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Jointed goatgrass (*Aegilops cylindrica* Host.) is a serious weed problem in wheat (*Triticum aestivum* L.) production in the United States. Studies were conducted to determine the outcrossing rate, competitive ability, and effectiveness of certain control practices on jointed goatgrass. A field study was conducted over two years at four locations to determine outcrossing rates of four jointed goatgrass populations. There were no differences in outcrossing rates among the four populations. In the first year of the study, outcrossing was not different at any of the sites and averaged 1.28%. In the second year, outcrossing ranged from 0.38% to 2.24%. Outcrossing rates also were measured for wheat. Wheat outcrossing average was 0.09%, but rates ranged from 0% to 0.30%. A second study compared the competitive ability of plants derived from seed from the primary and secondary floret position within jointed goatgrass spikelets with winter wheat. This study consisted of three replacement series experiments that included pairwise combinations of the three plant types grown in five planting ratios. Jointed goatgrass plants from the seed in the secondary floret position were equally competitive with winter wheat and more competitive than plants from seed in the primary floret position. A third study was conducted to determine the effect of rate and timing of imazamox application on jointed goatgrass and imidazolinone-resistant wheat. At earlier timings, there was no difference in jointed goatgrass response to different herbicide rates. Wheat response was affected by herbicide rate at all application times. Pre-emergent herbicide treatments did not affect either species. When grown in 50:50 mixtures, final dry weights of jointed goatgrass and wheat were not affected by herbicide rate at either the early or late application time.

Jointed Goatgrass: Outcrossing, Competition with Winter Wheat, and Response to Timing and Rate of Imazamox

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Joshua B. Cannon, Author

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX TABLES

Table | Page

Jointed Goatgrass: Outcrossing, Competition with Winter Wheat, and Response to Timing and Rate of Imazamox

CHAPTER 1

Jointed Goatgrass (*Aegilops cylindrica*), a Brief Introduction

Jointed goatgrass is a problematic weed in wheat production throughout much of the United States. It is particularly troublesome in dryland winter wheat production areas where few economically feasible crop rotation options exist (Ball et al. 1999). Jointed goatgrass is also a problem in reduced tillage systems (Morrow et al. 1982; Schweitzer et al. 1988). With an increase in the use of these types of tillage practices, jointed goatgrass control has become an important issue facing wheat producers and weed scientists.

The first introduction of jointed goatgrass into the United States probably occurred in the late 19th century by means of contaminated 'Turkey' wheat seed imported from Russia. Jointed goatgrass was first reported in Delaware in 1870 and since then, has been found in 32 states (Donald and Ogg 1991; USDA 2005). Despite this widespread range of infestation, it is only a significant weed in wheat-producing areas, where it infests over 2 million ha of cropland. The economic losses from jointed goatgrass incurred by producers due to yield loss and reduction in grain quality have been estimated at $145 million annually (Anonymous 2005).

Biology

Jointed goatgrass (*Aegilops cylindrica*) is a cool season annual grass native to Eurasia. Culms of jointed goatgrass are erect and are between 40 and 60 cm in height (Hitchcock 1950). The seedhead of the jointed goatgrass plant is a spike, which is divided into 10-12 spikelets 5-10 cm in length. Each spikelet contains 2-5 florets. Usually only the first 2-3 florets set seed (Hitchcock 1950). Seed from the basal (primary) floret position are generally smaller than those from the apical (secondary) floret. A single jointed goatgrass plant can produce up to 3,000 seed when grown without competition (Gealy 1988).

According to Donald (1984), jointed goatgrass has a quantitative vernalization requirement in order to flower. As vernalization periods increased, the number of spikes as well as dry weight/spike increased and the number of days to flowering decreased. However the persistence of some jointed goatgrass plants in spring planted crops indicates that jointed goatgrass might be a more facultative winter annual than previously thought (Walenta et al. 2002). Studies of jointed goatgrass populations found in winter and spring wheat fields, Fandrich (2005) found that, although vernalization requirements varied among populations, all had a minimum number of vernalization days required for flowering. This result indicated that if spring temperatures are sufficiently cool, jointed goatgrass germinating in the spring can reproduce in that same year, but these are not true spring adapted types.

Studies by List et al. (1988) found that seed dormancy in jointed goatgrass depends on position within the spikelet, with the secondary seed being non-dormant and the other seed exhibiting cyclic dormancy. Studies on the effects of temperature on germination of after-ripened jointed goatgrass seed showed that secondary seed germinated at a much wider range of temperatures than did primary seed (Fandrich 2005). Although jointed goatgrass seed can stay viable for several years, studies have shown that after 3 years at a burial depth of 5 cm, few jointed goatgrass seed remained intact (Donald and Zimdahl 1987). Jointed goatgrass germination and emergence were affected by seed burial depth. Morrow et al. (1982) found that jointed goatgrass emerged best at depths of 2-3 cm and that no seedlings emerged from depths greater than 5 cm.

Jointed goatgrass is a problem in wheat largely because the two species are genetically related. Wheat and jointed goatgrass have a common ancestor, *Aegilops tauschii,* from which both species inherited the D genome (Maan 1976). This genetic similarity makes hybridization between the two species possible (Zemetra et al. 1998). The implications of this ability to hybridize will be discussed later in this chapter.

Jointed goatgrass causes crop losses by competing for resources and by decreasing grain quality (Donald and Ogg 1991). Mechanical separation of jointed goatgrass spikelets from harvested wheat is difficult. The presence of jointed goatgrass spikelets in winter wheat can result in reduced prices for, or rejection of the wheat (Donald and Ogg 1991). Infestations of jointed goatgrass between 54 and 86 plants m^{-2} have been shown to reduce wheat yields 25-29% (Rydrych 1983). In addition to weed density, the time of weed competition can affect crop yield response. Anderson (1993) found that 18 jointed goatgrass plants m^{-2} reduced yields by 27% when the two species emerged at the same time. Each day of delay in emergence of jointed goatgrass relative to the wheat emergence reduced grain loss by 0.3%. Jointed goatgrass emerging in the spring also was detrimental to wheat yield, causing a yield reduction of 6% (Anderson 1993). Despite studies such as these, predicting yield loss as a function of jointed goatgrass density remains difficult. Studies conducted at multiple sites across several years have revealed significant site to site and year to year variation in wheat yield response to jointed goatgrass infestations (Jasieniuk et al. 1999).

In replacement series experiments, jointed goatgrass was slightly less competitive than winter wheat, but was more competitive than downy brome (Fleming et al. 1988). Jointed goatgrass is reportedly more winter hardy and more competitive under drought stress than winter wheat (Donald and Ogg 1991).

Control

The best way to avoid losses from jointed goatgrass is to prevent infestations from occurring. Since jointed goatgrass is spread by seed movement, planting clean seed is essential for keeping jointed goatgrass out of fields. A study conducted in Oregon found that 20% of farmers were planting seed contaminated with jointed goatgrass (Swan 1984). A similar study in Utah in 1988 found jointed goatgrass contamination in 5.8% of drillboxes surveyed (Dewey and Whitesides 1990). Cleaning equipment after use in infested areas before moving to jointed goatgrass-free areas also can minimize spreading (Westra 1989).

Once a field is infested with jointed goatgrass, a number of cultural practices can be implemented to control the weed. Where it is possible, crop rotation can allow for control of weeds, especially when the rotational crops have different life cycles (Blackshaw et al. 1994). Switching to spring planted crops or using extended fallow periods can reduce jointed goatgrass infestations (Donald 1991). However, jointed goatgrass can germinate in the spring and set seed before wheat harvest (Walenta et al. 2002). Later planting of spring wheat reduced jointed goatgrass seed production, but also caused reductions in wheat yields (Young et al. 2003).

Wheat planting density and geometry can improve crop competitiveness with jointed goatgrass. Increasing wheat seeding rates reduced reproductive success in jointed goatgrass (Kappler et al. 1997). In several studies in Washington, planting wheat in paired rows reduced jointed goatgrass spikelet production compared to single row wheat planting (Young et al. 1999).

Careful management of fertilizers is another way to improve wheat competitiveness with jointed goatgrass. Mesbah and Miller (1999) found that deep banding nitrogen fertilizer 5 or 10 cm below the surface adjacent to wheat rows improved competitiveness of the wheat over jointed goatgrass. In these studies, wheat yield increased 7-10%. Although jointed goatgrass density was not affected, the number of spikes/plant and joints/spike as well as total jointed goatgrass biomass were reduced. Timing of fertilizer application can also favor wheat over jointed goatgrass. Applying nitrogen fertilizer in the spring of the fallow year in conjunction with the planting of taller varieties reduced jointed goatgrass seed production by more than 40% (Anderson 1997).

Tillage can be used to control jointed goatgrass in wheat. V-blade sweeping and disking have been shown to reduce jointed goatgrass populations by 75%, while deeper tillage reduced jointed goatgrass populations by 95% (Westra 1989). Delayed planting in conjunction with rod weeding before planting also can be an effective way to reduce jointed goatgrass competition with crops (Donald and Ogg 1991).

Burning has been shown to effectively control jointed goatgrass (Willis et al. 1989; Young et al.1990). In studies on the effects of post-harvest field burning on jointed goatgrass, jointed goatgrass spikelet density on the soil surface was reduced by as much as 97% (Young et al. 1990). Burning, however, is not allowed in many areas due to fire hazard and air quality concerns. Burning also changes moisture availability in the soil and removes crop residue. For these reasons, burning may not be a viable control option for many farmers.

When soil conservation is a concern, and tillage and burning can not be used, farmers must rely largely on herbicides to control jointed goatgrass. Chemical control of jointed goatgrass in fallow periods is possible using a broad-spectrum, non-selective herbicide such as glyphosate (Wiese et al. 1995). However, due to their developmental and genetic similarity, selective chemical control of jointed goatgrass in wheat was not possible until the introduction of herbicide-resistant wheat (Ball et al. 1999). Imazamox-resistant wheat is currently available and efforts have been made towards the release of glyphosate-resistant wheat (Ball et al. 1999; Lyon et al. 2002).

Herbicide-resistant varieties offer several benefits to farmers. These crops make possible the control of weeds that were previously difficult to control. With herbicide-resistant crops there is also the possibility of having a longer window of application time and greater crop safety (Lyon et al. 2002).

Despite these benefits and the apparent simplicity of the system, concerns have been raised about possible problems that could arise from the use of this technology. Increased reliance on one herbicide could lead to rapid evolution of herbicide-resistant weeds. This is especially true of herbicides such as acetolactate synthase inhibitors, including imidazolinones, which are known to rapidly select resistant populations (Tranel and Wright 2002). Herbicide-resistant volunteer wheat plants could become weed problems and act as green bridges for pests and pathogens

(Lyon et al. 2002). Another major concern about herbicide-resistant wheat is the potential for resistance genes to move from the crop to closely related weeds (Zemetra et al. 1998). These concerns and others should be carefully considered when deciding whether or not to use a particular herbicide-resistant wheat.

Gene flow

The potential for gene flow between wheat and jointed goatgrass has been the subject of much study in recent years (Zemetra et al. 1998; Wang et al. 2000; Guadagnuolo et al. 2001; Wang et al. 2001; Morrison et al. 2002). Gene flow has been defined as the "incorporation of genes into the gene pool of one population from one or more populations" (Futumya 1998). If a cultivated species can produce fertile hybrids with a wild relative, then it may be possible for genes to move into the wild population through back-crossing (Ellstrand and Hoffman 1990).

Hybridization between wheat and jointed goatgrass was observed as early as the 1920's, but hybrid plants were incorrectly believed to be sterile (Morrison et al. 2002a). Seed production of hybrid plants has now been well documented (Snyder et al. 2000; Wang et al. 2001; Morrison et al. 2002b). In a study by Wang et al. (2001), female fertility of wheat by jointed goatgrass hybrids was found to be 0.87%. In the same study after one generation of backcrossing, female fertility increased and male and self-fertility were partially restored. Self-fertility continued to increase with successive backcrosses until it was fully restored with as few as three backcross generations (Zemetra et al. 1998).

Herbicide resistance traits have been found in wheat by jointed goatgrass hybrids located near experimental plots where herbicide-resistant wheat was being grown (Seefeldt et al. 1998; Mallory-Smith, unpublished data). If a gene that confers a fitness advantage introgressed into individuals in a weed population, it will become readily established in that population (Jenczewski et al. 2003). Herbicide resistance is generally a neutral trait as long as there is no selection pressure from the herbicide. If the herbicide is present, then the resistance trait will constitute a fitness advantage and the allele will increase in frequency within the population.

Herbicide-resistant weeds could undermine the usefulness of herbicide-resistant wheat and reduce control options. Loss of control options is potentially serious, especially in situations such as reduced tillage systems, where farmers have few choices for weed control. In order for the herbicides currently in use to continue to be effective, careful management of herbicide-resistant wheat is imperative. Understanding gene flow is an important component of developing appropriate management strategies.

Despite the many advancements that have been made in the understanding of jointed goatgrass, there is still much to be learned. Information pertinent to the discussion of gene flow, such as jointed goatgrass outcrossing rate, is missing from the literature. Further research into the biology and ecology of this species is necessary to insure effective management.

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Chapter 2

Outcrossing Rates in Four Jointed Goatgrass (*Aegilops cylindrica*) Populations

Jointed goatgrass is a common weed in wheat production systems in the United States. Because of its genetic and developmental similarity to wheat, selective control of jointed goatgrass has presented a challenge to growers. Recently, innovations have made herbicide-resistant wheat available and selective chemical control of jointed goatgrass is now possible. The ability of wheat to hybridize with jointed goatgrass in the field is well documented. The introduction of herbicide resistance into wheat has generated some concern about the possibility of resistance genes moving to jointed goatgrass populations. When assessing the potential risk of gene flow, it is important to understand how genes move within weed populations. To help understand how genes move in jointed goatgrass populations, field studies were conducted at three locations in Oregon and one location in Colorado, over two years, to determine the outcrossing rates of four jointed goatgrass populations. There were no differences in outcrossing rates among the four populations. In the first year of the study, outcrossing was not different at any of the sites and averaged 1.28%. In the second year, outcrossing ranged from 0.38% to 2.24%. Outcrossing rates also were measured for wheat. Wheat outcrossing average was 0.09%, but rates ranged from 0% to 0.3%.

Nomenclature: Jointed goatgrass, *Aegilops cylindrica* Host., AEGCY; winter wheat, *Triticum aestivum* L.

Key Words: Gene flow, outcrossing

Gene flow between crops and weeds has been documented in several species (Ellstrand et al. 1999). Futumya (1998) defined gene flow as "incorporation of genes into the gene pool of one population from one or more populations". Gene flow can occur seed or vegetative propagule movement, or via pollen movement. Factors affecting pollen-mediated gene flow include sexual compatibility of species, coincidence of flowering time, abundance of pollinators and receptors, and distance between plants (Jenczewski et al. 2003). Gene flow has recently become the subject of more study because of the introduction of transgenic crops. Transgenic traits such as herbicide resistance are easy markers to detect, making the occurrence of gene flow more readily observable.

Hybridization occurs in nature and is an important evolutionary process. Much of the genetic diversity found in nature is a result of hybridization events. If fertile hybrids between a crop and a weed develop, it is possible that genes from crops can be transferred through back-crossing to the weed population (Ellstrand and Hoffman 1990). Traits such as competitiveness, winter-hardiness, and disease and herbicide resistance are desirable in crops plants. These same traits, if expressed in weeds, could increase weed interference, limit control options and potentially have deleterious ecological effects. For this reason, when placing these traits in crop plants through traditional breeding or through genetic engineering, it is important to consider the possibility of the genes 'escaping' into related weed species and what the consequences of this might be.

Wheat is a generally self-pollinated grass (Hucl 1996). Depending on variety and environmental conditions, outcrossing rates in wheat can be as high as 5.6%

(Martin 1990), but outcrossing rates are normally below 1% (Hucl 1996). Despite this low percentage of outcrossing, hybridization with jointed goatgrass, a related species, does occur under field conditions (Morrison et al. 2002). Jointed goatgrass is a winter annual grass that is closely related to wheat. Jointed goatgrass (CD) has the D genome in common with wheat (ABD) and hybrids form readily in the field. Although these hybrids are male sterile, Wang et al. (2001) found female fertility rates of 0.87% and seed production on hybrids in field conditions has been documented (Snyder et al. 2000). Self-fertility can be partially restored after only two generations of back-crossing and can be fully restored as early as the third back-cross generation (Zemetra et al. 1998).

Herbicide resistance genes in wheat have been shown to be transferable to jointed goatgrass (Seefeldt et al. 1998). It has been suggested that gene transfer can be avoided by placing a resistance gene on the A or B genomes that do not occur in jointed goatgrass. However, translocation or chromosome retention can occur, making gene transfer possible regardless of the genome on which the genes are located (Wang et al. 2000). There is ample evidence that pollen-mediated gene flow can occur between wheat and jointed goatgrass. What is not known is the fate of genes once they have become introgressed into the weed populations.

Some genes can be present in weeds, but not expressed. In other cases, the gene might confer a trait with no fitness advantage, or even be a disadvantage. If this occurs, the frequency of the allele will not increase in the population, or may actually decrease until it disappears. In the case of herbicide resistance, as long as the herbicide is present, weeds with the resistance trait have a significant fitness advantage over those that do not. However, in the absence of the herbicide, resistance is generally considered a neutral trait (Tranel and Wright 2002).

The introduction of herbicide-resistant wheat varieties also may lead to increased selection pressure on weed populations. Under such conditions, resistance can evolve to the particular herbicide. Whether a resistance gene is present in a population as a result of hybridization or selection, understanding the outcrossing rate of a species is important in predicting how a gene will move within and among populations of that species.

Jointed goatgrass is considered to be a predominately self-pollinated species, but no studies have been conducted to determine the outcrossing rate of jointed goatgrass. Since jointed goatgrass generally has a longer period of anthesis than wheat, it would likely have a higher outcrossing rate than wheat. To determine outcrossing rates, field experiments were conducted to determine outcrossing rates of four populations of jointed goatgrass and two winter wheat cultivars.

Materials and Methods

Field experiments were conducted at four locations (Pendleton, Corvallis, and Moro, OR, and Fort Collins, CO) over two years (2002-2003, 2003-2004) to determine the outcrossing rates of jointed goatgrass and winter wheat. Four populations (A, B, C, and D) of jointed goatgrass and two winter wheat varieties (Madsen and Stephens) were used as receptors. Populations A, B, C, and D were collected at Helix, OR, Bickleton, WA, Fort Collins and Paoli, CO, respectively. A pubescent population (P) of jointed goatgrass, originally from Bickleton, WA was used as the pollinator.

Pubescence is a dominant trait and was used in this study as a morphological marker to detect outcrossing to the glabrous jointed goatgrass populations A, B, C, and D. Blue aleurone wheat was used as a pollinator for the wheat. The blue seeded wheat used had a mixture of maturity types to ensure that some plants would be flowering at the same time as the receptor plants.

Single rows of receptor plants were grown between paired pollinator rows. Rows were 2 m in length and 20 cm apart. An additional pollinator row was planted perpendicular to the receptor rows at both ends of the treatment plots. Each treatment was replicated four times. For jointed goatgrass, 50 spikelets were sown in each pollinator row and 100 spikelets were sown in each receptor row. Jointed goatgrass spikelets usually contain two seeds (Hitchcock 1950), so the actual seeding rated was approximately 100 seeds per 2 m row for pollinators and 200 seeds per 2 m row for the receptors. Wheat was seeded at 50 seeds per row for the pollinator rows and 100 seeds per row for the receptor rows. Winter barley was sown in 60 cm bands around each replication to minimize the possibility of contamination from pollen outside the cross blocks. Jointed goatgrass treatments were planted at all four experimental sites, while wheat treatments were only planted at the three Oregon locations.

In 2002, the experiment was planted at Corvallis on October 15, at Pendleton on October 17, at Moro on November 7, and at Fort Collins on September 30. The planting dates for those locations in 2003 were October 13, October 20, October 21, and September 19, respectively. Planting dates for the experiment corresponded approximately to typical local wheat planting times at the different locations. At maturity, seed from all plants in the receptor rows were harvested and bulked by row.

Number of plants per row and number of tillers per plant were counted to determine the plant density.

After harvesting, all seed were stored at room temperature and allowed to dry. Wheat heads were threshed by hand. Total seed number as well as blue seed number from each receptor row were counted. The percent outcrossing was calculated as the number of blue seeds per row, divided by the total number of seed in that row. Jointed goatgrass seed were allowed to after-ripen until October 30, then planted at Corvallis. Seed from each receptor row were grown in individual rows. The following year, when the plants had reached maturity, seed from any pubescent plants found in the growout rows were collected. Twelve seed from each pubescent plant were planted in a greenhouse and seedlings from these were evaluated for segregation. If segregation of glabrous and pubescent seedlings was observed, the mother plant was most likely a product of outcrossing. If no segregation occurred, then the mother plants must have been homozygous for the dominant allele, a condition that could not have resulted from outcrossing between a pubescent pollinator and a glabrous mother plant. Pubescent plants whose progeny did not segregate were not included in the calculation of percent outcrossing and were considered contaminants. The numbers of pubescent plants with non-segregating progeny collected from the growout rows were 47 and 12 for the first and second years, respectively.

There was some uncertainty as to the reliability of differentiating between pubescent and glabrous seedlings at early stages of development. During the first year of the study, to test the accuracy of these early evaluations, seedlings were evaluated at 14 d after planting, and then vernalized for 8 wk at 4 C. After vernalization, the seedlings were transplanted to individual cones and grown to maturity. At maturity, the plants were evaluated again for pubescence. The results of the second evaluation did not differ from the 14 d evaluation so it was concluded that the early seedling evaluations were accurate. Consequently, progeny of pubescent plants found in the growout rows during the second year of the study were only evaluated 14 d after planting and not grown to maturity.

The number of plants per growout row was estimated by counting the number of plants in three 1 m sections of each row to obtain an estimate of average number of plants per meter. The row lengths were then measured and plants per meter for each row were multiplied by the length of the row in meters.

Percent outcrossing results for wheat and jointed goatgrass were subjected to ANOVA. Replications were not a significant source of variation and data from all replications were pooled. Averages of sites, biotypes and years were compared using Duncan's multiple range test.

Results and Discussion

Jointed Goatgrass

A high level of variability in percent outcrossing of jointed goatgrass was observed in both years of the study. However, similar studies conducted with wheat also show that a large degree of variability in outcrossing is to be expected (Hucl 1996; Martin 1990). ANOVA revealed that there was no difference in percent outcrossing among the four jointed goatgrass populations at any of the sites in either year. Therefore, data for all populations at each site were combined. However, there was a significant site by year interaction so data could not be combined over the two years. The means for each site and year, along with the standard error for each mean are provided in Table 1. The year by site interaction was a significant source of variation, but population was not, suggesting that outcrossing rates in jointed goatgrass may be more affected by environmental conditions than by genetic factors.

Table 1. Jointed goatgrass seed produced by outcrossing as a percent of total number of seeds produced by year and location.

Year	Pendleton, OR	Moro, OR	Corvallis, OR	Ft. Collins, CO	Year Mean
	Outcrossing %				
2002-2003	0.99 (0.22)[a]	0.99 (0.37)	1.13 (0.29)	2.00 (0.57)	1.28 (0.2)
2003-2004	0.65 (0.3)	2.24 (0.55)	0.38 (0.19)	1.26 (0.26)	1.19 (0.2)

[a] Standard errors are shown in parentheses

Wheat

Wheat outcrossing rates varied by year and site. Wheat outcrossing rates and standard errors are shown in Table 2. Outcrossing rates were higher in the first year at all sites. No difference in outcrossing rates was detected between the two varieties of wheat. The average percent outcrossing over all years and sites was 0.09%. This result agrees with the outcrossing rates reported by Hansen et al. (2005) for blue seeded wheat to Madsen and Brundage 96 varieties. At each site in both years, jointed goatgrass had greater outcrossing rates than wheat.

Table 2. Winter wheat seed produced by outcrossing as a percent of total number of seeds produced by year and location

Year	Pendleton, OR	Moro, OR	Corvallis, OR	Year Mean
	Outcrossing %			
2002-2003	0.30 (0.16)[a]	0.11 (0.11)	0.01 (0.01)	0.14 (0.07)
2003-2004	0.06 (0.02)	0.06 (0.04)	0 (0.0)	0.04 (0.01)

[a] Standard errors are shown in parentheses

Implications

Based on these outcrossing rates, it is possible to model how a resistance gene might move in a population. Models have been created to predict the development of herbicide resistance in jointed goatgrass based on management practices (Hanson et al. 2002). Knowledge of the actual rate of outcrossing of jointed goatgrass can help augment such models. Whether the gene is present as a result of hybridization or selection by a herbicide, does not change how the gene would move. Since herbicide resistance usually is a dominant trait (Jasieniuk et al. 1996), successive backcross generations will lead to a more phenotypically homogeneous population, but will never completely eliminate the recessive allele. This is especially true in cases such as resistance to acetolactate synthase inhibitors, which is conferred by a single, dominant or semidominant, nuclear gene (Mallory-Smith et al. 1990). In such cases, heterozygous plants will be of the resistant phenotype, ensuring that some recessive alleles will remain in the population.

Figure 1 shows an example of a jointed goatgrass population that has 100 individuals and 1 of them is heterozygous (Rr) for the resistance trait and the rest are homozygous (rr) recessive. If a herbicide is applied and 95% of the goatgrass plants are killed, there will be 5 plants left to reproduce the next year, 1 resistant and 4 susceptible. Using the average outcrossing rate for jointed goatgrass observed in this study, 1.23% of the seeds on the resistant plant will result from cross-pollination with susceptible plants. Half of that 1.23% will be Rr and half will be rr. The susceptible plants will receive pollen from both the resistant plant and the other susceptible plants. On any one of the susceptible plants, 1.23% of the seed will be the result of outcrossing with 1 resistant and 3 susceptible pollinators. The remainder of the seeds on the resistant plant will be a result of self-pollination. Because the plant is Rr, half the selfs will result in Rr offspring, one quarter will result in rr and one quarter will result in RR offspring. All selfs on the susceptible plants will result in susceptible offspring.

Jointed goatgrass plants can produce up to 3000 seeds per plant when grown without competition (Gealy 1988). However, when grown in competition with winter wheat, jointed goatgrass seed production is usually 100-300 seeds per plant. Given the population above, if each plant produces 130 seed, in the second year there would be 552 rr seed, 66 Rr seed and 32 RR seed. The number of seed that will successfully germinate and emerge depends on environmental conditions and cultural practices. The average emergence of jointed goatgrass seed planted in the outcrossing study was 30%. Assuming that the resistance trait does not affect germination or emergence, at 30% emergence, the numbers of RR, Rr, and rr plants in the second year would be 10, 20, and 165, respectively.

Figure 1. Flow chart of genotypes in a hypothetical jointed goatgrass population

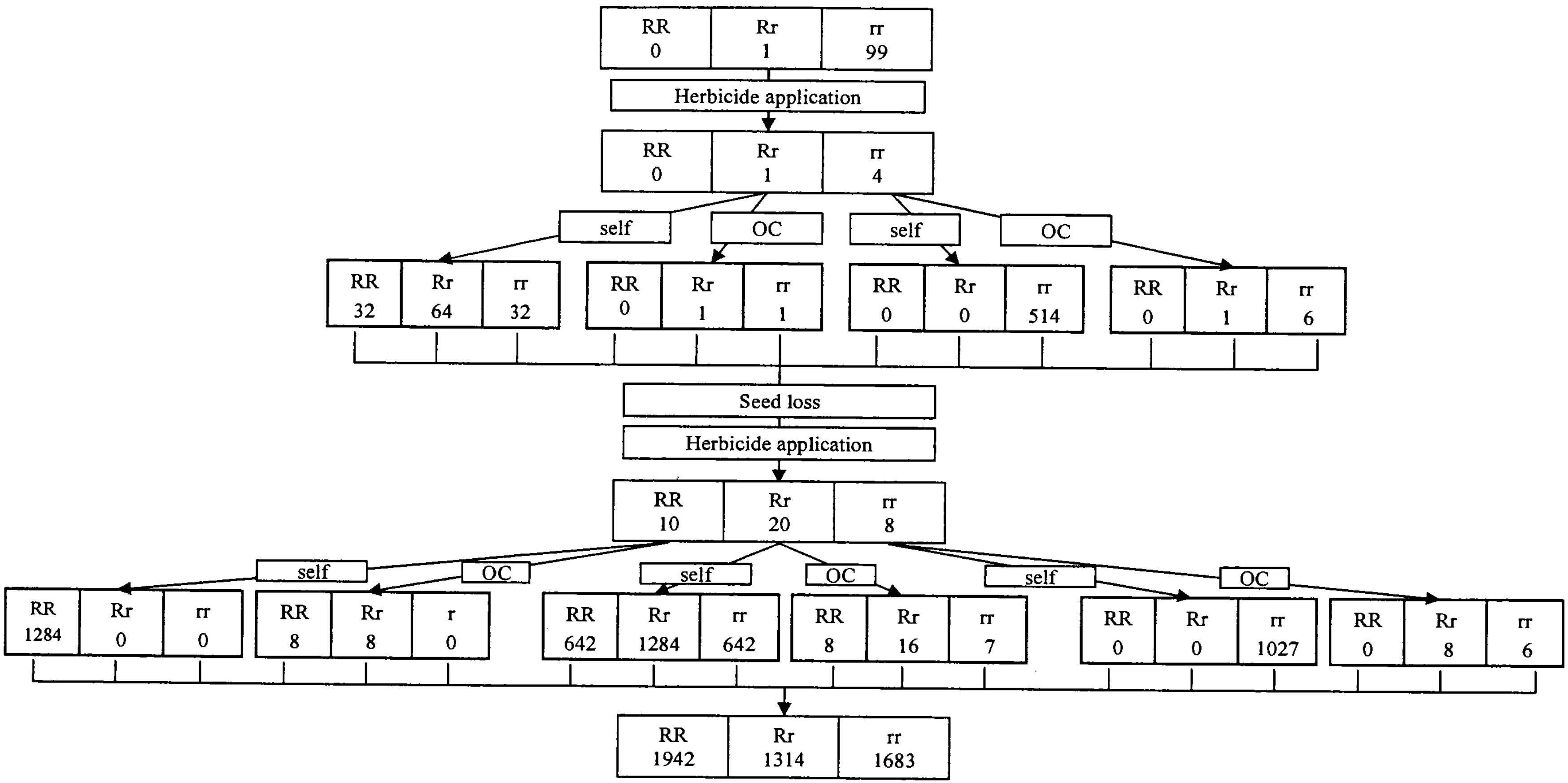

Figure 1. The numbers of each genotype in a hypothetical jointed goatgrass population with 99 susceptible individuals and 1 resistant individual, assuming 1.23% outcrossing (OC), 130 seed plant^{-1}, 95% control by the herbicide and 30% germination and emergence of jointed goatgrass seed.

An application of herbicide with the same efficacy as the first application would leave 30 resistant plants and 8 susceptible plants in the field. If these plants are allowed to reproduce, there would be 1942 RR seeds, 1314 Rr seeds, and 1683 rr seeds produced. This represents a change in frequency of resistance from 1% to 66% after just 2 years of herbicide treatment.

Outcrossing may be an important source of introduction of new genes into jointed goatgrass populations. However, at the low rates at which jointed goatgrass outcrosses, it is not likely to greatly affect the allele frequency in populations. Environmental and cultural factors could affect the total rate of outcrossing and emergence. Since jointed goatgrass is primarily self-pollinated (98.77%), the dominant and recessive alleles would remain in the population at nearly the same rate, if there is no selection pressure by the herbicide. Intense selection pressure from herbicides would drive the population towards resistance at a rapid rate.

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Chapter 3

Effect of Seed Position Within the Spikelet on Competition between Jointed Goatgrass (*Aegilops cylindrica*) and Winter Wheat

Studies have been conducted in the past to examine competition between wheat and jointed goatgrass. These studies, although insightful, neglect to take into account the fact that jointed goatgrass spikelets generally contain multiple seeds. These seeds have been shown to have differing biological characteristics based on position within the spikelet. The purpose of this study was to determine if competitive ability of jointed goatgrass plants is related to the position of the seed within the spikelet. Greenhouse studies were conducted to assess the relative competitive ability of winter wheat seedlings and seedlings of jointed goatgrass derived from different positions within the spikelet. Three replacement series experiments compared paired mixtures of the three plant types. Relative yields and relative crowding coefficients were calculated to evaluate competitive ability. Plants grown from primary jointed goatgrass seed were less competitive than plants grown from secondary jointed goatgrass seed or wheat. Secondary jointed goatgrass and wheat plants were equally competitive.

Nomenclature: Jointed goatgrass, *Aegilops cylindrica* Host., AEGCY; winter wheat, *Triticum aestivum* L.

Key words: Competition; replacement series.

Jointed goatgrass is a winter annual grass that is a common weed in cereal production throughout the United States. It infests over 2 million ha of cropland and costs growers an estimated $145 million annually in yield losses and reduced quality (Anonymous 2005). Jointed goatgrass causes losses in two major ways: reduction of quality via seed contamination and by competition for resources.

Competition has been defined as, “an interaction of individuals brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth, and/or reproduction of the individuals concerned” (Grace and Tillman 1990). Understanding competitive relationships between weeds and crops can help get maximum utility from resources expended for weed control. By knowing which weeds compete most with crops and when, growers are better equipped to perform cost/benefit analysis of potential control strategies.

Replacement series experiments have been widely used to show relative competitiveness of different biotypes (de Wit 1960). This type of experiment measures the ability of two species or plant types to capture and convert resources to biomass at varying proportions of each type at a constant total plant density. Although this design is limited in its ability to determine the importance of inter- vs. intra-specific competition (Cousens 1991), and does not address the possibility of a total density effect on plant competition (Rejmanek et al. 1989), it gives sufficient information about the relative competitiveness of the two species grown in mixture (Roush et al. 1989). It is possible using data from replacement series experiments to calculate the relative yield (RY) and relative yield total (RYT), which describe how the two plant types in the mixture share resources. It is also possible to assess the relative competitiveness of the two plant types by calculating the relative crowding coefficient (RCC).

The flowering portion of the jointed goatgrass plant is a spike that is 'jointed' into several spikelets. The florets of the spikelet are enclosed in two glumes which become rigid at maturity. Each spikelet typically contains two seeds (Donald and Zimdahl 1987). Seed size and dormancy vary depending on relative position within the spikelet. The primary (basal) seed in the spikelet is generally smaller and more dormant than the secondary (apical) seed. Primary dormancy in both seed positions can be overcome by after-ripening, but secondary dormancy may be induced in the primary seed, causing delayed germination (Fandrich 2005). Studies have been conducted on the competitive relationships between jointed goatgrass and winter wheat (Fleming et al. 1988). Winter wheat and jointed goatgrass have been shown to have approximately equal competitive ability, information about the relative competitiveness of plants derived from seed from the primary and secondary position in the spikelet has not been reported.

Since secondary jointed goatgrass seed are larger and produce earlier emerging, faster growing seedlings (Fandrich 2005), it seems likely that plants derived from these seeds would be more competitive against primary jointed goatgrass seed and against winter wheat. To test this hypothesis, three replacement series experiments were conducted to evaluate the relative competitiveness of the three plant types.

Materials and Methods

Competition between primary and secondary jointed goatgrass, primary goatgrass and winter wheat, and secondary goatgrass and winter wheat were evaluated in three replacement series using five planting ratios (100:0, 75:25, 50:50, 25:75, 0:100) at a constant total density of 16 plants per 15.5 cm diameter pot. The experiment was conducted as a randomized complete block design with four replications and was repeated.

Jointed goatgrass spikelets were collected from plants grown in a nursery in Corvallis, Oregon in 2003. These plants were descendents of populations originally collected at Moro, Athena, and Pendleton, Oregon in 2001. Seed were removed from the spikelets and separated by floret position. Seed from the three jointed goatgrass populations were bulked. Winter wheat 'ORCF101' seed, primary, and secondary jointed goatgrass seed were planted individually in 3 cm by 3 cm cells and placed in a greenhouse with 12 hour photoperiods. Daytime and nighttime temperatures were 25 and 20 C, respectively. Time of emergence was recorded for all individuals of each plant type. Ten days after planting, seedlings were transplanted to the large pots, which were filled with 4 liters of commercial potting mix. The pots were then separated into blocks and kept in the greenhouse with the same temperature and light conditions listed previously. Plants were watered regularly and pots within each block were rearranged periodically to decrease variation.

Tiller number and plant height were recorded weekly for each plant until harvest 35 d after transplanting. Above-ground biomass from each pot was cut, separated, and bulked by plant type, dried at 60 C for 72 hr, and weighed.

Dry weights per pot for each plant type were used to calculate the RY, RYT and RCC. RY and RYT were calculated as described by Radosevich (1988), using the following formula:

$$RY_a = Y_{ab}/Y_{aa} \quad [1]$$

and,

$$RYT_a = RY_a + RY_b \quad [2]$$

where Y_{ab} is the biomass (g) of the 'a' biotype grown in 50:50 mixture and Y_{aa} is the biomass (g) of the 'a' biotype grown in monoculture. The RCC (de Wit 1960) was calculated as:

$$RCC = (Y_{ab}/Y_{ba})/(Y_{aa}/Y_{bb}) \quad [3]$$

Relative yields, RYT, RCC, tiller number and plant height were subjected to ANOVA using SAS (1999). The experiment by treatment effects were not significant and data conformed to a test of heterogeneity of variance so data from the repeated experiments were combined.

Results and Discussion

Plant Height and Tiller Number

Seedling emergence was uniform among all plant types and plant height did not differ at the time of transplanting.

Throughout the course of the experiment, neither plant height nor tiller number for any plant type was affected by any of the treatments (Figure 1). At the time of harvest, wheat had the greatest total biomass, but was the same height as the secondary jointed goatgrass and only slightly taller than the primary jointed goatgrass.

The two jointed goatgrass types had equivalent numbers of tillers at harvest, nearly twice the number of tillers that the wheat plants had. Neither tiller number nor height varied among treatments so no information about differential competition could not be derived from these data.

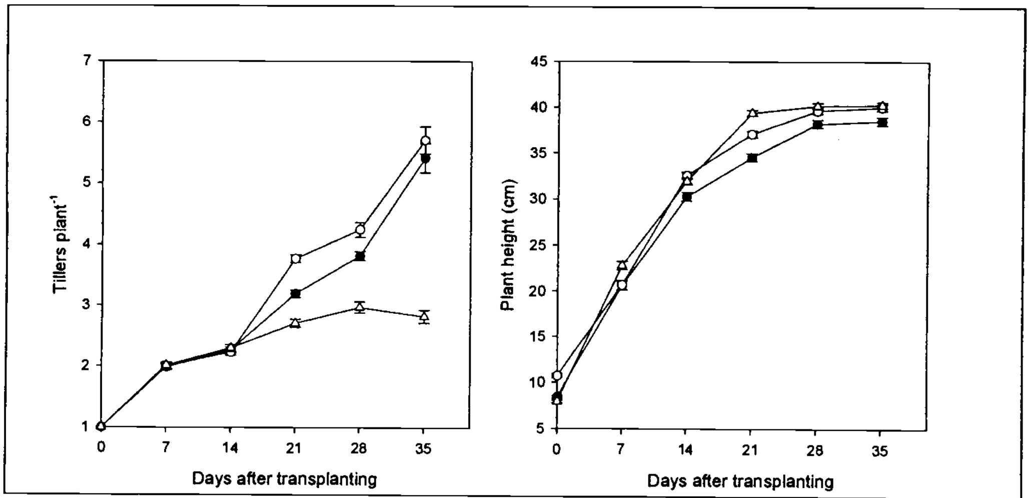

Figure 1. Tiller number and height per plant for wheat, △; secondary jointed goatgrass, ●; and primary jointed goatgrass, ○.

Relative Yield and Relative Crowding Coefficient

Resource complementarity is the degree to which the two biotypes share the same limited resources (Satorre and Snaydon 1992). In situations where there is no competition, there is complete resource complementarity and the RY's of plants grown in each mixture will be 1. If no resource complementarity is occurring, then the RY's of plants grown in each mixture will be less than 1. An RYT of 1 indicates that the two biotypes are competing for the same resources. When this is the case, the RCC can be used as a measure of the relative competitiveness of each plant type (de Wit, 1960; Fleming et al. 1988). RYT for each comparison did not differ significantly from 1 (Figure 2), which indicated that there was no resource complementarity occurring and that the biotypes were competing for the same limiting resources.

The RCC values from each pairwise comparison are shown in Table 1. Relative crowding coefficient values for comparisons between primary and secondary jointed goatgrass seed were significantly less than and greater than 1, respectively. The same was true for primary jointed goatgrass seed vs. wheat. Neither RCC value was significantly different from 1 in the case of secondary jointed goatgrass seed vs. wheat, indicating that these two plant types are equally able to accumulate biomass when grown in competition with at this density.

Table 1. Relative crowding coefficients for each plant type in all three pairwise comparisons

	Relative Crowding Coefficient		
	Biotype		
	Primary JGG	Secondary JGG	Wheat
Mixture:			
Primary vs. Secondary JGG	0.80*	1.26*	--------------------
Primary JGG vs. Wheat	0.66*	--------------------	1.66*
Secondary JGG vs. Wheat	--------------------	0.97	1.08

* indicates values that are significantly different from 1, which indicates a difference in relative competitive ability

The RY for each type compared to the hypothetical yields based on plant biomass in the monocultures are shown in Figure 2.

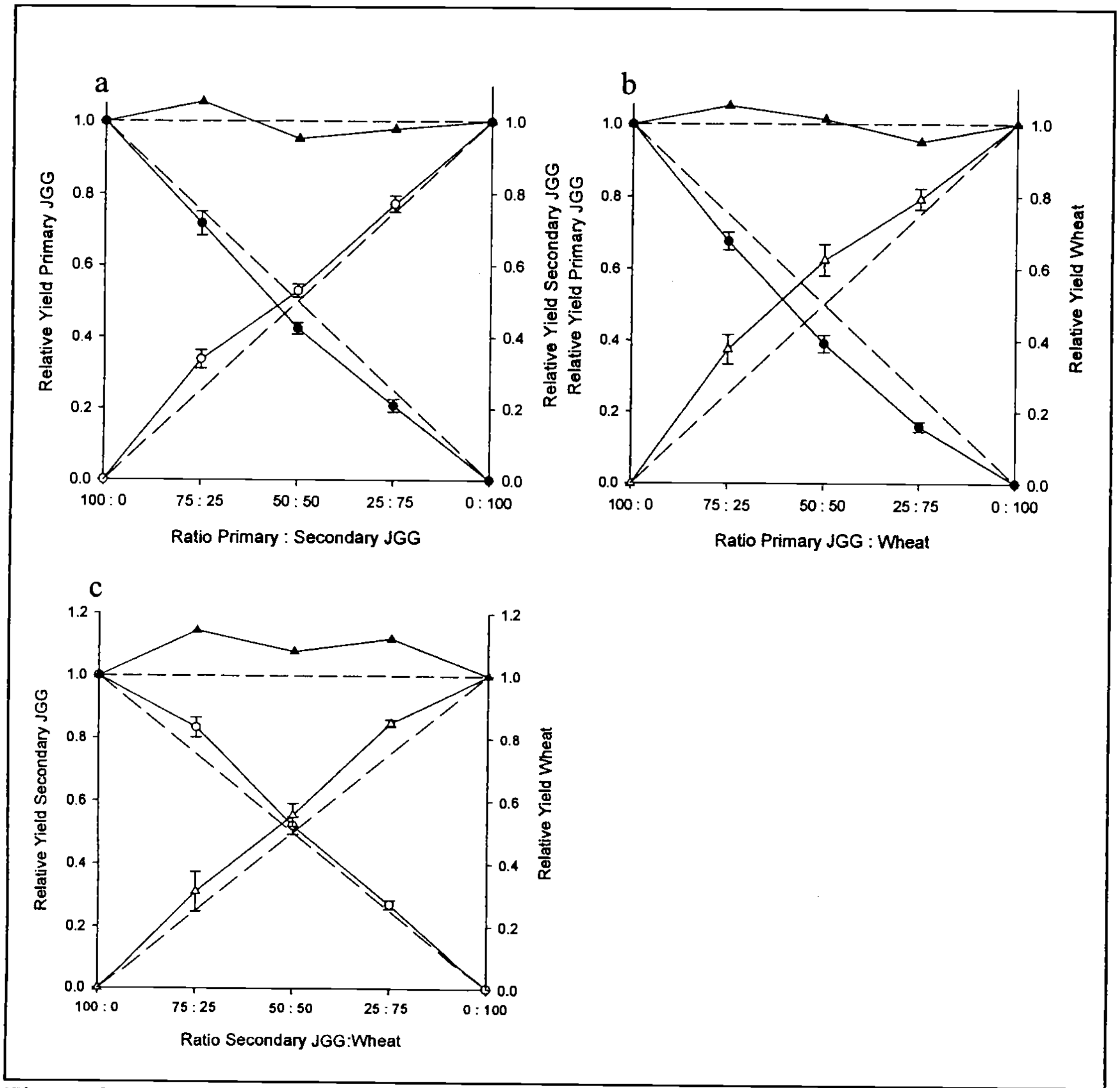

Figure 2. Relative yields for wheat, △; secondary jointed goatgrass, o; primary jointed goatgrass, •; and relative yield total, ▲, for each pairwise comparison. Dashed lines represent theoretical yields for equal competition. Vertical bars represent standard errors.

The comparison of relative yields of primary jointed goatgrass and secondary jointed goatgrass grown in competition is shown in Figure 2a. Relative yields for primary jointed goatgrass vs. wheat and secondary jointed goatgrass vs. wheat are shown in Figures 2b and 2c, respectively.

If a plant type acquires more biomass when grown in mixture with other plant types than when grown in monoculture, it is more competitive than the other plant types. As described in Harper (1977), the shape of the yield lines is indicative of the competitive ability of each respective plant type. In this case, a convex line indicates that a particular plant type is performing better in the mixture than in the monoculture. A concave line indicates the opposite. This is illustrated in the case of primary jointed goatgrass seed vs. wheat (Figure 2b). Wheat, represented by the convex line is more competitive than the jointed goatgrass, represented by the concave line.

Based on the results of this study, plants from primary jointed goatgrass seed are less competitive than plants from secondary jointed goatgrass seed or wheat and secondary jointed goatgrass and wheat plants are equivalent in their competitive abilities. Fleming et al. (1988) also found that secondary jointed goatgrass and wheat were equally competitive. In the experiments used to arrive at that conclusion, primary jointed goatgrass seed were not used. The results of the study described in this chapter show clearly that there is a difference in the relative competitive ability of jointed goatgrass plants derived from seed in the primary and secondary seed position within the spikelet.

Although the secondary jointed goatgrass seed began to germinate earlier than the primary jointed goatgrass seed, the average emergence times of the two types were not different. This is not how the seeds would germinate if left in the glumes. Fandrich (2005) suggested that differences between primary and secondary jointed goatgrass seed dormancy may be due to differing physical restrictions on germination imposed by the glumes. In field conditions, plants from the secondary jointed goatgrass seed would not only germinate first, but as has been illustrated by this study, would out-compete the plants from the primary jointed goatgrass seed. This emphasizes the importance of early-season control to kill the earlier emerging, more competitive jointed goatgrass plants.

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Chapter 4

Effect of Application Rate and Timing of Imazamox on Jointed Goatgrass (*Aegilops cylindrica*) and Imidazolinone-Resistant Wheat

Jointed goatgrass is a serious weed problem throughout much of the winter wheat production area of the United States. Recently, herbicide-resistant wheat varieties have been introduced that allow growers to selectively kill weeds, including jointed goatgrass, in wheat. Two greenhouse studies were conducted to determine the effect of application timing and rate on jointed goatgrass and imidazolinone-resistant winter wheat. In the first study, the effects of imazamox rate and application timing on wheat and jointed goatgrass were evaluated. Jointed goatgrass response was only affected by herbicide application rate at the latest timing, when the plants had more than 2 tillers and were over 30 cm in height. Herbicide rate had a significant effect on wheat biomass at all post-emergent timings. Neither jointed goatgrass nor wheat was inhibited by pre-emergent imazamox application. In the second experiment, jointed goatgrass and imidazolinone resistant wheat were grown in a 50:50 mixture and treated with imazamox at 5 rates and 2 timings. Imazamox rate did not affect the response of either wheat or jointed goatgrass at either timing.

Nomenclature: Imazamox, jointed goatgrass, *Aegilops cylindrica* Host., AEGCY; winter wheat, *Triticum aestivum* L.

Key words: Herbicide-resistant wheat, Clearfield wheat

Jointed goatgrass is a problematic weed in cereal production in the United States, particularly in reduced-tillage and dryland winter wheat-fallow systems (Donald and Ogg 1991). It is a winter annual grass genetically related to wheat (Hitchcock 1950: Maan 1976). The genetic and developmental similarity between wheat and jointed goatgrass limits chemical control options and makes selective control of difficult (Anderson 1993). Recently, herbicide-resistant wheat varieties have been developed, which allow selective chemical control of many weeds, including jointed goatgrass in wheat (Anderson et al. 2004; Ball et al. 1999).

The effects of herbicide timing and rate on jointed goatgrass control have been studied for several herbicides (Geier and Stahlman 1996, Geier et al. 2001). Understanding how imazamox application timing affects jointed goatgrass control and crop safety can be useful in obtaining optimal results from the use of imidazolinone-resistant wheat. If herbicides are applied too early, subsequent weed flushes may not be adequately controlled. Late applications may not sufficiently control weeds and increase the amount of time that the weeds have to interfere with the crops (Gower et al. 2003). The period of time during which weeds must be controlled to minimize yield loss is known as the critical period of weed control. Before this period, weeds are not competing with crops for resources. The presence of weeds after this period does not affect crop yield (Hall et al. 1992).

The critical time for implementing a weed management practice such as an herbicide treatment depends on the properties of the herbicide, the crop being grown, and the weed species present as well as the environmental conditions. Studies in corn (*Zea mays*) have shown that if two glyphosate applications are made, the most effective time of application was when weeds were less than 10 cm in height and no later than 23 d after planting. However, if only one application of glyphosate was made, the most effective, consistent control of weeds was achieved by delaying application until weeds are 15 cm or taller (Gower et al. 2003). Diclofop was effective at controlling wild oat at early developmental stages, while difenzoquat and flamprop more effectively control wild oat later in development (Bailey et al. 2003).

Although jointed goatgrass has similar development to wheat, jointed goatgrass seed are heteromorphic, and dormancy and germination vary among seeds (Donald and Ogg 1991; Donald and Zimdahl 1987), making timing of herbicide application difficult. The objectives of this study were to examine the effects of rate and timing of imazamox on jointed goatgrass and imidazolinone resistant wheat.

In field conditions, environmental factors can affect herbicide efficacy. Temperature and moisture can play a role in timing of herbicide application. In the studies described here, environmental conditions were the same for all treatments. Thus, the difference in treatments was a reflection of plant size and maturity.

Materials and Methods

Experiment 1: Application of 2 rates of imazamox at 8 timings

Jointed goatgrass seed were separated from the glumes and separated by floret position within the spikelet. Only seed from the secondary position were used. Seed from this position in the spikelet are not dormant and are the most likely to germinate and emerge at the same time as the wheat (Fandrich 2005). Jointed goatgrass seed used in the study came from plants grown in a nursery in Corvallis, OR. Wheat used in the study was Clearfield 'ORCF101'.

Jointed goatgrass and wheat plants were grown in individual pots and imazamox was applied at 2 rates at 8 different timings. Seed were planted in 6 cm x 6 cm, 267 ml, square pots filled with commercial potting mix[1]. Pots were placed in a greenhouse with a 12 hr photoperiod and temperatures of 25 C/20 C day/night. Seed were planted every 3 d for 21 d. Plants were watered regularly. Twenty-six days after the initial planting, imazamox was applied to each of the planting dates at rates of 34.4 g ai/ha, and 68.8 g ai/ha plus a nonionic surfactant at 0.025% v/v. An untreated control was included. Each treatment was replicated six times and the experiment was repeated. At the time of herbicide application, plants from the first 7 planting dates had emerged, but for the last planting date, the treatment was pre-emergent. Plant height, leaf number and tiller number for each plant were recorded at the time of spraying.

Two weeks after spraying, above-ground biomass was harvested and dried for 72 hr at 60 C. Dried samples were weighed and dry weights were converted to a percent of the dry weight of the untreated control. Plant height and tiller number were recorded for each plant at the time of harvest. Leaf number also was recorded for each jointed goatgrass plant.

Dry weights as a percent of the untreated control were subjected to ANOVA and treatments were compared using Duncan's multiple range test. ANOVA revealed that neither replications nor the repeated experiment accounted for a significant amount of variation in the data ($\alpha = 0.05$), and data were pooled across replications and experiments.

Experiment 2: Early and late applications of 5 rates of imazamox to wheat and jointed goatgrass grown in competition

A second experiment was conducted to measure the effects of different application rates and timings of imazamox on jointed goatgrass and imidazolinone-resistant wheat grown in mixture. Jointed goatgrass seed were extracted from the glumes and planted individually in 3 cm by 3 cm cells. Wheat seed of the same variety used in experiment 1 also were planted individually in cells. Ten days after planting, jointed goatgrass seedlings were transplanted in 50% mixture with wheat seedlings in 4 L, 15.5 cm diameter round pots. Jointed goatgrass and wheat plants were arranged in a pattern such that each plant had the same number of adjacent plants of each plant type and all plants were equally spaced. Pots were placed in a greenhouse with the same temperature and light conditions described previously.

Imazamox was applied to the pots at rates of 0, 4.3, 8.6, 17.2, 34.4, and 68.8 g/ha at two application times. The first application was to jointed goatgrass at the 2-leaf stage and the second application was to jointed goatgrass with 4-5 tillers.

Forty-five days after planting, (30 d after spraying for the early treatment, 15 d after spraying for the late treatment), above ground biomass was harvested, separated by biotype, and dried at 60 C for 72 hr. Dry weights of plants from treated pots were converted to percent of dry weights of the plants from the untreated control.

Experiment 2 was a randomized block design. Dry weights as a percent of the untreated control for each treatment were subjected to ANOVA.

Results and Discussion

Experiment 1

Although jointed goatgrass was inhibited slightly by the pre-emergent imazamox application, the response did not differ significantly from that of the wheat at either rate. The percent of injury for wheat and control ofjointed goatgrass at each rate for the pre-emergent treatment are shown in Table 1. Although imazamox is not labeled for pre-emergent control of jointed goatgrass in wheat, it has been shown to have some residual effects in the soil (Ball et al. 2003; Cobucci et al. 1988). These effects are related to soil characteristics including soil moisture, texture, temperature, pH, and organic matter content (Loux and Reese 1993). The pre-emergent applications in this study did not provide acceptable jointed goatgrass control.

Table 1. Response of wheat and jointed goatgrass to pre-emergent imazamox applications

Imazamox	Wheat	Jointed goatgrass
g ai ha^{-1}	% of untreated control (standard error)	% of untreated control (standard error)
34.4	107 (21)	71 (16)
68.8	99 (23)	70 (12)

In the post-emergent applications, imazamox rate only affected jointed goatgrass response in the earliest planting date, where the 68.8 g/ha rate had slightly better control than the 34.4 g/ha rate. Changing the herbicide rate had a significant effect on wheat response at all planting dates. Average plant height, as well leaf and tiller number at the time of imazamox application for each planting date are shown in Table 2.

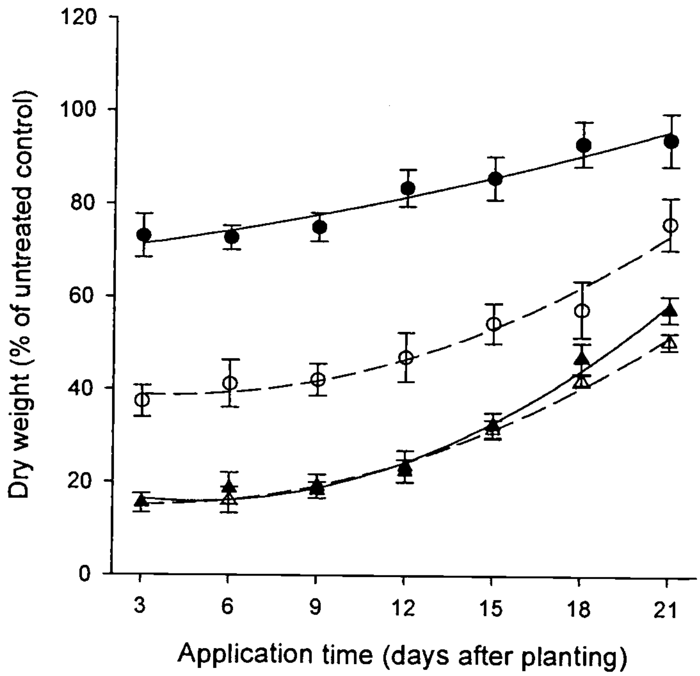

Figure 1. Effect of application time on dry weight of jointed goatgrass and wheat. Jointed goatgrass: 68.8 g/ha, △; 34.4 g/ha, ▲. Wheat: 68.8 g/ha, ○; 34.4 g/ha, ●. Vertical bars represent standard errors.

Imazamox rate had a much greater effect on response of wheat than it did on jointed goatgrass (Figure 1). For wheat, the difference in biomass reduction between 68.8 g/ha and 34.4 g/ha decreased as the application times got later and the plants got bigger. The opposite was true for the jointed goatgrass. This suggests that when the wheat crop is smaller, using a lower rate can reduce crop injury without sacrificing any control of jointed goatgrass. At later stages of development, a higher rate controlled jointed goatgrass more effectively than the lower rate.

Table 2. Tiller number, plant height, and leaf number for jointed goatgrass and wheat at each postemergent application time.

Application time	Days after planting	Plant height (cm)		Tiller number		Leaf number
		Jointed goatgrass	Wheat	Jointed goatgrass	Wheat	Jointed goatgrass
1	3	3.4	5.2	1.0	1.0	1.5
2	6	5.8	6.3	1.0	1.0	1.8
3	9	10.7	7.9	1.0	1.0	2.2
4	12	15.0	12.7	1.3	1.3	2.6
5	15	20.7	22.8	2.0	1.7	3.0
6	18	26.4	28.5	2.2	2.0	3.7
7	21	32.5	31.9	2.3	2.3	4.4

Experiment 2

At the 2-leaf stage application, all the jointed goatgrass plants were killed by the herbicide, regardless of rate. There was no difference in wheat response based on rate. The wheat plants were initially injured by the herbicide at the higher rates, but in the absence of competition, the plants were able to recover between spraying and harvest. At the late application, both wheat and jointed goatgrass plants were very large and were not inhibited by any of the herbicide rates used. The dry weights of wheat and jointed goatgrass plants as a percent of untreated control from Experiment 2 are show in Table 3.

The early application was too early to see any dose response and the late application was too late. This illustrates that if applied too early or too late, changing imazamox rate will not affect weed or crop response. Additionally, if the herbicide provides little or no residual control, applying as early as the 2-leaf stage may allow subsequent flushes of jointed goatgrass to emerge and compete with the crop to cause losses in crop yield. The critical time for imazamox application lies somewhere between these two application times. According to the imazamox label, the herbicide should be applied when the jointed goatgrass plants have a maximum of 4-5 leaves. Another experiment with the same rates and more, intermediate application times might yield more information on the effects of competition on response to timing and rate of imazamox.

Table 3. Response of jointed goatgrass and wheat grown in mixture to early and late applications of imazamox

	Early application		Late application	
Rate	Jointed goatgrass dry weight	Wheat dry weight	Jointed goatgrass dry weight	Wheat dry weight
g ai ha^{-1}	% of control		% of control	
4.3	39	97	90	103
8.6	39	95	89	112
17.2	42	91	91	99
34.4	32	83	102	115
68.8	28	92	94	111

Both of the experiments illustrate that the effect of imazamox rate on wheat and jointed goatgrass varies with the application timing. In early applications, a lower rate of imazamox can be used to reduce crop injury without reducing jointed goatgrass control. As the plants grow and mature, the difference in crop injury between high and low rates diminishes, but the difference in jointed goatgrass control between the two rates increases. Thus, at later stages of development higher rates of imazamox provide the most effective control of jointed goatgrass. After the critical time of weed control, however, increasing the rate of imazamox will not improve control, nor will it result in increased crop yields. Other factors, such as crop rotation, local climate, and presence of other weeds also would influence optimum herbicide timing and rate.

Source of Materials

[1] Sunshine Mix #1 potting mix, Sun Gro Horticultural Distribution Inc., 15831 N. E., 8th Street, Suite 100, Bellevue, WA 98008

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Chapter 5

Summary and Conclusion

The area infested by jointed goatgrass increases every year, as does the number of acres in production systems where jointed goatgrass is particularly problematic. Unless developments in the control of jointed goatgrass are made, it will continue to be a costly and increasingly troublesome weed. In order to effectively control a weed, it is necessary to understand the biology and ecology of the species. For optimal management, it is also important to examine the possible effects of control measures. The experiments described in this thesis have helped increase our understanding of jointed goatgrass biology, ecology, and control.

Outcrossing

The difficulty in controlling jointed goatgrass has led to the development and use of herbicide-resistant wheat varieties. Hybridization between wheat and jointed goatgrass is a well documented phenomenon. The advent of herbicide-resistant wheat raised concerns over the possibility of gene flow between wheat and jointed goatgrass. This gene flow has been the subject of research in recent years and pollen-mediated gene flow has been documented between the two species. Understanding the outcrossing rates in jointed goatgrass is important for predicting the fate of wheat genes once they move into jointed goatgrass populations.

Once a gene has been introgressed into a weed population, the phenotype associated with that particular gene will also help determine the fate of the gene in that population. Traits that confer a fitness advantage will increase more rapidly in populations than will neutral traits. Traits that confer a fitness disadvantage will decrease in frequency in the population. Herbicide resistance is generally considered a neutral trait when there is no selection pressure from the herbicide. However, In the presence of the herbicide, resistance is an advantageous trait and will increase in frequency in the population as long as the herbicide is present in sufficient quantities to reduce the fitness of the susceptible plants.

In the outcrossing experiments outlined in the second chapter of this thesis, jointed goatgrass outcrossing rates were determined for four jointed goatgrass populations and two winter wheat varieties. Experiments were conducted over two years with four locations for jointed goatgrass and three locations for wheat each year. Jointed goatgrass outcrossing rates varied among years and locations, but not among populations. The populations used were collected from different geographic and climatic regions. Despite the differences in origin of the populations, their outcrossing rates did not vary at any location in either year. This indicates that outcrossing rates are affected more by environmental conditions more than genetic differences.

The average outcrossing rate of jointed goatgrass was 1.28% in the first year of the experiment and 1.19% in the second year. Jointed goatgrass outcrossing was greater than wheat outcrossing in both years at all sites. Average wheat outcrossing rate was 0.14% in the first year and 0.04% in the second year. Outcrossing rates in wheat did not vary between the two varieties.

Environmental factors such as humidity, temperature, and wind at the time of anthesis can affect outcrossing rates of plants. Due to the distance between experimental sites, the time of anthesis of the plants in these outcrossing experiments is not known. If the time of anthesis were known, it might be possible to correlate weather data from the different sites with differences in outcrossing rates. With the data collected in this study, no such correlations could be made. Future research should include experiments to determine the effects of specific environmental conditions on jointed goatgrass outcrossing.

Competition

Understanding how weeds interact with crops is essential for effective weed control. Jointed goatgrass competes with wheat for resources such as light, water, and nutrients. This competition can result in reduced grain yields and quality. Past research has shown jointed goatgrass and wheat to be equally competitive for resources when grown in competition with each other. However, jointed goatgrass spikelets generally contain two or more seeds and these seeds have been shown to have differing biological characteristics based on position within the spikelet.

Seed from the primary floret position in the spikelet are smaller, germinate later, and more likely to be induced into secondary dormancy than seed from the secondary floret position. Because of these factors, at various times throughout the growing season or crop rotation, the jointed goatgrass plants competing with the wheat crop might be predominately derived from one or the other of these floret positions.

The relative competitive ability of jointed goatgrass from primary and secondary seed, and wheat grown in all possible pair-wise mixtures was compared in three replacement series experiments. The results of these experiments demonstrated that secondary jointed goatgrass plants were equally competitive with winter wheat plants and more competitive than primary jointed goatgrass plants.

Since secondary jointed goatgrass plants are more competitive and emerge earlier than primary jointed goatgrass plants, early control of jointed goatgrass is advisable for control of the plants that can do the most harm to wheat yield. In wheat fallow situations, if no jointed goatgrass plants are allowed to set seed during the fallow year, most of the seed left in the seedbank will be primary seed. This is because secondary dormancy is more likely to be induced in primary jointed goatgrass seed. As a result, jointed goatgrass plants after one year of fallow could be less competitive than jointed goatgrass plants in fields where wheat is grown in consecutive years.

Plants grown in this study were harvested while still in a vegetative state. Because of this, the effect of competition among the three seed types on final yield and seed production is not known. Similar experiments could be conducted with the plants allowed to grow to maturity. Replacement series experiments are useful for observing relative competitive abilities. However, the effect of total plant density on competition can not be determined by such experiments. Additive designs and three-way mixtures might give further insight to the importance of seed position within the spikelet on competitive ability of jointed goatgrass plants.

Imazamox Rate and Timing

Herbicide application rate and timing affect weed control efficacy and crop safety. Introduction of imidazolinone-resistant wheat has provided the opportunity to control weeds that were previously difficult to control. One such weed is jointed goatgrass. In order for herbicide-resistance technology to be used most effectively, optimum application rates and timings need to be implemented.

Two experiments were conducted to evaluate the effect of rate and timing of imazamox on jointed goatgrass and imidazolinone-resistant wheat. The first experiment compared the response of individual wheat and jointed goatgrass plants to two rates of imazamox at seven post-emergent and one pre-emergent application times. Imazamox rates were 34.4 g ai/ha and 68.8 g ai/ha, which is the maximum labeled rated for imazamox in wheat. Post-emergent application times were at 3 d intervals.

Jointed goatgrass response to both rates was the same at all but the latest post-emergent application time, when the higher rate had slightly better control than the lower rate. Wheat response to rate was different at all post-emergent application times. The higher rate reduced wheat biomass much more than the lower rate at all application times. However, the difference in wheat response to rate decreased at the later application times. Pre-emergent applications of imazamox did not affect seedling biomass of either species.

Based on these results, at early application times (i.e. 0-18 d after emergence) lower rates of imazamox could be used to reduce crop injury, without sacrificing jointed goatgrass control. At later timings however, higher rates are more effective at controlling jointed goatgrass than the lower rates and less injurious to the wheat than the same rate at an earlier time.

The second experiment studied the effect of five rates of imazamox on jointed goatgrass and imidazolinone-resistant wheat grown in 50:50 mixtures at an early and a late application timing. Plants for this experiment were grown in a greenhouse in pots with 16 plants in each pot. Imazamox rates ranged from 4.3 g ai/ha to the maximum labeled rate of 68.8 g ai/ha. The early application occurred when the plants were in the 2-leaf stage. The later application occurred when the jointed goatgrass plants had between 4 and 5 tillers.

All jointed goatgrass plants were killed by the early application at all rates of imazamox. The wheat plants were visibly injured by the higher rates, but recovered fully by the time the plants were harvested 30 d after treatment. None of the rates in the second application affected biomass production of either wheat or jointed goatgrass. Based on the results of this experiment, it is possible to apply imazamox too early or too late for rate to make a difference in jointed goatgrass control or crop safety.

An experiment combining elements of these two experiments might yield some additional information about the effects of timing and rate of imazamox on jointed goatgrass control. Combining more application times, as in the first experiment, with more rates, as in the second experiment, might give an idea of what rate to use at a given time for maximum control of jointed goatgrass and minimal crop injury. The effects of the treatments in these experiments were measured by comparing the biomass of treated plants with that of untreated plants. Using final seed yields as a measure of treatment effect might give further insight into the optimal rate and timing of imazamox in imidazolinone-resistant wheat.

Conclusion:

The research presented in this thesis addresses relevant questions in the current discussion of jointed goatgrass control in wheat. Agricultural systems are dynamic and as such, the problems and issues faced by those involved in agricultural production will continue to change. New technologies such as herbicide-resistant wheat are important for farmers to be able to adapt to these changes. Of equal importance is continuing research to increase our understanding of the biology and ecology of jointed goatgrass that infests crop lands. This will enable new technologies to be utilized to their fullest extent and to remain efficacious well into the future.

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APPENDIX

Table A-1. ANOVA tables of outcrossing study

Jointed Goatgrass Outcrossing

Source	DF	SS	MS	F-value	P
Year	1	0.43397889	0.43397889	0.21	0.6514
Population	3	7.13556510	2.37852170	1.12	0.3421
Location	3	23.97077156	7.99025719	3.78	0.0125
Year*Loc	3	24.64919752	8.21639917	3.89	0.0109

Wheat Outcrossing

Source	DF	SS	MS	F-value	P
Year	1	0.12200833	0.12200833	2.26	0.1399
Variety	1	0.00083333	0.00083333	0.02	0.9017
Location	2	0.24257917	0.12128958	2.25	0.1179

Table A-2. ANOVA tables of competition study

Primary Jointed Goatgrass vs. Secondary Jointed Goatgrass Relative Yields

Source	D.F.	SS	MS	F-value	P
Experiment	1	0.00143994	0.00143994	0.91	0.3720
Block	6	0.02321148	0.20542375	2.44	0.1339
Plant Type	1	0.04170305	0.04170305	26.34	0.0014

Primary Jointed Goatgrass vs. Wheat Relative Yields

Source	D.F.	SS	MS	F-value	P
Experiment	1	0.00008700	0.00008700	0.01	0.9404
Block	6	0.03828151	0.00638025	0.44	0.8316
Plant Type	1	0.20542375	0.20542375	14.17	0.0070

Secondary Jointed Goatgrass vs. Wheat Relative Yields

Source	D.F.	SS	MS	F-value	P
Experiment	1	0.01066301	0.01066301	0.75	0.4150
Block	6	0.03901640	0.20542375	0.46	0.8200
Plant Type	1	0.00304267	0.00304267	0.21	0.6576

Table A-3. ANOVA tables of imazamox rate and timing study

Effect of Rate and Timing on Jointed Goatgrass Plants Grown Without Competition

Source	D.F.	SS	MS	F-value	P
Experiment	1	0.00079	0.00079	2.45	0.1195
Block	5	0.00313	0.00063	1.93	0.0913
Herbicide Rate	1	0.00194	0.00194	5.99	0.0154
Herbicide Timing	7	1.03171	0.14739	455.52	<.0001
Rate*Timing	7	0.00076	0.00076	2.36	0.0253

Effect of Rate and Timing on Jointed Goatgrass Plants Grown in Competition

Source	D.F.	SS	MS	F-value	P
Experiment	1	0.00082400	0.00082400	0.02	0.8856
Block	4	0.19517814	0.00063	1.23	0.3022
Herbicide Rate	4	0.05540155	0.00194	0.35	0.8440
Herbicide Timing	1	1.68901857	1.68901857	42.60	<.0001
Plant Type	1	0.49855556	0.49855556	12.75	0.0006