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Review

Review of Volunteer Wheat (*Triticum aestivum*) Seedling Emergence and Seed Longevity in Soil[1]

RANDY L. ANDERSON and GEOFF SOPER[2]

Abstract: Herbicide-resistant cultivars may improve some aspects of weed management in wheat. However, negative consequences such as gene transfer among species, increased development of resistant weeds, or less effective volunteer wheat control may result from their use. Therefore, we reviewed literature on volunteer (self-sown) wheat seedling emergence and seed longevity in soil for insight in managing herbicide-resistant wheat. Data from classical burial studies suggested that wheat seeds were short-lived in soil, persisting less than 1 yr. Yet, in field studies, volunteer wheat seedlings were still emerging 16 mo after harvest; occasionally, seedlings have been observed 2 yr after harvest. Volunteer wheat emergence was extremely variable; causes of the variability are numerous and include genotypic, environmental, and production factors. This variability makes it difficult to predict volunteer wheat infestations in future years. Diverse cropping systems will enable producers to accrue the benefits of herbicide-resistant cultivars and yet still manage wheat volunteers, minimize gene flow by pollen, and avoid transfer of herbicide resistance. In regions where alternative crops are not viable, a key concern will be controlling volunteers and gene transfer in the next wheat crop.

Nomenclature: Wheat, *Triticum aestivum* L.

Additional index words: Dormancy, environment, gene transfer, herbicide resistance.

INTRODUCTION

Current production systems for wheat have favored the proliferation of difficult-to-control weeds. In winter wheat, jointed goatgrass (*Aegilops cylindrica* Host) in the United States and rigid ryegrass (*Lolium rigidum* L.) in Australia are now common, whereas wild oat (*Avena fatua* L.) continues to infest spring wheat in North America. These weeds proliferate because their life cycles are almost identical to that of wheat (Anderson 1998a; Powles et al. 1997). Herbicides are not always effective either because of genetic similarities, such as those between winter wheat and jointed goatgrass (Zemetra et al. 1998), or because weeds are resistant to currently used herbicides (Friesen et al. 2000; Powles et al. 1998).

The recent development of herbicide-resistant crops offers producers opportunities to control these weeds. The use of glyphosate (Ogg and Isakson 2001) or imazamox (Ball et al. 1999) will expand the spectrum of weeds that can be controlled in wheat, including jointed goatgrass and wild oat.

Yet, herbicide-resistant wheat may have negative consequences. Crop seeds dispersed during harvest can establish as volunteers during intervals between crops. A critical component of semiarid wheat production is storage of precipitation in soil during noncrop periods (Peterson et al. 1993). No-till systems, especially effective in storing precipitation (Peterson et al. 1996), rely extensively on glyphosate for weed control during this fallow period. If wheat volunteers are resistant to glyphosate, producers may till for volunteer control, primarily for economic reasons; tillage will minimize the water benefits gained with no-till production.

A second concern with herbicide-resistant volunteers is the transfer of resistant genes to other plants. For example, volunteer canola (*Brassica napus* L.) has been found to be resistant to glyphosate, glufosinate, and imazethapyr. This phenomenon was attributed to pollen flow among herbicide-resistant canola cultivars (Hall et al. 2000). Although gene transfer by pollen flow was expected with plants that naturally cross-pollinate, such as the *Brassica* species, it was hypothesized that gene transfer by self-pollinating species such as wheat would be minimal (Powles et al. 1997). Yet, gene transfer also

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occurs with wheat. Imazamox resistance has been transferred from winter wheat cultivars to hybrids of jointed goatgrass and winter wheat. This resistance transfer occurred within 2 yr of the initial application of imazamox and was attributed to pollen flow (Seefeldt et al. 1998).

An additional concern is the continuing development of weeds resistant to herbicides (Powles et al. 1997). Imazamox controls weeds by inhibiting the acetolactate synthase enzyme. Several weed species common in winter wheat, such as kochia [*Kochia scoparia* (L.) Schrad.] and prickly lettuce (*Lactuca serriola* L.), are already resistant to herbicides with this mode of action (Lyon et al. 1996). Cross-resistance occurs with this class of herbicides (Mallory-Smith et al. 1999), so it is probable that imazamox will favor the development of weeds resistant to this mode of action. With glyphosate, it was believed that development of resistance would be rare because of its unique mode of action (Kishmore et al. 1992). Yet, four weed species have been identified as resistant to glyphosate (Heap 2002), including rigid ryegrass and horseweed (*Conyza canadensis* L.), common weeds in winter wheat.

Herbicide-resistant cultivars may expand weed management options in wheat, but we are concerned that herbicide-resistant wheat may generate negative consequences such as gene transfer to wild species, increased weed resistance, or less effective volunteer wheat control. Therefore, we reviewed literature on volunteer wheat seedling emergence and seed longevity in soil for insight to guide management decisions with herbicide-resistant wheat. Our goal is to suggest production strategies that use herbicide-resistant cultivars without weakening future weed management.

VOLUNTEER WHEAT ECOLOGY

Extent of Seed Loss in Wheat. Shedding of grain occurs naturally in wheat at maturation. This natural shedding, where kernels fall or ''shatter'' from the spikelet, is further accentuated during harvest operations. G. Soper (unpublished data), summarizing field surveys in the U.K., found that harvest losses of wheat averaged 2% of yield, with 95% of the surveyed on-farm cases recording grain losses of less than 6%. Grain loss during harvest also varies with type of combine harvester; Komatsuzaki and Endo (1996), summarizing field surveys in Japan, reported that grain loss at harvest was greater with head-feeding (also known as stripper header) combines compared with combines with conventional grain headers. Loss of grain during harvest occurs both with grain entry at the cutter bar and with screenings discarded after threshing (Hughes 1974).

Natural shedding and shattering during harvest operations can leave a surprising number of wheat kernels on the soil surface. For example, 2% grain loss at harvest with a yield of 3,000 kg/ha and a 1,000-kernel weight of 25 gm will leave approximately 240 kernels/m^2. If combine loss approaches 6%, more than 700 kernels/m^2 could be left on the soil surface. An additional factor affecting kernel density on soil is that combines vary in dispersing screenings after threshing; some combines concentrate screenings in a narrow band behind the combine, whereas other combines are equipped with effective straw and chaff spreaders.

Seed Longevity After Shedding. Producers have long noted that weed seeds persist in soil. To understand this phenomenon, scientists conducted a series of experiments known as the classical burial studies, where seeds were buried in soil to determine their length of survival. Whereas initial studies, such as Beal's study (Darlington 1951), focused on weed seeds, later studies included crop seeds. Longevity of wheat seed viability was evaluated by Duvel (1905) in Virginia, Kjaer (1940) in Denmark, and Lewis (1958) in Wales. With each study, crop seeds were placed in retrievable containers, buried at several depths in soil, and recovered at designated intervals to determine seed survival. The studies showed that wheat seeds generally persisted less than 1 yr, leading the authors to conclude that ''cereal grains are short-lived in soil.''

Seedling Emergence in Field Studies. Results from field studies, however, contrast with the conclusion of classical burial studies. In the U.S. Central Great Plains, volunteer winter wheat seedlings emerged more than 15 mo after shedding at harvest (Anderson and Nielsen 1996). In the next growing season after wheat harvest, volunteer wheat seedlings emerged from April through October (Figure 1), with most seedlings emerging during August and September. Averaged across 4 yr, more than 40 seedlings/m^2 emerged after September 1, 14 mo after wheat harvest. Other scientists also have observed volunteer wheat (G. Wicks, personal communication) and barley (*Hordeum vulgare* L.) seedlings 2 yr after harvest (Davies and Wilson 1993).

The difference in seed longevity between field studies and the burial studies may be attributed to three factors. First, cereal grains require an after-ripening period before seeds can germinate (Hilhorst and Toorop 1997). The process of after-ripening can last from 0 to 7 mo

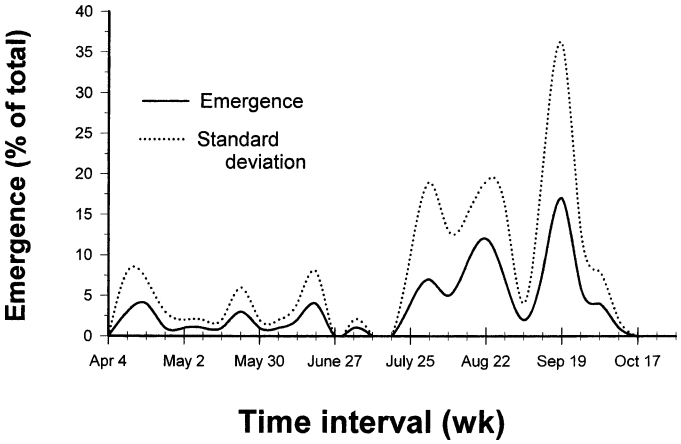

Figure 1. Seedling emergence pattern for volunteer wheat at Akron, CO. Grain was harvested in early July, and seedling emergence was recorded the following year, 9 to 15 mo later; the study was repeated across 4 yr. Dotted line represents one standard deviation. (Adapted from Anderson and Nielsen 1996.)

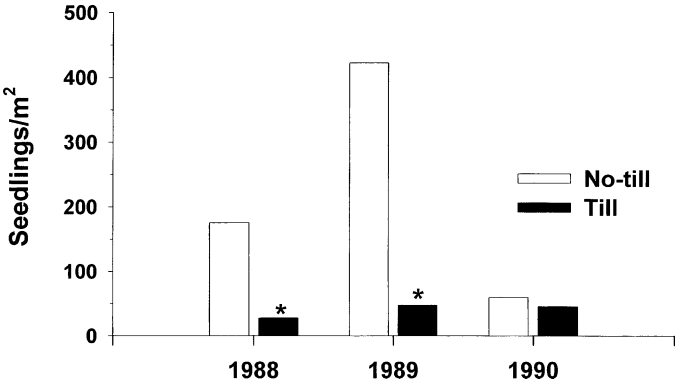

Figure 2. Seedling emergence of volunteer wheat during fallow in no-till and till systems at Akron, CO. Data collected from April 1 to November 1, 1988 through 1990. Asterisk signifies that means within a year differ at the 0.05 level of probability. (Adapted from Anderson and Nielsen 1996.)

depending on cultivar and environmental conditions (Pickett 1989). In the classical burial studies, wheat seeds were stored 6 to 9 mo before studies were started, thus eliminating the effect of after-ripening on seed development (J. Lewis, personal communication) (Duvel 1905; Kjaer 1940; Lewis 1958; Martin et al. 1976). In field studies, the after-ripening period likely delayed germination and prolonged seed survival.

The second factor in the burial studies was that seeds were buried at densities far in excess of natural occurrence in the soil seedbank. We suggest that the mass of germinating seeds within containers provided an excellent medium for microorganisms, thus enhancing microbial decomposition of the remaining seeds and reducing seed survival. The third factor is that precipitation levels are higher at the classical burial locations than in the semiarid regions where wheat is commonly grown. Seeds likely decayed earlier in the more moist conditions in the burial studies.

A striking characteristic of volunteer wheat emergence in the field was its variability; seedling emergence among years ranged from 28 to 423 plants/m^2 (Anderson and Nielsen 1996). One cause of this difference was tillage; averaged across years, fivefold more seedlings emerged in no-till than with tillage with a sweep plow.[3] This effect is attributed to tillage within 1 mo after wheat harvest, burying seeds in soil and stimulating seedling emergence in the autumn after wheat harvest. Autumn germination most likely reduced seedbank density of volunteer wheat in the following growing season. Tillage affects other grasses similarly; autumn emergence of both jointed goatgrass and downy brome (*Bromus tectorum* L.) increased with tillage after harvest (Anderson 1998b).

Yet, volunteer wheat responded differently to tillage in Australia; seedling density was almost 10-fold greater with tillage during fallow than with no-till (Wicks et al. 2000). The authors attributed this trend to less favorable conditions for germination and emergence in tilled treatments during the early period of fallow. The contrast in results between the two studies indicates that environmental factors can modify the effect of tillage on seedling emergence.

The difference in seedling emergence between no-till and tillage in the Colorado study also varied among years (Anderson and Nielsen 1996). In 1988 and 1989, seedling emergence was more than sixfold greater in no-till when compared with the tilled treatment; in contrast, seedling density did not differ between tillage treatments in 1990 (Figure 2). The difference in 1990 cannot be attributed to rainfall anomalies; thus, we are unable to explain the lack of tillage effect in 1990. Another variation was timing of volunteer wheat emergence in no-till (Figure 3). Comparing seasonal emergence between July 13 and November 2 among the 3 yr, seedlings emerged between August 24 and October 10 in 1988, whereas in 1990, all seedlings emerged before August 24. In 1989, volunteer wheat emerged from July 27 to October 29, differing with emergence in both 1988 and 1990.

Possible Causes of Variability. Being able to predict longevity and emergence characteristics of volunteer wheat would help producers in devising management

[3] A sweep plow comprises V-shaped blades that sever weed roots without inverting soil, tilling to a depth of 5 to 8 cm.

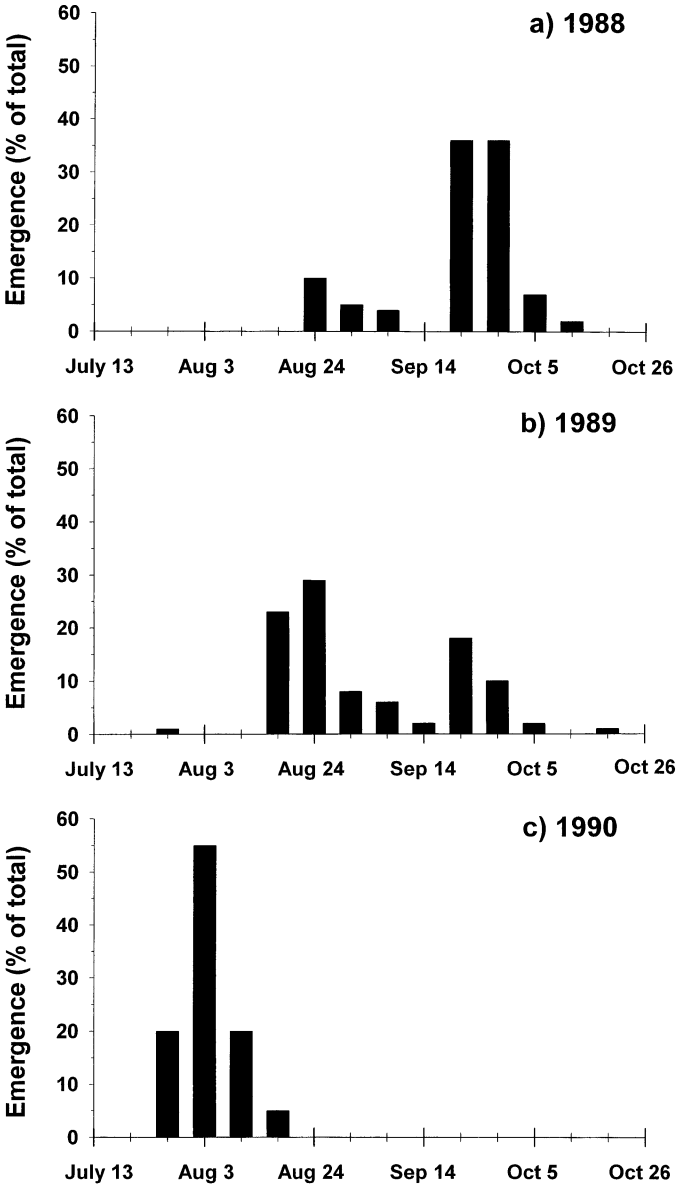

Figure 3. Seedling emergence of volunteer wheat between July 27 and November 2 for (a) 1988, (b) 1989, and (c) 1990. Data were collected during fallow in a no-till system at Akron, CO. (Adapted from Anderson and Nielsen 1996.)

strategies. As noted above, volunteer wheat emergence is extremely variable. Understanding the causes of this variability will help producers identify situations where seed longevity may be favored.

Shedding. Harvest efficiency can vary considerably; seed losses at harvest range from 0.8 to 6% of crop yield (Cussans 1978; Komatsuzaki and Endo 1996). Harvest efficiency also is affected by relative humidity because more shattering occurs under drier conditions (Pickett 1993).

Wheat cultivars differ in natural seed shedding before harvest. Pickett (1993) found that cultivars varied threefold in natural shedding; one cultivar lost 16% of its seeds before harvest. Also, natural shedding is accentuated when harvest is delayed because shedding increases with plant age. Cultivars also differ in ease of threshing; some cultivars retain more seeds in spike or head remnants dispersed with screenings. If seeds remain within glumes of the head, they remain dormant longer (Horovitz 1998; Komatsuzaki and Endo 1996). Hail is prominent in some regions where wheat is grown. Not only is shattering increased by hail, but also heads containing seeds are often broken off. Extensive head loss will prolong seedling emergence.

Dormancy. Wheat seeds usually are dormant at maturation. This condition, referred to as primary dormancy, is a period of time when a seed will not germinate even if environmental conditions are favorable (Foley 2001). Transition of dormant seeds to a germinable state is called after-ripening and involves chemical and physiological changes in the seed. With wheat, some initial short-term dormancy is desirable to prevent preharvest sprouting (Picket 1989).

With volunteer wheat, duration of primary dormancy can vary considerably. One source of variability is cultivar genetics; Komatsuzaki and Endo (1996) found that the duration of dormancy varied sixfold among cultivars. Another cause of variation in dormancy is environmental conditions during seed formation; extremes of temperature and moisture may increase dormancy (Pickett 1989). Hilhorst and Toorop (1997) suggested that a crop's ''wild'' background may reappear if seeds form under stress conditions. Seed dormancy has been quantified for two ancestral species of winter wheat, jointed goatgrass (Donald and Zimdahl 1987) and wild emmer (*Triticum turgidum* var. *dicoccoides*) (Horovitz 1998). One year after seed shedding, more than 20% of jointed goatgrass and wild emmer seeds were still alive in soil, whereas more than 2% of seeds of both species persisted 2 yr. Thus, volunteer wheat has a genetic background favoring dormancy.

Nitrogen management also affects wheat dormancy. Morris and Paulsen (1985) found that wheat seed dormancy was related to nitrogen concentration in seeds. Preharvest sprouting of wheat was more prominent if high rates of nitrogen fertilizers were applied during the growing season. However, this relationship varied among cultivars and also interacted with environmental conditions during seed development.

Seed dormancy also is affected by environmental con-

ditions after shedding. Pickett (1993) reported that after-ripening is delayed if seeds remain in moist conditions, whereas it is enhanced by extremely dry conditions. In contrast, dry conditions during optimum soil temperatures preclude germination, subsequently lengthening seed longevity in soil. Because environmental conditions vary considerably in semiarid regions, it will be difficult to predict stress-induced dormancy with volunteer wheat.

A further concern is that hybrids of winter wheat and jointed goatgrass are present in winter wheat fields (Snyder et al. 2000). Hybrid seeds may persist longer than volunteer wheat because hybrids express genetic traits of both parents. With jointed goatgrass, more than 2% of the seeds were still alive 2 yr after burial in soil, and some seeds persisted for 3 yr (Donald and Zimdahl 1987).

Production choices. Producers also can affect volunteer density in wheat by their management decisions. In northeastern Colorado, the optimum seeding period for winter wheat is September 10 to September 25. Yet, on soils prone to wind erosion, producers plant winter wheat in late August to increase plant growth in the fall; the greater biomass helps minimize wind erosion. Also, untimely rain can delay planting such that winter wheat may be planted in early October. Volunteer wheat emergence can differ considerably between these seeding dates. Using the 1988 emergence pattern from the Colorado study as an example (Anderson and Nielsen 1996), 153 volunteer seedlings would have emerged in winter wheat planted on August 31, contrasting with only 16 seedlings if winter wheat was planted on October 1. Seedling emergence differed almost 10-fold between the two seeding dates.

MANAGEMENT IMPLICATIONS

Production systems with herbicide-resistant wheat will need to address two characteristics of volunteer wheat. First, volunteer wheat seeds can survive in soil for at least 16 mo and may, in some situations, survive for 2 yr. Second, seedling emergence and seed longevity in soil is extremely variable, as shown by differences in seedling emergence among years in the Colorado study (Figure 2).

Factors influencing volunteer wheat dormancy are numerous (Figure 4); the multitude of possible interactions among these factors makes it difficult to predict seed longevity. For example, nutrient levels or water availability can vary within a field (Carr et al. 1991). Variable nitrogen levels will lead to different nitrogen concentrations in seeds; consequently, dormancy as affected by nitrogen concentration can vary in grain from different areas in the field. Pickett (1989) also suggested that organic matter level in soil affects seed longevity; more organic matter favors microbial consumption of seeds. Because organic matter levels can vary considerably within a field (Williams et al. 2001), seed survival may vary among areas of the same field.

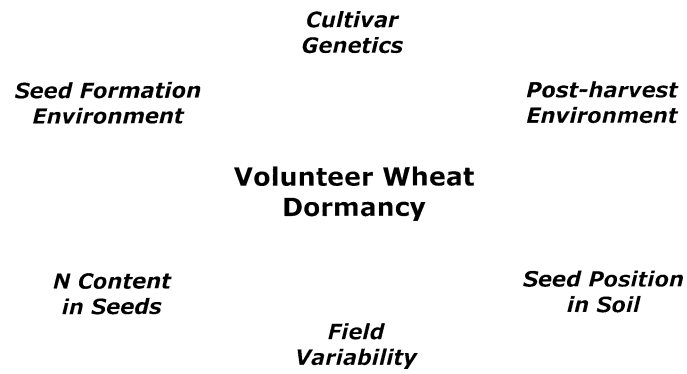

Figure 4. Multiple factors that influence development and persistence of dormancy in volunteer winter wheat.

Success in managing volunteer wheat will be influenced by how frequently wheat is grown in the rotation. In areas where alternate crops are available, producers can easily integrate herbicide-resistant wheat into their production systems. Crops other than wheat provide more options to control volunteers of herbicide-resistant wheat, whereas longer intervals between wheat crops reduce the probability of volunteers infesting future wheat and transferring genes by pollen flow. Especially favorable would be rotations designed in a cycle of 4 yr with different crops, such as winter wheat–corn (*Zea mays* L.)–sunflower (*Helianthus annuus* L.)–fallow (Anderson et al. 1999). The 3-yr interval between wheat crops in these rotations drastically reduces volunteer wheat density, whereas crop diversity provides flexibility to choose herbicides with different modes of action to minimize the development of resistance.

In areas where alternative crops are not economically viable, the common rotation is either wheat–fallow or continuous wheat. Herbicide-resistant cultivars will increase weed control options in these rotations; yet, a key concern will be controlling volunteer wheat. These rotations are especially vulnerable to pollen flow because volunteer wheat will infest the following wheat crops. Even though wheat generally is self-pollinating, the probability of gene transfer can be high as outcrossing with some cultivars approaches 6% (Hucl 1996). Fur-

thermore, moisture stress during flowering increases outcrossing in wheat (Briggs et al. 1999).

A concern with glyphosate-resistant wheat is that effective and affordable herbicide options may not be available to control volunteers during noncrop periods (Lyon et al. 2002), leading producers to rely on tillage for control. Pickett (1993) suggested the following strategy for tillage based on ecological traits of volunteer wheat. After-ripening of seeds is favored by hot and dry conditions; leaving seeds on the soil surface after harvest will encourage after-ripening. When environmental conditions become more favorable for germination in the following months, tilling fields shallowly to incorporate seeds in soil will stimulate germination. Tillage should be shallow because seed persistence increases with depth in soil; Cussans (1978) suggested not tilling more than 9 cm deep to avoid burial-induced dormancy of volunteer grains.

However, tillage has negative consequences in semiarid production; water-use efficiency and crop yields are usually less if tillage occurs during fallow (Peterson et al. 1996). A second negative aspect is that tillage reduces residue cover, thereby increasing soil erosion. Spring wheat–fallow would be especially vulnerable to erosion because fallow lasts 22 mo.

Tillage would not be favorable for rotations with continuous winter wheat because volunteer wheat emergence is greater during the first fall with shallow tillage than with a no-till system (Anderson 1998b). Therefore, producers with continuous wheat will have to rely on herbicides with different modes of action to eliminate volunteers in wheat. A possible option with continuous wheat is to delay planting, thus allowing volunteer wheat that emerges before planting to be controlled. Yet, this strategy can be detrimental to crop growth and grain yield if wheat is planted too late (Cook and Veseth 1991).

Herbicide-resistant cultivars provide new opportunities to control weeds in wheat. Yet, volunteer wheat requires additional management to ensure that pollen flow is minimized, especially in rotations where wheat is grown frequently. A striking demonstration of this concern is the transfer of imazamox resistance to jointed goatgrass after only 2 yr of imazamox use (Seefeldt et al. 1998). Without considering volunteer wheat management, effectiveness of this technology may be compromised rapidly by pollen flow. Producers are facing a paradox with herbicide-resistant cultivars; rotations where this technology may be the most helpful for weed control are also the most favorable for volunteer wheat infestations and pollen flow.

LITERATURE CITED

Anderson, R. L. 1998a. Ecological characteristics of winter annual grasses. Weed Technol. 12:478–483.

Anderson, R. L. 1998b. Seedling emergence of winter annual grasses as affected by limited tillage and crop canopy. Weed Technol. 12:262–267.

Anderson, R. L., R. A. Bowman, D. C. Nielsen, M. F. Vigil, R. M. Aiken, and J. G. Benjamin. 1999. Alternative crop rotations for the Central Great Plains. J. Prod. Agric. 12:95–99.

Anderson, R. L. and D. C. Nielsen. 1996. Emergence patterns of five weed species in the Great Plains. Weed Technol. 10:744–749.

Ball, D. A., F. L. Young, and A. G. Ogg Jr. 1999. Selective control of jointed goatgrass with imazamox in herbicide-resistant wheat. Weed Technol. 13: 77–82.

Briggs, K. G., O. K. Kiplagat, and A. M. Johnson-Flanagan. 1999. Floret sterility and outcrossing in two spring wheat cultivars. Can. J. Plant Sci. 79:321–328.

Carr, P. M., G. R. Carlson, J. S. Jacobsen, G. A. Nielsen, and E. O. Skogley. 1991. Farming soils, not fields: a strategy for increasing fertilizer profitability. J. Prod. Agric. 4:57–61.

Cook, R. J. and R. J. Veseth. 1991. Wheat Health Management. St. Paul, MN: American Phytopathological Society Press. 152 p.

Cussans, G. W. 1978. The problem of volunteer crops and some possible means of their control. *In* Proceedings of the 1978 British Crop Protection Conference—Weeds. Brighton, UK: British Crop Protection Council. Pp. 915–921.

Darlington, H. T. 1951. The seventy-year period for Dr. Beal's seed viability experiment. Am. J. Bot. 38:379–381.

Davies, D. K. and G. W. Wilson. 1993. The impact of husbandry and rotation on volunteer barley—a Scottish experience. Asp. Appl. Biol. 35:223–229.

Donald, W. W. and R. L. Zimdahl. 1987. Persistence, germinability, and distribution of jointed goatgrass (*Aegilops cylindrica*) seed in soil. Weed Sci. 35:149–154.

Duvel, J. T. 1905. The Vitality of Buried Seeds. U.S. Department of Agriculture Bureau Plant Industry Bull. 83.

Foley, M. E. 2001. Seed dormancy: an update on terminology, physiological genetics, and quantitative trait loci regulating germinability. Weed Sci. 49:305–317.

Friesen, L. F., T. L. Jones, R. C. Van Acker, and I. N. Morrison. 2000. Identification of *Avena fatua* populations resistant to imazamethabenz, flamprop, and fenoxaprop-P. Weed Sci. 48:532–540.

Hall, L., K. Topinka, J. Huffman, L. Davis, and A. Good. 2000. Pollen flow between herbicide-resistant *Brassica napus* is the cause of multiple-resistant *B. napus* volunteers. Weed Sci. 48:688–694.

Heap, I. 2002. The International Survey of Herbicide Resistant Weeds: Web page: www.weedscience.com. Accessed: August 8, 2002.

Hilhorst, H. M. and P. E. Toorop. 1997. Review on dormancy, germinability, and germination in crop and weed seeds. Adv. Agron. 61:111–165.

Horovitz, A. 1998. The soil seedbank of wild emmer. *In* N. Zencirci et al., eds. Proceedings of International Symposium on *In Situ* Conservation of Plant Genetic Diversity; November 8, 1998; Antalya, Turkey. Antalya, Turkey: CRIFC. Pp. 185–188.

Hucl, P. 1996. Outcrossing rates for 10 Canadian spring wheat cultivars. Can. J. Plant Sci. 76:423–427.

Hughes, R. G. 1974. Cereals as weeds. *In* Proceedings of the 12th British Weed Control Conference. Brighton, UK: British Crop Protection Council. Pp. 1023–1029.

Kishmore, G. M., S. R. Padgette, and R. T. Fraley. 1992. History of herbicide-tolerant crops: methods of development and current state of the art—emphasis on glyphosate tolerance. Weed Technol. 6:626–634.

Kjaer, A. 1940. Germination of buried and dry stored seeds. I. 1934–1939. Proc. Int. Seed Test. Assoc. 12:167–190.

Komatsuzaki, M. and O. Endo. 1996. Volunteer wheat in upland fields. Weed Res. (Tokyo) 41:197–204.

Lewis, J. 1958. Longevity of crop and weed seeds. I. First interim report. Proc. Int. Seed Test. Assoc. 23:340–354.

Lyon, D. J., A. J. Bussan, J. O. Evans, C. A. Mallory-Smith, and T. F. Peeper. 2002. Pest management implications of glyphosate-resistant wheat (*Triticum aestivum*) in the western U.S.A. Weed Technol. 16:680–690.

Lyon, D. J., S. D. Miller, and G. A. Wicks. 1996. The future of herbicides in weed control systems of the Great Plains. J. Prod. Agric. 9:209–215.

Mallory-Smith, C., P. Hendrickson, and G. Mueller-Warrant. 1999. Cross-

resistance of primisulfuron-resistant *Bromus tectorum* L. (downy brome) to sulfosulfuron. Weed Technol. 47:256–257.

Martin, J. H., W. H. Leonard, and D. L. Stamp. 1976. Wheat. *In* Principles of Field Crop Production. New York: Macmillan. Pp. 430–490.

Morris, C. F. and G. M. Paulsen. 1985. Preharvest sprouting of hard winter wheat as affected by nitrogen nutrition. Crop Sci. 25:1028–1031.

Ogg, A. G., Jr. and P. J. Isakson. 2001. Agronomic benefits and concerns for Roundup-Ready wheat. Proc. West. Soc. Weed Sci. 54:80–90.

Peterson, G. A., A. J. Schlegel, D. L. Tanaka, and O. R. Jones. 1996. Precipitation use efficiency as affected by cropping and tillage systems. J. Prod. Agric. 9:180–186.

Peterson, G. A., D. G. Westfall, and C. V. Cole. 1993. Agroecosystem approach to soil and crop management research. Soil Sci. Soc. Am. J. 57: 1354–1360.

Pickett, A. A. 1989. A review of seed dormancy and longevity of self-sown wheat and barley. Plant Var. Seeds 2:131–146.

Pickett, A. A. 1993. Cereals: seed shedding, dormancy, and longevity. Asp. Appl. Biol. 35:17–28.

Powles, S. B., D. F. Lorraine-Colwill, J. J. Dellow, and C. Preston. 1998. Evolved resistance to glyphosate in rigid ryegrass (*Lolium rigidum*) in Australia. Weed Sci. 46:604–607.

Powles, S. B., C. Preston, I. B. Bryan, and A. R. Justin. 1997. Herbicide resistance: impact and management. Adv. Agron. 58:57–93.

Seefeldt, S. S., R. S. Zemetra, F. L. Young, and S. S. Jones. 1998. Production of herbicide-resistant jointed goatgrass (*Aegilops cylindrica*) × wheat (*Triticum aestivum*) hybrids in the field by natural hybridization. Weed Sci. 46:632–634.

Snyder, J. R., C. A. Mallory-Smith, S. Balter, J. L. Hansen, and R. S. Zemetra. 2000. Seed production on *Triticum aestivum* by *Aegilops cylindrica* hybrids in the field. Weed Sci. 48:588–593.

Wicks, G. A., W. L. Felton, R. D. Murison, and R. J. Martin. 2000. Changes in fallow weed species in continuous wheat in northern New South Wales, 1981–1990. Aust. J. Exp. Agric. 40:831–842.

Williams, M. M., D. A. Mortensen, A. R. Martin, and D. B. Marx. 2001. Within-field soil heterogeneity effects on herbicide-mediated crop injury and weed biomass. Weed Sci. 49:798–805.

Zemetra, R. S., J. Hansen, and C. A. Mallory-Smith. 1998. Potential for gene transfer between wheat (*Triticum aestivum*) and jointed goatgrass (*Aegilops cylindrica*). Weed Sci. 46:313–317.