

## Environmental Implications of Herbicide Resistance: Soil Biology and Ecology

Robert J. Kremer\*

Soil microbial community structure and activity are linked to plant communities. Weeds may alter their soil environment, selecting for specific rhizosphere microbial communities. Rhizosphere modification occurs for many crop and horticultural plants. However, impacts of weeds in agroecosystems on soil biology and ecology have received less attention because effective weed management practices were developed to minimize their impacts on crop production. The recent development of herbicide resistance (HR) in several economically important weeds leading to widespread infestations in crop fields treated with a single herbicide has prompted a re-evaluation of the effects of weed growth on soil biology and ecology. The objective of this article is to review the potential impacts of herbicide-resistant weeds on soil biological and ecological properties based on reports for crops, weeds, and invasive plants. Persistent weed infestations likely establish extensive root systems and release various plant metabolites through root exudation. Many exudates are selective for specific soil microbial groups mediating biochemical and nutrient acquisition processes. Exudates may stimulate development of microbial groups beneficial to weed but detrimental to crop growth or beneficial to both. Changes in symbiotic and associative microbial interactions occur, especially for arbuscular mycorrhizal fungi (AMF) that are important in plant uptake of nutrients and water, and protecting from phytopathogens. Mechanisms used by weeds to disrupt symbioses in crops are not clearly described. Many herbicide-resistant weeds including *Amaranthus* and *Chenopodium* do not support AMF symbioses, potentially reducing AMF propagule density and establishment with crop plants. Herbicides applied to control HR weeds may compound effects of weeds on soil microorganisms. Systemic herbicides released through weed roots may select microbial groups that mediate detrimental processes such as nutrient immobilization or serve as opportunistic pathogens. Understanding complex interactions of weeds with soil microorganisms under extensive infestations is important in developing effective management of herbicide-resistant weeds.

**Nomenclature:** Glyphosate.

**Key words:** deleterious rhizobacteria, microbial ecology, mycorrhizae, rhizodeposition, rhizosphere, soil microbial community, systemic herbicides, transgenic crops.

The increasing prevalence of herbicide-resistant (HR) weeds has generated interest in potential effects of weed infestations in crop production fields on soil and biological processes. Effects of weeds on the soil environment previously received little attention because greatest efforts were focused on aboveground management to reduce or eliminate weeds as a detrimental factor in crop production. However, weeds can have major impacts on soil microbial communities of agroecosystems. With the introduction of HR crops, use of a total weed management system based on prevention of weed seed production, prevention of weed seedling emergence, and control of growing weeds (Aldrich and Kremer 1997) was essentially abandoned in favor of a one-component strategy of controlling

weeds with a nonselective herbicide. This change in weed management led to herbicide overuse resulting in widespread and rapid evolution of weed biotypes resistant to one or more mechanisms of herbicide action (Mortensen et al. 2012; Powles and Yu 2010; Tranel 2011). These HR weed biotypes often escape current herbicide-based weed control programs resulting in production of seeds, many of which carry HR trait(s), to replenish the weed seedbank and ultimately generate difficult-to-control weed infestations. As weed infestations become more prevalent due to the evolution of numerous HR biotypes, they may have important implications for full expression of microbially mediated biological processes in soils and the impact of these changes on crop growth in current and subsequent seasons.

Many important processes including nutrient cycling, decomposition, plant-growth regulation, disease suppression, and air and water movement as affected by microbial contributions to soil structure, are mediated by the soil microbial community, which in turn is influenced by plants established in

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\* Research Microbiologist, USDA-ARS and Adjunct Professor, Department of Soil, Environmental & Atmospheric Sciences, University of Missouri, 302 Natural Resources Building, Columbia, MO 65211; Corresponding author's E-mail: bob.kremer@ars.usda.gov

the field. Evaluation of interactions of HR weed infestations with soil biology and ecology is essential to understand the potential effects on specific components of the microbial community and associated biological processes. It is also important to assess the persistence of the effects on soil function and crop growth within the current and subsequent seasons. If HR weeds are found to be detrimental to soil functions that are critical for crop growth, management practices implemented to address HR weed infestations might be adjusted or supplemented to simultaneously overcome the disruption to soil productivity and quality. Current recommendations for mitigating evolution of HR weeds encourage diversification of weed control practices including rotation of different class herbicides (Norsworthy et al. 2012), which, when consistently followed, should reduce potential long-term effects on soil ecosystems.

In order to address implications for HR weeds on soil biology and ecology, we need to investigate and characterize microbial community structure and function within the environments that evolve under weed infestations. Because so little is known specifically of impacts by HR weeds on soil microbial ecology, documented effects of “wild-type” or non-HR weeds in agroecosystems will be reviewed to provide a foundation for evaluation of similar effects of HR weeds. The objectives are to (1) provide background on soil microbial biology and ecology in relation to plant–root interactions; (2) characterize relationships between weeds and soil microbial communities in agroecosystems based on the limited information available; and (3) discuss the influence of HR weed infestations and herbicides on expression of these relationships.

## Plants and the Soil Microbial Community

Soil biology effectively centers on the microbial community, which is critical to the maintenance of soil function in both natural and agricultural ecosystems. Soil microbial communities are often difficult to fully characterize, mainly because of their immense phenotypic, genotypic, and physiological diversity and heterogeneity. Relative strengths of factors shaping microbial communities are shown in Figure 1, which depicts the relative forces exerted by plant, soil, and microbial types (Garbeva et al. 2004). The major determinants of soil microbial community structure are plant type and the soil in which microbial populations and plants co-exist (Bulgarelli et al. 2012; Garbeva et al. 2004). Plant type is a

major determinant of microbial community structure in soil, as plants are the main providers of specific carbon and energy sources that are readily available to soil microorganisms. Also, soil affects microbial community composition based on textural influence on the microhabitats adjacent to plant roots wherein communities in coarse-textured soils (sandy loam) are distinctly different from those developing in fine-textured soils (silty clay loam). Thus, the influence of different plants are mediated by soil in addition to the relative adaptability of microbial groups to alterations in microhabitats, which make these interactions complex in describing soil microbial communities present under plant communities, such as areas occupied by weeds at various densities.

In microbial terms, structural diversity describes the number of different types (species) and their relative abundance in a given community in a given habitat. Functional diversity refers to the occurrence and distribution of physiological and metabolic traits among community members and can be categorized into different functional groups, i.e., nitrifying bacteria, lignin-degrading fungi, etc. Functional diversity reflects the overall microbial diversity and is most important when evaluating alterations in biological processes in a soil ecosystem. A review of several studies on different plant species in different locations, using a range of cultural and culture-independent detection methods, indicated that plant type is indeed a major factor influencing the structure of microbial communities (Garbeva et al. 2004; Marschner 2012).

Using the model of Garbeva et al. (2004), different weed species can be inserted to illustrate how interrelationships can be inferred between the two factors, plant type and soil, in influencing soil microbial communities. Examples of interrelationships range from root surface colonization to intimate endophytic interactions, all of which may involve mutualistic or antagonistic associations (Hirsch and Mauchline 2012). Many of these interrelationships will be discussed later. In the following illustration, selected weeds are used as “strong” and “weak” plants based on their differential competitiveness (Aldrich and Kremer 1997; Zimdahl 1999) and contrasting vegetative and root growth characteristics (Davis et al. 1967; Weise 1968). Thus, as shown in Figure 1, giant ragweed (*Ambrosia trifida* L.) with its robust growth habit is shown as a relatively strong plant factor that selects for relatively weak pseudomonad bacteria as a major microbial component when growing in sandy loam, which exhibits a weak soil effect. In contrast,

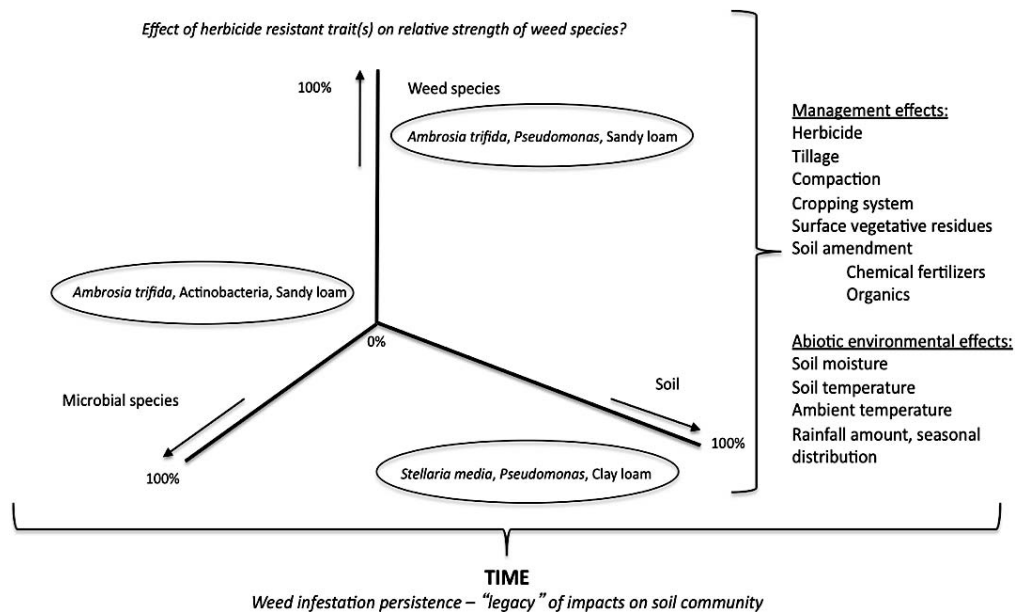


Figure 1. Conceptual diagram of relative strengths (0–100%) of factors shaping microbial communities in soil and rhizosphere environments. Axes depict relative forces exerted by weed, soil, and microbial type. Giant ragweed (strong) vs. common chickweed (weak), clay loam (strong) vs. sandy loam (weak), and actinobacterium (strong, recalcitrant) vs. *Pseudomonas* bacterium (weak, low recalcitrance) are depicted as models to illustrate the concept. Explanation: Giant ragweed, *Pseudomonas*, sandy loam: strong plant effect, weak soil effect, microorganism of low recalcitrance; Common chickweed, *Pseudomonas*, clay loam: weak plant effect, strong soil effect, microorganism of low recalcitrance; Giant ragweed, actinobacterium, sandy loam: strong plant effect, weak soil effect, recalcitrant microorganism. Expression of effects due to weed–soil–microorganism interactions are influenced further by herbicide input, management and environmental factors, and time that the weed infestation persists. (Modified from Garbeva et al. 2004.)

chickweed [*Stellaria media* (L.) Vill.], representing a weak plant type, may select for pseudomonads in the presence of clay loam, a representative strong soil factor. Other microorganisms may be virtually resistant to forces imposed in the soil environment, such as actinobacteria, whereas the pseudomonads are susceptible to stimulatory or disruptive effects due to their ability for rapid growth when available nutrients are enhanced (i.e., incursion of extensive root systems). This depiction may be useful in drafting a conceptual framework for documenting potential effects of weeds and soils on microbial ecology and biological processes. The overall lack of knowledge of the significance of altered microbial communities for plant (and ecosystem) function is still striking (Ehrenfeld et al. 2005). Imposition of management and abiotic factors on the weed–soil–microbe interactions further defines the microbial community in an agroecosystem. Additional overarching factors that need to be considered are to fully describe interactions involving HR biotypes that may influence the relative strength of the weed factor; and the time during which weed infestations persist that may determine the *long-term* microbial changes that potentially lead to legacy effects on the agroecosystem. The last two factors are those for which very little information has been developed. A basis for

potential legacy effects of weed infestations established in annual cropping systems is provided by impacts of the invasive weed garlic mustard [*Alliaria petiolata* (Bieb.) Cavara & Grande] that reduces soil densities of mycorrhizae and its colonization of native plants for up to 2 yr after removal of the infestation (Anderson et al. 2010).

### Weed Characteristics and Effects on Soil Biology and Ecology

Weed characteristics that contribute to effects on soil ecology and biology regardless of herbicide response include seed production, seedbank, and seedling phases and the associated microorganisms; weed growth rate and infestation density; root characteristics, root-released compounds including C amounts, composition and allelopathic properties; ability to form symbiotic and associative relationships with microorganisms; and products of vegetative residue decomposition (Table 1).

**Weed Seeds and Seedbank.** Limited research with common lambsquarters (*Chenopodium album* L.) and common chickweed demonstrated that distinct microbial communities associated with mature seeds on the mother plant were introduced into the soil during

Table 1. Different effects of weeds on soil biological and ecological properties.

Weed plant characteristic	Effect on soil biology/ecology	Representative references
Seed maturation and dispersal	Introduction of seedborne microorganisms into soil environment	Kremer 1987; van Overbeek et al. 2011
Seedling	Sustain introduced microorganism; rhizosphere select specific microbial groups from soil community	Cregut et al. 2009; Kennedy et al. 1991; Kremer et al. 1990
Root growth and extension into soil	Release C and N substrates in exudates into soil; Differential compounds in root exudates stimulate specific enzymatic activities, signals specific microbial groups, and enhances proportion within community; antagonistic compounds suppress selected microbial groups; suppression of rhizobia and nodulation of leguminous crops	DeAngelis et al. 2008, 2009; Vaicekonyte and Keesing 2012
Mycorrhizal	Mycorrhizal association develops, mobilize P, other nutrients, antagonize pathogens, aid soil structure, may encourage mycorrhizae for other plants	Jordan et al., 2012; Vatovec et al. 2005; Willis et al. 2013
Nonmycorrhizal	No impacts on nutrient mobilization, etc.; some (i.e., <i>Brassica</i> ) antagonistic to mycorrhizal propagules, etc. occurring in soil and to association with crops	Cipollini et al. 2012; Stinson et al. 2006
Vegetative, active rapid growth	Extraction of soil nutrients compete with soil microbial requirement; C4 plants (i.e., <i>Amaranthus</i> ) with high Mn demand for photosynthesis	Kering et al. 2009
Herbicide-resistant, no herbicide	Possible pleiotropic effect in <i>Lolium</i> for increased NAR may increase rhizodeposition of C compounds; Root exudate composition differs between herbicide-susceptible and HR <i>Brassica</i> ; invasive <i>Raphanus</i> disrupts mycorrhizae community in noncrop ecosystems	Li et al. 2013; Vila-Alub et al. 2005, 2009
Herbicide-resistant, with herbicide	Herbicide released into soil through root exudation; suppress mycorrhizal and rhizobial symbioses; alter rhizosphere microbial community through suppression or toxicity; select specific root colonizing and endophytic microorganisms; enhance potentially phytopathogenic fungi on root system; alter root exudate concentration and composition, indirect selective effect for specific microbial groups	Druille et al. 2013; Kremer et al. 2005; Mijangos et al. 2009; Rosenbaum et al. 2014; Schafer et al. 2012, 2013

seed dispersal (van Overbeek et al. 2011). Seeds retrieved from soil retained associated microorganisms that mostly originated from the mother plant and not from soil, indicating that the presence of a weed seedbank in arable soils can increase soil microbial diversity. Thus, a change in species composition or size of the weed seedbank, as a result of a change in crop management, could affect soil structural and functional microbial diversity. Seed production by major annual weeds with known HR biotypes including common lambsquarters at  $> 70,000$  seeds plant<sup>-1</sup> (Bassett and Crompton 1978) and weedy species of *Amaranthus* yielding from about 50,000 seeds plant<sup>-1</sup> for tumble pigweed to over 250,000 seeds plant<sup>-1</sup> for redroot pigweed (*Amaranthus retroflexus* L.), common waterhemp (*Amaranthus rudis* Sauer), smooth pigweed (*Amaranthus hybridus* L.), and Palmer amaranth [*Amaranthus palmeri* (S.) Wats.], depending on weed density (Sellers et al. 2003), is extremely high. Weed infestations of such high seed-producing weeds allowed to mature could indeed influence soil microbial

diversity (van Overbeek et al. 2011). The consequences of altered diversity and the extent to which microbially mediated soil processes are likely to be affected by weed seed-introduced microorganisms are unknown.

The microbial community associated with common lambsquarters seeds included bacterial species known to antagonize phytopathogens suggesting a potential for disease control in arable crop production (van Overbeek et al. 2011). However, presence of antagonists in weed seeds also may have a negative consequence on weed control because these microorganisms also can antagonize potential phytopathogens of the weed species. Suppression of phytopathogens by seedborne antagonistic microorganisms may contribute rapid emergence and establishment of annual weeds in arable soils (Kremer 1987, 1993). Therefore, the presence of putative antagonists of phytopathogens in soil weed seedbanks does not guarantee positive effects on crop plant growth promotion. Similar conclusions have been reported in a limited number of other

studies where potential weed phytopathogens were found. For example, between 35 and 65% of the tested bacterial isolates from various weed seeds suppressed seedling growth in bioassays; however, many isolates were not strictly bound to one host species, and pathogens associated with weeds may attack crops as well (Kremer 1987; Li and Kremer 2006).

Seedborne and soil microbial communities subsequently influence soil biology as a weed infestation develops. Microbial diversity within the zone of weed growth may shift both structurally and functionally as reported for wild oat (*Avena fatua* L.) (DeAngelis et al. 2009). The shifts in microbial community composition are also reflected in greater prevalence of specific fungal groups as noted for economically important *Fusarium* spp. associated with numerous weed hosts, which were suggested as an important reservoir for crop pathogens (Postic et al. 2012). Diversity of fungal communities associated with seeds varied among four common broadleaf weeds, velvetleaf (*Abutilon theophrasti* Medik.), woolly cupgrass [*Eriochloa villosa* (Thunb.) Kunth], Pennsylvania smartweed (*Polygonum pennsylvanicum* L.), and giant ragweed in cultivated soils (Chee-Sanford 2008). Multiple species of fungi on velvetleaf seed along with empirical observations of extensive seed deterioration suggest that fungal species may be associated with seed decay activities (Chee-Sanford 2008; Kremer 1986). Seedborne and soil-colonizing fungi and bacteria introduced with weed seed dispersal may protect seeds from antagonists; however, their role in initiating seed decay processes is yet unknown.

**Weed Seedlings.** Most of the information on weed seedling-associated microorganisms involves specific groups of bacteria that are the focus of exploratory research to discover unique and effective biological control microorganisms. Greatest efforts have focused on rhizobacteria, which are root-colonizing bacteria that may be classified as beneficial, deleterious, or having no effect on plants (Boyetchko 1996). Weed seedlings develop specific rhizobacterial associations, which may be influenced by crop and soil management in agroecosystems (Li and Kremer 2006). A proportion of weed seedling rhizobacteria is consistently found to possess phytotoxic activity and thereby considered potential biological control agents (Boyetchko and Mortensen 1993; Kennedy et al. 1991; Kremer et al. 1990). In contrast, plant-growth promoting rhizobacteria characterized for six weed species (Sturz et al. 2001) were suggested as potentially desirable to benefit

subsequent crops as a soil conditioning strategy. Although little to no information is available on development of the soil microbial community during the growth progression of a weed infestation from seedling to vegetative stages during the crop season, inferences can be made from research conducted with “weed-related plant species.” A study examining the rhizosphere bacterial community of winter rape (*Brassica napus* L.) or winter barley (*Hordeum vulgare* L.), representing Brassicaceae and Poaceae species, respectively, growing in a clay loam was carried out over 75 d from vegetative to seed development stages during which rhizosphere soils were periodically sampled (Cregut et al. 2009). Each plant exhibited contrasting rhizosphere bacterial communities with actinobacteria and pseudomonads predominating on roots of barley and rape, respectively. Further, sulfur-mineralizing bacteria dominated rhizosphere soils of rape, which was attributed to selective effects of rhizo-deposited sulfur-containing compounds. Thus, the findings suggest that related weed species may foster specific seedling microbial communities and affect functional processes in the soil environment. However, impacts of environmental disturbance due to management, including herbicide application, have not been extensively studied.

**Established Weed Infestations, Root Development, and Release of Substrates.** Root growth and incursion into the soil during the development of a weed infestation is central to establishment of weed-specific soil microbial communities. Many annual weed species exhibit rapid growth rates early in the growing season, and an infestation may establish adequate root biomass to effectively supply C to sustain activities of the soil microbial community. For example, Palmer amaranth, common cocklebur (*Xanthium strumarium* L.), and quackgrass [*Elymus repens* (L.) Gould] rapidly established root systems in 15 d with a root elongation rate that surpassed that of grain sorghum (Weise 1968). Root biomass accumulation of 17 weed species measured at 6 wk was similar to rates for wheat and canola in a fertilizer response trial suggesting that, depending on density of the infestation, annual weeds establish root systems comparable to crops early in the growing season (Blackshaw et al. 2004). Subsequently, roots may readily proliferate and compete with crop plants within a relatively short time and quickly establish a distinct plant community within a production field if no weed control measures are taken. For example, roots of common cocklebur and redroot pigweed proliferated rapidly and

attained root profiles of 7.25 and 4.55 m<sup>2</sup> by 10 wk after germination, respectively, compared to a 3.16-m<sup>2</sup> profile attained by grain sorghum (Davis et al. 1967). Rooting depths were nearly 2 m for both weeds, and it was noted that the rapid root development of pigweed, reaching 88% of its mature root-profile area at 10 wk, was no doubt a major factor in its ability to compete successfully with row crops. Similarly, grasses such as downy brome (*Bromus tectorum* L.) that emerge in cereal grains may establish high root densities and persist overwinter at cool soil temperatures by extending roots deep into warmer soil (Skipper et al. 1996). Rapid primary root elongation and early initiation of adventitious root growth contribute to development of about 75% of the root mass within the top 10 cm of soil and over 90% in the top 30 cm, allowing downy brome to rapidly absorb nutrients and moisture available at the soil surface.

Numerous reports describe the intimate relationship between plant roots and soil microorganisms culminating in modification of soil microbial structure and biological functions (Berg and Smalla 2009). One of the main influences roots have on the soil microbial community is serving as a source of readily available substrates that are introduced into the rhizosphere, a process known as rhizodeposition (Lynch and Whipps 1990). Estimates of rhizodeposition rates vary widely depending on plant species and age, and whether C compounds are actively (exudation) or passively (diffusion and sloughing) released from roots, but these range from 5 to 60% of photosynthetically fixed C released to rhizosphere (Bais et al. 2006; Berg and Smalla 2009; Brinecombe et al. 2001; Kumar et al. 2006; Lynch and Whipps 1990).

The amount and composition of organic C in the soil environment is critical for sustaining microbial activity and soil biological functions (Berg and Smalla 2009; Walker et al. 2003). Soil microbial communities rely on available C supplied from roots to drive metabolic pathways, including many transformations resulting in accumulation of labile nutrients required for plant uptake. It is now known that the level of readily available or soluble C provided by plant roots to rhizosphere microorganisms greatly influences the amount of microbially derived N that is released for plant uptake (Averill and Finzi 2013). Recent research reported that certain C-4 plants including *Amaranthus* species possesses the nicotinamide adenine dinucleotide (NAD)-malic enzyme involved in photosynthesis, which has a 20-fold higher manganese (Mn)

requirement compared to C3 plants (Kering et al. 2009). This suggests that not only is the demand for soil Mn higher but the greater rate of photosynthesis by *Amaranthus* results in higher C inputs, related to greater accumulation of root biomass, possibly increasing the microbial community structure and activity in the rhizosphere. The implications of weeds differing in photosynthetic pathways and their subsequent effects on soil microbial function have yet to be determined.

Plant roots release a wide variety of compounds into the surrounding soil, including sugars, amino acids, organic acids, vitamins, polysaccharides, ethylene, and enzymes (Bais et al. 2006; Brinecombe et al. 2001; Garbeva et al. 2004) and create unique environments for the microorganisms living in association with plant roots. Production of secondary metabolites by weedy species induces important effects on ecosystem organisms and key biological processes, which help determine how the ecosystem functions (van der Putten et al. 2007) when challenged with a weed infestation. Soil microorganisms respond differently depending on plant species, thus different root exudate compositions from individual plants often select different rhizosphere communities (Ehrenfeld et al. 2005). Slender wild oat (*Avena barbata* Pott ex Link) roots release compounds that signal soil microorganisms to increase production of N-mineralizing enzymes (proteases and glucosaminidases) that increase ammonium content in the rhizosphere for uptake by the plant (DeAngelis et al. 2009). This may not only endow a competitive edge for growth of the weed but also may contribute to depletion of soil organic N reserves. Also, root exudates of wild oat increased bacterial quorum sensing, a form of chemical-based communication, required for extracellular enzyme activity (DeAngelis et al. 2008). Compounds released from members of *Brassicaceae* including glucosinolates and other cyanide-containing substances are toxic to a range of soil microorganisms and may be part of a strategy to facilitate establishment of weed species in this family (Vaicekonyte and Keesing 2012).

**Symbiotic Associations.** A majority of plants inhabiting native and agroecosystems form symbioses with rhizosphere microorganisms, including mycorrhizal fungi, nitrogen-fixing bacteria, and other plant growth-promoting rhizobacteria (PGPR). These microorganisms stimulate plant growth and reproduction by increasing access to limited nutrients (i.e., N, P) and protection from pathogens. In exchange,

plants provide carbon substrates for microbial metabolism. Such symbioses have been studied extensively in economically important plants; however, there is only a limited amount of research on the importance of symbiotic associations on weeds, how the symbionts affect their competitive ability, or how weeds affect these associations with crops.

Weeds are loosely categorized as strong to weak mycorrhizal hosts or as nonhosts, based on extent of root colonization (Vatovec et al. 2005). For example, common ragweed (*Ambrosia artemisiifolia* L.) is considered “strong” and yellow foxtail [*Setaria lutescens* (Poir.) Roemer & J.A. Schultes] “weak” mycorrhizal hosts while the pigweeds (*Amaranthus* spp.) are “nonhosts.” Thus, considerable variation in mycorrhizal colonization of weeds exists. Strong hosts may actually increase diversity and abundance of mycorrhizae, whereas nonhosts may be antagonized by mycorrhizae, although some Brassicaceae, i.e., garlic mustard, may disrupt mycorrhizal associations with desirable plants (Stinson et al. 2006). Mycorrhizae may suppress some agriculturally important weeds in a manner similar to biological control (Jordan et al. 2000; Rinaudo et al. 2010). A number of annual weeds with HR biotypes are nonmycorrhizal or have low mycorrhizal dependency; these include members of the *Brassica*, *Amaranthus*, and *Chenopodium* genera (Cipollini et al. 2012). Some nonmycorrhizal weeds may produce allelochemicals that directly suppress arbuscular mycorrhizal fungi thereby altering the mycorrhizal soil environment to favor one that is more conducive to its growth and development rather than to mycorrhizal-dependent plants, which include most annual crops (Stinson et al. 2006). Further actively competing weed infestations interfere with other plants by affecting mutualisms between the plants and soil organisms, with potentially major effects on community dynamics and on crop growth and development in annual systems (Jordan et al. 2012).

Impacts of weed infestations on nitrogen-fixing bacteria are related to inhibitory compounds of root exudates or vegetative extracts of species, including common lambsquarters, nutsedges (*Cyperus* spp.), and sunflower (*Helianthus annuus* L.) (Cipollini et al. 2012). These not only had direct effects on soybean (*Glycine max*) seed germination and seedling growth, but also severely reduced or eliminated nodulation by *Bradyrhizobium japonicum*. PGPR comprise many species of free-living bacteria, including *Pseudomonas fluorescens*, *Bacillus*

*subtilis*, and other species, that associate with plant roots and provide benefits in the form of enhanced growth and disease resistance (Kloepper et al. 2004). During screening trials for deleterious rhizobacteria for potential use as weed biological control agents, numerous bacteria have been identified as PGPR suggesting that a component of the weed rhizosphere may benefit weed growth (Li and Kremer 2000, 2006). The weed PGPR associate with annual weed roots as epiphytes on surfaces or as endophytes within root tissue and stimulate root growth through production of plant growth regulating compounds including indole-3-acetic acid (Kim and Kremer 2005).

Vegetative residues accumulated from persistent weed infestations and deposited on the soil surface or incorporated in soils may affect microbial community structure and activity. Limited research has focused on direct effects of weed residues in the soil environment other than on effects on other organisms due to allelopathic properties of the plant tissues (Aldrich and Kremer 1997; Zimdahl 1999). Inhibition of decomposition and nitrification by residues of certain plants in natural ecosystems (Rice 1984) indicates that similar inhibitory effects could develop with weeds in cropping systems. However, amendment of soil with velvetleaf residues from plants of different growth stages did not affect or stimulate microbial respiration, an indicator of decomposition (LaBarge and Kremer 1989). Specific substances such as phenolic compounds that tend to accumulate in many weed species directly impact soil microorganisms by selectively repressing certain microbial groups such as those involved in symbiotic associations with crop plants (Siqueira et al. 1991). Interestingly many *Amaranthus* spp. release low molecular weight volatile organic compounds that are highly bioactive and allelopathic toward developing seedlings such as tomato (*Solanum lycopersicum* L.) and disruptive of soil ecological processes (Connick et al. 1989).

## HR Weed Biotypes and Soil Biology and Ecology

Plant characteristics of HR weeds that contribute to effects on soil ecology and biology are similar to herbicide-susceptible weed biotypes with the additional consideration of potential expression of traits not related to resistance, or pleiotropy (Table 1). Addition of herbicide to HR weeds without killing the plant adds an additional factor to the weed-microbe interaction that would not be exhibited by herbicide-susceptible biotypes.

**No Herbicide Application.** As concluded for studies on transgenic HR crop cultivars (Powell and Dunfield 2007), the functional consequences of HR weeds on the structure of soil microbial communities have not been adequately addressed. Main areas of study concerning such effects may be the possibility of horizontal transfer of genes coding for herbicide resistance to the soil microbial community or direct effects on the community via contact within the weed rhizosphere. To date few, if any, attempts have been made to investigate these possibilities in the absence of herbicide treatment. A limited number of studies examining conventional and transgenic HR crop cultivars for effects on soil microbial communities serve as a reference for similar investigations of HR weeds. For example, Dunfield and Germida (2003) found differences between the bacterial communities associated with genetically modified *Brassica napus* and conventional varieties, which were presumably linked to differences in root exudate composition of these plants. Such studies might serve as a template for further work with brassicaceous HR weeds. Wild radish (*Raphanus raphanistrum* L.) is a widespread, economically important dicot weed of Australian and global agriculture, with most infestations possessing a high level of evolved resistance to acetolactate synthase (ALS)-inhibiting herbicides (Walsh et al. 2007). Not only has HR wild radish become widespread across millions of ha of Australian cropland but also infests large areas of fencerows, field edges, and other noncropland sites where this nonmycorrhizal plant likely disrupts mycorrhizal habitat (Willis et al. 2013) due to the difficulty in readily and economically controlling this HR weed. Also, foliar phytopathogens used as mycoherbicides are similarly infective and pathogenic on both imazaquin-susceptible and -resistant biotypes of common cocklebur (Abbas and Barrentine 1995). This suggests that interactions of the biotypes with soilborne microorganisms may be similar as well. However, studies directly addressing these comparisons should be conducted to confirm the hypothesized effects on the soil microbial community (Hirsch and Mauchline 2012).

Limited evidence suggests that the soil microbial community may be affected due to pleiotropic effects associated with development of HR in certain weed species. Rigid ryegrass (*Lolium rigidum* Gaudin) with P450 enhanced herbicide metabolism exhibits reduced relative growth and net assimilation (NAR) rates (Vila-Alub et al. 2005, 2009). The reduced NAR implies reduced C released through roots and could very well

impact microbial community function. Interestingly, ALS gene resistance in wild radish is not associated with pleiotropic effects (Li et al. 2013). Although pleiotropic effects of transgenic crops are considered relatively nonsignificant based on numerous safety assessments (Herman and Price 2013), more evaluation is required to confirm whether similar effects are an environmental concern with HR weeds.

**With Herbicide Application.** Herbicide-related factors that likely contribute the impact of HR weeds on the soil environment include herbicide chemistry, rate, and frequency of application; herbicide translocation within plant, allocation to roots; amount applied to infestation before resistance trait is realized; effect of different herbicides applied to resistant infestation as rescue treatments; and persistence of infestation and the legacy of impact on soil microbial community. Impacts of herbicides on interaction of both target and nontarget plants with soil microorganisms, primarily soilborne phytopathogens, have been detailed nearly since the onset of herbicide use as a weed management practice (Altman and Campbell 1977). Enhanced release of organic substances from roots due to herbicide application as a cause for increased pathogenic activity was well established. Several routinely applied herbicides were also implicated in poor infection or colonization of crop roots by mycorrhizae (Altman and Campbell 1977). Thus, in order to understand all possible impacts of current HR weeds on the soil environment, it is necessary to consider circumstances in which herbicides are present either as a nonefficacious treatment due to undetected HR in the weed infestation or as the alternative treatment for controlling weeds with resistance to another herbicide.

Most effort on impact of herbicide combined with herbicide resistance has focused on glyphosate and glyphosate-resistant (GR) weed biotypes. Early research showed that glyphosate applied to plant foliage was transported systemically toward roots and eventually released into rhizosphere soil (Couland and Casely 1979). Microbial activity may increase in rhizospheres of glyphosate-treated plants where it is subject to metabolism by specific microbial groups with potential changes in functional diversity of the heterotrophic microbial community (Mijangos et al. 2009). Glyphosate and altered composition of organic substances released from roots of glyphosate-treated GR soybean were similarly associated with altered microbial community structure in the rhizosphere (Kremer et al. 2005). Situations in which manage-



ment of GR weed infestations is continued with frequent and variable rather than using alternative herbicides may serve as conduits for delivering glyphosate into the soil environment.

Evaluations of GR weed biotypes including giant ragweed, common lambsquarters, and horseweed [*Conyza canadensis* (L.) Cronq.] demonstrated that glyphosate applied at label rates enhanced root colonization and infection by the fungi *Fusarium* spp. and *Pythium* spp. (Schafer et al. 2012, 2013). The selected soil microorganisms increased activity of glyphosate on glyphosate-susceptible giant ragweed and common lambsquarters but not on GR horseweed or GR common lambsquarters. It was concluded that because the level of fungal root colonization differed among the GR biotypes for each weed species, the resistance mechanism evolved in each weed influenced the rhizosphere microbial community structure and therefore, generalizations simply due to glyphosate resistance cannot be made. Soil microorganisms played an important role in herbicidal activity of glyphosate on giant ragweed causing root infection thereby contributing to plant death (Schafer et al. 2012). However, because the GR biotypes survived with enhanced root colonization, the soil fungal community is likely enriched with these species, at least for the season, to carry out or enhance some detrimental or beneficial function in the soil environment. Similarly, Rosenbaum et al. (2014) evaluated the association of *Fusarium* spp. on GR and susceptible biotypes of common waterhemp and found enhanced control of the susceptible biotype even though low levels of root colonization (approximately 25%) were recorded. The different responses by each common waterhemp biotype treated with glyphosate to soilborne fungi may be due to differential translocation within the plant. This has been demonstrated for three *Conyza* species, all of which systemically translocated glyphosate differently throughout the plant, with varying amounts reaching the root system (Gonzalez-Torralva et al. 2010). The persistence of potential root pathogens in soil and possible subsequent association with future weed infestations was not investigated. However, other research on application of glyphosate to soil from long-term GR cropping system fields detected no shift in microbial community structure suggesting an adaptation of the soil microbial community exposed to annual applications of glyphosate (Dick et al. 2010). Thus infestations of GR weeds that receive continuous glyphosate might also sustain a “glyphosate-adapted microbial community,” in which struc-

tural or functional diversity changes occurred early and have been maintained. However, management of GR weeds with alternate herbicides may restore the soil microbial community to its capacity prior to exposure to glyphosate.

Other potential impacts of glyphosate introduced into rhizosphere by translocation through roots include reduction in mycorrhizal spore germination and root colonization (Druille et al. 2013). Long-term (3+ yr) selection GR *Brassica* led to dominance in nonfield plant communities due to selection by glyphosate drift from adjacent crop fields for increased fitness of *Brassica* with the CP4 EPSPS transgene (Watrud et al. 2011). The increased HR *Brassica*, a mycorrhizal nonhost, may likely “indirectly negatively impact” ecosystem services associated with mycorrhizae, specifically by reducing biomass production and mycorrhizal infection of leguminous cohort plants in these ecosystems. Many herbicides including glyphosate alter the amounts and composition of compounds released from roots of the treated plants (Altman and Campbell 1977; Kremer et al. 2005); root exudates from herbicide-treated HR weeds containing altered chemical composition may then selectively enhance rhizosphere microorganisms that are either beneficial or detrimental to the plant community in the field or to soil ecosystem processes.

A relevant concern involves potential effects of herbicides applied to weeds resistant to a different herbicide class as a means of control. For example, foliar-applied mecoprop, an auxinic herbicide, increased certain rhizosphere and endophytic bacteria in wheat (Greaves and Sargent 1986). Effects of the selected bacterial community were not reported; however, it is likely that rhizosphere microbial diversity was altered with parallel changes in functions mediated both by the selected bacteria and by those microbial components that were adversely affected. These effects may have been positive or detrimental to soil function and, with the current trend to use similar auxinic herbicides to manage GR weeds, the potential compounding effects of two herbicide classes on the soil ecosystem merit new assessments of these effects on functional and structural diversity and their relationship to crop productivity.

## Summary and Management Implications

Impacts of HR weeds on soil biology and ecology are not well known. Previous research on effects of weed infestations regardless of herbicide suscepti-

bility currently serves as a template for potential effects of HR weeds on the soil environment. Understanding of any impacts involves dynamics of a complex system including interactions of plant, soil, microbial community, management system imposed on the agroecosystem, and time. “Monocultures” of infestations of HR weeds will likely select specific microbial communities and alter functional diversity with consideration of the particular soil and management, as well as use of herbicide as an additional factor.

Time is a major factor determining whether changes in soil biology and ecology are short-term or persist for several cropping cycles. Limited information suggests that although annual weed infestations are transient, their ability to provide an influx of very high numbers of seeds, often with associated and persistent seedborne microorganisms (van Overbeek et al. 2011), lead to establishment of weeds with specific rhizosphere microbial communities within a relatively short time (Cregut et al. 2009). The established weeds may release specific metabolites through root exudation or other deposition processes that affect both soil microbial and plant communities similar to effects of invasive weeds display in less disturbed ecosystems (Bais et al. 2006; Ehrenfeld et al. 2005; Willis et al. 2013).

Thus, understanding potential impacts of HR weeds on soil ecology and biology may be important for weed management for developing effective management approaches to control HR weeds in crop production systems. Their ability to establish and thrive in the field environment, condition the soil microbial community, and take advantage of factors in the conventional crop production system including widespread POST herbicide use, tillage, short crop rotations, and use of chemical fertilizers suggest that altering or increasing cropping system diversity may minimize the impact of HR weeds (Davis et al. 2012). Because HR weeds increasingly play an important role in weed management based on transgenic crops, an improved understanding of their behavior in agroecosystems is necessary to better control impacts on crop production.

Multidisciplinary approaches are needed to gain this understanding and should include weed scientists, microbiologists, soil scientists, ecologists, economists, and educators to develop and implement new or adapted technologies for understanding, monitoring, and minimizing potential risks from HR weeds to both the soil ecosystem and to crop productivity. Research is urgently needed in the following areas: (1) the critical period of HR weed infestation that

leads to long-lasting effects on soil microbial processes and on crop-microbial interactions; (2) investigation of similarities between invasive plant effects and their HR weed counterparts to better understand and predict impacts on soil biological processes, crop interactions, and environmental quality; and (3) the potential of multiple effects of two or more herbicide classes used for HR weed control on functional and structural diversity of soil microbial communities and crop interactions.

Many practices that are components of current diverse management systems including long rotations with diverse crops, herbicide rotation, cover crops, and organic amendment of soils have been eloquently described in previous reports (Davis et al. 2012; Forcella 2014). Indeed cover cropping has been shown to restore mycorrhizae in soils previously devoid of these organisms due to intensive cultivation (Lehman et al. 2012). A return to adoption of total weed management programs (Aldrich and Kremer 1997) and implementation of practices to keep the soil environment in balance through careful monitoring of soil to ensure the integrity of the biological and ecological ecosystem may minimize effects of HR weed infestations on soil biology and ecology.

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