, 1988) to three fold (Menalled et al., 2007) compared to CT systems, but again it is not clear if it is due to NT, residue retention, or their interaction. Allelopathic suppression of weed seed germination via surface residue may be more effective in NT since seeds are concentrated near the soil surface, where allelopathic compounds will be released by the residue.

5.2. Tillage practice interactions with crop rotation

Most studies show crop rotation reduces weed densities compared to monocultures irrespective of tillage regime. However, for a given crop rotation, whether zero tillage results in higher weeds relative to tilled systems is not clear and probably depends on other factors. Some studies show NT works synergistically with rotations to further reduce weed densities compared to tilled systems (Kegode et al., 1999; Anderson, 2005; Murphy et al., 2006). Other studies show medium-disturbance tillage enhances control of certain weeds compared to NT + Res (Schreiber, 1992; Blackshaw, 1994; Cardina et al., 2002; Legere et al., 2011). Interestingly, of the studies showing more weeds in NT + Res compared to CT + Res, ones that report both yield and weed densities show that despite having more weeds, yields in rotated NT + Res are either equal to or higher than those in the rotated CT + Res systems (Schreiber, 1992; Legere et al., 2011). This may be because weed density may not be representative of weed biomass, which is more important when considering crop competition and yield reductions. Another possibility is that all systems had weed densities below yield reducing populations, and yields were constrained by other factors. In these cases, although yields may not have been negatively affected in the study year, the legacy of those weeds on future yields must be included when considering threshold weed populations.

Yields notwithstanding, in all rotation-tillage interaction studies the treatment with the highest weed densities was a monoculture grown in NT + Res (Schreiber, 1992; Blackshaw, 1994; Anderson et al., 1998; Kegode et al., 1999; Blackshaw et al., 2001; Cardina et al., 2002; Sosnoskie et al., 2006). Utilizing crop rotation in NT + Res systems is crucial for weed control. Moyer et al. (1994) found that successful weed management in NT + Res systems involved sequences of three or more crops. Even in environments where two or more crops are grown each year, altering the pattern of crops in NT + Res is vital for weed management (Chauhan and Mahajan, 2012). The potential for carefully designed crop rotations to enhance weed control in CA systems is discussed further in Section 6.7.

Cropping sequences interact with tillage practice to create distinct communities of weeds (Bàrberi et al., 2001; Blackshaw et al., 2001; Sosnoskie et al., 2006). Two studies compared monocultures to three-year rotations under various tillages, and both found the most diverse communities in the three-year rotation NT systems (Stevenson et al., 1997; Murphy et al., 2006). In a 14 year study done in the Mid-western US Buhler et al. (1994) found there was an increase in perennial weeds as tillage intensity was reduced, but this increase was greater in a maize monoculture as compared to a two-year rotation of maize and soybean, indicating that crop rotation may help combat establishment of perennial weeds in NT.

6. Additional cultural practices for weed control in CA

Without tillage, CA systems must rely on herbicides and agronomic practices for weed control. Here we briefly discuss tactics that may offer CA practitioners additional options for weed control, with an emphasis on increasing the competitiveness of the crop with weeds. Cultural practices discussed include adjusting the crop planting date, planting density, and/or spatial arrangement; resource management; preventing weed seed recruitment; using microbial bio-controls; and intentionally designing crop rotation for weed control.

6.1. Adjusting the crop planting date

Due to dormancy processes, many weeds germinate during specific seasons. If the approximate date of emergence is known for problem weeds, crop planting dates can be adjusted so that either (i) the crop emerges before the weeds for a competitive advantage or (ii) weeds are allowed to germinate and are controlled before or during crop planting. Planting earlier by even a few days can give the crop a significant competitive advantage over weeds (Mohler, 2001c). The potential weed suppression offered by early crop planting is demonstrated by the case of *Phalaris minor* in rice-wheat systems of the Indo-Gangetic plains. Adoption of NT permitted wheat crops to be planted 1–2 weeks earlier, allowing the crop to establish before emergence of the still dormant *Phalaris minor* (Chhokar and Malik, 1999; Wall, 2007; Chauhan et al., 2012). While the change in tillage and residue management may have contributed to the weed's reduced emergence (Chhokar et al., 1999; Franke et al., 2007), the earlier planting date played a significant role (Singh, 2009; Chauhan and Mahajan, 2012). Delaying planting, however, may be more risky, especially in temperate zones. Models and field data generally show that unless weed infestations are severe, planting the crop later in order to accommodate early season weed control is counter-productive with respect to yield (Mohler, 2001d).

6.2. Adjusting the crop density

Increasing the crop density increases the proportion of resources used by the crop compared to weeds, and may be desirable for several reasons. Planting density recommendations are made based on weed-free research environments, where crop biomass quickly increases then plateaus with higher planting densities. In the presence of weed competition, both models and field data suggest the relationship becomes more linear, with the benefit from increased planting density being greatest when weed densities are highest (Mohler, 2001c). While the goal of increased crop density is to increase crop biomass, this may not always result in significantly higher yields. However, in non-water limiting conditions field studies have shown utilizing crop densities higher than 150 plants m^{-2} in wheat (Lemerle et al., 2004), 4 plants m^{-2} in maize (Tollenaar et al., 1994), and 100 plants m^{-2} in rice (Zhao et al., 2007) has been shown to lower weed densities and increase yields. The weed control and subsequent yield advantages compared to the increased cost of seed should be evaluated, but increasing crop densities is a potential tool for weed control tool in CA systems.

6.3. Spatial arrangement of the crop

Researchers have used stochastic and 3-dimensional models to mathematically predict plant arrangements that best suppress weed growth (Fischer and Miles, 1973; Colbach et al., 2014). They found that, theoretically (i) weed-occupied space decreases as between-row spacing approaches within-row spacing of plants, i.e. when the uniformity of the arrangement is maximized, (ii) random sowing doubles the ratio of weed to crop space compared to uniform planting, and (iii) planting in clusters is the poorest design, allowing weeds to occupy a large amount of space.

In practice, the majority of studies confirm that reducing crop row spacing reduces weeds, although it does not necessarily increase yields (Mohler, 2001c). The effectiveness of reduced row spacing on weed control depends on several other factors, including water limitations, nutrient placement, crop to weed height ratio, and crop versus weed emergence timing. However, several recent studies have shown increased uniformity can work cooperatively with increased planting density to significantly reduce weed biomass and raise yields in a variety of crops (Weiner et al., 2001; Olsen et al., 2012; Marín and Weiner, 2014). For some producers, row spacing is dictated by tractor tire spacing; for non-mechanized production it may be possible to adapt closer row spacing.

Directional orientation of row crops can increase the amount of light captured by the crop, thus limiting the amount of light available for weed growth. When feasible, north-south orientation of crop rows is desirable for most latitudes (Mohler, 2001c).

6.4. *Resource management*

6.4.1. *Fertilizer*

In general weeds have more aggressive nutrient uptake compared to crops (Vengris et al., 1953), therefore altering timing, placement, and source in order to preferentially provide the crop with better access to nutrients is desirable. In soils with low background levels of fertility, banding of fertilizers can reduce weed biomass compared to broadcasting, with deep banding being more effective than surface banding (Di Tomaso, 1995; Liebman and Mohler, 2001; Derksen et al., 2002). The source of fertilizer can also favor certain weeds and therefore offers an opportunity to shift weed species (Liebman and Mohler, 2001).

6.4.2. *Water*

In irrigated environments, spatial and temporal variation of soil moisture offers opportunities for weed control. When the top layer of soil is dry, planting large-seeded crops into deep soil moisture can provide crops with an initial advantage over weeds (Liebman and Mohler, 2001). Another option under these conditions is to apply irrigation to germinate weeds, terminate them using herbicide, then plant the crop into the clean seed bed (Shaw, 1996; Chauhan et al., 2012; Mulvaney et al., 2014). The type of irrigation used can also change the location and density of weeds (Liebman and Mohler, 2001).

6.5. *Cultivar selection*

Certain varieties have been shown to be more competitive with weeds than others (see references within Mohler, 2001c; Zhao et al., 2006; Marín and Weiner, 2014). Additionally, the role of CA-specific cultivars for weed competitiveness under CA conditions is an active area of research (Mahajan and Chauhan, 2013). Designing breeding programs to select for competitive ability under CA is challenging due to the complexity of characteristics and large variation between location and year, but development of such varieties would be highly beneficial not only for weed control, but for other CA-specific characteristics (Herrera et al., 2013).

In select cases, herbicide-tolerant crops may facilitate adoption of no-till practices (Givens et al., 2009) but may also restrict crop rotations (Alister and Kogan, 2005). Herbicide-tolerant crops must be used in conjunction with other weed control methods, particularly rotational use of herbicidal mode-of-actions to avoid resistance issues. Additionally, while herbicides are a useful tool, they have limitations due to the potential build-up of resistance (Heap, 2014), their expense and limited availability (Ngwira et al., 2014), and associated health concerns (Wesseling et al., 1997; Ecobichon, 2001).

6.6. *Microbial weed control*

The microbiome offers a huge, largely untapped resource for bio-control of weeds (Kennedy, 1999). Hundreds of microorganisms have shown potential for biological weed control including bacteria, fungi, and actinomycetes (Kennedy and Kremer, 1996; Li et al., 2003). Microorganisms that suppress growth of many common agricultural weeds have been identified and commercial development is underway (Stubbs and Kennedy, 2012). Although the optimal method of application of these bio-controls is still being researched, it does not require tillage and is projected to be very low cost; application of microbial bio-controls may therefore represent a promising method to compliment CA weed management.

6.7. *Prevention of weed seed introduction*

Weed seed may be directly imported into agricultural fields via manure, crop seed, and irrigation water (Kelley and Bruns, 1975; Dastgheib, 1989). Obtaining clean crop seed, sifting contaminated crop seed, and filtering irrigation water are simple but effective tools for reducing these types of weed seed recruitment. Utilizing a seed cart to collect and remove chaff containing weed seeds as it passes through the combine can be effective in removing new weed seeds from the field (Shirtliffe and Entz, 2005; Walsh and Powles, 2007; Walsh and Powles, 2014).

6.8. *Intentionally designed crop rotations*

Rotation designs involving four years or more have been shown to drastically reduce herbicide use in both tilled and un-tilled systems (Anderson, 2008, 2015; Liebman et al., 2008). Including perennial forages such as alfalfa in a rotation has been shown to contribute weed control for up to three years, and can be particularly effective in NT systems (Entz et al., 1995; Ominski et al., 1999; Ominski and Entz, 2001).

We acknowledge that environmental, market, and equipment constraints can restrict rotation options (for example to a single season or crop family). Both field and modeling studies have shown that changing management (which is often associated with crop rotation, but can occur within the same crop) may account for a greater percentage of the weed control than the actual changes in crops (Doucet et al., 1999; Davis et al., 2004). When rotation options are limited, changing the timing of activities or alternating between early- and later-maturing cultivars may assist in controlling infestations of weed species that have complementary growth habits to a given crop. Adjustment of planting dates is also a viable option that was discussed previously.

A relatively new rotation schedule for systems utilizing in-season herbicide use is ‘stacked rotations’, in which rotated crops are grown for two consecutive years before rotating. As an example in a three-crop, six-year rotation, weeds are forced through one crop’s selection pressure for two years, followed by a four-year break. Stacking may involve identical crops or crops with similar growth cycles (e.g. two cool season crops). In NT systems of the Northern Great Plains of the United States (US) and Canada, stacked rotation designs offer superior weed control compared to yearly rotations (Derksen et al., 2002; Anderson, 2004, 2005). Garrison et al. (2014) used models to show this may be due to increased intra-weed competition in stacked rotations. Other modeling studies have suggested that the proportion of winter versus spring crops used in the past more strongly defines weed dynamics than the exact order of crops (Colbach et al., 2013). Despite the apparent promise, to our knowledge few field studies have investigated stacked rotations, and more research outside of the Northern Great Plains is certainly warranted.

6.9. *General considerations*

Many weed control methods are not effective when used alone, but when used together can interact to cumulatively reduce weeds.

Numerous studies have shown the disproportionate benefits of using several methods in tandem (Derksen et al., 2002; Anderson, 2005; Westerman et al., 2005). Using several methods provides insurance against one method failing, and provides a buffered system of weed control that will be effective in changing and unpredictable environments; a tactic that has been coined ‘many little hammers’ (Liebman and Gallandt, 1997).

A major criticism of CA is its enhanced reliance on herbicides as compared to tilled systems. In particular, glyphosate may be heavily used, especially to control perennial weeds (Moyer et al., 1994). Despite these concerns, we are unaware of any side-by-side comparisons of herbicide use in CA and conventionally managed systems. In Canada adoption of NT has not increased herbicide use significantly (Derksen et al., 1996), and in the US Great Plains NT wheat systems have controlled weeds using cultural tactics and reduced herbicide usage by 50% compared to CT (Anderson, 2005). Additionally, in many areas targeted by CA, herbicides are unavailable or prohibitively expensive, thus weed control must occur through other means (Ngwira et al., 2014). When herbicides are utilized, higher rates of use can lead to herbicide resistance, and utilizing different herbicides is crucial to avoid infestations of herbicide resistant weeds (Heap, 1997; Valverde and Gressel, 2006; Owen et al., 2007; Powles, 2008).

7. Transitioning to CA

Weed management during transition to CA systems is crucial, and it may take 4–10 years for yield, soil characteristics, and weed populations to reach equilibrium (Swanton et al., 1993). In many parts of the world CA is adopted in parts (Giller et al., 2009; Kienzler et al., 2012) or step-wise (Kassam et al., 2009), often beginning with reduced tillage (Andersson and D’Souza, 2014). This adoption process may make weed control even more challenging, as it does not take advantage of the synergistic effects from combined use of the three principles.

Implementing NT will be most successful in systems that also implement at the minimum a two-year crop rotation plus residue retention (cover cropping is another option that is widely utilized in US NT systems). Even if producers may not want to incorporate all three pillars of CA in the long term, utilizing crop rotation and residue retention during a transition period would likely be beneficial for long term weed control under NT.

Weed models have been used to offer significant insight into the interaction between weeds, management, and environments (e.g., Davis et al., 2009; Kenkel et al., 2009; Colbach and Mézière, 2013). These models can be used to identify where in a CA system weed control should be targeted, and could offer understanding into how to best transition from a certain system to CA. These types of models are becoming more valuable as computing power becomes more accessible. Additionally, meta-analyses could use currently available data to quantify how weeds respond to CA adoption under certain conditions, similar to the study done by Pittelkow et al. (2015).

It can be expected that a greater amount of herbicide might be necessary in the first years of transitioning. As many CA programs begin year zero with an intensive tillage-leveling regime, producers could take advantage of the residue-free soil surface during year zero by using a broad-spectrum herbicide to kill recruited weed seedlings before crop emergence; this would significantly reduce the surface weed seedbank in the first season, which has been identified as an effective intervention point for weed management (Jordan et al., 1995; Davis et al., 2004). The initially large number of weeds immediately following transition to CA should not be discouraging, as it can be a transitory phenomenon. With vigilant control of seed production and continued emphasis on reducing the weed seedbank, a drastic reduction in the numbers of viable weed seeds in the soil occurs within 1–4 years (Schweizer and Zimdahl, 1984).

8. Conclusion

This review indicates that the principles of CA, particularly crop rotation and surface residue retention, are in themselves methods of weed control. The combined use of all three principles can offer disproportionate advantages, and weed problems are more likely to occur if only one CA practice is utilized. For CA, it appears the synergistic effects of utilizing multiple control tactics are even more crucial and their importance cannot be over-emphasized. With respect to weed control, NT should never be implemented in monoculture systems and vice versa. Additional options for weed control in CA systems may include selecting new varieties with more competitive crop canopies; altering crop planting dates, planting densities, row-spacing and/or fertilizer placement; utilizing microbial weed controls; and implementing long (4+ years) rotations designed with weed management in mind. Few breeding programs are actively developing cultivars specifically for the CA environment, although initial work appears promising. Further research is needed concerning interactions between CA practices with regard to weed control, particularly tillage and residue retention. Models are increasingly being used to explore cropping system scenarios and their predicted effects on weed populations; they could prove to be a valuable tool for investigating the effects of CA in various environments. Developing a standardized template for data collection could aid in performing meta-analyses, which could offer further insights into weed responses to CA adoption. Exploring the weed-suppressive potential of stacked and longer-term crop rotations is another promising area that has received little attention.

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