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DISSERTATION

WINTER ANNUAL GRASS WEED MANAGEMENT IN WINTER WHEAT

Submitted by

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In partial fulfillment of the requirements

for the degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2001

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COLORADO STATE UNIVERSITY

December 12, 2000

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY **TODD A. PESTER** ENTITLED **WINTER ANNUAL GRASS WEED MANAGEMENT IN WINTER WHEAT** BE ACCEPTED AS FULLFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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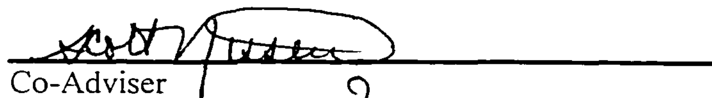
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ABSTRACT OF DISSERTATION

WINTER ANNUAL GRASS WEED MANAGEMENT IN WINTER WHEAT

The objective of this dissertation was to enhance integrated weed management strategies for controlling winter annual grass weeds in winter wheat. The research consisted of a three-pronged approach evaluating cultural practices, herbicide-resistant crop technology, and weed genetic diversity. Field studies were conducted to evaluate the effects of combining multiple cultural practices on controlling jointed goatgrass in a winter wheat-fallow cropping system. Jointed goatgrass growth and population were effectively reduced in treatments that included a tall wheat cultivar with a more open-crown growth habit, increased wheat planting density, and reduced-tillage. Delayed planting usually reduced wheat yield without reducing jointed goatgrass production and sub-surface nitrogen applications did not significantly increase wheat competitive advantage. Wheat cultivars with resistance to imazamox herbicide are being developed that will facilitate selective control of jointed goatgrass, downy brome, and feral rye. These three weed species respond differently to imazamox postemergence treatments with feral rye demonstrating more tolerance than jointed goatgrass or downy brome. A series of laboratory studies identified that imazamox absorption was >90% in all three species and the differential control of jointed goatgrass and feral rye was attributed to differences in herbicide translocation and metabolism. Weed genetic diversity influences genetic response to selection pressure and may influence the success of chemical and cultural

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weed management practices. For example, the level of genetic diversity within jointed goatgrass may influence introgression of herbicide-resistant genes from wheat to jointed goatgrass through herbicide-resistant allele frequencies. RAPD and AFLP fingerprinting techniques generated over 650 molecular markers among eight U.S. and 50 Eurasian jointed goatgrass accessions of which 5% were polymorphic. Cluster analyses showed relatively small genetic distances among jointed goatgrass accessions. The lack of genetic diversity within jointed goatgrass suggests the evolution of the species was relatively recent and the subsequent polyploidy provided sufficient plasticity for adaptation to a wide geographic range without significant mutation and selection. The results of this research have increased our knowledge of winter annual grass weed biology and ecology and should contribute to the development of successful integrated management systems for these weeds in winter wheat.

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DEDICATION

To my wife, Dawn, and my son, Hayden.

My inspiration.

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CHAPTER 1

A review of jointed goatgrass (*Aegilops cylindrica*) biology, ecology, and management.

Abstract

Jointed goatgrass is a winter annual grass weed that is believed to have been introduced into North America as a contaminant in winter wheat (*Triticum aestivum* L.) seed. Although jointed goatgrass was first discovered in some states early in the 20th century, changing wheat production practices during the past 25 yrs have encouraged its spread and increase. Winter wheat producers in the western United States are concerned about the lack of adequate selective control measures for this weed. Jointed goatgrass and wheat have the D genome in common and have similar growth habits. Jointed goatgrass lowers winter wheat yield by competing for growth requirements, reducing harvesting efficiency, and lowering crop quality by contaminating harvested grain. Jointed goatgrass is well adapted to stubble-mulch or reduced tillage crop production, particularly in regions where climate limits cropping options to the winter wheat-fallow rotation or continuous wheat. Cultural practices have been shown to suppress jointed goatgrass growth and seed production, but control is often erratic. Development of new herbicide

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resistant winter wheat cultivars should provide effective control of jointed goatgrass but stewardship of this technology will be critical to reduce the potential for introgression of herbicide resistant genes from wheat into jointed goatgrass.

Jointed Goatgrass Introduction into the United States

There were multiple times and sites of introduction of jointed goatgrass into North America. Jointed goatgrass probably was first introduced into the United States in contaminated winter wheat seed. Johnston and Parker (1929) speculated that it was transported into Kansas in the late 19th century from the eastern Mediterranean, possibly in 'Turkey' winter wheat brought from Russia by Mennonite settlers (Johnston and Parker 1929; Mayfield 1927). Mayfield (1927) added that it also was probably brought into Kansas in introductions of Turkey or 'Kharkof' wheat made by the U.S. Department of Agriculture or by private seed firms and individuals during the early 1900s. Herbarium samples collected in 1910 indicated that it had escaped from experimental plots on the South Dakota State University campus at Brookings, SD. It was first identified by botanists in Kansas in 1917 (Johnston and Parker 1929), in Washington about 1917 (Swan 1984), in Oregon in 1926 (Rydrych 1983), and in Oklahoma in 1946 (Chaffin 1947; Featherly 1946), although it was probably introduced much earlier.

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Plant Description

Morphology

Two varieties of *Aegilops cylindrica* are recognized: vars. *rubiginosa* and *cylindrica* (Hitchcock 1950). Variety *rubiginosa* has pubescent outer glumes on the spikelets, whereas *cylindrica* has glumes that are glabrous (Johnston and Parker 1929; McGregor 1987). These two varieties of jointed goatgrass were first found in Kansas in the late 1920s. Whether these varieties differ in their susceptibility to herbicides or tillage has not been reported. Most studies involving jointed goatgrass selections have not described which varieties were studied.

Jointed goatgrass is a winter annual species. Culms of jointed goatgrass are erect (40 to 60 cm tall) and branch at the base. Isolated plants can produce up to 50 erect flowering stalks. Leaves are alternate and 2 to 3 mm wide. Leaf length varies from 5 to 12 cm; leaves near the seedhead and at the base of the plant are shorter than elsewhere on the shoot. Auricles at the juncture of the leaf sheath and blade are hairy (Donald and Ogg 1991).

The jointed goatgrass seedhead is a spike 5 to 10 cm long with rachis internodes every 6 to 8 mm (Hitchcock 1950). Like the wheat spike, the jointed goatgrass spike is sessile with alternately arranged spikelets on opposite sides of the rachis, the main axis of the spike. Joints of the rachis thicken at their distal tips. At maturity, the spike disarticulates between the spikelets along the rachis. Spikelets are 8 to 10 mm long and generally have two flowers each. Awn length varied from 3.8 to 7.1 cm on nine

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selections from across the western U.S. (Gealy 1988). Only the glumes on the uppermost spikelet have long awns.

Normally, there are one to two seed per joint (Hitchcock 1950), but three occur rarely (McGregor 1987). Seed are reddish-brown, grooved, 6.5 to 9 mm long, and 2 mm wide. Seed account for 48% of the joint weight. Unlike winter wheat, jointed goatgrass seed adhere to the lemma and palea of the glumes which makes them difficult to remove from joints (McGregor 1987). Entire disarticulated spikelets are cylindrical and often are mistaken for small pieces of wheat straw (Johnston and Parker 1929). Farmers can identify jointed goatgrass seedlings most easily by digging up the plants to observe the joint attached to the mesocotyl (Westra and Davis 1988).

Jointed goatgrass selections collected from nine western states were similar to one another in growth, development, and germination when they were grown at the same location in Washington (Gealy 1988; Gealy 1989; Gealy and Buman 1989). Germination of seed one month after harvest ranged from 52 to 75%, and did not differ greatly among the nine selections. Also, five selections collected in Oregon were similar to each other for the following characteristics: temperature dependence of germination, timing of emergence and flowering in the field, leaf and stem dry weight, spikes per plant, and spikelets per plant.

Genomics

Both diploid and polyploid species are found in the genera *Aegilops* and *Triticum* (Zohary 1965). Polyploidy in *Aegilops* may contribute to its wide ecogeographic range and its weedy nature (Zohary 1965). Genetic relationships between these genera have

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been reviewed (Bowden 1959; Kihara 1954). The CD genome of jointed goatgrass is polyploid and may give this species the potential for wide distribution and adaptation to a range of ecogeographic areas. The D chromosome confers cold tolerance and adaptation to continental climates (Simmonds 1974). The chromosome number (2N=CD) of jointed goatgrass is 28, whereas that of wheat (2N=ABD) is 48. Evidence indicates that the D chromosome of tetraploid jointed goatgrass was derived from a diploid progenitor of wheat, *A. squarrosa* L. (Kofoid and Maan 1982; Maan 1976). Thus, jointed goatgrass is genetically related to wheat since both have a D chromosome. Occasionally, jointed goatgrass and winter wheat cross in fields and seed from these crosses produce sterile F1 hybrids that are intermediate in form between these species (Seefeldt et al. 1998).

Economic Importance

Detrimental Economic Impact

Jointed goatgrass reduces winter wheat yields by interference (Rydrych 1983) and lowers harvested grain quality. Direct combine harvesting causes unshattered joints to disarticulate and contaminate harvested winter wheat grain. When jointed goatgrass joints contaminate winter wheat as dockage, farmers' grain is discounted (Anonymous 1988). If joints are not removed by grain cleaning, jointed goatgrass is considered as foreign matter and can reduce grain grade.

In three yrs of competition studies in Oregon, 54 to 86 jointed goatgrass plants m^{-2} reduced winter wheat yields 25 to 29%, respectively (Rydrych 1983). More research is

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needed to accurately predict wheat yield losses from jointed goatgrass. Jointed goatgrass interference reduced the water use efficiency of winter wheat in the field in Montana but did not affect the pattern of water use in the soil profile (Coble and Fay 1985). Half of the stored water used by winter wheat came from the top 60 cm of the soil whether or not jointed goatgrass was present. In replacement series experiments in pots, winter wheat was only slightly more competitive than jointed goatgrass, both of which were much more competitive than downy brome (*Bromus tectorum* L.) (Fleming et al. 1988). Apparently, the three species were competing for the same resources, as judged by the relative yield total. Jointed goatgrass displayed a competitive advantage with winter wheat in the growth chamber under stress conditions (high temperature of 27/10 C and water potential of –300 kPa), but winter wheat had a competitive advantage under favorable growing conditions (18/10 C and –33 kPa).

Because the cross sectional area of jointed goatgrass joints is similar to the cross sectional area of winter wheat seed, joints are not removed easily by conventional seed cleaning methods (Fenster and Wicks 1976). Either length graders, such as indent disc and indent cylinder seed cleaners, or gravity tables can separate jointed goatgrass joints from winter wheat seed. Such seed cleaners are slow and costly to operate for grain handling businesses; consequently, this cost is passed on to farmers. Because there is a zero tolerance for jointed goatgrass seed in certified winter wheat seed in many states, discovery of even one jointed goatgrass plant in a field prevents the wheat from being certified.

Jointed goatgrass is an over-wintering host for pests that attack winter wheat. These pests include the Russian wheat aphid, leaf spot, pink mold, foot rot, root browning,

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damping off, and karnal bunt (Farr et al 1989; Hammon et al 1989; Warham et al. 1983). Pests of winter wheat may be managed better by controlling jointed goatgrass in wheat fields, in fence rows, along field edges, along roadsides, in land enrolled in the Conservation Reserve Program (CRP), and on wasteland (Johnston and Parker 1929).

Beneficial Economic Impact

Wheat breeders have used germplasm from jointed goatgrass and other *Aegilops* species to improve winter wheat tolerance to environmental stresses, diseases, and insects (Maan 1976). Selections of jointed goatgrass have been studied as sources of rust and karnal bunt resistance for use in winter wheat breeding (Warham et al. 1983). Hybridization has been used for creating amphidiploids with improved drought resistance, productive vigorous growth, and adaptation to infertile sites (Priadcencu et al 1967). The CD chromosomes of jointed goatgrass and related *Aegilops* species are a source of cold tolerance for winter wheat breeding equal to those of the winter wheat variety 'Norstar' which contains the ABD genome (Limin and Fowler 1985). Apparently, the D genome is more cold tolerant than the A genome. Chromosomes 4D and 5D are associated with cold tolerance in hexaploid wheat.

Cattle graze both jointed goatgrass and winter wheat in parts of the Central Great Plains during fall and winter (McGregor 1987). Jointed goatgrass joints separated from wheat have been ground and used as an animal feed (Heyne 1950). Joints contained 11.7% protein, 1.4% ether extract, 26.1% crude fiber, 8.2% moisture, 5.8% ash, and 46.8% nitrogen-free extract. Seed contained most of the protein in joints.

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Geographic Distribution

Worldwide Distribution

The genus *Aegilops* is distributed worldwide and contains at least 23 species (Priadcencu et al 1967). According to Holm et al. (1979), jointed goatgrass is a problem weed only in Turkey and the U.S., although other species of *Aegilops* are weeds in Morocco, Portugal, Iran, Jordan, and Israel. Reportedly, it was a common weed of cereals around the Mediterranean, Caspian, and Black Seas early in this century (Johnston and Parker 1929). Jointed goatgrass is believed to be native to southern Europe and Russia (Gunn 1958).

North American Distribution

Although jointed goatgrass is not native to North America, it is now widely distributed in the U.S. (Hitchcock 1950; Schweitzer et al. 1988). It is considered one of the most common weeds of cereals in Colorado, Kansas, New Mexico, Oklahoma, Oregon, Utah, Washington, and Wyoming, infesting a total of 2.5 to 3.0 million acres of winter wheat in the U.S., and it is still spreading (Elmore 1988). Despite the presence of jointed goatgrass throughout the Corn Belt, weed scientists there have not reported it as a commercial problem in winter wheat. Perhaps, widespread use of rotation of spring-sown corn (*Zea mays* L.) and soybean [*Glycine max* Merr. (L.)] with winter wheat has limited its impact on crop production in that region.

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Climatic Requirements

Because jointed goatgrass is as widely distributed in North America as winter wheat, edaphic factors are unlikely to limit its final distribution. Whether jointed goatgrass is better adapted to certain soil types or rainfall areas than winter wheat requires further study. Annual rainfall ranges from 25 to 55 cm in many parts of its distribution. Differences in jointed goatgrass seed persistence in Colorado, Kansas, and Nebraska may be related to climate (Donald and Zimdahl 1987).

Growth and Development

Phenology and Physiology

The phenology and vegetative shoot growth of jointed goatgrass is similar to winter wheat. The two species germinate together and develop at about the same rate throughout the growing season (Dotray 1989; Dotray and Young 1988; Fenster and Wicks 1976). In dry yrs, jointed goatgrass emerges in the wheat row, presumably because of better soil moisture and soil-seed contact. In wet yrs or when the soil seed bank is large, jointed goatgrass germinates both within the row and between rows. Reportedly, jointed goatgrass seedlings can emerge from the same depths as winter wheat.

Jointed goatgrass tillers more profusely than does winter wheat. Gealy (1988) noted that one selection of jointed goatgrass from Washington produced as many as 138 tillers per plant. In another study (Dotray and Young 1988), the two species produced similar

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numbers of tillers and similar total root length, but wheat had a greater shoot to root dry weight ratio and twice as much leaf area.

Jointed goatgrass is somewhat more winter hardy than winter wheat and survives winters that cause widespread winter killing of winter wheat (Johnston and Parker 1929). Jointed goatgrass is similar to wheat in its photosynthetic capacity and transpiration (Gealy 1987; Gealy 1989). Both species are C3 plants (Gealy 1987; Waller and Lewis 1979). In the greenhouse, net photosynthesis, transpiration rate, leaf diffusive resistance, and stomatal density of nine selections from across the western U.S. were also similar. (Gealy 1987; Gealy 1989).

Jointed goatgrass seed matures before or with winter wheat in the Central Great Plains (Heyne 1950; Johnston and Parker 1929) but can mature as much as two weeks before winter wheat in the Pacific Northwest. Its seedheads form at or below winter wheat spikes in the plant canopy, but high enough to be cut during combining. Abscission layers are present at the base of the joint and the distal end of the attached rachis. At harvest, seedheads and foliage of some selections of jointed goatgrass become purple colored, aiding detection in straw colored wheat (Mayfield 1927). Shattered jointed goatgrass joints can lie on the soil surface until washed away in runoff water or until buried by sweep sub-tillage, disking, or cultivation during fallow. Stubble mulch tillage practices leave joints near the soil surface (Donald and Zimdahl 1987) where the percentage of germination is much greater.

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Floral Biology

Winter wheat flowering in the greenhouse is promoted by vernalization at 5 to 7 C for 6 to 10 weeks under an 8 to 10 h photoperiod followed by a photoperiod of 14 to 16 hours, and a daytime temperature range of 15 to 20 C and a night temperature range of 10 to 16 C (Allan 1980). Like winter wheat, jointed goatgrass has a quantitative requirement for vernalization to produce seed and imbibed seed can be vernalized (Donald 1984).

Seed Production

Isolated jointed goatgrass plants can produce as many as 3000 seed each (Gealy 1988). Under highly competitive conditions with winter wheat, few (3 to 5) joints form per spike. Under more favorable conditions, 11 or 12 joints may form per spike on isolated plants. Isolated jointed goatgrass plants growing without interference may produce over 100 tillers and as many as 1,500 joints per plant (Gealy 1988).

Seed Dispersal

Joint disarticulation aids in local seed dispersal by wind, machinery, and man (Johnston and Parker 1929). Man has played a major role in transporting and spreading jointed goatgrass by (a) planting contaminated winter wheat seed, (b) allowing joints to blow from passing trucks hauling grain, and (c) transporting joints from field to field and region to region by combines.

Resowing contaminated winter wheat seed from earlier harvests is common on wheat farms. In a drill box survey of winter wheat sown in Oregon in the 1970s, 20% of farmers were planting jointed goatgrass-contaminated winter wheat (Swan 1984). Even

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if contaminated winter wheat seed were cleaned commercially before being resown, most grain elevators lack proper cleaning equipment to remove all joints. However, proper seed cleaning equipment has become more widely available in recent yrs. Because some states do not have seed laws denying certification for winter wheat seed contaminated with joints; therefore, jointed goatgrass has been spread across state boarders via sale of contaminated certified winter wheat seed (Donald and Ogg 1991).

Because jointed goatgrass joints float, seed can be moved by runoff water and infestations may become dense in moist depressions or draws in fields, or along drainageways where seed collect. Tillage equipment can transport joint-contaminated soil from moist depressions across fields to infest new areas. Because joints are large, seed are unlikely to be moved far by wind (Donald and Ogg 1991).

Seed Dormancy Mechanisms and Germination

Dormancy in jointed goatgrass has not been thoroughly studied. However, the origin of the mother plant and the condition under which seed matured in the joints on the spike influenced later germinability of *A. ovata* (Datta et al. 1970; Datta et al. 1972) and *A. kotschy* (Wurzberger and Leshem 1974). In both species, germination of seed removed from joints was greater than germination of seed left in intact joints. Because seed removal did not overcome dormancy completely, embryo factors, possibly endogenous gibberellins, were suggested to contribute to germinability in addition to germination inhibitors in the joint (Wurzberger and Leshem 1967). Exposure to exogenous GA improved germination of seed removed from the joint (Wurzberger and Leshem 1974).

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A balance of endogenous gibberellins in the embryo and germination inhibitors in the joint was suggested as a regulator of germination in this species.

Jointed goatgrass emerged best from shallow depths of 0 to 5 cm (Cleary and Peeper 1980). Emergence from below 10 cm was limited and no seed emerged from below 15 cm (Cleary and Peeper 1980). Depth of emergence has not been reported from the field on different soil types or under different moisture regimes. However, more seedheads of jointed goatgrass were produced by plants that germinated from the soil surface than seed buried 5 or 16 cm deep (Cleary and Peeper 1980). Reduced-tillage soil conservation practices, such as shallow disking for primary tillage, left 70 to 75% of the soil seed reserve of jointed goatgrass in the top 3.8 cm of the soil profile (Donald and Zimdahl 1987). The bulk of the remaining seed was buried between 3.8 and 7 cm deep, the working depth of the disk. Total joint densities in the soil varied from 1,730 to 3,720 joints m^{-2}.

That growers and researchers have observed better emergence and establishment of jointed goatgrass in wheel tracks of combines and tractors than on uncompacted soil suggested that compaction favors good contact between the seed and soil and enhances subsequent germination and emergence of jointed goatgrass.

Seed persistence

Jointed goatgrass seed viability remained unchanged after 2 yrs of dry storage in the laboratory (Lish et al. 1988). Dormancy was cyclical during each yr but total viability, as measured by germination and the tetrazolium test, remained high.

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Jointed goatgrass seed in soil persisted from 3 to 5 yrs depending upon site (Donald and Zimdahl 1987). Seed survival of undisturbed seed buried 5, 15, or 30 cm deep at five locations in Kansas, Nebraska, and Colorado decreased rapidly over the first 3 yrs of burial. By the third yr, less than 8% of seed survived at 5 cm in the soil at all locations. By the third, fourth, and fifth yrs, there was total loss of seed buried 5 cm deep at one, two, and four sites, respectively.

Management and Control

Cultural Practices

Survey data of 44 fields in Montana indicated that jointed goatgrass was more frequent on farms using conservation-tillage than on conventionally-tilled fields (Schweitzer et al. 1988). As reported, the rate of establishment of jointed goatgrass seed lying on the soil surface was 96% compared with only 30% for winter wheat. The ability of seed to germinate on the soil surface makes jointed goatgrass adapted to conservation- or no-tillage winter cereal production.

Combinations of crop management practices have been shown to effectively suppress jointed goatgrass and reduce winter wheat yield loss (Daugovish et al. 1999). Cultural control methods that may reduce the severity of jointed goatgrass include (a) fallowing for one or more growing seasons, (b) deep moldboard plowing, (c) burning stubble after wheat harvest, (d) long-term crop rotations with winter wheat grown only once every 3 or 4 yrs, and (e) delayed seeding in fall so that seedbed preparation destroys emerged

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jointed goatgrass seedlings. Thus, control measures must prevent further increases of jointed goatgrass seed in the soil seed bank and must speed the loss of seed in soil.

Burning cereal fields is used occasionally to either eliminate cereal crop residues or decrease diseases that overwinter on residues. Burning fields after wheat harvest in August killed most jointed goatgrass seed in joints lying on the soil surface (Willis et al. 1988; Willis et al. 1989; Young et al. 1990). The potential of fire as a cheap management strategy for CRP acreage remains to be determined if this land is ever returned to production. Nevertheless, air pollution and safety concerns may limit widespread burning to control jointed goatgrass (Donald and Ogg 1991). Cultural practices are only partially effective for suppressing jointed goatgrass because dormant seed persist in soil and can later reinfest land.

Response to Herbicides and Other Chemicals

Because jointed goatgrass is genetically related to winter wheat, it is not surprising that there are no registered herbicides that selectively control it in winter wheat. Preemergence herbicides applied at commercial rates typically result in only 50 to 60% control (Dyer and Fay 1983). When soil applied herbicides were used before planting winter wheat, the type of planter influenced jointed goatgrass control (Westra 1988; Westra and D'Amato 1989). Drills with hoe openers move herbicide-treated soil away from the winter wheat row, allowing jointed goatgrass to emerge through untreated soil within the wheat row. Persistence of some soil applied herbicides (1 to 2 yrs) during the fallow period in arid western states limits rotational crop options after chemical fallow. Registered selective postemergence grass herbicides used in winter have not been

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effective in controlling jointed goatgrass either (Fandrich et al. 2000; Geier et al. 1998). Seed safeners have had limited success but none have proven effective in protecting winter wheat (Schirman 1978).

Herbicide-Resistant Winter Wheat

Herbicide-resistant crops facilitate the use of currently available postemergence herbicides that were lacking crop selectivity. Imidazolinone herbicides are used throughout the world because they control a broad spectrum of weeds at low use rates with low mammalian toxicity and environmental impact (Shaner et al. 1996). Imidazolinone-resistant crops including corn and canola have provided additional weed management options for producers (Harker et al. 2000; Sprague et al. 1997). More recently, wheat cultivars with resistance to imazamox have been developed (Newhouse et al. 1992). This technology should provide good selective control of jointed goatgrass in winter wheat; however, potential exists for introgression of the resistance genes from winter wheat into jointed goatgrass (Seefeldt et al. 1998; Snyder et al. 2000; Zemetra et al. 1998).

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CHAPTER 2

Integrated management systems for jointed goatgrass (*Aegilops cylindrica*) in the Central Great Plains

Abstract

Three related studies were conducted in eastern Colorado during four cropping seasons from 1996 to 2000 to evaluate the effects of combining multiple cultural practices on controlling jointed goatgrass (*Aegilops cylindrica*) in a winter wheat (*Triticum aestivum*)-fallow cropping system. Cultural practices included three wheat cultivars, two planting densities, three tillage systems, two planting dates, and two methods of nitrogen placement. Growth parameters were determined for winter wheat and jointed goatgrass, including plant height, reproductive tiller number, biomass, spikelet number, and seed mass, in addition to wheat grain yield, jointed goatgrass dockage, and jointed goatgrass soil seedbank. 'Akron' was the most competitive wheat cultivar against jointed goatgrass and possessed taller plant height and a more open-crown growth habit compared to 'Lamar' and 'TAM 107'. Increased planting density from 45 to 67 kg ha^{-1} decreased jointed goatgrass biomass 18% and increased wheat yield 12%, and reduced-tillage resulted in wheat yields 5 and 9% higher than conventional- and no-till systems,

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respectively. Delaying planting resulted in 40% lower wheat grain yield and an unexpected two-fold increase in jointed goatgrass growth. Winter wheat and jointed goatgrass growth were not significantly influenced by fertilizer placement methods.

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

Key words: Crop-weed competition, nitrogen placement, planting date, planting density, tillage system, winter wheat.

Jointed goatgrass (*Aegilops cylindrica*) is a winter annual grass weed that infests dryland winter wheat (*Triticum aestivum*)-fallow production areas of the western United States. Jointed goatgrass is troublesome because its germination, growth, and development is similar to winter wheat, which limits effective control methods (Donald and Ogg 1991). Selective herbicide control options are currently not available to effectively manage this weed, largely because tetraploid jointed goatgrass (CCDD) and hexaploid wheat (AABBDD) share a common D genome. Thus, producers must employ cultural practices to minimize jointed goatgrass interference (Anderson 1997).

Several cultural practices have been identified that negatively affect jointed goatgrass growth and reproduction in winter wheat. Wheat cultivars with tall plant height, early canopy closure, and more reproductive tillers are more competitive toward weeds (Challaiah et al. 1986; Ogg and Seefeldt 1999). Anderson (1997) reported that a tall

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wheat cultivar reduced jointed goatgrass spikelet production 42% more than a semidwarf wheat cultivar; however, the tall cultivar yielded 14% less on average. Competitiveness against jointed goatgrass remained high and wheat yield loss was diminished by increasing seeding rate and narrowing row spacing. These cultural practices have also been shown to reduce cheat (*Bromus secalinus*) production in winter wheat (Koscelny et al. 1991).

Tillage systems have continually been evaluated for their impact on crop production, weed management, and environmental quality. Conventional tillage operations such as tandem disking and moldboard plowing often bury weed seeds 10 and 25 cm deep, respectively. Morrow et al. (1982) showed that jointed goatgrass seedlings did not emerge from below 6 cm in laboratory studies even though germination occurred. Unfortunately, burial of weed seeds often extends their longevity (Donald and Zimdahl 1987) and repeated deep tillage operations return viable seeds to the surface thereby increasing the probability of subsequent crop infestations.

Reduced- and no-till systems, used for erosion control and soil moisture conservation, have created a more favorable environment for jointed goatgrass, and infestations have increased (Donald and Ogg 1991). This is likely due to the ability of jointed goatgrass to germinate on the soil surface (Donald and Ogg 1991) and enhanced seedling emergence rates, as high as 74% of the total seedbank, from shallow tillage operations (Anderson 1998), despite knowledge that seed remaining on the soil surface is subject to predation and decreased viability due to weathering (Baskin and Baskin 1988).

Delayed winter wheat planting has been effective at reducing downy brome (*Bromus tectorum*) (Anderson 1996; Wicks 1984), but detrimental consequences for this practice

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often include reduced grain yield (Musick and Winter 1994) and increased disease susceptibility (Cook and Veseth 1991). Fertilizer placement is another cultural practice that has proven effective in enhancing wheat competitiveness (Singh et al. 1976). In competition with jointed goatgrass, Mesbah and Miller (1999) found that placing nitrogen below the wheat seed in a deep band or injected with a spoke-wheel increased wheat yield 7 and 10%, respectively, over broadcast applications to the soil surface. Further, jointed goatgrass biomass was reduced 15 and 21% with deep band and spoke-wheel treatments.

Addition of an extra fallow yr or a summer crop into the winter wheat -fallow rotation lengthens time between wheat crops and favors natural decline of the soil seedbank (Daugovish et al. 1999). However, producers are hesitant to change from winter wheat - fallow because of possible summer crop failure. A limitation to crop rotation as a control strategy is survival of jointed goatgrass seeds for 3 to 5 yrs (Donald and Zimdahl 1987). Because winter wheat is the most profitable and consistent crop in this region, producers are reluctant to use rotations that do not include wheat for three or more yrs.

Producers may possibly increase the effect of cultural practices on weed management by combining several practices into one system (Holtzer et al. 1996). For example, in a two-yr study, Anderson (1997) combined three cultural practices (tall cultivar, high seeding rate, and nitrogen placement) and reduced seed production of jointed goatgrass 40% compared to conventional practices. The long-term effects of combining multiple cultural practices into integrated management systems for controlling jointed goatgrass are unknown. Therefore, the objective of this study was to compare combinations of five cultural practices (cultivar, planting density, tillage system, planting date, and nitrogen

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placement) within a winter wheat -fallow system during six cropping seasons. A full factorial of the five cultural practices was not feasible so they were divided into three studies. The first study combined cultivar, planting density, and tillage system; the second study combined cultivar and planting date; and the third study combined cultivar and nitrogen placement. This dissertation chapter presents data from the first four yrs of this ongoing study.

Materials and Methods

Site Description

Three studies were conducted during four cropping seasons from 1996 to 2000. The studies were established under dryland conditions on a Weld silt loam soil (fine, montmorillonitic, mesic Aridic Paleustoll) with 1.4% organic matter and pH 6.6. Monthly precipitation and the 92-yr average are listed in Table 2.1. Precipitation was measured at the USDA-ARS Research Station near Akron, CO, located 24 km NW of the study area. The studies were established on winter wheat stubble in an area that had been in a winter wheat -fallow rotation for several yrs and was naturally infested with jointed goatgrass. Plots were 9 by 15 m arranged in a randomized complete block design with four replications and every treatment was present in each yr.

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Cultivar, Planting Density, and Tillage System Study

Eighteen management systems were compared for their effect on jointed goatgrass growth and seed production. Management systems included combinations of three cultural practices: winter wheat cultivars, winter wheat planting densities, and tillage systems. Three locally adapted wheat cultivars were compared: 'Akron', a medium-tall cultivar with a more open-crown growth habit, 'Lamar' a tall cultivar, and 'TAM 107', a semidwarf cultivar (J. Quick, personal communication); two wheat planting densities: 45 and 67 kg ha^{-1}; and three tillage systems: conventional-till, reduced-till, and no-till. The conventional-till system consisted of sweep tillage after harvest, two or three sweep tillage operations during the fallow period as required to control weeds, and a tandem disk operation prior to planting to prepare the seedbed. The reduced-till system consisted of sweep tillage after harvest, 1.1 kg ha^{-1} glyphosate applied two or three times during the fallow period as required to control weeds, and a tandem disk operation prior to planting. The no-till system consisted of glyphosate applications after harvest and throughout the fallow period. All possible combinations of these systems were evaluated.

Cultivar and Planting Date Study

Six management systems were compared for their effect on jointed goatgrass growth and seed production. Treatments included: the three cultivars listed above planted at 45 kg ha^{-1}; and two planting dates (Table 2.2) that represented the average planting date for the region, September 15, and a delayed planting approximately 2 to 3 wk later to allow an additional cohort of jointed goatgrass to be controlled prior to planting.

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Cultivar and Nitrogen Placement Study

Six management systems were compared for their effect on jointed goatgrass growth and seed production. Treatments included: the three cultivars listed above planted at 45 kg ha^{-1}; and two methods of nitrogen placement. Nitrogen placement treatments consisted of broadcasting 56 kg ha^{-1} dry nitrogen fertilizer on the soil surface or injecting by spoke wheel 56 kg ha^{-1} aqueous nitrogen fertilizer 10 cm deep and 5 cm to the side of the wheat row in the spring after plants began actively growing.

Plant Establishment and Measurements

Table 2.2 lists the dates of winter wheat planting and data collection of wheat and jointed goatgrass growth parameters. In all three studies, winter wheat was planted in rows spaced 30 cm apart with a no-till drill. During study establishment, the natural jointed goatgrass population was augmented with jointed goatgrass cylinders applied broadcast and incorporated throughout the top 10 cm of soil with a tandem disk. Four soil cores, 5 cm diameter by 10 cm deep, were taken from random locations within each plot. Jointed goatgrass cylinders were elutriated from the soil cores using a high-pressure water bath system. An average of 0.4 jointed goatgrass spikelets was detected per soil core, equal to a baseline population of 462,000 spikelets ha^{-1} (46.2 m^{-2}). Prior to planting each yr, 56 kg ha^{-1} nitrogen and 22 kg ha^{-1} phosphorus were applied as liquid and incorporated within the top 5 cm with a tandem disk to prepare the seedbed. Broadleaf and grass weeds were controlled during the fallow period with sweep tillage and glyphosate applications as needed. Broadleaf weeds were controlled in winter wheat in the spring with 0.43 kg ha^{-1} metsulfuron + 0.14 kg ha^{-1} bromoxynil.

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Jointed goatgrass seedling densities were determined each fall prior to planting from five equidistantly spaced 1 m^2 quadrat sample locations along two transecting lines per plot (Figure 2.1). Jointed goatgrass seedlings were subsequently controlled with tillage or glyphosate prior to wheat planting. Jointed goatgrass and winter wheat seedling densities were determined from the same five 1-m^2 quadrat samples per plot each spring after plants began actively growing. One to five days prior to wheat harvest, two randomly placed 1-m^2 quadrat samples (Figure 2.1) were used to obtain winter wheat and jointed goatgrass height, reproductive tiller number, spikelet number, seeds per spike, seed weight, and naturally dried mature biomass. Wheat grain yield was determined by combine harvesting the center 3.6 by 9 m of each plot (Figure 2.1). Jointed goatgrass dockage per plot was determined from a sub-sample of the harvested grain. The remaining wheat was harvested and removed ensuring wheat chaff remained in each respective plot. Jointed goatgrass seedbank was determined each fall from four random soil cores per plot.

Statistical Analyses

All experiments were repeated over time. All data were subjected to ANOVA, tested for homogeneity of variance using Bartlett's test (Gomez and Gomez 1984), and means were separated using Fisher's protected LSD test ($P \leq 0.05$). Correlation coefficients were calculated between winter wheat yield and each jointed goatgrass growth attribute measured.

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Results and Discussion

Cultivar, Planting Density, and Tillage System Study

Cultivar. Mean number of jointed goatgrass reproductive tillers and winter wheat grain yields varied across yrs (Table 2.3). The study was established on winter wheat stubble resulting in low sub-surface moisture available for wheat growth the first yr. Consequently, wheat yields were much lower in 1997 than the following three yrs. Heterogeneity of error variance was detected across yrs so data could not be pooled; therefore, discussion will be limited to the 1997-1998 cropping season when winter wheat yielded the highest and most effectively competed against jointed goatgrass.

Adoption of new cultural practices for weed management by producers is often associated with large economic costs of retooling field equipment and the risk of yield loss if the new practice fails. Producers are familiar with selecting crop cultivars that perform well on their farm. Selecting a crop cultivar that is more competitive against weeds would eliminate retooling expenses; however, a weed-competitive cultivar must also return maximum net profit (Pester et al. 1999).

Cultivars in this study represent a range in plant height and growth habit. In 1998, these cultivars differed in yield but not in their ability to reduce jointed goatgrass growth when averaged over planting density and tillage system (Table 2.4). Lamar was the tallest cultivar but it was the lowest yielding. TAM 107 yielded 3 and 22% more than Akron and Lamar, respectively. Further, treatments including TAM 107 resulted in the lowest jointed goatgrass growth. These results do not agree with those reported by

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Anderson (1997), who identified Lamar as lower yielding than TAM 107, but more competitive with jointed goatgrass. Akron was selected for its medium-tall height and more open-crown growth habit, which have been identified as desirable traits for weed competitiveness (Challaiah et al., 1986). Interestingly, Akron performed similarly to TAM 107 and, in many individual treatments, was more effective at reducing jointed goatgrass reproductive tillers (Table 2.3). For example, when Akron was planted at 67 kg ha^{-1} in the reduced-till system it yielded higher than TAM 107 two out of four yrs and resulted in lower jointed goatgrass reproductive tillers every yr.

Winter wheat and jointed goatgrass compete for the same resources (Ogg and Seefeldt 1999). Thus, when growing in limited nutrients and moisture wheat yield should be negatively correlated with jointed goatgrass growth. Correlation coefficients were calculated between winter wheat yield and jointed goatgrass growth parameters. Results were similar for each jointed goatgrass parameter measured, so data presented is limited to biomass and number of reproductive tillers (Table 2.5). In 1998, Akron and Lamar wheat yields were strongly negatively correlated to jointed goatgrass growth in the no-till treatments. TAM 107 yield was less negatively correlated to jointed goatgrass growth in these treatments indicating that it was less competitive. Positive correlations may be the result of several factors. Wheat yield was determined from the center 3.6 by 9 m of each plot with a combine while jointed goatgrass parameters were determined from two 1-m^2 quadrat samples, resulting in larger variation. Spatial variation in jointed goatgrass population was observed within each plot and likely contributed to large variation in sampling data. In addition, if nutrients and moisture were non-limiting in isolated areas, competition between species would be minimal.

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Planting density. Increasing planting density from 45 to 67 kg ha^{-1} resulted in lower jointed goatgrass growth and reduced spikelets returned to the soil seedbank 45% in 1998 (Table 2.4). Winter wheat yield increased 15 %, averaged over cultivar and tillage system in 1998. Similar results have been found in wheat competition against jointed goatgrass (Anderson 1997) and cheat (*B. secalinas*) (Koscelny 1991). In the no-till system during 1998, negative correlation coefficients between wheat yield and jointed goatgrass biomass and reproductive tillers decreased with increased planting density (Table 2.5). This may be a function of increased wheat intra-specific competition at higher plant density.

Tillage system. In 1998, the reduced-till system supported the largest wheat growth and yield while resulting in the lowest jointed goatgrass production, averaged across cultivar and planting density (Table 2.4). Surprisingly, the no-till treatments yielded lower than either conventional- or reduced-till. Moisture is often limited in the Central Great Plains and research has shown that residue remaining on the surface helps increase stored soil moisture, reduce evapotranspiration, (Smika 1990) and minimize the probability of drought-induced crop failure (Peterson et al. 1993). Anderson (1998) reported that one shallow tillage operation effectively reduced a majority of the jointed goatgrass seedbank. The reduced-till system in this study employed a single sweep tillage operation after wheat harvest and subsequent control of jointed goatgrass cohorts with herbicide. The sweep plow, which consists of V-shaped blades that sever weed roots with minimal soil disturbance, is commonly used by wheat producers in the Great Plains because it only buries 10% of the residue with each operation (Good and Smika

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1978). Therefore, the reduced-till system provided good weed control and likely increased precipitation retention in the soil to enhance wheat yield.

In this study, the best combination of cultural practices that reduced jointed goatgrass growth while maintaining winter wheat yield was Akron planted at 67 kg ha^{-1} in the reduced-tillage system (Table 2.3). Although not statistically valid, Appendix Table A2.1 shows the main effect treatment means of data pooled across yrs. Many significant differences within treatments were masked by variation across yrs. However, Akron most effectively reduced jointed goatgrass growth parameters; increasing planting density increased wheat yield 12% and decreased jointed goatgrass biomass 18%; and reduced-tillage resulted in wheat yields 5 and 9% higher than conventional- and no-till systems, respectively.

Cultivar and Planting Date Study

Heterogeneity of error variance prevented these data from being pooled across yrs. Treatment means are provided for jointed goatgrass reproductive tillers and winter wheat grain yield during the four cropping seasons (Table 2.6). Winter wheat yields were highest in 1998, and again resulted in the lowest number of jointed goatgrass tillers produced. The study area received below average precipitation in July and August of 1998 and sub-soil moisture was extremely low. Winter wheat stands were about 75% in November 1998 and no jointed goatgrass had emerged (data not shown). Surprisingly, jointed goatgrass density was high in spring 1999 and the open wheat canopy provided a niche for a 10-fold increase in jointed goatgrass reproductive tillers compared to 1998 (Table 2.6).

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Jointed goatgrass emerges between late August and mid-November and between late February and early March (Anderson 1993), thus raising the question of whether spring emerging plants will flower and produce seed. Jointed goatgrass has a quantitative vernalization requirement for flowering, which means that cold temperatures hasten floral initiation but are not an absolute requirement (Donald 1984). Small plants overwintering as seedlings or vernalized as imbibed seed and germinating in the spring have adequate time to flower, mature, and shed seed prior to winter wheat harvest (Donald 1984).

Spring emergence and seed set resulted in a recharge of the jointed goatgrass soil seedbank in 1999 (Table 2.6). Stump and Westra (2000) reported similar results for feral rye (*Secale cereale*), another winter annual grass weed. Favorable environmental conditions during the final yr of their seed burial study permitted a dramatic increase in feral rye seed production, negating four yrs of incremental seedbank depletion.

Table 2.7 presents the main effect treatment means for the cultivar and planting date study in 1998. Jointed goatgrass growth was similar for all three wheat cultivars. We expected a decrease in jointed goatgrass growth in the delayed wheat planting treatments due to removal of an additional cohort in the fall. In contrast, delaying planting resulted in more than a two-fold increase in jointed goatgrass growth and 40% lower wheat grain yield. Producers should be cautious about delayed planting for jointed goatgrass control because planting winter wheat outside of its optimum period can be detrimental. For example, Musick and Winter (1994) found that grain yield was reduced 4 to 8% for each week delay after the optimum period.

Few negative correlations were detected between wheat grain yield and jointed goatgrass biomass and reproductive tillers among cultivar and planting date treatments

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within each yr (Table 2.8). However, pooled data identified negative correlations for all three wheat cultivars planted during the optimal period, indicating increased competitiveness against jointed goatgrass compared to delayed planting.

Cultivar and Nitrogen Placement Study

Bartlett's tests detected heterogeneity of error variance and prevented pooling these data across yrs. Means for the cultivar and nitrogen placement treatments are listed in Table 2.9. Similar trends in wheat yield and reduced jointed goatgrass production occurred in 1998 as described above in the other studies. Averaged across nitrogen placement treatments, jointed goatgrass spikelet production was 46 and 60% higher when competing with Lamar than with Akron and TAM 107 wheat cultivars, respectively (Table 2.10).

Winter wheat biomass, tillers, and yield were not significantly influenced by fertilizer placement methods, although data trends indicated sub-surface treatments enhanced wheat growth (Tables 2.9 and 2.10). In a similar study, Mesbah and Miller (1999) reported that sub-surface nitrogen applications reduced jointed goatgrass biomass, number of spikes plant^{-1}, and joints spike^{-1} compared to broadcast applications; however, jointed goatgrass population was not influenced. In contrast, we found that sub-surface nitrogen placement tended to increase jointed goatgrass height, reproductive tillers, cylinders, and biomass; although variation in the data masked significant differences (Tables 2.10 and A2.3).

TAM 107 grain yield was negatively correlated to jointed goatgrass biomass and reproductive tillers in most yrs (Table 2.11). Akron was negatively correlated to jointed

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goatgrass growth, but only in the sub-surface treatments during the last three yrs. Thus, Akron gained a competitive advantage from sub-surface nitrogen applications.

Management Implications

During the past four yrs, environmental conditions fluctuated resulting in winter wheat yield variation. Adequate soil moisture in the fall is required for good winter wheat establishment. Uniform crop stands allow winter wheat to compete with jointed goatgrass and reduce its emergence and growth. For example, favorable growing conditions during 1997-1998 contributed to uniform winter wheat emergence in the fall and aggressive growth during the following spring and summer. Consequently, jointed goatgrass plant populations and seed production were the lowest among the three yrs of this study.

Early growth, plant vigor, and plant height facilitate light interception, and thus, enhanced winter wheat competition against winter annual grass weeds (Challaiah et al. 1986). Akron winter wheat was typically more competitive against jointed goatgrass than either Lamar or TAM 107. Further, Akron possesses a more open-crown growth habit, and is often 4 to 5 cm taller that the other two cultivars in this study. These traits appear to be effective in reducing jointed goatgrass production with no significant cost in wheat yield.

Increasing winter wheat competitiveness against weeds may be achieved through plant breeding efforts if selections are made from breeding materials growing in competition with weeds (Callaway 1992; Ogg and Seefeldt 1999; Pester et al. 1999). Due to large variability, significant differences between cultivar means were seldom

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detected within the other cultural treatments from tests conducted at $P<0.05$; however, many more significant differences would have been detected at $P<0.20$ (data not shown). Plant breeders seldom make selections for quantitative traits, such as yield, based on $P<0.05$ (Orf 1995); therefore, P values greater than 0.05 should be used when selecting for increased weed competitiveness.

Integrated weed management involves numerous optional control components, such as cultural, mechanical, biological, and chemical practices. Individual components may provide only partial control on their own, but combining several components may achieve effective control. Rotating to spring planted crops provides additional management opportunities (tillage and herbicide) to control jointed goatgrass throughout the growing season but, as mentioned earlier, many producers are reluctant to assume the economic risks associated with cropping system changes. Consequently, alternative jointed goatgrass management practices need to be developed for the winter wheat - fallow system.

These three studies have identified several cultural practices that may be combined to achieve acceptable jointed goatgrass control. They include a competitive cultivar, such as Akron, increased planting density, reduced- or minimum-tillage, optimal planting date, and sub-surface fertilizer placement. Future research should evaluate combining all five of these factors into a single management system, and subsequent comparison of this system to other conventional production practices.

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Table 2.1. Precipitation during the four cropping seasons and the 92-yr average at Akron, CO.

Month	Cropping season				
	1996-1997	1997-1998	1998-1999	1999-2000	92-yr average
	cm				
August	7.5	8.8	6.2	16.4	5.3
September	8.7	2.7	0.9	4.0	3.1
October	1.0	6.1	2.4	1.1	2.3
November	0.1	0.7	2.1	1.2	1.4
December	0.0	1.1	0.6	1.4	1.0
January	1.3	0.1	0.2	0.6	0.8
February	1.3	3.2	0.4	0.8	0.9
March	0.2	0.4	0.7	5.7	2.1
April	2.4	2.0	5.7	3.0	4.2
May	5.7	2.5	5.5	1.9	7.6
June	7.9	0.9	8.7	1.9	6.3
July	2.9	9.8	6.9	6.8	6.9
Total	38.8	38.2	40.3	44.9	42.0

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Table 2.2. Time of planting and data collection for winter wheat and jointed goatgrass during four cropping seasons at Platner, CO.

	Cropping season			
	1996-1997	1997-1998	1998-1999	1999-2000
Jointed goatgrass seedling density removed prior to planting	——	Sep. 08, 1997	Sep. 14, 1998	Sep. 14, 1999
Wheat planting date				
Average	Oct. 09, 1996	Sep. 18, 1997	Sep. 18, 1998	Sep. 24, 1999
Delayed	Oct. 16, 1996	Oct. 09, 1997	Oct. 09, 1998	Oct. 07, 1999
Jointed goatgrass soil seedbank, determined with soil cores	Oct. 30, 1996	Nov. 05, 1997	Oct. 30, 1998	Oct. 26, 1999
Nitrogen placement treatments	Apr. 07, 1997	Apr. 13, 1998	Apr. 01, 1999	Apr. 10, 2000
Jointed goatgrass and wheat seedling density	May 15, 1997	May 18, 1998	May 12, 1999	Apr. 14, 2000
Jointed goatgrass and wheat growth attributes at maturity	July 07, 1997	July 13, 1998	June 30, 1999	June 29, 2000
Wheat harvest	July 11, 1997	July 18, 1998	July 20, 1999	July 01, 2000

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Table 2.3. Mean jointed goatgrass reproductive tillers and winter wheat grain yields for different tillage systems, planting densities, and cultivars during four yrs at Platner, CO.

Treatments			Jointed goatgrass reproductive tillers				Winter wheat grain yield			
	Winter wheat									
Tillage system	Planting density	Cultivar	1997	1998	1999	2000	1997	1998	1999	2000
	kg ha^{-1}		no. m^{-2}				kg ha^{-1}			
Conventional	45	Akron	110	88	405	121	267	2060	1218	1341
		Lamar	103	17	515	76	470	2011	1286	903
		TAM 107	96	31	492	104	230	2099	1352	1427
	67	Akron	74	28	270	65	355	2345	1368	1605
		Lamar	90	32	347	63	488	2546	1446	1204
		TAM 107	132	32	464	71	578	2430	1799	1382
Reduced	45	Akron	92	30	306	64	147	2421	1228	1688
		Lamar	114	70	481	92	365	1809	1217	1033
		TAM 107	131	58	301	171	386	2480	1246	1699
	67	Akron	134	10	378	111	479	2918	1373	1652
		Lamar	139	31	594	58	516	2146	1375	1081
		TAM 107	156	30	401	117	373	2829	1719	1823
No-till	45	Akron	107	78	272	70	348	1958	1746	1204
		Lamar	135	119	500	350	601	1140	2199	608
		TAM 107	122	78	263	192	406	1523	2176	1241
	67	Akron	77	57	246	241	199	1761	1523	1268
		Lamar	87	84	283	143	541	1125	2366	703
		TAM 107	94	32	235	142	368	2458	2098	1267

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Table 2.4. Main effect treatment means of jointed goatgrass and winter wheat production for different cultivars, planting densities, and tillage systems in 1998 at Platner, CO.

Treatments		Jointed goatgrass				Winter wheat			
		Seedlings	Biomass	Tillers	Spikelets	Biomass	Tillers	Spikelets	Yield
		no. m^{-2}	g m^{-2}	no. m^{-2}	no. m^{-2}	g m^{-2}	no. m^{-2}	no. $tiller^{-1}$	kg ha^{-1}
Cultivar	Akron	18	11	48	386	549	309	15.5	2244
	Lamar	18	13	59	442	500	297	16.3	1796
	TAM 107	16	12	43	343	561	327	13.5	2303
	LSD (0.05)	NS	NS	NS	NS	NS	NS	0.5	488
Planting density	45 kg ha^{-1}	18	15	63	502	488	285	15.3	1945
	67 kg ha^{-1}	17	9	37	278	585	337	14.9	2284
	LSD (0.05)	NS	4	19	156	73	33	0.4	NS
Tillage system	Conventional	17	9	37	293	551	324	15.3	2249
	Reduced	17	9	38	284	627	349	15.0	2434
	No-till	19	18	75	593	433	260	14.9	1661
	LSD (0.05)	NS	5	23	191	89	41	NS	488

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Table 2.5. **Correlation coefficients of winter wheat grain yield with jointed goatgrass biomass and reproductive tillers for different tillage systems, planting densities, and cultivars during four yrs at Platner, CO.**

Treatments			Jointed goatgrass biomass					Jointed goatgrass reproductive tillers				
	Winter wheat											
Tillage system	Planting density	Cultivar	1997	1998	1999	2000	Pooled[a]	1997	1998	1999	2000	Pooled
	kg ha^{-1}											
Conventional	45	Akron	.53	-.77	.20	-.28	-.16	.71	-.74	.44	-.30	-.10
		Lamar	.22	-.72	.48	-.51	.04	-.12	-.92	.63	-.46	.00
		TAM 107	-.03	-.67	.29	.53	.00	-.25	-.29	.43	.56	.03
	67	Akron	.61	.40	.41	.87	-.13	.49	.99	.94	.72	.00
		Lamar	.13	.51	.64	.88	.04	-.71	.61	.63	.89	.02
		TAM 107	.92	-.53	.63	-.39	.06	.97	-.46	.43	-.50	.04
Reduced	45	Akron	.50	.44	.85	-.86	-.20	.53	-.52	.44	-.87	-.24
		Lamar	.99	-.53	.29	.86	.03	.99	-.67	.64	.96	.09
		TAM 107	.91	-.80	-.22	.31	-.41	.85	-.87	-.49	.22	-.30
	67	Akron	.74	.38	.90	.89	-.23	.77	.61	.92	-.11	-.23
		Lamar	-.86	-.05	.57	-.60	.05	-.93	-.07	.64	-.72	.02
		TAM 107	-.34	.70	-.95	.63	-.33	-.16	.51	-.90	.03	-.26
No-till	45	Akron	.99	-.85	.36	.56	.05	.99	-.99	.70	.63	.14
		Lamar	.12	-.90	-.68	-.63	.56	.26	-.99	-.62	-.47	.26
		TAM 107	-.99	-.58	.38	.11	.27	-.99	-.30	.34	.13	.27
	67	Akron	.99	-.62	.42	.92	.32	.97	-.51	.31	.93	.37
		Lamar	.81	-.41	.51	.99	.76	.08	-.01	.47	.98	.67
		TAM 107	.03	.69	-.83	.18	-.05	.13	.64	-.66	.23	-.05

[a]Correlation coefficients for data pooled across all four yrs.

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Table 2.6. Mean jointed goatgrass reproductive tillers and winter wheat grain yields for different planting dates and cultivars during four yrs at Platner, CO.

Treatments		Jointed goatgrass reproductive tillers				Winter wheat grain yield			
Winter wheat									
Planting date	Cultivar	1997	1998	1999	2000	1997	1998	1999	2000
		no. m^{-2}				kg ha^{-1}			
Average	Akron	112	38	417	75	232	2219	1198	1346
	Lamar	120	40	542	99	222	2409	1188	1099
	TAM 107	143	31	353	71	192	2059	1172	1160
Delayed	Akron	135	92	421	40	233	1344	1490	1426
	Lamar	68	87	267	40	188	1202	1115	1120
	TAM 107	91	75	393	30	311	1473	1141	1602

Table 2.7. Main effect treatment means of jointed goatgrass and winter wheat production for different planting dates and cultivars in 1998 at Platner, CO.

Treatments		Jointed goatgrass				Winter wheat			
		Seedlings	Biomass	Tillers	Spikelets	Biomass	Tillers	Spikelets	Yield
		no. m^{-2}	g m^{-2}	no. m^{-2}	no. m^{-2}	g m^{-2}	no. m^{-2}	no. tiller^{-1}	kg ha^{-1}
Cultivar	Akron	14	18	65	549	524	283	16.5	1782
	Lamar	14	18	64	517	535	323	17.5	1805
	TAM 107	14	18	53	451	478	259	15.4	1766
	LSD (0.05)	NS	NS	NS	NS	NS	45	1.4	NS
Planting date	Average	14	11	36	289	574	329	16.9	2229
	Delayed	14	25	85	723	450	247	16.0	1340
	LSD (0.05)	NS	2	14	91	101	36	NS	423

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Table 2.8. Correlation coefficients of winter wheat grain yield with jointed goatgrass biomass and reproductive tillers for different planting dates and cultivars during four yrs at Platner, CO.

Treatments		Jointed goatgrass biomass					Jointed goatgrass reproductive tillers				
Winter wheat											
Planting date	Cultivar	1997	1998	1999	2000	Pooled[a]	1997	1998	1999	2000	Pooled
Average	Akron	.93	.19	.78	.76	-.11	.94	-.10	.88	.77	-.14
	Lamar	.81	-.58	-.47	.36	-.10	.82	.43	-.53	.35	-.12
	TAM 107	.81	.52	.49	.47	-.14	.83	.68	-.13	.20	-.23
Delayed	Akron	.58	.45	.89	.97	.31	.40	.40	.60	.99	.30
	Lamar	-.92	.41	.82	.93	.21	-.81	.34	.89	.94	.28
	TAM 107	-.77	.88	.05	.88	-.05	-.94	.57	-.45	.88	-.05

[a]Correlation coefficients for data pooled across all four yrs.

Table 2.9. Mean jointed goatgrass reproductive tillers and winter wheat grain yields for different nitrogen placements and cultivars during four yrs at Platner, CO.

Treatments		Jointed goatgrass reproductive tillers				Winter wheat grain yield			
Nitrogen placement	Cultivar	1997	1998	1999	2000	1997	1998	1999	2000
		no. m^{-2}				kg ha^{-1}			
Broadcast	Akron	70	25	215	62	50	2259	2200	1092
	Lamar	54	18	262	58	32	2168	1859	583
	TAM 107	73	14	285	45	67	1862	2000	978
Sub-surface	Akron	64	19	391	82	66	2441	1907	1198
	Lamar	61	48	273	191	62	2250	1785	1047
	TAM 107	89	16	277	102	120	2231	1896	1350

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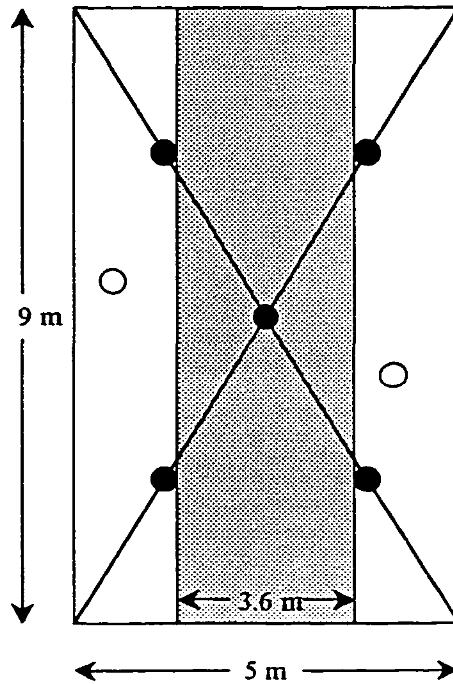
Table 2.10. Main effect treatment means of jointed goatgrass and winter wheat production for different cultivars and nitrogen placements in 1998 at Platner, CO.

Treatments		Jointed goatgrass				Winter wheat			
		Seedlings	Biomass	Tillers	Spikelets	Biomass	Tillers	Spikelets	Yield
		no. m^{-2}	g m^{-2}	no. m^{-2}	no. m^{-2}	g m^{-2}	no. m^{-2}	no. $tiller^{-1}$	kg ha^{-1}
Cultivar	Akron	12	6	22	138	596	300	17.6	2350
	Lamar	11	11	33	257	552	268	17.9	2209
	TAM 107	12	5	15	103	515	282	14.3	2046
	LSD (0.05)	NS	5	16	134	NS	NS	0.7	NS
Nitrogen placement	Broadcast	11	6	19	136	527	282	17.0	2096
	Sub-surface	12	9	28	197	581	284	16.2	2307
	LSD (0.05)	NS	NS	NS	NS	NS	NS	0.5	NS

Table 2.11. Correlation coefficients of winter wheat grain yield with jointed goatgrass biomass and reproductive tillers for different nitrogen placements and cultivars during four yrs at Platner, CO.

Treatments		Jointed goatgrass biomass					Jointed goatgrass reproductive tillers				
Nitrogen placement	Cultivar	1997	1998	1999	2000	Pooled[a]	1997	1998	1999	2000	Pooled
Broadcast	Akron	.54	.55	.09	.73	.29	.56	.64	.00	.99	.31
	Lamar	.99	.73	-.66	.82	.28	.99	.91	-.73	.75	.23
	TAM 107	-.09	-.15	-.65	-.69	.37	-.44	.01	-.71	-.22	.30
Sub-surface	Akron	.44	-.91	-.68	-.72	.11	.39	-.91	-.58	-.83	.09
	Lamar	.97	.35	-.21	.13	.20	.94	.31	.20	.19	.19
	TAM 107	-.29	-.58	.76	.61	.22	-.26	-.26	-.25	.78	.13

[a]Correlation coefficients for data pooled across all four yrs.



● Five equidistantly spaced 1 m^2 quadrat sample locations along two transecting lines per plot.

○ Two randomly located 1 m^2 quadrat samples outside the center 3.6 m by 9 m harvested for grain yield.

Figure 2.1. Individual plot sampling methods for jointed goatgrass and wheat seedling densities and growth parameters.

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CHAPTER 3

Absorption, translocation, and metabolism of imazamox in jointed goatgrass (*Aegilops cylindrica*) and feral rye (*Secale cereale*).

Abstract

Wheat (*Triticum aestivum*) cultivars resistant to imazamox are being developed. These new cultivars will facilitate selective chemical control of many winter annual grass weeds including jointed goatgrass (*Aegilops cylindrica*), downy brome (*Bromus tectorum*), and feral rye (*Secale cereale*). These three weed species respond differently to imazamox postemergence treatments with feral rye demonstrating more tolerance than jointed goatgrass or downy brome; therefore, growth chamber studies were conducted to evaluate imazamox absorption in all three weed species and translocation and metabolism in jointed goatgrass and feral rye. Adding nonionic surfactant (NIS) or methylated seed oil (MSO) increased absorption in jointed goatgrass and feral rye but not downy brome, compared to imazamox applied alone. Imazamox + NIS + urea ammonium nitrate (UAN) resulted in the highest absorption in each species, 97, 91, and 92% of applied ^{14}C for jointed goatgrass, downy brome, and feral rye, respectively at 48 h after treatment (HAT). Imazamox translocation from the treated leaf was similar for jointed goatgrass and feral rye across harvest intervals. Shoot tissues of jointed goatgrass and feral rye

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accumulated 17 and 14% of applied ^{14}C by 96 HAT, respectively. Differential translocation of imazamox into root tissue was observed by 12 HAT, with 20% of applied ^{14}C translocated to jointed goatgrass roots by 96 HAT compared to 27% for feral rye. Imazamox is readily metabolized in both weed species. At 96 HAT, metabolism in the treated leaves of jointed goatgrass and feral rye reached 73 and 88% of applied ^{14}C, respectively. Metabolism was consistently higher in feral rye than jointed goatgrass in each plant part 96 HAT. When determined on a whole plant basis, metabolism was 25% greater in feral rye than jointed goatgrass. The differential control of jointed goatgrass and feral rye with foliar applications of imazamox was attributed to differences in translocation and metabolism.

Nomenclature: Imazamox; *Aegilops cylindrica* L. AEGCY, jointed goatgrass; B*romus tectorum* L. BROTE, downy brome; *Secale cereale* L. SECCE, feral rye; *Triticum aestivum* L. wheat.

Key words: herbicide-resistant crop, imidazolinone, winter annual grass weed management, winter wheat.

Cropping systems in the Central Great Plains and the Pacific Northwest have predominately relied on winter wheat (*Triticum aestivum*)-fallow rotations. These rotations have selected for several winter annual grass weed species including jointed goatgrass (*Aegilops cylindrica*), downy brome (*Bromus tectorum*), and feral rye (*Secale*

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cereale) (Anderson 1998; Blackshaw and Hamman 1998; Donald and Ogg 1991; Pester et al. 2000; Stump and Westra 2000). Selective control of these weeds in the winter wheat crop has been difficult because they all have winter annual growth habits. New sulfonylurea herbicides are labeled for selective control of downy brome but they do not provide adequate control of jointed goatgrass or feral rye (Fandrich et al. 2000; Geier et al. 1998; Olson et al. 1999); therefore, producers have relied on alternative management methods. Cultural practices including competitive crop cultivars (Challaiah 1986; Ogg and Seefeldt 1999), increased crop density (Koscelny et al. 1991), and fertilizer placement (Mesbah and Miller 1999) provide some weed suppression, but control is erratic (Anderson 1998). Extended crop rotations that include summer annual crops or increase the fallow period provide additional opportunities for weed management (Daugovish et al. 1999), but these cropping systems are often less profitable, particularly in yrs when precipitation is low (Anderson 1998).

Herbicide-resistant crops facilitate the use of currently available postemergence herbicides that were lacking crop selectivity. Imidazolinone herbicides are used throughout the world because they control a broad spectrum of weeds at low use rates with low mammalian toxicity and environmental impact (Shaner et al. 1996). Imidazolinone-resistant crops including corn and canola have provided additional weed management options for producers (Harker et al. 2000; Sprague et al. 1997). More recently, wheat cultivars with resistance to imazamox have been developed (Newhouse et al. 1992).

Imazamox is an imidazolinone herbicide that controls many grass and broadleaf weeds (Blackshaw 1998; Nelson and Renner 1998) including several winter annual grass

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species (Ball et al. 1999). In Colorado, preliminary field studies indicated that jointed goatgrass, downy brome, and feral rye respond differently to imazamox. Jointed goatgrass appears to be the most susceptible, downy brome control is intermediate, and feral rye is the most tolerant. Spring treatments controlled jointed goatgrass, downy brome, and feral rye 98, 95, and 60%, respectively (Table A3.1). Feral rye was adequately controlled if treatments were applied prior to tillering. Treatments applied in early fall (1-5 leaf), late fall (1-5 tiller), or spring provided 97, 95, and 95% control of jointed goatgrass, respectively, compared to 96, 57, and 45% control of feral rye (Table A3.2).

Differences in absorption, translocation, and metabolism could be involved in the differential response of these grasses to imazamox. Adjuvants and nitrogen can increase absorption of many foliar applied herbicides (Foy 1993; Kirkwood 1993). Miller et al. (1999) reported that adding urea ammonium nitrate (UAN) increased sulfosulfuron + nonionic surfactant (NIS) absorption in jointed goatgrass and downy brome 27 and 54%, respectively. Once absorbed, herbicide translocation can be affected by many factors including plant growth stage, photosynthetic rate, phloem mobility, and sink strength (Little and Shaner 1991). Olson et al. (1999) found that temperature affected sulfosulfuron translocation in jointed goatgrass, downy brome, and wild oat (*Avena fatua*). Chao et al. (1997) reported that presence of early tillers in wild oat affected imazamethabenz translocation pattern but not efficacy. Differential metabolism is the primary mechanism for imidazolinone selectivity (Shaner and Mallipudi 1991). For example, imazaquin is metabolized more slowly in susceptible common cocklebur (*Xanthium strumarium*) compared to more tolerant velvetleaf (*Abutilon theophrasti*)

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(Shaner and Robson 1985). There is no information available on the behavior of imazamox in winter annual grass weeds; therefore, growth chamber studies were initiated to characterize imazamox absorption in jointed goatgrass, downy brome, and feral rye, and imazamox translocation and metabolism in jointed goatgrass and feral rye.

Materials and Methods

Plant Material

Jointed goatgrass, downy brome, and feral rye seeds were pre-germinated at 25 C in petri dishes and planted in 6.5-cm-diam by 25-cm-long cones[1] filled with an organic potting mix[2] for the absorption studies or washed silica sand[3] for the translocation and metabolism studies. Downy brome seeds were started 5 d before jointed goatgrass and feral rye, which provided uniform growth stages for all three species. Plants were grown in a growth chamber[4] (16 h photoperiod , 22/18 C day/night, PPF of 400 µmol m^{-2} s^{-1}), and watered daily with 15 ml half-strength Hoagland's solution (Hoagland and Arnon 1938). Plants were allowed to grow for approximately 2 wk until the 3 leaf stage.

Absorption

The second, fully expanded, leaf of each plant was covered with aluminum foil and plants were oversprayed with an overhead track sprayer. Treatment solutions consisted of commercially formulated imazamox at a rate equivalent to 45 g ha^{-1} in an application volume of 125 L ha^{-1}. Four treatments included: imazamox applied alone; imazamox +

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1% methylated seed oil (MSO)[5](v/v); imazamox + 0.25% NIS[6](v/v); and imazamox + NIS + 1% 28% UAN (v/v). Following herbicide application, the aluminum foil was removed and the protected leaf on each plant was treated with four 0.5 μl droplets of radiolabeled imazamox (200 Bq leaf^{-1} ^{14}C-imazamox, specific activity 4,292 MBq mg^{-1}). Treatments were applied to the adaxial leaf surface, two droplets on each side of the midrib. Radiolabeled treatment solutions were prepared from technical grade ^{14}C imazamox, commercial grade imazamox, distilled water, and adjuvants. Following treatment, plants were immediately returned to the growth chamber until harvest.

Plants harvest intervals were 24 and 48 hr after treatment (HAT). Treated leaves were excised and vortexed for 30 s in a 5-ml wash solution containing 10% methanol and 0.25% NIS (v/v). Leaves were removed from the wash, and 15 ml of liquid scintillation cocktail[7] were added to each vial. Radioactivity of the leaf wash solution was determined by liquid scintillation spectroscopy[8] (LSS) and used to estimate herbicide absorption. Four leaves of each species were treated and immediately washed to determine the amount of radioactivity applied to each leaf. Percent absorption was determined by the difference between the amount of radioactivity applied and the amount recovered in the leaf wash.

Glass cover slips were used to determine ^{14}C volatilization. Cover slips were spotted with radiolabeled imazamox solutions as described for the treated leaves, placed in petri dishes near the plants in the growth chamber, collected at each respective plant harvest, and washed. Radioactivity was determined by LSS.

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Translocation and Metabolism

Jointed goatgrass and feral rye were selected for this experiment because they represented the largest differential response among the three weed species in preliminary field studies (Tables A3.1 and A3.2). Imazamox + NIS + UAN treatment solutions were prepared and applied as described for the absorption experiment. Total radioactivity applied to each leaf was 5 MBq.

Plant harvest intervals were 3, 6, 12, 24, 48, and 96 HAT. At harvest, each plant was divided into treated leaf, remaining shoot, and root. Treated leaves were washed as described for the absorption experiment to remove non-absorbed ^{14}C. Roots were rinsed in glass jars containing 100 ml distilled water to remove sand, and blotted dry on paper hand towels to remove excess water. All harvested plant tissues were frozen in liquid nitrogen and stored at –20 C until analysis.

Total radioactivity translocated to the roots was determined as the combination of radioactivity from root tissue, sand rooting media wash, and root leachate. Silica sand from each cone was placed in a glass jar containing the respective root rinse. Samples were shaken for 30 min, allowed to stand for 1 hr to settle particulate, and 5 ml subsamples of supernatant were used to determine radioactivity by LSS. Leachate resulting from daily watering between time of treatment and 24, 48, and 96 h harvests was collected from each cone and used to determine root release of radioactivity by LSS.

Imazamox and metabolites were extracted from the treated leaf by grinding samples for 90 s in a 15-ml solution containing 95% methanol (v/v) using a tissue homogenizer[9]. Tissue samples were shaken for 1 h followed by 15 min centrifugation at 10,000 rpm, and supernatant subsamples (100 µl) were analyzed for radioactivity by LSS. Remaining

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supernatant was reduced to 2 ml under vacuum followed by 15 min centrifugation at 5,000 rpm, and a 10 μl subsample was taken to measure total radioactivity using LSS. Subsamples (300 μl) were fractionated by C_{18}[10] HPLC[11] coupled with in-line ^{14}C detection[12]. The solvents were (A) 72% water:25% methanol:2% tetrahydrofuran:1% acetic acid (v/v), and (B) 47% water:50% methanol:2% tetrahydrofuran:1% acetic acid (v/v). The compounds were fractionated with a binary gradient of 10% min^{-1} from 0% B to 100% B, with an 18 min total run time.

Data Analyses

Experiments were arranged in a randomized complete block design with replications as blocks. The absorption experiments had four replications and the translocation and metabolism experiments had five replications. Bartlett's tests for homogeneity of variance indicated that data from replicated experiments could be pooled. Mean values for absorption data were compared using Fisher's protected LSD ($P \leq 0.05$). Means and standard errors are presented for translocation and metabolism data with regressions calculated from raw data.

Results and Discussion

Absorption

Imazamox absorption, when applied without surfactant or nitrogen, was lowest for all three weed species (Table 3.1). Downy brome absorbed 16 and 34% more imazamox

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than jointed goatgrass or feral rye, respectively, when applied without adjuvants (48 HAT); however, adding MSO or NIS without nitrogen did not increase absorption in downy brome above the amount absorbed when imazamox was applied alone. Imazamox + NIS increased imazamox absorption in jointed goatgrass and feral rye 30 and 42%, respectively, 48 HAT. Imazamox + MSO increased feral rye absorption compared to imazamox + NIS at 48 HAT, but did not increase absorption in jointed goatgrass or downy brome. Absorption was greater than 90% in each species with imazamox + NIS + UAN. In a similar study, Miller et al. (1999) found that adding nitrogen to NIS significantly increased sulfosulfuron absorption in jointed goatgrass and downy brome. Analysis of cover slip wash solutions detected minimal loss of ^{14}C-imazamox due to volatilization.

Translocation and Metabolism

The treatment combination of imazamox + NIS + UAN was used for the translocation and metabolism study. Recovery of applied ^{14}C-imazamox ranged from 80 to 94% for both weed species at all harvest times. Imazamox absorption continued throughout the translocation and metabolism experiment; however, > 60% of the ^{14}C was absorbed by 3 HAT with maximum absorption by 12 HAT for both jointed goatgrass and feral rye (Figure 3.1). Jointed goatgrass consistently absorbed approximately 10% more imazamox than feral rye between 24 and 96 HAT, but this amount is likely not large enough to explain the differential response.

Imazamox translocation from the treated leaf was similar for jointed goatgrass and feral rye across harvest intervals (Figure 3.2). Radioactivity in the treated leaf of jointed

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goatgrass and feral rye reached a maximum of 54 and 46% of applied, 12 HAT, respectively. By 96 HAT, radioactivity in the treated leaf was reduced to 26 and 24% for jointed goatgrass and feral rye, respectively. Translocation of radioactivity into the untreated shoot tissue was slightly greater in jointed goatgrass than in feral rye with 17 and 14% of the applied ^{14}C detected by 96 HAT, respectively. Accumulation of radioactivity in roots was greater in feral rye than jointed goatgrass. Twenty-seven percent of the applied ^{14}C was recovered in the roots of feral rye, while 20% was detected in jointed goatgrass at 96 HAT. Radioactivity was detected in sand rooting media 3 HAT in jointed goatgrass and 6 HAT in feral rye (data not shown). By 96 HAT, 11% of the applied ^{14}C was detected in jointed goatgrass leachate and sand wash and 22% was detected in feral rye leachate and sand wash (Figure 3.2). These differences in retention may partially explain the differential control observed with jointed goatgrass and feral rye. Feral rye exuded twice the amount of radiolabel into the sand media compared to jointed goatgrass, making it less readily available for biological activity in the plant; however, exuded imazamox may be available for root absorption by other plants. Environmental conditions also can affect herbicide translocation. Olson et al. (1999) found that jointed goatgrass translocated more sulfosulfuron than downy brome at 25/23 C (day/night) temperatures and visa versa at 15/13 C, and both species translocated more herbicide as soil moisture increased from one-third to full field capacity.

Imazamox was readily metabolized in both weed species. Imazamox and its associated metabolites were successfully separated from tissue samples and similar metabolite profiles were produced in each species; however, no attempt was made to identify metabolites. Differential metabolism in the treated leaf became apparent at 24

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HAT with 38 and 52% of the radioactivity identified as metabolites in jointed goatgrass and feral rye, respectively (Figure 3.3). Metabolism in the treated leaf of jointed goatgrass reached 73% of applied radiolabel compared to 88% for feral rye, 96 HAT.

Imazamox metabolism in feral rye shoot and root tissues increased linearly over time reaching a maximum of 69 and 72%, respectively, by 96 HAT (Figure 3.3). In jointed goatgrass, metabolism remained at approximately 30% across harvest intervals so a regression line could not be fit to these data. In root tissue, the fitted regression lines for metabolism indicate an interaction between species and time; however, significant differences were not detected between jointed goatgrass and feral rye until 96 HAT (Figure 3.3). Differences in metabolism between jointed goatgrass and feral rye shoots and roots were most pronounced after 48 h. Imazamox recovered from feral rye shoots was less than half the amount recovered from jointed goatgrass shoots at 96 HAT and 22% more metabolites were detected in feral rye roots than jointed goatgrass roots.

Plant tolerance to imidazolinone and sulfonylurea herbicides is usually due to enhanced metabolism in the tolerant species relative to the susceptible species (Shaner and Mallipudi 1991). Both primisulfuron and nicosulfuron have half-lives < 4 h in tolerant corn (*Zea mays*) (Hinz and Owen 1996). Woolly cupgrass (*Eriochloa villosa*) is controlled by nicosulfuron but not by primisulfuron and the corresponding half-lives for these two herbicides are >72 h and <4 h, respectively (Hinz and Owen 1996). Biological half-lives for imazamox in jointed goatgrass and feral rye were determined on a whole plant basis and can be estimated from the fitted curves for both species (Figure 3.4). Fifty percent of imazamox was metabolized within 42 h in feral rye and 84 h in jointed goatgrass.

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The differential response of jointed goatgrass and feral rye to foliar applications of imazamox can be attributed to differences in both translocation and metabolism. Feral rye translocated more imazamox to the root tissue and exuded a large proportion of the radiolabel into the sand media. Differential metabolism may be an explanation for the lower activity of imazamox on feral rye because feral rye metabolized 25% more ^{14}C-imazamox than jointed goatgrass by 96 HAT (Figure 3.4).

Preliminary field studies showed that feral rye could be adequately controlled with imazamox prior to tillering (Table A3.2). A similar response has been observed for wild oat (*Avena fatua*) control with imazamethabenz (Smith and Chow 1990), but it was determined that the presence of early tillers during herbicide application did not influence imazamethabenz efficacy (Chao et al. 1997). Future research should evaluate the fate of imazamox in feral rye before and after tiller initiation.

Sources of Materials

[1]Cones, Stuewe and Sons, Inc., Corvalis, OR 97333-9461.

[2]Metro-Mix 350 organic potting mix, Scotts-Sierra Horticultural Products Co., Marysville, OH 43040.

[3]Sakrete washed silica sand, US Mix Products Co., Denver, CO 80223

[4]Conviron Controlled Environments Limited (Model 15), Winnipeg, MB, Canada.

[5]MSO, methylated seed oil, Sun-It II, AGSCO, Grand Forks, ND 58201.

[6]NIS, nonionic surfactant, Loveland Industries, Greeley, CO 80537.

[7]ScintiSafe Plus 50%, scintillation cocktail, Fisher Scientific, Fair Lawn, NJ 07410.

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[8]Packard Tri-Carb (Model 2500 TR), Packard Instrument Co., Meriden, CT 06450.

[9]Tempest Homogenizer, Virtis Company, Gardiner, NY 12525.

[10]Zorbax Eclipse XDB-C_{18}, 3 × 150 mm, 3.5 μm particle size, Mac-Mod Analytical, Inc., Chadds Ford, PA 19317.

[11]Hitachi Instruments, Inc., San Jose, CA 95134.

[12]βRAM Detector, IN/US Systems, Inc., Tampa, FL 33610-4809

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Table 3.1. ^{14}C-imazamox absorption by three winter annual grass weeds as affected by surfactant and nitrogen 24 and 48 HAT.

	Absorption[a]						
	Jointed goatgrass		Downy brome		Feral rye		
Treatment[b]	24[c]	48[c]	24	48	24	48	LSD[d]
	% of applied						
Imaz	58	63	54	79	44	45	20
Imaz + NIS	87	90	62	80	70	77	9
Imaz + MSO	94	96	78	87	85	95	7
Imaz + NIS + UAN	96	97	80	91	86	92	4
LSD	11	14	15	10	12	11	

[a]Percentage absorption calculated by the difference between amount applied and amount recovered in leaf wash.

[b]Imaz = imazamox, 45 g ha^{-1}; NIS = nonionic surfactant, 0.25% (v/v); MSO = methylated seed oil, 1% (v/v); UAN = 28% urea ammonium nitrate, 1% (v/v).

[c]24 and 48 HAT.

[d]LSD values valid for comparing weed species within a treatment at 48 HAT.

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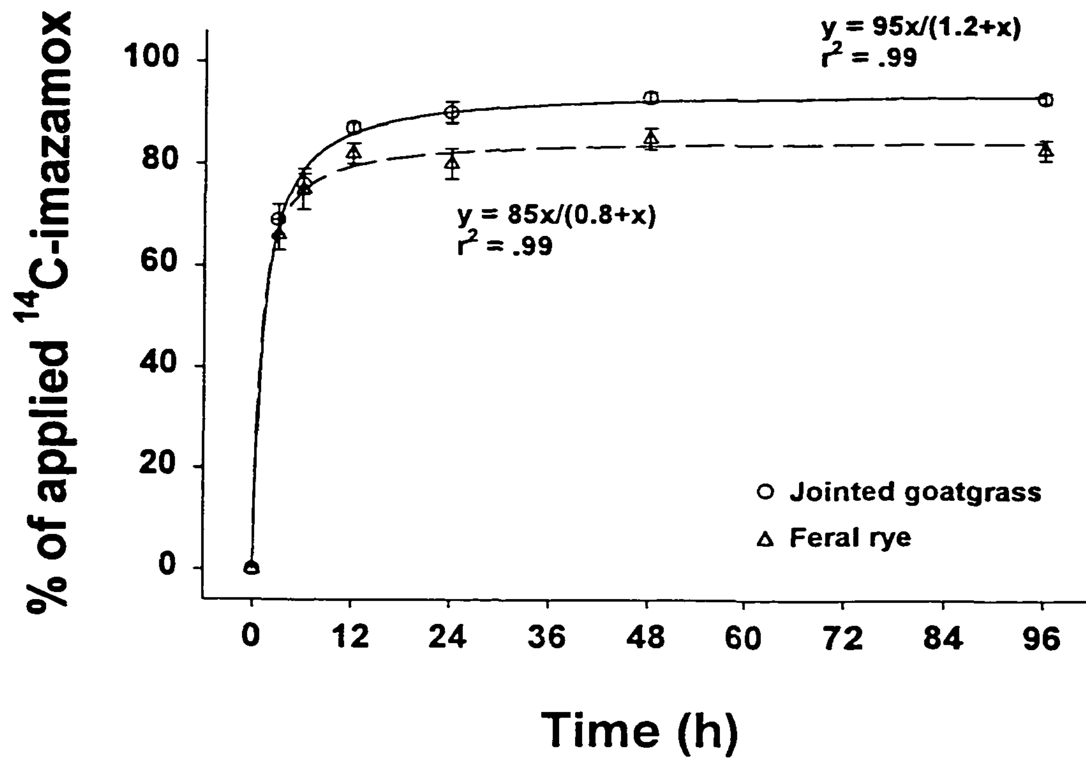

Figure 3.1. Foliar absorption of ^{14}C-imazamox in jointed goatgrass and feral rye during 96 HAT.

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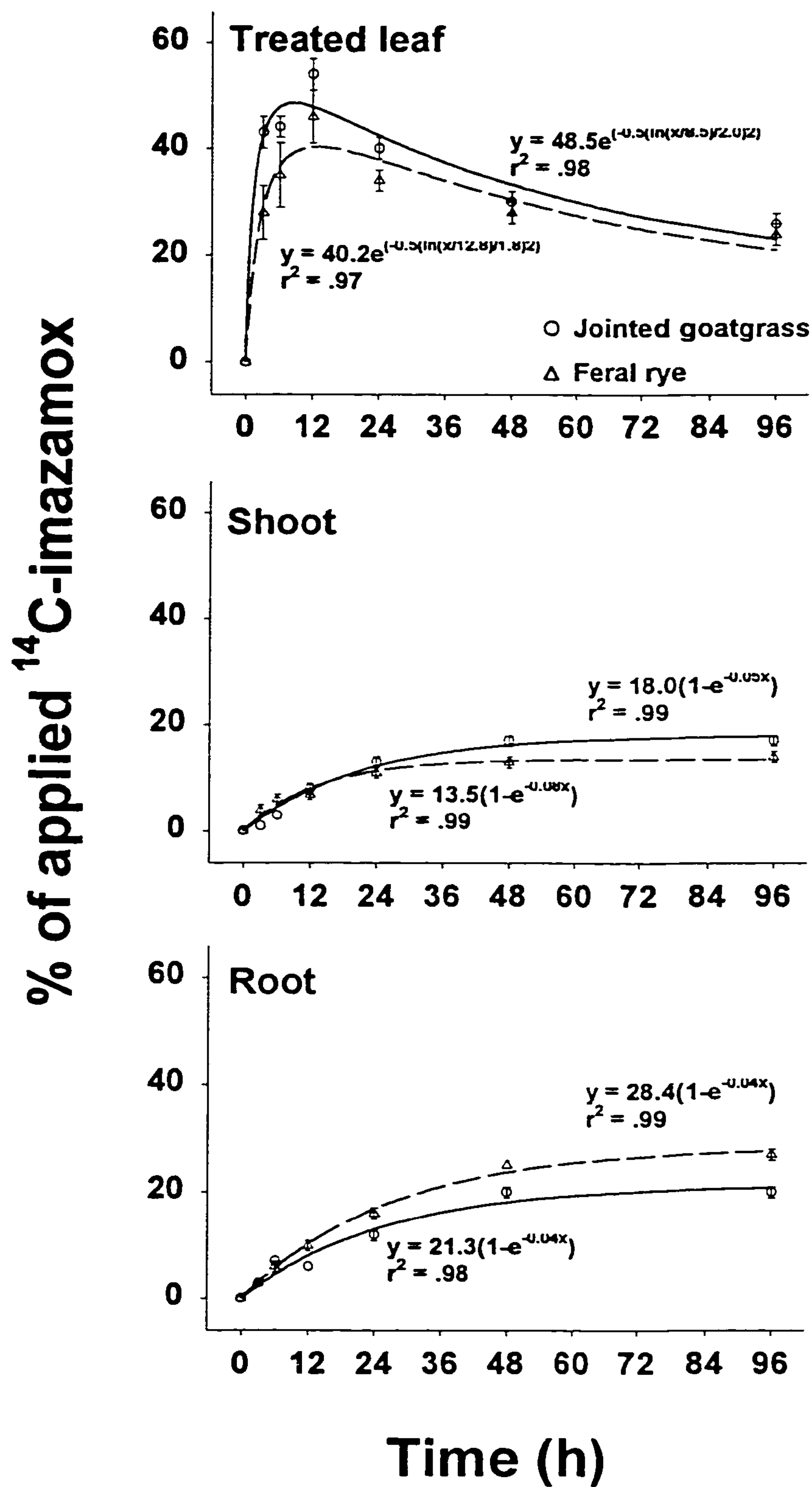

Figure 3.2. Translocation of ^{14}C-imazamox within treated leaves, shoots, and roots of jointed goatgrass and feral rye during 96 HAT.

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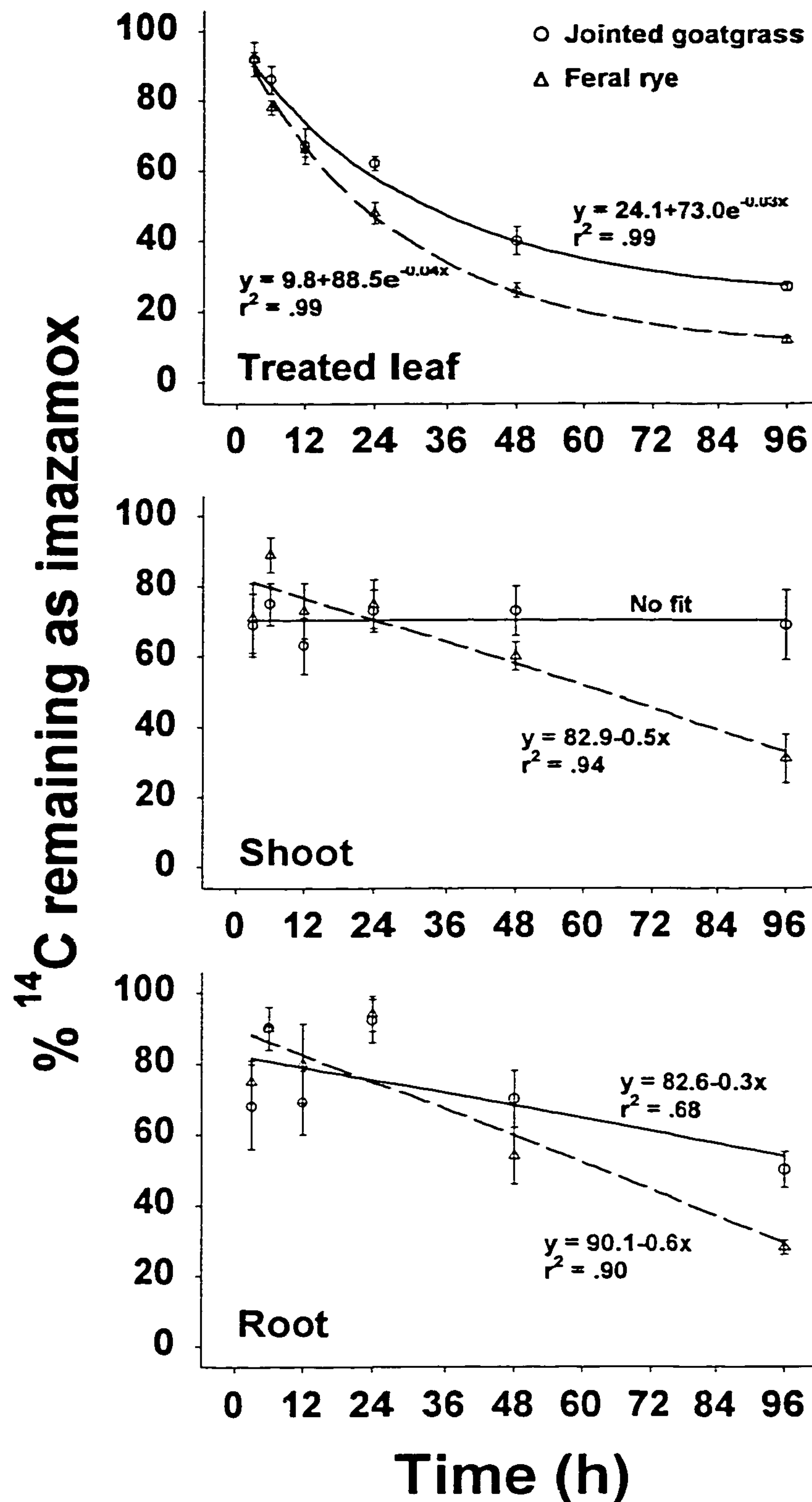

Figure 3.3. Metabolism of ^{14}C-imazamox within treated leaves, shoots, and roots of jointed goatgrass and feral rye during 96 HAT.

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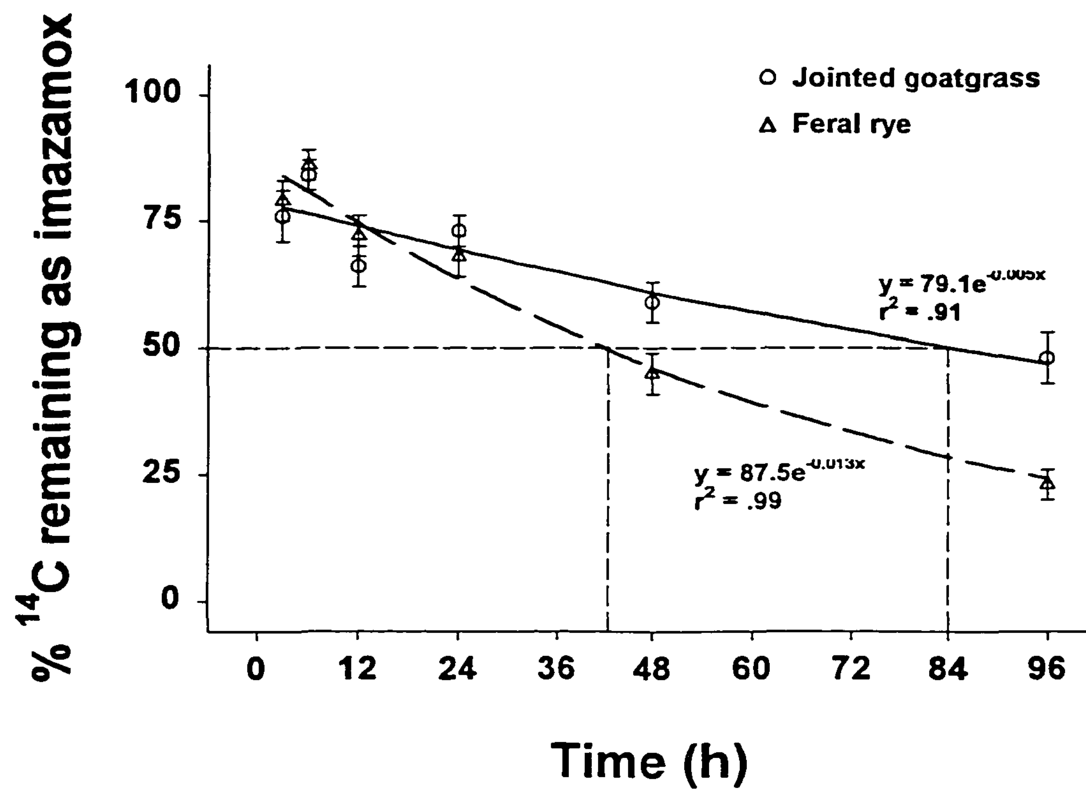

Figure 3.4. Half-life of ^{14}C-imazamox in jointed goatgrass and feral rye determined on a whole plant basis during 96 HAT.

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CHAPTER 4

Genetic diversity of jointed goatgrass (*Aegilops cylindrica*) determined with RAPD and AFLP markers.

Abstract

Molecular marker techniques were used to evaluate the genetic diversity of jointed goatgrass (*Aegilops cylindrica*). Random amplified polymorphic DNA (RAPD) assays were performed using 30 random decamer primers. The frequency of scorable polymorphic bands within jointed goatgrass was 6 out of 90 (6.7%) across 8 U.S. and 50 Eurasian accessions. Cluster analysis of RAPD data showed relatively small genetic distances among jointed goatgrass accessions with values of 0.005 or less obtained between all accessions. Two polymorphisms identified in a Washington accession resulted in its dissimilarity to other U.S. accessions. RAPD techniques successfully detected slightly more genetic diversity among six accessions of *Aegilops triuncialis* supporting the usefulness of these techniques for evaluating sympatric species. Amplified fragment length polymorphism (AFLP) assays were performed on three U.S. and 13 Eurasian accessions. Ten primer combinations generated 560 scorable bands of which 28 (5%) were polymorphic. While many more scorable bands were produced per run compared to RAPDs both methods detected only a small amount of genetic diversity.

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Cluster analysis of AFLP data showed a slightly smaller range in genetic distance (0 to 0.002) among accessions compared to RAPD results; however, AFLPs successfully separated all but two of the 16 accessions. Both techniques identified only minimal amounts of genetic diversity within jointed goatgrass.

Nomenclature: *Aegilops cylindrica* L. AEGCY, jointed goatgrass.

Key words: DNA fingerprinting, weed genetics.

Jointed goatgrass (*Aegilops cylindrica*) is a problem weed in winter wheat (*Triticum aestivum*) producing regions (Ball et al. 1999). It has been suggested that jointed goatgrass was introduced to North America from the eastern Mediterranean probably through wheat imports made by the U.S. Department of Agriculture or by private seed firms and individuals during the early 1900s (Johnston and Parker 1929; Mayfield 1927), but the actual number of jointed goatgrass sources and introductions are unknown. Although jointed goatgrass is not native to North America, it is now widely distributed in the U.S.

Jointed goatgrass and winter wheat are genetically related with the D genome in common. Jointed goatgrass is an allotetraploid (CCDD) (van Slageren 1994) and winter wheat is an allohexaploid (AABBDD) (Poehlman and Sleper 1995). The D genome for each species was contributed by *A. tauschii*. *A. tauschii* has served as a source of germplasm for wheat improvement and confers many stress resistant genes including

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heat, drought, and cold tolerance (Simmonds 1974), thereby facilitating the wide geographic distribution of these two species (Zohary 1965). Development of selective control methods for jointed goatgrass in winter wheat has been difficult primarily because the two species have similar growth habits and they are genetically related with the D genome in common (Bowden 1959; Kihara 1954). Herbicide-resistant wheat cultivars are currently being developed (Newhouse et al. 1992) that will facilitate selective control of jointed goatgrass (Ball et al. 1999); however, the potential for introgression of the herbicide resistance gene from winter wheat into jointed goatgrass has been demonstrated (Seefeldt et al. 1998; Snyder et al. 2000; Zemetra et al. 1998).

Since jointed goatgrass is an introduced exotic species, classical biological control remains a viable option. Efforts to control weeds, including downy brome (*Bromus tectorum*), using classical biological control or biological control with indigenous soil bacteria have been implemented but success has been limited (Kennedy and Kremer 1996). If the origins of U.S. jointed goatgrass populations were identified, these locations could serve as a source of natural enemies to be used as biological control agents and limit the search for candidate biological control organisms to smaller geographic areas.

To improve the potential for success with these herbicide and biological control strategies it is critical to determine the genetic diversity among jointed goatgrass populations throughout the U.S. and Eurasia. Genetically diverse populations of jointed goatgrass may have evolved in response to local or regional environmental and edaphic conditions in which case integrated weed management strategies implemented to manage jointed goatgrass populations may have different effects among populations (e.g.,

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introgression of herbicide resistance genes from winter wheat cultivars). If the level of genetic diversity is too great, efforts to identify and obtain a successful biological control agent may be fruitless (Burdon and Marshall 1981). A primary center of diversity of the genus *Aegilops* is considered to be the 'Fertile Crescent', because a larger number of the *Aegilops* species are found there than other areas (van Slageren 1994). If U.S. and Eurasian populations are genetically similar, sites of origin from the 'Fertile Crescent' could serve as a source of biological control agents. Finally, if unique biotypes of jointed goatgrass have evolved in the U.S., efforts to identify and obtain exotic biological control agents could be shifted toward indigenous organisms.

Limited previous research on the genetic diversity of jointed goatgrass has been inconclusive. Several studies have examined physiological and morphological relationships among diverse jointed goatgrass populations. In the greenhouse, net photosynthesis, transpiration rate, leaf diffusive resistance, and stomatal density of nine accessions from across the western U.S. were similar (Gealy 1987; Gealy 1989). In a common nursery study at Colorado State University, examining 53 jointed goatgrass accessions collected from 11 western states identified differences in morphological characteristics including cylinder color and pubescence, height, maturity, and vigor, but results of growth attributes were inconsistent over yr (T. Pester, unpublished data). Morphological traits have traditionally been used to describe genetic diversity and relationships in plant species with the assumption that common morphological features indicate close genetic relationships. This method has proven to be inadequate because morphological traits are limited in number, can be strongly influenced by environment,

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and often have polygenic inheritance that limits their use in the detection of hybridization and lineage determination (Newbury and Ford-Lloyd 1993).

More recently, protein profiles (allozymes) have been used to document genetic variation in many organisms, including weed species (Warwick 1990). Watanabe et al. (1994) conducted isozyme analysis of 426 Eurasian jointed goatgrass accessions and identified six variants in α–amylase isozymes but no genetic differences were identified in 27 North American accessions. Allozyme marker systems provide a relatively inexpensive tool for assessing genetic variation at the molecular level; however, allozyme variation can be too low for analysis of genetic diversity within and among populations because it is unable to detect changes in DNA sequence (Holt 1994; Warwick 1990).

Molecular techniques such as RAPDs have proven to be particularly useful in determining genetic diversity within a plant species. The power of this technique for the identification, classification, and characterization of closely related genotypes is illustrated by the fact that RAPD markers have been used to identify cereal crop varieties (Weining and Langridge 1991) and screen genetic resources held in genebanks (Newbury and Ford-Lloyd 1993). Okuno et al. (1998) used RAPD techniques to assess the genetic diversity among several *Aegilops* species from Central Asia and north Caucasia. They reported that RAPD techniques adequately divided *Aegilops* species into two major groups corresponding to the D genome species and the U genome species; however, jointed goatgrass accessions from north Caucasia were genetically uniform and accessions from Central Asia were only slightly more diverse. The AFLP technique is based on selective polymerase chain reaction (PCR) amplification of restriction fragments from total genomic DNA (Vos et al. 1995). AFLP uses primers specific to the

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adapter and restriction site sequence, whereas RAPD utilizes arbitrary primers. AFLP also has the capacity to inspect a much greater number of loci for polymorphism than RAPDs, such that the number of polymorphisms detected per reaction are much higher. Finally, AFLP is superior in terms of the number of sequences amplified per reaction and their reproducibility. The markers produced are reliable and reproducible within and between laboratories, and are relatively easy and inexpensive to generate.

The objectives of this research were to use RAPD and AFLP molecular markers to determine genetic diversity in U.S. and Eurasian jointed goatgrass accessions at the DNA level and establish relatedness among Eurasian and U.S. populations to provide evidence for origins of the U.S. introductions.

Materials and Methods

Plant Material

The 58 jointed goatgrass accessions used in this study originated from eight western U.S. states and 13 Eurasian countries (Table 4.1). Six additional accessions of a related species, *Aegilops triuncialis* (UUCC), from six Eurasian countries were also evaluated. U.S. jointed goatgrass accessions were provided by several University researchers and extension agents throughout the western states, while Eurasian accessions of both species were provided by the USDA-ARS National Small Grains Collection in Aberdeen, ID. Plants were grown in a greenhouse (22/18 C day night, 16 h photoperiod, natural light supplemented with metal halide lamps, PPF of 400 μmol m^{-2} s^{-1}) in individual plastic pots

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(9 × 9 × 6 cm) filled with an organic potting mix[1] until leaves were harvested for total genomic DNA extraction.

DNA Extraction

Fresh leaf tissue (3 g) was ground to a fine powder in liquid nitrogen, and total genomic DNA was extracted using the method of Tai and Tanksley (1990). The concentration of each DNA sample was measured using a spectrophotometer[2] and standardized to a concentration of 100 ng μl^{-1} DNA dissolved in 0.5 ml TE buffer (10 m*M* Tris-Cl pH 8, 1 m*M* EDTA).

RAPD Amplification and Electrophoresis

All 58 U.S. and Eurasian jointed goatgrass accessions plus the six *A. triuncialis* accessions were subjected to RAPD analyses (Table 4.1). RAPDs were generated using a set of 30 random decamer primers[3] on all jointed goatgrass accessions (Table 4.2). A subset of 20 primers (609 to 646, Table 4.2) was used on the six *A. triuncialis* accessions. Each 25 µl reaction contained 10 ng genomic DNA, 0.2 m*M* of each dNTP, 0.5 µ*M* primer, 2.5 µl 10 × polymerase buffer[4] containing 1.5 m*M* $MgCl_2$, and distilled H_2O. Reaction mixtures were overlaid with 20 µl mineral oil, placed in a thermal cycler[5], and heated to 99 C for 5 min to ensure complete denaturation of genomic template DNA. The block was then cooled to 85 C and 1 unit of *Taq* polymerase[6] was added to each tube. The samples were then subjected to 45 cycles of 92 C for 1 min, 35 C for 2 min, and 72 C for 2 min, followed by a final extension cycle of 72 C for 8 min. Two replicates of each genomic DNA-primer combination were amplified on each run, together with a

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control containing all components of the reaction mixture except the template DNA. Amplifed DNA fragments were separated on a 1.2% agarose gel, stained with ethidium bromide, and photographed under UV light.

AFLP Amplification and Electrophoresis

A subset of 16 jointed goatgrass accessions was selected for AFLP analyses, three U.S. accessions representing a large geographic range (16, 42, 45), and one accession from each of the 13 Eurasian countries in our collection (101, 103, 105, 106, 107, 110, 111, 112, 113, 114, 119, 144, 147) (Table 4.1). Template DNA was prepared in a single restriction-ligation reaction. Genomic DNA (500 ng) was digested with *Eco*R I and *Mse* I at 37 C for 3 h. The mixture was incubated at 70 C for 15 min to inactivate the restriction endonucleases and placed on ice for 5 min. The DNA fragments were ligated to *Eco*R I and *Mse* I adapters[7] at 20 C for 2 h. The digestion-ligation mixture was diluted 10-fold with TE. Preselective amplification using provided primers[7] was performed in a thermal cycler programmed for 20 cycles at a profile of 94 C for 30 s, 56 C for 1 min, and 72 C for 1 min; then, held at 4 C. The preselective amplification mixture was diluted 5-fold with TE. A 5-μl aliquot of each preselective amplification was resolved on a 1.2% agarose gel and stained with ethidium bromide to verify proper amplification.

Selective amplification of restriction fragments was performed using 10 different combinations of *Eco*R I and *Mse* I primers[7] with three selective nucleotides attached to the 3' end (Table 4.4). Subsamples (2 μl) of the diluted preamplified fragments were used as template DNA and mixed with EcoR I and Mse I primers[7] (30 ng each) also containing dNTPs, 2 μl 10 × PCR buffer[7] (200 m*M* Tris-HCl, 15 m*M* $MgCl_2$, 500 m*M*

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KCl), 1 unit of *Taq* polymerase, and brought to 20 μl final volume with distilled H_2O. The PCR amplification program was one cycle at 94 C for 30 s, 65 C for 30 s, and 72 C for 1 min; then 12 cycles reducing the annealing temperature 0.7 C each cycle (65.0 to 56.6 C); followed by 23 cycles at 94 C for 30 s, 56 C for 30 s, and 72 C for 1 min; then, held at 4 C.

Samples were mixed with an equal volume of loading buffer (98% formamide, 10 m*M* EDTA, 0.15% Bromophenol Blue, 0.15% Xylene Cyanol), denatured at 95 C for 5 min, and placed on ice. Subsamples (5 μl) of the selective amplifications were separated by electrophoresis at a constant power[8] (75 W) in a 1 × TBE running buffer for 3.5 h on 0.4-mm thick 5.3% (wt/vol) polyacrylamide gels (40.56 g urea, 12 ml 40% acrylamide, 18 ml 5 × TBE). Gels were soaked for 30 min in fixing solution (10% acetic acid), rinsed three times with distilled water, soaked for 30 min in a silver staining solution (2 g silver nitrate and 3 ml 37% formaldehyde in 2 L water), rinsed with distilled water, soaked in developing solution (60 g sodium carbonate, 3 ml 37% formaldehyde, and 400 μl sodium thiosulfate in 2 L water) until DNA bands were visible. The reaction was stopped by adding fixing solution, gels were rinsed with distilled water, and air-dried overnight at room temperature. Dried gel images were digitized with a flat-bed scanner.

Statistical Analyses

Binary data matrices were constructed by scoring the presence or absence of amplified bands for each primer-accession combination in RAPD and AFLP experiments. RAPD data were combined for the 20 primers used on the 58 jointed goatgrass accessions

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and the six *A. triuncialis* accessions. The index proposed by Nei (1972) was used to calculate the genetic distance, GD_{ij}, between two accessions i and j:

$$GD_{ij} = 2N_{ij}/(N_i + N_j)$$

where N_{ij} is the number of bands common to i and j, and N_i and N_j are the number of bands for accessions i and j, respectively. The resulting genetic distance data were analyzed using a group average method (unweighted pair-group method with arithmetical averages, UPGMA) to create dendrograms providing a visual representation of the similarity matrices. All analyses were performed using NTSYS-pc software[8].

Results and Discussion

RAPD Analysis

Aegilops cylindrica. The set of 30 primers used on the eight U.S. jointed goatgrass accessions generated a total of 90 reproducible bands with only three bands (3%) being polymorphic between two or more accessions (Table 4.2). Primer 619 produced a polymorphism was unique to the Washington accession (Figure 4.1) and primer 612 produced a polymorphism shared by Washington and Oregon. The third polymorphism was produced by primer 624, and was shared by Colorado and Nebraska. Genetic relatedness between these spatially related accessions seemed logical due to the geographic separation between the Pacific Northwest and the Central Great Plains regions, thus supporting allopatric speciation. The low number of polymorphisms indicated a limited amount of genetic diversity in the U.S. accessions. We initially

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hypothesized that this result would be consistent with the loss of allelic variation due to founder effect and the limited amount of time in the new environment to increase genetic diversity by outcrossing. Three additional polymorphisms were detected in the 50 Eurasian accessions (primers 636, 637, and 648), so overall the frequency of scorable polymorphic bands within jointed goatgrass was 6 out of 90 (6.7%) across 58 U.S. and Eurasian accessions (Table 4.2).

Cluster analysis showed relatively small genetic distances among jointed goatgrass accessions (Figure 4.2). On a genetic distance scale from 0 (identical) to 1 (different for all criteria studied) values of 0.005 or less were obtained between all accessions, with the largest values arising between 45 (Washington) and a group of three U.S. accessions (2-Nebraska, 42-Oklahoma, and 47-Utah). The Eurasian accessions, except two from Turkey (133 and 141), were divided into three major clusters each with no genetic diversity. The Colorado accession (16) was included with a cluster consisting mostly of accessions from Turkey.

Aegilops triuncialis. Six *A. triuncialis* accessions were evaluated to determine if RAPDs could detect genetic variation between accessions in a species sympatric with and similar to jointed goatgrass. A subset of 20 primers (609 to 646, Table 4.2) was used to evaluate the *A. triuncialis* accessions. Data were pooled with jointed goatgrass data from the same primers. A total of 63 scorable bands were generated, of which 27 (43%) were polymorphic between two or more accessions. Figure 4.3 shows that the two species were correctly separated by a relatively large genetic distance. A considerable degree of polymorphism was detected at the interspecific level; although, over half of the amplified bands were common to both species. At the intraspecific level, a larger degree of

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polymorphism was detected within *A. triuncialis* compared to jointed goatgrass. Only one tie occurred within the six *A. triuncialis* accessions compared to the three large groups of tied jointed goatgrass accessions. Interestingly, jointed goatgrass was clustered identically with 20 versus 30 primers (Figures 4.2 and 4.3), indicating that the additional 10 primers did not detect additional genetic diversity within jointed goatgrass. Although this is likely an artifact of selecting against primers that did not detect polymorphisms when the subset of 20 primers was selected for evaluating the *A. triuncialis* accessions.

AFLP Analysis

A subset of 16 jointed goatgrass accessions were selected for AFLP analysis to further evaluate genetic diversity within the species. Accessions were selected to represent a large geographic range, three from the U.S. and 13 from Eurasia (one from each country in our collection) (Table 4.3).

Ten AFLP primer combinations produced 560 scorable bands, of which 28 (5%) were polymorphic (Table 4.4). While many more scorable bands were produced per run compared to RAPDs (Figures 4.1 and 4.4), both methods detected only a small amount of genetic diversity. Cluster analysis of the AFLP data showed genetic distance ranging from 0 to 0.002 (Figure 4.5). This distance is smaller than detected by RAPD analyses (Figure 4.2); however, AFLPs separated nearly all of the accessions with only one tie (105-Azerbaijan and 110-Greece). As noted earlier, AFLP is a much more robust procedure than RAPDs for detecting genetic diversity among closely related accessions. Therefore, the increased separation among Eurasian accessions at more stringent genetic distances with AFLPs is logical. Both RAPD and AFLP results separated Colorado (16)

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and Oklahoma (42) accessions and showed they were less genetically similar to Washington (45) and other Eurasian accessions.

These results suggest either multiple introductions of jointed goatgrass into the U.S. or genetic divergence within U.S. populations since their introduction. It has been suggested that multiple introductions occurred early in the 20th century (Johnston and Parker 1929; Mayfield 1927). These introductions likely originated from different geographic locations and contained genetically different jointed goatgrass genotypes. Due to the relatively recent introduction of jointed goatgrass into the U.S., ample time for genetic mutation and selection seems unlikely.

Colorado and Oklahoma accessions share genetic similarity with accessions from Afghanistan, Azerbaijan, and Greece, while the Washington accession was more genetically similar to the accession from Israel (Figure 4.5). There does not appear to be a logical geographic grouping of the Eurasian accessions but this is likely due to the homogeneity of the accessions indicated by the small relative genetic distances and number of ties between accessions found with RAPDs (Figure 4.2).

The results of our RAPD and AFLP analyses support previous research on the genetic diversity within jointed goatgrass. Watanabe et al. (1994) found only six variants in α–amylase isozymes among 426 Eurasian jointed goatgrass accessions and no differences among 27 North American accessions. Okuno et al. (1998) evaluated 112 accessions among five *Aegilops* species including *A. cylindrica* (jointed goatgrass), *A. tauschii* (DD), *A. crassa* (DDMM), *A. biuncialis* (UUMM), and *A. triuncialis*. They found that RAPDs could adequately differentiate species with cluster analyses but accessions within jointed goatgrass were virtually identical.

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The homogeneity of jointed goatgrass does not necessarily place the species at an evolutionary disadvantage. Polyploid genomes typically have a high level of plasticity and gene expression is regulated by environmental interactions including biotic and abiotic stress. As stated earlier, the D genome shared by jointed goatgrass and winter wheat provides these species with a large capacity to respond to diverse growing conditions including moisture, temperature, and nutrient stress. Consequently, both of these species are adapted to a large geographic range and limited mutation and selection events have been required for these species to proliferate. This would also explain the limited genetic diversity detected in the Eurasian accessions. These competitive traits have permitted jointed goatgrass to successfully invade winter wheat cropping systems in Eurasia and the U.S., and establish and maintain vigorous weedy populations.

One of the objectives for evaluating the genetic diversity of jointed goatgrass was to determine the implications for managing introgression of herbicide resistant genes between jointed goatgrass and winter wheat. The low amount of diversity detected implies that introgression will be more largely influenced by environmental conditions that affect pollen viability and flowering synchronicity than genetic components including multiple alleles, mutation rate, and sexual compatibility. The rate of outcrossing of jointed goatgrass has not been reported but it is traditionally treated as a primarily self-pollinating species (van Slageren 1994). Therefore, gene flow among spatially separated populations would likely be greater through seed movement than through pollen flow or natural mutation. A second objective was to identify genetic relatedness between U.S. and Eurasian accessions. The lack of genetic variation within jointed goatgrass makes it difficult to determine the site of origin for U.S. introductions;

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however, if successful biological control agents are identified they will likely be effective on spatially and temporally separated populations of jointed goatgrass, not withstanding environmental interactions.

Sources of Materials

[1]Metro-Mix 350 organic potting mix, Scotts-Sierra Horticultural Products Co., Marysville, OH 43040.

[2]Spectrophotometer, SmartSpec 3000, Bio-Rad Laboratories, Hercules, CA.

[3]Decamer primers, University of British Columbia.

[4]Polymerase buffer, Promega, Madison, WI

[5]Thermal cycler, PTC-100 Programmable Thermal Controller, MJ Research, Inc.

[6]*Taq* polymerase, Promega, Madison, WI

[7]GibcoBRL, AFLP™ Analysis System I, AFLP Starter Primer Kit, Life Technologies.

[8]Power source, PC 3000 Power Supply, Bio-Rad Laboratories, Hercules, CA

[9]NTSYS-pc ver. 2.02j, Numerical taxonomy and multivariate analysis system, Exeter Software, Setauket, NY.

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Table 4.1. Origin of *Aegilops* species and accessions used for RAPD evaluation.

Species	Accession	Location	
		Country	State
A. cylindrica	2	United States	Nebraska
	16	United States	Colorado
	42	United States	Oklahoma
	45	United States	Washington
	47	United States	Utah
	49	United States	Kansas
	51	United States	South Dakota
	54	United States	Oregon
	101	Afghanistan	Faryab
	102	Afghanistan	Faryab
	103	Armenia	
	104	Armenia	
	105	Azerbaijan	
	106	China	
	107	Georgia	
	108	Georgia	
	109	Georgia	
	110	Greece	Macedonia
	111	Iran	Zanjan
	112	Iraq	
	113	Israel	
	114	Macedonia	
	115	Macedonia	
	116	Macedonia	
	117	Macedonia	
	118	Macedonia	
	119	Turkey	Gumushane
	120	Turkey	Erzurum
	121	Turkey	Kars
	122	Turkey	Kirsehir
	123	Turkey	Ankara
	124	Turkey	Van
	125	Turkey	Hakkari
	126	Turkey	Hakkari
	127	Turkey	Van
	128	Turkey	Van
	129	Turkey	Hakkari
	130	Turkey	Mus
	131	Turkey	Bitlis
	132	Turkey	Mus
	133	Turkey	Hakkari
	134	Turkey	Hakkari
	135	Turkey	Hakkari
	136	Turkey	Hakkari
	137	Turkey	Hakkari
	138	Turkey	Bilecik
	139	Turkey	Cankiri
	140	Turkey	Cankiri
	141	Turkey	Cankiri
	142	Turkey	Ankara
	143	Turkey	Ankara
	144	Uzbekistan	
	145	Uzbekistan	
	146	Uzbekistan	
	147	Yugoslavia	Serbia
	148	Yugoslavia	Serbia
	149	Yugoslavia	Serbia
	150	Yugoslavia	Serbia
A. triuncialis	213	Iran	East Azerbaijan
	214	Yugoslavia	Montenegro
	215	Macedonia	
	216	Syria	
	217	Greece	Thessaly
	218	Turkey	Cankiri

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Table 4.2. Random primers used in RAPD analyses of 8 U.S. and 50 Eurasian jointed goatgrass accessions.

Primer		Scorable bands	Polymorphisms	
			U.S.	Eurasian
609	5'-ACA GCA CCA T-3'	4		
612	5'-CCG TGA GTA T-3'	2	1	
613	5'-TGC ACC CAC G-3'	5		
615	5'-CGT CGA GCG G-3'	3		
616	5'-CGG AAG AAA C-3'	4		
617	5'-CGG ACT ATG T-3'	3		
619	5'-TTC CCT AGC G-3'	3	1	
620	5'-TTG CGC CCG G-3'	3		
621	5'-GTC TGC GCT A-3'	3		
624	5'-GTG ATA AGC C-3'	3	1	
626	5'-CCA AGC CCG G-3'	4		
627	5'-GGA TTC ACA G-3'	1		
633	5'-CGT TGT ATC C-3'	3		
634	5'-CCG TAC ACG C-3'	4		
635	5'-CTC AGC TCA G-3'	1		
636	5'-GGG ATA TCG C-3'	3		1
637	5'-CCC TAA AGC G-3'	2		1
641	5'-TGG AAC CAT G-3'	3		
644	5'-TCG TAT TGG G-3'	3		
646	5'-GTC CAC TTC C-3'	3		
648	5'-GCA CGC GAG A-3'	3		1
649	5'-AAT GCT GGA C-3'	5		
650	5'-AGT ATG CAG C-3'	4		
652	5'-CCC AAC ACA C-3'	3		
653	5'-CAT GCA AGA C-3'	3		
654	5'-CCC TGG TCT G-3'	1		
655	5'-GCA TTT CCC G-3'	3		
656	5'-CGT AAC CTT G-3'	1		
669	5'-GTT ACA CCA C-3'	3		
688	5'-GCA GGA GCG T-3'	4		
Total		90	6	

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Table 4.3. Origin of jointed goatgrass accessions used for AFLP evaluation.

	Location	
Accession	Country	State
16	United States	Colorado
42	United States	Oklahoma
45	United States	Washington
101	Afghanistan	Faryab
103	Armenia	
105	Azerbaijan	
106	China	
107	Georgia	
110	Greece	Macedonia
111	Iran	Zanjan
112	Iraq	
113	Israel	
114	Macedonia	
119	Turkey	Gumushane
144	Uzbekistan	
147	Yugoslavia	Serbia

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Table 4.4. **Combinations of *Eco*R I and *Mse* I primers with three selective nucleotides attached to the 3' end, and the number of scorable bands and polymorphisms produced in AFLP selective amplifications.**

Combination	*Eco*R I primer +	*Mse* I primer +	Scorable bands	Polymorphisms
1	ACC	CAG	56	6
2	ACT	CTG	71	2
3	ACA	CTA	86	7
4	ACG	CTC	67	8
5	ACG	CAA	58	2
6	AAC	CAT	84	1
7	AGG	CAC	55	
8	AAG	CTT	55	2
9	AAC	CAA	5	
10	AGC	CTA	23	
Total			560	28

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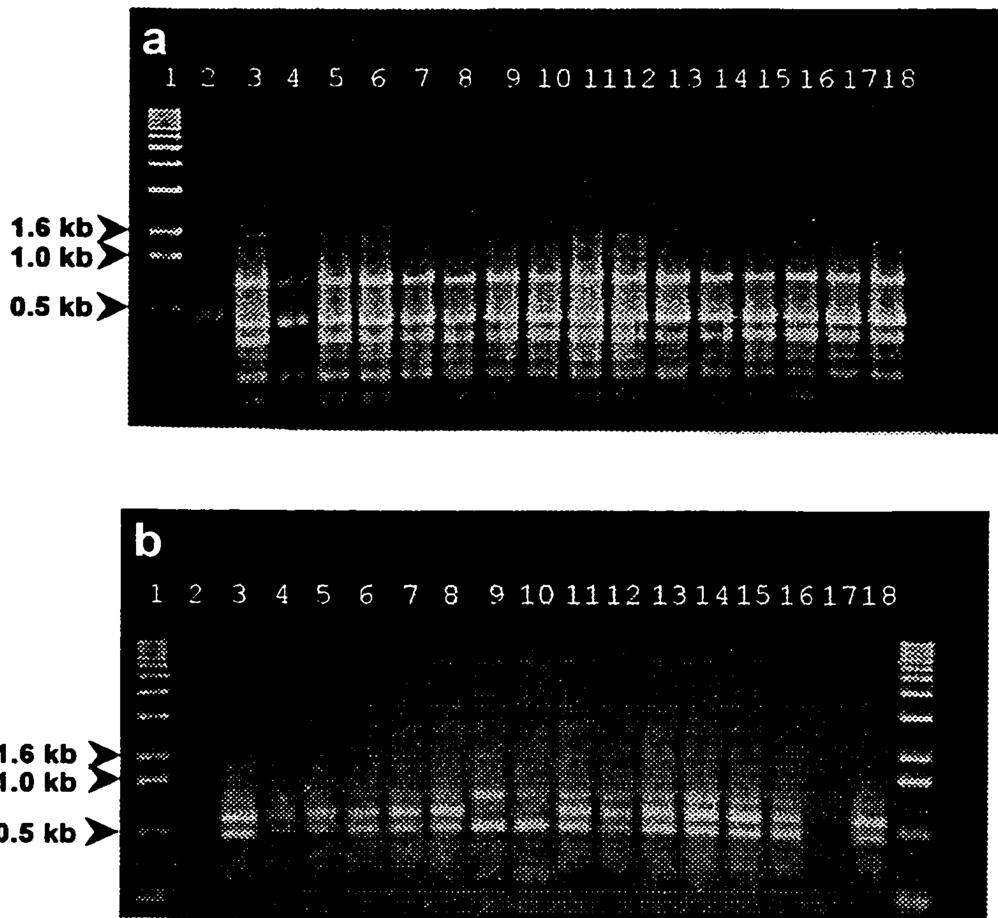

Figure 4.1. RAPD profiles for eight U.S. jointed goatgrass accessions (Table 4.1) amplified with UBC primers 609 and 619 (Table 4.2) for gels (a) and (b), respectively. Accessions were duplicated in adjacent lanes. Lane 1: 1 Kb ladder (GibcoBRL, Rockville, MD), lane 2: control, lanes 3-4: Nebraska, lanes 5-6: Colorado, lanes 7-8: Oklahoma, lanes 9-10: Washington, lanes 11-12: Utah, lanes 13-14: Kansas, lanes 15-16: South Dakota, lanes 17-18: Oregon.

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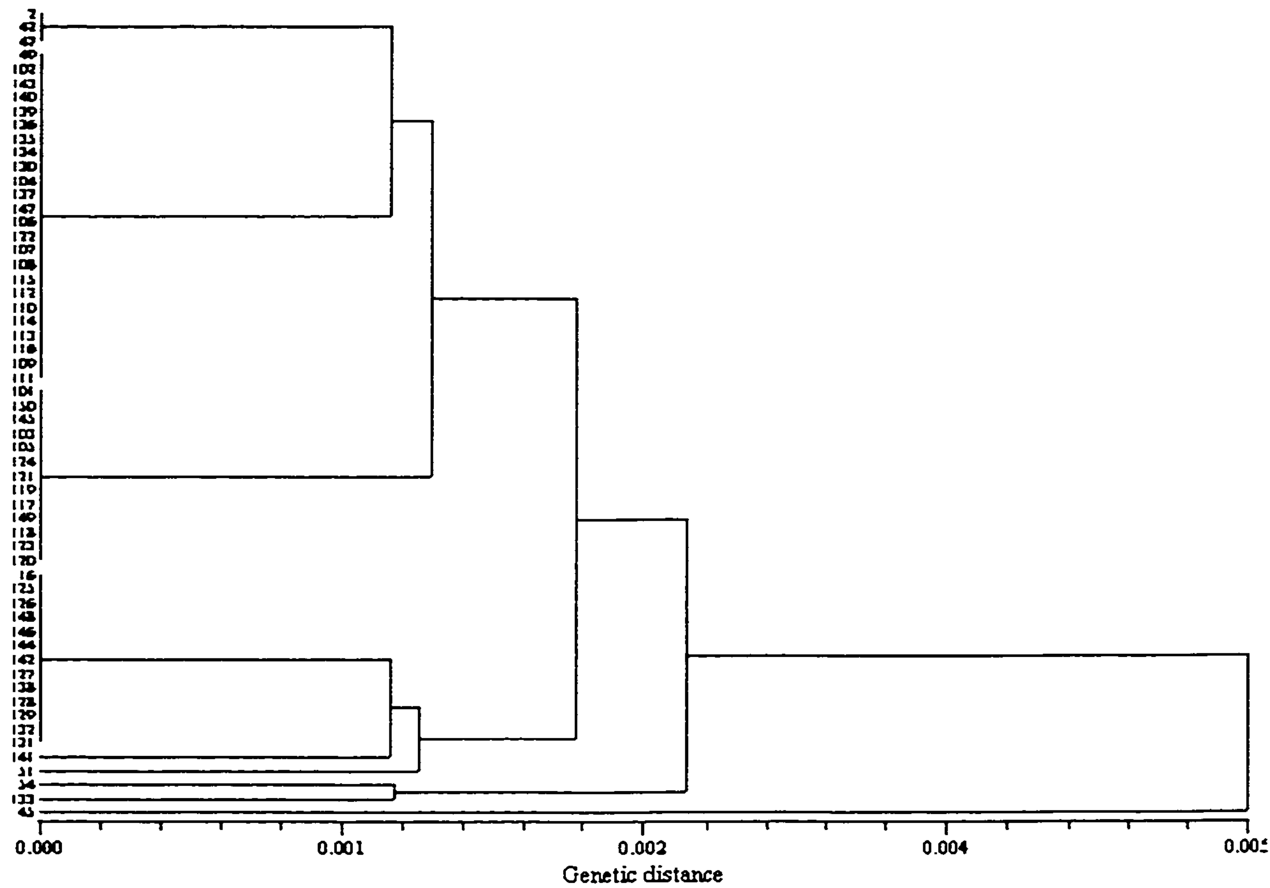

Figure 4.2. Dendrogram for 8 U.S. and 50 Eurasian jointed goatgrass accessions (Table 4.1) generated by cluster analysis (UPGMA) of genetic distance values from RAPD data using 30 random decamer primers (Table 4.2). Relative branch lengths indicate relative genetic distances between accessions.

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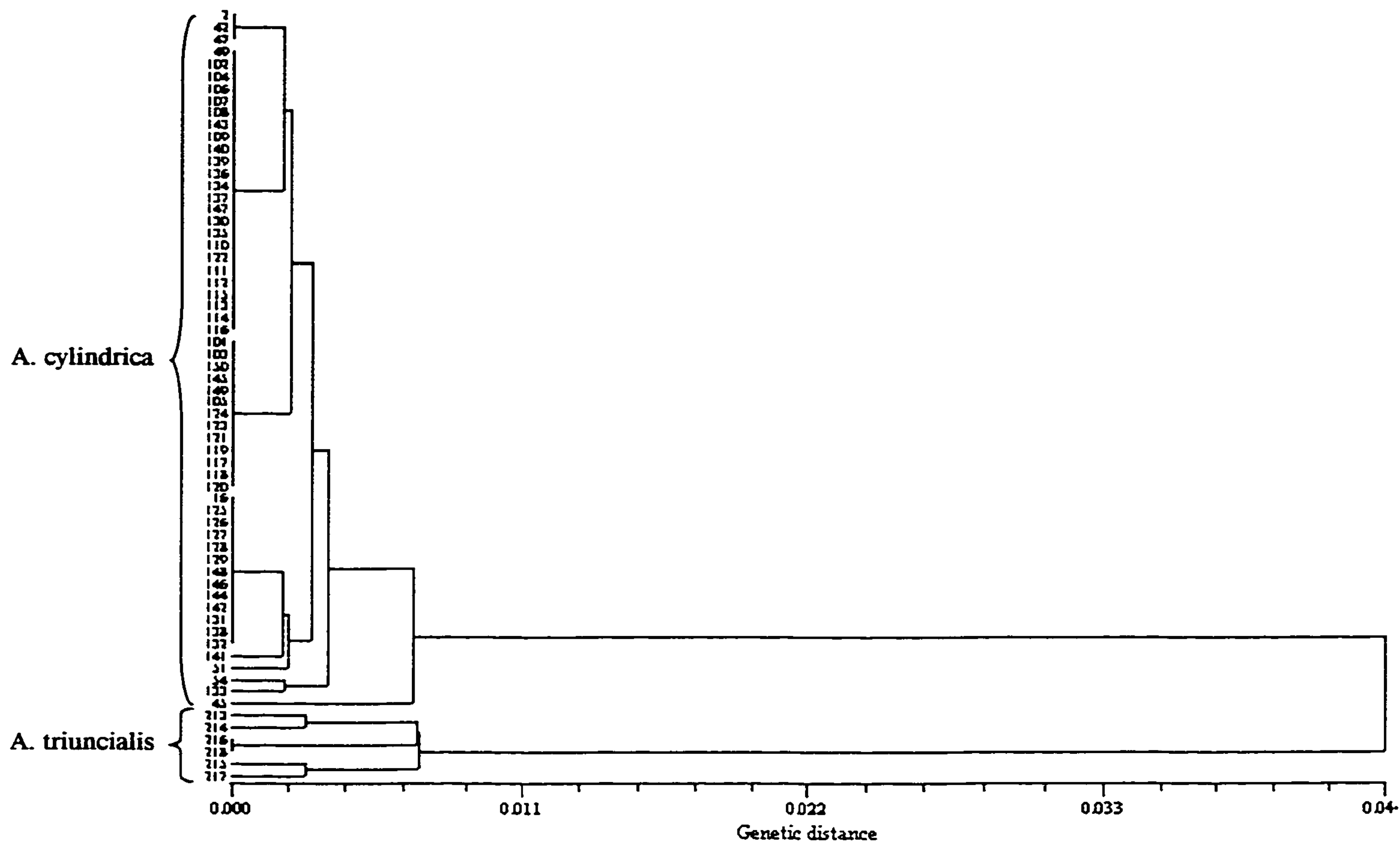

Figure 4.3. Dendrogram for jointed goatgrass and *Aegilops triuncialis* accessions (Table 4.1) generated by cluster analysis (UPGMA) of genetic distance values from RAPD data using 20 random decamer primers (First 20, Table 4.2). Relative branch lengths indicate relative genetic distances between accessions.

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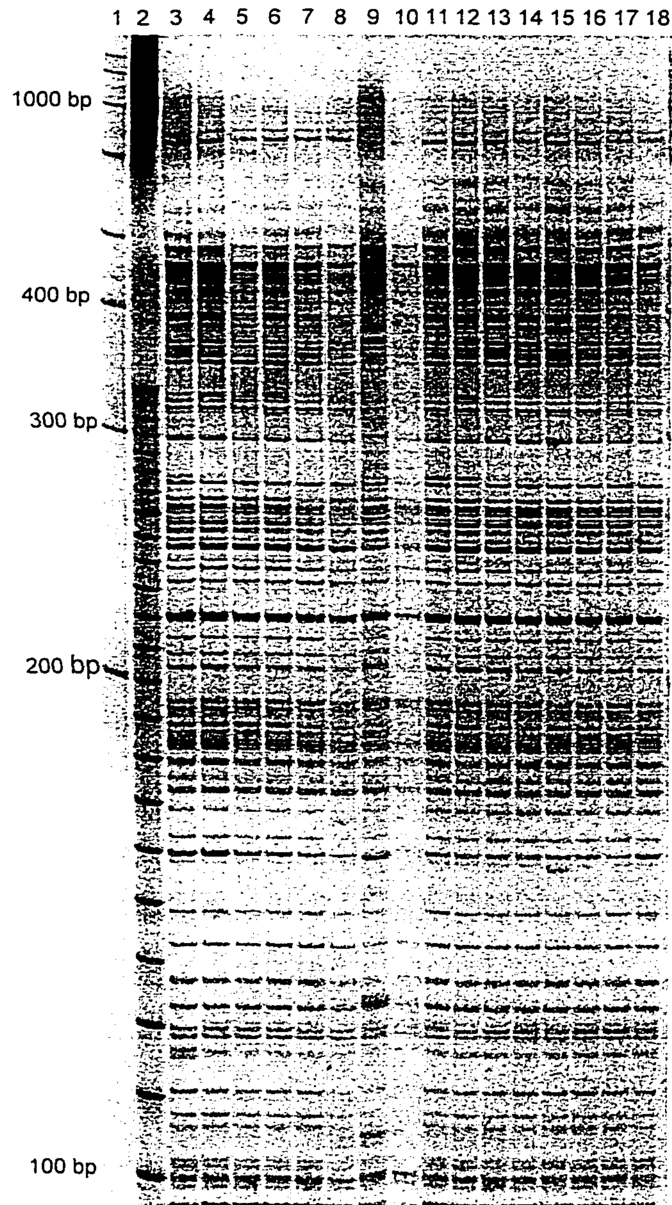

Figure 4.4. AFLP profiles for three U.S. and 13 Eurasian jointed goatgrass accessions (Table 4.3) amplified with primer combination 3 (Table 4.4). Lane 1: Amplisize ladder (Bio-Rad, Hercules, CA), lane 2: 10 bp ladder (GibcoBRL, Rockville, MD), lane 3: 16, lane 4: 22, lane 5: 42, lane 6: 101, lane 7: 103, lane 8: 105, lane 9: 106, lane 10: 107, lane 11: 110, lane 12: 111, lane 13: 112, lane 14: 113, lane 15: 114, lane 16: 119, lane 17: 144, lane 18: 147.

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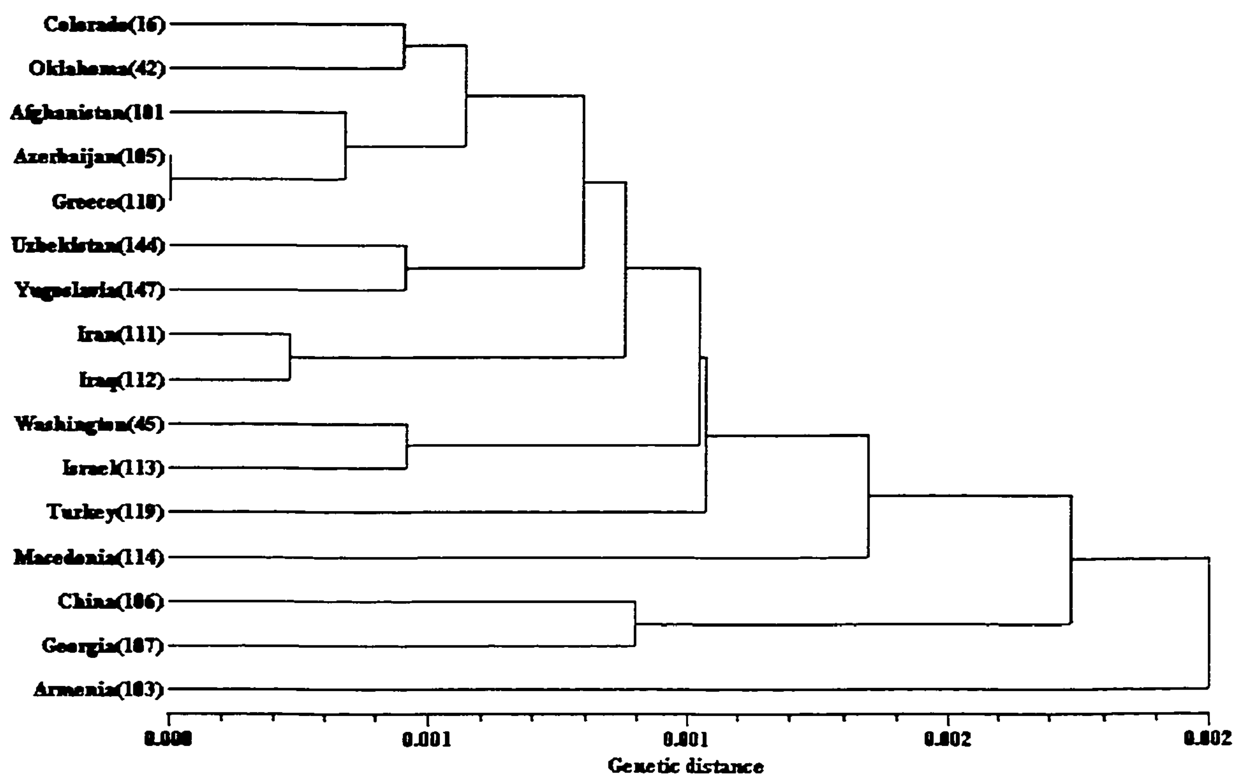

Figure 4.5. Dendrogram for three U.S. and 13 Eurasian jointed goatgrass accessions (Table 4.3) generated by cluster analysis (UPGMA) of genetic distance values from AFLP data. Relative branch lengths indicate relative genetic distances between accessions.

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APPENDIX

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Table A2.1. Main effect treatment means of *Aegilops cylindrica* and winter *Triticum aestivum* production for different cultivars, planting densities, and tillage systems during four cropping seasons from 1997 to 2000 at Platner, CO.

Treatments		*A. cylindrica*				Winter *T. aestivum*			
		Seedlings	Biomass	Tillers	Spikelets	Biomass	Tillers	Spikelets	Yield
		no./m^2	g/m^2	no./m^2	no./m^2	g/m^2	no./m^2	no./tiller	kg/ha
Cultivar	Akron	16	47	143	1213	393	301	14.0	1353
	Lamar	17	62	188	1601	375	287	14.6	1216
	TAM 107	17	54	164	1387	382	295	12.1	1474
	LSD (0.05)	NS	NS	41	356	NS	NS	0.3	NS
Planting density	45	17	60	176	1505	361	279	13.8	1265
	67	16	49	154	1295	406	309	13.4	1431
	LSD (0.05)	NS	10	NS	NS	NS	NS	NS	122
Tillage system	Conventional	16	55	159	1382	379	295	13.7	1342
	Reduced	16	58	169	1443	406	305	13.5	1417
	No-till	18	50	167	1376	365	283	13.4	1284
	LSD (0.05)	NS	NS	NS	NS	NS	NS	NS	NS

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Table A2.2. Main effect treatment means of *Aegilops cylindrica* and winter *Triticum aestivum* production for different cultivars and planting dates during four cropping seasons from 1997 to 2000 at Platner, CO.

Treatments		*A. cylindrica*				Winter *T. aestivum*			
		Seedlings	Biomass	Tillers	Spikelets	Biomass	Tillers	Spikelets	Yield
		no./m^2	g/m^2	no./m^2	no./m^2	g/m^2	no./m^2	no./tiller	kg/ha
Cultivar	Akron	16	56	166	1468	356	279	14.7	1186
	Lamar	16	54	158	1376	349	276	15.3	1068
	TAM 107	16	51	148	1330	324	252	13.0	1139
	LSD (0.05)	NS	NS	NS	NS	NS	20	0.7	NS
Planting date	Average	17	57	170	1477	360	284	14.3	1208
	Delayed	15	52	145	1305	326	254	14.4	1054
	LSD (0.05)	NS	NS	NS	NS	31	17	NS	116

Table A2.3. Main effect treatment means of *Aegilops cylindrica* and winter *Triticum aestivum* production for different cultivars and nitrogen placements from 1997 to 2000 at Platner, CO.

Treatments		*A. cylindrica*				Winter *T. aestivum*			
		Seedlings	Biomass	Tillers	Spikelets	Biomass	Tillers	Spikelets	Yield
		no./m^2	g/m^2	no./m^2	no./m^2	g/m^2	no./m^2	no./tiller	kg/ha
Cultivar	Akron	12	49	116	959	425	299	14.5	1402
	Lamar	11	37	121	1035	423	281	15.1	1223
	TAM 107	12	44	112	973	377	279	12.2	1313
	LSD (0.05)	NS	NS	NS	NS	NS	NS	NS	NS
Nitrogen placement	Broadcast	11	34	98	834	400	284	13.9	1263
	Sub-surface	12	53	134	1144	416	289	13.9	1363
	LSD (0.05)	NS	NS	NS	NS	NS	NS	NS	NS

Table A3.1. **Weed control of four winter annual grass weeds with imazamox at two spring application timings at Fort Collins, CO in 1998.**

Treatment[b]	Rate	Control[a]			
		AEGCY[c]	BROJA	BROTE	SECCE
	lb ai/a	%			
Early POST					
Imazamox + NIS + UAN	0.016	42	17	3	13
	0.024	95	83	53	20
	0.032	100	80	67	33
	0.040	98	97	95	60
	0.048	100	83	88	42
LSD (0.05)		13	32	36	27
Imazamox + MSO	0.016	27	13	13	7
	0.024	88	48	50	8
	0.032	75	45	37	10
	0.040	95	67	90	17
	0.048	100	75	92	22
LSD (0.05)		11	53	15	7
Late POST					
Imazamox + NIS + UAN	0.016	97	63	43	63
	0.024	100	93	77	88
	0.032	100	98	95	97
	0.040	100	98	95	92
	0.048	100	100	93	95
LSD (0.05)		5	39	35	15
Imazamox + MSO + UAN	0.016	98	63	30	67
	0.024	100	95	87	90
	0.032	100	95	95	90
	0.040	100	97	98	97
	0.048	100	100	97	95
LSD (0.05)		2	40	17	21
LSD (0.05) across all four treatments		8	34	25	16

[a]Visual percent control evaluated 6/30/98.
[b]Early POST, applied 4/22/98; Late POST, applied 5/21/98; NIS, nonionic surfactant (0.25% v/v); MSO, methylated seed oil (1% v/v); UAN, urea ammonium nitrate (1% v/v).
[c]AEGCY, jointed goatgrass; BROJA, Japanese brome; BROTE, Downy brome; SECCE, feral rye.

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Table A3.2. **Visual percentage control of jointed goatgrass and feral rye in Clearfield winter wheat at Fort Collins, CO in 1999 – 2000, determined June 21, 2000.**

		Fall applied				Spring applied	
		1-5 Leaf		1-5 Tiller		Tillered	
Product	**Rate**	AEGCY[a]	SECCE	AEGCY	SECCE	AEGCY	SECCE
	lb ai/a	% control					
Imazamox	0.032	97	94	88	35	82	22
	0.040	97	96	95	57	95	45
	0.048	97	97	97	48	92	43
Maverick	0.031	10	0	0	0	0	0
LSD		10	4	3	17	10	31

[a]AEGCY = *Aegilops cylindrica* (jointed goatgrass); SECCE = *Secale cereale* (feral rye).

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