

Field-scale spatial distribution, water use, and habitat of wild oat in the semiarid Northern Great Plains
by Lee Russell Van Wychen

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Land Resources and Environmental Sciences
Montana State University
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Abstract:
Wild oat (Avena fatua L.) is widely dispersed throughout the Northern Great Plains (NGP), typically occurring in patchy distributions at the field-scale. If weeds are patchy, the environmental impact of weed control and input costs can be reduced through site-specific weed management (SSWM). However, the mechanisms regulating wild oat spatial distribution and the cost effectiveness of SSWM in the NGP need to be understood.

Field experiments were conducted to map wild oat distributions and quantify the. accuracy of continuous weed presence/absence maps produced by crop consultants for use in SSWM. The accuracy of wild oat seedling maps was 70%. SSWM of wild oat could be profitable compared to a traditional broadcast herbicide application, even with the associated technology cost and seedling map inaccuracy.

Greater increases in SSWM profitability could be realized if scouting and management efforts were directed to field areas with suitable wild oat habitat. I hypothesized that wild oat habitat may be limited by field-scale heterogeneity in plant available water. The effects of water stress on wild oat growth and fecundity was quantified in a greenhouse experiment. Lower soil matric potentials reduced wild oat relative growth rate and unit leaf rate due to an allometric tradeoff of assimilates from leaf tissue in favor of root tissue, but allowed wild oat to reproduce under adverse climatic conditions. Wild oat was estimated to produce seed above soil matric potentials of-1.66 MPa.

In three grower-managed cereal grain fields, wild oat was seeded in areas with and without historic wild oat patches to delineate field-scale habitat quality. Almost all wild oat habitat-defining variables (leaf area growth rate, harvest biomass, seeds per plant, biomass water use efficiency, and competitive ratio) were similar between existing patch and non-patch areas. Wild oat grew and produced seed regardless of existing patch boundaries and field-scale heterogeneity in soil water use. Wild oat habitat may be unlimited in agroecosystems of the NGP. Future research efforts should focus on limiting weed fecundity and dispersal instead of correlating soil properties to predict wild oat distribution.

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APPROVAL

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This dissertation has been read by each member of the dissertation committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Wild oat (*Avena fatua* L.) is widely dispersed throughout the Northern Great Plains (NGP), typically occurring in patchy distributions at the field-scale. If weeds are patchy, the environmental impact of weed control and input costs can be reduced through site-specific weed management (SSWM). However, the mechanisms regulating wild oat spatial distribution and the cost effectiveness of SSWM in the NGP need to be understood.

Field experiments were conducted to map wild oat distributions and quantify the accuracy of continuous weed presence/absence maps produced by crop consultants for use in SSWM. The accuracy of wild oat seedling maps was 70%. SSWM of wild oat could be profitable compared to a traditional broadcast herbicide application, even with the associated technology cost and seedling map inaccuracy.

Greater increases in SSWM profitability could be realized if scouting and management efforts were directed to field areas with suitable wild oat habitat. I hypothesized that wild oat habitat may be limited by field-scale heterogeneity in plant available water. The effects of water stress on wild oat growth and fecundity was quantified in a greenhouse experiment. Lower soil matric potentials reduced wild oat relative growth rate and unit leaf rate due to an allometric tradeoff of assimilates from leaf tissue in favor of root tissue, but allowed wild oat to reproduce under adverse climatic conditions. Wild oat was estimated to produce seed above soil matric potentials of –1.66 MPa.

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CHAPTER 1

PROLOGUE

Nothing in biology makes sense, except in the light of evolution, then, equally, very little in evolution makes sense, except in the light of ecology.

–T. H. Dobzhansky

Ecology has the distinction of being peculiarly confronted with uniqueness: millions of different species, countless billions of genetically distinct individuals, all living and interacting in a varied and ever-changing world. One of the earliest plant ecologists in America, Cowles (1901), recognized that plant succession never reaches an equilibrium state due to continuous climatic fluxes and described succession as a variable approaching a variable rather than a constant. The same can be said about weed population dynamics in agroecosystems. An agroecosystem represents a stochastic, highly disturbed, anthropomorphically manipulated system, which undoubtedly influence weed distributions within a field. The presence of weeds in crop fields and across the agricultural landscape is uncertain because seed dispersal is sufficiently probabilistic that there must always be some degree of chance involved in which a species is able to establish persistent populations (Gleason 1926, Hubbell 1995). For a specific field in a specific season, when weeds will germinate, how fast they will grow in relation to the crop, how much seed they will produce, and how effective crop growth and weed control practices are difficult to predict (Ghersa and Holt 1995). Weeds can have retrogressive

and progressive phases of population growth, depending on the stochastic outcome of fecundity, dispersal, habitat, and management.

This thesis will explore the field-scale spatial distribution, habitat and water use of wild oat (*Avena fatua* L.) in dryland agroecosystems. Wild oat occurs throughout the world in cooler climates between 30 and 60° latitude (Figure 1.1) causing large economic losses in dryland cereal grain systems (Chancellor and Peters 1976). Wild oat is widely dispersed in the Northern Great Plains (NGP), but typically occurs in patchy distributions at the field-scale (Colliver et al. 1996). Entire books (Jones 1976) and symposiums (Smith 1983) have been published on wild oat, yet little research has attempted to delineate wild oat's potential habitat at any scale. Odgaard (1972) concluded that wild oat occurs widely on arable soils in temperate climates in the northern hemisphere, but Kuhnel (1965) suggested, with no elaboration, that climate-soil interactions limit wild oat incidence.

Despite the patchiness of wild oat, farmers have traditionally managed inputs according to mean field conditions. Site-specific weed management (SSWM) can reduce the environmental impact of weed control and reduce input costs if weeds are patchy. Luschei et al. (2001) estimated that if less than 72% of a field was infested with wild oat, SSWM was as profitable as a broadcast treatment to the entire field based on the assumption that the weed maps used in SSWM were 100% accurate (all wild oat were identified). However, the accuracy and future cost effectiveness of GPS-based weed maps was unknown because of the impact of wild oat escapes (field areas with wild oat that were unmapped and, thus not managed). Initial field experiments were conducted to map

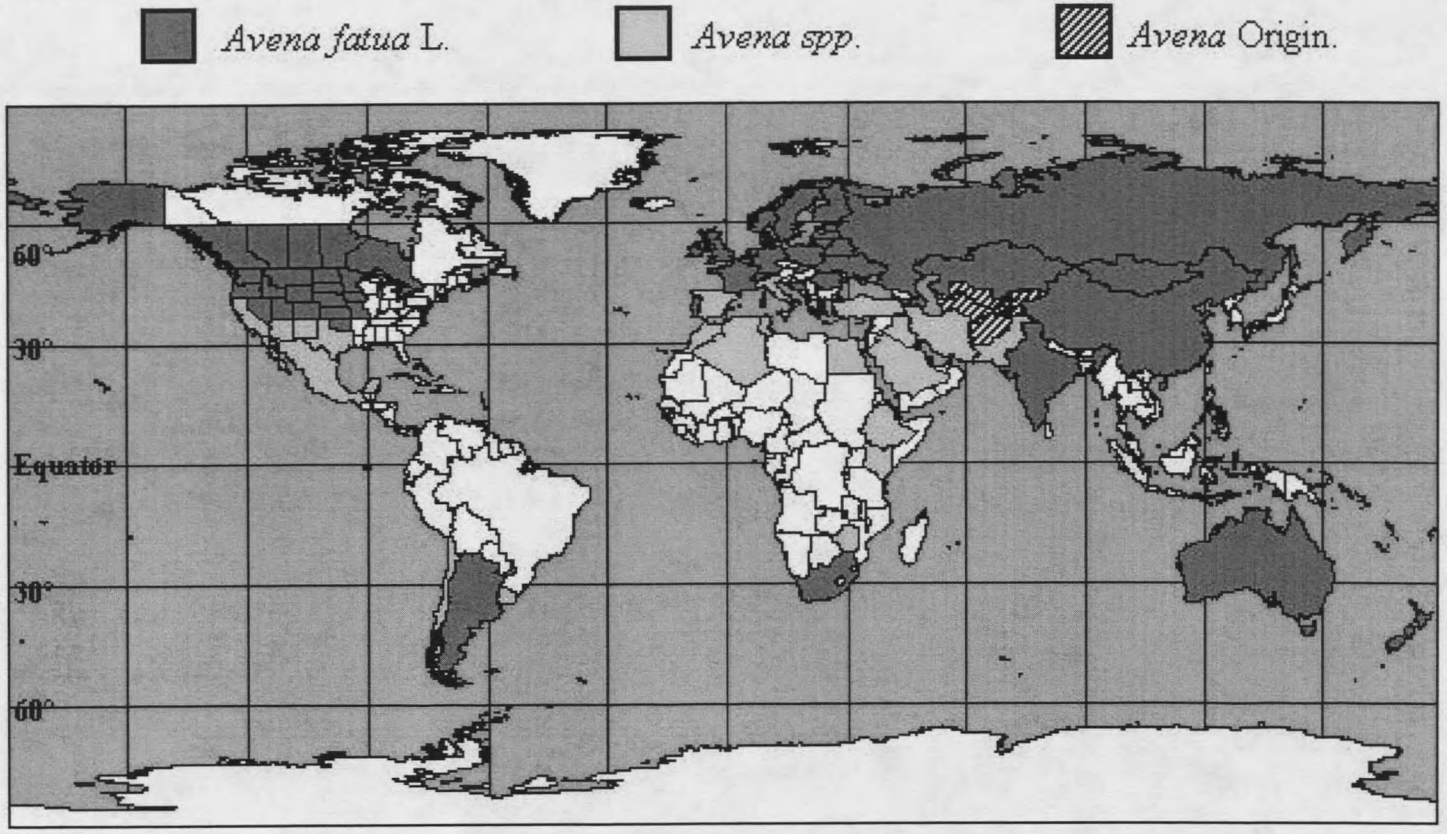


Figure 1.1. Countries, states or provinces with reported infestations of *Avena fatua* L. (spring wild oat), other *Avena* species (*A. ludoviciania, A. sterilis, A. barbata*), and the origin of *Avena* species in the Pamir (Thurston and Phillopson 1976).

wild oat distributions and quantify the accuracy of continuous weed presence/absence maps produced by crop consultants for use in SSWM.

The Cost of Weed Maps and the Information Provided

Little attention has focused on continuous weed presence/absence maps because the maps do not provide weed density information. Weed density maps of entire fields are needed for density-based threshold strategies or variable rate herbicide applications. The use of weed density maps for threshold management of weeds is a philosophically sound concept for integrated weed management, but the practical application of thresholds in the field has suffered because 1) weed density maps have been expensive to produce because of the time and labor involved (Clay et al. 1999; Wiles and Schweizer 1999), 2) farmers tend to be risk averse rather than profit maximizing (Pannell 1990; Reichelderfer 1980), and 3) the technology is still maturing for other weed identification techniques such as real-time optical sensors (Thompson et al. 1991) or remote sensing (Medlin et al. 2000). As an alternative SSWM strategy, the sprayer operator may turn the spray boom on or off during post-emergence herbicide application, thus forgoing the use of weed maps altogether. Threshold studies assume weed density is known across the field, but the cost of assessing density is typically not accounted for when calculating economic thresholds (Lindquist et al. 1999) or economic optimum thresholds (Bussan and Boerboom 2001; Cousens 1987; Munier-Jolain et al. 2002).

The cost-effectiveness and accuracy of GPS-based weed presence/absence maps may provide enough information on weed spatial distributions to support SSWM until

other weed mapping technologies mature. The objectives of my first paper were to quantify the accuracy of GPS-assisted continuous sampled wild oat presence/absence maps made: 1) after crop emergence but prior to herbicide application (seedling map); and 2) during crop harvest (panicle map); and 3) to determine the economic significance of inaccuracy when the wild oat seedling map was used for SSWM.

Characterizing Weed Spatial Distributions

The economics of SSWM could be improved if we could predict weed distribution and abundance from previous weed maps. The question is raised: Why do wild oat patches occur in some areas of fields and not others? Both spatial and non-spatial techniques have been used to characterize weed distributions. Non-spatial methods such as the negative binomial (Hughes 1990); mean/variance ratio (Lloyd 1967), or Lloyd's mean crowding index (Wiles et al. 1992) cannot be used to estimate the density, location, or arrangement of weeds (Mortensen et al. 1993). Geostatistical techniques provide more quantitative information suggestive of the causative processes associated with weed spatial distributions, but a good deal of subjectivity is involved in selecting the best linear unbiased predictor for the appropriate spatial scale (Rew et al. 2001; Rew and Cousens 2001). In addition, many weed populations do not follow a normal distribution and the use of geostatictics is invalidated (cf. Rew et al. 2001). Other statistical techniques related to spatial correlation (canonical correspondence analysis, cluster analysis, principal components analysis) can provide insights into site factors associated with weed patches, but the associated factors do not imply the cause of weed distributions even though they

may account for a large part of the variation explaining weed spatial distributions. Correlative techniques are dependent on the sample size and the subjective selection of independent variables.

Dale et al. (1992) conducted an extensive study correlating weed community composition in spring-seeded crops in Canada. They investigated the relationship between weed communities and variables related to crop management and soil-climatic zones in Saskatchewan (2244 fields over 4 years) and Manitoba (864 fields over 3 years). In the Saskatchewan data, there was a clear and consistent separation of the species into groups along an axis correlated with the gradient in soil-climatic zones. Kochia, Russian thistle, Persian darnel, and foxtail barley were found in the relatively warm and semiarid Brown soil-climatic zone. Common groundsel, field horsetail, common chickweed, and sheperdspurse were found in the cooler and more humid Gray Wooded soil-climatic zone. Species that occurred in high abundance throughout all five soil-climatic zones in Saskatchewan were green foxtail, wild oat, field bindweed, and field pennycress.

All of the above mentioned studies concerning weed spatial distributions are investigative techniques, but the mechanisms driving the spatial patterning of weeds cannot be discerned unless the plant population is perturbed experimentally (Harper 1977; Tilman and Kareiva 1997). In Chapter 4, we propose that the spatial distributions of annual weeds in agroecosystems are a function of fecundity, seed dispersal, management, and habitat (Figure 4.1).

Water as a Limiting Resource

Water is often the most limiting resource in agroecosystems of the Northern Great Plains (NGP) frequently resulting in terminal moisture stress (Padbury et al. 2002). The general perception among producers and researchers is that wild oat occurs mainly in field depressions that are likely to collect more moisture than surrounding areas. Based on observations during the initial wild oat mapping studies, I hypothesized that field-scale heterogeneity in plant available water may limit potential wild oat habitat in dryland agroecosystems. Few studies have quantified wild oat response to decreasing water potential (Akey and Morrison 1984; O'Donnell and Adkins 2001; Sharma et al. 1977) and none provide a complete description of vegetative growth, biomass allocation and reproductive output in response to drought stress. The goal of Chapter 3 was to quantify the impact of limiting water supply on wild oat growth and fecundity under controlled greenhouse conditions.

In the fields where I had quantified wild oat density and spatial distribution during the SSWM research, wild oat patch and non-patch areas were delineated. If lower water availability and use in non-patch areas resulted in less wild oat leaf area growth, shoot biomass and fecundity compared to existing patch areas, we could conclude that grain production fields in the NGP differ in field-scale wild oat habitat availability under the assumptions of uniform response to management and enough seed dispersal to supply seed to the entire field. Thus, proactive weed management efforts could be directed to field areas with suitable wild oat habitat, not just areas where infestations exceed an economic density threshold.

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CHAPTER 2

ACCURACY AND COST EFFECTIVENESS OF GPS-ASSISTED WILD OAT MAPPING IN SPRING CEREAL CROPS

Abstract

Managing weed infestations in a spatially precise manner requires accurate and cost-effective weed identification techniques. The goal of our research was to quantify the accuracy of continuous weed presence/absence maps and assess how management based on those maps may affect producer net returns. Each continuous sampled map covered the entire field and contained vector polygons labeled as either wild oat presence or wild oat absence. The accuracy of the continuous wild oat maps at each sampling time was determined from georeferenced quadrats of wild oat densities. The accuracy of the continuous wild oat seedling maps ranged from 48.3 to 87.1% among the six site-years. The accuracy of the wild oat seedling maps improved by at least 8% when a 10-m buffer was included around areas mapped as wild oat presence. The accuracy of continuous wild oat panicle maps from the combine at harvest ranged from 65.8 to 90.9% among the six site-years. The variation in accuracy for the wild oat seedling maps among sites was greater than the accuracy of the panicle maps. Net returns ($ ha^{-1}) for four site-years were calculated and compared for four possible weed management approaches on each field. A site-specific herbicide application to areas mapped as wild oat presence always generated higher net returns than a herbicide application over the entire field for four sites. A site-specific herbicide application to areas mapped as wild oat presence plus a surrounding 10-

m buffer area only resulted in a higher net return in one of 12 site-years compared to a site-specific herbicide application without the 10-m buffer. This site had the lowest (48.3%) wild oat seedling map accuracy and uncontrolled wild oat had a high yield impact. This research indicates that using a continuous weed sampling method based on presence or absence for site-specific herbicide application can be profitable over a herbicide application to the entire field, even with the associated technology cost and seedling map errors.

Introduction

In fields where weeds are heterogeneously distributed, site-specific weed management (SSWM) has the potential to improve producer net returns and environmental quality (Johnson et al. 1997; Oriade 1995). Many studies have demonstrated the economic benefits of SSWM over broadcast herbicide application (Felton et al. 1991; Lindquist et al. 1998; Luschei et al. 2001; Maxwell and Colliver 1995; Medlin and Shaw 2000). In addition to direct savings from reduced herbicide use, there are indirect benefits like fewer sprayer refills resulting in reduced water costs and faster application times.

An essential component of SSWM requires special technology to detect weeds at the time of management or concerns the acquisition of weed distribution information within a field. Real-time decisions require expensive equipment to recognize weed patches that construct binary spray/no-spray actions (Paice et al. 1995; Stafford and Miller 1993; Thompson et al. 1991). In the 'map-based' approach weeds are mapped in

one operation and sprayed in a later field operation (Johnson et al. 1997). The map-based approach requires labor-intensive field sampling to quantify weed spatial distributions that direct spray/no-spray actions in a later operation (Clay et al. 1999; Medlin and Shaw 2000; Mortensen et al. 1993; Rew et al. 1996). The advantage of map-based weed management is the ability to manage when the weeds are not visible (i.e. preemergence herbicides).

Weed spatial distribution maps can be generated with discrete or continuous sampling techniques (Rew and Cousens 2001). Discrete sampling constructs weed spatial distribution maps by counting weed density within unique points from a predetermined grid. Wiles and Schweizer (1999) estimated the cost of collecting weed density at each point to be $0.08. They did not include the global positioning system (GPS) or data processing costs to transform the seedling counts into a weed distribution map. Intensive grid sampling of a whole field is impractical because of the time, cost and labor required (Clay et al. 1999; Medlin and Shaw 2000). Thus, construction of weed distribution maps has focused on discrete weed-sampling techniques in conjunction with spatial statistics (Cardina et al. 1995; Colbach et al. 2000; Rew and Cousens 2001). Weeds such as wild oat are heterogeneously distributed (Maxwell and Colliver 1995), suggesting that weed maps could be generated based on the spatial correlation exhibited by the species (Cardina et al. 1995; Johnson et al. 1995). However, intensive sampling is still required because large grid sizes (distances between sample points) increase the possibility of losing information due to weed spatial variation (Wiles et al. 1993).

For the continuous sampled map, data are collected over the entire area. In other words, 100% of the area is covered in vector polygons of various shapes depending on the type of qualitative description being recorded (i.e. presence/absence). Continuous sampling may be more appropriate for SSWM because it is less costly and labor intensive. Continuous sampling lacks the site specificity of discrete point samples and thus is less suitable for ecological studies. However, detailed weed counts are not required for SSWM if a herbicide spray-boom is to be switched on and off when weeds are present or absent. Several new methods of continuous weed mapping are now possible because GPS/geographic information system (GIS) technology is more accessible and affordable for producers and crop consultants (Stafford et al. 1996). Crop consultants have traditionally mapped weeds using hand drawn maps recorded during several visits to the field (Mortensen et al. 1998). Currently, the crop consulting business is expanding and adapting to provide the expertise necessary for producing spatially referenced weed maps (Mortensen et al. 1998). The least time consuming mapping method is marking weed presence/absence using GPS. The crop consultant can produce continuous sampled weed maps by toggling a switch to indicate weed presence or absence while driving at a moderate rate of speed (5-10 km hr^{-1}) in a predetermined swath width over fields. While this mapping method has the advantage of being efficient, it gives no indication of weed density, which may be useful for more refined weed threshold based management. Theoretically, the faster the mapping method, the less accurate it becomes. Regardless of the weed mapping method used in SSWM, there are likely tradeoffs between accuracy of the method and its cost.

Little attention has focused on continuous weed seedling map accuracy and the resulting impact on net returns. The success of GPS-assisted weed mapping for implementing SSWM will depend on the tradeoff between the accuracy of the method and the costs associated with the technology. The first two objectives of this research were to quantify the accuracy of GPS-assisted continuous sampled wild oat presence/absence maps made: 1) after crop emergence but prior to herbicide application (seedling map); and 2) during crop harvest (panicle map). The third objective was to determine the economic significance of inaccuracy when the wild oat seedling map was used for SSWM.

Materials and Methods

Two fields were mapped for weeds in 1998 and four fields in 1999. All fields were located in north central Montana, historically seeded to cereal grain, and either continuously cropped or in a crop-fallow rotation depending on environmental conditions. Relevant field information and dates for planting, wild oat mapping, spraying, and harvesting are presented in Table 2.1. All site-years were planted with spring wheat except Fife 1998, which had barley. The two sites in 1998 were planted about a week earlier than average Montana planting dates. The sites in 1999 were planted in a timely fashion except the Box Elder site, which was delayed due to several rainfalls in early and mid May. At all sites, the producer applied either 0.17 or 0.23 kg a.i. ha^{-1} of glyphosate to manage any emerged weeds prior to planting. At each site, four separate wild oat maps were created using a differential global positioning system

(DGPS). Both a continuous and discrete map was generated at the wild oat seedling and panicle stages of development.

The continuous wild oat seedling map was created using an all-terrain vehicle (ATV) mounted with a DGPS receiver and a computer[1]. Mapping occurred during the 2 to 6 leaf stage of wild oat. A crop consultant in the North Central region of Montana was hired to generate all the continuous sampled wild oat seedling maps. The two sites in 1998 were mapped using a patch perimeter method. The perimeter of each patch was determined as the outermost occurrence of wild oat seedlings. The ATV was driven around wild oat infested areas following the perceived patch edge until the area was enclosed. The four sites in 1999 were mapped with the same equipment. Instead of using the patch perimeter method, the ATV was systematically driven across the field on transects spaced 9.2 m apart. When the ATV encountered wild oat seedlings at any point within the 9.2 m transect a button on the computer would be turned on indicating wild oat presence. An analogy would be driving a 9.2 m wide sprayer back and forth across the field with the driver turning the sprayer on and off based on wild oat presence and absence. The crop consultant changed methods in order to decrease the time needed to map an equivalent area, but the cost remained the same. The differences in accuracy between the patch perimeter method used in 1998 and the swath-width method used in 1999 appeared to be negligible. Misclassifications of wild oat seedlings were equally likely to occur between the two types of continuous sampling methods (DeImna Heiken, personal communication).

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[1] Ashtech Ag Navigator, Model RDAC, Magellan Corp., 469 El Camino Real, Santa Clara, CA. 95050.

The data for the discrete sample wild oat seedling map was collected just before or shortly after herbicide application (Table 2.1) by walking parallel transects in the specified grid patterns described below. Wild oat density was counted in 0.29 m^{-2} rectangular quadrats laid perpendicular to the crop row at all sites. Each quadrat count was georeferenced with a DGPS receiver and computer[1]. The density of both wild oat and crop were recorded. The 1998 Sun River site was sampled on a 10- by 10-m grid in 1/3 of the field (100 quadrats ha^{-1}) and a 50- by 10-m grid in the remainder of the field (20 quadrats ha^{-1}). The 1998 Fife site was sampled on a repeating, stratified grid pattern of 20- by 20-m followed by a 5- by 20-m pattern (40 quadrats ha^{-1}). All sites in 1999 were sampled on a 20- by 20-m grid pattern (25 quadrats ha^{-1}).

The data for the discrete wild oat panicle maps was collected 2-4 wk before crop harvest (Table 2.1). Wild oat density was counted in 0.29 m^{-2} rectangular quadrats laid perpendicular to the crop row at all sites. Each quadrat count was georeferenced separately with a DGPS receiver and computer[1]. The density of both wild oat panicles and crop tillers were recorded. The 1998 sites were sampled on a semi-systemic grid resulting in approximately 15 quadrats ha^{-1} at Sun River and 19 quadrats ha^{-1} at Fife. All sites in 1999 were sampled on a 20- by 20-m grid pattern (25 quadrats ha^{-1}).

The continuous wild oat panicle maps were generated from a combine during harvest at each site. This was accomplished by using a DGPS receiver and computer[1] to 'tag' wild oat location as the 9.2 m combine header entered and exited patches. The wild oat entering the header was rated into one of four abundance categories and separated later into presence or absence classifications.

Table 2.1. Agronomic information and GPS-assisted wild oat mapping dates for six experimental site-years in North Central Montana.

Year	Site	Field size	Row spacing	Planting	Discrete seedling map	Continuous seedling map	Herbicide application	Discrete panicle map	Harvest
		ha	cm	Date					
1998	Sun River	24.3	30.5	April 22	May 28	May 18	May 29	July 26	August 18
1998	Fife	25.9	30.5	April 16	June 4	May 20	June 5	July 28	August 13
1999	Sun River	24.3	30.5	April 25	June 15	June 7	June 10	July 29	August 17
1999	Fife	25.9	30.5	May 4	June 14	June 2	June 7	July 28	August 19
1999	Box Elder	20.2	22.9	May 25	June 23	June 21	June 22	July 29	August 26
1999	Chester	12.1	30.5	May 5	June 23	June 15	June 18	July 29	August 18

Wild Oat Map Accuracy Assessment

The accuracy of the continuous sampled wild oat maps was determined at two separate sampling times; wild oat seedlings and wild oat panicles. We used the discrete sampled map with known wild oat densities to determine the continuous sampled map (wild oat presence/absence) accuracy. No comparisons were made in map accuracy between the seedling and panicle stages of wild oat. A 2 × 2 contingency table was constructed for each site at each wild oat sampling time (seedling and panicle stage). The contingency table quantified the accuracy of the continuous wild oat presence (A_{PRES}) or absence (A_{ABS}) areas relative to the discrete wild oat density samples (Figure 2.1). At each respective sampling time, we used GIS software[2] to overlay the discrete sampled map with the continuously sampled map on the same coordinate system. In this way, the data from the continuous sampled map can be ground-truthed at the exact position were the wild oat density was recorded. The combined data file was then sorted into one of four possible outcomes. These outcomes were: 1) zero wild oat m^{-2} classified as absence; 2) ≥1 wild oat m^{-2} classified as presence; 3) zero wild oat m^{-2} classified as presence; 4) ≥ 1 wild oat m^{-2} classified as absence. The first two outcomes are correct classifications and the last two outcomes are incorrect classifications. Accuracy was calculated as the number of correct classifications divided by the total number of classifications. The accuracy of the continuous sampled maps remained constant for a site whether 20, 40, 60 or 80-m grid points were used to assess the accuracy (data not shown).

Two additional methods were used to assess wild oat map accuracy. The first method used a wild oat detection threshold of ≤ 5 m^{-2} as counted in the discrete point

observations. Thus, any discrete samples of wild oat ≤ 5 m^{-2} did not decrease the accuracy of continuous sample wild oat map when they were classified as absence by the crop consultant. The second method used GIS software[2] to place a 10-m buffer (A_{BUF}, Figure 2.1) around areas mapped as wild oat presence. Thus, any wild oats observed in the discrete point maps that occurred within 10-m of an area mapped as wild oat presence was counted as a correct classification.

Cost Effectiveness of Wild Oat Seedling Maps

Crop yield and net returns were predicted from the continuous wild oat seedling maps. The average wild oat seedling density for A_{PRES}, A_{ABS}, A_{BUF} and A_{OUT} (Figure 2.1) were calculated from the discrete sampled seedling maps. The Sun River 1998 and 1999 sites are omitted from analysis of crop yield and net returns due to spurious yield data acquisition. Crop yield loss was predicted from a linear yield response model for the decision scale analysis (DSA) method outlined by Luschei et al. (2000). Luschei et al. (2000) concluded that the DSA method was the best way to relate site-specific crop yield to georeferenced weed densities for these sites. The DSA method used spatial averaging to determine crop yield and a calibrated consultant map (CCM) procedure to determine weed density values. The CCM procedure combines the information from the quadrat (0.29 m^{-2}) and the continuous sampled weed presence/absence map (9.2 m width) to predict weed density at the decision scale (16-m spray boom). Crop yield loss parameter values of the intercept (expected weed-free yield) and slope (per unit yield impact of

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[2] ArcView GIS, Version 3.2, Environmental Systems Research Institute, Inc., 380 New York St., Redlands, CA. 992373

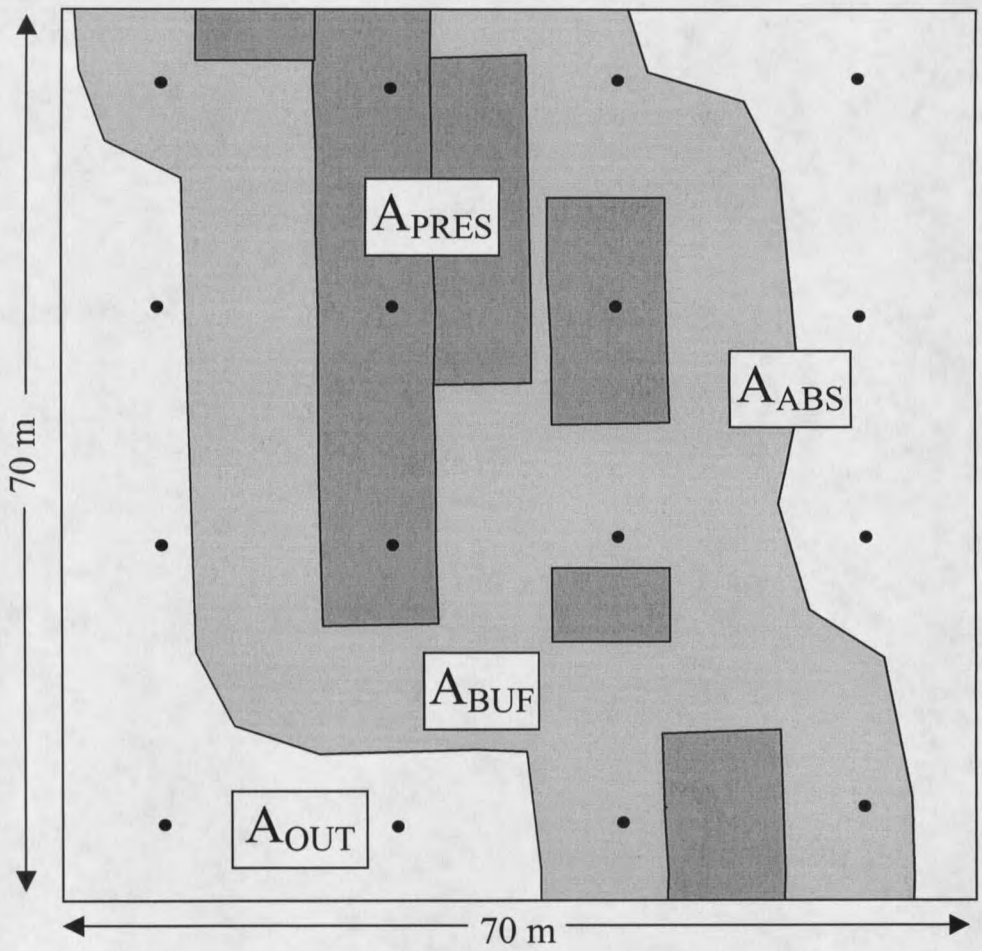


Figure 2.1. Example map of continuous and discrete sampled wild oat methods. The discrete sampling method contains point data of wild oat density (●). The continuous sampling method contains areas classified as wild oat presence (A_{PRES}) and wild oat absence (+ A_{ABS}). The A_{ABS} was then geoprocessed into 10-m buffer area (A_{BUF}) surrounding A_{PRES}, with the remaining area categorized as outside (A_{OUT}) the buffer, but within the field boundary.

weeds) were generated from the measured yield data (Luschei et al. 2000). The crop yield data were obtained with a yield monitor coupled with DGPS on the producer's combine. The low and high crop yield impact slopes were calculated using a 0.002 and 0.01 yield loss per wild oat, respectively. These values represent the extremes generated by other wild oat interference studies (Chancellor and Peters 1976).

The expected yield for the whole field was calculated from the proportion of the continuous map classified as A_{PRES} or A_{ABS} including its inaccuracies, expected weed free yield, and wild oat impact on crop yield:

$$Y_{fld} = A_{pres}Y\left(\bar{N}_p\right) + A_{buf}Y\left(\bar{N}_b\right) + A_{out}Y\left(\bar{N}_a\right) \tag{2.1}$$

where Y_{fld} is the predicted yield for the field, A_{pres} is the area of the field classified as wild oat presence, Y is the crop yield (T ha^{-1}) as influenced by wild oat and management (Luschei et al 2000), $\bar{N}_p$ is the average wild oat density within A_{pres}, A_{buf} is the area of the field in the 10-m buffer surrounding A_{pres}, $\bar{N}_b$ is the average wild oat density within A_{buf}, A_{out} is the remaining area of the field outside of A_{pres} and A_{buf}, and $\bar{N}_a$ is the average wild oat density in areas mapped as wild oat absence (Figure 2.1).

The net return ha^{-1} was predicted for four different weed management approaches: herbicide application over entire field (H+), no herbicide (H-), a site-specific herbicide application to A_{PRES} (SS), and a site-specific herbicide application to A_{PRES} plus A_{BUF} (SS+B):

$$NR = \left(\frac{Y_{fld}}{A_{tot}}\right)p - \gamma C_{herb} - \beta C_{tech} \tag{2.2}$$

where *NR* is net return in \$ ha^{-1}, A_{tot} is the total area of the field, p is the crop price = \$114 T^{-1}, γ is the proportion of the field sprayed, C_{herb} is the herbicide cost = \$44.48 ha^{-1}, β is 0 for H+ and H- and 1 for SS and SS+B weed management treatments, and C_{tech} is the cost of precision herbicide technology = \$12.36 ha^{-1}. The technology cost includes \$9.89 ha^{-1} for continuous wild oat mapping and \$2.47 ha^{-1} for site-specific herbicide application. Technology cost represents the prices charged for these services in Montana in 1999. The *NR* does not include other crop husbandry costs (e.g. planting and harvesting). This method of calculation allowed us to determine if the value of lost yield due to wild oat escapes in SSWM exceeds the difference in herbicide costs between site-specific and whole-field weed management given the inaccuracies in continuous sampled weed maps.

Results and Discussion

Wild Oat Map Accuracy Assessment

Seedling Maps. The most accurate wild oat seedling map occurred at Sun River 1999 (Table 2.2). The high accuracy reflects the lack of spatial variability in the wild oat population. We expected the crop consultant to obtain high continuous sampled map accuracy in fields with a spatially homogenous wild oat population. Spatially homogenous could mean either, a field completely infested with wild oat, or a field with no wild oat infestation. At Sun River 1999, 99% of the field was infested with wild oat (607 out of 613 quadrats had at least 1 wild oat m^{-2}). The least accurate wild oat seedling map occurred at Fife 1998, which had an intermediate level of wild oat infestation with

Table 2.2. Accuracy of the continuous wild oat seedling maps. Accuracy is based on the number of correct and incorrect classifications of wild oat seedling presence or absence before (or shortly after) a post-emergence herbicide application. The accuracy is also presented for two post-mapping accuracy improvement methods, a 5 wild oat m^{-2} detection threshold and 10-m buffer area. Percent infestation indicates the number of observations of wild oat seedling densities greater than zero divided by the total number of discrete sampled quadrat counts taken at each site.

			Wild oat presence		Wild oat absence			
Year	Site	Accuracy method	Correct	Incorrect	Correct	Incorrect	Accuracy	Infestation
			Number of quadrat observations				%	
1998	Sun River	Original	294	102	533	236	71.0	45.4
		Density threshold	294	102	612	157	77.8	
		10-m buffer area	458	102	533	72	85.1	
1998	Fife	Original	95	5	328	447	48.3	61.9
		Density threshold	95	5	422	353	59.1	
		10-m buffer area	268	5	328	274	68.1	
1999	Sun River	Original	532	4	2	75	87.1	99.0
		Density threshold	532	4	6	71	87.8	
		10-m buffer area	606	4	2	1	99.2	
1999	Fife	Original	326	28	118	218	64.3	78.8
		Density threshold	326	28	180	156	73.3	
		10-m buffer area	511	28	118	33	91.0	
1999	Box Elder	Original	86	80	385	91	73.4	27.6
		Density threshold	86	80	431	45	80.5	
		10-m buffer area	140	80	385	37	81.8	
1999	Chester	Original	45	32	223	48	77.0	26.7
		Density threshold	45	32	243	28	82.8	
		10-m buffer area	83	32	223	10	87.9	

poorly defined patches (difficult to detect edges). The 48.3% accuracy at Fife 1998 resulted mainly from A_{ABS} that contained at least 1 wild oat m^{-2}. The classification error resulted from germination of subsequent wild oat cohorts after the continuous seedling map was created. The 15-d between the continuous and discrete sampled wild oat maps was longer than anticipated due to several rainfalls (Table 2.1). This introduces a critical issue regarding timing of weed mapping and potential efficacy of SSWM. Depending on the weed species, several rainfalls immediately after mapping a field would most likely delay any control measures while also stimulating several new cohorts. This also indicates that timing is critical for any weed mapping procedure given the fast weed growth rates typical during the beginning of June in the Northern Plains.

The accuracy of the continuous mapping method improved by at least 5.% at all sites except Sun River 1999 when using a detection threshold of 5 wild oat m^{-2} (Table 2.2). Sun River 1999 had very few low wild oat density areas. A 10-m buffer area improved the continuous map accuracy at least 8 %. The accuracy of the continuous wild oat seedling map at Fife 1999 improved from 64.3% to 91.0% when a 10-m buffer area was included in the calculation. The 26.7% increase in accuracy at Fife 1999 is related to the subsequent emergence of wild oat cohorts near A_{PRES}. The 10-m buffer area improved accuracy at every site more than using a 5 wild oat m^{-2} detection threshold. Wild oat classified as absence on the continuous map when $\geq$1 wild oat m^{-2} actually occurred is potentially the most costly error. We refer to this error type as a wild oat escape. Bivariate histograms of wild oat escapes from the continuous seedling maps indicate a majority of the mapping errors occurred at low densities or within short

distances of A_{PRES} (Figure 2.2). The Fife 1998 site had the lowest accuracy with many errors occurring at wild oat densities >5 m^{-2} and distances >10 m from A_{PRES}. A 10-m buffer surrounding A_{PRES} would include a large percentage of the wild oat escapes at the Sun River 1998 and 1999 and Fife 1999 sites. The wild oat escapes at Box Elder and Chester 1999 (wild oat infestation < 28%) were mostly at densities less than 10 m^{-2} and distances within 10 m of A_{PRES}. Most wild oat escapes >10 m away from A_{PRES} were at low densities, which decreases the chance to produce new patches and minimizes crop yield loss. At Sun River 1999 (wild oat infestation of 99%) only one discrete sample of wild oat seedlings occurred greater than 10 m from A_{PRES}. There was a counterintuitive sense of trying to find areas not infested with wild oat when creating the continuous seedling map at Sun River 1999.

Panicle Maps. The accuracy of continuous wild oat panicle maps produced during crop harvest ranged from 65.8 to 90.9% among the six site-years using the original weed maps (Table 2.3). The lowest accuracy (Box Elder 1999) resulted from scattered low-density wild oat panicles. Discrete sampled quadrats had a low probability of capturing a single wild oat panicle that would be classified as wild oat presence during harvest. A 10-m buffer area provided a greater accuracy than a 5 wild oat m^{-2} detection threshold at all sites. The 10-m buffer area increased accuracy 3.1 to 11.9% compared to the original wild oat panicle map created during harvest.

Incorrectly classified wild oat panicles during crop harvest most often resulted in errors within a short distance of areas mapped as having wild oat (Figure 2.3). Although Box Elder 1999 had the least accurate wild oat panicle map, only six discrete samples

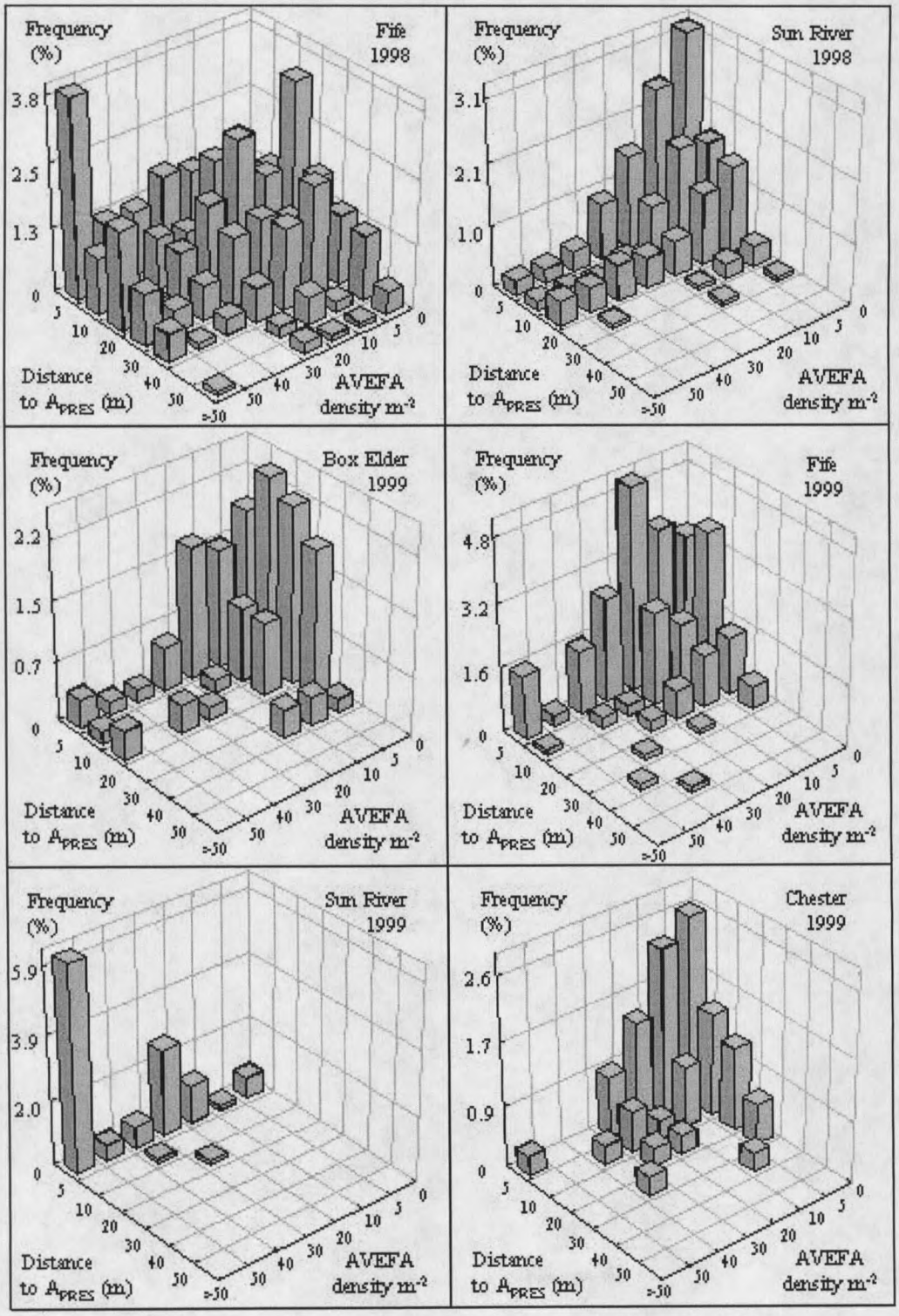


Figure 2.2. Bivariate histograms of incorrectly classified wild oat seedlings. Each histogram represents wild oat seedlings observed during the discrete sampling, but not classified as wild oat presence during the continuous sampling for each site. The x-axis indicates the distance (m) to the nearest area classified as wild oat presence (APRES) and the z-axis is the wild oat (AVEFA) seedling density at each distance.

Table 2.3. Accuracy of the continuous wild oat panicle maps. Accuracy is based on the number of correct and incorrect classifications of wild oat panicle presence or absence during crop harvest. The accuracy is also presented for two post-mapping accuracy improvement methods, a 5 wild oat m^{-2} detection threshold and 10-m buffer area. Percent infestation indicates the number of observations of wild oat panicle densities greater than zero divided by the total number of discrete sampled quadrat counts taken at each site.

			Wild oat presence		Wild oat absence			
Year	Site	Accuracy method	Correct	Incorrect	Correct	Incorrect	Accuracy	Infestation
			Number of quadrat observations				%	
1998	Sun River	Original	336	16	2	18	90.9	95.2
		Density threshold	336	16	3	17	91.1	
		10-m buffer area	354	16	2	0	95.7	
1998	Fife	Original	220	72	154	48	75.7	54.3
		Density threshold	220	72	165	37	77.9	
		10-m buffer area	249	72	154	19	81.6	
1999	Sun River	Original	478	37	18	48	85.4	90.5
		Density threshold	478	37	22	44	86.1	
		10-m buffer area	526	37	18	0	93.6	
1999	Fife	Original	277	115	149	80	68.6	57.5
		Density threshold	277	115	164	65	71.0	
		10-m buffer area	351	115	149	6	80.5	
1999	Box Elder	Original	108	162	262	30	65.8	24.6
		Density threshold	108	162	279	13	68.9	
		10-m buffer area	137	162	262	1	71.0	
1999	Chester	Original	12	56	241	16	77.8	8.6
		Density threshold	12	56	244	13	78.8	
		10-m buffer area	22	56	241	6	80.9	

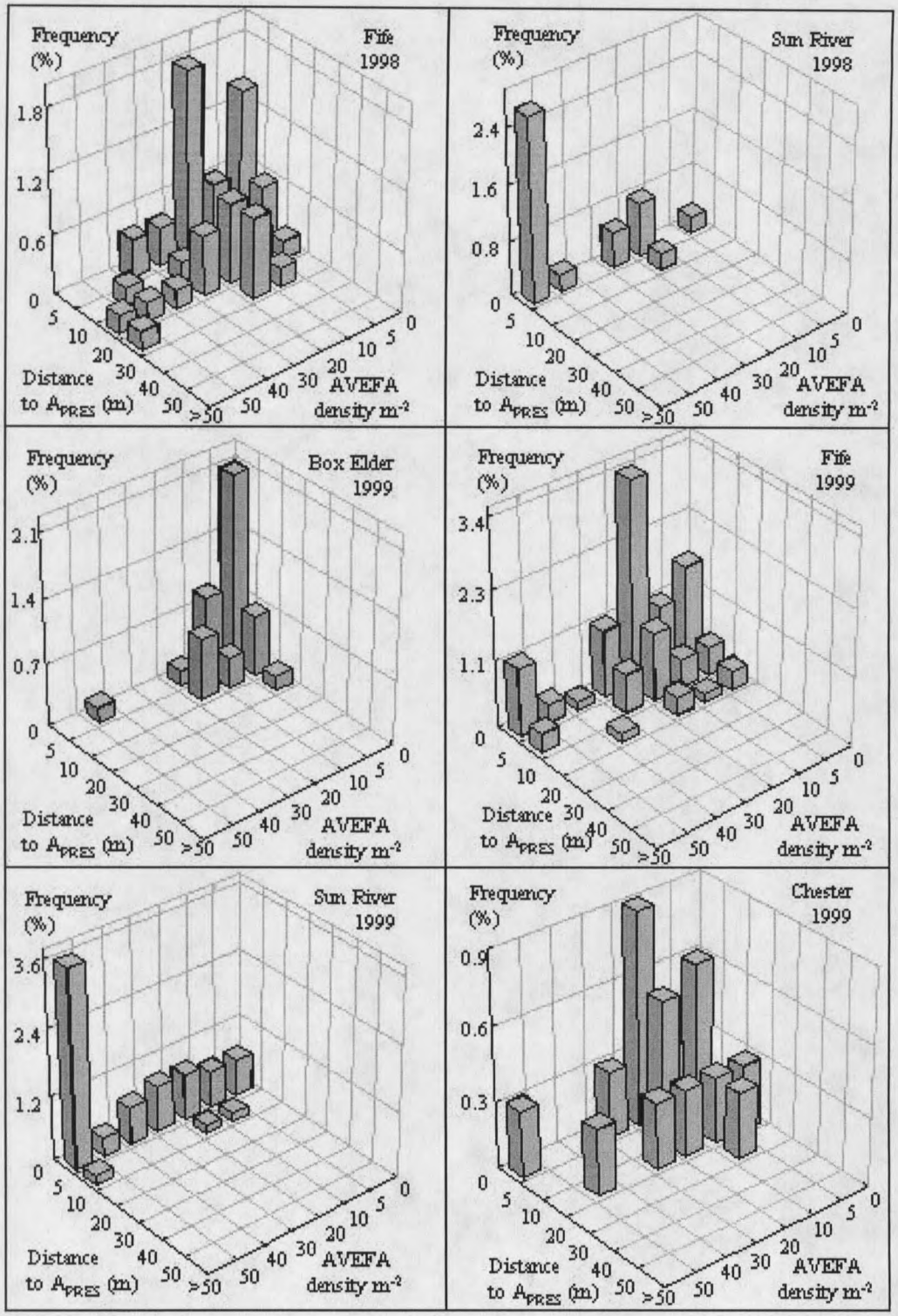


Figure 2.3. Bivariate histograms of incorrectly classified wild oat panicles. Each histogram represents wild oat panicles observed during the discrete sampling, but not classified as wild oat presence during the continuous sampling for each site. The x-axis indicates the distance (m) to the nearest area classified as wild oat presence (APRES) and the z-axis is the wild oat (AVEFA) panicle density at each distance.

exceeded five wild oat m^{-2} greater than 10-m from A_{PRES}. All incorrect classifications of wild oat panicles for Sun River 1998 and 1999 were within 10-m of the nearest correctly mapped area. However, 90% of those fields where infested with wild oat at harvest.

Seedling vs. Panicle Map. The panicle maps had greater accuracy than the seedling maps when comparing the overall accuracy of the original wild oat maps (Table 2.4). The variation in accuracy among site-years was also greater for the seedling maps for both accuracy improvement methods compared to the panicle maps. Identifying mature wild oat plants growing above the cereal grain canopy at harvest was easier than identifying seedlings growing within the cereal grain canopy. When adding the 10-m buffer area to calculate accuracy, the seedling maps had a slightly greater accuracy than the panicle maps. This may have been due to the inability to see low-density lodged wild oat plants from the combine. However, the wild oat panicle maps were still the most accurate continuous mapping method because of the ease in identification between wild oat and cereal grains at maturity compared to the seedling stage.

Table 2.4. Overall accuracy for the continuous wild oat seedling and panicle mapping methods across all sites. The accuracy is also presented for two post-mapping accuracy improvement methods, a 5 wild oat m^{-2} detection threshold and 10-m buffer area.

		Overall accuracy	
Wild oat sampling time	Accuracy method	mean	sd
		%	
Seedling stage	Original	70.2	13.1
	Density threshold	76.9	10.0
	10-m buffer area	85.5	10.4
Panicle stage	Original	77.4	9.6
	Density threshold	79.0	8.5
	10-m buffer area	83.9	9.2

Two issues affecting the usefulness of the panicle maps are how they relate to true wild oat distributions as influenced by management, and how well maps created during harvest will relate to seedling maps during the next growing season. Initial results from anisotropic semivariograms indicate that wild oat infested areas are elongated in the direction of machinery travel suggesting wild oat maps in following years may be influenced by harvest or tillage equipment. Further insights into the spatial and temporal dynamics of wild oat patches could improve the prediction of future spatial distribution of wild oat, and subsequent site-specific management recommendations.

Cost Effectiveness of Wild Oat Seedling Maps

The highest average wild oat density occurred in A_{PRES} at all site-years (Table 2.5). Average wild oat density in A_{BUF} was 30 to 80% less than A_{PRES}. Wild oatdensities were the lowest in A_{OUT} at all site-years. The predicted crop yield was lower for H- in A_{PRES} compared to H+ for all site years. Crop yield increased for both H+ and H- in A_{ABS} compared to A_{PRES} at Fife 1998 and 1999. At Box Elder 1999, the predicted crop yield was the same for all areas of the field with H+ because of a small yield impact due to low wild oat densities. At Chester 1999, the H+ resulted in greater crop yield in A_{PRES} than in A_{ABS} because of the overall reduction in wild oat density and decreased competition. The average wild oat density was only 22.9 m^{-2} in A_{PRES} at Chester 1999, which occurred mostly in the lower areas of the field. It should be noted that the lowest wild oat densities did not necessarily indicate the highest crop yields. All of these North Central Montana sites typically endure some period of drought stress. Plant available water across sites would likely help explain why the Fife 1998 and 1999 sites had the highest predicted

Table 2.5. The size, average wild oat density, and predicted crop yield for each classification area based on the accuracy of the continuous wild oat seedling map. The continuous sampling method contains areas classified as wild oat presence (A_{PRES}) and wild oat absence (A_{ABS}). The A_{ABS} was further divided into a 10 m buffer area (A_{BUF}) surrounding A_{PRES} and the area remaining outside the buffer (A_{OUT}) (Figure 2.1). The crop yield was predicted for each area sprayed with a herbicide or left untreated. The predicted yield is based on the parameters generated from the measured yield data for each site and presented in Luschei et al. (2000).

		Wild oat seedling classification			Predicted yield	
Year	Site	Area	Size	Density	Sprayed	Untreated
			ha	m^{-2}	—— T ha^{-1} ——	
1998	Fife	A_{PRES}	3.0	98.4	2.18	1.60
		A_{ABS}	22.9	16.4	2.76	3.00
		A_{BUF}	6.6	32.0	2.65	2.73
		A_{OUT}	16.3	10.1	2.80	3.11
1999	Fife	A_{PRES}	13.3	31.3	2.30	2.04
		A_{ABS}	12.6	10.4	2.47	2.41
		A_{BUF}	9.5	12.4	2.45	2.37
		A_{OUT}	3.1	4.4	2.51	2.51
1999	Box Elder	A_{PRES}	5.2	11.8	1.17	1.10
		A_{ABS}	15.0	2.2	1.17	1.24
		A_{BUF}	6.8	3.2	1.17	1.23
		A_{OUT}	8.1	1.4	1.17	1.25
1999	Chester	A_{PRES}	2.7	22.9	0.76	0.28
		A_{ABS}	9.4	2.0	0.71	0.58
		A_{BUF}	5.4	2.8	0.71	0.57
		A_{OUT}	4.1	0.9	0.70	0.60

crop yields, nearly two-fold of any other site regardless of wild oat density. The mean growing season precipitation was at least 6-cm greater at Fife during both years than the other sites (Data not shown).

The H- treatment had the highest NR given the observed yield at each site (Table 2.6). The economic threshold (return of increased crop yield exceeds the cost of the treatment) was only exceeded twice with a high crop yield impact from wild oat at Fife 1998 and 1999. These results indicate the marginal economic benefit of single-season

herbicide applications for low-return wheat-fallow systems in the Northern Great Plains. No herbicide application would clearly be the treatment of choice if no subsequent penalty is assessed for future wild oat populations. However, it was not within the scope of this research to analyze long term NR and economic optimum thresholds so only single year returns are discussed.

Comparing the NR of SS versus H+, the SS treatment had higher NR at every site except Fife 1999. The H+ resulted in \$0.95 ha^{-1} higher NR at Fife 1999 compared to the SS treatment with a high crop yield impact from wild oat. If the site-specific herbicide application technology cost were doubled (= \$24.72 ha^{-1}) then H+ would result in higher NR than SS for 4 out of 12 cases (Table 2.6). The SS had higher NR than the SS+B in every case except one. The only site with the highest NR for the SS+B was Fife 1998, with a 1% T ha^{-1} crop yield loss per wild oat. This site also had the lowest seedling map accuracy (Table 2.2), which suggests a 10-m buffer can be economically effective for controlling nearby wild oat escapes, but only when the escapes cause a high crop yield loss. Rew et al. (1996) noted that adding a 4-m buffer would compensate for sampling errors in their mapping, but that it would also increase the area treated, potentially decreasing the economic benefits of SSWM.

Increasing the predicted cost of herbicides resulted in the H- treatment having the highest NR in 11 of 12 site and herbicide cost scenarios (Table 2.7). The general effect of increasing herbicide cost was a shift in higher NR towards SS and lower NR for H+. The SS+B always had lower NR than the SS for any herbicide cost between \$20-\$80 ha^{-1}. The NR for SS+B was higher than H+ for any herbicide cost at Fife 1998, but lower than

Table 2.6. Net return ha^{-1} for each weed management approach based on low, predicted (Y_{Pred}), and high yield impact due to wild oat competition. The four weed management approaches were herbicide application over entire field (H+), no weed control (H-), a site-specific herbicide application to areas mapped as wild oat presence (SS), and a site-specific herbicide application to areas mapped as wild oat presence plus the surrounding 10-m buffer areas (SS+B). Net return is calculated as the gross crop yield value for the entire field minus total herbicide cost (44.48 ha^{-1}) for the proportion of the field treated. The SS and SS+B treatments include a \$12.36 ha^{-1} weed mapping and application technology fee.

			Net Return			
Year	Site	Yield Impact[a]	H+	H-	SS	SS+B
				\$ ha^{-1}		
1998	Fife	Low	269.63	351.69	335.81	315.33
		Y_{Pred}	258.97	315.96	306.12	292.26
		High	269.63	262.75	280.51	284.41
1999	Fife	Low	236.71	282.37	249.44	230.58
		Y_{Pred}	226.31	251.21	231.43	218.41
		High	236.71	230.80	235.76	227.65
1999	Box Elder	Low	88.85	143.32	117.39	98.79
		Y_{Pred}	88.79	136.75	114.75	97.55
		High	88.85	137.49	115.10	97.75
1999	Chester	Low	35.94	68.56	49.48	34.78
		Y_{Pred}	37.48	58.19	48.04	35.32
		High	35.94	64.66	48.40	34.41

[a] The low and high yield impact slopes were calculated using 0.002 and 0.01 crop yield loss per wild oat, respectively.

H+ for any herbicide cost at Fife 1999. This can be attributed to the increase in wild oat infestation at Fife from 1998 to 1999.

The cost analysis results are consistent with the notion that the economic advantage of using SSWM depends mainly on the proportion of the field to be targeted with herbicide. Luschei et al. (2000) quantified the break-even weed infestation level as 72% of the field. This infestation level is generated from the same technology cost (\$12.36 ha^{-1}) and weed control cost (\$44.48 ha^{-1}) used in this paper to calculate net

Table 2.7. Net return ha^{-1} for each weed management approach based on potential herbicide costs. The four weed management approaches were herbicide application over entire field (H+), no weed control (H-), a site-specific herbicide application to areas mapped as wild oat presence (SS), and a site-specific herbicide application to areas mapped as wild oat presence plus the surrounding 10-m buffer areas (SS+B). Net return is calculated as the value of the predicted crop yield for the whole field minus total herbicide cost ($20 to $80 ha^{-1}) for the proportion of the field treated. The SS and SS+B treatments include a $12.36 ha^{-1} weed mapping and application technology fee.

Year	Site	Herbicide cost	Net Return			
			H+	H-	SS	SS+B
			$ ha^{-1}			
1998	Fife	20	283.45	315.96	308.92	301.30
		40	263.45	315.96	306.63	293.91
		60	243.45	315.96	304.35	286.53
		80	223.45	315.96	302.06	279.15
1999	Fife	20	250.79	251.21	243.98	239.98
		40	230.79	251.21	233.72	222.35
		60	210.79	251.21	223.46	204.73
		80	190.79	251.21	213.20	187.11
1999	Box Elder	20	113.27	136.75	121.08	112.16
		40	93.27	136.75	115.91	100.23
		60	73.27	136.75	110.74	88.29
		80	53.27	136.75	105.57	76.36
1999	Chester	20	61.96	58.19	53.45	51.57
		40	41.96	58.19	49.03	38.29
		60	21.96	58.19	44.60	25.02
		80	1.96	58.19	40.18	11.74

returns. All of the sites analyzed for NR had weed infestation levels less than 72% except Fife 1999, which had 78.8% initial wild oat infestation (Table 2.2). Fife 1999 was the only site where NR was greater for H+ than SS, but only when using the high crop yield impact estimate for wild oat (Table 2.6). In theory, it should have been more profitable for H+ across all yield impact scenarios at Fife 1999 than SS. However, the 72% weed infestation estimation (Luschei et al. 2001) does not account for adverse yield

impact resulting from herbicide injury, weed escapes, or early season competition prior to herbicide application.

These results only apply to dryland spring grain production in the Northern Plains. Some of the sites with predicted weed-free yields under 2 T ha^{-1} are marginally profitable without any input costs associated with SSWM (Table 2.5). Alternatively, increased returns due to improved environmental quality were not considered. The economic value of improved environmental quality is impossible to assess. No government program currently pays producers for improved environmental quality. The price of wheat ($114 T^{-1}) used in the calculations for net return is generous given the market conditions of 1998-2000. The Fife 1998 site would not have as high a NR if the price of barley ($80 T^{-1}) were used in the net return calculation.

This research clearly indicates that using continuous sampled weed seedling maps based on presence/absence can provide enough accuracy to be used in SSWM. From a cost effectiveness viewpoint, a H+ treatment is only justified over SS when high initial weed infestation occurs throughout a field and the weeds cause high crop yield loss. When adding errors associated with continuous sampled weed maps and the cost of the technology, economic net returns can still be increased over H-. Continuous weed map accuracy under 60% can be improved with a 10-m buffer around areas classified as weed presence. Otherwise, continuous sample weed seedling maps without any accuracy improvement method appear accurate enough to increase NR from SS over H+ given a reasonable technology cost (< $20 ha^{-1}) for the weed maps and associated GIS costs. Use of buffers within a SSWM system may improve NR if weed escapes cause significant

crop yield loss. Producers should consider using spatially referenced continuous weed presence/absence maps for SSWM, especially if less than 70% of their field is infested. There is a tradeoff between the cost and accuracy of producing a spatially referenced weed map. Decreasing the cost of GPS-assisted weed maps should be a high priority. Weed map accuracy greater than 70% will be effective enough to provide higher NR for SSWM within wheat-fallow systems of the Northern Great Plains compared to whole-field herbicide applications. As crop value, weed impacts, and pressure to reduce chemical inputs to the environment increase, the cost of generating maps with improved accuracy may be justified to ensure economic and environmentally optimal weed management decisions.

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CHAPTER 3

RESPONSE OF WILD OAT GROWTH, CARBON PARTITIONING AND FECUNDITY TO A RANGE OF SOIL MATRIC POTENTIALS

Abstract

Weeds will respond to environmental stresses, but the manner and magnitude of the response is often unknown. We used an ecophysiological approach to quantify wild oat response to drought stress in order to elucidate the mechanisms that determine its field-scale habitat range in dryland cropping systems. Wild oat root, leaf, stem, and reproductive tissues were quantified with 12 destructive harvests from early vegetative growth through maturity in greenhouse pot experiments at three soil matric potentials (-0.03, -0.5, and -1.2 MPa). Wild oat allocated about 10% more carbon to roots at the expense of leaf tissue under water stress resulting in a two-fold increase in the root to shoot ratio between 393 and 597 growing degree days (GDD, 5°C base). However, wild oat could only maintain increases in root mass up to 750 GDD at –0.5 MPa. At –1.2 MPa, water stress was severe enough to reduce root relative growth rate (RGR) compared to -0.5 MPa. Despite higher carbon allocation to roots the ratio of root length to root mass did not increase and overall root mass declined because of the relatively lower assimilates available under water stress due to decreased whole plant RGR and unit leaf rate. Seed production decreased fourfold from the wettest to the driest treatment, but wild oat may grow and produce seed above an estimated soil matric potential of –1.66 MPa. The allometric tradeoff of assimilates from leaf tissue in favor of root tissue and

the inability of wild oat to remobilize assimilate from stem and leaf tissues around anthesis carries a physiological cost of reduced seed production, but allows wild oat to reproduce at some minimal level under adverse climatic conditions.

Introduction

Wild oat (*Avena fatua* L.) occurs throughout the world in cooler climates (~ 30 to 60° latitude) (Thurston and Phillipson 1976) causing large economic losses in dryland cereal grain systems (Chancellor and Peters 1976). Water is typically the most limiting resource in agroecosystems of the Northern Great Plains (NGP), frequently resulting in summer drought (Campbell et al. 1993). In Havre, MT, mean annual precipitation is 302 mm with 168 mm occurring from April through July while potential evapotranspiration is 608 mm during the same growing season (Padbury et al. 2002). Thus, in the dry regions wild oat must be water-use-efficient to survive and reproduce, especially in the presence of a crop. Wild oat is widely distributed throughout this region, but typically occurs in patchy distributions at the sub-field scale. Resource availability temporally fluctuates in this landscape making it difficult to identify the relationship between patterns of spatial abundance of wild oat and resource availability, and subsequent competition intensity with crops. The general perception among producers and researchers is that wild oat occurs mainly in field depressions that are likely to collect more moisture than surrounding areas. In a field study near Calgary, Alberta, Faechner et al. (2000) found the highest densities of wild oat correlated with convergent backslopes where water accumulates. Infrequent precipitation events during the growing season often result in

soil matric potentials that frequently limit plant growth. Field areas that can maintain soil matric potentials above the wilting point for the longest periods during the growing season are the ones that support weed and crop growth best.

Understanding the relative morphological and physiological response of crops and weeds to resource supply rates is crucial for understanding mechanisms of plant competition and predicting fecundity of each species (Kropff 1988; Spitters 1989). When soil water and nutrient resources are unlimited, the potential (maximum) growth and reproduction of a species is only limited by temperature, light, and ability to escape pathogens and predators. Quantifying a plant's morphological and physiological changes to decreasing amounts of soil water under those same temperature and light conditions will help define its sub-field scale habitat range.

Few studies have quantified wild oat response to decreasing water potential (Akey and Morrison 1984; O'Donnell and Adkins 2001; Sharma et al. 1977) and none provide a complete description of vegetative growth, biomass allocation and reproductive output in response to drought stress. There are many morphological and physiological measures of plant growth and development. We chose to quantify shoot and root morphological components both directly and indirectly through common growth metrics to characterize the physiological responses of wild oat under water stress. Primary processes affected by water stress include cell expansion, photosynthesis, and dry matter allocation while plant fecundity is affected secondarily by water stress (Ritchie et al. 1998; Turner 1997).

Leaf area expansion and root extension are forms of cell expansion that are important responses to plant water deficits. As soil matric potential decreases, cell turgor

pressure is reduced, subsequently decreasing cell expansion (Neumann 1995). However, there is evidence that water deficits increase the rate of root elongation (Hsiao and Jing 1987). Turner and Begg (1978) have shown that leaf expansion in many grass species is more sensitive to water stress than is photosynthesis. Water stress primarily reduced barley yields by a reduction in light interception arising from smaller leaves during vegetative growth (Legg et al. 1979). Reductions in weed leaf area relative to the crop have been shown to reduce crop yield loss (Kropff and Spitters 1991).

A useful index to quantify plant growth is relative growth rate (RGR), which is the rate of biomass production per unit biomass (Hunt and Cornelissen 1997). High and low maximum RGR have been shown to be general properties of species in resource-rich and resource-poor natural environments, respectively (Grime and Hunt 1975). If wild oat were a better competitor in wetter areas of fields, we would expect significantly higher RGR in soils near field capacity (-0.03 MPa) water content. However, using RGR to predict competitive success among plant species has had mixed results (Bubar 1992; Dunan and Zimdahl 1991; Holt and Orcutt 1991; Roush and Radosevich 1985). By separating RGR into a physiological component, the unit leaf rate (ULR, the rate of biomass production per unit leaf area), and a morphological component, the leaf area ratio (LAR, the quotient of leaf area and plant biomass), further insights can be gained on the primary assimilation and allocation processes affected by water stress. We hypothesized that wild oat reduces leaf area during vegetative growth under drought stress to reduce water loss. The tradeoff in reduced leaf area with potential

photosynthesis or the ability to maintain photosynthetic efficiency under water stress may determine the ability of a wild oat population to persist at sub-field scales in the NGP.

Water stress can also alter the carbon allocation patterns of plants. A common response of many crop species to water stress is that more assimilate is channeled to roots compared to leaf and stem tissues during vegetative growth resulting in a higher root to shoot ratio (R/S) (Brown 1984; Lucero et al. 1999; Turner and Begg 1981). Such an allocation pattern would be particularly important in the vegetative phase and is a likely consequence of the greater sensitivity of leaf expansion than photosynthesis to water deficits (Wardlaw 1969). The preferential development of the root over the shoot under water stress enables the plant to explore a greater soil volume for water, particularly if there is an increase in ratio of root length to root mass. The pattern of wild oat carbon allocation in response to reduced soil matric potentials has not been quantified during its vegetative growth.

The net effects of prolonged water stress will undoubtedly affect plant fecundity. Wild oat relies on seed production and dispersal for increasing population density and spatial extent. Periods of water stress will affect seed numbers and potentially seed weight and viable tillers. O'Donnell and Adkins (2001) reported that wild oat seed numbers were significantly reduced at lower soil matric potentials. The ratio of seed number per unit of mature biomass can be used to gauge the seed production efficiency (SPE) of a plant under limited resources (Steinmaus and Norris 2002). Wild oat seed production efficiency will be dependent of the type of primary responses that result from water stress during early vegetative growth.

The goal of this research was to quantify the impact of limiting water potential on wild oat growth and fecundity in order to elucidate the mechanisms that determine its field-scale habitat range in dryland cropping systems. We hypothesized that wild oat maintains enough morphological and phenological plasticity to allow it to grow and produce seed under season long water stress. Wild oat growth was quantified by root, leaf, stem, and panicle mass as well as leaf area and root length. The specific objectives were to measure the impact of moisture stress on wild oat: 1) RGR, ULR, and LAR; 2) dry matter distribution and R/S; and 3) fecundity and SPE.

Materials and Methods

A greenhouse experiment was conducted twice in the Plant Growth Center at Montana State University. The experiment consisted of three treatments with six destructive harvests and was replicated five times for a total of 90 pots. Treatments consisted of three soil matric potentials at -0.03, -0.5 and -1.2 MPa. A matric potential of –0.03 MPa was considered field capacity for the soil. The soil used in both trials consisted of an equal mix of silt loam, washed concrete sand, and Canadian sphagnum peat moss. Soil pH was 6.6 to 7.4 and organic matter was 5.6 to 5.8%. A soil water retention relationship was determined using a pressure plate apparatus. Resulting data were fitted to van Genuchten's (1980) parametric equation to facilitate interpolation of soil matric potential based on measured gravimetric soil water contents (Wraith et al. 1995). The estimated mass water content was 17.2, 11.7 and 10.8% for soil matric potentials of -0.03, -0.5, and -1.2 MPa, respectively. The soil was dried for two wk at 50

C, filled into pots, and weighed to calculate the gravimetric target wt for the desired soil matric potential for each pot. Pot size increased with destructive harvest time from 2.5 L to 9.7 L. Pots were watered to field capacity (-0.03 MPa) at planting to ensure proper germination and then allowed to dry down to the desired soil matric potential. Water treatments for individual pots were maintained by adding water until each pot reached its target mass. Pots were weighed and watered every day in the first experiment with the exception of four separate days, and every other day in the second experiment. The effect of watering every other day compared to every day did not alter wild oat growth because we were able to combine data from the two experiments (described below).

Wild oat seed was collected from a small grain production field near Great Falls, MT. The seed was cleaned with a 2 mm mesh sieve and scarified to improve germination and emergence. Ten seeds were planted in each pot. Each pot was thinned to one wild oat plant 10 d after planting (DAP) by removing the earliest and latest emerging plants to establish a consistent emergence time in all pots. Water-soluble 20-10-20 (N, P, K) fertilizer was applied at 10 mg kg^{-1} soil according to soil weight in split applications at 2, 40, and 54 DAP for both experiments.

Natural light was supplemented with metal halide lamps[1] at 280 μmol m^{-2} s^{-1} of photosynthetically active radiation (PAR). Day length and temperature were set to mimic climatic conditions of the NGP during the typical growing season for wild oat. Day length periods, each 30-d long, were 15.25, 16.25, 15.5, and 14.5 hr. Minimum and maximum air temperature were set to 13/21, 15/24, 15/26, and 15/26°C, respectively,

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[1] GE Multi-Vapor MVR1000/C/U, General Electric Company, Nela Park, Cleveland, OH 44112.

with each temperature regime 30-d long. Temperature data was recorded with three temperature probes attached to a data logger[2] because actual air temperature in the greenhouse varied due to outside conditions. Growing degree days (GDD, °C) from the time of planting were calculated using a 5°C base temperature for wild oat (Cudney et al. 1989).

A wet and dry wt of a representative subsample of soil from each pot at each harvest was used to calculate mass water content to ensure the proper matric potential was maintained. Actual water content averaged across the 12 harvests was 17.4 ± 1.1, 11.6 ± 0.8, and 10.8 ± 0.8% for the –0.03, -0.5, and –1.2 MPa treatments, respectively. In the second greenhouse trial we added a replication of pots without wild oat in order to estimate evaporation. Transpiration per plant was calculated by subtracting the estimated evaporation from the water added per pot and plotted as a function of GDD for each matric potential treatment.

Data Collection

Destructive sampling for growth analysis was carried out at 437, 539, 729, 881, 947, and 1428 GDD in trial one and at 393, 597, 831, 1040, 1209, and 1632 GDD in trial two. At each harvest, shoots were clipped at the soil surface and separated into leaf, stem, and panicle fractions. The wild oat green leaf area was measured on a moving belt area meter[3]. All tissues were dried to constant wt and biomass was recorded.

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[2] 107-L Temperature Probe and CR10X Datalogger, Campbell Scientific, Inc., 815 W. 1800 N., Logan, UT 84321.

[3] LI-COR 3000 Leaf Area Meter, LI-COR, Inc., P.O. Box 4425, Lincoln, NE 68504.

Wild oat roots and soil were removed from pots and placed in a 2 mm mesh sieve. A large portion of the soil and organic matter was removed from the roots by dry sieving. The roots and remaining soil were placed in a 0.25 mm mesh sieve under running water for further cleaning. The roots were placed in jars containing 20 % ethyl alcohol solution and stored at 5°C. The final processing involved placing the roots in a tray under water to remove any remaining organic matter with tweezers.

Seeds plant^{-1}, 100 seed wt, and viable tillers plant^{-1} were quantified for the last two harvests. All seeds were counted for each plant after the panicles were dried and weighed. All tillers with at least one internode were counted and considered viable if at least two spikelets were visible on the panicle. One hundred seeds were randomly selected from each plant to obtain an estimate of seed wt.

Quantitative Analysis

A general F test was used to test whether whole plant wt (root + shoot), root wt, shoot wt (leaf + stem + panicle), leaf wt, and green leaf area over thermal time at each soil matric potential from each greenhouse trial could be combined into one data set. The natural log transformed data was regressed on GDD using a second order polynomial. The F statistic for the test was (Afifi and Clark 1984):

$$F = \frac{\left[SS_{res}(H_0) - SS_{res}(H_1)\right] / \left[df(H_0) - df(H_1)\right]}{SS_{res}(H_1) / df(H_1)} \qquad (3.1)$$

where SS_{res} is the residual sums of squares, df is the degrees of freedom, H_0 is the regression for the combined data, and H_1 is the sum of each regression performed separately for trial 1 and 2. In all cases, the regression using the combined data from the

two trials conducted at different times did not differ ($P > 0.05$) from the regressions using separate data sets, so the data were combined to improve the resolution of the growth analysis.

A flexible growth function was used to facilitate comparisons between sigmoid growth curves of differing symmetry. The Richards function was chosen because biological meaning can be derived from its parameter estimates (Causton and Venus 1981; Steinmaus and Norris 2002), only three parameters need to be fitted (if the start of the growth curve is maintained at $t = 0$), and it can account for asymmetry about its point of inflexion in describing sigmoidal growth (Richards 1959). Use of thermal time for wild oat growth eliminated differences due to fluctuations in the greenhouse temperature regime (Dunan and Zimdahl 1991), thus GDD was used. The Richards function took the form of (Richards 1959):

$$w = A(1 - \exp(-k \times GDD))^{1/(1-m)} \qquad (3.2)$$

where w was the dependent variable (e.g. whole plant wt), A was the asymptotic or maximal value of w, k was the RGR over the entire growth period, and m was the Richards parameter. As the parameter m increases, so does the relative size at which the growth rate peaks. For certain values of m, Equation 3.2 assumes the form of special classical growth models. When $m = 0$, the function reduces to the monomolecular growth function (growth rate declines linearly with increasing wt), and when $m = 2/3$ the von Bertalanffy model results. As $m \rightarrow 1$ it can be shown that the limiting form of the model is the Gompertz function, if it is assumed that $X_{t \rightarrow \infty} \rightarrow A$ (Pienaar and Turnbull 1973).

The Richards function was fitted to all the observed data for whole plant wt (root + shoot), root wt, shoot wt (leaf + stem + panicle), leaf wt, and green leaf area after the individual plants were ranked by size within each harvest time (1 through 5) at each soil matric potential. The Richards function was fit separately to each of the five size rankings over the experimental growth period to derive the mean and standard deviation of A, k, m, from the five regression fits. The coefficients of determination (R^2) (75 total, 5 variables at 3 matric potentials with 5 size-ranked fits) were all greater than 0.91. All A, k, and m parameters were significant at $P < 0.01$.

The Richards function has no parameter that can account for senescing plant tissue after it has reached its maximum (A), thus the function was only fit up to the asymptotic values for leaf dry weight at 1209 GDD and green leaf area at 1040 GDD. The inverse of the variance within a harvest was used to weight the nonlinear least squares estimation because the variance around the mean became proportionately larger as plant size increased. The Richards function was fit using the Hooke-Jeeves (1961) pattern moves estimation method in nonlinear estimation module of STATISTICA with a convergence criterion of 10^{-5} (StatSoft Inc., 2000).

The combined interaction of ULR and LAR at the whole plant level can provide further insight into water stress effects on wild oat physiological and morphological responses. The instantaneous values of LAR were calculated for each of the sized ranked plants at the point of maximum leaf area (1040 GDD). ULR was calculated at RGR/LAR for each of the respective size-ranked values from each treatment. Analysis of variance

(ANOVA) was conducted on the estimates of whole plant, root, and shoot RGR, and whole plant ULR and LAR with means separated using Tukey's HSD test ($P = 0.05$).

Measuring the changes in dry matter distribution quantifies the emphasis placed upon internal source-sink relationships in regulating growth and fecundity under reduced soil matric potentials. The dry wt of the root, leaf, stem, and panicle were each divided by the whole plant wt at that sampling time to calculate dry wt proportion relative to the whole plant wt. The sums of all tissue fractions equal 100% of the whole plant wt at any sampling time and were plotted in a stacked area graph over GDD. The tissue fractions at the commencement of growth (0 GDD) used the same values for the three matric potential treatments, which were 35% root and 65% shoot tissue based on the values reported for cereal crops (Welbank et al. 1973), with the shoot fraction set to 5% stem tissue and 60% leaf tissue. The R/S was calculated as the ratio of belowground to aboveground biomass produced. The growth period was split into three time intervals: 393 to 597, 729 to 947, and 1040 to 1632 GDD, which corresponded to the periods with the highest, intermediate (declining), and final R/S during the wild oat life cycle.

Reductions in potential seed yield of wild oat are mostly the secondary effects of water stress resulting from decreased photosynthesis and cell expansion, and altered carbon allocation during vegetative growth. However, the seed is the principal unit determining population growth and subsequent future impacts of wild oat. Wild oat SPE, as a further measure of water stress on seed production, was calculated as seeds g^{-1} shoot wt for each plant. Wild oat seed $plant^{-1}$, 100 seed wt, viable tillers, and SPE were linearly regressed on soil matric potential with the significance determined at $P = 0.05$.

Results and Discussion

Impact on RGR, ULR, and LAR

Temperature and solar radiation play an important role in regulating cell expansion and photosynthesis, respectively, but water stress over prolonged periods is also important (Ritchie et al. 1998; Turner 1997). The increase in dry organ wt (root, leaf, stem, and panicle) is a direct surrogate for carbon assimilation via photosynthesis even though a minor fraction of mass growth occurs from mineral elements. Leaf area response can identify water stress effects on cell expansion. The greatest asymptotic values (*A*) for all the mass and expansion growth variables occurred at -0.03 MPa followed by -0.5 MPa, with –1.2 MPa resulting in the lowest *A* (Table 3.1), which corresponded to wild oat water use. The estimated transpiration per plant over the length of the second trial was 15.3, 11.9, and 11.0 L at –0.03, –0.5, and -1.2 MPa, indicating that the lower matric potential treatments were effective in limiting wild oat water uptake the results, but the apparent trend is that decreasing soil matric potential significantly reduces wild oat growth (photosynthesis) during vegetative growth resulting in substantial reductions in final biomass. None of these experiments presented root wt or leaf wt as a function of soil matric potential.

The –0.03 MPa treatment resulted in the highest whole plant and shoot RGR, but was intermediate for root RGR (Figure 3.2). Reductions in shoot RGR at –0.5 MPa were greater than whole plant RGR compared to –0.03 MPa, but relative final biomass for the shoot and whole plant were similar. This indicates that water stress increased root RGR at the expense of shoot RGR, but could not maintain growth due to prolonged water

Table 3.1. Means and standard deviations (±) of Richards function parameter estimates for whole plant wt (root + shoot), root wt, shoot wt (leaf + stem + panicle), leaf wt, and leaf area of wild oat grown at -0.03, -0.5 and -1.2 MPa soil matric potential.

Variable	Parameter	-0.03 MPa	-0.5 MPa	-1.2 MPa
Whole plant wt (g)	A	28.19 (4.55)	16.83 (4.59)	12.73 (3.06)
	$k \times 10^{-3}$	4.66 (0.48)	4.18 (0.52)	3.05 (0.01)
	m	0.985 (0.003)	0.968 (0.006)	0.945 (0.012)
Root wt (g)	A	2.54 (0.75)	1.41 (0.38)	1.11 (0.20)
	$k \times 10^{-3}$	4.42 (0.18)	4.89 (0.61)	3.80 (0.34)
	m	0.973 (0.003)	0.962 (0.015)	0.932 (0.011)
Shoot wt (g)	A	24.72 (3.65)	15.26 (3.59)	11.29 (3.17)
	$k \times 10^{-3}$	5.02 (0.26)	4.06 (0.29)	3.30 (0.29)
	m	0.990 (0.003)	0.976 (0.005)	0.960 (0.009)
Leaf wt (g)	A	5.73 (0.76)	4.02 (0.70)	2.88 (0.17)
	$k \times 10^{-3}$	6.56 (0.37)	5.50 (0.25)	5.49 (0.73)
	m	0.992 (0.002)	0.985 (0.006)	0.984 (0.007)
Leaf area (cm^2)	A	740.13 (73.50)	561.07 (93.06)	342.27 (87.98)
	$k \times 10^{-3}$	5.29 (0.13)	4.38 (0.48)	4.34 (0.73)
	m	0.972 (0.015)	0.963 (0.017)	0.958 (0.014)

stress. Indeed, the root RGR was highest at -0.5 MPa, but was not statistically greater than –0.03 MPa (Figure 3.2B). The fact that root RGR at –0.5 MPa was greater than at -1.2 MPa suggests that initially decreasing soil matric potential stimulates root growth, but more severe matric potentials retard root growth. The final root biomass (A) was still highest for -0.03 MPa meaning that root growth at –0.5 MPa likely experienced a shortage of assimilate due to reduced leaf area.

Reductions in RGR have been recorded for other species under drought stress such as wheat (Kalapos et al. 1996), white clover (Lucero et al. 1999), and seedling growth of *Albizia procera*, a subtropical tree species (Khurana and Singh 2000).

Conversely, wild oat RGR did not differ among three different temperature regimes when water was provided in adequate supply (Wall 1993). Hunt and Cornelissen (1997) demonstrated that doubling PAR to 250 μmol m^{-2} s^{-1} had a slight effect on RGR of 59 temperate plant species. The results of this and other research would indicate that water stress directly affects RGR more than other abiotic variables.

The maximum green leaf area occurred near anthesis (Zadoks 59-65) then gradually senesced to zero at maturity. Water stress reduced maximum leaf area by 24 and 54% at –0.5 and -1.2 MPa, respectively, compared to the leaf area produced at field capacity (Table 3.1). Soil matric potentials at –0.5 and –1.2 MPa caused similar reductions in both mass and expansion growth of leaf tissue compared to –0.03 MPa. However, the effects of water stress on green leaf area was more obvious earlier because leaf area expanded slower, *k*, and peaked earlier, *m*, relative to leaf wt, which would indicate that photosynthesis continued to occur under increasing water stress resulting in

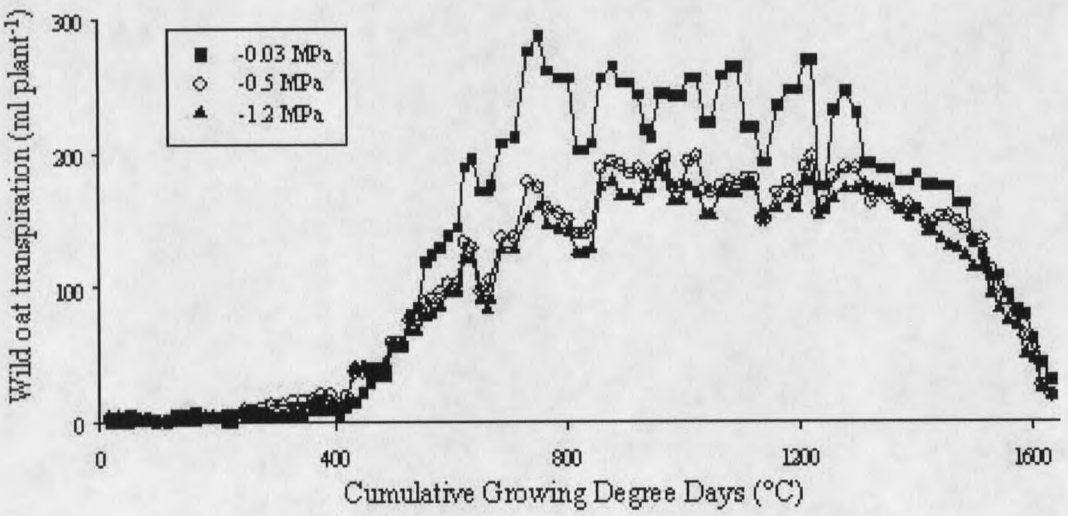


Figure 3.1. Estimated wild oat transpiration as a function of GDD over the length of the second trial at soil matric potentials of –0.03, -0.5, and –1.2 MPa.

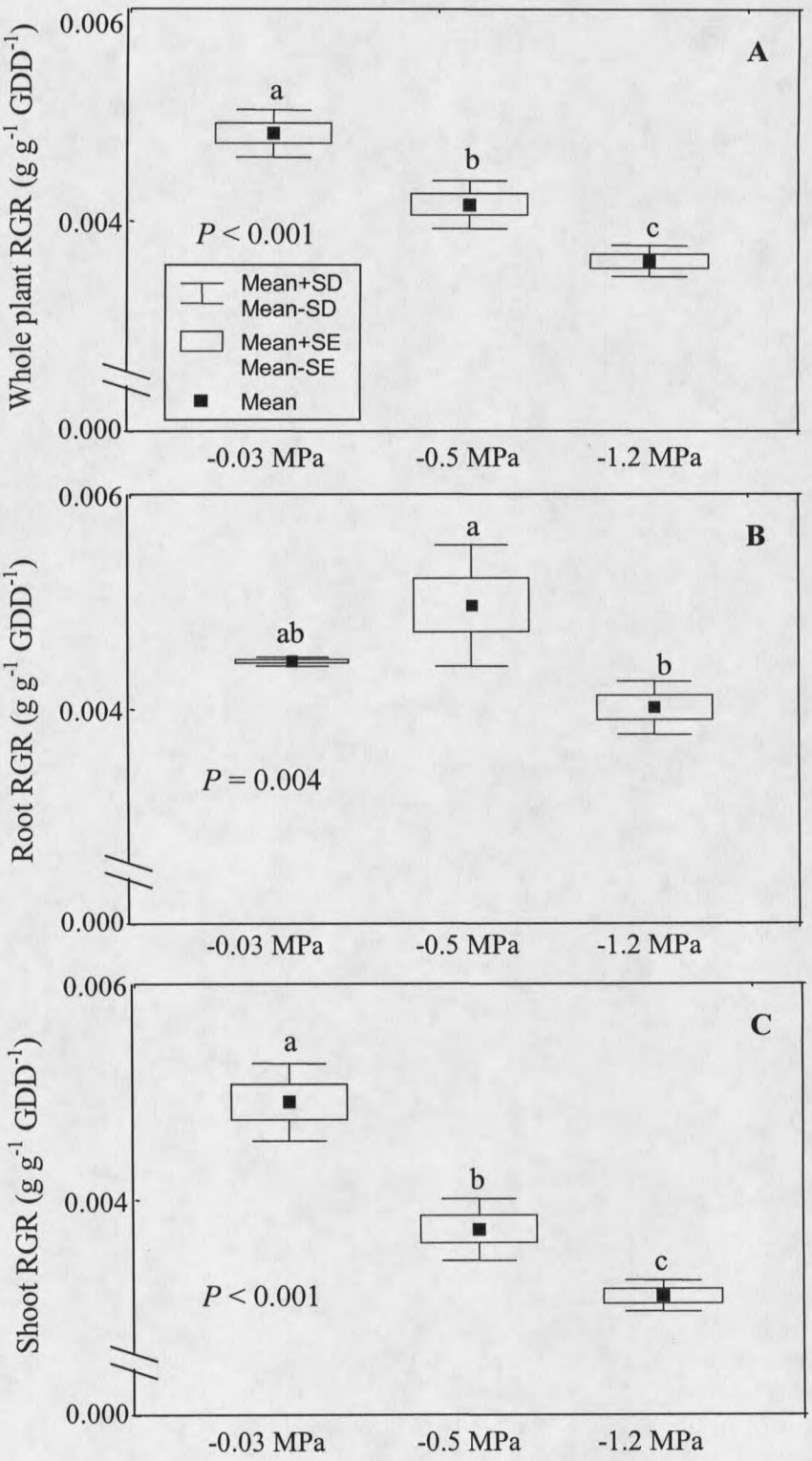


Figure 3.2. Estimated relative growth rate (RGR) for whole plant (A), root (B), and shoot wt (C) over the length of the experiments for wild oat grown at soil matric potentials of -0.03, -0.5, and -1.2 MPa.

an increase in leaf wt, but not in leaf area. Turner and Begg (1978) have shown that leaf expansion in many grass species is more sensitive to water stress than photosynthesis. If soil moisture stress was only temporary, we could assume that leaf area expansion would resume at its normal rate because of the limited ability of wild oat to increase root mass under water stress (Table 3.1). Akey and Morrison (1984) report similar wild oat maximum leaf area to that measured in this experiment at –1.2 MPa. However, field soil matric potential was only lower than –0.4 MPa for the week prior to maximum leaf area, when soil matric potential declined to –1.1 MPa (Akey and Morrison 1984). This suggests that the magnitude and timing of declining soil matric potentials will both affect wild oat leaf area expansion.

The redundant interaction of ULR and LAR provides a clearer picture of wild oat physiological and morphological response to water stress. The whole plant ULR over the course of the season was greatest at –0.03 MPa, but did not differ between –0.5 and –1.2 MPa (Figure 3.3A). The LAR, measured at the time of maximum leaf area (1040 GDD) was lower at –0.03 MPa compared to the water stress treatments, which did not differ in LAR (Figure 3.3B). The greater LAR under water stress indicated that there was the same leaf area with less biomass because a greater fraction of the plant was composed of root, stem, and reproductive tissue at -0.03 MPa compared to the water stressed wild oat (Figure 3.4 at 1040 GDD). The water stressed wild oat had relatively less assimilate available during vegetative growth because of a reduction in leaf area, ULR, and transpiration (Figure 3.1, 600 to 1000 GDD). The transpiration efficiency based on whole plant wt up to 1040 GDD was 2.3, 1.9, and 1.2 g L^{-1} at soil matric potentials of

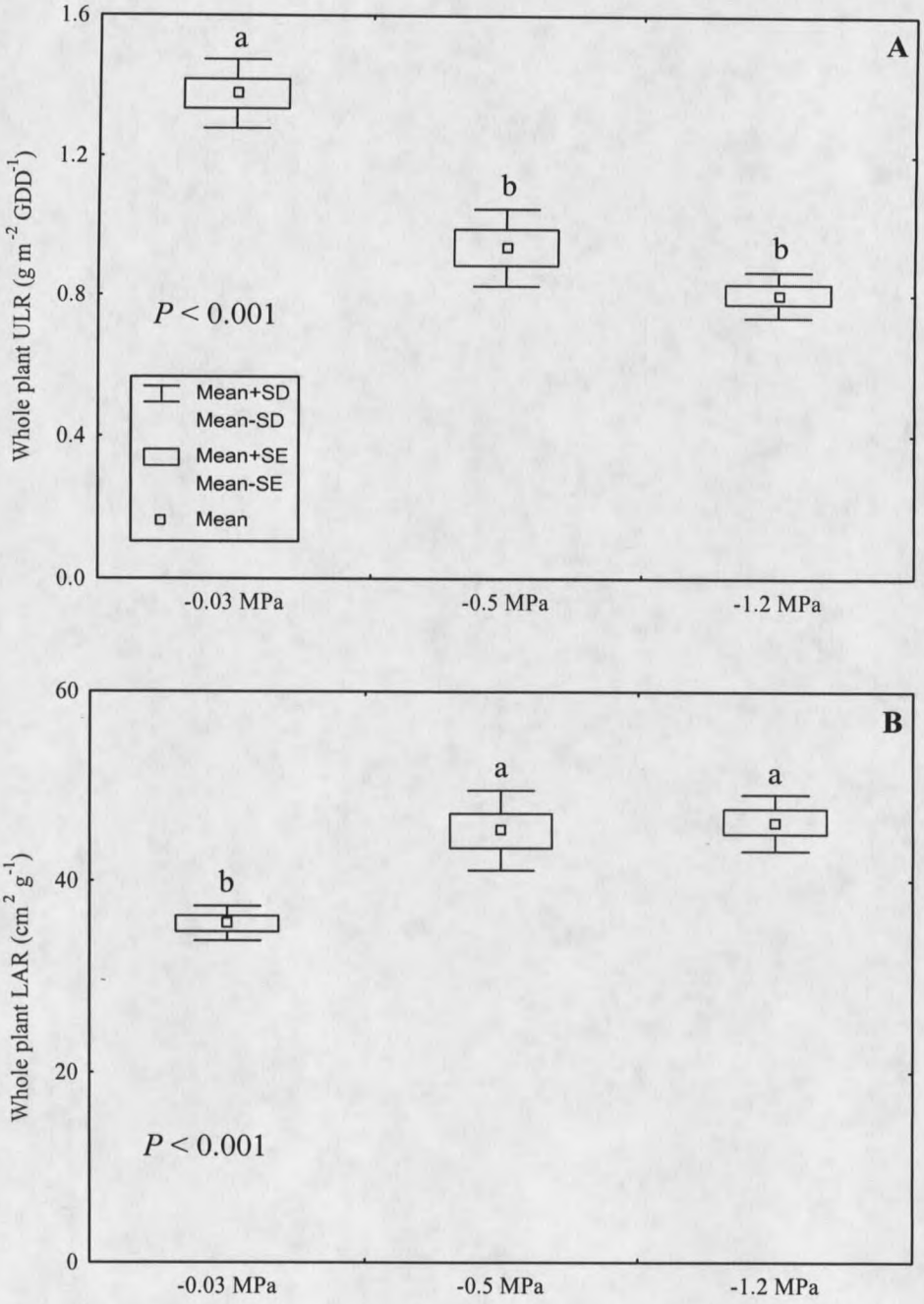


Figure 3.3. Estimated unit leaf rate (ULR) (A) and leaf area ratio (LAR) (B) based on wild oat whole plant wt (root + shoot) grown at soil matric potentials of -0.03, -0.5, and –1.2 MPa.

-0.03, -0.5, and –1.2 MPa, respectively. Van Den Boogaard and Villar (1998) report a similar finding in explaining the differences that occurred between wheat and *Aegilops* species' RGR, ULR, and LAR.

While derivation of ULR is useful in describing assimilation efficiency, caution must be exercised in its interpretation. The ULR does not measure real photosynthesis since it represents the net result of photosynthetic gain over respiratory loss and may therefore vary according to the magnitude of respiration (Watson 1952). Because respiration increases and LAR decreases with plant age, the ULR could fall irrespective of change in photosynthetic activity. Nevertheless, the whole plant ULR was highly correlated with RGR (0.94, $P < 0.001$) and negatively correlated with LAR (-0.80, $P < 0.001$). Xue and Stougaard (2001) report spring wheat had greater ULR than wild oat during early development stages, but Dunan and Zimdahl (1991) did not observe any differences in ULR between wild oat and barley. Dunan and Zimdahl (1991) concluded barley was a better competitor than wild oat under both greenhouse and field conditions, despite wild oat having a greater LAR than barley over the course of the experiments. Thus, LAR may be a poor index of crop-weed competition under water stress for cereal grain cropping systems in the NGP.

In this experiment, water stress reduced wild oat net photosynthesis and leaf area expansion resulting in a significantly slower RGR compared to the field capacity treatment. However, differences in wild oat and cereal grain RGR have not been a reliable predictor of competitive success (Bubar 1992; Dunan and Zimdahl 1991). Roush and Radosevich (1985) also found that RGR was a poor predictor of aggressivity among

four annual weed species. However, *Echinochloa crus-galli,* the species with the highest aggressivity of the four weeds tested, had the greatest shoot wt and ULR, but the lowest LAR (Roush and Radosevich 1985). Using the *E. crus-galli* results as a model, the aggressivity of wild oat would decline under water stress because wild oat shoot wt and ULR were lowest and LAR was highest under water stress than wild oat at field capacity. Grime (1979) stated that the relative importance of competition between species is negatively correlated with the level of stress. Thus, in field areas of prolonged drought stress wild oat potential aggressivity would decline, but reductions in leaf area and net photosynthesis would reduce water loss in order to ensure survival to maturity to attain reproduction (Harper 1977).

Impact on Dry Matter Distribution and R/S

Plant responses to water stress also affect the source-sink relationships among individual organs. Both fast- and slow-growing species have been shown to allocate their carbon and nitrogen in a manner that will maximize their RGR (Van der Werf et al. 1993). Species can respond to environmental stresses, but what makes species different from one another is perhaps the manner in which they are able to respond to those stresses (Lambers et al. 1998).

The leaf wt proportion of wild oat grown at –0.03 MPa remained constant during vegetative growth while it slowly decreased at lower soil matric potentials due to relative increase in root wt (Figure 3.4). The growth of leaf tissue contributed a major proportion of total shoot growth up to 700 GDD at all water potential treatments. These results show that wild oat partitions increasing amounts of assimilated carbon to root tissues at

the expense of leaf tissues under drier conditions. Biomass allocation to each organ (root, leaf, stem, and panicle) can be calculated by dividing the change in wt of the respective organ between two samplings by the change in total plant wt (Kropff and van Laar 1993) and should not be confused with the proportional wt of each organ at a given time. During early vegetative development (up to 500 GDD), wild oat allocated about 40% of its assimilate to root tissue and 50% to leaf tissue under water stress, while at field capacity, allocation was 30% to root and 65% to leaf tissue. Kropff and van Laar (1993) showed that three crops and two weeds never increased the initial carbon allocation to roots after emergence under adequate water supply. In this experiment, wild oat increased carbon allocation to roots by 10% under water stress, but could only maintain this allocation pattern up to 600 GDD after planting. As a result, lower RGR and ULR occurred because of less available leaf area (Table 3.1) and decreased transpiration (Figure 3.1). Kalapos et al. (1996) reported similar biomass partitioning patterns for wheat under decreasing water availability where the reduction in RGR was associated with increased biomass allocation to roots and less to leaves. Likewise, Villar et al. (1998) showed *Aegilops* species from locations with lower annual rainfall invested more biomass in roots and less in shoots (leaves and stems) and had a lower RGR.

For the period between 393 and 597 GDD, the average R/S was 0.35, 0.73, 0.76 for the –0.03, -0.5, and -1.2 MPa, respectively (Table 3.2). The R/S during 729 to 947 GDD decreased by about 50% at each soil matric potential compared to the initial time interval. By the last four harvests (1040 to 1632 GDD), the R/S differed only 3% among treatments. The R/S of wild oats competing with barley under adequate moisture levels

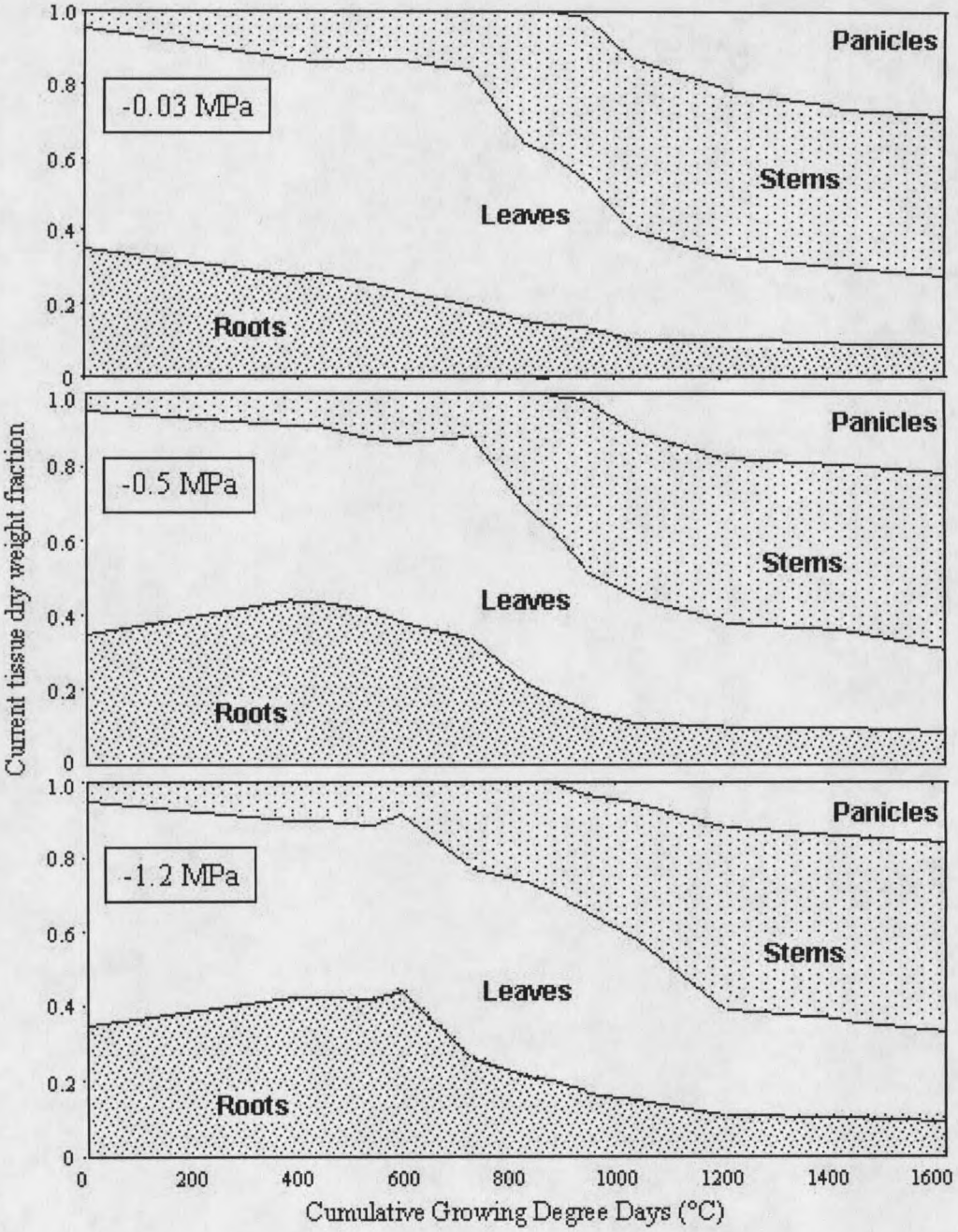


Figure 3.4. Root, leaf, stem, and panicle dry wt fraction of the whole plant wt for soil matric potentials of –0.03, -0.5, and –1.2 MPa. Dry wt fractions sum to one and represent the proportion of the total dry wt at the current sampling time. Dry wt proportions at 0 GDD are based on values reported for cereal grains (Welbank et al. 1973).

(Dunan and Zimdahl 1991) was similar to the R/S reported here at –0.03 MPa.

We can draw three conclusions about the R/S relationship under water stress from Figure 3.4. First, wild oats initially allocated assimilate to root tissue under water stress at the expense of leaf tissue. Second, water stress increased R/S, but wild oat maintained a higher R/S for about 150 GDD longer at -0.5 MPa compared to -1.2 MPa. Third, a decrease in R/S under water stress coincided with an increase in the ratio of stem wt to whole plant wt. Despite the limited increase in root wt during vegetative growth, wild oat was not able to increase the ratio of root length to root mass, which remained constant among all soil matric potentials at 306 m of root length per g of root dry wt (data not shown).

An annual plant must eventually shift carbon allocation to reproduction. By 900 GDD, the panicles became a carbon sink mostly at the expense of leaf tissue regardless of soil matric potential. However, the panicle wt fraction relative to the whole plant at the final sampling time was 0.29, 0.22, and 0.16 at –0.03, -0.5, and –1.2 MPa, respectively (Figure 3.4). Whole plant wt at maturity consisted of more leaf and stem tissue at the lower soil matric potentials, while root wt was about 9% of final dry wt in all treatments. Because wild oat under water stress had relatively greater fractions of stem and leaf wt at maturity suggests wild oat was not as efficient in remobilizing pre-anthesis assimilate

Table 3.2. Mean root to shoot ratio (R/S) between the first, middle, and last four destructive harvests of wild oat grown at -0.03, -0.5 and -1.2 MPa soil matric potential.

Time Interval	-0.03 MPa	-0.5 MPa	-1.2 MPa
393 to 597 GDD	0.35	0.73	0.76
729 to 947 GDD	0.18	0.30	0.29
1040 to 1632 GDD	0.10	0.11	0.13

from stem and leaf to reproductive tissue compared to wild oat grown at field capacity (Ludlow and Muchow 1990). This point is reiterated with calculations of the partitioning coefficients. The carbon allocated to panicles decreased under water stress where the stems became a larger proportion of the carbon sink after anthesis.

Water stress altered the carbon allocation pattern of wild oat. An increase in the R/S was expected, but the magnitude of the increase was unknown. Soil matric potentials at –0.5 MPa resulted in higher root RGR that maintained the R/S for about 150 GDD longer compared to –1.2 MPa. This suggests wild oat will invest assimilate in root tissue at the expense of photosynthetic potential under water stress, but more severe matric potentials will eventually retard root growth. Wild oat can alter carbon partitioning to ensure survival, but lacks the physiological plasticity required to maintain photosynthetic efficiency (ULR) and thus maintain high fecundity under water stress. Wild oat still adhered to phenological cues of thermal time and photoperiod for initiating reproductive growth, but lack of stored pre-anthesis assimilate under water stress resulted in lower panicle dry wt fractions. However, seed was still produced, even at season long soil matric potentials of -1.2 MPa.

Impact on Fecundity and SPE

Quantifying weed seed production and its subcomponents is not nearly as common as quantifying crop yield, especially under water stress. Any inference of wild oat population dynamics under differential water availability requires information on wild oat fecundity. There was always a positive slope estimate ($P < 0.04$) for each of the measured fecundity variables and increasing soil matric potential. Wild oat seed plant^{-1}

had the steepest slope (529 ± 60, $P < 0.001$) indicating that the greatest increase in seeds per plant occurred as soil matric potential approached field capacity (-0.03 MPa). Wild oat produced 823, 370, and 180 seeds plant^{-1} at –0.03, –0.5 and -1.2 MPa, respectively.

Wild oat seed wt was least affected by water stress (slope = 0.15 ± 0.04, P = 0.002). The average wt of one wild oat seed was 9.2 mg at –0.03 MPa and 7.4 mg at –1.2 MPa. The seed wt values at all soil matric potentials reported here were lower than those reported by Sharma et al. (1977) and Thurston (1959). The lower seed wt values may be due to smaller seed size from the parent population (Sharma et al. 1977). We did not measure seed wt of the parent population and little information exists in the literature on the effects of biotic and abiotic variables on wild oat seed wt. Thurston (1959) reported that seed wt slightly decreased as nitrogen content increased. Small wild oat seeds would indicate decreased competitive ability and population growth through lower dry wt and decreased emergence (Sharma et al. 1977). Even though seed wt had the lowest slope, water stress still reduced seed wt.

Wild oat produced 13.1, 11.2, and 10.6 viable tillers plant^{-1} at –0.03, –0.5 and -1.2 MPa, respectively, which was generally higher than reported in the literature (Cousens et al. 1991; Morishita and Thill 1988; Morishita et al. 1991; Sharma et al. 1977; Wall 1993). Tiller numbers reported here are assumed to be near the genetic potential for this population of wild oat at field capacity as limiting resources were prevented. Wild oat tiller initiation is a highly plastic response variable in terms of being able to predict from abiotic resource levels (Akey and Morrison 1984; Wall 1993), or community composition (Cousens et al 1991; Morishita and Thill 1988). The trend suggested from this and other

research is that the amount of light, particularly the three components of PAR reaching the canopy may be more important in tiller initiation than water stress.

The harvest index (quotient of seed wt to shoot wt) is a common descriptor of crop yield efficiency, but does not provide information about actual seed numbers. The quotient of seed numbers per g of shoot biomass may be a better measure of weed seed production efficiency (SPE) in response to increasing drought stress. Wild oat produced 34.9, 27, and 19.5 seeds g^{-1} shoot biomass at –0.03, -0.5, and –1.2 MPa, respectively. The only other published study (that we are aware of) that reported both biomass and seed numbers is Thurston (1959), who quantified wild oat response to nitrogen. Wild oat produced 20.7, 18.4 and 20.5 seeds g^{-1} total biomass at 0, 90, and 180 kg ha^{-1} N, indicating that wild oat was able to maintain SPE with reduced nitrogen concentrations. Steinmaus and Norris (2002) report SPE for velvetleaf grown under various light environments. Velvetleaf produced 32 seeds g^{-1} shoot biomass in full sunlight and only 17 seeds g^{-1} shoot biomass in competition with corn. The similarity in the values with wild oat is probably a coincidence, but the pattern suggests that weed SPE may be a good indicator of light and water availability, but not nitrogen availability. If we calculate seeds per L of water transpired (Figure 3.1), then wild oat produced 53.8, 31.1 and 16.4 seeds L^{-1} at –0.03, -0.5, and –1.2 MPa, respectively. The most efficient spring wheat under dryland conditions in Australia produced about 66 seeds L^{-1} of transpired water (French and Schultz 1984).

Measuring transpiration in a field setting compared to shoot biomass is a more difficult task, even though seeds L^{-1} transpired water is a better indicator of SPE as a

function of water use. The most water use efficient plants adapted to drier areas would be expected to maintain SPE under moderate water stress. In other words, the weed would produce the same amount of seeds per unit of biomass (or transpired water) regardless of water stress. However, this did not occur in this experiment. Alternatively, if SPE decreased under water stress as it did here, probability would indicate that higher wild oat densities are more likely to occur where water availability was greatest. A nearly two-fold reduction in wild oat seeds per unit of biomass and three-fold reduction in seeds L^{-1} transpired water suggests that periods of sub-optimal soil moisture will reduce future densities and may explain the patchy distributions of this weed under dryland conditions.

Reductions in wild oat seed production were more severe than biomass reductions at lower soil matric potentials because the amount of new carbon allocated to panicles decreased under water stress. The stems became a larger proportion of the carbon sink after anthesis (Figure 3.4). The mean wild oat fecundity response to lower soil matric potentials in this study was in the range of fecundity values reported by O'Donnell and Adkins (2001), the only other study that reported wild oat fecundity as a function of soil matric potential. If we combine our wild oat fecundity data with that reported by O'Donnell and Adkins (2001), fecundity was reduced 49, 55, 56, and 78% at -0.1, -0.5, -1.0, and –1.2 MPa, respectively, compared to field capacity. Some caution should be used in interpreting the combined results, but the apparent trend indicates that wild oat has two fecundity thresholds as soil matric potential decreases. The first threshold occurs at about -0.1 MPa, not far below field capacity. In the NGP, soil matric potentials near

field capacity are rarely maintained during the entire growing season. This suggests that wild oat is still able to produce enough seed over a majority of years to maintain persistent patches. The second fecundity threshold occurs at soil matric potentials around -1.0 MPa. Wild oat seed production per plant begins declining significantly at this point towards some theoretical minimum tolerable soil matric potential required for seed production. If wild oat seeds L^{-1} of transpired water (reported above for this study only) are linearly regressed on soil matric potential, the regression fit crosses the x-axis at -1.66 MPa, slightly below the conventionally established permanent wilting point (-1.5 MPa). If soil matric potential is maintained below -1.66 MPa for length of the growing season, wild oat will not produce seeds. We realize that this is below the conventional permanent wilting point of –1.5 MPa, but this serves as a reference to habitat suitability. Angus and Van Herwaarden (2001) provide evidence that vigorous wheat crops extract soil water down to –3.0 to –5.0 MPa between 30 and 100 cm. Thus, it might be possible to plant crops that would prevent wild oat fecundity, but crop yield would likely be uneconomical.

This study revealed the ability of wild oat to acclimate to a range of moisture stress by morphological and physiological responses. Water stress during early vegetative growth of wild oat reduced growth and fecundity, but our hypothesis that wild oat maintains enough morphological and phenological plasticity to allow it to grow and produce seed under season long water stress could not be rejected. Many researchers have shown wild oat time of emergence relative to the crop to be an important predictor of crop yield loss (Cousens et al. 1987; O'Donovan et al. 1985; Peters and Wilson 1983).

The relative competitiveness of a crop would also be affected by early drought conditions. In field areas of prolonged drought stress wild oat potential aggressivity would decline, but reductions in leaf area and net photosynthesis and increased carbon partitioning to roots would reduce water loss and increase the chance for water uptake in order to ensure survival to maturity to attain reproduction under adverse climatic conditions.

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CHAPTER 4

WILD OAT HABITAT MAY BE UNLIMITED IN CEREAL GRAIN CROPPING SYSTEMS OF THE NORTHERN GREAT PLAINS

Abstract

The advent of site-specific weed management has generated research aimed at predicting weed spatial distributions from existing weed maps or correlations with soil properties and edaphic factors. Forecasting the spatial distribution of annual weeds requires knowledge of the fecundity, dispersal, crop management and suitable habitat distribution. We hypothesized that wild oat habitat was limited by field-scale heterogeneity in plant available soil water, thus patches would be distributed in areas with greatest plant available water. Wild oat was seeded in areas with and without historic wild oat patches in monoculture and mixture with spring wheat in three grower-managed fields. Wild oat habitat was quantified by wild oat leaf area growth rate, mature shoot biomass, seeds per plant (SDPP), biomass water use efficiency and competitive ratio (CR) with spring wheat. Sand and clay content and plot elevation correlated with existing wild oat patch areas in individual fields, but no site properties correlated with wild oat patch areas over all 3 fields. Total water use per plant and almost all habitat-defining variables for wild oat were similar between existing patch and non-patch areas. Wild oat CR, based on SDPP, was greater in patch than non-patch areas at the site with the lowest crop yields. Even though wild oat SDPP did not statistically differ between habitat areas, wild oat in patch areas had a 56% probability of producing more SDPP

compared to wild oat in non-patch areas suggesting that small relative differences in soil seedbank populations may govern the long-term stability of wild oat patches. However, wild oat grew and produced seed regardless of existing patch boundaries and field-scale heterogeneity in soil water use. This research demonstrated that wild oat habitat may potentially be unlimited in agroecosystems of the Northern Great Plains and that research efforts should focus on limiting weed fecundity and dispersal instead of correlating soil properties to predict wild oat distribution.

Introduction

Agricultural fields represent simplified ecosystems. Uniform distributions of weeds rarely occur in these simplified systems despite the homogeneity in crop management practices (Cardina et al. 1995; Colbach et al. 2000; Clay et al. 1999; Mortensen et al. 1993; Wilson and Brain 1991). Many researchers have recognized the importance associated with being able to predict weed species abundance and spatial distribution (Cardina et al. 1995; Luschei et al. 2001; Mortensen et al. 1993; Rew and Cousens 2001; Van Wychen et al. 2002), but a framework is lacking to identify the relative contribution of mechanisms driving weed population occurrence and dynamics (Figure 4.1).

Studies have reported that weed species were correlated to certain site properties or soil characteristics at both field (Dieleman et al. 2000a; Ervio et al. 1994; Hausler and Nordmeyer 1995; Walter et al. 2002) and regional scales (Andreasen et al. 1991; Dale et al. 1992). However, correlating soil attributes to weed populations does not imply

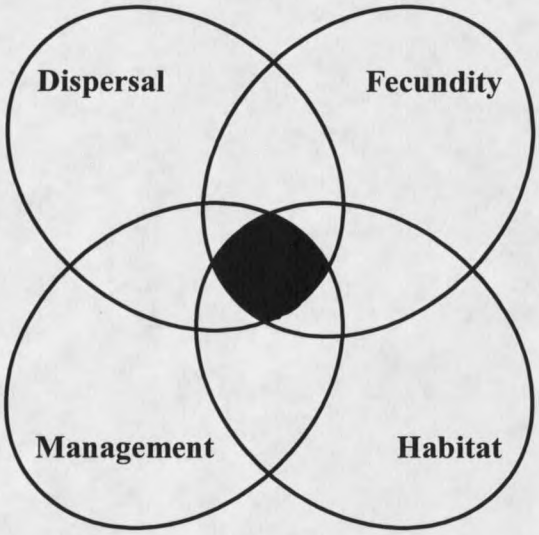


Figure 4.1. The interactions among factors that determine when and where a weed patch will persist in a cropped field. The shaded area indicates where weed seed density surpasses a threshold and is maintained above the threshold to express a metapopulation (patch).

causation for weed distributions and thus cannot be reliably used to predict weed distributions. None of those studies had a 'null pattern' with which to compare field measurements. Plant ecologists spent many decades attempting to correlate vegetation with underlying soil conditions (Knapp 1974). Field-scale variation in the five primary soil forming factors: parent material, climate, biota, topography and time (Jenny 1941), naturally result in non-uniform spatial patterns of soil properties with the consequence that plant species are likely to be aggregated in areas according to their relative abilities to utilize limiting resources. Thus, finding that weed spatial distributions are not random tells us nothing that we did not already know (Crawley 1997). Similarly, plants might be aggregated due to limited dispersal around parents, or differential weed management efficacy. Williams et al. (2001) showed that variation in soil properties within a field altered the efficacy of a soil-applied herbicide on velvetleaf by 12-fold. Evidence from

studies that have mapped spatial weed distributions for at least five consecutive years suggested that predicting future distribution of densities from existing weed maps did not produce consistent results (Colbach 2000; Wilson and Brain 1991). Years in which the patchy distributions were related were not always consecutive and were often separated by years of apparently unrelated distributions.

Harper (1977) stated that the dynamics of plant populations are unlikely to be understood simply by observing and recording plant abundance. A population needs to be perturbed if the factors that determine its characteristics are to be exposed. Researchers and farmers alike have the means to perturb factors effecting annual weed populations occurring in agricultural fields. However, in order to be experimental one needs a list of factors that can be manipulated. The factors must represent processes that contribute to the majority of variation in weed spatial distribution. Cousens and Mortimer (1995) provide a list of factors determining the dynamics of weed populations, which include intrinsic species characteristics such as growth, dispersal, and seed production, and extrinsic factors like habitat, weather, management and succession. We simplified this list of factors in order to provide a framework of manageable factors to quantify the spatial dynamics of wild oats in small grain production in the Northern Great Plains (NGP). The spatial distributions of annual weeds in agroecosystems are a function of fecundity, seed dispersal, management, and habitat (Figure 4.1).

Farmers possess the means to manage seed production and dispersal, but manipulating habitat requires long-term management. Cousens and Mortimer (1995) define habitat as: The sum of the factors at a point in space that may affect a plant's

ability to survive and to contribute offspring to the next generation. However, we propose a narrower definition of habitat: The type of site in an agricultural production field where a weed can grow and reproduce given the inherent variation in climate. Thus, under our climate-constrained definition, habitat quality may vary over time. Annual weeds in agroecosystems represent a range of habitat generalists and specialists. By definition, the most successful annual weeds are generalists in that they can maintain fitness over a wide range of habitat gradients due to phenotypic plasticity or genetic polymorphism, given the inherent variation in soil attributes, climate and management (Crawley 1997). We can assume that an existing weed distribution in an agricultural field has reached its habitat limit if dispersal has allowed enough propagules to reach all areas of the field and management has had a uniform effect on the population.

Boyd et al. (2002) classified wild oat as a generalist based on germination success at various seed depths, soil textures, and soil moisture contents, which contributes to the explanation of wild oat's worldwide geographic distribution (Thurston and Phillipson 1976). Wild oat is well dispersed throughout cereal grain cropping systems of the NGP, but infestations vary widely from field to field (Van Wychen et al 2002). We hypothesized that field-scale heterogeneity in plant available soil water may limit potential wild oat habitat in dryland agroecosystems. Water is often the most limiting resource in agroecosystems of the NGP frequently resulting in terminal moisture stress. Average 30-yr growing season precipitation (March to August) for the sites where this study was conducted is about 255 mm while potential evapotranspiration exceeds 500 mm (Padbury et al. 2002). Faechner et al. (2000) found the highest wild oat densities on

convergent backslopes where their digital elevation model predicted the most water would accumulate, yet some wild oat was also found on toeslopes and hilltops. Van Wychen (2002) reported that wild oat seed production decreased fourfold from season long soil matric potential treatments of –0.03 MPa to –1.2 MPa, but estimated that wild oat would grow and produce seed above a soil matric potential of –1.66 MPa, slightly below the conventional permanent wilting point.

The main question this research attempted to answer is "Why do wild oat patches occur in some areas of a field and not others?" In order to research this question, we considered fecundity, dispersal, management, and habitat. We intentionally seeded high densities of wild oat seed in field areas with and without a history of wild oat infestation in grower-managed fields. Auld (1988) intentionally seeded wild oat into two pastures where it had not been observed previously and reported that wild oat had successfully established and rates of spread remained constant for the duration of the study. We hypothesized that wild oat habitat-defining variables would be more favorable in patch compared to non-patch environments, where the environment was understood to be a mix of biotic and abiotic driving factors (with water as the most limiting resource). Habitat-defining variables included wild oat competitive ratio (CR) with spring wheat, leaf area growth, shoot biomass, water use efficiency, and fecundity. We could thereby conclude that grain production fields in the NGP differ in field-scale wild oat habitat availability under the assumptions of uniform response to management and sufficient seed dispersal to supply seed to the entire field. Proactive weed management efforts could then be directed to field areas with suitable wild oat habitat, not just areas where infestations

exceed an economic density threshold. The objectives of this research were to compare and quantify the effects of existing wild oat patch and non-patch areas on wild oat growth, fecundity and water use efficiency in monoculture and in mixed culture with spring wheat.

Materials and Methods

Experiments were conducted in three farmer-managed production fields located at Box Elder (48° 13′N, 109° 57′W), Fife (47° 14′N, 111° 01′W), and Sun River (47° 09′N, 111° 43′W), MT in 1999. Selected fields were historically seeded to a cereal grain, had a history of wild oat infestation, and differed in soil attributes such as elevation, soil texture, rooting depth, and annual rainfall (Table 4.1). Field size was 20.2 to 25.9 ha with a wild oat infestation in 25 to 91% of the entire field (Van Wychen et al. 2002). Wild oat was the predominant weed species at all three sites. Treatments consisted of a factorial combination of two wild oat habitat types (historic presence or absence of wild oat) and three plant communities (wild oat or spring wheat monoculture or wild oat mixed with spring wheat) arranged in a split-plot treatment design with six replicates. Wild oat habitat was treated as whole plots and plant community as subplots. Wild oat habitat was selected for historic presence or absence of wild oat based on previous geo-referenced maps of wild oat seedling and panicle distributions as well as producer knowledge of where wild oat patches frequently occurred. Historic wild oat presence was defined as field areas where wild oat grew in the previous two years and frequent infestations occurred based on the producer's past experience. Historic wild oat absence was defined

Table 4.1. Site properties for field-scale wild oat habitat (patch or non-patch areas) at Box Elder, Fife, and Sun River.

	Box Elder		Fife		Sun River	
Site Properties	Patch	Non-Patch	Patch	Non-Patch	Patch	Non-Patch
1998 wild oat panicle density (m^2)	79	1	85	2	214	6
1999 wild oat seedling density (m^2)	209	165	174	179	223	169
1999 spring wheat seedling density (m^2)	108	119	102	133	58	67
1999 mixture total density (m^2)	286	255	256	270	280	247
1999 total whole plot density (m^2)	603	539	532	582	561	483
Emergence rate (%): wild oat mono[a]	31	37	18	41	2	29
wild oat mix	21	29	18	30	8	36
spring wheat mix	47	50	38	54	19	28
Spring wheat cultivar	Amidon		Mc Neal		Earnest	
Sand-silt-clay (%, 0 – 0.2 m)	68-15-17	58-19-23	20-44-36	22-44-34	33-45-22	32-41-27
Average elevation (m)	826.8	835.2	1075.6	1067.6	1097.6	1098.3
1999 Rainfall (mm) Planting to harvest	115		166		110	
1999 GSP[b] (mm)	160		285		178	
30-yr Average GSP (mm)	240		281		246	

[a] Mono: monoculture subplot; mix: wild oat and spring wheat mixture subplot.
[b] GSP: growing season precipitation (March through August).

as field areas where no wild oat occurred in the previous two years and infestations were infrequent or never occurred based on the producer's past observations. We use the terms historic wild oat presence and absence interchangeably with patch and non-patch, respectively. Plant community treatments consisted of three subplots randomly selected for wild oat monoculture, spring wheat monoculture, and a mixture of wild oat and spring wheat. The subplot community treatments allowed us to quantify differences in water use in wild oat and spring wheat mixtures (realized niche) compared to monocultures of each species (fundamental niche) in wild oat patch and non-patch areas (cf. Crawley 1997; Hutchinson 1957). The experimental unit was a 2 m by 2 m subplot with 1 m separating each of the three subplots in the whole plot.

The producer at each site conducted all agronomic practices as under normal management. Glyphosate was applied at either 0.17 or 0.23 kg a.i. ha^{-1} to manage any emerged weeds before planting at each site. Seedbeds were prepared with one pass of a harrow prior to planting at Box Elder and Fife, while Sun River was under no-till management. Each producer applied fertilizer according to soil test results based on Montana State University recommendations for spring wheat (Lichthardt and Jacobsen 1999). Spring wheat was planted with an air-seeder at 66 kg ha^{-1} on May 25, May 4, and April 25 at Box Elder, Fife, and Sun River, respectively. Planting at Box Elder was delayed compared to normal planting dates due to several rainfalls in early and mid May. Row spacing was 23 cm at Box Elder and 30 cm at Fife and Sun River. After spring wheat was seeded, the 12 plots (2 whole plot treatments replicated 6 times) within a field were staked, and spring wheat was removed from one of the subplots in each plot with a

hoe to establish the wild oat monoculture subplot. Wild oat seed was broadcast by hand at 5 g m^{-2} (~500 seeds) and raked into the top 2 ± 0.5 cm of soil 1 d after spring wheat was planted at Fife and 2 d after spring wheat was planted in Box Elder and Sun River. The wild oat seed planted in this experiment was collected from a small grain production field near Great Falls, MT in 1998. The seed was cleaned with a 2 mm mesh sieve and placed in cool dry storage over winter. Immediately prior to planting, the wild oat seed was scarified to improve germination and emergence. The plant community in both subplots was maintained by hand weeding all other undesired species, but the desired species in each community were not thinned, thus enabling normal seedling recruitment and cohort establishment. By seeding wild oat at relatively high densities in both historic wild oat presence and absence areas under similar crop management, we eliminated three of the four factors that affect patch persistence: fecundity, dispersal, and management, which allowed us to quantify the effects of wild oat habitat.

Data Collection and Analyses

Daily minimum and maximum air temperature and rainfall were recorded on site with a data logger[1] at Box Elder and by the producer at Sun River. The producer at Fife recorded daily rainfall on site, but minimum and maximum temperature were obtained from Malmstrom Air Force Base (12 km from the field). Growing degree days (GDD, °C) from the time of planting were calculated using a 5°C base temperature for wild oat (Cudney et al. 1989) to calculate leaf area growth rates.

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[1] 107-L Temperature Probe, TE525 Tipping Bucket Rain Gauge, and CR10X Datalogger, Campbell Scientific, Inc., 815 W. 1800 N., Logan, UT 84321.

Soil water was measured at the center of each subplot from 2 wk after wild oat was planted until harvest approximately every other week with a neutron moisture gauge[2] at 20 cm increments to a depth of 120 cm. Some access tubes could not be installed to 120 cm because of rock, particularly at Sun River, thus, measurements were made to the deepest 20 cm increment. The neutron moisture gauge was calibrated for each soil type according to the Soil Survey Geographic Database[3] against volumetric soil water contents collected at the time of access tube installation and from soil cores taken after harvest in each plot. The 20 cm depth measurement was used to calculate the equivalent depth of water in the 0 to 30 cm depth followed by 20 cm soil layers thereafter (i.e. the 40 cm depth measurement was used to calculate the equivalent depth of water for the 30-50 cm depth). Soil water use (SWU) was calculated as the equivalent depth of water in the soil profile at planting minus the equivalent depth of water at harvest. Total water use (TWU) was SWU plus precipitation between planting and harvest. The volume of water used in each subplot was calculated as the equivalent depth of water in a 1-m^2 area surrounding each neutron access tube. Soil particle size was estimated from the Bouyoucos method for the 0 - 0.2 m depth for each subplot as described in Gee and Bauder (1979). Plot elevation was determined from a differential global positioning system[4].

Wild oat response in patch and non-patch environments was quantified by early season leaf area growth rate per plant (LAGR), shoot biomass per plant at maturity

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[2] 503DR Hydroprobe, CPN International, Inc., 2830 Howe Rd., Martinez, CA 94553.

[3] Soil Survey Geographic Database (SSURGO), National Cartography and Geospatial Center, USDA National Resource Conservation Service, P.O. Box 6567, Fort Worth, TX 76115.

[4] AgGPS 124, Trimble, 645 North Mary Avenue, Sunnyvale, CA. 94088.

(BIO), and seeds per plant (SDPP). We chose early season leaf area growth because of the strong sensitivity of the competition process to early growth characteristics (Kropff and van Laar 1993). Wild oat BIO indicates the amount of resources extracted during the season and SDPP provides a measure of reproductive success. Variables were calculated on a per plant basis to minimize differences in seedling establishment and subsequent density differences between habitat types. Because we augmented existing wild oat seedbanks in patch areas by sowing equal rates of seed in both patch and non-patch areas, wild oat seedling emergence rate was estimated from the difference between number of emerged seedlings in 1999 and the corresponding wild oat panicle density in 1998 and then divided by the seeding rate in 1999 (~500 seeds m^{-2}).

Ten wild oat seedlings in the monoculture and mixture subplots were destructively harvested at three separate times before 600 GDD (before LAI reached 1.0) at each site to calculate LAGR. At each harvest, shoots were clipped at the soil surface and separated into leaf and stem fractions. The wild oat green leaf area was measured on a moving belt area meter[5]. Wild oat LAGR was calculated from the slope of a natural log regression of natural log transformed leaf area per plant on GDD accumulated from planting. A natural log regression fit provided a better fit than a linear regression (as determined from a general F test) indicating that leaf area expansion rates were not exponential up to an LAI of 1.0.

Wild oat and spring wheat was harvested between Zadoks stage 85-93. All plant shoots were clipped at the soil surface in each subplot in a randomly located 0.29 m^2

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[5] LI-COR 3000 Leaf Area Meter, LI-COR, Inc., P.O. Box 4425, Lincoln, NE 68504.

quadrat within 0.5 m of the neutron moisture gauge access tubes and density was recorded. Wild oat spikelets were counted for each plant and multiplied by 2.0 to estimate wild oat SDPP (Thurston 1962). All tissues were dried to a constant wt and biomass was recorded. Spring wheat seed heads were mechanically threshed and weighed.

Biomass water use efficiency (WUE_B) for each species was calculated as the shoot biomass at harvest (in a 0.29 m^2 quadrat) divided by the TWU and was reported as kg ha^{-1} mm^{-1}. TWU was assumed to be equal to evapotranspiration. The actual WUE_B might be underestimated with this equation because TWU (the denominator) would usually be larger than the true evapotranspiration because of precipitation loss due to runoff and deep percolation (Peterson et al. 1996). However, runoff and deep percolation were assumed to be negligible under these dryland conditions.

As a measure of the relative competitive ability between wild oat and spring wheat in patch and non-patch areas, the competitive ratio (CR) (Willey and Rao 1980) was calculated as:

$$CR_a = \left(\frac{Y_{ab}}{Y_{aa}} \div \frac{Y_{ba}}{Y_{bb}} \right) \times \frac{Z_{ba}}{Z_{ab}} \qquad (4.1)$$

where CR_a was the competitive ratio for species a, Y_{ab} was the yield per plant of species a in mixture with species b, Y_{aa} was the yield per plant of species a in monoculture, Y_{ba} was the yield per plant of species b in mixture with species a, Y_{bb} was the yield per plant of species b in monoculture, Z_{ba} was the proportion of the mixture sown to species b, and Z_{ab} was the proportion of the mixture sown to species a. Wild oat CR with spring wheat was calculated for both BIO and SDPP. We assumed spring wheat 1000 seed wt was 30

g in order to calculate the seeds per plant of spring wheat. The CR value gives the exact degree of competition by indicating the number of times one species is more competitive than the other (Willey and Rao 1980) and is identical to the relative crowding coefficient used by de Wit (1960), except the CR allows for calculation of other ratios of component species and not just 1:1 mixtures. The reciprocal of the CR value for wild oat is the CR value for spring wheat.

The purpose of the experiment was to test whether wild oat responded differently between field areas with a historic presence or absence of wild oat. A comparison of response variables among fields was not a primary objective because we expected crop and weed growth to differ among fields due to climatic variation. A separate split-plot analysis of variance (ANOVA) for each field was used to analyze the combined effects of wild oat history (patch or non-patch areas) and plant community (wild oat or spring wheat monoculture, or wild oat mixed with spring wheat) on SWU (mm per 1.2 m soil profile) and TWU (L plant^{-1}) for each field using the General ANOVA/MANOVA module of Stastica (StatSoft Inc. 2000). If the interaction between habitat and community was significant ($P < 0.05$), a post-hoc Tukey's HSD test was used to separate differences between whole plot and subplot factors at ($P < 0.05$). Only wild oat in monoculture or in mixture with spring wheat was used as the plant community factor for the split-plot ANOVA on wild oat LAGR, BIO, SDPP, and WUE_B. A paired t-test was used to separate mean wild oat CR between patch and non-patch areas.

Because wild oat seed is the principal unit determining population growth and subsequent future impacts, we calculated a frequency distribution for the probability of

more wild oat SDPP in patch compared to non-patch areas over the three sites. Wild oat SDPP was randomly selected 100 times from each of two arrays representing patch and non-patch areas. If SDPP in patch areas were greater than in non-patch areas, then the result was equal to 1 and if the opposite scenario occurred, the result equaled 0. The 100 random draws were repeated 1000 times. The mean of the 1000 simulations represented the probability of more wild oat SDPP occurring in historic patch areas compared to outside a previous wild oat patch.

Results and Discussion

Differences in Wild Oat Habitat and Site Attributes

We hypothesized that field-scale heterogeneity in plant available water may limit potential wild oat habitat in dryland agroecosystems. Sand-silt-clay (%) in the upper 20 cm of soil and plot elevation in patch and non-patch areas (Table 4.1) were correlated with existing wild oat patches. Site property correlations with wild oat patch areas differed for each field. At Box Elder, wild oat patch areas had 8% more sand, 6% less clay, and were 8.4 m lower compared to areas with a historic absence of wild oat resulting in patch areas that correlated with the percent sand ($r = 0.42$, $P = 0.042$), the percent clay ($r = -0.47$, $P = 0.022$), and plot elevation ($r = -0.70$, $P < 0.001$). At Fife, existing wild oat patches were 8 m above non-patch areas resulting in a positive correlation with elevation ($r = 0.46$, $P = 0.024$). At Sun River, wild oat patch areas had 5% less clay compared to non-patch areas and were negatively correlated with clay content ($r = -0.57$, $P = 0.003$). No site attributes were correlated with historic wild oat

patches when analyzed across all three fields. If this experiment was conducted in a smaller geographic area or in fields with similar site properties, we might have reached different conclusions. Dieleman and Mortensen (1999) and Dieleman et al. (2000) identified combinations of site properties such as soil texture, elevation, organic carbon and macronutrient concentration that were related to *Setaria* spp. and *Abutilon theophrasti* abundance and occurrence, which have a broad geographic range, but associations were only based on two NE fields and weed populations were not planted in other areas of those fields.

Soil water use (SWU) averaged across plant community areas did not differ between patch and non-patch areas at any site (Figure 4.2). If precipitation was added to SWU and estimated on an area basis across plant community types, patch and non-patch total water use (TWU) would not differ because we assumed precipitation did not differ among plots within a field. However, TWU averaged across plant communities on a per plant basis was greater ($P = 0.046$) in patch compared to non-patch areas at Fife, but not at Box Elder or Sun River (Figure 4.3). Density independent water use and adequate growing season precipitation (GSP, March – August) at Fife might explain why the combined water use of wild oat and spring wheat in monocultures and mixed culture in patch areas was greater than in non-patch areas on a per plant basis, but was similar on an area basis. The GSP was 33 and 28% below the 30 yr average at Box Elder and Sun River, respectively, while 1999 GSP at Fife was near the 30 yr average (Table 4.1). The drought-like conditions at Box Elder and Sun River resulted in 64 and 74% reductions in average crop yields, respectively, compared to the 1990-99 average spring wheat yield in

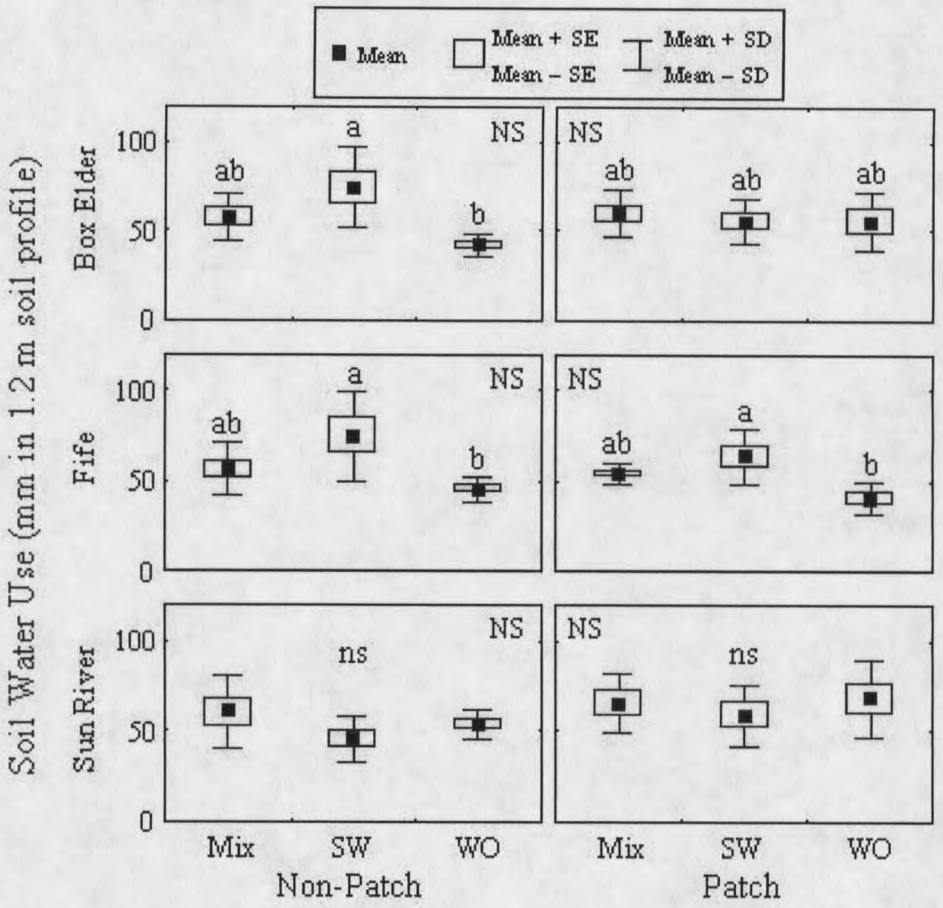


Figure 4.2. Equivalent depth of soil water use (SWU) in a 1.2 m soil profile from planting to harvest for mixtures of wild oat and spring wheat (Mix), monoculture spring wheat (SW), and monoculture wild oat (WO) in fields with a history of wild oat patch or non-patch areas at Box Elder, Fife, and Sun River, MT. Upper case letters indicate differences within a site between patch and non-patch area water use and lower case letters indicate differences within a site between Mix, SW, and WO at $P < 0.05$.

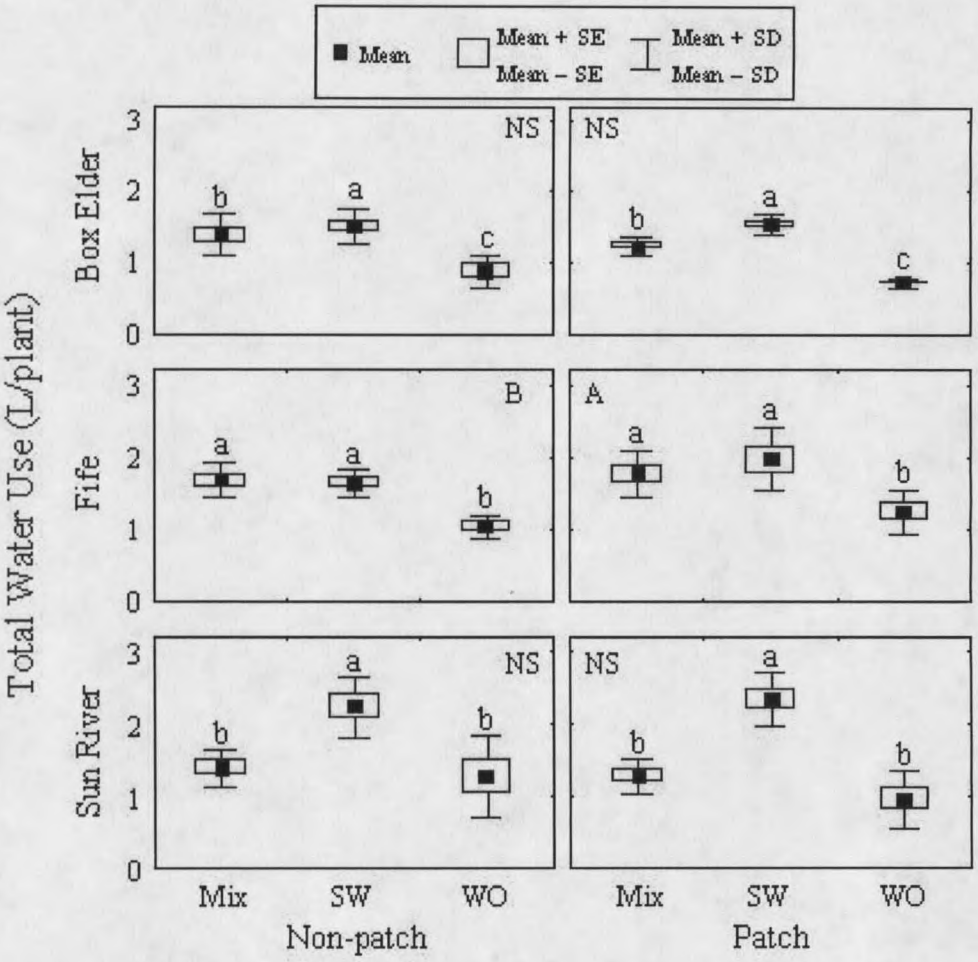


Figure 4.3. Total water use (soil water use + precipitation) per plant in a 1.2 m soil profile from planting to harvest for mixtures of wild oat and spring wheat (Mix), monoculture spring wheat (SW), and monoculture wild oat (WO) in fields with a history of wild oat patch or non-patch areas at Box Elder, Fife, and Sun River, MT. Upper case letters indicate differences within a site between patch and non-patch area water use and lower case letters indicate differences within a site between Mix, SW, and WO at $P < 0.05$.

MT of 2030 kg ha^{-1} (MT Ag Statistics 2001). In addition, total whole plot densities in patch areas at Fife averaged 532 plants m^{-2}, which was the lowest among all sites in patch areas while total whole plot densities in non-patch areas at Fife averaged 582 plants m^{-2}, which was the highest among all sites in non-patch areas (Table 4.1). Thus, fewer areas compared to non-patch areas, but the plasticity of both the weed and the crop allowed the whole-plot plant community to extract nearly all plant available water within the area regardless of the established densities in this experiment. This point is reiterated at Sun River where rainfall between planting and harvest was the lowest of any site, but spring wheat monocultures used the greatest volume of water per plant of any plant community at any of the three sites because crop density was half that of crop density at other sites (Table 4.1).

Spring wheat SWU in monocultures was greater than wild oat SWU in monocultures in non-patch areas at Box Elder and in both patch and non-patch areas at Fife on an area basis (Figure 4.2). However, mixtures of spring wheat and wild oat did not differ in SWU per area compared to either wild oat or spring wheat in monoculture. On a per plant basis, spring wheat always extracted more water than wild oat in both patch and non-patch areas at all sites (Figure 4.3). It should be noted that the water use by mixtures of spring wheat and wild oat (on a per plant or area basis) never equaled the sum of the respective monocultures in each plot. This suggests that the fundamental niche of spring wheat and wild oat in monocultures is different than their realized niche in mixed culture and may be the result of root growth inhibition. Ellenberg (1953) conducted one of the earliest experiments on fundamental and realized niches with five

grass species in monoculture and mixture and found similar results as reported here (Crawley 1997).

We hypothesized that field-scale heterogeneity in plant available water would delineate existing wild oat habitat. Based on the resource use patterns reported above, we could conclude that plant communities of spring wheat and wild oat in monoculture and mixed culture did not differ in field-scale water use between existing patch and non-patch areas which suggests that the variance in field-scale soil water capacity will not control wild oat population carrying capacity as much as GSP. Furthermore, correlations of soil properties and existing wild oat habitat among all three fields within the region could not account for differences in field-scale habitat. In order to make definitive conclusions about wild oat habitat and limiting resources, we need to examine wild oat growth and fecundity between both patch and non-patch areas.

Habitat Effects on Wild Oat Growth and Fecundity

By planting wild oat in field areas with and without historic wild oat patches in three different production fields that varied in climate and soil characteristics, we could account for: 1) temporal and spatial interactions associated with variability in weed distributions; and 2) differences in previous dispersal events and seedbank numbers that may have limited wild oat population distributions. Wild oat LAGR, BIO, SDPP, and WUE_B did not differ between field areas with existing patches compared to non-patch areas in any of the three fields (Table 4.2). In addition, habitat availability was not limited by wild oat emergence because the emergence rates of the spring-seeded wild oat were greater in non-patch areas compared to patch areas (Table 4.1). There was no

Table 4.2. Mean wild oat early season (<600 GDD) leaf area growth rate per plant (LAGR, $d°C^{-1}$), shoot wt at maturity (BIO, g $plant^{-1}$), seeds produced per plant (SDPP), and biomass water use efficiency (WUE_B, kg ha^{-1} mm^{-1}) at Box Elder, Fife and Sun River as affected by wild oat history (patch and non-patch) and plant community (wild oat monoculture or mixed culture with wheat).

	Box Elder				Fife				Sun River			
Source of Variation	LAGR	BIO	SDPP	WUE_B	LAGR	BIO	SDPP	WUE_B	LAGR	BIO	SDPP	WUE_B
Wild oat history (H)												
Patch	1.45	0.83	34.7	12.6	3.07	1.46	50.0	13.9	2.45	1.11	39.9	14.3
Non-patch	1.61	0.76	29.9	10.0	3.06	1.23	49.3	13.3	2.24	1.16	38.8	13.5
$P > F$	0.250	0.429	0.089	0.058	0.965	0.163	0.806	0.693	0.243	0.657	0.718	0.627
Community (C)												
Monoculture	1.48	0.81	32.6	10.6	3.14	1.53	54.4	13.5	2.47	1.28	42.9	12.9
Mixed culture	1.58	0.76	32.0	12.0	2.98	1.15	44.9	13.7	2.22	0.99	35.8	14.9
$P > F$	0.459	0.680	0.804	0.269	0.460	0.029	0.004	0.878	0.165	0.020	0.036	0.269
Interaction, $P > F$												
H×C	0.053	0.539	0.180	0.599	0.227	0.778	0.628	0.619	0.059	0.410	0.416	0.278

apparent trend in the wild oat response variables among all three sites. Because wild oat grew and produced seeds equally across each field suggests wild oat habitat may be unlimited in cereal grain production fields in the NGP.

Wild oat interspecific competition with spring wheat reduced wild oat BIO and SDPP at Fife and Sun River compared to intraspecific competition in the wild oat monoculture, but LAGR and WUE_B did not differ between intraspecific and interspecific competition at any site (Table 4.2). Wild oat BIO and SDPP at Box Elder followed the same pattern between inter- and intra-specific competition as the other two sites, but did not statistically differ. Possible reasons for lack of differences in wild oat BIO and SDPP between intraspecific and interspecific competition at Box Elder include time of planting and water use. Spring wheat was planted late in the growing season (May 25) at Box Elder compared to Sun River (April 25) and Fife (May 4) while wild oat was seeded within 2 d after the crop at each site. Late sowing of spring cereals can reduce wild oat growth and fecundity, but crop yield also suffers (Sexsmith 1955). Average TWU in wild oat monocultures (averaged across patch and non-patch areas) was also about 0.3 L less per plant at Box Elder compared to Fife and Sun River (Figure 4.3), which may have been the result of coarser textured soils at Box Elder with lower plant available water capacity and the lowest GSP of the three sites (Table 4.1). Consequently, the wild oat at Box Elder had the slowest LAGR, and lowest BIO, SDPP, and WUE_B regardless of the plant community compared to the other two sites.

The competitive ratio (CR) for wild oat BIO and SDPP did not differ between patch and non-patch areas at any site except for SDPP at Sun River (Figure 4.4). The

wild oat CR for SDPP at Sun River was greater in patch compared to non-patch areas suggesting that wild oat had an advantage in response to some edaphic factor that occurred in patch areas but not in areas where wild oat had been historically absent. Soil water use (Figure 4.2) and total water use (Figure 4.3) could not account for differences between wild oat CR based on SDPP at Sun River. In general the CR for wild oat BIO and SDPP was slightly higher in patch areas at each site compared to non-patch areas, which would support the hypothesis that once wild oat becomes established in an area, it may modify the soil medium in a manner that is either beneficial for its growth and reproduction or unfavorable for crop growth or both. Possible mechanisms that could be responsible for an increase in wild oat competitive ability include allelopathy (Perez and Ormeno 1991) and species-specific microbe associations that enhance resource uptake (Bagyaraj and Varma 1995; Rillig et al. 1998) or alter biochemical efficiency (Lambers et al. 1998).

Across all three fields, wild oat LAGR was correlated with BIO ($r = 0.59$, $P < 0.001$) and SDPP ($r = 0.70$, $P < 0.001$) indicating that early season leaf area growth is a good predictor of final biomass and fecundity at the regional scale. However, at the field-scale wild oat LAGR was not correlated with BIO and SDPP at any of the sites individually except with BIO at Sun River ($r = 0.54$, $P = 0.006$). Thus, predictions of wild oat BIO and SDPP based on LAGR might not be attainable at the field-scale because: 1) precipitation, solar radiation, and fertilizer are often homogenously distributed across an agricultural field, and 2) heterogeneous site-properties affecting the availability of those resources (particularly precipitation and fertilizer) can only account

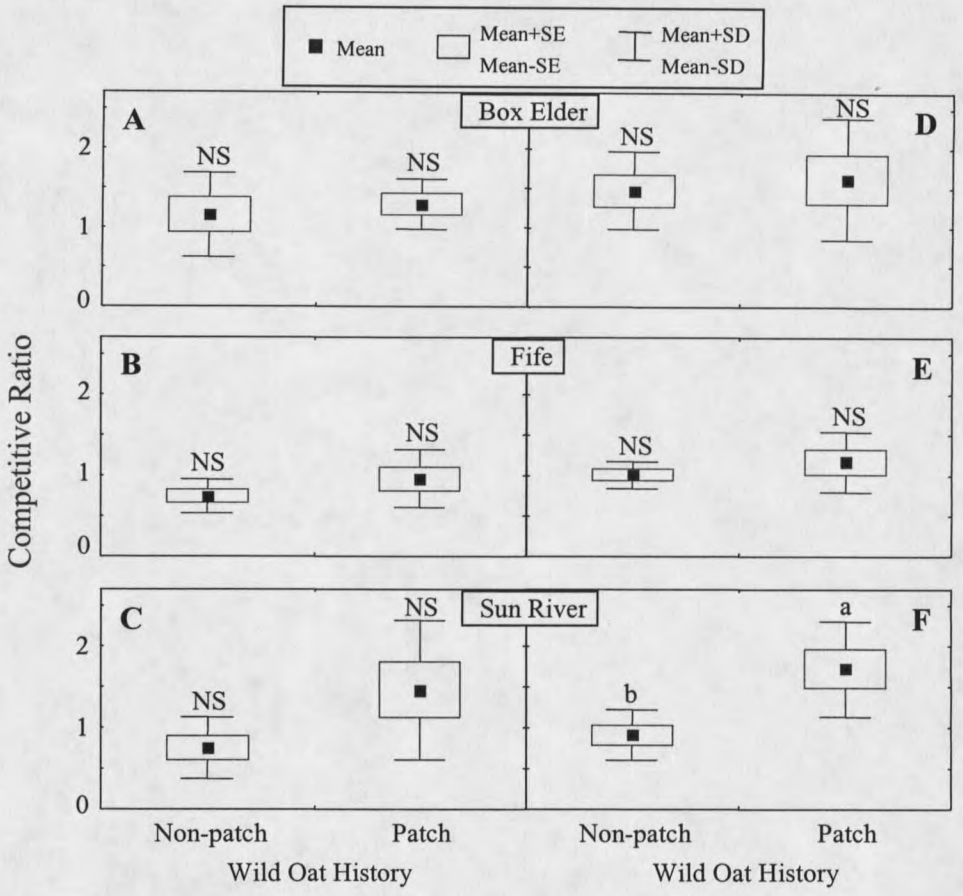


Figure 4.4. Wild oat competitive ratio (CR) with spring wheat calculated for shoot biomass per plant at maturity (A-C) and seeds per plant (D-F) as effected by wild oat patch and non-patch areas at Box Elder, Fife, and Sun River, MT. Different letters within a box plot indicate significant differences for wild oat CR between patch and non-patch areas within a site at $P = 0.05$.

for a small proportion of the resource availability at the field-scale (e.g. even in drought conditions, stored soil water at planting accounted for less than 30% of the total water use). If conditions are favorable for wheat growth in a field, wild oat will grow.

Average wild oat SDPP did not differ between patch and non-patch areas at all sites. However, we calculated a frequency distribution for the probability of more wild

oat SDPP in patch compared to non-patch areas over the three sites (Figure 4.5). Using 1000 draws from the patch and non-patch data it was determined that patch areas produce more SDPP 56% of the time. Alternatively, we could say that 44% of the time wild oat produced more SDPP in non-patch areas. Thus, the question is raised: Could a slight advantage of producing more seed in areas where patches occur make the difference in maintaining a patch? Stochastic climate events will affect seed rain as well as other life history processes from year to year, making it difficult if not impossible to predict wild oat spatial distributions over time based on demographics alone.

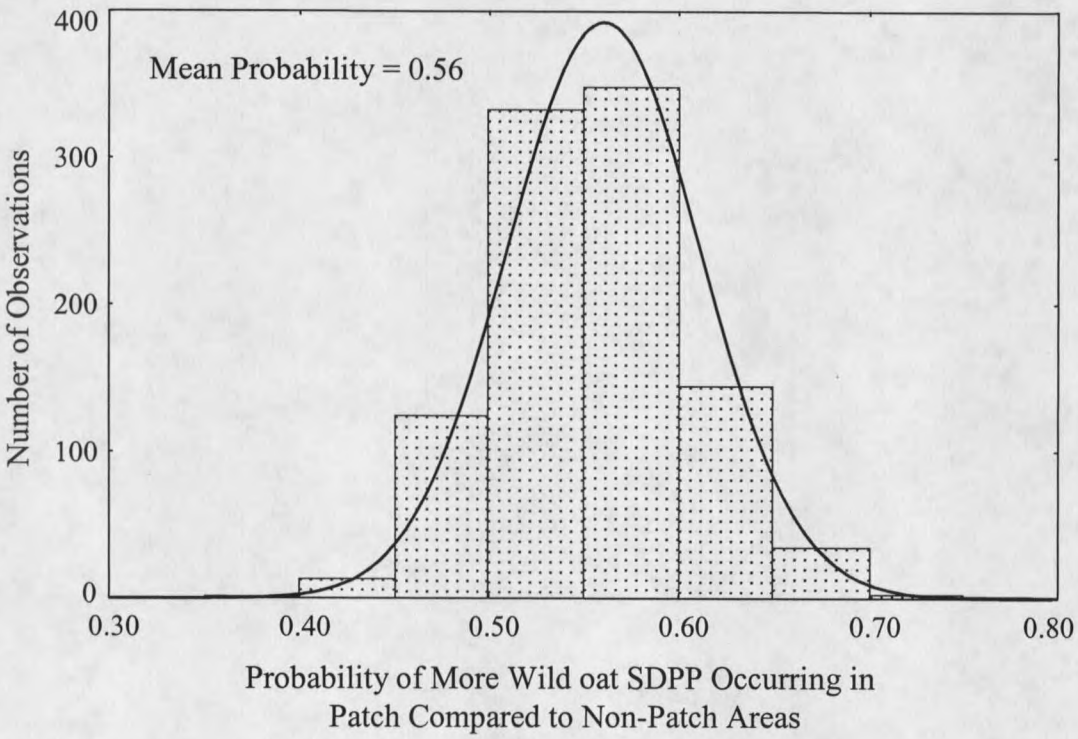


Figure 4.5. Frequency distribution (1000 simulations) of the number of times when wild oat seed per plant (SDPP) was greater in patch compared to non-patch areas at Box Elder, Fife, and Sun River, MT. The mean probability indicated that more wild oat SDPP occurred 56 times out of 100 in patch areas compared to non-patch areas.

Our plot areas only represented a small fraction of the entire field at each site (< 0.05%), but care was taken to locate plots in previous high wild oat density areas (patches) and over a range of topography in each field. Additional wild oat density data was collected in randomly placed quadrats throughout these same fields before and during this study (Table 4.3). The density correspondence data suggested that wild oat patches were continually expanding because the sample frequency of seedling and mature wild oat panicles (density > 0) increased from 1998 to 1999 at each site. However, field areas without wild oat in the previous year never increased to greater than 100 wild oat m^{-2} (considered a patch core area) over one season. In addition, core areas never declined to zero wild oat m^{-2}. Thus, core areas may be relatively stable in occurrence even if density fluctuates.

Table 4.3. Wild oat density correspondence between 1998 at harvest and spring 1999 (randomly placed quadrats within 2 m of each other) at Box Elder, Fife, and Sun River, MT. Frequency is the percent of spatially explicit quadrats within a site meeting the wild oat density selection criteria in the first two columns.

Wild Oat Sampling Time and Density		Wild Oat Sample Frequency		
1998 Panicles	1999 Seedlings	Box Elder	Fife	Sun River
——— No. m^{-2} ———		——— % ———		
0	0	62	31	0
≥1	≥1	18	38	96
0	≥1	12	28	4
≥1	0	9	3	0
0	≥100	0	0	0
≥100	0	0	0	0
≥100	≥100	0	3	29

We cannot reject our null hypothesis that wild oat habitat is unlimited in cereal grain production fields of the NGP. Wild oat grew and reproduced everywhere we

planted it under typical cereal grain management for the region. Formation of new wild oat patches within a field will depend on the right combination of stochastic events influenced by management, fecundity and dispersal. The results of this study suggest little variation in wild oat habitat and thus there is potential for a patch in any given area. Wild oat patches (core areas with relatively dense stands) may have reduced densities in years of good weed management, but unless complete control is achieved for many years, the seedbank may ensure that the patch core area persists. Relatively low-density areas however, may vary from year to year in a stochastic manner making it difficult to predict weed locations for directed pre-emergence herbicide applications before crop planting. In addition, variation due to density dependent differential mortality from herbicides can increase the change of patch persistence and encourage stable core areas (Dieleman et al. 1999). Gonzalez-Andujar et al. (1999) predicted that the most heavily infested blackgrass patches persisted longer than 10 yr, even with the use of an efficacious herbicide. Predicting pre-emergence spatial distribution within a field would require complete knowledge of the size and location of the seedbank across a field and even then, seed dormancy and cohort emergence would need to be considered to be predictive of low density patch locations. One may conclude that future site-specific wild oat management research should focus on using aerial or satellite imagery for producing weed maps prior to post-emergence weed control or the use of real-time optical sensors to ensure management of low density infestations. The risk of leaving low-density wild oat infestations unmanaged is that they have the potential to become stable core areas regardless of edaphic conditions.

Based on our results and observations, habitat variability and fecundity play minor roles in determining where wild oat patches will occur in a field. Thus, we may want to focus on variability in management efficacy and seed dispersal as more important factors to predict wild oat patch occurrence (Figure 4.1). Sun River had the greatest wild oat infestation and Box Elder the least (Table 4.3), which corresponds with seed sanitation methods practiced by the grower at each site. The grower at Box Elder consistently cleaned harvest equipment after each field and planted certified weed-free seed most of the time, unlike the grower at Sun River. Even though crop management and herbicide use was almost identical among sites, weed sanitation methods were quite different based on our subjective assessment. This demonstrates that preventative weed management methods may be significant in the long-term. In the case of wild oat, our results demonstrated that poor weed management will result in geometric increases in population size, but cannot continue unrestricted growth because the field becomes saturated.

Preventing weed seed dispersal might be the best way to manage wild oat (Jones and Medd 1997; Shirtliffe et al. 2000). Maxwell and Ghersa (1992) demonstrated with a simulation model that managing weed seed dispersal had a more important influence on crop yield than managing crop-weed competition. Two primary management tools for preventing wild oat dispersal are planting weed-free crop seed and avoiding mature wild oat patches during crop harvest. Wild oat matures before spring wheat in the NGP, but the amount of wild oat seeds remaining on the plant at the time of crop harvest varied from 10 to 50% (Feldman and Reed 1974; Shirtliffe et al. 2000). Maxwell and Ghersa

(1992) recommend using a combine harvester as a 'weed seed predator' compared to a weed seed dispersal agent. Future research and extension programs should place more effort in determining the cost effectiveness of limiting seed dispersal.

Weed spatial distribution and habitat suitability will differ for other species. However, researchers should proceed cautiously when extrapolating correlative results between soil properties and weed distributions, especially for weeds with a wide geographic distribution. The effects of fecundity, seed dispersal, management, and habitat need to be considered when predicting weed population distributions across agricultural landscapes. Farmers possess the management tools to change crop rotations and prevent or dramatically reduce weed invasions by preventing seed production and dispersal of weeds, even for a generalist weed like wild oat with a habitat as large as the NGP.

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CHAPTER 5

EPILOGUE

General Summary

This dissertation represents three papers that will contribute to the future management of wild oat and weed science in general. Mapping wild oat seedlings using a continuous presence/absence map was accurate enough to provide cost-saving site-specific management of wild oat, even with the associated technology costs. These findings imply that farmers could reduce environmental weed control impacts and reduce input costs over the long-term by using the presence/absence maps to conduct SSWM.

I could not reject the null hypothesis that wild oat habitat is limited by field-scale heterogeneity in plant available water. Even though increasing water stress reduced wild oat growth and fecundity in a greenhouse study, wild oat was estimated by extrapolation to produce seeds at soil matric potentials slightly below the conventionally accepted permanent wilting point.

In the field, wild oat habitat is likely to be unlimited in the NGP where cereal grain crops produce economic yield. Wild oat grew and produced seed regardless of environmental conditions between existing wild oat patch and non-patch areas. If we assume wild oat transpiration was about two thirds of the water use in the field, wild oat produced the same amount of seeds per L of transpired water compared to a single plant growing at field capacity in the greenhouse.

Correlating geographic and site properties to weed distributions can identify hypothetical sources of variation when a large sample size is used (Dale et al. 1992). However, studies relating weed spatial distribution and abundance within a field based on correlations from only a few sites may miss the inherent adaptability of weeds and thus draw false conclusions.

A framework was proposed for studying the distributions of annual weeds in agroecosystems (Figure 4.1). Wild oat was seeded at high densities throughout fields under similar crop management in order to delineate wild oat habitat at the field-scale. The population in question must be manipulated to eliminate or reduce the variation contributing to its spatial dynamics (Harper 1977). Gradations of habitat may exist and certain species (specialists with a narrow niche breadth) will be limited by potential habitat. However, because wild oat evolved with other cereal grain crops over several millennia, it is not surprising that it has the phenotypic plasticity and genetic variability to be widely distributed throughout the cereal grain regions of the world (Figure 1.1).

Wild oat seed per plant did not differ between patch and non-patch areas, but it was determined that patch areas produce more SDPP 56% of the time compared to non-patch areas (Figure 4.5). Furthermore, wild oat patches (core areas with relatively dense stands) may have reduced densities in years of good weed management, but unless complete control is achieved for many years, the seedbank may ensure that the patch core area persists (Table 4.3). A possible answer to "Why do wild oat patches occur in some areas of fields and not others?" is that the frequency of positive outcomes for wild oat fecundity, dispersal, management, and habitat over the long term is greater than the

frequency of negative outcomes, which allows for the maintenance of wild oat patches through a seedbank density threshold.

Hindsight

As much as I like applied fieldwork, I realize I should not have approached the field until my thesis proposal was solidified. Looking back, I could have generated most of the data and practically have written the paper before I set foot into the field. Alternatively, the observation of the agricultural system I was working in and the hands-on work with the GPS equipment and software was probably the best way to learn it, regardless of the slope of the learning curve.

In the wild oat map accuracy study, I would not have tried to map entire fields. I would have used smaller areas in more fields increasing the number of site-years, statistical precision, and sampling accuracy. After learning about the intricacies of spatial statistics, the weed density sampling pattern would have been an order of magnitude less than the scale of the methods for which the accuracy was being quantified. I also would have established permanent quadrats to follow wild oat population growth rate over time.

The greenhouse growth analysis study could have been improved by including wheat as well as wild oat. The relative response between the crop and weed in mixture and monoculture would have provided more meaningful results than a single species experiment. In regard to growth analysis, half of the destructive harvests would have occurred within a month after planting to increase the precision of the plant growth response to early season resource capture. The matric potentials for each treatment

would have been established before planting and the first destructive harvest would have occurred within 100 GDD after planting (possibly before some plants emerged).

The wild oat habitat study could have been more conclusive had I been able to conduct the study for another year while monitoring the seedbank fate. While analyzing the data, I would have been able to calculate more indices of competition had I maintained equal seedling density ratios in my field experiment. However, each species was seeded at the same rate. Our small plot competition experiments typically provide greater precision, but as ecologists, we have to encompass the variation surrounding crop and weed seedling recruitment when working in 'real' environments, which depict the variation prevalent across agricultural landscapes from year to year. Ecological studies almost always occur within the scope of the desired environment. Experiment station research has applicability within the scale of the conducted research, but GPS technology allows us to search for 'rules of thumb' across farm and regional landscapes.

My foray into the mechanistic modeling area was a trying, but valuable learning experience. A mechanistic model forces you to think about mechanisms, and the overlying structure provides heuristic limits for separate but related processes. The crop ecophysiology models are well established and could be very effective learning tools for on-farm agronomic management when properly parameterized. However, building and parameterizing crop-weed interaction models will be a monumental if not impossible task for resource limited conditions. The biggest problem with predicting weed growth and fecundity is accounting for the genetic polymorphism and phenotypic plasticity within a population. The DSSAT crop growth models have five genetic coefficient parameters

that account for differences among cultivars within a crop species. Keep in mind that this occurs for crops where much of the variation has been removed through conventional breeding programs. Existing weed growth and population models will serve as teaching tools and may improve as the scale of predictability becomes more site-specific.

Weed Management Durability

Durable is defined as: Able to endure or continue in a particular condition; lasting; not perishable or changeable. Weed management durability could be defined as a highly proactive plethora of tactics aimed to keep an undesired species off balance, which would be analogous to the "many little hammers" approach (Liebman and Gallandt 1997). Weed management durability integrates both ecological and technological principles in a manner that is environmentally sound, economically viable, socially just, and culturally acceptable. An integrated weed management system uses multiple management tactics based on biological knowledge of the weed. Buhler (2002) listed 11 weed management tactics for use in an integrated weed management system. Given the results of my thesis, and observations and comprehension of the wild oat literature, the most promising three tactics of integrated wild oat management are: 1) prevention; 2) crop rotation; and 3) crop competitiveness.

The concept of prevention has been de-emphasized in recent times because of the availability of effective herbicides and mechanical control measures and increasing farm size (Buhler 2002). If farmers invested as much money into prevention techniques as they did herbicides, they might achieve greater return on their investment. The most obvious

preventative tactic is to plant weed-free crop seed. The fourth chapter of my thesis clearly showed that "if you plant them, they will come", analogous to the movie *Field of Dreams*. Improved seed cleaning equipment virtually eliminated *Agrostemma githago* and *Lolium temulentum*, weeds that had been extremely difficult to remove from small grains with prior methods (Elliot et al. 1977). Other prevention tactics are: 1) cleaning field equipment between fields; 2) avoiding wild oat patch core areas during crop harvest; 3) chaff collection during harvest; and 4) selective spray topping (seed kill methods) prior to harvest. Pandey and Medd (1991) determined that seed rain by uncontrolled wild oat plants was the life stage that had the greatest influence on weed population size and persistence through the use of intensive studies on population dynamics, simulation modeling, and bioeconomic modeling.

I rank crop rotation ahead of crop competitiveness because it might be the only option farmers have to reduce highly infested fields of wild oat. Crop rotation should not only rotate to other annual crops, but to perennial forages and grasses. Derksen et al. (2002) make the case for more diversified cropping systems, which increase resource utilization by crops and varies the selection pressure on weeds. Farmers in the Canadian prairies are diversifying cropping systems and minimizing summer fallow hectares leading to more stable net returns over time (Zentner et al. 2002).

Third, I feel crop competitiveness is being underutilized in our current agronomic management and breeding programs. Crop seedling establishment can be quite variable in MT, even under controlled conditions (Holman 2002). Research conducted on 100 farms in the U.S. and Canada showed that investing $1.25 per acre in planter calibration and

maintenance resulted in $11.70 per acre return due to increase in crop yield from uniform seed placement (Mowitz 2002). Xue and Stougaard (2002) showed that the combined effect of increasing spring wheat seed size and seeding rate reduced wild oat biomass and seed production by 45%.

The greatest spring wheat emergence rates occurring at any of my field sites was 54%, based on a seeding rate of 220 seeds m^{-2} (Table 4.1). A more troubling aspect was that spring wheat growing in mixture with wild oat had lower emergence rates in patch compared to non-patch areas at all sites. One hypothesis may be that once wild oat becomes established at high densities, wild oat modifies the site through some unknown mechanism that is detrimental to spring wheat emergence. Cereal grains may not be the best choice for providing more competitive conditions against wild oat because of similar life cycles and long-term co-evolution with them. Another hypothesis may be that more organic matter and detritus resulting from wild oat infested areas attract more seed and seedling predators or other seed decay organisms.

Other elements of an integrated weed management program that will probably not work for wild oat management include tillage and fertility management. These elements will not be able to provide effective wild oat management due to the similarities between wild oat and cereal grain crops. How many more tillage and fertility trials will be done with wild oat? The only general rule of thumb is that no-till may lead to a shift in perennial species. Contrary to popular opinion, one might expect no-till to lead to a shift away from wild oat; however, the worst infested field in my study was under no-till management for nearly a decade. Over 40 yr ago, Thurston (1959) concluded that the

application of nitrogen to infested fields would not likely alter the balance between wild oat and the crop. Kirkland and Beckie (1998) state that broadcast-applied fertilizer was more effective than banded fertilizer in promoting wild oat emergence and growth over the growing season. However, Kirkland and Beckie's conclusion was misleading because wild oat biomass at harvest did not differ between broadcast-applied and banded fertilizer at any of the six site-years in the study. In addition, spring wheat biomass response to fertilizer placement in their study was nearly identical to that of wild oat. Reinerstsen et al. (1984) conducted a similar study to Kirkland and Beckie (1998) over a decade earlier and found that broadcast-applied N increased wild oat density compared to banded N, but wild oat biomass was similar at maturity between the two application methods because wild oat tillered more profusely in banded N plots.

Other weed management tactics such as cover crops and intercropping will probably not work in Montana's climate due to limited precipitation over the long term. Three other wild oat management tactics, which I would neither fully endorse nor reject due to inconclusive or unknown evidence, are thresholds, organic amendments (wild oat suppressive soils), and biological control of wild oat with other organisms.

Weed Generalists and Coexistence

By definition, the most successful annual weeds are generalists in that they can maintain fitness over a wide range of habitat and management practices due to phenotypic plasticity or genetic polymorphism (Crawley 1997). Ecologists widely accept the idea that selection for coexistence may be the rule more than the exception (Gliessman 1998).

However, Shmida and Ellner (1984) have observed, "coexistence depends on the spatial patterning of suitable microsites, not just on the characteristics of species and microsites". Coexistence among similar plant species often share the same habitat where niches highly overlap. A consequence of working on large spatial and temporal scales is a tendency to be impressed by how spatially variable and ephemeral ecological communities are. For example, the composition and species mixtures of plant communities change greatly from small scales (Whittaker 1956) to large scales (Gleason 1926), with few if any sharp community boundaries. Gleason (1926) saw the relationship of coexisting species as simply the results of similarities in their requirements and tolerances and partly the result of chance. Harms et al. (2001) suggested that local habitat specialization plays a limited role in the maintenance of species diversity in tropical forests, to the extent that habitat association reflects habitat specialization. Condit et al. (1996) showed that tree species have their abundance and distribution guided more by random drift than deterministic interactions.

The unified neutral theory of biodiversity and biogeography (Hubbell 2001) attempts to bridge two long-standing divergent perspectives on the nature of ecological communities: the niche assembly perspective, and the dispersal assembly perspective. To explain most of the variability in natural communities and still adhere to the niche-assembly hypothesis, one need only postulate the existence of sufficient environmental heterogeneity in limiting resources on the appropriate spatial and temporal scale (e.g. Tilman 1987). On the other hand, while it is not difficult to demonstrate the existence of environmental heterogeneity (Kolasa and Pickett 1991), it is considerably harder to prove

that this heterogeneity is actually causing observed patchy distributions and spatial variability among communities (Naeem and Colwell 1991). Also, by using small-scale heterogeneity as a universal explanation, proponents of niche assembly undermine their case for communities as persistent and predictable assemblages of coevolved niche specialists (Hubbell 2001).

Farming activities have resulted in homogenization of ecological conditions (Holzner 1978) so that differences in the floristic composition of fields might not be expected. Farmers use various cropping practices such as summer fallow, tillage, and fertilization to attempt to create conditions that are optimal for the crop. Thus, agricultural production fields can be considered to be resource rich. Weeds with requirements near to those of the crop species will be favored if plant-plant interactions are the major determinants of fitness. Weeds that are better adapted to other conditions (e.g. low fertility or lack of tillage) will not be able to compete and will either be reduced in density or disappear. In many of the fields in north central MT, wild oat is the predominant weed. Because cohabitating species (wheat and wild oat) experience similar selection pressures, they frequently converge to some similar evolutionary solutions for survival under a given set of conditions. Other examples of co-evolving weed-crop relationships (that cannot hybridize) are barnyardgrass-rice, common cocklebur-soybean, velvetleaf-corn. In summary, weed scientists should encourage frequent weed population shifts, because the longer that a particular weed species coevolves with a particular crop, the harder that weed species will be to manage. Very little in evolution makes sense, except in the light of ecology.

Future Research

How do we quantify/identify other mechanisms driving wild oat population dynamics? I concluded in Chapter 4 that wild oat has the potential to form high-density patches in any area of a small grain field in the Northern Great Plains. Thus, attention needs to be focused on management, dispersal, and fecundity. Farmers will not be able to eradicate wild oat and herbicide resistance is inevitable under constant selection pressure from herbicides (Beckie et al. 2002; Maxwell 1992). Hartzler and Roth (1993) found that weed management efficacy in the current year was strongly influenced by weed management efficacy in the preceding year and that the outcome of weed management practices was directly linked to weed population size. In the section above, I propose that prevention, crop rotation, and competition are the best tools we have in our wild oat management toolbox. Future wild oat research should focus on the mechanisms allowing wild oat patch core areas to persist. Four hypotheses and their rationale are proposed below.

1. Hypothesis: Potential wild oat habitat in other cropping systems in other regions is only limited by dispersal.

Rationale: Why isn't wild oat a problem in other cropping systems prevalent in the Midwest or northeastern U.S.? Does habitat, dispersal, fecundity, or management or a combination of those factors limit wild oat population distribution in other agroecosystems? Possible mechanisms of wild oat population limitation could be lack of cereal grains in the cropping rotation (dispersal limited), higher wild oat

seed decay rates in wetter conditions (habitat limited), or more competitive crops (fecundity limited).

2. Hypothesis: Wild oat-specific microbe associations increase the likelihood that wild oat patch core areas will persist due to enhanced competitive ability (fecundity) through habitat modification.

Rationale: Data from the wild oat habitat study indicates that wild oat competitive ratio with spring wheat was slightly greater in patch areas compared to non-patch areas at all sites. If wild oat modifies its habitat, how long and at what densities does wild oat have to be present for this to occur? We may not have the particular assays needed to detect species-specific microbe associations.

3. Hypothesis: A seedbank density threshold exists for persistent wild oat patches over the long-term (greater than 5 years).

Rationale: In Chapter 4, I demonstrated that patch areas produce more SDPP 56% of the time compared to non-patch areas (Figure 4.5). This suggests that higher seed rain may be critical in maintaining wild oat patches over the long term. Stochastic climate events will affect seed rain as well as other life history processes from year to year, but wild oat patch core areas may remain persistent until seedbank numbers decrease below a critical seedbank threshold that is required to maintain patches in the long-term.

4. Hypothesis: Wild oat patch core areas can be mapped with a core/non-core area classification system from the combine at harvest for directed pre-emergence application in the following spring.

Rationale: Despite wild oat habitat availability in the NGP, proactive wild oat management may be possible for existing high-density patch core areas. From supplemental density correspondence data in Chapter 4 (Table 4.3), if wild oat panicle density in the previous year was greater than 100 m^{-2}, wild oat seedlings were always present in the following spring.

The Bigger Picture

Site-specific technology should continue to be explored for on-farm management, especially for large-scale producers. Staver (2001) argues that precision agriculture will likely follow the technology transfer diffusion model that has been employed for the promotion of other purchased inputs in crop production. However, as scientists teach farmers to be better scientists, large-scale farmers will benefit from spatially explicit field knowledge and environmental issues can be better addressed. The sensing and data processing technologies will likely come from off-farm sources, but the technology represents a fixed cost that will improve management decisions over time, unlike the fixed costs of chemical inputs and equipment. Small-scale producers on the other hand can more easily make conclusions about spatially explicit processes. There is a place for small-scale and large-scale farmers. Both groups will have to be innovative and efficient to survive economically, while being ecologically responsible.

Local perspectives on how to innovate in crop production and weed control have been sidetracked by input-linked credit programs and promotion activities of the commercial input sector (van der Ploeg 1993). The Precision Agriculture Research Association (PARA) of MT is a real first step in overcoming the "herd mentality". Site-specific data identifies problems particular to an individual producer as well as general problems. Farm groups have been formed in the past for educational learning, but site-specific data forces farmers to think at smaller-scales in order to deal with relevant problems.

Site-specific management has the potential to reduce fossil fuel inputs. Three decades ago, Odum (1967) and Pimentel et al. (1973) argued the case that the technical improvements in agriculture due to fossil energy use did not provide any real 'emancipation' of production from the natural resources base. A wide debate has since ensued, concerning the environmental consequences of agricultural activities, when heavily boosted by technical inputs and the viability of yield increases in the long run (Gever et al. 1991; Pimentel and Hall 1984; Vitousek et al. 1986). The main problem with the increasing dependency of food production on fossil energy is related to the fact that the rate of consumption of fossil energy is certainly faster than that of its production (Martinez-Alier 1987), implying that current agricultural techniques are unsustainable in the long run (ceteris paribus: all things being equal) since present consumption of fossil energy has the effect of reducing consumption availability for future generations. In the last two centuries, technical development has always been able to generate increases in productivity even when some of the previously used resources were exhausted. The

question is thus, will the proved ability of human ingenuity be able to find substitutes for fossil fuel energy sources if the remaining stocks become limiting? Certainly, the confrontation between 'Neo-Malthusian pessimism' and 'Cornucopian optimism' reaches peaks of high intensity when the debate focuses on energy and food security in the next century (cf. Daly 1992). My opinion is that site-specific technology is a way to hedge against our dependence on fossil fuels through optimized resource management at the sub-field scale. Both ecology and technology will continue to ensure an adequate food supply for the human population.

As an agroecologist I have covered both tails of the weed science distribution. Weed management durability must evolve faster than the species it is directed toward. We are still a long way from mimicking the structure and function of natural systems, but at least we are becoming more environmentally responsible. I hope that a broad perspective in both ecology and technology will provide me with the tools to clarify issues and establish relevant agroecological research in the future management of weeds.

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APPENDICES

APPENDIX A

ADDITIONAL GREENHOUSE EXPERIMENT DATA

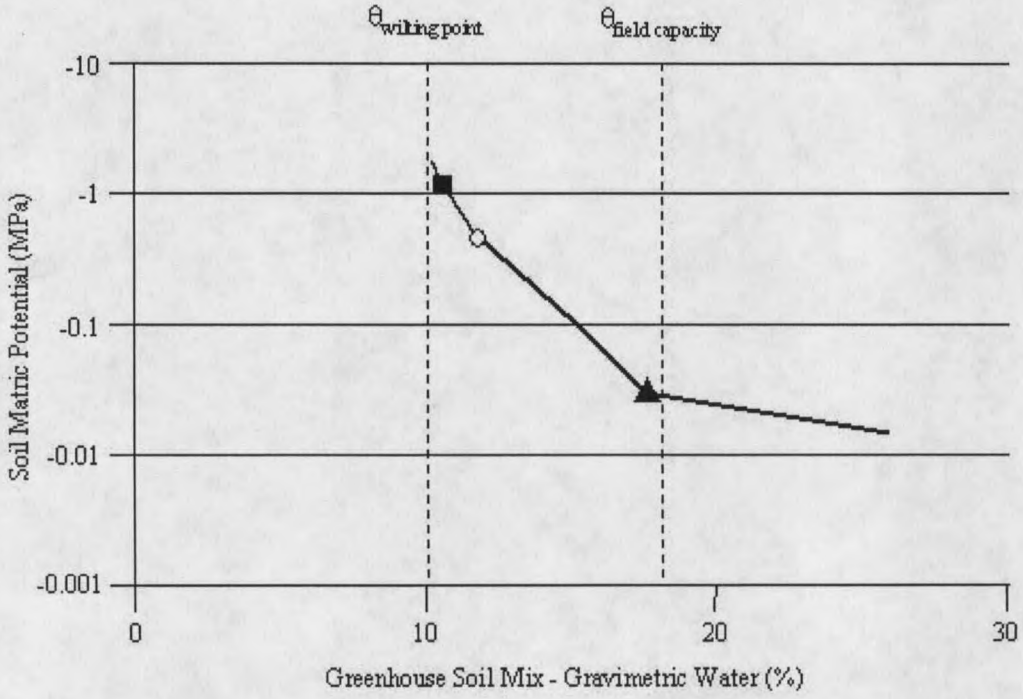


Figure A.1. Estimated soil matric potential curve for greenhouse soil mix as a function of gravimetric water content.

Table A.1. Greenhouse experiment information for pot size and wild oat harvest times for the six destructive harvests in a repeated greenhouse trial. Cumulative growing degree days (GDD) from planting, days after planting (DAP), Zadoks stage, and the approximate wild oat phenological stage at each destructive harvest are provided.

		Pot size					
Trial	Harvest	Depth	Volume	GDD	DAP	Zadoks Scale	Phenological Stages
		cm	L	°C	d	0-99	
1	1	15	2.5	437	31	13-14, 21	3 to 4 leaf, first tiller visible
	2	15	2.5	539	38	14, 21-22, 30-32	4 leaf, tillering, stem elongation
	3	20	4.8	729	49	14-16, 21-26, 32-35	Tillering, stem elongation
	4	20	4.8	881	58	15-16, 26-29, 36, 45	Boot stage to head emergence
	5	46	9.7	947	64	26-29, 36, 47-55	Elongation of peduncle, anthers visible
	6	46	9.7	1428	98	75-91	50% mature, apical seed dehiscence
2	1	20	4.8	393	25	13-14, 20-21	3 to 4 leaf, first tiller visible
	2	20	4.8	597	40	14-15, 21-23, 30-33	4 to 5 leaf, tillering, stem elongation
	3	46	9.7	831	55	15-16, 24-29, 34-37, 41	Last internode elongation, flag leaf visible
	4	46	9.7	1040	70	29, 39, 59-65	End of stem extension, anthers visible
	5	46	9.7	1209	82	69-83	Seed fill
	6	46	9.7	1632	111	87-93	100% mature, seed dehiscence

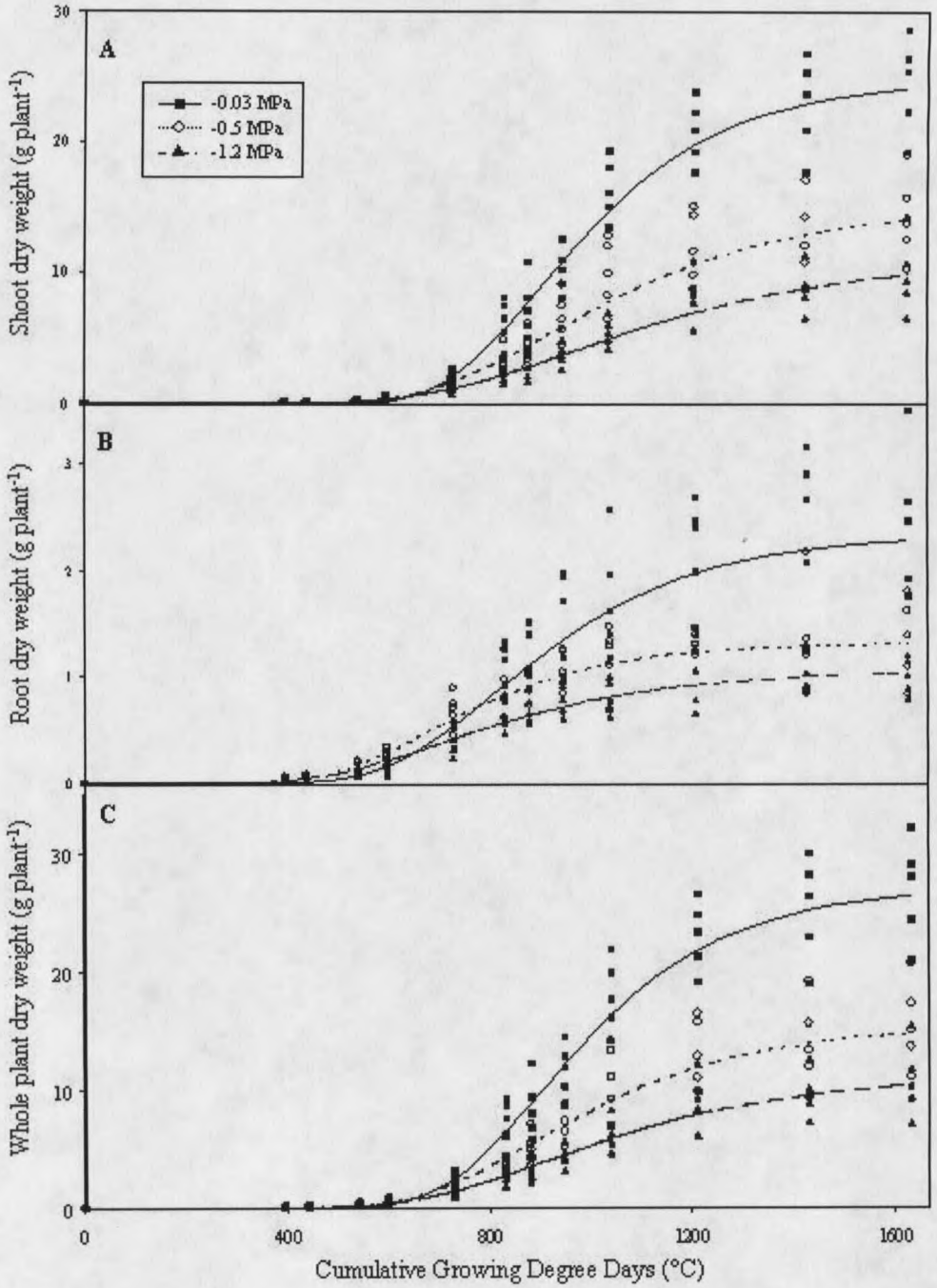


Figure A.2. Observed (symbols) and predicted (lines) shoot wt (A), root wt (B), and whole plant wt (C) for wild oat grown at soil matric potentials of -0.03, -0.5, and –1.2 MPa. Data were fitted to the Richards function (Equation 3.2) as a function of growing degree days from planting.

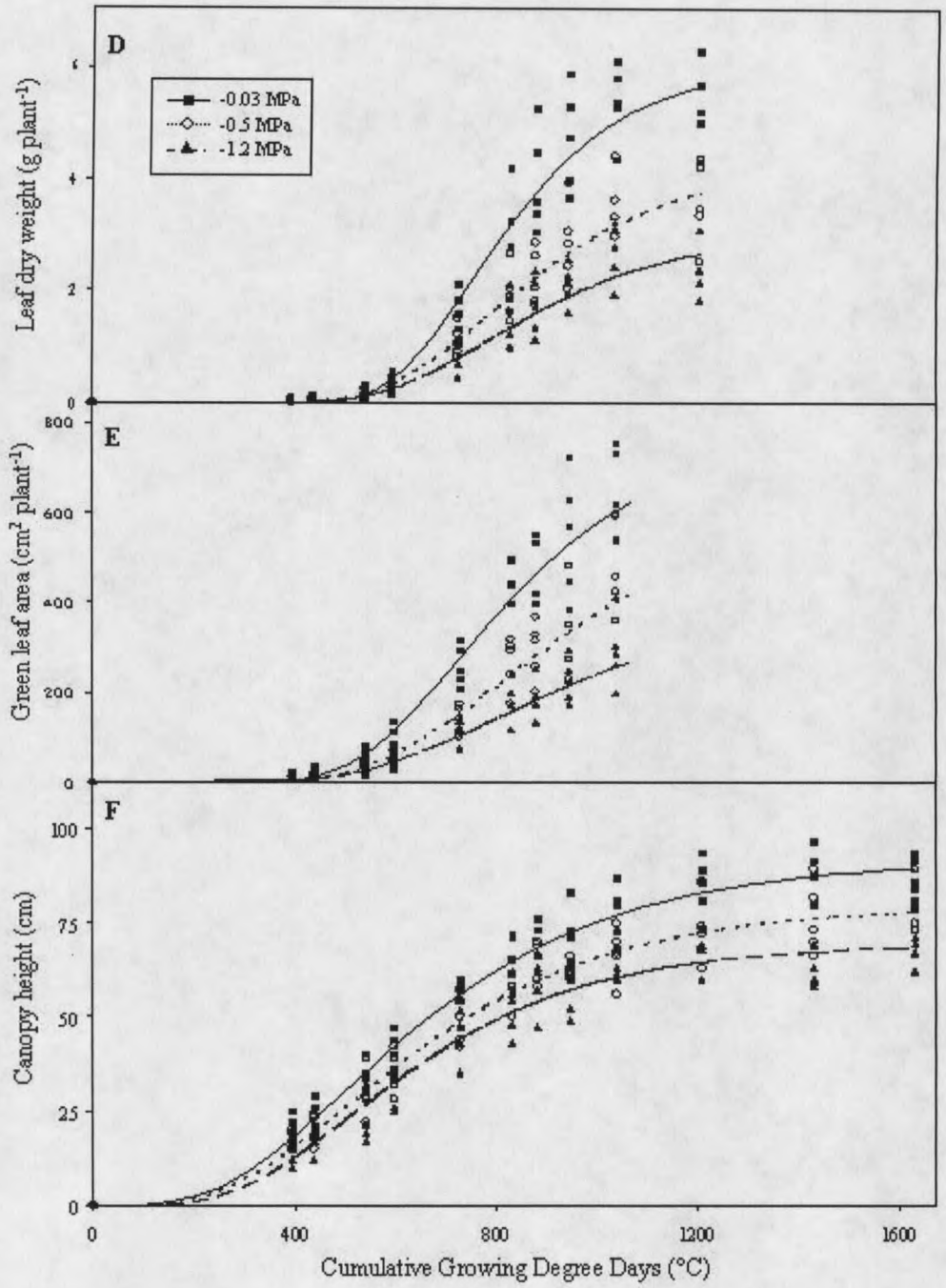


Figure A.3. Observed (symbols) and predicted (lines) leaf dry wt (D), green leaf area (E), and canopy height (F) for wild oat grown at soil matric potentials of -0.03, -0.5, and –1.2 MPa. Data were fitted to the Richards function (Equation 3.2) as a function of growing degree days from planting. The asymptotic size for leaf area and leaf wt occurred at 1040 and 1209 GDD, respectively.

CALCULATING PARTITIONING COEFFICIENTS

The percent of new dry matter production partitioned to each tissue type was calculated as a function of GDD from the mean of size ranked pairings of individual plants between two subsequent harvests. The partitioning coefficient (PC_k) for tissue k was calculated by dividing the change in weight of tissue k between two samplings by the change in total plant weight (Kropff and van Laar 1992). The PC_k for the root, leaf, stem, and panicle for the midpoint of the time interval, time (t_j) to time (t_{j+1}), was calculated as:

$$PC_k(t_{j+0.5}) = \left(\frac{k(t_{j+1}) - k(t_j)}{w(t_{j+1}) - w(t_j)} \right) \qquad \text{(A.1)}$$

where $k(t)$ is the root, leaf, stem, or panicle tissue dry weight at time, t and $w(t)$ is the total plant dry weight at time, t. If the change in weight of a specific tissue was negative, no growth was assumed. Standard errors were estimated from the square root of the variance for each PC_k divided by the number of size ranked pairings.

Table A.2. Wild oat partitioning coefficients (PC) ± standard errors for assimilate allocated to root, leaf, stem, and panicle (Pan.) tissues as a function of cumulative growing degree days (GDD). The PC and its standard error (SE) were calculated from the ranked size pairing of plants in subsequent harvests (Equation A.1).

	-0.03 MPa				-0.5 MPa				-1.2 MPa			
GDD	Root	Leaf	Stem	Pan.	Root	Leaf	Stem	Pan.	Root	Leaf	Stem	Pan.
°C	PC (SE)											
197	27 (1)	60 (2)	13 (2)	0 (0)	45 (1)	47 (1)	9 (1)	0 (0)	43 (2)	47 (1)	10 (1)	0 (0)
415	32 (7)	52 (5)	16 (3)	0 (0)	40 (8)	50 (5)	10 (3)	0 (0)	43 (2)	47 (2)	10 (1)	0 (0)
488	22 (2)	64 (3)	14 (1)	0 (0)	37 (5)	44 (5)	18 (3)	0 (0)	40 (1)	47 (3)	12 (2)	0 (0)
568	20 (3)	68 (5)	12 (4)	0 (0)	36 (3)	50 (2)	14 (1)	0 (0)	47 (4)	49 (3)	4 (2)	0 (0)
663	18 (1)	64 (1)	18 (1)	0 (0)	32 (2)	59 (2)	10 (2)	0 (0)	18 (2)	52 (3)	30 (2)	0 (0)
780	14 (1)	43 (5)	44 (6)	0 (0)	10 (1)	41 (2)	49 (1)	0 (0)	18 (2)	53 (1)	29 (3)	0 (0)
856	8 (7)	38 (8)	54 (6)	1 (1)	7 (7)	31 (7)	60 (9)	2 (2)	13 (5)	39 (4)	48 (8)	0 (0)
914	12 (2)	24 (2)	57 (9)	7 (3)	5 (1)	25 (4)	67 (4)	4 (2)	4 (1)	40 (5)	36 (5)	20 (7)
994	4 (3)	11 (3)	51 (4)	34 (2)	2 (3)	30 (7)	37 (5)	31 (3)	9 (3)	29 (3)	52 (6)	10 (1)
1125	7 (4)	0 (0)	41 (8)	52 (8)	6 (3)	0 (0)	44 (9)	51 (12)	3 (1)	0 (0)	71 (2)	26 (2)
1319	0 (0)	0 (0)	23 (12)	77 (12)	0 (0)	0 (0)	51 (9)	49 (9)	0 (0)	0 (0)	61 (21)	39 (21)

SPECIFIC ROOT LENGTH ANALYSIS

At least one root within each harvest time at each soil matric potential (Table A.1) was randomly selected for root length analysis. The last harvest (1632 GDD) in trial 2 was not analyzed as the biomass was within the range of biomasses already analyzed. The selected roots were washed after the final cleaning procedure to remove any remaining ethyl alcohol and stained for 1 d in a methyl blue solution that contained 1 g methyl blue to 100 ml of water. The stained roots were mounted on transparencies with tweezers and dissecting needles with care taken not to overlap any root segments. The larger root samples required over 100 separate transparencies to ensure non-overlapping root segments. The transparencies with the mounted roots were scanned (Scan Jet 4c Scanner with Transparency Adapter. Hewlett Packard, 3000 Hanover St., Palo Alto, CA 94304) at a resolution of 600 dpi. The roots were removed from the transparency, dried and weighed. Root length was estimated from the digital images using the ROOTEDGE software program (ROOTEDGE software. Tom Kaspar, USDA-ARS, National Soil Tilth Laboratory, 2150 Pammel Dr., Ames, IA 50011. *http://www.nstl.gov/software/rootedge*). The accuracy of the estimated root length was determined from 10 sub samples that were hand-measured. The estimated root lengths were consistently within 2% of the measured root length.

Specific root length (SRL) is an indicator of a plants ability to avoid water stress. If SRL increases, there is more root length per unit of root wt. Wild oat root length was linearly regressed on root dry wt for each soil matric potential treatment constraining the y-intercept to zero. SRL is the slope of this relationship. A general F test was used to

test whether the three linear regressions statistically differed between the soil matric potential treatments. The null hypothesis of similar SRL among treatments was not rejected, thus the linear regression on the pooled data is given along with its R^2. Root length data over the last five harvests (only 1 sample at each harvest) for each treatment were analyzed with ANOVA with means separated using Tukey's HSD test at $P = 0.05$.

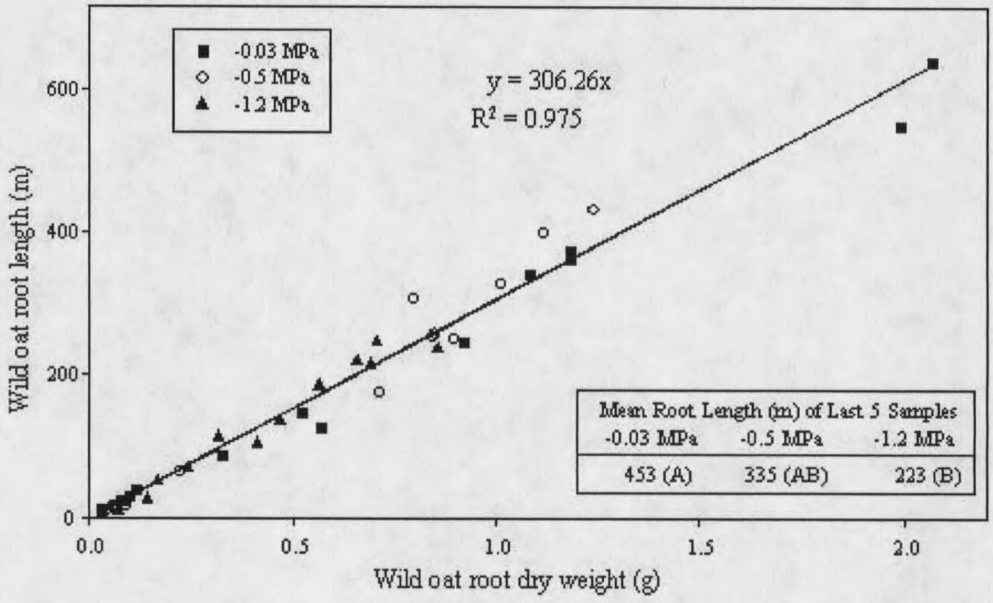


Figure A.4. Relationship between observed (symbols) wild oat root length and root wt at soil matric potentials of –0.03, -0.5, and –1.2 MPa. The box in the lower right hand corner shows the mean root length (m) over the last five harvests (only 1 sample at each harvest) at each soil matric potential with letters in parentheses indicating significant differences at $P = 0.05$.

YIELD COMPONENT ANALYSIS

Wild oat yield component data (seeds/plant, spikelets/plant, seeds/spikelet, 100 seed wt, tillers/plant, and viable tillers/plant) was pooled for the last two sampling periods (1428 and 1632 GDD) within each matric potential treatment. Each yield variable was linearly regressed on soil matric potential. The data was natural log transformed because some yield variables had heteroscedastic variances. The transformation did not alter the initial results so the primary data was used. The significance of the slope was determined at $\alpha = 0.05$. As a further measure of water stress on seed production, wild oat seed production efficiency was calculated as the number of seeds per g shoot dry wt for each plant and was analyzed the same as the other yield components.

Table A.3. Soil matric potential effects on wild oat yield components. The average for each wild oat yield component within the last two harvests is given. Each yield component variable was regressed on soil water matric potential. The linear regression slope estimate, its standard error (SE) and p-value are presented.

	-0.03 MPa	-0.5 MPa	-1.2 MPa	Linear regression slope		
Yield variable	——— Avg. ———			Estimate	SE	P-value
Seeds plant^{-1}	823	370	180	529.42	59.50	0.00000
Spikelets plant^{-1}	419	219	120	247.44	31.35	0.00000
Seeds spikelet^{-1}	2.0	1.7	1.5	0.39	0.11	0.00150
100 seed wt (g)	0.92	0.80	0.74	0.15	0.04	0.00221
Tillers plant^{-1}	13.1	11.2	10.6	2.04	0.96	0.04147
Viable tillers plant^{-1}	11.7	9.4	8.5	2.63	1.09	0.02229
Seed g^{-1} shoot wt (SPE)	34.9	27.0	19.5	13.04	2.56	0.00002

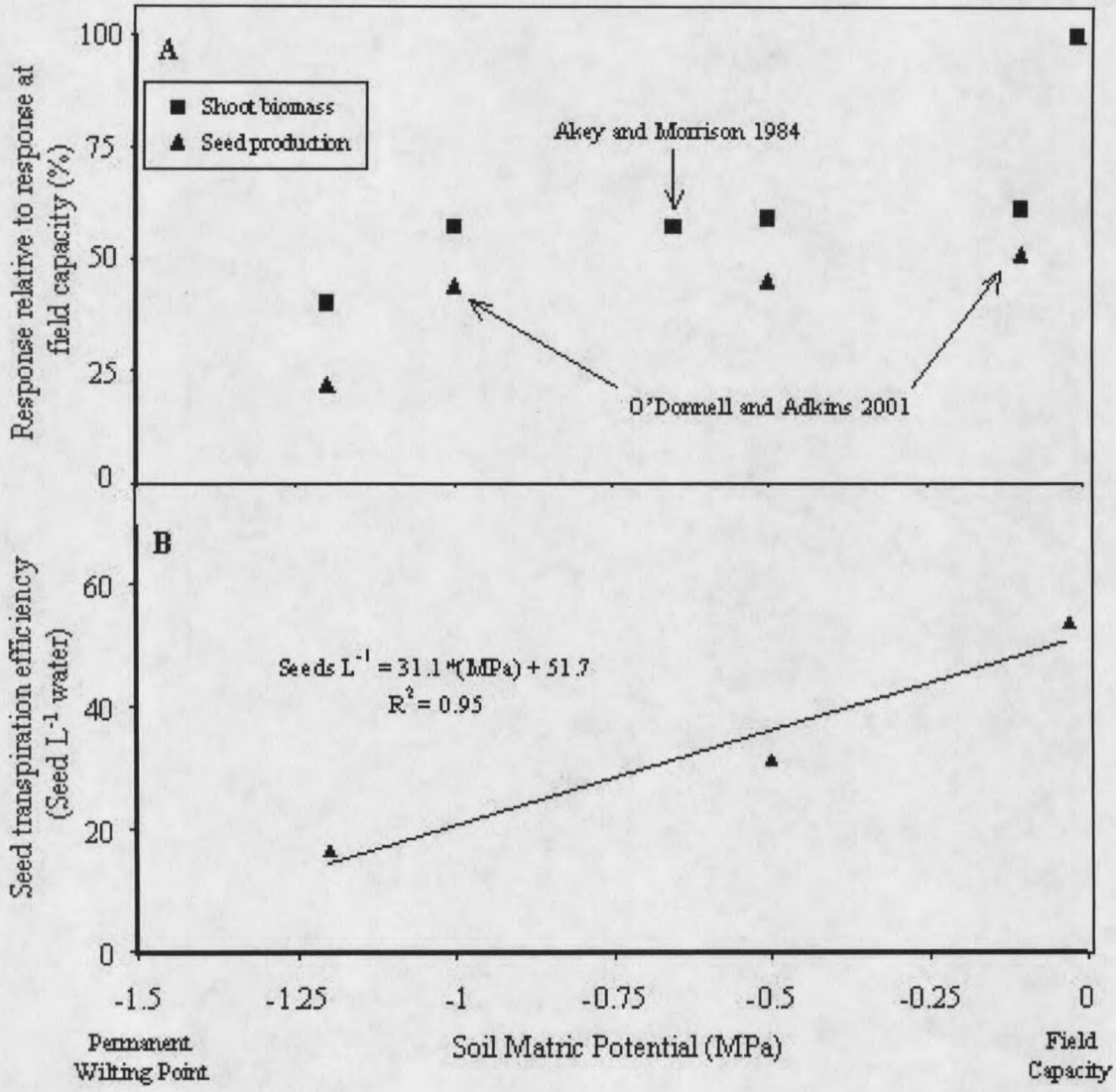


Figure A.5. Wild oat mature shoot biomass and seed production response relative to the response at field capacity for this and two other studies (A) and wild oat seeds L^{-1} of transpired water estimated from this study (B) as function of soil matric potential. The shoot biomass and seed production values at -0.5 and –1.2 MPa in A are from this study, values at –0.1 and –1.0 MPa was from O'Donnell and Adkins (2001), and the shoot biomass at –0.65 MPa was from Akey and Morrison (1984).

APPENDIX B

ADDITIONAL WILD OAT HABITAT EXPERIMENT DATA

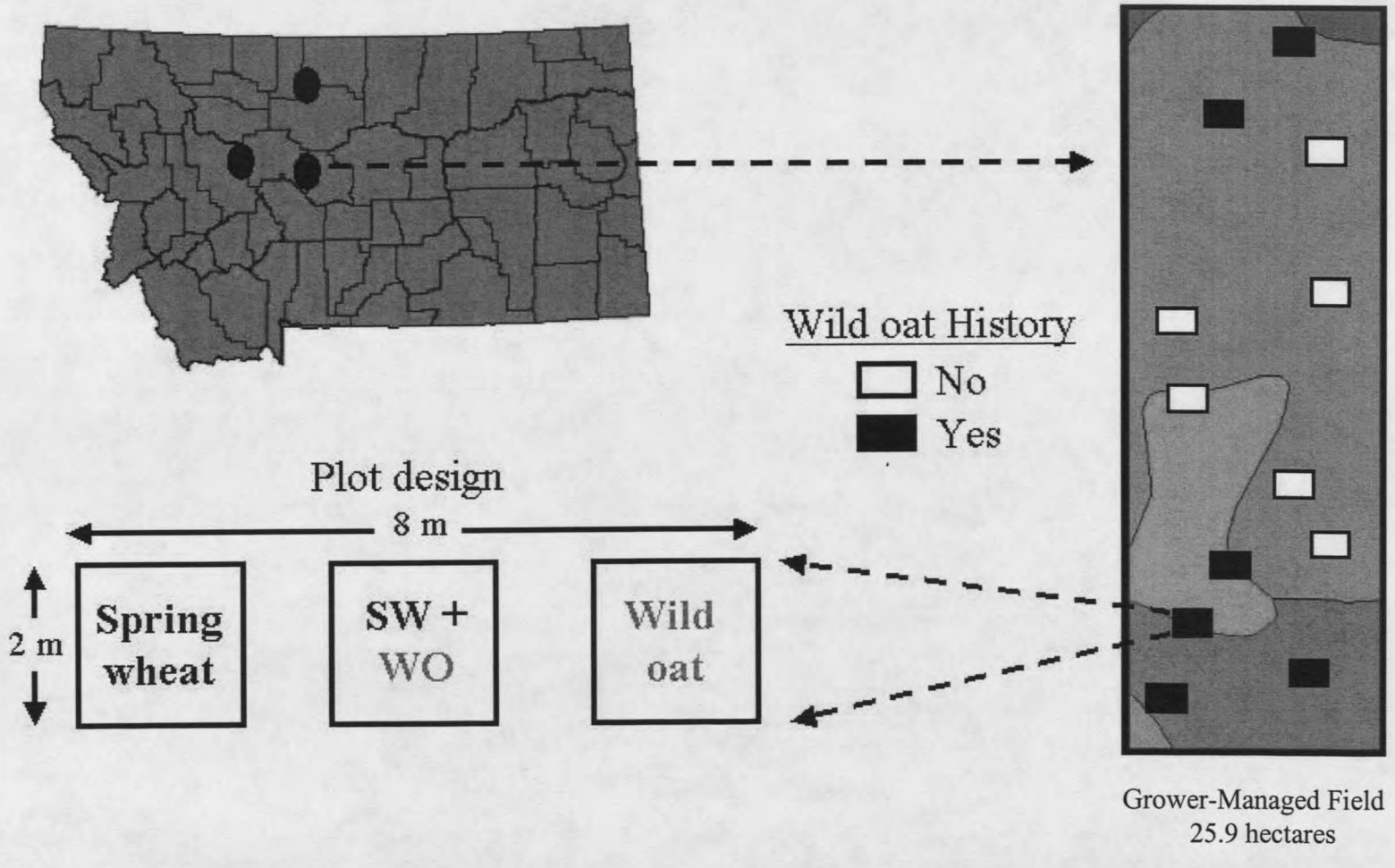


Figure B.1. Montana field sites and plot design for wild oat history and plant community type. Each field had 12 plots, six of each in wild oat patch and non-patch areas. Each plot had a subplot of monoculture wild oat, monoculture spring wheat and a mixture of both species.

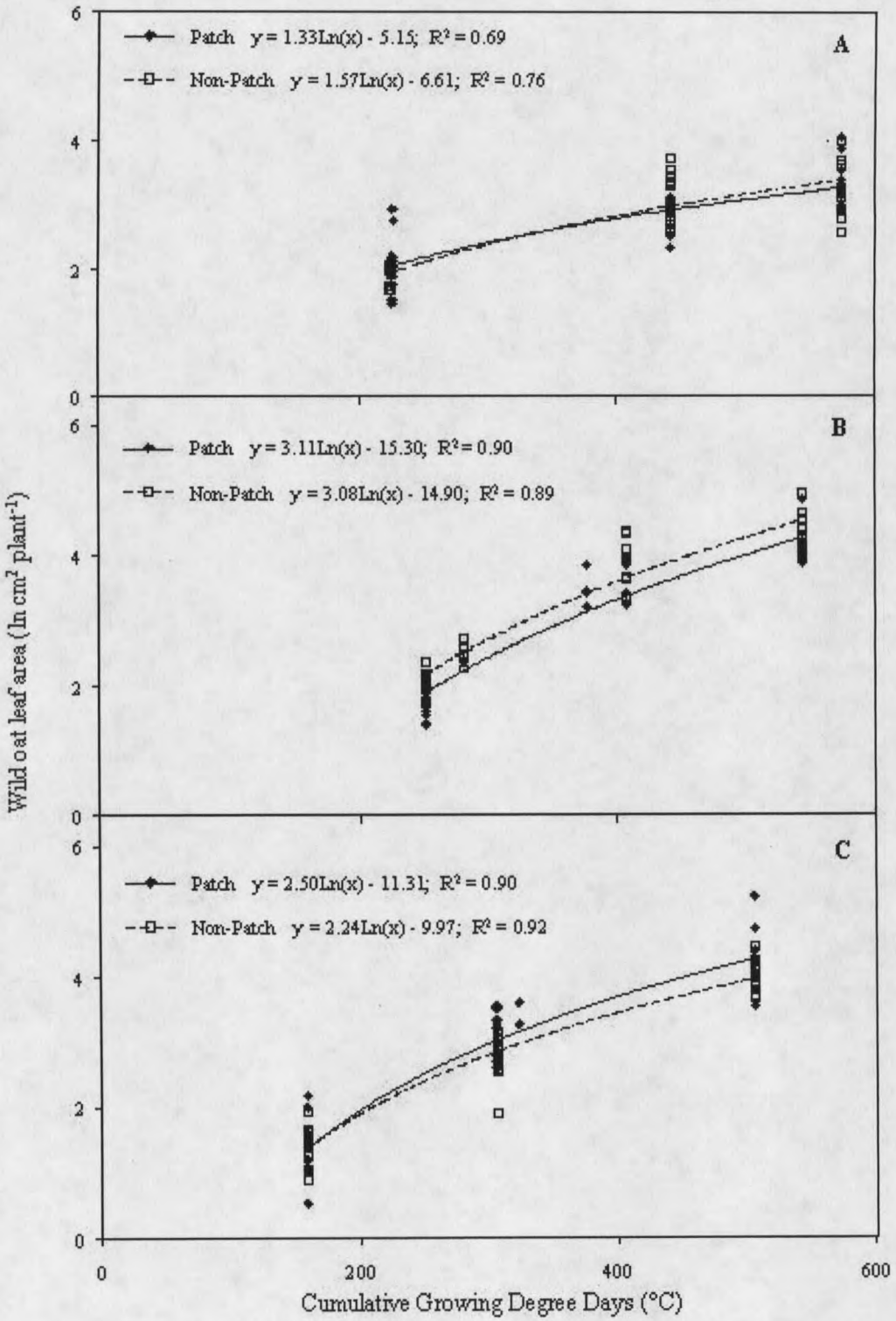


Figure B.2. Observed (symbols) and predicted (lines) values of natural log transformed leaf area per plant as a function of cumulative growing degree days for wild oat in patch and non-patch areas at Box Elder (A), Fife (B), and Sun River (C).

Table B.1. Mean spring wheat early season leaf area growth rate per plant (LAGR), shoot wt at maturity, and grain yield at Box Elder, Fife and Sun River, MT as affected by wild oat history (patch and non-patch areas) and plant community (spring wheat monoculture or mixed culture with wild oat).

Source of Variation	Box Elder			Fife			Sun River		
	RGRL	Shoot	Yield	RGRL	Shoot	Yield	RGRL	Shoot	Yield
	$d°C^{-1}$	—— g $plant^{-1}$ ——		$d°C^{-1}$	—— g $plant^{-1}$ ——		$d°C^{-1}$	—— g $plant^{-1}$ ——	
Wild oat habitat (H)									
Patch	0.96	1.56	0.49	2.93	2.73	1.13	2.16	2.18	0.70
Non-patch	1.62	2.05	0.71	3.10	2.98	1.14	2.23	2.65	0.078
$P > F$	0.008	0.059	0.016	0.329	0.375	0.945	0.750	0.186	0.487
Community (C)									
Monoculture	1.29	2.50	0.87	3.00	3.81	1.62	2.06	3.32	1.09
Mixed culture	1.30	1.11	0.33	3.02	1.89	0.65	2.33	1.58	0.40
$P > F$	0.961	<0.001	<0.001	0.940	<0.001	<0.001	0.181	<0.001	<0.001
Interaction, $P > F$									
H×C	0.573	0.909	0.448	0.974	0.699	0.641	0.555	0.090	0.157

Table B.2. Spring wheat total water use (TWU) and biomass water use efficiency (WUE_B) at Box Elder, Fife and Sun River, MT as affected by wild oat history (patch and non-patch areas) and plant community (spring wheat monoculture or mixed culture with wild oat).

Source of Variation	Box Elder		Fife		Sun River	
	TWU	WUE_B	TWU	WUE_B	TWU	WUE_B
	mm	kg ha^{-1} mm^{-1}	mm	kg ha^{-1} mm^{-1}	mm	kg ha^{-1} mm^{-1}
Wild oat habitat (H)						
Patch	116.5	14.5	150.1	19.9	97.5	15.4
Non-patch	133.3	18.9	169.0	24.6	100.2	22.1
$P > F$	0.042	0.099	0.044	0.113	0.706	0.058
Community (C)						
Monoculture	179.3	16.7	235.3	21.6	162.3	15.1
Mixed culture	70.6	16.6	83.8	22.9	35.4	22.4
$P > F$	<0.001	0.975	<0.001	0.652	<0.001	0.040
Interaction, $P > F$						
H×C	0.777	0.763	0.384	0.846	0.033	0.095

Average wild oat WUE_B across all fields was 12.9 kg ha^{-1} mm^{-1} (Table 4.2) while average spring wheat biomass water use efficiency was 19.2 kg ha^{-1} mm^{-1}, meaning that spring wheat was more efficient in assimilating biomass per unit of water (assumed evapotranspiration) than wild oat.

Table B.3. Mean wild oat and spring wheat yield loss per plant at Box Elder, Fife and Sun River, MT as affected by wild oat history (patch and non-patch areas).

Source of Variation	Box Elder		Fife		Sun River	
	Wild oat	Spring wheat	Wild oat	Spring wheat	Wild oat	Spring wheat
	Yield loss (%)					
Wild oat habitat						
Patch	1.2	66.1	16.1	61.6	23.0	74.4
Non-patch	0.0	58.2	20.1	56.8	11.6	49.4
$P > F$	0.646	0.409	0.796	0.489	0.943	<0.001

Spring wheat yield loss averaged 61% across all sites. Crop yield loss did not differ between wild oat patch and non-patch areas within a field at Box Elder or Fife. At Sun River, spring wheat yield loss was 74% in wild oat patch areas and 49% in non-patch areas ($P < 0.001$). Most of this effect was likely due to higher wild oat densities in patch areas compared to non-patch areas ($P = 0.048$) and lower spring wheat WUE_B in patch compared to non-patch areas ($P = 0.058$) (Table B.2). Spring wheat WUE_B was lower in patch areas compared to non-patch areas at all three sites which suggests long-term wild oat patch areas may modify the soil matrix in a manner which is detrimental to spring wheat water use efficiency. Furthermore, existing wild oat habitat was negatively correlated with both spring wheat biomass and grain yield water use efficiency across all three sites ($r = -0.33$, $P = 0.004$; and $r = -0.27$, $P = 0.024$, respectively).

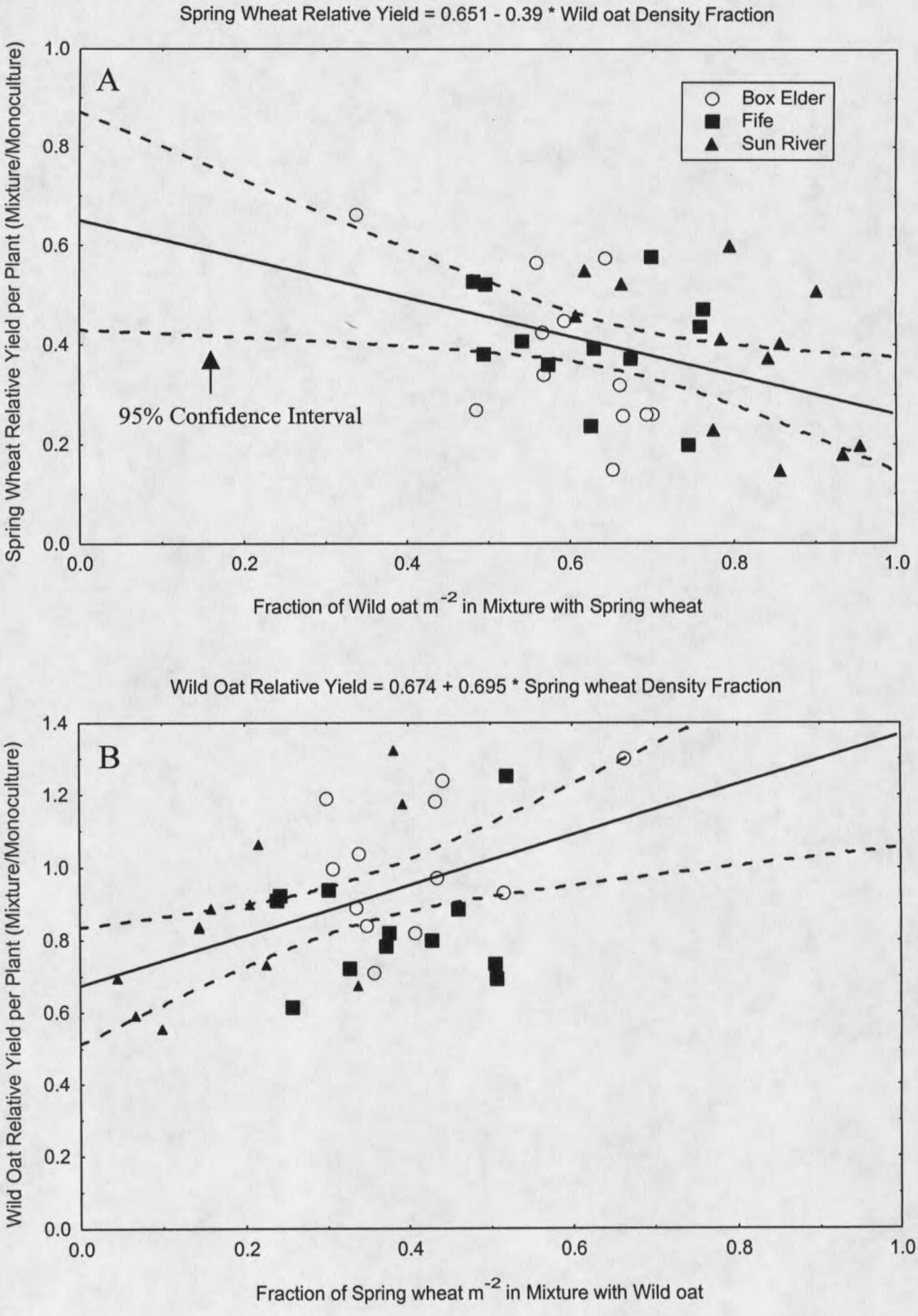


Figure B.3. Relationship between spring wheat relative yield and the wild oat density fraction in mixture (A) and the wild oat relative yield and the spring wheat density fraction in mixture (B) at Box Elder, Fife, and Sun River, MT

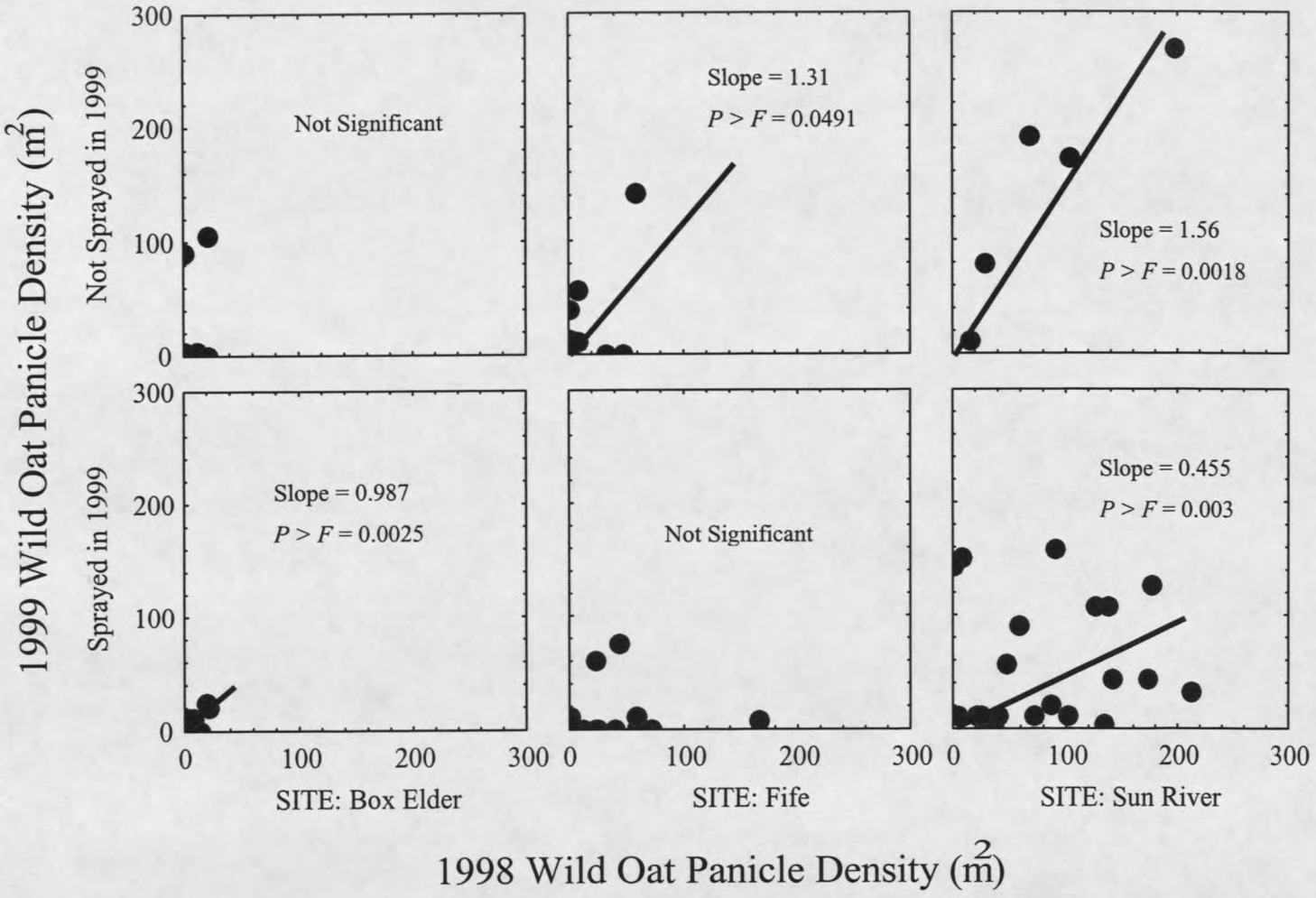


Figure B.4. Wild oat panicle density correspondence between 1998 and 1999 for field areas sprayed and not sprayed in 1999 at Box Elder, Fife, and Sun River, MT.

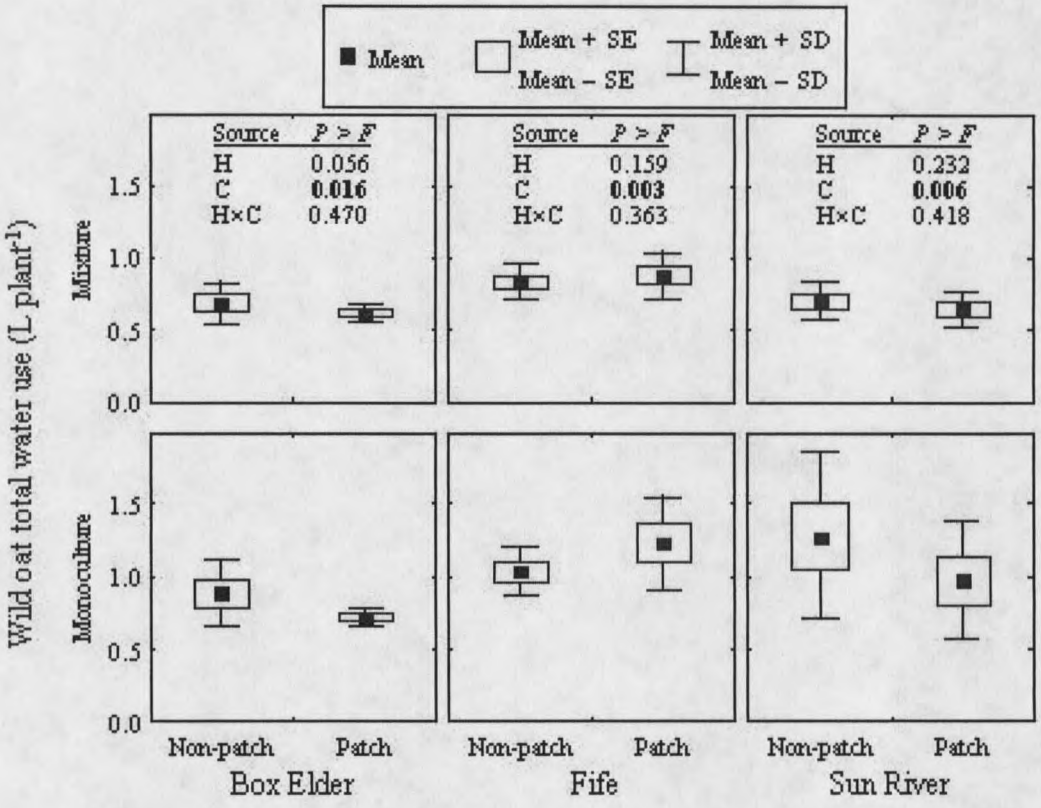


Figure B.5. Main effects and interaction between wild oat history (H, patch or non-patch) and plant community (C, wild oat monoculture or mixed culture with spring wheat) for wild oat total water use (TWU, assumed evapotranspiration during the season) at Box Elder, Fife, and Sun River, MT.

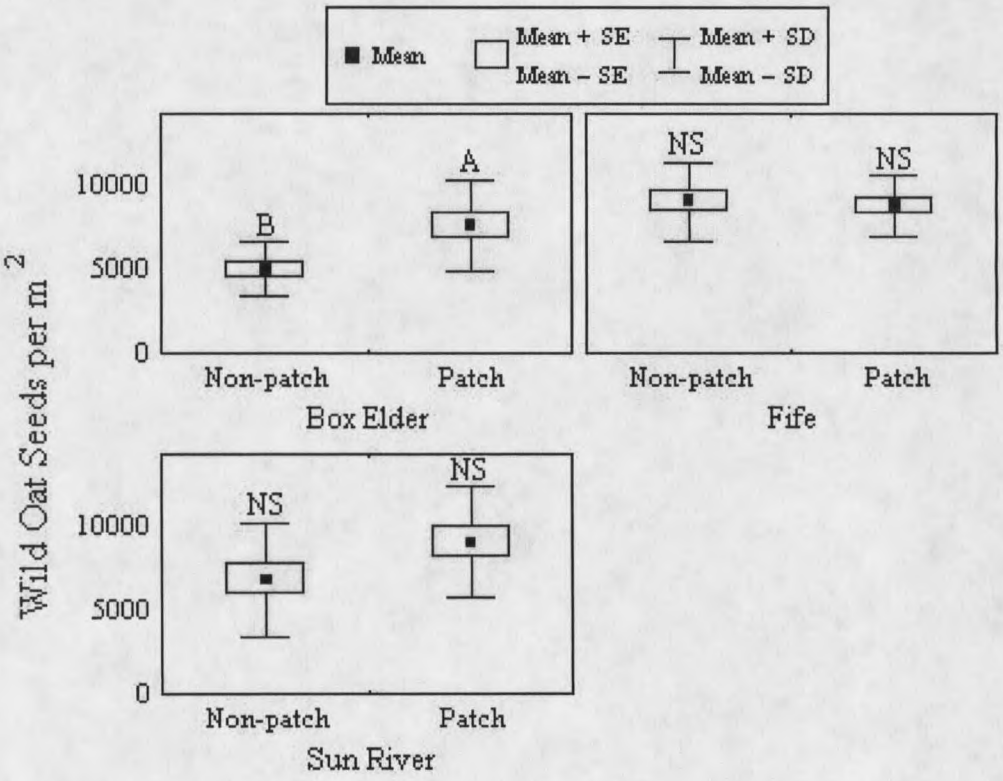


Figure B.6. Wild oat seeds per square meter in fields with a history of wild oat patch or non-patch areas at Box Elder, Fife, and Sun River, MT. Letters indicate differences within a site between patch and non-patch areas at $P < 0.05$.

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