AN ABSTRACT OF THE THESIS OF

Jeremy R. Snyder for the degree of Master of Science in Crop Science presented on February 26, 1999. Title: Introgression Between Jointed Goatgrass (*Aegilops cylindrica*) and Wheat (*Triticum aestivum*).

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Carol A. Mallory-Smith

Hybrids between wheat and jointed goatgrass have long been presumed to be sterile; however, seed were found on hybrid plants in 1990. Field studies were conducted in 1995 and repeated in 1996. One to ten hybrid plants were planted in variable populations of wheat and jointed goatgrass to determine the rate of seed set and viability of seed produced on hybrids. An average of 2.3% of florets set seed in 1995 and 3.8% of florets set seed in 1996. Seed were set in all treatments. Hybrid population had no effect on seed set. The BC_1 (first backcross) seed produced in the field studies were separated according to seed condition, full or shrivelled, and were tested for germination. Ninety-four percent of the full seed germinated in each year and 79% and 84% of the shrivelled seed germinated in 1995 and 1996, respectively. Field studies were conducted in 1996 and 1997 using seed set on hybrids grown in populations of 150 jointed goatgrass or 150 wheat plants in the previous year's field study. Ten BC_1 plants were planted into plots containing 100 jointed goatgrass plants. From 0.25 to 20.29% of florets per plot set seed. Greenhouse studies were conducted in 1997 and repeated in 1998 using BC_1 seed produced in the previous year's field study. Seed resulting from self-pollination occurred on 4.1% or 59 plants in 1997 and

2.1% or 16 plants in 1998. Percent seed set ranged from 0 to 80.22% on a per plant basis. Parental population and seed set on BC_1 plants can not be predicted based on coleoptile color, germination day, leaf width, number of veins in the leaf, presence or number of hairs on leaf margin, plant posture, number of spikes produced, culm height, spike length, or resemblance to parents.

Introgression Between Jointed Goatgrass (*Aegilops cylindrica*)

and Wheat (*Triticum aestivum*)

by

Jeremy R. Snyder

A THESIS

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Major Professor, representing Crop Science

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Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Jeremy R. Snyder, Author

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CONTRIBUTION OF AUTHORS

Dr. Carol Mallory-Smith assisted in the design, implementation, data collection, analysis, and writing of the following manuscripts. Dr. Robert Zemetra assisted in the design, data collection, and editing of both manuscripts. My sincere appreciation is extended to both.

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INTRODUCTION

Jointed goatgrass (*Aegilops cylindrica* Host) is one of the worst weed problems faced by winter wheat (*Triticum aestivum* L.) producers. This weed directly competes with the crop for light, nutrients, and moisture, and thereby greatly reduces yield (Baltensperger et al. 1990). As wheat and jointed goatgrass are closely related, the use of herbicides to selectively control jointed goatgrass in wheat is not currently possible (Callihan et al. 1990; Cook and Veseth 1991). Cultural control methods are the only viable options. These include the use of rotational crops, enabling producers to alter the system in which jointed goatgrass thrives, and also planting as late as possible so that the weed can be either sprayed out or rouged out (Anderson 1995; Donald 1993). The recent increase of land in minimum and no-till management strategies has resulted in the increased prevalence of jointed goatgrass in wheat (Anderson 1992; Lyon 1995).

A new strategy on the horizon for wheat producers to control jointed goatgrass is herbicide-resistant wheat. This technology enables wheat to be sprayed with herbicides that would otherwise kill the plant. The wild-type population of jointed goatgrass will be killed by the herbicide treatment while wheat will remain uninjured. Winter wheat has been produced with resistance to the imidazolinone herbicide, imazamox (Newhouse et al. 1992), and glyphosate (Sally Metz, personal communication 1998).

This new technology comes with concerns, however. One major question is the risk associated with transferring the herbicide-resistance gene(s) from wheat to jointed goatgrass via a hybrid bridge. Wheat could hybridize with jointed goatgrass to produce the F_1 generation. This F_1 plant, if not completely sterile, could then backcross to jointed goatgrass repeatedly over several generations, resulting in a jointed goatgrass plant, which in its genetic makeup contains the herbicide-resistance gene. This process is called introgression. This scenario has been noted with several other crops and weedy relatives. Examples include corn (*Zea mays* L.) hybridizing with wild teosintes (Doebley 1990), numerous cucurbit species hybridizing with wild cucurbit relatives (*Cucurbita* spp.) (Kirkpatrick and Wilson 1988; Wilson 1990; Wilson et al. 1994), and cultivated and wild radish (*Raphanus sativus* L.) (Klinger and Ellstrand 1994; Klinger et al. 1991). Oilseed rape (*Brassica napus* Metzger) crossing with wild hoary mustard (*Hirshfeldia incana* L. Lagreze-Fossat) (Lefol et al. 1996), crop sorghum (*Sorghum bicolor* L.) hybridizing with Johnsongrass (*Sorghum halepense* L.) (Arriola and Ellstrand 1996) and crossing between wild and cultivated sunflower (*Helianthus annuus* L.) (Arias and Rieseberg 1994) also have been noted. Extensive reviews of introgression between crops and weeds have been published including one by Raybould and Gray (1993), and an article discussing not only crop to weed gene flow but also the role of introgression in producing some important present day crops including *T. aestivum* (Small 1984).

Wheat is an allohexaploid with three genomes, AABBDD. Each genome arose from a different ancestor, the A genome from *T. urartu* Gandilyan, the B possibly from *T. speltoides* Tausch, and the D from *A. tauschii* Coss., according to the taxonomic treatment by Chapman et al. (1976) and Slageren (1994). Winter wheat is an annual grass germinating in the fall, overwintering, and senescing in the following summer. Primarily a self-pollinated crop, wheat has up to 2% outcrossing under natural conditions (Poehlman and Sleper 1995; Weise 1991). Jointed goatgrass shares a very similar life cycle. Jointed goatgrass is an allotetraploid, CCDD. As with wheat, both genomes arose from distinct ancestors, the C from *A. markgraffi* (= *A. caudata*) (Greuter) Hammer and the D from *A. tauschii* (Slageren 1994). Interestingly, there has been much debate as to the correct generic identification of jointed goatgrass. Many scientists have placed the species in the *Triticum* genus, *T. cylindricum* (Baenziger 1992; Gould and Shaw 1983; Hafliger and Scholz 1981; Stubbendieck et al. 1995).

Intergeneric hybridization attempts with *T. aestivum* have been successful with several genera including *Secale*, *Hordeum*, and *Agropyron* (Maan 1987). Researchers also have investigated the possible use of several *Aegilops* species to increase the genetic diversity of wheat. In 1984, Warham et al. screened several species in the *Aegilops* genus for resistance to *Neovossia indica*, the causal organism of karnal bunt. They reported a 10% or less infection rate of *A. cylindrica* when inoculated in the boot stage with the organism; however, they did not report the rate of infection with this species when backcrossed to *T. aestivum*. Kofoid and Maan (1982) screened several alloplasmic lines, created by the substitution backcrossing method, of *T. aestivum* with cytoplasm from one of several *Aegilops* and *Haynaldia* species including *A. cylindrica*. They found that the lines with the cytoplasm from *Aegilops* had better bread loaf volume and higher protein content that those lines with the *Triticum* cytoplasm. These findings suggest that the *Aegilops* genus could hold important and yet undiscovered diversity needed by breeders to continue to improve wheat.

Having the D genome in common allows wheat and jointed goatgrass to hybridize under field conditions (Anonymous 1975; Callihan et al. 1990; Kimber and Sears 1987; Priadcencu et al. 1967). This has been noted almost as early as the existence of jointed goatgrass in the United States. These hybrids generally have a taller stance and larger spikes than either parent, displaying overall hybrid vigor. The plants take an intermediate form between the two species; the spikes resemble wheat with respect to awnedness, and have the compact spike morphology of jointed goatgrass. The culms are approximate in size to those of wheat plants. It was noted by Johnston and Parker (1929) and Mayfield (1927) that these hybrids between wheat and jointed goatgrass were almost always sterile. Priadcencu et al. (1967) reported a germination rate of hybrid seed of approximately 50%; however, of the 74 plants investigated, all were sterile. Donald and Ogg (1991) also noted the occurrence and the sterility of the hybrids in the review article on jointed goatgrass biology and control, stating that the hybrids were never fertile.

Preliminary work conducted by Mallory-Smith et al. (1996) found viable seed on hybrids between wheat and jointed goatgrass in 1990. This discovery brought to light many new questions regarding the sterility of the crosses. Studies were initiated in 1995 and repeated in 1996 to determine the rate at which hybrids between wheat and jointed goatgrass would set seed in variable populations of wheat and jointed goatgrass and also to determine the germination of the seed. Studies were conducted in 1996 and 1997 to determine the rate at which the first backcross generation, BC_1, would set seed in populations of pure jointed goatgrass, leading to the BC_2 or BC_1S_1 generation. Greenhouse studies were conducted in 1997 and repeated in 1998 to determine the rate of restoration of self-fertility in the BC_1 generation, and also to identify one or more morphological characteristics that could be used to determine the probable identity of the pollen donor during fertilization in the F_1 generation.

MANUSCRIPT I

INTROGRESSION BETWEEN WHEAT (*TRITICUM AESTIVUM*) AND JOINTED GOATGRASS (*AEGILOPS CYLINDRICA*) – HYBRID GENERATION

Jeremy R. Snyder, Carol A. Mallory-Smith, and Robert S. Zemetra

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Lawrence, Kansas; March 1999.

ABSTRACT

Field experiments were conducted in 1995 and repeated in 1996 to determine the rate of seed set on hybrids between wheat and jointed goatgrass and to determine the viability of the seed produced. One to ten hybrids were planted into varying populations of jointed goatgrass and wheat. Percent seed set ranged from 0 to 5.5% in 1995 and from 0 to 9.2% in 1996. In both years, seed was set in all treatments. The average seed set was 2.29% in 1995 and 3.84% in 1996. No differences in seed set were found among treatments in either year. The seed produced were separated according to seed condition, either full or shrivelled, and tested for germination. The germination of the seed produced on the hybrids was not significantly different between years. The percent of seed germinating was higher for the full seed condition than the shrivelled seed condition. The average germination for full seed was 94% in both years, and 79% and 84% for shrivelled seed in 1995 and 1996, respectively. The germination percent was not influenced by hybrid population. Results from this study indicate that hybrids between wheat and jointed goatgrass have the ability, although limited, to backcross with either parent under field conditions and set seed. Furthermore, the seed produced will be viable and germinate. These results clearly show that introgression between wheat and jointed goatgrass can occur via a hybrid bridge.

Nomenclature.

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

Key Words.

Hybrid, gene movement, backcross, AEGCY.

INTRODUCTION

Jointed goatgrass (*Aegilops cylindrica* Host) is a problem weed of winter wheat (*Triticum aestivum* L.) production areas. Because of the high degree of similarity between the two species, selective control of jointed goatgrass with the use of herbicides is unavailable (Miller 1995). Cultural control methods are the only viable options currently available.

Wheat is an allohexaploid with three genomes, AABBDD. Each genome arose from a different ancestor, the A genome from *Triticum urartu* Gandilyan, the B possibly from *T. speltoides* Tausch, and the D from *A. tauschii* Coss., according to the taxonomic treatment of Chapman et al. (1976) and Slageren (1994). Winter wheat is an annual grass germinating in the fall, overwintering, and senescing in the following summer. Jointed goatgrass shares a similar life cycle. Jointed goatgrass is an allotetraploid, CCDD. As with wheat, each genome arose from distinct ancestors, the C from *A. markgraffi* (= *A. caudata*) (Greuter) Hammer and the D genome from *A. tauschii* (Slageren 1994). Interestingly, there has been much debate as to the correct general epithetical identification of jointed goatgrass. Many scientists have placed the plant in the *Triticum* genus, *T. cylindricum* (Baenziger 1992; Gould and Shaw 1983; Hafliger and Scholz 1981; Stubbendieck et al. 1995).

A new strategy on the horizon for wheat producers to control jointed goatgrass is herbicide-resistant wheat. This technology enables wheat to be sprayed with herbicides that would otherwise kill the plant. The wild-type population of jointed goatgrass will be killed by the herbicide treatment and the wheat will remain uninjured. Winter wheat has been produced with resistance to the imidazolinone herbicide, imazamox (Newhouse et al. 1992), and glyphosate (Sally Metz, personal communication 1998).

This new technology comes with concerns, however. One major question is the risk associated with transferring the herbicide-resistance gene(s) from wheat to jointed goatgrass via a hybrid bridge. Wheat could hybridize with jointed goatgrass to produce the F_1 generation. This F_1 plant, if not completely sterile, could then backcross to jointed goatgrass repeatedly over several generations, resulting in a jointed goatgrass plant, which in its genetic makeup contains the herbicide-resistance gene. This process is called introgression.

Because wheat and jointed goatgrass have the D genome in common, hybrids between the two species have long been known to occur. These hybrids, however, were always presumed to be sterile or nearly sterile (Donald and Ogg 1991; Johnston and Parker 1929; Mayfield 1927; Priadcencu et al. 1967). The shared genome is thought to allow the hybrids to form, allowing sufficient pairing during pollination and subsequent seed set (Zemetra et al. 1998). This scenario has been reported to have occurred in research plots testing the effectiveness of imazamox on herbicide-resistant wheat (Seefeldt et al. 1998). Two resistant hybrid plants were discovered in plots where the herbicide had previously been applied. A fertility rate of approximately 2% on these hybrids was reported. Both species are primarily self-pollinated; however, 1 to 2% outcrossing does occur under natural conditions in wheat (Kimber and Sears 1987; Poehlman and Sleper 1995; Weise 1991). Several intergeneric hybridization attempts have been successful using *T. aestivum* and species from genera including *Secale*, *Hordeum*, and *Agropyron* (Maan 1987). This research investigates the rate at which hybrids between *T. aestivum* and *A. cylindrica* will set seed when grown in differing populations of wheat and jointed goatgrass, and the proportion of seed produced that will germinate.

MATERIALS AND METHODS

In the fall of 1995 and 1996, 1 m by 1 m plots were planted at Hyslop Field Laboratory, Corvallis, Oregon, to varying populations of jointed goatgrass plants and 'Madsen' soft white winter wheat plants (150/0, 100/50, 75/75, 50/100, 0/150). Into each plot 1, 5 or 10 hybrid plants were transplanted, (Table I-1). The hybrid seed used for the experiment were produced using the approach breeding technique using 'Madsen' wheat as the female parent and jointed goatgrass as the male parent (Zemetra et al. 1998). The treatments were randomly assigned to plots. The soil was Woodburn silt loam. Plots were hand-weeded throughout the growing season.

Table I-1. Hybrid plot populations for field experiments in 1995 and 1996.

Treatment	Jointed goatgrass plants	Wheat plants	Hybrid plants
1	150	0	1
2	100	50	1
3	75	75	1
4	50	100	1
5	0	150	1
6	150	0	5
7	100	50	5
8	75	75	5
9	50	100	5
10	0	150	5
11	150	0	10
12	100	50	10
13	75	75	10
14	50	100	10
15	0	150	10

The experimental design was a randomized complete block factorial with four replications. In July 1996 and 1997, all plants were harvested and spikes of all species were counted. Florets were counted on each spike from the hybrid plants and hand-threshed. The number of florets present was established by counting the number of spikelets and doubling this number. Two florets per spikelet was estimated based on published numbers of jointed goatgrass and wheat florets per spikelet (Gates 1936; Hafliger and Scholz 1981; Slageren 1994). Percent seed set was determined by dividing the number of reproductively successful florets by the total number of florets present. Seed produced were divided according to seed condition, full or shrivelled. Percent germination of the seed then was determined.

RESULTS AND DISCUSSION

Seed set on hybrid plants was lower in 1995 than in 1996 ($F=35.64$, $p=0.0001$). This possibly could be due to different weather conditions between the two years. Temperature data of both experiment years are presented in Figure I-1 and precipitation data of both experiment years are presented in Figure I-2.

Figure I-1. Temperature at Hyslop Field Laboratory, Corvallis, Oregon, during field experiments in 1995 and 1996.

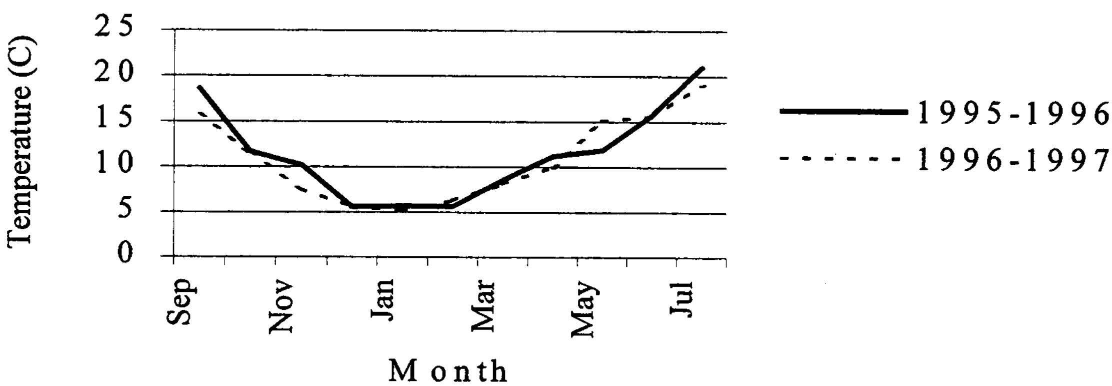
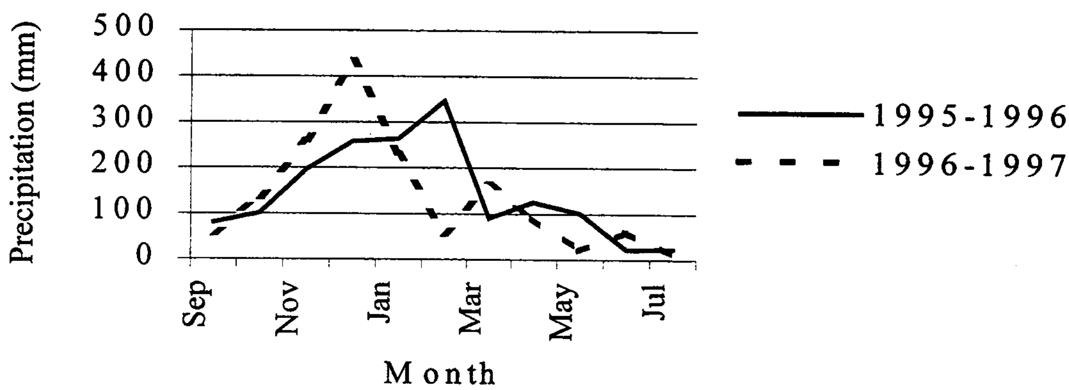


Figure I-2. Precipitation at Hyslop Field Laboratory, Corvallis, Oregon, during field experiments in 1995 and 1996.



When anthesis was occurring in May and June, the weather was wetter and cooler in the first year than it was in the second year. Pollen movement and dispersal is inhibited by wet and cool weather (Robert Zemetra, personal communication 1999). This may partially explain why seed set was lower in the first year than in the second year.

Hybrid spikelets remained open approximately three weeks, much longer than expected, so it is likely that seed set resulted from cross-pollination, not self-pollination. This hypothesis is further supported by earlier work conducted by Mallory-Smith et al. (1996) when investigating similar hybrids. The chromosome numbers present did not match the expected value if self-fertility was occurring with the hybrids; therefore, it was concluded that seed set on hybrids did not arise from self-pollination.

In both years, seed was set in all treatments. The average seed set was 2.29% in 1995 and 3.84% in 1996. No differences in seed set were found among treatments in 1995 (F=0.76, p=0.7030), or in 1996 (F=1.56, p=0.1300). Average seed set per plot ranged from 0 to 5.5% in 1995 and from 0 to 9.2% in 1996. This indicates that hybrids between wheat and jointed goatgrass have the ability to backcross with either parent and produce seed regardless of surrounding populations. These data are summarized in Table I-2.

Table I-2. Summary of seed set on hybrids in 1995 and 1996 at Hyslop Field Laboratory, Corvallis, Oregon.

Treatment	1995 Seed set range	1995 Average seed set	1996 Seed set range	1996 Average seed set
	%			
1	0.9-3.9	2.4	2.4-7.2	4.1
2	1.0-5.5	2.9	2.1-3.2	2.7
3	2.6-3.8	3.2	0.0-3.8	1.9
4	1.4-4.1	2.2	2.0-6.3	3.3
5	1.0-2.5	1.8	3.0-9.2	6.0
6	1.9-2.9	2.3	2.8-5.0	3.6
7	1.9-3.4	2.3	2.7-4.9	3.7
8	0.0-3.0	1.7	3.0-6.2	4.5
9	1.2-2.3	1.7	2.4-6.3	4.2
10	1.7-2.9	2.2	2.6-7.3	4.8
11	1.7-2.5	2.2	2.1-3.7	2.9
12	1.7-2.5	2.4	2.2-4.8	3.9
13	1.8-3.1	2.2	0.0-6.0	2.8
14	2.2-2.5	2.4	3.0-5.7	4.1
15	1.4-3.7	2.4	2.9-8.2	5.2

The germination of the seed produced on the hybrids was not significantly different between years. Also, the germination percent was not different among treatments. The percent of seed germinating was significantly higher for the full seed condition than the shrivelled seed condition (F=11.75, p-value=0.0014). The average germination for full seed was 94% in both years, and 79 and 84% for shrivelled seed in 1995 and 1996, respectively. These data are summarized in Table I-3.

Table I-3. Summary of germination of BC_1 seed produced on hybrids during field experiments in 1995 and 1996.[a]

Year	Seed condition	Average germination
		%
1995	Full	94.0 a
1995	Shrivelled	79.0 b
1996	Full	93.8 a
1996	Shrivelled	83.6 b

[a] Means followed by the same letter are not different according to Fischer's Protected LSD Test at P = 0.05.

These results indicate that hybrids between wheat and jointed goatgrass are not completely sterile and do have the ability to backcross to either parent. Furthermore, the seed produced on the hybrids will be viable and will produce the subsequent generation, BC_1. The fertility rate is independent of parental population, thus seed could potentially be produced by hybrids in any population, ranging from 100% wheat to 100% jointed goatgrass. These findings directly contradict earlier reports of hybrid sterility. Gene flow can occur between wheat and jointed goatgrass by way of the hybrid bridge; therefore, a gene responsible for herbicide resistance may indeed be moved from wheat into nearby populations of jointed goatgrass. Investigations should be made to determine ways to reduce or eliminate the risk of gene flow. The longevity and usefulness of technology is largely determined by the way in which it is implemented; consequently, careful assessments must be made when wheat is released with novel characteristics.

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MANUSCRIPT II

INTROGRESSION BETWEEN WHEAT (*TRITICUM AESTIVUM*) AND JOINTED GOATGRASS (*AEGILOPS CYLINDRICA*) – FIRST BACKCROSS GENERATION

Jeremy R. Snyder, Carol A. Mallory-Smith, Robert S. Zemetra, and Sarah Balter

Submitted to *Weed Science*
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Lawrence, Kansas; March 1999.

ABSTRACT

Field studies were conducted in 1996 and 1997 to determine the rate of seed set on BC_1 plants produced from hybrids between wheat and jointed goatgrass when grown in populations of 100 jointed goatgrass plants. Six studies were conducted, four studies used seed produced on hybrids between wheat and jointed goatgrass grown in populations of 150 jointed goatgrass plants and two studies used seed produced on hybrids grown in populations of 150 wheat plants. The ratio of BC_1 spikes to jointed goatgrass spikes was not different among studies. The average number of florets per BC_1 spike was not different among studies. Percent seed set per plot ranged from 0.25 to 20.29%. All plots contained BC_1 plants that set seed. Greenhouse studies were conducted in 1997 and 1998 to evaluate the rate of self-fertility of the BC_1 generation and to identify morphological characteristics that could be used to identify the probable recurrent parent and to predict the occurrence of seed set. A total of 59 or 4.1% of BC_1 plants in 1997 and 16 or 2.1% of BC_1 plants in 1998 set seed. The average seed set was 0.3% in 1997 and 0.06% in 1998. Results from the field and greenhouse experiments indicate that the first backcross generation in crossing between wheat and jointed goatgrass will have the ability, though limited, to backcross to jointed goatgrass and this generation will recover a degree of self-fertility. Results from the greenhouse studies indicate that it is not possible, using any morphological characteristic measured, to determine the identity of the recurrent parent serving as pollen donor in the previous generation or to predict the occurrence of seed set in the BC_1 generation.

Nomenclature.

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

Key Words.

Hybrid, gene movement, backcross, AEGCY.

INTRODUCTION

Jointed goatgrass (*Aegilops cylindrica* Host) is an allotetraploid with genomes CCDD. It is an annual grass generally germinating in the fall, overwintering, and senescing the following summer. Winter wheat shares a very similar life cycle. Wheat is an allohexaploid with genomes AABBDD. Primarily a self-pollinated crop, wheat has up to 2% outcrossing under natural field conditions (Poehlman and Sleper 1995; Weise 1991). Several intergeneric hybridization attempts between wheat and genera including *Secale*, *Hordeum*, and *Agropyron* have been reported (Maan 1987). Hybridization attempts using the genus *Aegilops* also have been reported. Warham et al. (1984) screened several species in the genus for resistance to the causal organism of karnal bunt, *Neovossia indica*. These researchers found that *A. cylindrica* had a 10% or less infection rate following inoculation in the boot stage, though they did not report the rate of infection when backcrossed to *T. aestivum*. Kofoid and Maan (1982) found that alloplasmic lines of wheat with the cytoplasm of *Aegilops* species had both a better bread loaf volume and higher protein content than the lines with the *Triticum* cytoplasm.

Because wheat and jointed goatgrass are highly related and share the D genome in common, hybrids occur under natural field conditions (Zemetra et al. 1998). The existence of hybrids between wheat and jointed goatgrass was noted as early as 1927 (Mayfield 1927). These hybrids were presumed to be sterile or nearly sterile (Donald and Ogg 1991; Johnson and Parker 1929; Priadcencu et al. 1967). However, preliminary work conducted by Mallory-Smith et al. (1996) found seed on hybrids between wheat and jointed goatgrass. In order to determine if introgression is possible between these two species, field studies were conducted in 1995 and 1996. It was concluded from the data from these studies that hybrids between jointed goatgrass and wheat are not completely sterile and do have the ability to produce viable seed (see Chapter One).

With the advent of new genetic and breeding technologies, wheat can now be produced with novel characteristics such as herbicide resistance (Newhouse et al. 1992). This technology comes with many new questions and concerns. Of primary concern is the risk of introgression occurring between wheat and jointed goatgrass. If this were possible, genes could be transferred from wheat to jointed goatgrass over several generations. This scenario has been reported to have occurred in research plots testing the effectiveness of imazamox on herbicide resistant wheat (Seefeldt et al. 1998). Two resistant hybrid plants were discovered in plots where the herbicide had previously been applied. The fertility rate of these two hybrids was reported as approximately 2%.

The objective of field research was to evaluate the rate at which the first backcross generation, seed set on a hybrid with wheat or jointed goatgrass as the pollen donor, would set seed when planted into populations of 100% jointed goatgrass under natural field conditions. Objectives of greenhouse studies were twofold, first to evaluate the rate of self-fertility of the first backcross generation leading to BC_1S_1 (backcross-one self-one) seed. The second objective was to determine if any morphological characteristics could be used to ascertain, with any degree of accuracy, the identity of the parent serving as the pollen donor to produce the BC_1 seed.

MATERIALS AND METHODS

Field Experiments.

In October 1996 and 1997, 1 m by 1 m plots were roto-tilled to a depth of approximately 15 cm and 100 jointed goatgrass spikelets were planted in each plot at Hyslop Field Laboratory, Corvallis, Oregon. The soil type was Woodburn silt loam. Studies 1 through 4 used BC_1 seed produced in a previous field study on hybrids grown in plots that contained 150 jointed goatgrass plants. Studies 5 and 6 used BC_1 seed produced on hybrids grown in plots that contained 150 wheat plants. The design was a randomized complete block with five replications. Seed were planted in Sunshine Mix #1[1] in 560 ml pots in a greenhouse at 21/18 C day/night temperature. Germinated seed were allowed to grow to the 2 to 3 leaf stage, and then were placed outdoors to acclimate for a period of 10 to 12 days. Ten BC_1 plants were then transplanted into each plot. Plots were hand-weeded throughout the growing season.

At harvest, the number of jointed goatgrass spikes and BC_1 spikes were counted. The total number of florets present on each BC_1 spike was established by counting the number of spikelets and doubling this number. Two florets per spikelet was estimated based on previously published numbers of jointed goatgrass and wheat florets per spikelet (Gates 1936; Hafliger and Scholz 1981; Slageren 1994). Percent seed set for each plot was calculated by dividing the number of reproductively successful florets by the total number of florets present in the plot. Data were subjected to analysis using ANOVA. Percent seed set was log transformed prior to analysis; however, data are reported as untransformed.

Greenhouse Experiments.

Greenhouse studies using BC_1 seed produced on hybrids of jointed goatgrass and wheat under field conditions were conducted. The seed were separated by seed condition, full or shrivelled. These seed were placed in germination boxes with blotter paper presoaked with distilled water and then placed in the dark in a growth chamber set at 24 C. Seed were checked for germination at 2, 4, and 6 days, and the day of germination was recorded. The germinated seed were removed, transplanted into Jiffy pots[2], and placed in a greenhouse at 21/18 C day/night temperature. Supplemental lighting resulted in a total day length of 12 h. Coleoptile color, either red or green, was recorded at day 10.

A maximum of 30 plants, 15 from the full seed group and 15 from the shrivelled seed group were randomly selected from each hybrid plot to be used for morphological measurements. The seedlings were allowed to reach the 2 to 3 leaf stage and then were vernalized for 6 weeks in a growth chamber at 4 to 6 C with

10/14 h light/dark. Following the vernalization period, plants were returned to the greenhouse and allowed to acclimate 1 to 2 days, and then were transplanted into 4.5 by 4 by 9 cm black 3-mil grow-out bags containing Sunshine Mix #1[1].

At the 4 to 6 tiller stage, morphological characteristics on the uppermost fully extended leaf of five tillers on each plant were measured. Leaf width 5 cm from the juncture of the blade and sheath was measured. The number of veins 5 cm from the juncture and the number of hairs on the leaf margins from 3 to 7 cm from the juncture were counted. A relative value of plant posture was assigned to each plant, ranging from 1 for entirely prostrate to 5 for entirely upright. The plants were allowed to mature and senesce. At harvest, the height of five culms, from the soil surface to the base of the spike, was recorded for each plant, as well as the length of five spikes from the base of the spike to the top of the terminal spikelet, excluding awn length. A relative assessment of plant appearance, ranging from jointed goatgrass-like to hybrid-like to wheat-like was made.

The total number of spikes produced on each plant was recorded. The total number of florets present on each spike was estimated by counting the number of spikelets and doubling this number, assuming that each spikelet averaged two florets (Gates 1936; Hafliger and Scholz 1981; Slageren 1994). Percent seed set of each plant was calculated by dividing the number of reproductively successful florets by the total number of florets present. Data were subject to statistical and correlation analysis using ANOVA and Pearson correlation coefficients.

RESULTS AND DISCUSSION

Field Experiments.

Several plants were identified as potential outliers due to the extremely high percentage of seed set. Data were analyzed with and without these plants. It was found that these plants had no effect on the conclusions and thus remained in the data set. The ratio of BC_1 spikes to jointed goatgrass spikes were not different among studies (F=0.05, p=0.7695). This indicates that each plot likely had very similar environments with respect to the availability of jointed goatgrass pollen. The average number of florets per BC_1 spike was not different among studies (F=2.26, p=0.0877); therefore, no study had an increased chance of seed set due to higher average number of florets per spike present. Percent seed set per plot ranged from 0.25% in 1997 to 20.3% in 1998. No differences in percent seed set were found among studies (F=1.80, p=0.1320). All plots contained BC_1 plants that set seed. These data are summarized in Table II-1.

Table II-1. Summary of BC_1 plants setting seed in populations of 100 jointed goatgrass plants in the 1997 and 1998 field experiments.

Year	Study	Parental Population	Seed set range	Average Seed set	Average seed/plot
			------------------ %	-------------	
1997	1	Jointed goatgrass	0.25-5.23	2.77	66.0
1997	2	Jointed goatgrass	1.26-3.40	2.13	71.6
1998	3	Jointed goatgrass	4.06-20.29	10.33	181.2
1998	4	Jointed goatgrass	1.61-6.87	4.63	107.2
1998	5	Wheat	1.11-7.04	3.26	82.8
1998	6	Wheat	0.67-12.79	4.22	133.2

These results indicate that the first backcross generation is not completely sterile. These BC_1 plants either self-pollinated or backcrossed to jointed goatgrass and formed viable BC_1S_1 or BC_2 seed, respectively. It is clear that a proportion of BC_1 plants have the ability to produce viable seed regardless of the population, either 150 jointed goatgrass plants or 150 wheat plants, in which the hybrid was grown. These findings are in direct contradiction to previous reports regarding the sterility of hybrids and backcrosses of wheat and jointed goatgrass (Johnston and Parker 1929; Mayfield 1927); however, do support the findings of Zemetra et al. (1998).

Greenhouse Experiments.

A total of 59 or 4.1% of the BC_1 plants in 1997 and 16 or 2.1% of the BC_1 plants in 1998 set seed of varying amounts in the greenhouse experiments. The number of plants investigated in 1998 was lower than expected due to death of plants resulting from failure of growth chambers during vernalization. This is one explanation of the low quantity of plants setting seed in the greenhouse in 1998. The average percent seed set in 1997 was 0.30% and 0.06% in 1998. These plants were isolated from both wheat and jointed goatgrass pollen; thus, seed that was produced resulted from self-pollination. The seed set indicates that a proportion of the BC_1 plants will recover some self-fertility. These data are summarized in Table II-2. Hybrid plant treatments refer to the population in which the hybrid plants were grown, refer to Table I-1.

Table II-2. Summary of BC_1 plants producing BC_1S_1 seed in greenhouse experiments during 1997 and 1998.

Hybrid Plant Treatment	1997			1998		
	BC_1 plants setting seed	Highest seed set	Average seed set	BC_1 plants setting seed	Highest seed set	Average seed set
	----- # -----	--------- %	-----------	----- # -----	--------- %	-----------
1	3	2.22	0.052	3	2.50	0.087
2	2	0.53	0.009	0	---	0.000
3	2	3.13	0.038	0	---	0.000
4	1	0.62	0.013	0	---	0.000
5	1	80.22	2.865	2	2.50	0.082
6	5	46.15	0.799	4	14.50	0.390
7	9	38.36	0.861	1	6.25	0.110
8	7	29.05	0.444	3	0.71	0.026
9	3	1.86	0.028	0	---	0.000
10	7	8.56	0.268	2	1.04	0.026
11	4	4.87	0.083	0	---	0.000
12	5	14.02	0.183	0	---	0.000
13	5	1.25	0.032	0	---	0.000
14	5	25.60	0.345	1	4.72	0.079
15	0	---	0.000	0	---	0.000

Figure II-1 is a representative photograph taken in 1997 of BC_1 spikes produced in the greenhouse, and clearly illustrates the vast amount of variation seen in the greenhouse experiment. All of the heads shown are from the same generation, BC_1, and are arranged based on the appearance of the spikes. Each spike pictured was taken from a different plant.

Figure II-1. Representative BC_1 spike appearance in greenhouse experiments.

Similar variation as seen in the spikes also was seen on the whole plant level. Figure II-2 is a photograph also taken in 1997 of BC_1 plants in the greenhouse. Though most plants resembled the hybrid generation, some plants closely resembled jointed goatgrass or wheat plants. These plants are from the BC_1 generation and are arranged according to resemblance to parents; those plants closely resembling jointed goatgrass appear on the left side of the photograph and wheat on the right.

Figure II-2. Representative BC_1 plant appearance in greenhouse experiments.

While many plants were consistently wheat-like or jointed goatgrass-like with respect to leaf characteristics and overall appearance, it was common to see a BC_1 plant that closely resembled wheat with respect to spike appearance and leaf width, but which had a prostrate posture similar to jointed goatgrass. The reverse also could readily be found, namely a plant that had leaf and spike characteristics very similar to jointed goatgrass but which had the upright posture of wheat. The statistical analyses conducted were in agreement with the observations made. No correlations were found among any morphological characteristics measured when analyzed using both data plots and Pearson's correlation coefficients. The probable recurrent pollen donor parent can not be identified by coleoptile color, leaf width, number of hairs on the leaf margin, presence of hairs on the leaf margin, number of veins in the leaf, spike appearance, spike length, plant height, plant posture, or number of spikes produced on the BC_1 plant. Furthermore, and perhaps more importantly, none of these aforementioned characteristics can be used to predict the occurrence of seed set on BC_1 plants arising from self-pollination.

The conclusions drawn from both the BC_1 field and greenhouse experiments are of vital importance as new genetic and breeding techniques are introduced. Based on these results, it has now been proven that hybrids and subsequent generations of crosses between wheat and jointed goatgrass are not sterile. As a direct result of this work, we now understand that introgression between wheat and jointed goatgrass is a definite possibility. New technologies intent on improving or altering the genetic constitution of wheat in any way must take into account the risk of transferring these traits to nearby jointed goatgrass populations. Adequate risk assessments must be made such that it will be possible to decrease the chance of introgression.

Sources of Materials.

[1] Sunshine Mix #1, Sungro Horticulture, Inc., 110 110th Ave. NE Suite 490, Bellevue, WA 98004.

[2] Jiffy pots, Jiffy Products of America, Inc., Batavia, IL 60510.

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SUMMARY AND CONCLUSIONS

Jointed goatgrass is a major weed problem facing winter wheat producers in the United States. Selective control of jointed goatgrass with the use of herbicides is currently not possible. However, new genetic and breeding technology may change this with the advent of herbicide-resistant wheat. Of primary concern with this technology is the protection of any added resistance to prevent escape to weed populations. Because wheat and jointed goatgrass have the D genome in common, hybridization between the two species does occur. Scientists have believed that these hybrids were completely sterile almost as early as the hybrids were observed (Johnston and Parker 1929). If these hybrids are not completely sterile, the resistance gene(s) could move from wheat to jointed goatgrass via a hybrid bridge. In this scenario, wheat and jointed goatgrass cross and form the F_1 generation, the hybrid. This hybrid plant can backcross to jointed goatgrass. Occurring over several generations, the result is a jointed goatgrass plant that in its genetic makeup contains the resistance gene. This is an example of introgression.

The discovery of seed on hybrid plants in 1990 brought to light many new questions regarding the sterility of the crosses between wheat and jointed goatgrass (Mallory-Smith et al. 1996). Reports also have been made of hybrids acquiring resistance genes from herbicide-resistant wheat (Seefeldt 1998).

Field studies were conducted to determine the rate of seed set on hybrids and to determine the viability of seed produced. Hybrid plants were planted into varying populations of wheat and jointed goatgrass in Corvallis, Oregon in 1995. This study was repeated in 1996. The average seed set on the hybrid plants was 2.3% in the first year and 3.8% in the second year. Seed set was independent of hybrid population. The seed produced on the hybrids were separated according to seed condition, either full or shrivelled. Approximately 94% of the full seed germinated in both years and 79 and 84% of the shrivelled seed germinated in 1997 and 1998, respectively. Percent germination was independent of hybrid population.

Field studies were conducted to evaluate the rate of seed set on BC_1 plants. First generation backcross plants were planted into populations of 100 jointed goatgrass plants in Corvallis, Oregon, in 1996 and 1997. Six studies were conducted; four used seed produced on hybrids grown in populations of 150 jointed goatgrass plants, two studies used seed produced in plots containing 150 wheat plants. The percent seed set per plot ranged from 0.25 to 20.3%. Average seed set on BC_1 plants arising from hybrids grown in jointed goatgrass was 4.96% and from hybrids grown in wheat was 3.74%. No differences in percent seed set were found among studies.

Greenhouse studies were initiated to determine the rate of self-fertility restoration and also to identify any morphological characteristics that could be used to determine the probable identity of the recurrent pollen donor. A total of 59 or 4.1% of plants in 1997 and 16 or 2.1% of plants in 1998 showed varying ranges of self-fertility restoration. Percent seed set per plant ranged from 0 to 80.2%. No correlations were found among any morphological characteristics measured. These characteristics included coleoptile color, day of germination, plant posture, number of veins in the leaf, presence and number of hairs on leaf margin, width of leaf, height of plant, length of spike, number of spikes produced, and resemblance to jointed goatgrass or wheat. This means that it is not possible, using any of the characteristics measured, to predict seed set or determine parental population.

The conclusions drawn from these experiments are of vital importance as new genetic and breeding techniques are introduced. Based on the results, it has now been proven that hybrids between wheat and jointed goatgrass are not sterile and will have the ability, though limited, to produce viable seed. Furthermore, subsequent generations of crosses between wheat and jointed goatgrass will recover a moderate level of self-fertility and have the capacity to backcross additional times to jointed goatgrass. As it is not possible to conclude the probable identity of the recurrent parent using readily available morphological characteristics, all crosses must be managed carefully.

Introgression between wheat and jointed goatgrass has occurred and will continue to occur. New technologies intent on improving or altering the genetic constitution of wheat in any way must take into account the risk of transferring these traits to nearby jointed goatgrass populations. Studies should be conducted to evaluate the risk associated with gene flow from wheat to jointed goatgrass. These studies will allow adequate risk assessments to be made such that it will be possible to increase both the longevity and usefulness of wheat with novel characteristics.

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APPENDIX

Table A-1. Pearson correlation coefficients for morphological characteristics during greenhouse experiments in 1997 and 1998.

Characteristic	Hybrid number	JGG/wheat population	Coleoptile color	Seed condition	Plant Morphology	Leaf width	Veins	Hairs	Posture	Height	Spike length	Seed set
Hybrid number	1.00	---	---	---	---	---	---	---	---	---	---	---
JGG/wheat population	0.00	1.00	---	---	---	---	---	---	---	---	---	---
Coleoptile color	-0.32	0.27	1.00	---	---	---	---	---	---	---	---	---
Seed condition	-0.13	-0.36	-0.32	1.00	---	---	---	---	---	---	---	---
Plant morphology	-0.10	0.55	0.44	-0.29	1.00	---	---	---	---	---	---	---
Leaf width	-0.48	0.26	0.65	-0.28	0.46	1.00	---	---	---	---	---	---
Veins	-0.40	0.36	0.21	-0.62	0.27	0.59	1.00	---	---	---	---	---
Hairs	-0.34	-0.61	-0.08	0.43	-0.48	-0.13	-0.28	1.00	---	---	---	---
Posture	-0.21	0.38	0.29	-0.38	0.67	0.68	0.62	-0.36	1.00	---	---	---
Height	-0.18	0.16	0.46	0.11	0.09	0.47	0.02	-0.11	0.03	1.00	---	---
Spike length	-0.46	-0.48	-0.28	0.54	-0.58	-0.21	-0.22	0.76	-0.56	0.15	1.00	---
Seed set	0.08	-0.36	-0.12	-0.18	-0.31	-0.03	-0.04	0.21	-0.01	0.04	0.17	1.00