

**A Study of Wild Oat, Green Foxtail, and
Barnyardgrass Associations in an Arable Field**

By
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The University of Manitoba

In Partial Fulfillment of the Requirements
For the Degree of

Master of Science

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**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University
of Manitoba in partial fulfillment of the requirements of the degree**

of

Master of Science

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Abstract

Many researchers are acknowledging the need to address multiple weed species interaction. The objective of this project was to assess the associations between wild oat, green foxtail, and barnyardgrass, discuss the practical implications of these results, and the possible mechanisms responsible for the association of these species.

At the University of Manitoba's Carman research station two, 10 m x 10 m sites were surveyed for the presence or absence of weed seedlings at a scale of 10 cm x 10 cm, in 1998 and one repeated site in 1999. These sites contained wild oat, green foxtail, and barnyardgrass.

Visual maps were created which provided an overall view of the species associations. Statistical analysis of the three species was performed using unadjusted Chi-square analysis, and autocorrelation was adjusted for using the Random Patterns and Patch Model tests. Spatial patterns cannot be used to prove which process is responsible for their formation, but can be used to suggest possible processes which led to their formation. Wild oat and green foxtail were found to be significantly negatively associated at sites 1 and 2 in 1998. Wild oat and barnyardgrass were found to be significantly negatively associated at sites 1 and 2 in 1998, and significantly positively associated at site 1 in 1999. Green foxtail and barnyardgrass were found to be significantly positively associated at site 1 in 1998 and 1999.

Positive and negative associations of weed species may reflect their ability to establish in and dominate an area, which may have applications in

patch dynamics models. Positive and negative associations of weed species may also have implications for the suitability of additive or non-additive effects in yield loss prediction models.

A replacement series experiment revealed that wild oat was more competitive than green foxtail or barnyardgrass, and that green foxtail and barnyardgrass were relatively equal competitors. However, at site 1, from 1998 to 1999 the area occupied by green foxtail and barnyardgrass increased relative to the area occupied by wild oat, indicating that, under field conditions, green foxtail and barnyardgrass may be better able to invade an area. The association values for wild oat, green foxtail, and barnyardgrass may have been affected more by seed dispersal than by competition. Comparison of soil cores taken in the spring of 1999 to weed seedling infestations measured in the spring of 1999, revealed that there was only a relatively high relationship of association between the seed bank and seedlings of barnyardgrass. Environmental differences at site 1 between 1998 and 1999 may have affected the species associations, mainly due to the differences in the relative emergence time of the weed species, and the time of seeding.

In conclusion, the detection of spatial association patterns allows one to discuss the mechanisms which might be responsible for their creation. The detection of spatial association patterns between species may have important implications for the parameters of weed population dynamics models, and the suitability of additivity assumptions for yield loss prediction models.

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1.0 Introduction

Historically, the majority of weed scientists have focused on single crop-weed interactions. Recently weed ecology has shifted focus to a more holistic approach to weed control. Scientists have begun to question the validity of many yield loss prediction models due to their underlying single species assumptions. Limited information, however, is available on multi-species interference patterns occurring in field situations. Important considerations include whether multi-weed species interactions occur at all, and if so between which species and to what extent.

The objective of this project was to quantify the spatial associations occurring among several common weed species in Manitoba's arable fields. The null hypothesis for this survey was that no species associations would be detected, while the alternative hypothesis was that positive or negative species associations would exist. We will examine the spatial association of key weed species interactions with particular emphasis on species associations. Insight gained from the spatial relationships will be used to justify the study of interactions occurring between multiple weed species. A determination of the extent of multiple weed species associations will help scientists to better understand the practical effect on agricultural production systems, and on weed population biology.

Agricultural fields examined on a coarse scale appear as monoculture production systems. However, when examined on a finer scale they clearly consist of a wide variety of plant species. This project was based at the

University of Manitoba's Carman research station. In the project we investigated wild oat (*Avena fatua* L.), green foxtail (*Setaria viridis* (L.) Beauv.), and barnyardgrass (*Echinochloa crus-galli* (L.) Beauv.) over two 10 m x 10 m sites at 10 cm x 10 cm grids. This information was coupled with gravimetric soil moisture measurements and seed bank analysis. Spatial analysis consisted of Chi-square and corrected Chi-square procedures, which related the degree of weed species associations. Pair wise replacement series experiments involving wild oat, green foxtail, and barnyardgrass were also performed to help quantify relative competitiveness among these species.

Gaps in the understanding of multiple weed species interaction presently exist and hamper further improvement of weed ecology models. This project focused on gaining insight into the spatial associations of multi-weed species associations. A survey of weed species was performed over both space (snapshot), and time (trajectory). The study of weed ecology and weed management requires that one study weed populations over a period of years to assess the long-term trends within the system. A better understanding of the spatial associations occurring within multi-weed species patches enhances the ability of researchers to predict weed patch movement and thus future crop yield losses due to competition. Knowledge in this area could be useful for the modification of weed population dynamics and yield loss predication models. They may then better reflect the reality of multiple weed species infestations in arable fields.

2.0 Literature Review

2.1. Justification for studying multi-species weed interactions

Good weed management is key for profitable agriculture (Cowan et al. 1998). Kropff and Lotz (1992) stated that increasing herbicide resistance, rising costs, and environmental concerns have all contributed to the pressure on producers to reduce herbicide use. To support this movement towards reducing herbicide applications the Manitoba Guide to Crop Protection (2000) includes yield loss thresholds for many weed-crop combinations. Swinton et al. (1994) noted that most studies used to assess parameters for economic yield loss thresholds only considered competition between single weed-crop combinations. Combellack and Friesen (1992) stated that in reality, producers are often faced with more than one weed species infestation, resulting in the need to address multiple-weed species interference. As a result, adjustments of patch dynamics and yield loss prediction models are necessary to adequately reflect modern arable agriculture.

2.1.1 Single weed species interference studies

Kropff and Spitters (1991) noted that a variety of single weed-crop empirical models have been investigated in the past. The most important parameters considered were weed density (Spitters 1983), and relative time of weed emergence with respect to the crop (Cousens et al, 1987). However, many studies conducted to develop yield loss predictions have not taken into account the non-additive affects of multiple weed species interactions (Beckett et al. 1988; Knezevic et al. 1994; Cousens et al. 1986; Bauer and Mortensen 1992).

Combellack and Friesen (1992) noted single species experiments were narrow sighted, as they failed to recognize that weed infestations often consist of more than one weed species.

2.1.2 Multiple weed species interference studies

Van Acker et al. (1997) stated that it is important to use parameters established from multiple weed species experiments, when developing multiple weed species empirical yield loss prediction models. Van Acker (1996) stated that multiple weed species experiments have been avoided in the past because of the large number of treatments needed, and the increased complexity of analyzing multiple weed species infestations. Swanton et al. (1999) stated that the objective of most studies involving multiple weed species interference has been to determine if the effect of the weeds in the multi-species complex was additive or non-additive in nature. Additive yield loss occurs when the yield loss caused by two interacting species is equal to the sum of the yield loss caused by each individual species. Non-additive yield loss occurs when the yield loss caused by two interacting species is not equal to the sum of the yield loss caused by each individual species. Non-additive yield loss infers that weeds are affecting one another.

Blackshaw and Schaalje (1993) investigated the interference between two weed species redstem filaree (*Erodium cicutarium* L.), and round-leaved mallow (*Malva pusilla* Sm.) under controlled environmental conditions. The authors disagreed with Spitters (1983), who developed a model that assumed that competition effects were independent of plant density and that this assumption

would hold true for other competition experiments. As a result, Blackshaw and Schaalje (1993) added a linear-by-linear interaction term to account for the lack of independence, which only slightly increased the complexity of the model. Results indicated that, when grown in monocultures, round-leaved mallow grew taller and produced more shoot biomass than redstem filaree. When grown in mixtures, round-leaved mallow gained leaf area and shoot biomass, at the expense of redstem filaree, indicating that it was the superior competitor. This suggested that the weed species would have a non-additive effect on one another. Competition ratios indicated that round-leaved mallow was about twice as competitive as redstem filaree. The authors concluded that significant competition was occurring between these weed species, but that their extended reciprocal yield model would require additional testing with other weed species.

Haizel and Harper (1973), studied multiple weed species interactions between wild oat, wild mustard (*Sinapis alba* L.), and barley (*Hordeum vulgare* cv. Proctor). A rating of aggressiveness of the three species studied was derived from comparisons between the species. For example, in a crop of barley, volunteer barley caused the greatest yield reduction followed by wild oat, and then wild mustard. The effects of the weeds on the crop were not strictly additive, in that a doubling of the weed population density did not double the crop yield loss. Doubling the density of the weed population produced a stress which was shared between the crop and weed populations. This was noted in the barley crop containing wild mustard and wild oat; and in the wild oat populations containing wild mustard and volunteer barley. Thus the mixtures of

weed species produced less than additive effects. The authors also noticed an apparent synergistic effect between weeds, as the production of wild mustard was reduced more by a mixture of barley and wild oat than expected.

Blackshaw et al. (1987) studied the interference of wild mustard and lamb's quarters (*Chenopodium album* L.) in spring rapeseed (*Brassica napus*) to quantify the response of rapeseed dry weight and yield to varying infestation levels of wild mustard and lamb's quarters. Rapeseed yield was reduced 36 and 25% by 20 plants per m² of wild mustard and lamb's quarters, respectively. However, when these weeds were combined at these densities the yield reduction was 39%, only slightly greater than the loss caused by wild mustard alone. The authors noted that these non additive results indicated that there was a great difficulty in reliably predicting crop yield losses from single weed species experiments when more than one weed species was present.

Alex (1970), investigated the competition of wild mustard and cow cockle (*Saponia vaccaria* L.) in wheat (*Triticum aestivum*) to test the hypothesis that cow cockle was able to increase in abundance when wild mustard was controlled by 2,4-D; and to measure the competition effect on wheat and the two weed species. Alex noted that 125 wild mustard per m² reduced wheat grain yield by 38%, and 2.5 times as many cow cockle reduced the wheat yield by only 36%. Wild mustard was not affected by the presence of cow cockle, while in the presence of wild mustard, cow cockle seed and dry weight were reduced by 50%. The study indicated that the two weed species competed with each other as well as with the wheat. The competitive effects of wild mustard and cow

cockle were not completely additive because the effects of one species obscured the effects of the other. Thus their combined effect on wheat was only a little greater than the effect of each species individually.

Sims and Oliver (1990) studied the mutual influence of seedling johnsongrass (*Sorghum halepense* (L.) Pers.) and sicklepod (*Cassia obtusifolia* L.) on soybean (*Glycine max* (L.) Merrill). Their objective was to study the magnitude of soybean yield reduction caused by both weeds in combination. Results indicated that soybean yield was reduced 31% by sicklepod and 14% by johnsongrass, alone. Both weeds grown together caused a yield reduction in soybean of 36%, indicating a non additive effect.

Toler et al. (1996) investigated interference between johnsongrass, smooth pigweed (*Amaranthus hybridus* L.), and soybean. Their objective was to compare the competitive effects of single and multi-species johnsongrass and smooth pigweed populations, on soybean seed yield using a field experiment and modeling programs. The results indicated that multi-species populations of johnsongrass and smooth pigweed were more competitive with soybean than johnsongrass alone; but no detectable differences were found between the effects of these multi-species populations and the smooth pigweed population. Relative crowding coefficients revealed that inter-specific competition between weed species occurred at relatively low densities and increased as densities increased. For neutral associations between weed species, the additive response model (ARM) was developed and was the sum of the calibrated marginal responses. Weed densities and environmental conditions that

enhanced inter-specific competition and interactive relations were better represented by a product response model (PRM). Based on monospecific responses ARM and PRM were used to predict yield reductions caused by multi-species weed populations. Under ideal cropping conditions and lower weed densities the models both gave close predictions of yield loss compared to those observed. Under less ideal cropping conditions and with higher weed populations, ARM and PRM models overestimated yield losses by 14 and 6%, respectively. These results indicated that the weeds were behaving in a non-additive fashion, and that the PRM was best able to accommodate the non-additive effects of weed-weed competition.

Street et al. (1985) investigated the competition of sicklepod, and a complex of red root (*Amaranthus retroflexus*) and smooth pigweeds in cotton (*Gossypium hirsutum*). Their objective was to compare the competitive influences of monospecific vs bispecific weed stands on cotton. Results indicated that one pigweed and one sicklepod plant per 7.5 m row reduced yields by 9 and 9.7%, respectively. At these low levels of infestation the competitive effects of pigweed and sicklepod were additive. At high levels of infestation individual populations of pigweed and sicklepod densities reduced yield by 44% and 56%, respectively. However, when pigweed and sicklepod species were grown together at high densities they reduced yields by a maximum of 66%. Thus at higher densities the competitive effects of sicklepod and a complex of redroot and smooth pigweed were not additive in nature.

Van Acker et al. (1997) investigated the effects of yield loss due to interference from volunteer barley and chickweed (*Stellaria media*) in flax (*Linum usitatissimum*) and faba bean (*Vicia faba*). The authors tested Kropff and Spitters yield loss model (Kropff and Spitters, 1991), and determined that including an additional parameter into the model that accounted for asymptotic yield loss was not needed for either weed species in the single weed species experiments. It was recognized that although the existence of an interaction between chickweed and barley and their effect on flax and faba bean yield was not proven, the presence of barley might influence chickweeds competitiveness. Authors discussed including a parameter that accounted for asymptotic yield loss was necessary for chickweed in the presence of barley for the two-weed species model. The addition of the parameter accounting for asymptotic yield loss and the presence of barley affected the damage coefficients for chickweed in the two-weed species compared to the single-weed species models. This suggested that barley and chickweed exhibited non-additive yield loss in the presence of one another. Using single weed species parameters in two species yield loss prediction models resulted in overestimations of yield loss and unnecessary weed control practices.

2.2 Weed competition

Competition is a mechanism which can affect the association of weed species (Dale 1999). Competition is a negative form of interference caused by the influence of one plant upon another (Burkholder 1952). Barbour et al. (1987) defined competition as the mutually adverse effects of plants that utilize a

resource in short supply. Weeds compete with associated plant species for light, water, and nutrients (Crafts and Robbins 1962; Fryer and Evans 1970; Klingman 1966). Radosevich et al. (1997) stated that competition for light, water, and nutrients can be considered individually or as a unified concept called space.

Competition between two or more species can be studied using replacement series experiments. A replacement series experiment includes pure stands and mixtures where the proportion of the two species studied is changed (Radosevich et al. 1997). In this type of experiment total density is held constant. This is in contrast to an additive experiment in which the density of one species is held constant while the density of the other species is varied. Radosevich et al. (1997) stated that replacement series experiments are appropriate for determining the relative effects of intra- and inter-specific competition, and for determining competitive hierarchies among species.

2.2.1 Competition for Light

Donald (1961) stated that competition for light occurs under all cropping situations except when plants are very young or very sparse. Radosevich et al. (1997) stated that light has the ability to regulate plant competition through both quality and quantity via shading and light interception and reflectance, respectively. These alterations in light include the depletion of light energy in the 400-700 nm range, as well as red: far red light ratio changes.

Fennimore et al. (1984) noted that beans which germinated earlier than barnyardgrass and black nightshade (*Solanum nigrum*) reduced light penetration, and caused significant reductions in weed height and leaf area. Makowski and

Morrison (1989) noted that round-leaved mallow caused significant crop losses, particularly in crops which did not fully shade the ground. Friesen et al. (1992) studied the effects of round-leaved mallow in wheat and flax fields. They noted that from week 4 to 10 after emergence photosynthetically active radiation penetration in the wheat canopy was decreased by 80-90% though increasing canopy development. Penetration of photosynthetically active radiation through the flax canopy was not reduced as early or to the same extent as wheat.

Dunan and Zimdahl (1991) found that barley's superior competitive ability with wild oat was due to its larger leaf area; which allowed for greater interception of incoming photosynthetically active radiation from the beginning of the growing season. Tanji et al. (1997) have also found that the larger photosynthetic area of wheat leaves early in the growing season gave it a competitive advantage over rigid ryegrass (*Lolium rigidum*) and cowcockle (*Vaccaria hispanica*).

Jones et al. (1997) reported that plant height could also influence light interception. Clipping sicklepod and common cocklebur (*Xanthium strumarium* L.) to progressively lower heights decreased the sap flow of the weeds, and increased the sap flow of the soybean. When sicklepod was clipped to levels below the soybean canopy, soybean sap flow, dry weight, and yield were equivalent to weed-free soybean. Caton et al. (1997) found that shade cast by redstem onto rice (*Oryza sativa* L.) decreased shoot and grain production, and increased rice tiller mortality. An increase in LAI was also noted to increase the

competition for light and consequently cause a reduction in the light transmission ratio and the light ratio 0 and 10 cm above ground level.

Légère and Schreiber (1989) reported that leaf area distribution patterns suggested that soybean and pigweed were competing for light even though soybean had produced more leaf area than pigweed. Redroot pigweed leaf area was concentrated in the upper strata of the canopy when grown in combination with soybean; thus reducing the light available to soybean leaves lower in the canopy. This pattern implied that redroot pigweed distributed a greater percentage of its leaf area into the higher regions of the plant when grown in mixed stands.

Regnier and Stoller (1989) have studied interference caused by common cocklebur, jimsonweed (*Datura stramonium* L.), and velvetleaf (*Abutilon theophrasti* Medic.) in soybean. They noted that velvetleaf and jimsonweed did not share the same aboveground niche with soybeans due to the placement of their leaves above rather than within the soybean canopy. However, common cocklebur had a similar height to the soybean crop and caused more intense competition for light between these two species. Authors concluded that interference of common cocklebur with soybean resulted primarily from shoot height differences and competition for light within the soybean canopy.

Stoller and Woolley (1985) have found that interference from jimsonweed and velvetleaf infestation in soybean was caused by light competition. Lee and Cavers (1981) found that green foxtail grew taller when shaded. Vanden Born (1971) stated that green foxtail required high levels of photosynthetically active

radiation to prevent reductions in vegetative and reproductive growth and development. Sharma et al. (1977) noted that low light intensity restricted wild oat biomass, and the plants grew taller under low light conditions.

2.2.2 Competition for Water

Radosevich et al. (1997) stated that competition for water occurs under all cropping situations except under intense irrigation. Competition for water can begin at the time of seed germination. Competition for water between plants intensifies as soon as the root systems of two plants interact.

Weeds which possess C_4 photosynthetic systems such as redroot pigweed, barnyardgrass, and green foxtail have a competitive advantage under situations of high light intensity and limited water availability (Purohit and Tregunna 1974; Elmore and Paul 1983). Patterson and Flint (1983) found that C_4 weed species were 2-3 times as efficient in water use compared to C_3 weed species. Conversely, Pearcy et al. (1981), noted that lamb's quarters (a C_3 species) was able to out compete redroot pigweed (a C_4 species) by limiting water availability to pigweed via its own poor stomatal control.

Water availability can affect a plant's ability to complete its lifecycle and successfully compete with other plants. Nadeau (1983) noted that tiller number per plant, plant height, and leaf area of green foxtail decreased with reduced water availability. Nadeau and Morrison (1983) also reported that green foxtail growth decreased with decreasing soil water potential.

The attributes of individual species root systems have also been noted to confer a competitive advantage. Rahn et al. (1968) found that barnyardgrass

roots could penetrate as deep as 116 cm, enabling the species to withstand drought conditions. Siriwardana and Zimdahl (1984) found that barnyardgrass was more competitive than redroot pigweed when soil moisture was increased from 30-50% field capacity, to 100% field capacity. Thullen and Keeley (1980) noted that the roots of Japanese millet (*Echinochloa crus-galli* var. *frumentacea*) successfully competed with yellow nutsedge (*Cyperus esculentus* L.) via competition for both water and nutrients.

Okafor and De Datta (1976) studied the competition occurring between upland rice and purple nutsedge (*Cyperus rotundus* L.), and noted that greater soil moisture depletion developed in the mixed weed species plots. This indicated that mixed species plots exhibited greater competition for water than the single weed species plots. The authors also noted that there was a greater competition for water at higher levels of nitrogen fertilizer.

2.2.3 Competition for Nutrients

Radosevich et al. (1997) stated that plants compete for both micro and macro nutrients, any of which can be limited through competition. The nutrient which first becomes limiting can most drastically affect a plant's growth, and its ability to compete with other plants. In southern Manitoba, the nutrients which are generally most limiting are nitrogen and phosphorous. However, increasing a particular nutrient will only prevent competition until the next most limiting nutrient reaches a deficiency point.

Species have differing abilities to compete for specific nutrients. Henson and Jordan(1982) conducted an experiment in which they investigated wild oat

and wheat competition for nitrogen. They determined that wheat was more competitive than wild oat in stands of equal maturity and density. They also noted that although wheat was more competitive for nitrogen, wild oat was still able to reduce wheat yields significantly.

Sanders et al. (1981) noted that different weeds including jimsonweed, common cocklebur, large crabgrass (*Digitaria sanguinalis* (L.) Scop.), and tall morning glory (*Ipomoea purpurea* (L.) Roth.) accumulated different levels of nutrients within their tissues. For example they found that jimsonweed leaves contained the greatest concentration of N, P, K, and S. Common cocklebur leaves were usually high in Ca and Mg. Large crabgrass leaves were low in N, P, Ca, and S. Tall morning glory leaves were low in P and S. The authors suggested that weeds which required lower amounts of nutrients may have a distinct advantage over others in low fertility situations. Under more fertile situations, weeds which were able to use a larger supply of the available nutrients would have a competitive advantage over those crops or weeds which could not.

Okafor and De Datta (1976) noted that as nitrogen was added from 0 to 120 kg/ha the total nitrogen uptake by both purple nutsedge and rice cultivars increased. At each increase in purple nutsedge population density, the total nitrogen taken up by the purple nutsedge increased, and the amount taken up by the rice decreased. As a result, the total amount of nitrogen taken up by the purple nutsedge was negatively correlated with rice grain yield.

Vengris et al. (1953) noted that yield losses in crop plants resulted from barnyardgrass' ability to accumulate considerable amounts of macro nutrients, especially when the nutrients were present in low amounts. It was also noted that barnyardgrass had a higher phosphorus content than onions or potatoes, which implied that barnyardgrass was more efficient in absorbing phosphorus from the soil.

Chisaka (1977) reported that the ability of weeds to compete with crop species can also change with respect to their growth stage. For example, barnyardgrass has been noted to have lower nitrogen content than rice in earlier growth stages; and similar content when both species were close to maturity.

2.2.4 Competition for space

Radosevich et al. (1997) stated that space can be considered as both an individual item for competition, and an entity called *integrated space* that holds all other resources and conditions that relate to competition. Space can be thought of as an individual item for competition which plants need for growth. After germination, plants begin to experience both intra and inter-species competition for space. Competition for space can arise from an already limited resource, or create deficiencies in an area of high resources for an individual plant. The advantage of considering space as an integrated entity is that one can study the effects of proximity between individuals without concern for the actual cause of the interaction. Considering space as an integrated entity may simplify the spatial study of plant interactions.

2.3 Plant spatial relationships

2.3.1 Purpose of studying spatial relationships

Dale and Zbigniewicz (1995) stated that spatial pattern can be defined as the non-random arrangement of plant species in space. Leps (1990) stated that spatial patterns alone cannot indicate underlying processes; however changes over time in spatial patterns are highly indicative of underlying community interactions. Kenkel (1988 and 1993) suggested that the detection of a statistically significant regular pattern could be used to infer the processes causing the pattern of particular plant species. Mahdi and Law (1987) reported that studying spatial relationships among plant species helps one to understand processes, which could have operated to give spatial structure, or emphasize how the observed spatial structure will influence processes in the future. Mahdi and Law (1987) also stated that understanding spatial organization is the key to understanding the interactions of sedentary organisms. Hill (1973) suggested that one purpose for analyzing spatial patterns is to suggest and check theories about establishment and competition within plant communities. Researchers have stated that spatial pattern has important consequences in areas such as competition, which is usually between neighbors, or plants in a localized neighborhood (Mack and Harper 1977, and Goldberg 1987). Navas and Goulard (1991) stated that the pattern of sexual and vegetative propagules originate from the dispersal pattern caused by the parent plant, and the spatial distribution of resources and environmental conditions. As a result the modeling of spatial components of weed infestations is of economic and biological importance

because it enables a spatial comparison of the effects of different control strategies, prediction of infestation levels, and detection of spreading mechanisms.

2.3.2 Purpose of studying spatial relationships of weeds

Researchers have stated that the spatial arrangement of weed species is often ignored, causing the inappropriate management of weed populations (Hughes 1989, Pannell 1990, and Brain and Cousens 1990). Some researchers have noted that weeds often occur in aggregated patches throughout a field, and these non-uniform distributions make uniform prophylactic control techniques inefficient (Cardina et al. 1995, Mortensen et al. 1993, and Marshall 1988). Cardina et al. (1997) stated that describing, predicting, and managing weed populations requires knowledge of the spatial arrangement of weeds and the consequences of this distribution for population processes.

2.3.3 Creation of patterns

Franco and Harper (1988) stated that spatial pattern is determined by asymmetric competition between plants. Asymmetric competition can occur due to a canopy opening, soil variation, or an innate genetic trait. Anderson (1970) reported that several Australian desert sites have revealed that younger plants are aggregated, and that this spatial pattern disappears as the plants grow larger and exert more influence on one another. Phillips and MacMahon (1981) noted that the spatial pattern of plant species tends to follow a clumped, to random, to regular dispersion patterns over their lifecycle. Biotic interference may, however,

occur during the lifecycle which prevents regular dispersion patterns in adult plant populations.

Conversely, Aarssen and Turkington (1985a) reported that competition may promote a random spatial arrangement in plant communities. They (Aarssen and Turkington 1985 b,c) went on to state that this arrangement favors genotypes with sufficient competitive ability to avoid being excluded, and has been documented in pasture communities. Czaran and Bartha (1989) found that the spatial limits of dispersal and competition may result in the increased persistence of weak competitors, moderate the realized competitive effects of strong species, and shape the spatial coalition structure of the community.

Competition and resulting spatial pattern between species was also determined to be highly affected by vertical root stratification. Researchers have stated that significantly higher levels of competition existed between species with roots systems of similar depth (Yeaton and Cody 1976; Yeaton et al. 1977). Martens et al. (1997) stated that greater intra- than inter-species competition has also been detected for semi-arid woodland tree species found to be undergoing intra-specific competition for water. Van der Laan (1979) noted that variation in space was also detected for dune species due to differences in water table height.

2.3.4 Effect of climate on spatial patterns

Although spatial patterns are affected by plant competition, they may also arise due to microclimate effects on developing plant species. Phillips and MacMahon (1981) stated that perfectly regular dispersion can only be expected

from perfectly homogeneous environments. As a result, regular dispersion patterns found in adult populations may not fit expected values. Yeaton et al. (1977) found that segregation in response to microhabitat variation could mask any competitive interactions which might occur. Yeaton and Cody (1976) noted that to solve this problem in studies of spacing and competition it was of the utmost importance to choose sites in which the limiting resource was evenly distributed. Phillips and MacMahon (1981) noted that macro-climatic differences in desert ecosystems for example do not appear to be of overriding importance in determining plant spatial patterns. As a result they concluded that macroclimate effects have less effect on an ecosystems spatial distribution, than localized effects.

2.3.5 Niche effects on spatial arrangement

Yeaton and Cody (1976) found that two taxonomically related and structurally similar desert species showed a very strong competitive interaction. This is not surprising because the two species had partially overlapping resource niches. Duncan (1991) noted that in order to allow a sharing of community space, it was determined that coexisting tree species could avoid inter-specific competition by obtaining resources from spatially different regions of forest floor micro relief and substrate type.

Conversely, coexistence between grassland species in a given area may occur if conspecific neighbors producing isolated ramets create more intra- than inter-specific competition. Mahdi and Law (1987) noted that niche differentiation may give rise to greater intra- than inter-specific competition, thus affecting plant

spatial patterns. Researchers have noted that intra-specific competition has also been found to keep tree species spatial distributions from clumping to more regular patterns (Phillips and MacMahon 1981; Kenkel 1988).

2.3.6 Suitability of desert, grassland, and forest ecosystems for studying species spatial associations

Some researchers have noted that grassland and desert shrub communities are some of the few communities which one can manipulate, and provide direct evidence of competitive interaction (Fowler 1986; Chapin et al. 1989). Other researchers have noted that desert ecosystems present unique situations for studying the effect of competition on plant spacing (Woodell et al. 1969 and Anderson 1971). Often plants in desert communities are spaced widely enough to remove competition for sunlight, but the plants compete intensely for water and nutrients. Veresoglou and Fitter (1984) noted that plants in grassland communities are strongly limited by water and nutrients. As a result of the relatively short lived and annual nature of many cropping systems the study of weed communities lend themselves to studies of spatial patterns. Harper (1977) noted that it is more difficult to directly measure competition as affected by spatial patterns in long-lived forests, resulting in the need to study density dependent relationships.

2.3.7 Factors affecting the study of weed spatial distribution

Cardina et al. (1997) stated that weed spatial distributions are heterogeneous, making their spatial study difficult. A lack of "*a priori*" information about weed communities results in difficulties in blocking and replication, hampering traditional experimentation techniques. Forcella et al.

(1992) noted that weeds have heterogeneous spatial distributions and weed competition experiments may have coefficients of variation as high as 60-100%.

In addition, statistical analysis of weed species has often been hampered by autocorrelation, which has caused overly liberal interpretations of data. This problem was addressed by Dale et al. (1991), who found that a deflation of statistical output was necessary to adequately represent multi-species data. The authors used a Monte Carlo approach to provide a solution to the problem of auto-correlation within the data. Dale et al. (1991) also noted that the amount of deflation required to test the associations between all species involved decreased with the number of species involved, and with the spatial independence of each species sampled. The authors suggest that if large numbers of species (such as 20) are considered, deflation will be virtually unnecessary, especially if the species have little spatial autocorrelation.

Firbank et al. (1993) found that increasing the environmental variation, caused the proportion of variance accounted for by competitive effects to become smaller, compared to that accounted for by environmental factors. Thus different experiments on the same system can give substantially different results for inter-specific interactions and the relative importance of competition. As a result, more sophisticated experiments can be designed which are sensitive to both species interactions and substantial environmental variation. Law et al. (1993) stated that in more homogeneous environments, species interactions including competition could be studied.

2.3.8 Weed spatial distribution

Thornton et al. (1990) reported weed seedlings found in arable fields had an aggregated spatial distribution. Wiles et al. (1992) noted that the spatial distribution of broad-leaved weeds including common cocklebur, common lamb's quarters, and redroot pigweed in a soybean field revealed that weed species exhibited a negative binomial distribution. The negative binomial distribution has two parameters including the mean quadrat count (μ), and a value inversely related to the degree of patchiness (K). Weed populations which fit a negative binomial distribution have a clumped distribution. This implies that the weeds are aggregated, which would facilitate patch spraying, and thus help to reduce the need for blanket herbicide application. Rew (1996) also stated that fields with weed populations which had negative binomial distributions would have aggregated weed populations suitable for patch spraying. *Elymus repens* was found to have a patchy nature allowing for herbicide spray reduction through patch spraying. Rew (1996) also stated that weed patch morphology and infestation level affected the suitability of a particular patch for spraying.

Mulgeta and Boerboom (1999) noted that seedling giant foxtail (*Setaria faberi* Herrm.), common lamb's quarters, and velvetleaf had spatial aggregations which differed among cohorts; likely due to seed dispersal, germination, and seedling emergence. Thornton et al. (1990) reported differences in the level of aggregation among cohorts, resulting in the need for weed management strategies to be cohort specific. Wild oat have been found to cover only 18% of an infested field, of which 94% was lightly infested and only 6% was heavily

infested. The patchy nature of wild oat makes them good candidates for patch control via herbicides and cultural techniques.

Researchers have described weed populations as fractal in nature. Fractals describe an occurrence when the parts of a structure resemble the structure as a whole. This means that the weed populations found in patches are distributed as clumps of clumps across a field. For example, Shirtliffe (1999) investigated wild oat infestations and determined that the spatial pattern could be described by fractals. Wallinga (1995) investigated Cleavers (*Galium aparine* L.) and determined that their spatial pattern was of a fractal nature. For these species the spatial pattern of the weed species should be made up of pieces which resemble the whole.

Johnson et al. (1995) noted that weeds have been found to exhibit varying degrees of spatial and temporal stability. As a result Mulugeta and Boerboom (1999) stated that mapping the spatial distribution of weeds can provide meaningful information, that accounts for spatial and temporal distributions and that this information would be useful for managing future weed populations.

2.3.9 Distances of interference influence

Stauber et al. (1991) noted that the interference of barnyardgrass on rice cultivars was found to significantly increase with increasing proximity between weed and crop species. Significant yield interference caused by barnyardgrass in rice cultivars was found at 20 cm and non-significant interference at 100 cm. Monks and Oliver (1988) noted similar results with cocklebur and Palmer

amaranth (*Amaranthus palmeri* S. Wats.) in soybeans. However, other researchers have noted that cocklebur, devil's claw (*Proboscidea louisianica* (Mill.) Thellung) and velvetleaf were found to have much greater areas of influence on cotton neighbors, extending from 40 to 200 cm (Abney and Walker 1988; Bridges and Chandler 1986).

2.3.10 Plant size and distribution

Yeaton and Cody (1976) reported that plant sizes and relative distances were positively correlated indicating that competition was occurring between selected desert species. Researchers have stated that nearest-neighbor distances were found to be greater for larger individuals than for smaller ones (Pielou 1962 and Yeaton and Cody 1976). This indicated that under situations of competition larger individuals were more widely spaced than smaller ones. Fowler and Antonovics (1981) noted that plant species may be associated positively in space if they have similar environmental needs. They may also be negatively associated with one another due to competitive exclusion. Mack and Harper (1977) noted that individual plant weight was found to be inversely proportional to increasing neighborhood effects, and individual fecundity was closely correlated with plant weight. This indicates the important connection between competition and seed placement in space.

2.3.11 Parent seed dispersal

Harper (1977) noted that distributed weed seed tended to fall in an area which was relatively close to the parent plant. As a result, it was noted that a spatial relationship between the distribution of the parent plants and their

offspring may be expected over years. Gerhards et al. (1997) reported that the location of sunflower (*Helianthus annuus* L.), velvetleaf, and hemp dogbane (*Apocynum cannabinum* L.) patches were found to be very consistent in a field over four years.

McCanny and Cavers (1988) stated that the parent seed relationship may become obscured with the addition of combine harvesting, which has been found to disperse seed up to 50 meters from parent plants. Shirliffe (1999) stated that wild oat seed can spread 30 to 150 m with and without chaff collection, respectively, during combine harvest. Zhang and Hamill (1998) noted that to a lesser degree plowing may also limit the close association between weed parents and the spatial proximity of their seed.

Mulugeta and Boerboom (1999) determined that an aggregated distribution of seeds in the seedbank may not necessarily result in aggregated seedling distribution at any time during the growing season. This non parallel relationship may result from seed dispersal pattern (Harper 1977), vertical seed distribution (Mulugeta and Stoltenberg 1997b), percent seedling emergence in relation to seedbank density (Forcella et al. 1992), and relative abundance of species within the community (Mulugeta and Stoltenberg 1997a). Mulugeta and Boerboom (1999) stated that differences in the level of aggregation among cohorts derived from the seedbank could justify the concept of considering the spatial structure of weed seedling populations and resulting management decisions to be cohort specific. This may be difficult because weed communities often consist of varying species age groups and overlapping cohorts.

2.4 Methodological scales of plant species observation, and the effects on perceived spatial and temporal distribution

Levin (1992) stated that there is no single natural scale at which ecological phenomena should be studied. Ecological systems generally show characteristic variability at a range of spatial, temporal and, organizational scales. Steele (1978) noted that some systems are studied at scales to detect key features in the natural system, while at other times the scales are imposed on us by perceptual capabilities, technologies, or logistical constraints. Haury et al. (1978) stated that the level of variability observed in an ecological system is dependent upon the scale of the system; pertaining to both time from seconds to millennia, and to space from centimeters to kilometers. Researchers examine particular situations or species at various scales and this has implications on their ability to describe ecological phenomena.

Levin (1992) stated that to fully understand plant communities one must understand the scale of spatial patterns that occur within them. Typically, the mechanisms underlying observed patterns operate at different scales than those on which the patterns are observed. Watt (1947) noted that spatial and temporal patterns arise from several underlying processes such as establishment, growth, competition, reproduction, senescence, and mortality. Steele (1989) noted that the development of theoretical models which incorporate multiple scales, and guide the collection and interpretation of data is a major and exciting theoretical task for future studies.

2.4.1 The role of quadrat size

Greig-Smith (1964) stated that in addition to the scale of the overall scientific experiments, consideration must be given the scale of the quadrats used. For example the smaller the quadrat the larger the length of quadrat boundary per unit area, and consequently the greater the chances of edge effects within the experiment. In addition, as quadrat size increases and approaches the size of the experimental patches, the variance relative to the mean will rise sharply. If the patches are regular the variance will then fall off again ultimately reaching or even falling below the mean. If however, the patches are themselves randomly distributed the high variance will be maintained. The variance of measurements within experiments involving individuals which are more regular than random in pattern is affected by the use of very small quadrats; as they fail to detect departure from randomness, but larger quadrat sizes will detect this regular pattern. Many types of non-random arrangements sampled by random quadrat placements will appear random if measured using very small or large quadrats, but they will appear non-random if measured with intermediate sized quadrats.

Greig-Smith (1964) noted that it is clear that the information derived from association data which is based on a single sample size will be incomplete and difficult to interpret. To capture the effects of scale it is important to make observations at a number of sample scales. Using a plan of systematic sampling allows for a larger scale to be obtained by grouping smaller adjacent samples. In addition, using rectangular compared to square quadrats can change the

outcome of experiments. The elongated units are more likely to include portions of more than one of the density phases making up a population. In summary, careful choice of placement and size of quadrats can enhance the analytical opportunities in an experiment.

2.4.2 Single scale experiments

Many researchers have not considered the scale of their observation in their experiments. Bigwood and Inouye (1988) noted that the failure to recognize the importance of scale may result in incorrect interpretations of collected data. A population that appears to be clustered at one scale may appear to be random at a larger or smaller scale. The following examples show how researchers may achieve their objectives at one spatial scale; but fail to acknowledge or identify the possibility of alternate spatial arrangements at smaller or larger scales of study.

Phillips and MacMahon (1981) studied desert shrubs in 1 ha areas in the Sonoran and Mojave Desserts. The purpose of the study was to examine aspects of intra- and inter-specific spacing patterns in desert shrubs. Locations were divided into 100, 10 x 10 m plots of which 25 were chosen for sampling. Results showed that small shrubs tended to be clumped, medium sized ones tended to have a random arrangement, and large shrubs tended to have a regular pattern. In addition, they found a correlation between plant size and neighbor distance, root system overlap, and similar neighbor species. The authors conceded that the biotic interaction between individuals which produced the trend towards a uniform dispersion, were more likely to operate over

interplant distances in the order of 1 m. Thus quadrat sizes of 10 x 10 m were inappropriate for detection of these small scale interactions. The mismatching of quadrat size and biotic interaction explained the lack of regular patterns found by the variance mean tests performed.

In 1986 Donald (1994) investigated Canada thistle (*Cirsium arvense* L.) in an established patch area with no background crop. The purpose of the study was to use geostatistics to map Canada thistle shoot density and to characterize patch spatial heterogeneity. Canada thistle was surveyed in a 12 x 16 m area with quadrats centered on a 1.8 x 1.8 m grid. The shoot density was measured with 0.2 x 0.2 m circular quadrats. At this scale, results indicated that areas with the greatest shoot density co-occurred with the greatest underlying root biomass, and adventitious root buds.

In 1985 Dessaint and Caussanel (1994) sampled weeds in a corn field in order to obtain an assessment of the effects of weed spatial pattern on crop yield loss. Weed species in this experiment included *Polygonum persicaria* L., *Chenopodium album* L., and *Solanum nigrum* L. In a 25 x 40 m field, 80, 0.125 x 0.50 m quadrats were spaced on a 2.5 x 5 m grid. A spatial gradient was found for *Polygonum persicaria* L., and *Chenopodium album* L.; while *Solanum nigrum* L. existed in patches within the sampled area.

Dessaint et al. (1991) surveyed the weed seed bank of a grain field after harvest to establish the spatial pattern of weed species present. Weeds studied included *Thlaspi arvense* L., *Capsella bursa pastoris* (L.) Medik., *Avena fatua* L., *Chenopodium album* L., *Galium aparine* L., *Rumex crispus* L., and *Chenopodium*

polyspermum L.. In a 1.16 ha field an area of 7.5 x 10 m was chosen. Soil cores were taken at 0.5 m intervals and each was 0.046 m in diameter. At this spatial scale it was determined that most weed species present had patchy distributions; except for *Avena fatua* L. and *Chenopodium polyspermum* L. which had random seed distributions.

Yeaton et al. (1977) studied desert shrubs in the Sonoran desert to determine relative spacing and competition between several species. Data from 5 randomly placed quadrats in a 30 x 10 m area, were studied. At this spatial scale all intra-specific nearest neighbor comparisons showed that competition was occurring. In addition, *Larrea tridentata* competed with all species studied except *Carnegiea gigantea*. *Franseria deltoidea* competed only with *Larrea tridentata*, while there was no evidence of competition between *Carnegiea gigantea* and any of the other species.

In 1985 and 1986 Wiles et al. (1992) studied weed populations which were sampled in double cropped soybean; to verify the hypothesized patchy distribution of broad leaved weeds. Over 0.4 ha, 9 sites were chosen with equally spaced 9.1 x 0.16 m quadrats. Examples of weeds examined included *Xanthium strumarium* L., *Chenopodium album* L., and *Amaranthus retroflexus* L. At this scale their results indicated that the population of weeds as a whole had a patchy distribution, and that counts of individual species were positively correlated with each other in some fields.

In summary, the above experiments all met their objectives using one spatial scale. However, they failed to address the effects of using smaller or

larger scales, and this may have lead to erroneous conclusions regarding spatial patterns. Researchers with the objective of understanding spatial patterns, must use several scales of observation, while working within their logistical capabilities.

2.4.3 Large area surveys (Surveys at small scales)

Surveys have been conducted throughout Canada which took place over much larger areas. The logistics of these surveys dictated that observations could only be made at one spatial scale.

In 1979-81, 1986, and, 1997 Thomas and Wise (1984), Thomas and Wise (1986), and Thomas et al. (1998), respectively, surveyed weed populations in 500 fields including cereal and oilseed crops throughout Manitoba. Surveys were stratified on the basis of 7 ecoregions, which had similar environmental characteristics. After land class and crop type exclusion, remaining or substituted fields were sampled. A minimum of 20 fields was set as the limit for inclusion of a crop in the survey, to give a reasonable summary of the weeds found in the crop type. Individual fields were sampled by walking 100 paces along the edge of a field, and then 100 paces into the field. This was the location of the first 0.5 x 0.5 m sampling unit. The rest of each field was surveyed by walking at 45 degree angles to the field edges, and sampling quadrats at every 20 paces, until 20 sampling units were obtained. Thomas et al. (1997) used similar methods to compare weeds in zero and conventional tillage crop production systems throughout Manitoba in 1994. Thomas et al.

(1996) also used similar methods to assess cereal, oilseed, and pulse crops in 1995 in Saskatchewan fields.

Because of logistical challenges, weed surveys over large areas do not usually contain information at more than one scale. The primary purpose of these surveys was to capture a snapshot of weed flora, for a better understanding of weed presence and relative importance over an ecoregion or province. The objective of the surveys was met by use of a single sampling scale. However, the scale of these surveys was not fine enough to adequately assess spatial patterns within individual fields or to truly assess species associations.

2.4.4 Multi-scale experiments

Levin (1992) stated that the key to understanding how information is transferred across scales is to determine what information is preserved, and what information is lost as one moves from one scale to another. Generally, the goal of research into scaling is to discover what the most relevant macroscopic statistics are that relate lower level activities to higher level realities. Researchers have used several methodologies to capture spatial scale over a variety of species and environments.

For example, in a four year period from 1985-1990, Herben et al. (1993) studied the spread of Czechoslovakian mountain grass species. Four permanent plots of 0.5 x 0.5 m were established, and grids of 15 x 15 were overlaid to produce quadrats of 0.033 x 0.033 m. This study revealed that there was little net change of species type measured by persistence at the plot level,

and dynamic changes at the subplot level. The absolute level of persistence was defined as the tendency of a species not to leave its original position and not to colonize new subplots. A non-decreasing persistence curve indicated that the rate of change of a species was either greater or smaller than the scale of sampling. A decreasing persistence curve over time with an increasing time lag indicated that the spatial dynamics of the species was suitable to the scale of sampling, which was in the order of 3 cm for this experiment. The persistence varied between species and they could be divided into stable and moving species. Since a decreasing persistence curve was detected for some species within this study, the quadrat size was proper for addressing the author's objectives.

Martens et al. (1997) considered scale when investigating intra- and inter-specific tree species competition. Researchers found that the spatial dispersion of Juniper (*Juniperus monosperma*) and Pinon (*Pinus edulis*) varied with spatial scale. The univariate analysis of all mapped trees showed a strong aggregation at scales less than or equal to 6 m, with peak aggregation at 3 m, and random organization at scales greater than 6 m. Tree crowns were less aggregated than tree stems at scales of less than 5 m. Pinon stems showed aggregation at scales of 1 and 2 m. Pinon crowns were random at those scales and were less aggregated at scales smaller than 5 m. Juniper stems and crowns were aggregated at 2 to 4 m, but were random at the scale of 1 m. Juniper crowns were less aggregated than stems at scales smaller than 5 m. Bivariate analysis of tree species indicated a positive association between the species at scales

less than 5 m for both stems and crowns. The Pinon and juniper species were randomly associated at larger scales. Thus, spatial pattern of Pinon and juniper crowns and stems varied, depending upon the spatial scale considered.

From 1976-1993 Vacek and Leps (1996) investigated the effects of the scale of study on Norway spruce (*Picea abies*). The purpose of this 18 year research program was to study the effects of air pollution on the performance of individual members of the population, and the spatial pattern of tree species. Plot dimensions were 50 x 50 m, and were established at 5 elevations. Researchers used K-function statistical analysis to show that the largest increase in species regularity occurred at a scale of about 3 m indicating the radius of the mean area of influence of an individual. In 4 of the 5 plots L(h) values (indicating the degree of aggregation), had decreased from 1976-1993, at a scale of 2-5 m. This agrees with the theory that defoliation rate and tree mortality was higher in trees with close and large neighbors, causing spatial pattern to change towards regularity at a scale of 2-5 m. At the scale of 1 m the associations between species were unstable because the number of expected and observed neighbors closer than 1 m was low, and consequently the sampling error was large. At scales smaller than 5 m there was no pattern detected within the plots.

Occasionally unintentional manipulations of ongoing experiments have given rise to good examples of the influence of quadrat scale on experimental results. In 1992 and 1993 Johnson et al. (1996), studied velvetleaf and volunteer sunflower in a 4 ha area under corn and soybean rotations. Within this area, intensive surveying of an area of 189 x 224 m was conducted. In 1992

measurements were taken every 7 m using a 1 x 0.76 m quadrat. In 1993 measurements were taken every 7 m using a 1 x 0.38 m quadrat. To determine whether or not the change in quadrat size between 1992 and 1993 had an impact on comparisons made between years, further analysis was performed. The 1993 per quadrat density data were doubled to account for a doubling of quadrat size in 1992. Semivariograms and summary statistics were calculated based on this adjusted data and compared to the unadjusted data. No difference was detected between the 1992 and 1993 data with respect to spatial statistics, or the coefficients of variation for either the velvetleaf or sunflower population. As a result, the 1993 quadrat size did not need to be adjusted to maintain the integrity of the data. Thus authors accounted for differences in the spatial scales considered, although it had no effect on the end results.

In 1996 and 1997 Mulugeta and Boerboom (1999) studied 34 x 16 m blocks of soybean planted to investigate the effects of 18 and 76 cm row spacings on the emergence pattern and spatial aggregation of weed populations. In a 1.5 ha field, two 3 x 8 m plots were randomly assigned within each row spacing treatment. Weeds studied included giant foxtail, common lamb's quarters, and velvetleaf. Weed emergence was surveyed in 16, 0.25 x 0.25 m quadrats within each plot. Authors noted that at coarse spatial scale (1.5 ha), field aggregation declined with decreasing density. Thus, species with higher abundances such as giant foxtail, were more aggregated than less abundant species such as velvetleaf. In comparison, at fine spatial scale (24 m² plots), the level of seedling aggregation of all weed species decreased as seedling density

increased. These results indicated that within the density range evaluated, the aggregation of weed seedlings was directly related to increasing density in large areas; and inversely related to density in small areas. Thus the effects of spatial scale on the estimation of weed aggregation, implied that the sampling intensity to determine density and associated weed management decisions, could vary with the field size and spatial precision of the management practices. Authors noted that further research was needed on the effects of varying spatial scale when studying weed aggregation and associated weed management practices.

2.5 The biology and ecology of wild oat, green foxtail, and barnyardgrass

Wild oat, green foxtail, and barnyardgrass are all weeds commonly found on the Canadian prairies (Thomas et al. 1997). The importance of the study of multiple weed species associations has been previously noted. In this project we investigated weed species associations between wild oat, green foxtail, and barnyardgrass.

2.5.1 Wild oat

Wild oat (*Avena fatua* L.), is an important annual weed of the Canadian prairies causing significant economic losses in wheat (Bell and Nalewaja 1968), barley (Bell and Nalewaja 1968), flax (Bowden and Friesen 1967), and rapeseed (Dew and Keys 1976).

Thurston (1959) stated that seeds produced on panicles ripen over time creating a wide window of seed dissemination. Dadd (1953) stated that wild oat may produce up to 500 seeds per plant, but ranges from 100-150 are more common. Banting (1974) found that immediately after wild oat seeds shatter

onto the ground the mature seeds are usually completely dormant. Banting (1966) found that after shattering, wild oat seed have been found to after ripen more quickly when stored in warm dry conditions, and less quickly under cool moist conditions. Wild oat seed has a twisted lemma, which causes the seed to bury itself in soil clods and cracks in the soil.

Wild oat seed can emerge from as deep as 20 cm (Sharma and Vandeborn 1978), although more recently it has been noted that seedlings recruit from a maximum depth of 9.9 cm (duCroix Sissons 1999). Sharma and Vandeborn (1978) noted the first internode of wild oat has the ability to elongate allowing leaf tissue to be pushed large distances through the soil. This allowed wild oat to emerge from depths deeper than wheat, barley, and rye (*Secale cereale*). Wild oat plants have been reported to grow to 150 cm in height.

Thurston (1959) stated that in comparisons between wild oat and cultivated cereals of similar ages, wild oat were initially lower in total dry weight, nitrogen content, leaf areas and number of leaves. However, it was also noted that very young wild oat had higher net assimilation rates than the cultivated cereals, and the wild oat quickly caught up and surpassed the crop plants in the above categories. Some researchers have also identified the slow start of wild oat growth and development for up to two weeks after emergence followed by a rapid increase (Pavlychenko 1937; Sharma et al. 1977). Despite this slow start Chancellor and Peters (1976) have found significant competition between wild oat and crop species at and before the 2-3 leaf stage of wild oats. Pavlychenko

and Harrington (1934) noted that after 80 days the root system of wild oat was found to be more extensive than barley, wheat, spring rye, and oats (*Avena sativa*).

Sharma and Vanden Born (1978) noted that wild oat grew and reproduced better in some environments. Wild oat was not a serious weed in hot and arid areas of the Northern Plains. They are more likely to be found in the moister areas of fields, rather than on hilltops, or southern slopes. Banting (1974) stated wild oat prefers cool moist conditions, causing the majority of emergence to occur in the spring and early fall, with some germination occurring throughout the growing season. As a result most infestations occurred in fields which were planted early.

Sharma and Vanden Born (1978) stated that wild oat grew better in heavy clay and clay loam soils of parkland area, rather than in drier soils. Wild oat was found to occur in a wide variety of habitats including spring cereals, oil seeds, fallow land, roadsides, waste areas, and gardens. Sharma and Vanden Born (1978) stated that wild oat tended to most commonly proliferate in cultivated fields, at times forming very heavy patches.

In 1997 Thomas et al. (1998) surveyed seven ecoregions in Manitoba including fields of spring wheat, barley, oats, canola, and flax. Authors reported that the maximum density of wild oat found in the Manitoba weed survey was 167.6 wild oat per m², with an all field density of 7.1 per m². Wild oat occurred in 65.5% of all fields surveyed and wild oat ranked second in relative abundance in Manitoba. Wild oat was found to be one of the most common and abundant

weed species in the praries, and it was considered a dominant and persistent weed problem.

2.5.2 Green foxtail

Green foxtail (*Setaria viridis* (L.) Beauv.), is an important annual weed of the Canadian prairies causing yield loss in wheat (Blackshaw et al. 1981b), barley and oats Dryden and Whitehead (1963), sorghum (Robinson et al. 1964), and flax (Rahman and Ashford 1972b).

Vanden Born (1971) noted that green foxtail can produce from 350-500 seeds per panicle and 5,000-12,000 seeds per plant. Freshly shattered green foxtail seed has been found to range from nondormant (Martin 1943) to completely dormant (Vanden Born 1971). Burnside et al. (1981) noted that dormancy was affected by precipitation and soil texture.

Chepil (1946) found that most green foxtail plants emerged from May 15 to July 15, while Banting et al. (1973) found that the peak emergence occurred between May 24 and June 1. Wilson (1980) noted that emergence peaks tended to occur following periods of high rainfall. Banting et al. (1973) noted that green foxtail seedlings have been found to emerge in response to rainfall throughout the growing season. Blackshaw et al. (1981a) reported that field studies have shown that emergence of green foxtail was strongly related to average daily accumulation of soil temperature. Green foxtail has been noted to emerge from depths of 7.6 to 10 cm (Douglas et al. 1985), while others have noticed a maximum depth of emergence of 7.2 cm (du Croix Sissons 1999). Douglas et al. (1985) noted that unlike wild oat the first internode of green foxtail

seedlings does not elongate. It was also reported that green foxtail can grow from 10-100 cm in height.

Blackshaw et al. (1981b) noted that green foxtail is most competitive when it emerged with or shortly after the crop; while later emerging plants have less detrimental effects on yields. Rahman and Ashford (1972a) found that green foxtail did not have any significant effect on growth or yield of wheat plants when the wheat was seeded in early May. Blackshaw et al. (1981b) noted that green foxtail's competitive effects depended on the associated crop, weed density, time of emergence, and environmental conditions following emergence. Dryden and Whitehead (1963) found that barley and oats were more competitive with green foxtail than wheat. Sturko (1978) found that green foxtail must be removed from wheat at the one to three leaf stage of the crop to minimize yield reductions, but this was highly dependent upon environmental conditions following emergence.

Black et al. (1969) noted that green foxtail possessed a C₄ photosynthetic mechanism which meant that it required higher levels of photosynthetically active radiation for maximum growth potential. Vanden Born (1971) found corroborating evidence and noted that green foxtail required high levels of radiation to maximize both vegetative and reproductive growth and it is significantly hampered by reduced light levels. Lee and Cavers (1981) noted that green foxtail plants grew substantially taller in shaded versus unshaded conditions. Green foxtail was found to significantly increase the amount of biomass allocated to leaves making them larger and thinner; and decrease the allocation to stems and inflorescence as the amount of shading increased.

Bubar and Morrison (1984) reported that green foxtail reduced their tiller number in response to increased shading.

Alex et al. (1972) stated that green foxtail was usually found in temperate climate conditions. Frankton and Mulligan (1970) noted that green foxtail was found in grain fields, gardens, roadsides, and waste areas. Thomas and Wise (1983) noted that it is more prevalent in oat and rye crops, than in wheat, barley, flax, and rape crops.

Alex et al. (1972) stated that green foxtail frequency was found to vary with respect to soil type in Alberta and Saskatchewan. However, in Manitoba green foxtail occurrence was not related to soil texture, because the frequency of occurrence in fields, the extent to which each field was infested, and the maximum densities recorded in each infestation were uniformly high for all soil textural groups. In general, green foxtail appeared less commonly in fine textured soils, and relatively more frequently in medium to coarse textured soils.

Thomas et al. (1998) noted that the maximum density of green foxtail found in a 1997 Manitoba weed survey was 1693.2 green foxtail per m², with an all field density of 31.9 per m². Green foxtail occurred in 73.9% of all fields surveyed and were ranked first in the relative abundance in Manitoba in the 1997 weed survey of cereal and oilseed crops. In all 7 Manitoba ecoregions which included fields of spring wheat, barley, oats, canola, and flax, green foxtail was found to be the most common and abundant weed species, and was considered a dominant and persistent weed problem.

2.5.3 Barnyardgrass

Barnyardgrass (*Echinochloa crus-galli* (L.) Beauv.), an annual weed can cause significant crop yield losses in grain fields (Best et al., 1971), in rice (Smith 1983), potato (Vengris 1965), and Alfalfa (Vengris 1966).

Holm et al. (1977) stated that barnyardgrass could produce between 2,000–40,000 seeds per plant, depending on the environment at the time of seed production. Barrett and Wilson (1983) noted that freshly shattered seed of barnyardgrass exhibited dormancy which varied considerably in duration. Rahn et al. (1968) reported that fresh seeds had only 0.3–1.4% germination, while 4–8 month storage increased germination to 19–44%, respectively.

Dawson and Bruns (1962) noted that the maximum depth of seedling emergence was 10 cm, while others have found that the maximum depth of emergence was 7.5 cm (du Croix Sissons 1999). Maun and Barrett (1986) reported a maximum emergence of barnyardgrass seedlings in the beginning of June and continuation of emergence throughout the summer. It was also noted that barnyardgrass could grow up to 150 cm tall.

Maun and Barrett (1986) stated that barnyardgrass is a C₄ species giving it distinct advantages in warm and high light environments. Bayer (1965) noted that barnyardgrass was highly susceptible to shading, with greater biomass measured in the form of tillers and panicles when it was grown in full sunlight. Asano et al. (1981) noted an increased growth rate, leaf area, and net assimilation rate with higher light intensities and temperature.

Kennedy et al. (1980) noted that barnyardgrass seed can maintain active germination even under anaerobic conditions giving it a distinct advantage over other species in flooded areas. In addition, barnyardgrass has been found to grow better under wet conditions compared to other C₄ plants. Kennedy et al. (1980), and Kataoka and Kim (1978) have noted the inhibition of root and plumule elongation, and of leaf greening when barnyardgrass is subjected to relatively anaerobic conditions. Vengris et al. (1966) stated that dry soil conditions were found to decrease yield, height, and tiller number in barnyardgrass. Barrett (1983) suggested that barnyardgrass had a competitive advantage in rice, via rice mimicry.

Vengris et al. (1953) noted that barnyardgrass had an advantage over other crop species via its ability to accumulate large amounts of macronutrients such as N, P, K, Ca and Mg. Holm et al. (1977) reported that barnyardgrass could remove 60-80% of the applied nitrogen from the soil especially in the first half of the growing season.

Best et al. (1971) noted that barnyardgrass could be found in a variety of locations including grain, rice, row crops, root crops, gravel pits, roadsides, cultivated ground, manured soils, and disturbed habitats. Brod (1968) stated that barnyardgrass could be found on a wide variety of soil types including sandy loam, medium, and heavy soils. Frankton and Mulligan (1970) stated that barnyardgrass was more commonly found in relatively moist and fertile soils. Roche and Muzik (1964) reported barnyardgrass grew best under conditions of

35-65% soil moisture and required warm frost-free periods to allow adequate plant growth and seed dispersal.

Thomas et al. (1998) reported a weed survey carried out in 7 Manitoba ecoregions which included fields of spring wheat, barley, oats, canola, and flax. The maximum density of barnyardgrass found was 131.4 barnyardgrass per m², with an all field density of 1.5 per m². Barnyardgrass occurred in 18.1% of all fields surveyed and was ranked eighteenth in Manitoba fields on the basis of relative abundance.

2.5.4 Wild oat, green foxtail, and barnyardgrass associations

Dale and Thomas (1987) stated that little information existed on the phytosociological structure of weed species associations found in Canadian provinces. Even less information was published to explain why the associations exist, but several explanations have been offered including soil texture, pH, salinity, and herbicide selectivity. Dale and Thomas (1987) also noted that greater differences were detected between communities in differing soils, versus those in differing crops, suggesting that characteristics and or the associated climate conditions may exert a stronger influence on these communities than the crop or cultural practices.

Sharma and Vanden Born (1978) noted that wild oat was found to be associated in arable cereal and oilseed fields with many weeds including, redroot pigweed, common lamb's quarters, field horsetail (*Equisetum arvense* L.), *Fagopyrum tataricum* (L.) Gaertn., wild buckwheat (*Polygonum convovulus* L.), lady's thumb (*Polygonum persicaria* L.), pale smartweed (*Polygonum scabrum*

Moench.), cow cockle, green foxtail, wild mustard, and field pennycress (*Thlaspi arvense* L.). Hume (1993) investigated fields dominated by green foxtail, and noted that wild oat was found to be associated with green foxtail. Dale and Thomas (1987) have found many positive and negative associations using association analysis and cluster analysis for weed species in Saskatchewan fields. Wild oat was found to be positively associated with wild buckwheat, field pennycress (*Thlaspi arvense* L.), common lamb's quarters, cow cockle, wild mustard, perennial sowthistle (*Sonchus arvensis* L.), Canada thistle, European sticktight (*Lappula echinata* Gilib.), night flowering catchfly (*Silene noctiflora* L.), pale smartweed (*Polygonum lapthifolium* L.), shepherds purse (*Capsella bursa-pastoris* (L.) Medik.), field horsetail, narrowleaf hawksbeard (*Crepis tectorum* L.), common hempnettle (*Galeopsis tetrahit* L.), persian darnel (*Lolium persicum* Boiss. Hohen.), dandelion (*Taraxacum officinale* Weber.), wheat, barely, rape, common chickweed, barnyardgrass, and common groundsel (*Senecio vulgaris* L.). Wild oat was also noted to be negatively associated with Russian thistle (*Salsola iberica* Sennen and Pau.), redroot pigweed, and flixweed (*Descurainia sophia* (L.) Webb.).

Thomas and Wise (1983), and Thomas and Wise (1984) noted that green foxtail surveyed in Manitoba fields has been found to exist in close association with several weed species including wild buckwheat, wild oat, Canada thistle, lady's thumb, pale smartweed, perennial sowthistle, redroot pigweed, field pennycress, and barnyardgrass. Hume (1993) investigated yield loss caused by multi-species weed populations dominated by green foxtail; and noted that

several species coexisted with green foxtail including stinkweed, common lamb's quarters, wild buckwheat, wild mustard, prostrate pigweed (*Amaranthus blitoides* S. Wats.), redroot pigweed, wild buckwheat, and wild oat. Dale and Thomas (1987) surveyed Saskatchewan fields and noted that green foxtail was positively associated with wild buckwheat, wild oat, Russian thistle, common lamb's quarters, redroot pigweed, European sticktight, nightflowering catchfly, roses (*Rosa spp.*), wheat, barley, barnyardgrass, quackgrass (*Agropyron repens* (L.) Beauv.), and greenflower pepperweed (*Lepidium densiflorum* Schrad.). Green foxtail was also found to be negatively associated with wild mustard, perennial sowthistle, and Canada thistle.

Maun and Barrett (1986) noted that barnyardgrass tended to grow in association with several other weed species including quackgrass, creeping bentgrass (*Agrostis stolonifera* L.), daisy (*Chrysanthemum leucanthemum* L.), Bull thistle (*Cirsium vulgare* (L.) Scop.), Orchard grass (*Dactylis glomertata* L.), Kentucky bluegrass (*Poa pratensis* L.), Canada blue grass (*P. compressa* L.), heal all (*Prunella vulgaris* L.), yellow foxtail (*Setaria glauca* L.), green foxtail, dandelion, white clover (*Triflium repens* L.), red clover (*T. pratense* L.), and *E. Muricata*. Dale and Thomas (1987) found that barnyardgrass was positively associated with green foxtail, wild buckwheat, wild oat, redroot pigweed, nightflowering catchfly, and pale smartweed. They also noted that it was negatively associated with field pennycress, Russian thistle, and common lamb's quarters.

2.5.5 Differential herbicide control

While considering spatial relationships between weed species one must consider the effects of past and present herbicide regimes on infestations, species composition, and patch development. The Manitoba Guide to Crop Protection (Anonymous, 2000) stated that differential herbicide control exists within group 1 and 3 herbicides which results in varying control of wild oat, green foxtail, and barnyardgrass. Successive years of use of particular types of herbicides, may cause initial multi-species weed infestations to develop into unique species associations.

In barley, Avedex BW (trilalate) provides good control of wild oat while providing no control of green foxtail or barnyardgrass. Champion plus (fenoxaprop-p-ethyl, MCPA, 2,4-D, and thifensulfuron methyl), Fortress (trilalate and trifluralin), and Prevail ((Prevail A) tralkoxydim), provide good to excellent control of wild oat and green foxtail, respectively, but provide no control of barnyardgrass. Poor to good control of green foxtail is obtained with Linuron (linuron) + MCPA amine, Stampede EDF (propanil) +MCPA/2,4-D or Refine Extra (thifensulfuron methyl and tribenuron methyl), and Trifluralin (trifluralin) (foxtail control), but these products provide no control of wild oat or barnyardgrass. Trifluralin (grassy and broadleaf) provides good control of green foxtail and barnyardgrass, but no control of wild oat (Anonymous 2000).

In oat crops, few options are available for grassy weed control for green foxtail, while none exist for wild oat and barnyardgrass. Green foxtail control options in oat include Linuron and MCPA amine (providing poor green foxtail

control), and Stampede EDF and 2,4-D or MCPA or Refine Extra (providing good green foxtail control) (Anonymous, 2000).

Control options in rye or Triticale for wild oats, green foxtail, and barnyardgrass include of Hoe-grass 284 (diclofop-methyl), and Hoe-Grass II (diclofop methyl and bromoxynil) which provide good control. Good control of wild oat and green foxtail can also be obtained with Achieve (tralkoxydim) and Achieve Extra Gold (tralkoxydim, bromoxynil, and MCPA ester). Achieve and Achieve Extra Gold both provide unrated control of barnyardgrass (Anonymous 2000).

In flax, Fortress (trallate and trifluralin) provides good control of wild oat and green foxtail, but no control of barnyardgrass. Stampede EDF +MCPA/2,4-D, or Refine Extra provides good control of green foxtail, but no control of wild oats or barnyardgrass (Anonymous 2000).

In canola, control of wild oat, green foxtail and barnyardgrass can be achieved with Fortress, Pursuit (imazethapyr), and Round up Transorb (glyphosate) (Anonymous 2000).

In spring wheat, Accord (quinclorac) provides registered but unrated control of green foxtail and barnyardgrass, but no control of wild oat. Fortress, Horizon (clodinafop-propargyl), Platinum (clodinafop-propargyl, bromoxynil, and MCPA ester), Prevail, and Triumph Plus (fenoxaprop-p-ethyl, MCPA ester, and thifensulfuron methyl) provide good to excellent control of wild oat and green foxtail, but no control of barnyardgrass. Laser DF (fenoxaprop-p-ethyl, MCPA ester, and thifensulfuron methyl), Linuron+MCPA amine, Stampede EDF and

2,4-D or MCPA or Refine Extra, Trifluralin (foxtail control rate) provide control for green foxtail, but no control of wild oat or barnyardgrass. Assert, Avadex BW, Avenge, and Harmony Total (Refine Extra: thifensulfuron methyl and tribenuron methyl; Horizon: clodinafop-propargyl) provide good control of wild oat, but no control of green foxtail or barnyardgrass (Anonymous 2000)

2.5.6 Results of differential herbicide control

Thomas and Ivany (1990) reported that weeds which were not affected or only mildly affected by herbicides, were able to grow in most fields at high densities. They stated that unaffected weed species would fill the vacant niches left by the herbicide sensitive species. Holzner (1978) stated the activity of weeds replacing each other at various locations has been referred to as the compensation phenomenon.

Several examples of the results of differential herbicide control have been documented in the literature. Thomas and Ivany (1990) stated that differential herbicide practices used between Saskatchewan and Prince Albert Island may be responsible for the dominance and lack of dominance, respectively, of green foxtail in these provinces. Thomas (1985) noted that species sensitive to herbicides have been reduced in frequency and density over the years since the introduction of phenoxy herbicides. Thomas (1985) also stated that the effects of herbicide choice have been noted to affect the relative abundance ranking of weed species in Saskatchewan fields.

Steckel et al. (1997) noted that glufosinate was absorbed and differentially translocated, in giant foxtail, barnyardgrass, velvetleaf, and common lamb's

quarters resulting in differential sensitivity. As a result velvetleaf and common lamb's quarters recovered from doses of glufosinate, more readily than giant foxtail and barnyardgrass. Ballard et al. (1995) noted differential herbicide effects between common ragweed (*Ambrosia artemisiifolia* L.) and giant ragweed (*Ambrosia trifida* L.). Both weeds showed initial sensitivity to imazethapyr, but common ragweed regrew 10 to 14 days following the herbicide application. Alex (1970) noted that the superior competitive ability of wild mustard over cow cockle aided in the control of cow cockle before the use of 2,4-D. After the introduction of 2,4-D cow cockle was no longer suppressed by wild mustard, and its occurrence within fields increased.

Conclusions can also be drawn from the differential effects of herbicides on wild oat, green foxtail, and barnyardgrass. For example the Guide to Crop Protection (Anonymous 2000) indicated that Avadex BW used in barley crops provided control of wild oat, but no control of green foxtail or barnyardgrass. Thus, under conditions of high Avadex BW use, wild oat would have a competitive advantage over populations of green foxtail and barnyardgrass.

2.6 Summary

Data gathered under monoculture weed-crop experiments fail to truly characterize the dynamic interactions which occur in arable fields, as weeds often occur in multi-specific associations. As a result, researchers are beginning to examine multi-species weed interactions to obtain a more understanding of the effects of weed-weed interaction.

Changes over time in the spatial patterns of weed communities are indicative of underlying processes. Understanding the spatial patterns of weeds allows researchers to study the effects of different control strategies, predict future infestations, and detect spreading mechanisms.

Plant species interact on a variety of scales, and interact at some scales which may be beyond our immediate perceptual realization. As a result researchers must carefully consider plot and quadrat spatial and temporal scales. Failure to assess the importance of spatial or temporal scales may lead researchers to inadequately capture the true relationships among weed species.

In the past researchers have not quantified the true extent of weed species associations in arable fields at an appropriately fine scale. Wild oat, green foxtail, and barnyardgrass are all significant weed species found in Canada's arable fields. The objectives of this project were to quantify the spatial association of wild oat, green foxtail, and barnyardgrass, and to investigate and discuss the mechanisms responsible for the creation of these association patterns. Quantifying the spatial association of these weed species at a fine scale, may provide important insight into weed-weed interactions for weed ecology and yield loss prediction models.

3.0 Quantification of wild oat, green foxtail, and barnyardgrass associations

3.1 Introduction

Most research addressing weed species associations has not focused on fine scale experiments. According to Levin (1992) there is no correct scale at which to study biological systems. Assessing weed species associations at fine scales is a challenging task. This work is often tedious, and requires large amounts of time and effort to cover even small areas of weed infestation. To-date, much of the data collected for multiple weed species interactions has been from surveys designed to represent large areas.

Weed species have been noted to exist as multi-species associations (Combella and Friesen 1992). The study of weed-weed associations may provide important insight into multiple weed species infestations. Leps (1990) stated that the examination of the resulting patterns cannot be used to uniquely define the type of interaction occurring. Mahdi and Law (1987) stated that association measures can be used to recognize patterns worthy of further study. Mulugeta and Boerboom (1999) stated that mapping the spatial distribution of weeds can provide information which accounts for spatial and temporal distributions, and this can be used for managing future weed populations. The objective of this study was to characterize species associations in a complex of wild oat, green foxtail, and barnyardgrass in an arable field, and to discuss the implications of these results for patch dynamics and yield loss prediction models.

3.2 Materials and Methods

3.2.1 Survey location

The study was conducted at the University of Manitoba's Carman Research Station (legal land description of the station was N 1/2 26-6-5W). The dimension of the survey field was 60 m x 390 m and it was designated as block 7e. The field had been cropped using conventional tillage and crop rotations for at least four years prior to the survey.

3.2.2 Site preparation

On May 13, 1998, 23-23-0 fertilizer was broadcast on block 7e at a rate of 134 kg/ha. On May 19, 1999 5-0-0 fertilizer was broadcast at a rate of 26.1 kg/ha. On May 13, 1998 following fertilizer application the field was cultivated, harrowed, and packed. Rain caused a delay in the cultivation and seeding in May of 1999. On May 31, 1999 the field was cultivated, harrowed, and packed. On May 13, 1998 and June 1, 1999 the field was sown to flax (*Linum usitatissimum* cv. Flanders). Flax was seeded using a double disc press drill set at 15 cm row spacing.

After crop and weed emergence, two 10 m x 10 m were chosen based upon the presence of an adequate density of weed species including wild oat, green foxtail, and barnyardgrass. Within block 7e, site 1 was located on Winkler Series soil type, which had a mean pH of 6.52, a mean organic matter of 6.52%, 60% sand, 15.0% silt, and 25.0% clay. Site 2 was located on Eigenhof Series soil type, which had a mean pH of 6.68, a mean organic matter of 6.68%, 56.5% sand, 18.0% silt, and 25.5% clay. The corners of each 10 m x 10 m site

were permanently marked by placing a 0.45 m stake into the ground, leaving 0.05 m above ground as a reference point for the following year. Stakes 0.30 m in length were placed at 1 m intervals around each site. String was run between each stake in both north-south and east-west directions creating 100, 1 m² areas. No herbicide was applied to site 1 or 2 in 1998, but was applied in 1999.

3.2.3 Photographing weed infestations

Time limitations in capturing the location of seedlings created the need to photograph each of the 10 m x 10 m sites. Photographs were taken to assess seedling position and density within each 10 cm x 10 cm area. To aid in photographing these areas a 1 m² quadrat was constructed of wood. On each side of the quadrat 10, 0.015 m nails were placed at 0.010 m intervals. Yellow fluorescent string was then wound onto the nails in north-south and east-west directions creating 100, 10 cm² areas.

A camera stand was used that allowed photographs to be taken from directly over top of the plots. The top of the stand consisted of plywood with a hole, which allowed for the camera lens to be placed through and focused. The top of the stand was supported by four corner legs, which were 1.5 m in length. A 50 mm lens was used in the camera which allowed the resulting slides to capture a 0.25 m² area.

Photographs were taken when the majority of the wild oat, green foxtail, and barnyardgrass seedlings had reached the 1-4 leaf stage. In 1998, the photographs were taken from May 28-30. In 1999, the photographs were taken from June 14-16. The 1 m² wooden quadrat was placed into the 10 m x 10 m

sites. The quadrat was placed with the string as close to the ground as possible. This prevented the outer cells from appearing to contain less area compared to the centrally located cells within the 50 cm x 50 cm quadrat. In preparation for each photograph, each plot was marked with a card containing a number particular to that location. This number was photographed along with the plot and provided a permanent record of each photographs location. Four hundred photographs were taken per 10 m x 10 m site.

3.2.4 Slide analysis

Photographs were developed as slides. A slide projector was used to view the slides on an overhead screen. Each 10 cm² area of the slide was visually inspected for species type and number, and the data was recorded.

The data was entered into a spread sheet, using Microsoft Excel. Three species combinations and 3 site/years produced nine 10 000 cell spread sheets which were subjected to further visual and statistical analysis.

A species mapping program (Walker, 1999) was written in Visual Basic (Microsoft, 1997) and was used to map the locations of the weed species in each of the 10 m x 10 m sites. This program provided a visual representation of species absence, presence, or co-occurrence in 10 cm x 10 cm sub-quadrats. Different monochrome shades including white, light grey, dark grey, and black corresponded to each species lone presence, co-occurrence, and total presence. Twelve maps were created for each 10 m x 10 m site (species A, species B, co-occurring species A and B, and all locations in which species A and B occurred, and each of these for each of the 3 species combinations). In

figures 3.1, 3.3, and 3.5 a data block of 50 cm x 50 cm is missing in the top central area. The macro program was also used to create contingency tables for pairwise combinations of the 3 species.

3.2.5 Statistical analysis

The data was converted to species presence or absence in each of the 10 cm x 10 cm cells for association analysis. Chi-square analysis was used to assess the significance of species associations using the formula: $X^2 = \frac{(ad-bc)^2}{n(a+b)(c+d)(a+c)(b+d)}$. Where a is the number of cells with both species mutually occurring, b is the number of cells with species 1 occurring, c is the number of cells with species 2 occurring, d is the number of cells with both species mutually absent, and n is the total number of cells present (Steel and Torrie 1960). To minimize autocorrelation within the data, the random patterns test (Roxburgh and Chesson 1998) and the patch model test (Watkins and Wilson 1992) were implemented. These tests were performed using a program called Spatial.exe (Roxburgh and Chesson 1998). This program was used to conduct pairwise association tests for the presence-absence data.

The random patterns test creates two random species patterns, and then combines them. The cells are then interchanged in an attempt to make the randomized pattern more similar to the observed pattern. After a preset number of iterations, a Chi-square value is generated by comparison of the observed pattern to the newly created pattern.

Four algorithms were provided under the analysis options including the random patterns test, independent assignment, patch model test,

rotation/reflection and random shifts. The random patterns test was found to be liberal with data which had a strong gradient (Roxburgh and Chesson 1998). As a result, the patch model test was also implemented because it was conservative in its Chi-square evaluation. The patch model test has provided reliably accurate results when analyzing data with a strong gradient.

For the random patterns test, the plot area selected was 100 x 100, representing the entire 10 m x 10 m site. The number of iterations was set at 1000. This allowed the program to test pairwise associations 1000 times to find the best fit of the observed data to the randomized data. The plot was divided into 4 large blocks of cells, which were relocated to obtain a random pattern before the individual cells were relocated to create a fine tuned pattern. The purpose of dividing the plot into 4 large blocks was to increase the speed of the calculations. The large block attempts were set at 100, representing the maximum number of relocation attempts for the large blocks, before they were locked into place and individual cells were relocated. The small block attempts were set at 10 000, representing the maximum number of movement attempts for individual cells. The stopping limit was set at 0.01, which indicated that the randomized pattern was now sufficiently similar to the observed pattern.

Corrected Chi-square and associated p values were produced for each species combination analyzed.

Similarly, for the patch model test the plot size was set at 100 x 100, and the number of iterations was set at 1000. The patch size was set at 3. Similar

procedures as outlined for the random pattern test were used to generate the final adjusted Chi-square values and associated p values.

Point correlation coefficients (v) were calculated for each species combination, using the formula $v = \frac{ad - bc}{\sqrt{(a+b)(c+d)(a+c)(b+d)}}$. Where a is the number of cells with both species mutually occurring, b is the number of cells with species 1 occurring, c is the number of cells with species 2 occurring, and d is the number of cells with both species mutually absent.

This value depicted the level of association between the two species considered. Positive values indicated that the species were positively associated, while negative values indicated that the species were negatively associated.

3.3 Results

3.3.1 Species maps and contingency tables

Figures 3.1 and 3.2 visually represent the wild oat and green foxtail populations in site 1 from 1998 to 1999. In site 1 from 1998 to 1999 there was a decrease in the number of cells individually occupied by wild oat, and an increase in the number of cells individually occupied by green foxtail (tables 3.1 and 3.2). There was relatively no change in the number of cells mutually occupied or mutually unoccupied by wild oat and green foxtail (tables 3.1 and 3.2).

Figures 3.3 and 3.4 visually represent the wild oat and barnyardgrass populations in site 1 from 1998 to 1999. In site 1 from 1998 to 1999 there was a decrease in the number of cells individually occupied by wild oat, and an

increase in the number of cells individually occupied by barnyardgrass (tables 3.3 and 3.4). There was a decrease in the number of cells mutually occupied and mutually unoccupied by wild oat and barnyardgrass (tables 3.3 and 3.4).

Figures 3.5 and 3.6 visually represent the green foxtail and barnyardgrass populations in site 1 from 1998 to 1999. In site 1 from 1998 to 1999 there was a decrease in the number of cells individually occupied by green foxtail, and relatively no change in the number of cells individually occupied by barnyardgrass (tables 3.5 and 3.6). There was an increase in the number of cells mutually occupied, and a decrease in the number of cells mutually unoccupied by green foxtail and barnyardgrass (tables 3.5 and 3.6).

In summary, for site 1 in 1998 and 1999 wild oat and green foxtail appeared together in the least number of cells of all species combinations (tables 3.1 and 3.2). In 1998 wild oat and barnyardgrass appeared together in more cells than green foxtail and barnyardgrass (tables 3.3 and 3.4). However, in 1999 green foxtail and barnyardgrass appeared together in more cells than wild oat and barnyardgrass (tables 3.5-3.6).

At site 2 in 1998, barnyardgrass appeared in the largest number of cells, followed by green foxtail, and wild oat, respectively (tables 3.7-3.9). Species pairs, green foxtail, and barnyardgrass appeared together in the largest number of cells, followed by wild oat and barnyardgrass, and then by wild oat and green foxtail, respectively (tables 3.7-3.9).

3.3.2 Results of species association analysis

In 1998, wild oat and green foxtail were significantly associated in both site 1 and 2, but not at site 1 in 1999 (table 3.10). Wild oat and barnyardgrass were significantly associated at site 1 and 2 in 1998, and site 1 in 1999 (table 3.10). Green foxtail and barnyardgrass were significantly associated at site 1 in 1998 and 1999, but not at site 2 in 1998 (table 3.10).

Negative and positive point correlation coefficients indicate that two species are respectively, negatively or positively associated. Wild oat and green foxtail were negatively associated at site 1 and 2 in 1998, and at site 1 in 1999 (table 3.10). Wild oat and barnyardgrass were negatively associated at site 1 and 2 in 1998, and they were positively associated at site 1 in 1999 (table 3.10). Green foxtail and barnyardgrass were positively associated at site 1 and 2 in 1998, and at site 1 in 1999 (table 3.10).

The adjusted Chi-square values were lower than the unadjusted Chi-square values for species combinations at site 1 in 1998. This implies that there was some autocorrelation in the data for this site year, and that it was adjusted for by means of the random patterns test and the patch model test. The adjusted Chi-square values were similar to the unadjusted values at site 2 in 1998 and at site 1 in 1999. This suggests that there was little autocorrelation in the data for these site years.

3.4 Discussion

Understanding the inter-specific relationships of weed species provides a basis for further modification of patch dynamics and yield loss models. A key

component of studying multiple weed species is studying their association with one another. Dale (1999) defined association as the likelihood of different plant species to be found in close proximity more often than expected (positive association) or less often than expected (negative association). Mahdi and Law (1987) stated that studying spatial relationships between plant species would help in understanding the processes which could have given rise to spatial patterns. Dale (1999) stated that weed species which deviate from non-random associations and form positive or negative association patterns do so as a result of one or a combination of competition, response to environmental heterogeneity, and dispersal mechanisms.

Few surveys have been conducted to determine the association of multiple weed species, and those that do exist have been performed using a small scale. For example Wiles et al. (1992) studied broadleaved weeds in soybean at a relatively small scale using 9.1 x 0.16 m quadrats. Dale and Thomas (1987) sampled 20, 0.25 m² quadrats, in 4423 fields and determined that wild oat, green foxtail, and barnyardgrass were all positively associated with one another. Using 20, 0.25 m² quadrats per field, Thomas and Wise (1983 and 1984) determined that wild oat and barnyardgrass were associated with green foxtail in Manitoba and Saskatchewan fields. This project addresses weed-weed associations at a scale of 10 cm x 10 cm. It may not be appropriate to directly compare the results of this experiment to those performed at coarser scales. Other reports of species associations are general, and they infer a positive association between weed species. For example Sharma and Vanden Born

(1978) noted that wild oat was associated with green foxtail, and Maun and Barrett (1986) noted that barnyardgrass was associated with green foxtail. Neither reference indicated how these associations were determined.

3.4.1 Patch dynamics models

Understanding the ecological ramifications of weed species associations within multi-species infestations will provide insight into how these species exist in particular areas. Weed species associations may be indicative of the relative ability of a species to colonize and inhabit a particular area. As a result, the spatial association of weed species may become an important consideration in weed patch dynamics models.

Wild oat and green foxtail were found to be negatively associated (table 3.10). The negative weed species association detected is a result of one or a combination of competitive effects, differential response to environmental heterogeneity, or dispersal mechanisms. Negative associations of weed species may be indicative of species abilities to establish and dominate in a particular area.

Green foxtail and barnyardgrass were found to be positively associated (table 3.10). This suggests that they were not excluding each other from mutually inhabited areas. Weeds found in positive associations are not separated by the effects of competition, differential response to environmental heterogeneity, or dispersal mechanisms. The positive association of green foxtail and barnyardgrass may be indicative of neither species ability to dominate an area.

Wild oat and green foxtail, were found to be negatively associated. Since these species tend not to exist together, patches containing these species may be fairly unstable with respect to species composition. Green foxtail and barnyardgrass species were found to be positively associated. Since these species tend to exist together, patches containing these two species may be fairly stable with respect to species composition.

From 1998 to 1999, wild oat and barnyardgrass were found to change from negative to positive association. This may indicate that patches containing these two species will be subject to wide changes in species association over time. The changes in the wild oat and barnyardgrass associations noted in this survey may indicate that prediction of the patch make up (containing wild oat and barnyardgrass) will be unpredictable over time, and that the sustainability of the patches may be relatively variable. In contrast, patches containing mixtures of wild oat and green foxtail and green foxtail and barnyardgrass maintained their respective negative and positive associations over time. The consistency in associations may indicate that the patch make up will be relatively more predictable over time, and the sustainability of the patches may be more stable.

Those creating patch dynamics models might want to consider the influence of positive and negative associations between species, on the stability over time of a given species, within a weed patch.

3.4.2 Yield loss prediction models

If multiple weed species infestations are prevalent, an important consideration when addressing parameters for yield loss prediction models, is to

assess whether or not the species considered will have an additive or non-additive effect on crop yield. Swanton et al. (1999) stated that most of the research addressing multiple weed species interaction has been to determine if the effects of the weeds were additive. Understanding the positive and negative association of weed species may provide insight into the additivity or non-additivity of multiple weed species interference.

This survey indicated that wild oat and green foxtail (site 1 in 1998 and 1999), and wild oat and barnyardgrass (site 1 in 1998) were negatively associated (table 3.10). This indicated that these weed species were isolated from one another. As a result these weed species may act as mono-specific stands. This may indicate that infestations containing mixtures of wild oat and green foxtail or wild oat and barnyardgrass would result in additive yield loss.

Johnson et al. (1995) noted that weeds have been found to exhibit varying degrees of spatial and temporal stability. Fluctuations in environmental heterogeneity or dispersal mechanisms may outweigh localized competition and cause species which were once negatively associated to become positively associated. For example seed dispersal from barnyardgrass may have changed the association of wild oat and barnyardgrass from negative at site 1 in 1998, to positive in 1999 (table 3.10). Under these circumstances, weed species may interact with one another, and infestations containing wild oat and green foxtail, or wild oat and barnyardgrass may result in non-additive yield loss.

Green foxtail and barnyardgrass were positively associated with one another throughout this survey (table 3.10). Species which are positively

associated are not excluding each other from an area. These species may be experiencing relatively similar inter-specific and intra-specific competition, similar responses to environmental heterogeneity, and may have similar dispersal abilities, when compared to species which are negatively associated. As a result these species may have less influence on one another, possibly causing additive yield loss from the species combination. Since green foxtail and barnyardgrass were found to be positively associated, fields which contain mixtures of these two species may exhibit additive yield loss.

The concept of the additivity of weed species had been incorporated into many yield loss prediction models including those by Spitters (1983), Cousens (1985), and Kropff and Spitters (1991). The concept of additivity in yield loss may hold true under conditions of stable negative or positive weed species associations. This is in disagreement with other researchers who stated that multiple weed species infestations did not cause additive yield loss (Van Acker et al. 1997; Blackshaw and Schaalje 1993; Toler et al. 1996). The concept of non-additive yield loss may hold true for species combinations which change from negative to positive association, as observed with wild oat and barnyardgrass at site 1 from 1998 to 1999. In addition, even though wild oat and green foxtail, and wild oat and barnyardgrass were found to be negatively associated, they still occurred together to some extent (tables 3.1 - 3.6). Since species still occur together even if they are negatively associated, the potential still exists for non-additive yield loss effects due to multiple weed species interference.

Studying the association patterns of weed species could provide interesting ecological data for weed patch dynamics models, and practical information for the appropriateness of additivity assumptions in yield loss prediction models.

Patterns alone cannot be used to explain the factors which caused them. However, the study of patterns can provide a basis for a discussion of the factors which may have lead to their development. An important step in understanding multiple weed species interactions will be to discuss the effects of competition, environmental heterogeneity, and dispersal mechanisms on species association patterns.

Table 3.1. Contingency table for presence (+) and absence (-) of wild oat and green foxtail for 1998 site 1. Numbers represent quantity of 10 cm x 10 cm cells within 10 m x 10 m site

	Wild oat		Total	
	+	-		
Green foxtail	+	689	1368	2057
	-	2919	4999	7918
TOTAL		3608	6367	9975
<hr/>				
X ² value				8.03

Table 3.2. Contingency table for presence (+) and absence (-) of wild oat and green foxtail for 1999 site 1. Numbers represent quantity of 10 cm x 10 cm cells within 10 m x 10 m site

	Wild oat		Total	
	+	-		
Green foxtail	+	697	3288	3985
	-	1106	4909	6015
TOTAL		1803	8197	10000
<hr/>				
X ² value				1.30

Table 3.3. Contingency table for presence (+) and absence (-) of wild oat and barnyardgrass for 1998 site 1. Numbers represent quantity of 10 cm x 10 cm cells within 10 m x 10 m site

	Wild oat		Total	
	+	-		
Barnyardgrass	+	2131	5137	7268
	-	1477	1230	2707
TOTAL		3608	6367	9975
X ² value				544.3

Table 3.4. Contingency table for presence (+) and absence (-) of wild oat and barnyardgrass for 1999 site 1. Numbers represent quantity of 10 cm x 10 cm cells within 10 m x 10 m site

	Wild oat		Total	
	+	-		
Barnyardgrass	+	1727	7661	9388
	-	76	536	612
TOTAL		1803	8197	10000
X ² value				13.89

Table 3.5. Contingency table for presence (+) and absence (-) of green foxtail and barnyardgrass for 1998 site 1. Numbers represent quantity of 10 cm x 10 cm cells within 10 m x 10 m site

		Green foxtail		Total
		+	-	
Barnyardgrass	+	1636	5632	7268
	-	421	2286	2707
TOTAL		2057	7918	9975
X^2 value				58.33

Table 3.6. Contingency table for presence (+) and absence (-) of green foxtail and barnyardgrass for 1999 site 1. Numbers represent quantity of 10 cm x 10 cm cells within 10 m x 10 m site

		Green foxtail		Total
		+	-	
Barnyardgrass	+	3778	5610	9388
	-	207	405	612
TOTAL		3985	6015	10000
X^2 value				9.88

Table 3.7. Contingency table for presence (+) and absence (-) of wild oat and green foxtail for 1998 site 2. Numbers represent quantity of 10 cm x 10 cm cells within 10 m x 10 m site

	Wild oat		Total	
	+	-		
Green foxtail	+	769	3942	4711
	-	991	4298	5289
TOTAL		1760	8240	10000
<hr/>				
X ² value				10.01

Table 3.8. Contingency table for presence (+) and absence (-) of wild oat and barnyardgrass for 1998 site 2. Numbers represent quantity of 10 cm x 10 cm cells within 10 m x 10 m site

	Wild oat		Total	
	+	-		
Barnyardgrass	+	1109	5562	6671
	-	651	2678	3329
TOTAL		1760	8240	10000
<hr/>				
X ² value				13.16

Table 3.9. Contingency table for presence (+) and absence (-) of green foxtail and barnyardgrass for 1998 site 2. Numbers represent quantity of 10 cm x 10 cm cells within 10 m x 10 m site

		Green foxtail		Total
		+	-	
Barnyardgrass	+	3170	3501	6671
	-	1541	1788	3329
TOTAL		4711	5289	10000
X ² value				1.35

Table 3.10. Unadjusted, Random pattern, and Patch test Chi-square analysis of wild oat and green foxtail (GF), wild oat and barnyardgrass (BY), and green foxtail and barnyardgrass for site 1 and 2 in 1998, and site 1 in 1999, and point correlation coefficient (v) relating positive or negative species association

Plot	Unadjusted X ²	Random patterns X ²	Patch model X ²	p value	V value
WO-GF 1998 site 1	8.03	7.50	7.50	0.006	-0.0283
WO-GF 1999 site 1	1.30	1.30	1.30	0.253	-0.0114
WO-GF 1998 site 2	10.01	10.01	10.01	0.002	-0.0316
WO-BY 1998 site 1	544.30	527.09	527.09	<0.001	-0.2330
WO-BY 1999 site 1	13.89	13.89	13.89	<0.001	+0.0373
WO-BY 1998 site 2	13.16	13.16	13.16	<0.001	-0.0363
GF-BY 1998 site 1	58.30	61.26	61.26	<0.001	+0.0765
GF-BY 1999 site 1	9.88	9.88	9.88	0.002	+0.0314
GF-BY 1998 site 2	1.35	1.35	1.35	0.246	+0.0117

$X^2_{0.05,1}=3.841$

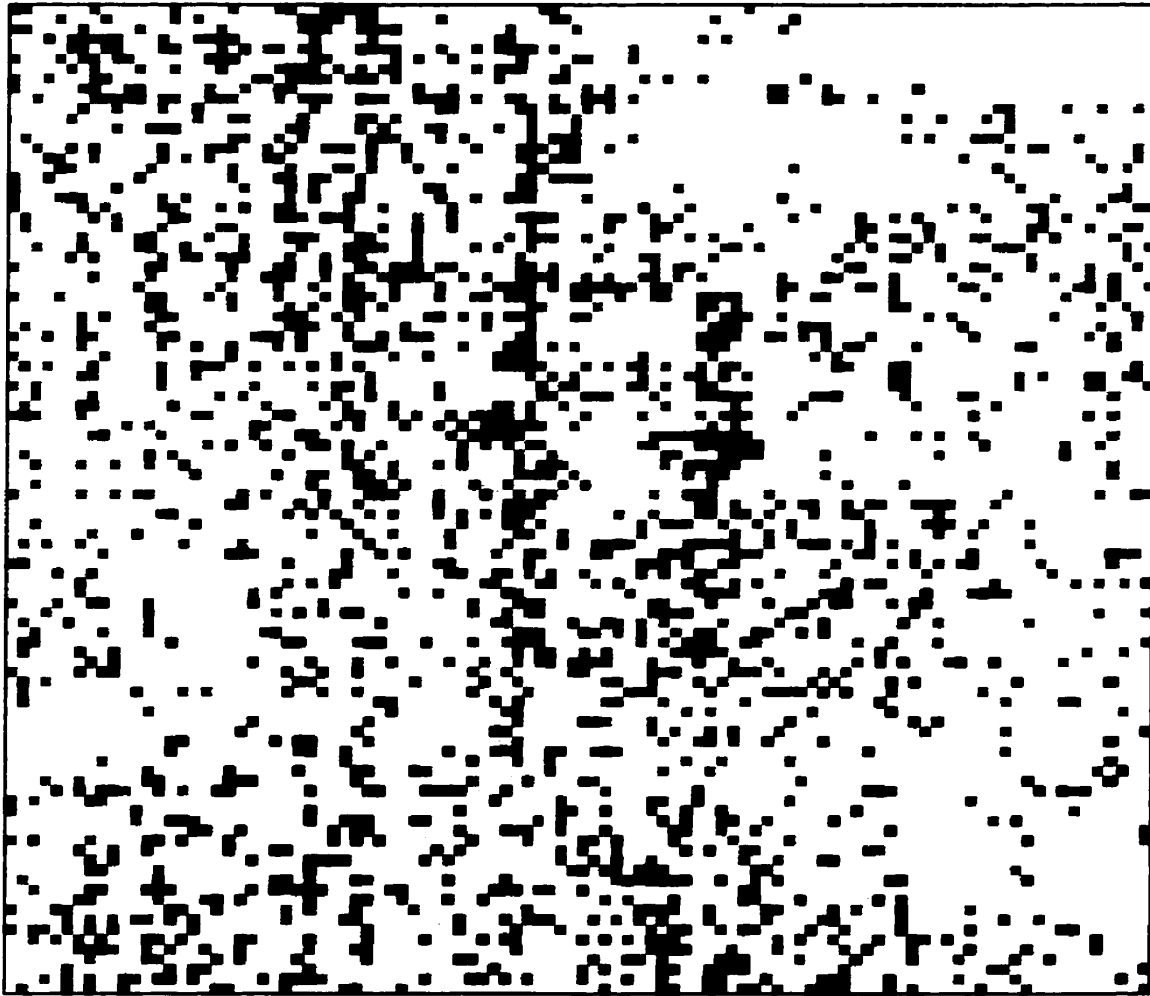


Figure 3.1. Map of 10 cm x 10 cm cells within 10 m x 10 m site 1 in 1998 showing individual species presence, mutual presence, and mutual absence of wild oat and green foxtail.

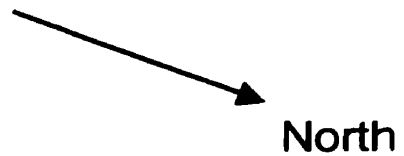
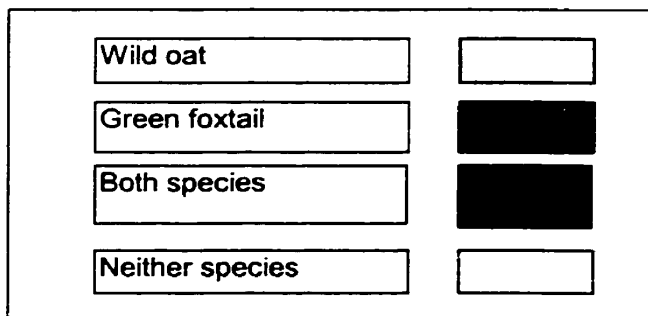
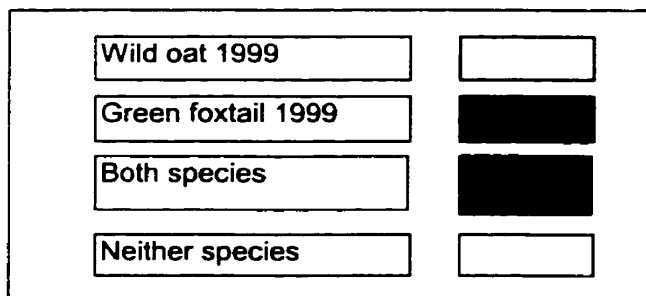




Figure 3.2. Map of 10 cm x 10 cm cells within 10 m x 10 m site 1 in 1999 showing individual species presence, mutual presence, and mutual absence of wild oat and green foxtail.



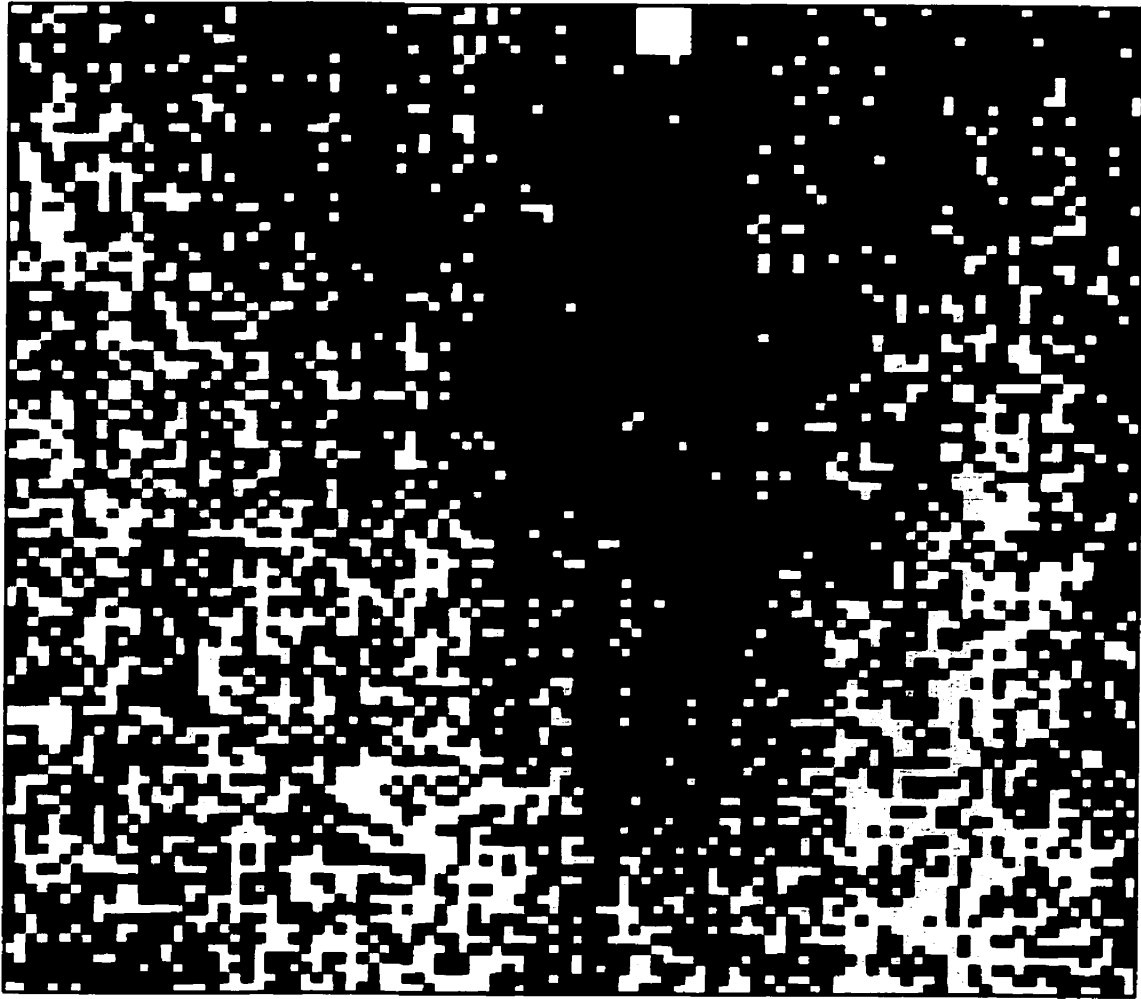
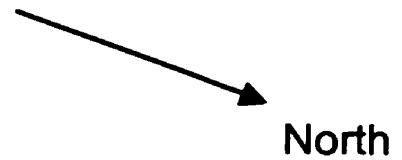
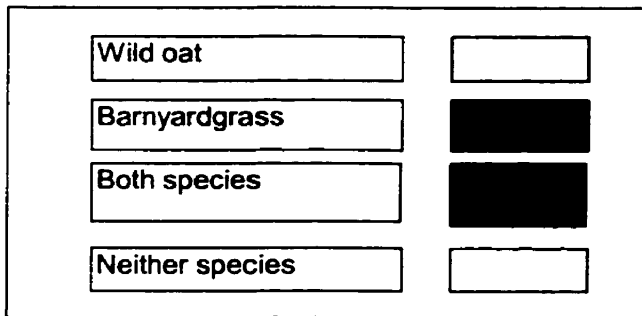


Figure 3.3. Map of 10 cm x 10 cm cells within 10 m x 10 m site 1 in 1998 showing individual species presence, mutual presence, and mutual absence of wild oat and barnyard grass.



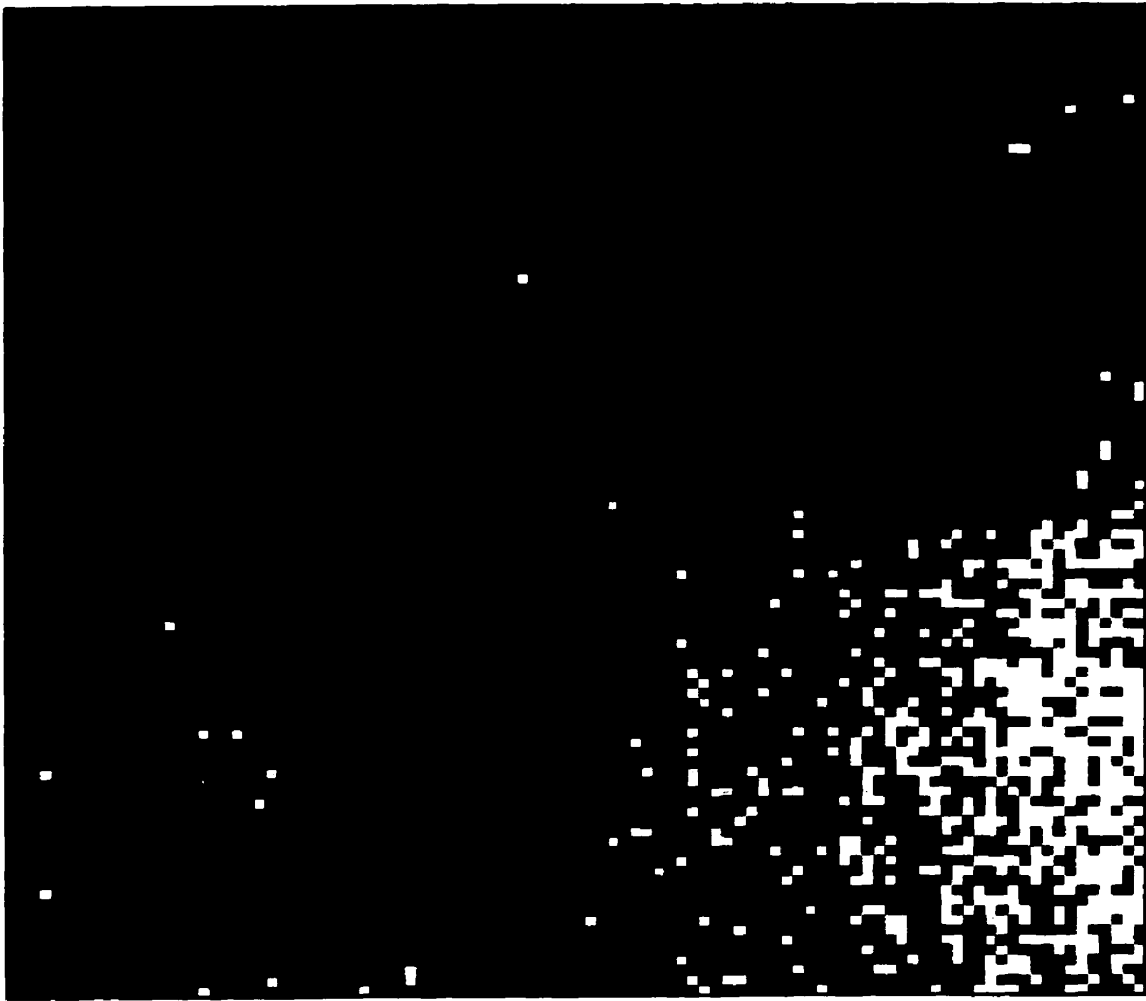
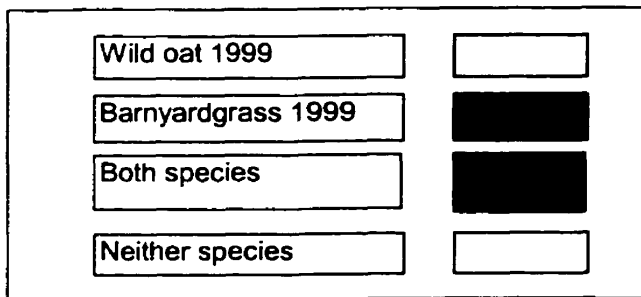


Figure 3.4. Map of 10 cm x 10 cm cells within 10 m x 10 m site 1 in 1999 showing individual species presence, mutual presence, and mutual absence of wild oat and barnyard grass.



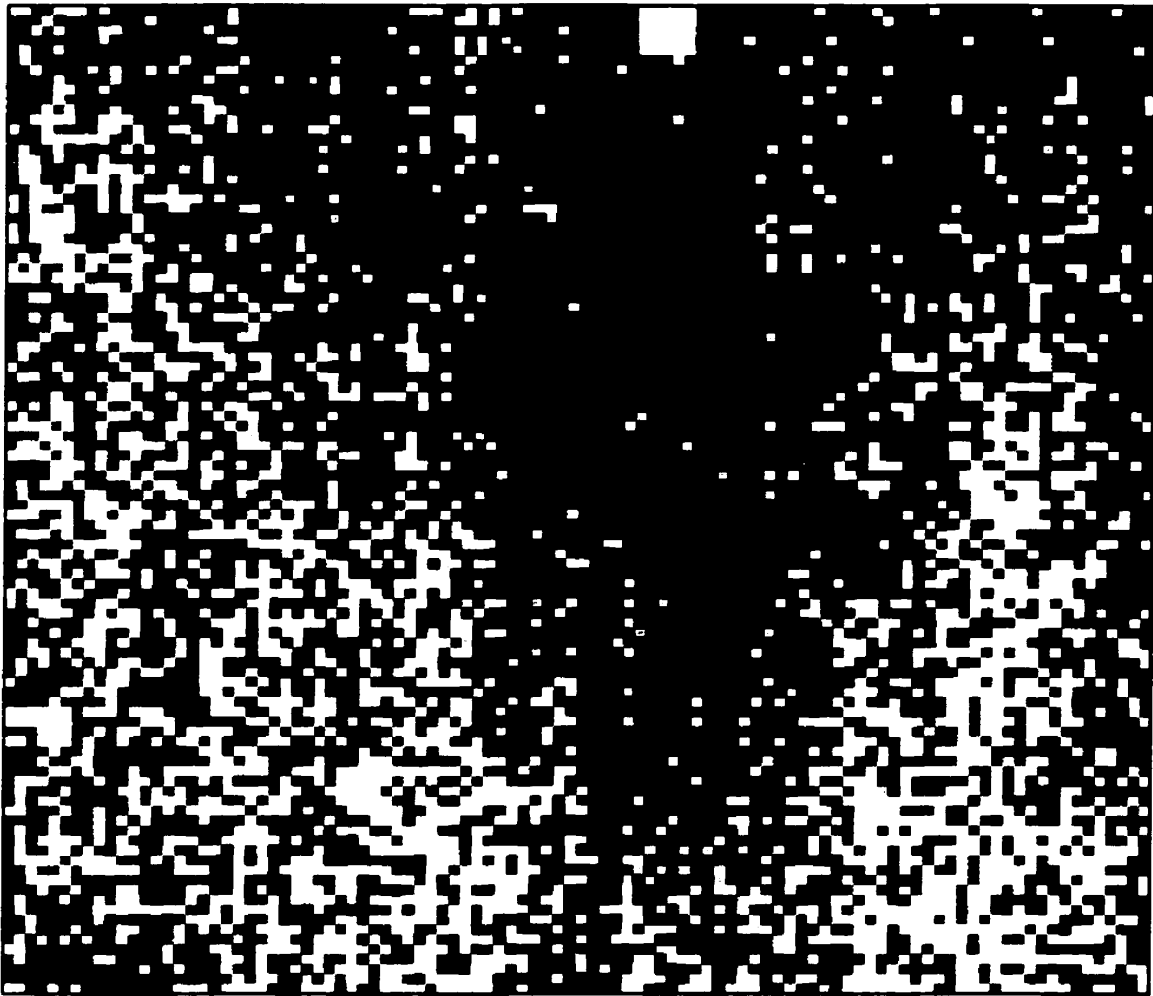
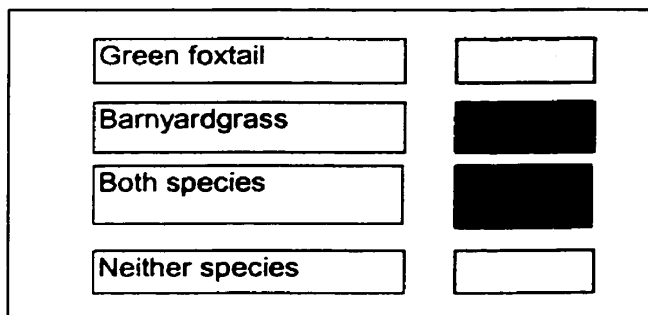


Figure 3.5. Map of 10 cm x 10 cm cells within 10 m x 10 m site 1 in 1998 showing individual species presence, mutual presence, and mutual absence of green foxtail and barnyardgrass.



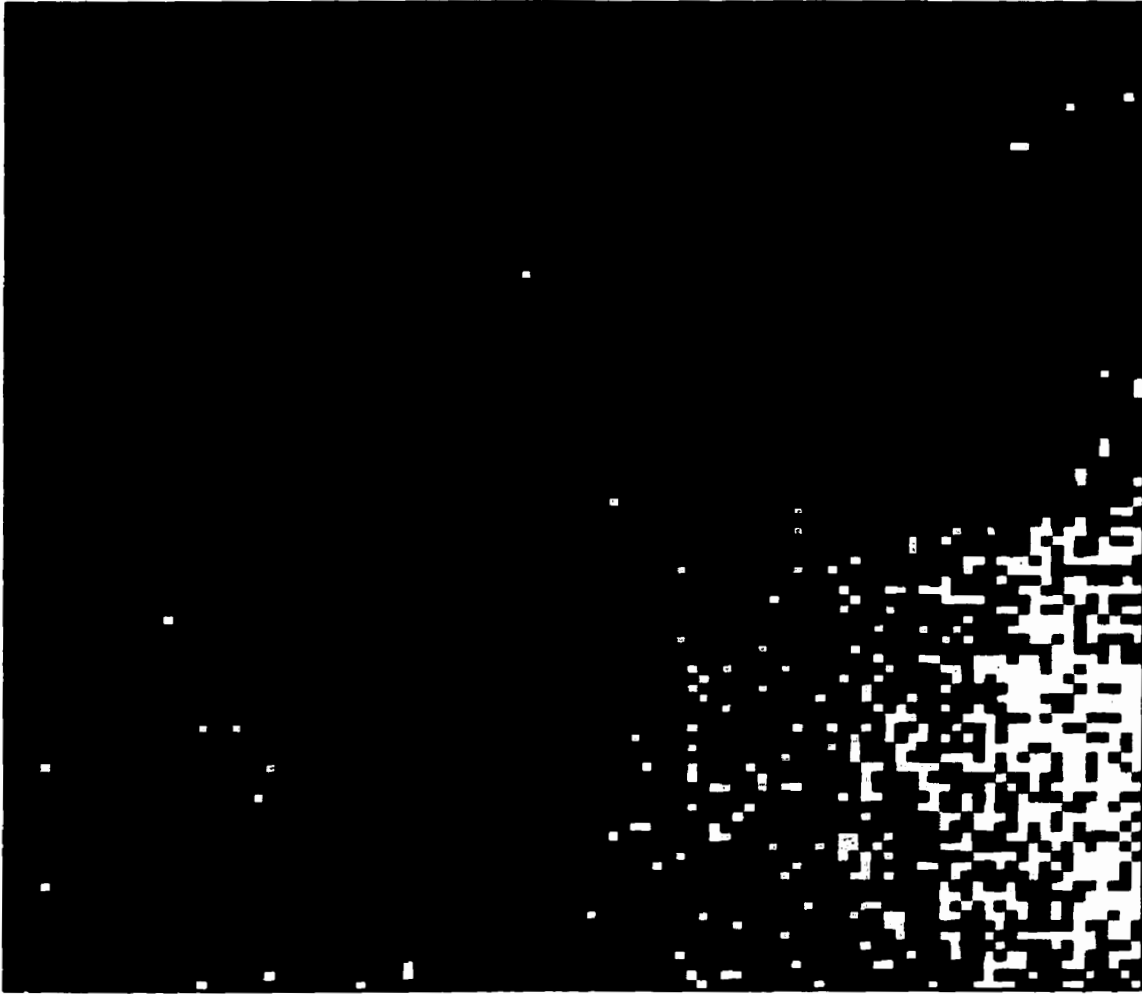


Figure 3.6. Map of 10 x 10 cm² cells within 10 x 10 m² site 1 in 1999 showing individual species presence, mutual presence, and mutual absence of green foxtail and barnyardgrass.

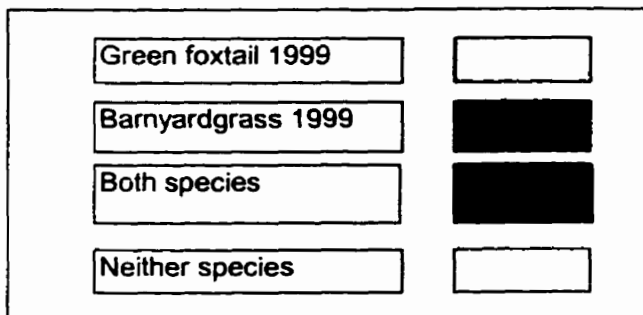
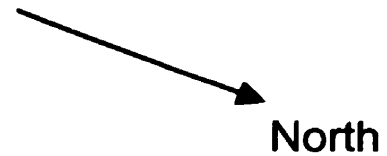
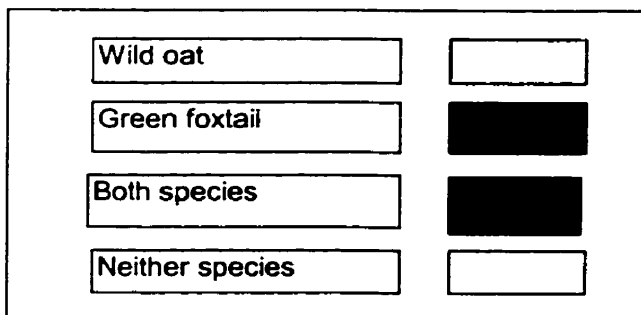




Figure 3.7. Map of 10 cm x 10 cm cells within 10 m x 10 m site 2 in 1998 showing individual species presence, mutual presence, and mutual absence of wild oat and green foxtail.



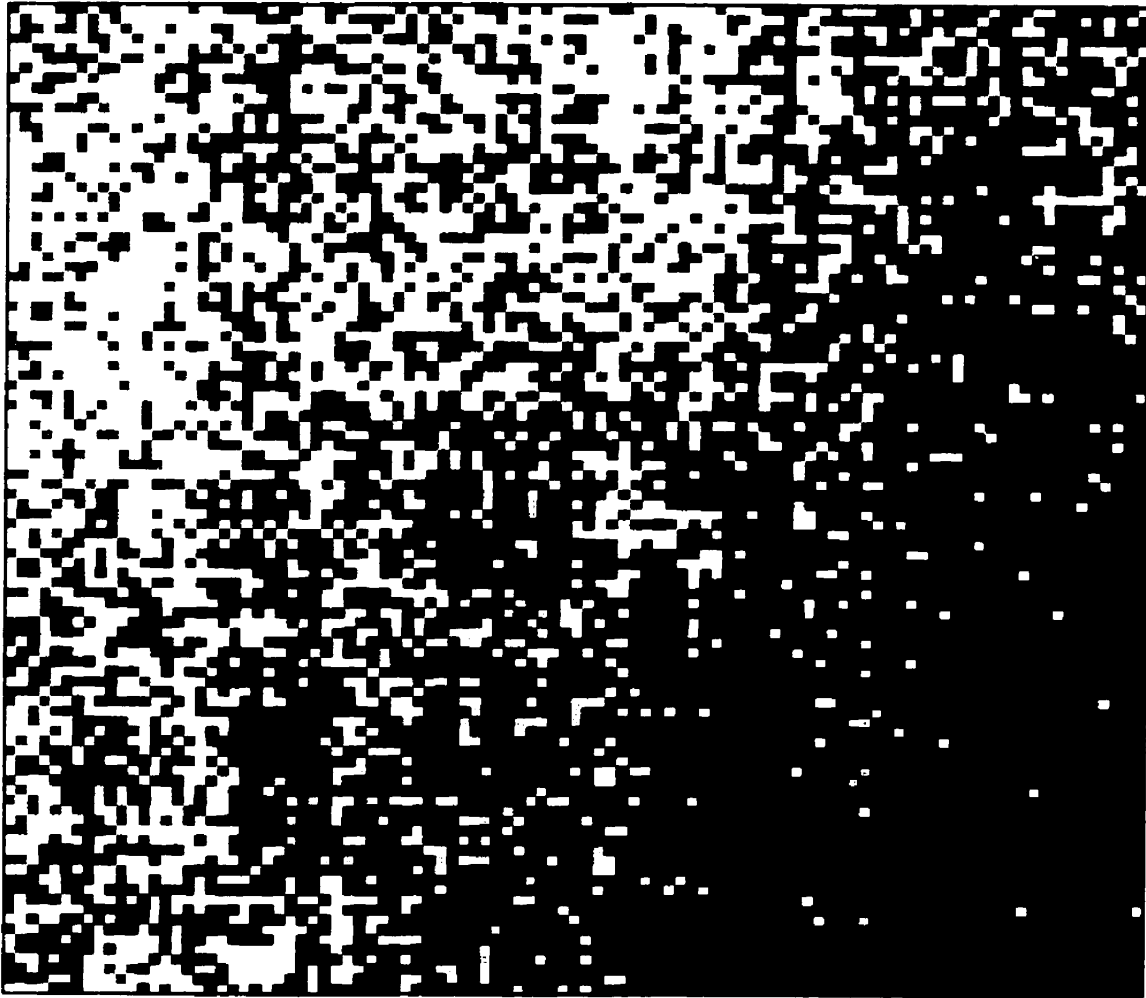
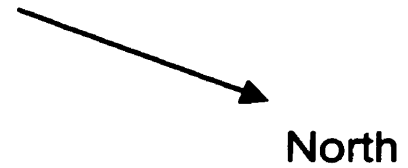
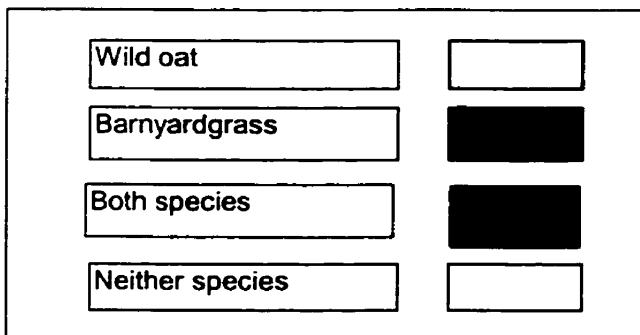


Figure 3.8. Map of 10 cm x 10 cm cells within 10 m x 10 m site 2 in 1998 showing individual species presence, mutual presence, and mutual absence of wild oat and barnyardgrass.



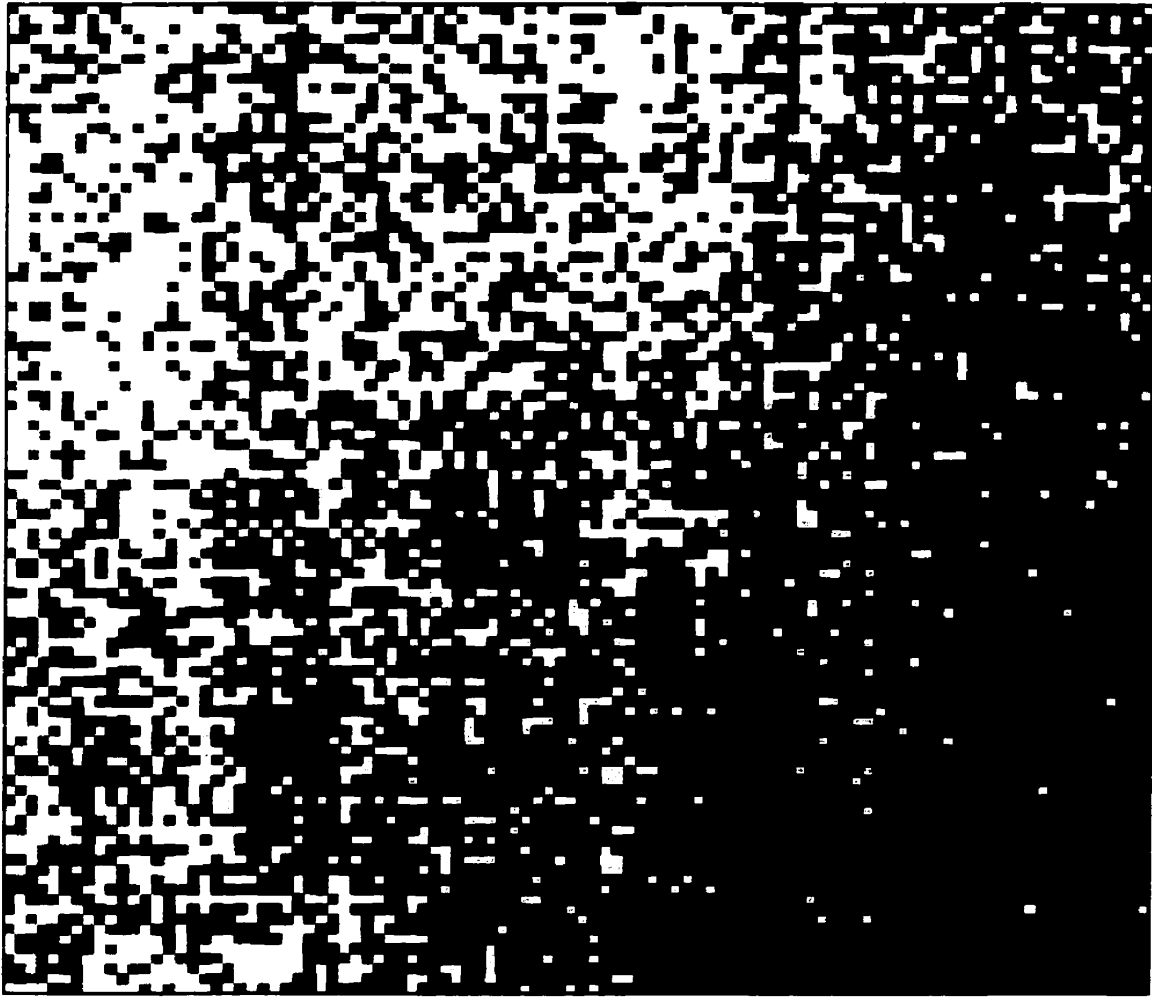
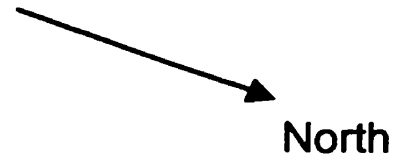
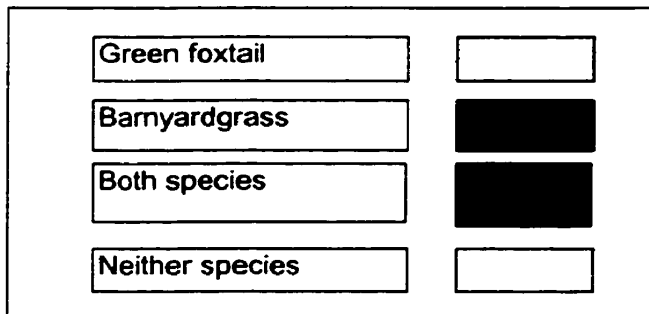


Figure 3.9. Map of 10 cm x 10 cm cells within 10 m x 10 m site 2 in 1998 showing individual species presence, mutual presence, and mutual absence of green foxtail and barnyard grass.



4.0 Mechanisms underlying wild oat, green foxtail, and barnyardgrass spatial association patterns

4.1 Introduction

Weed species have been noted to exist in multi-species associations (Combella and Friesen 1992). Studying weed-weed associations within arable fields can lead to the detection of patterns. Mahdi and Law (1987) stated that the study of patterns cannot decisively pinpoint the cause of the pattern, however, their study can provide insight into the factors which may have caused the patterns. Dale (1999) stated that spatial pattern can be affected by competition, environmental heterogeneity, and dispersal mechanisms. Discussing the mechanisms and their interaction will provide insight into why weed species form particular negative or positive associations.

The objective of this chapter was to discuss the mechanisms which may have affected the spatial association of wild oat, green foxtail, and barnyardgrass in site 1 from 1998 to 1999.

4.2 Materials and Methods

4.2.1 Replacement series experiment

A replacement series experiment was carried out to establish the relative competitive abilities of wild oat, green foxtail, and barnyardgrass.

Circular plastic pots used for the experiment had a height of 13 cm and a radius 6 cm. Soil was prepared by mixing soil, sand, and peat in a ratio of 2:2:1. The mix constituents were placed in a rotating drum for 2 minutes to ensure

adequate mixing.

Treatments included 3 species combinations; wild oat and green foxtail, wild oat and barnyardgrass, and green foxtail and barnyardgrass. The experiment included 2 total densities (low densities of 8 plants per pot (equivalent to 708 plants per m²), and high densities of 16 plants per pot (equivalent to 1416 plants per m²)), and two separate harvest dates (including seedling stage when wild oat was at 4th leaf , and early reproductive stage harvested when wild oat just flowering). There were 5 species ratios (100:0, 75:25, 50:50, 25:75, and 0:100), replicated 4 times.

A pattern template for planting was developed for both the low and high density replacement series. The seeding pattern template ensured equal spacing of all of the seeds.

The pots were filled with 10 cm of soil. The pattern was then laid out onto the soil and the seeds of each respective species were placed into each cut out hole. Once all of the seeds had been placed the pattern was removed and the seeds were covered with 2 cm of soil. The soil was then lightly packed to ensure proper seed-soil contact.

The experiment was carried out in a growth chamber with 14 hour days and 10 hour nights. The light intensity was 1500 micro mol/m² of PAR. The day-night temperature was 20 and 15 °C, respectively.

Watering was performed evenly over all treatments every 5 days. Fertilizer was applied to each pot every 14 days at a rate equivalent to 25 kg of nitrogen per hectare. Fertilizer was added 2 times to each pot for the seedling

harvest (resulting in 50 kg of nitrogen/ha), and 6 times to each pot for the early reproductive stage (resulting in 150 kg of nitrogen/ha) during this experiment.

The pots were randomized every 7 days. This was done to equalize edge effects and the effects of neighboring pots on one another.

Plants were harvested by cutting at the soil level. The species were separated and dried at 80 °C for 72 hours, and weighed.

This data was placed into a spread sheet format, and treatment means and standard errors were calculated. Tables and figures for the replacement series data were created for interpretation.

In a replacement series experiment the superior competitor's relative biomass is decreased less as it is replaced by an inferior competitor. When its relative dry biomass is plotted against species ratio a convex curve is created. The inferior competitor's relative dry biomass weight is decreased more as it is replaced by a superior competitor. When its relative dry biomass is plotted against species ratio a concave curve is created. When the relative yield total (RYT) species is above 1, equal to 1, or below 1 indicates partial niche overlap and synergistic effects, niche overlap, and complete niche overlap and additional antagonism, respectively.

4.2.2 Gravimetric soil moisture measurements

Soil samples were taken from both sites 1 and 2 on April 30, 1999. Soil was collected from the surface of the field in the center of each of the 100-1m² areas within each 10 m x 10 m site. Containers with a radius of 0.04 m and a height of 0.025 m and with tight fitting lids were used to collect the soil samples.

The entire sample including the soil, water, and containers were weighed (original total weight). The lids were removed from the samples and dried for 72 hours at 80 °C. The lids were replaced and the tins and dried soil were reweighed (container and dried soil weight). The weight of water in each soil sample was determined by subtracting the weight of the tin and dried soil from the original total weight.

4.2.3 Seed bank sampling

Soil cores were taken and analyzed to provide information on the content and location of the seed bank during this experiment. Soil cores were taken on August 15, 1998, May 2, 1999, and September 9, 1999. From each 10 m x 10 m site 30 soil cores were taken randomly and their exact location within the 10 m x 10 m site was recorded. Samples were taken using a soil corer with a radius of 0.05 m to a depth of 0.10 m. Each sample was placed into plastic bags for transport and storage. The samples were each placed into a 0.10 x 0.10 m tray and all samples were frozen. In order to assess species density in the seed bank samples we used the method as described by Cardina et al. (1996). After one month the trays were removed, allowed to thaw, and placed onto greenhouse benches. The soil was stirred, and weeds allowed to germinate and grow for one month. Following species identification seedlings were removed and soil samples were returned to the freezer. This procedure was repeated two more times, and the total density for each species in each sample was recorded. Using regression analysis the relationship was determined between the density of the seeds of each species from the seed bank from the spring of 1999, and

the density of seedlings in the spring of 1999.

4.2.4 Number of cells with single species infestations

From tables 3.1-3.6, a diagonal count of the number of cells with each species solely present was tabulated (table 4.1). For each combination of species A and B, this revealed the number of cells in which species A occurred alone, and the number of cells in which species B occurred alone.

4.3 Results

For both total density and both harvest dates, when wild oat and green foxtail were grown together the replacement series figures showed that the plot of wild oat relative dry biomass versus species ratio produced a convex shaped curve, and green foxtail relative dry biomass versus species ratio produced a concave shaped curve (figures 4.1-4.4). These curves indicate that wild oat is the superior competitor to green foxtail.

For both total density and both harvest dates, when wild oat and barnyardgrass were grown together the replacement series figures showed that the plot of wild oat relative dry biomass versus species ratio produced a convex shaped curve, and barnyardgrass relative dry biomass versus species ratio produced a concave shaped curve (figures 4.5-4.8). These curves indicate that wild oat is the superior competitor to barnyardgrass.

For both total density and both harvest dates, when green foxtail and barnyardgrass were grown together the replacement series figures showed that the plot of neither species showed a convex or a concave shaped curve (figures 4.9-4.12). These curves indicate that neither green foxtail nor barnyard

grass are superior competitors.

The relative yield totals ranged both above and below 1 for all species combinations for low and high total density for the seedling harvests, and for low total density for the early reproductive harvests. This implies that in these cases, there were no antagonistic effects beyond competition occurring between the species (Figures 4.1-4.3 and 4.5-4.7 and 4.9-4.11). The relative yield total for the high total density for the early reproductive harvest was consistently above one for all species pairs. This implies in these cases, that there was a synergistic effect occurring between the species (figures 4.4, 4.8, and 4.12).

For site 1 in 1999, gravimetric soil moisture measurements indicated that the mean water content was 10.5% v/v; and the range extended from a maximum value of 26.2% v/v, and a minimum value of 0.15% v/v (table 4.3).

For site 1 in 1999, the relationship between the seed bank from the spring of 1999, and the seedlings for barnyardgrass had an R^2 value of 0.376. The relationships between wild oat and green foxtail were weaker with R^2 values of 0.00107 and 0.0209, respectively.

4.4 Discussion

Visual observation of site 1 from 1998 to 1999 revealed that there were changes in the spatial pattern of wild oat, green foxtail, and barnyardgrass (figures 3.1-3.6). From 1998 to 1999 the number of cells containing green foxtail and the number of cells containing barnyardgrass increased, and the number of cells containing wild oat decreased (table 4.1).

A negative and positive point correlation coefficient indicated that two species were, respectively, negatively and positively associated. Wild oat and green foxtail were negatively associated at site 1 in 1998 and 1999 (table 3.10). Wild oat and barnyardgrass were negatively associated at site 1 in 1998, and positively associated at site 1 in 1999 (table 3.10). Green foxtail and barnyardgrass were positively associated at site 1 in 1998 and 1999 (table 3.10). The association pattern can be used to suggest possible mechanisms which might be responsible for its existence. Competition, differential response to environmental heterogeneity, and dispersal mechanisms are all factors which could influence the association patterns of these species.

Competition can affect the spatial association of weed species. The replacement series results indicated that wild oat was more competitive than green foxtail and barnyardgrass (figures 4.1-4.8), and that barnyardgrass and green foxtail were equally competitive toward each other (figures 4.9-4.12).

It is likely that the earlier emergence of wild oat caused it to have a greater competitive ability over green foxtail and barnyard grass. Green foxtail and barnyardgrass had relatively similar emergence times. Radosevich (1997) stated that the timing of emergence will affect the relative competitive hierarchy among plant species. In a replacement series experiment performed by Wall (1993) it was determined that wild oat was more competitive than green foxtail. In addition, O'Donovan (1985) reported that in wheat, 50 wild oat per m² would reduce yield by 24%, while green foxtail at the same density would reduce wheat yield by only 2%.

If competition were the most influential mechanism affecting the species association pattern, then field results should have revealed that wild oat would expand into the areas previously dominated by green foxtail and barnyardgrass. This is the opposite of what was observed at site 1, where green foxtail and barnyardgrass were found in a greater number of cells in 1999 versus 1998. (figures 3.1-3.6). This suggests that factors other than competition were having a greater influence on the species associations.

In this experiment the species considered had vastly different abilities to produce seed. The replacement series results indicated that wild oat was the superior competitor, however, because of their ability to produce greater amounts of seed, green foxtail and barnyardgrass may be superior invaders under field conditions. At site 1, the total number of cells occupied solely by either green foxtail or barnyardgrass increased considerably from 1998 to 1999 compared to wild oat (tables 3.1-3.6). Seed dispersal may therefore, be a very important factor affecting species association patterns.

Wild oat can produce between 100-500 seeds per plant (Dadd 1953), green foxtail between 5,000-12,000 seeds per plant (Vanden Born 1971), and barnyardgrass between 2,000-40,000 seeds per plant (Holm et al. 1977). Green foxtail and barnyardgrass have a much greater annual seed return than wild oat. This could give green foxtail and barnyardgrass an advantage, in that they are able to establish at relatively higher densities, in a relatively shorter time than wild oat.

The relative densities of species could also affect competition between

species and in turn the relative pattern of infestation in the field. At site 1, green foxtail was present in a smaller number of cells than wild oat in 1998, and a larger number of cells than wild oat in 1999 (table 4.1). In 1998 the occurrence density of wild oat and green foxtail, (the density in cells where they occurred) was 157 and 120 plants/m², respectively (table 4.2). In 1999 the occurrence density of wild oat decreased to 86 plants/m², while for green foxtail it increased to 203 plants per m². Because it was able to increase both the number of cells it occupied, and it's occurrence density within these cells, this may indicate that seed production may allow green foxtail to invade an area faster and at higher densities than wild oat.

At site1, barnyardgrass was present in a greater number of cells than either wild oat or green foxtail in both 1998 and 1999 (table 4.1). From 1998 to 1999 the occurrence density of barnyardgrass increased greatly from 249 plants/m² to 1043 plants/m² (table 4.2). Because it's occurrence density within these cells increased relative to wild oat and green foxtail, this may indicate that seed production may allow barnyardgrass to invade an area faster and at higher densities than the other species.

No herbicide was applied to site 1 in 1998, resulting in large amounts of weed seed shed. This may have accelerated weed species movement within the site, especially for green foxtail and barnyardgrass. This may explain the large increase in cell numbers occupied by the green foxtail and barnyardgrass populations in site 1 from 1998 to 1999, and the reduction in cell numbers occupied by wild oat in site 1 in 1998 versus 1999 (tables 3.1-3.6). The ability of

barnyardgrass to produce large amount of seed may also explain why the wild oat and barnyardgrass association changed from negative in 1998 to positive in 1999.

There was a strong relationship between the barnyardgrass seed bank measured in the spring of 1999 and resulting seedling occurrence in the spring of 1999 (Figure 4.15). There was no relationship between the spring 1999 seed bank and resulting seedling occurrence in spring 1999 for green foxtail, and no relationship for wild oat (tables 4.13 and 4.14). The relatively strong relationship between seed bank and seedling occurrence for barnyardgrass, indicates that seed occurrence is likely to result in barnyardgrass seedlings. The results of this survey indicate that there is no apparent relationship between the seed bank and seedling occurrence for green foxtail and wild oat. In general these results suggest that seedlings resulting from weed seed inundation in an area may be dependent upon the species type.

Seed dormancy may also affect species associations patterns. Wild oat (Banting 1966), green foxtail (Martin 1943; Vanden Born 1971), and barnyardgrass (Barrett and Wilson 1983) have all been noted to have variable dormancy depending upon environmental conditions, soil texture and soil moisture levels. Variable seed dormancy may affect the species emergence, which in turn may affect the formation of the spatial association pattern. The strong relationship found between the seed bank and the seedlings, as noted for barnyardgrass (spring 1999 seed bank, and spring 1999 seedlings) compared to wild oat and green foxtail, was likely a result of a large number of seed produced

by barnyardgrass, rather than lower seed dormancy.

Mechanical cultivation and harvesting could also have contributed to the associations and spatial patterns observed between the weed species in this experiment. Previous to this experiment the field was tilled and harvested in an east-west direction. McCanny and Cavers (1988) stated that the parent-seed relationship might become obscured with the addition of combine harvesting. Shirtliffe (1999) noted that wild oat seed can spread 30 to 150 m by combine harvesting. At site 1 in both 1998 and 1999, visual assessment of the field indicates that there is an east-west spatial pattern of the weed species infestation.

Environmental heterogeneity is another mechanism which can affect the spatial association of weed species. Temporal environmental heterogeneity may have been responsible for the change in spatial pattern in site 1 from 1998 to 1999. Cool spring environments suit wild oat emergence and growth, and wild oat has the ability to emerge earlier than either green foxtail or barnyardgrass. Green foxtail and barnyardgrass may compete more actively under warmer conditions such as those usually present in late spring or early summer. As a result wild oat may compete more actively with green foxtail and barnyardgrass in years of early cultivation and early seeding, and green foxtail and barnyardgrass may compete more actively with wild oat under years of late cultivation and late seeding.

In site 1 from 1998 to 1999 changes in the environment due to the time of seeding may have influenced the spatial pattern of wild oat, green foxtail, and

barnyardgrass. Site 1 in 1998 was seeded on May 13. Delays caused by a wet spring resulted in the 1999 site 1 being seeded on June 1. As of May 31, 1999 60% of wild oat had emerged in the Red River valley (Marginet, personal communication). Therefore, in 1999 many wild oat seedlings which emerged before May 31, 1999 were likely destroyed during field cultivation prior to seeding. The late seeding in 1999 may help to explain why at site 1 in 1999 versus 1998 fewer cells were occupied by wild oat, and more cells were occupied by green foxtail and barnyardgrass.

Gravimetric soil moisture measurements at each site revealed that there was considerable variation in the mean water content within each site (table 4.3). Areas with higher water content may favor wild oat (Sharma and Vandeborn 1978) and barnyardgrass (Roche and Muzik 1964), which are able to exist under relatively wet conditions. Conversely, areas with lower water content may favor green foxtail which prefers to exist in relatively dry conditions (Alex et al. 1972). Visual observation of the gravimetric soil moisture pattern did not resemble any species presence or absence pattern in site 1. Thus the species association patterns may have been relatively unaffected by moisture differences in site 1.

This survey was conducted over only two years. Over the short-term, competition may have relatively little effect on species association. Seed dispersal on the other hand may affect the spatial association pattern of weed species within one year.

In conclusion, although wild oat is a superior competitor (according to replacement series experiments) its presence and density in an area may be

diminished by the magnitude of seed produced by competitors (green foxtail and barnyardgrass), which appear nearby at higher base densities. Thus, the spatial association of the weed species in site 1, may have been influenced more by seed dispersal than by competition. The density of the initial population may have been an important factor influencing the dispersal mechanisms.

Environmental heterogeneity may have also influenced the spatial association of the weed species from 1998 to 1999, particularly, the late seeding in 1999 versus 1998. The detection of spatial association patterns within weed populations allows one to discuss mechanisms which might be responsible for their creation. Understanding the interaction of these mechanisms will provide insight into why weed species form particular negative or positive associations.

Table 4.1. Summary of contingency tables 3.1-3.9 for the number of 10 cm x 10 cm cells for site 1 in 1998 and 1999 containing only one of the two species for wild oat (WO) and green foxtail (GF), or wild oat and barnyardgrass (BY), or green foxtail and barnyardgrass combinations

Species combination	Site-Year	WO present	GF present	BY present
WO-GF	Site 1 1998	2919	1368	-
WO-GF	Site 1 1999	1106	3288	-
WO-BY	Site 1 1998	1477	-	5137
WO-BY	Site 1 1999	76	-	7661
GF-BY	Site 1 1998	-	421	5632
GF-BY	Site 1 1999	-	207	5610

Table 4.2. Occurrence density (density in areas in which species occurs) (plants/m²) of wild oat (WO), green foxtail (GF), and barnyardgrass (BY) for site 1 in 1998 and 1999

Species and site year	Occurrence density
WO 1998 site 1	157
WO 1999 site 1	86
GF 1998 site 1	120
GF 1999 site 1	203
BY 1998 site 1	249
BY 1999 site 1	1043

Table 4.3. Mean, minimum, and maximum soil water content measured gravimetrically (v/v) on April 30, 1999 at site 1 (100 samples taken)

Mean	10.5
Minimum	0.15
Maximum	26.2

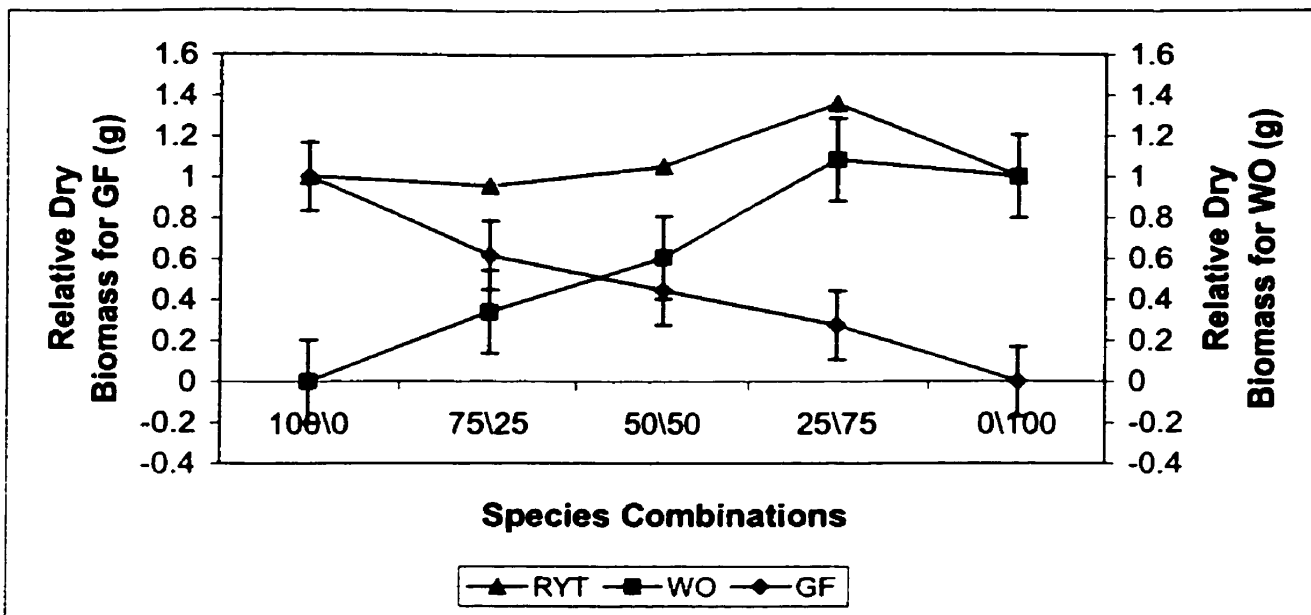


Figure 4.1. Results of replacement series experiment for green foxtail and wild oat showing relative dry biomass of green foxtail (GF) and wild oat (WO) and relative yield total (RYT). Experiment conducted at low total density (708 plants/m²), and plants harvested at early seedling stage. (4th leaf of wild oat).

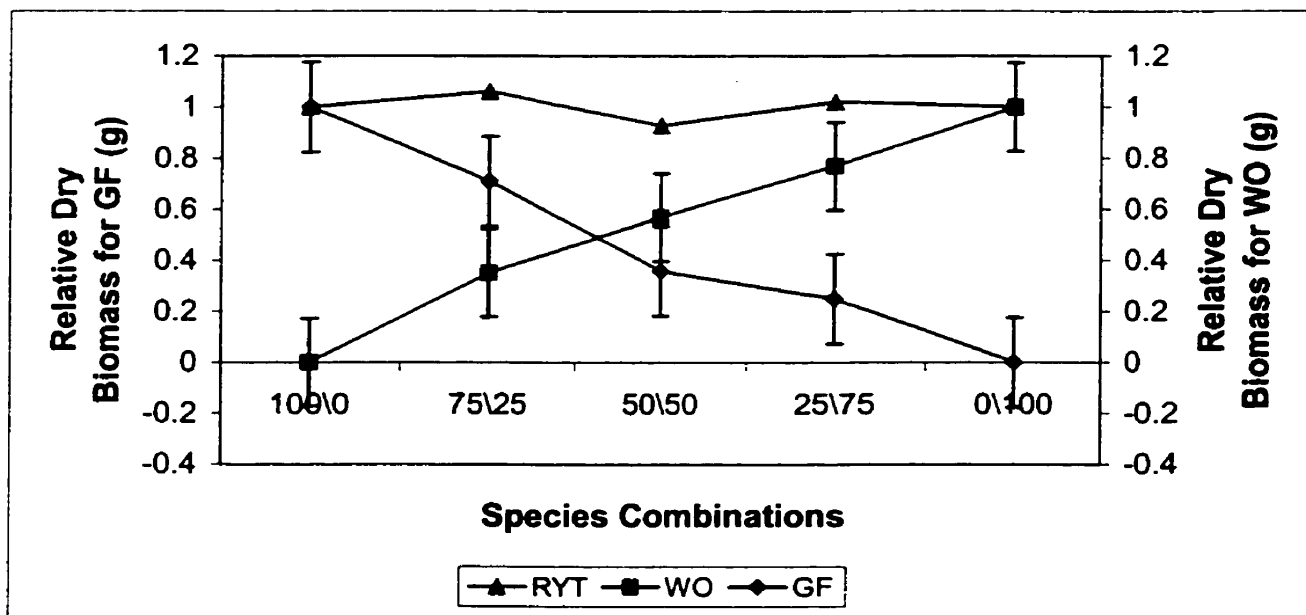


Figure 4.2. Results of replacement series experiment for green foxtail and wild oat showing relative dry biomass of green foxtail (GF) and wild oat (WO) and relative yield total (RYT). Experiment conducted at high total density (1416 plants/ m²), and plants harvested at early seedling stage. (4th leaf of wild oat).

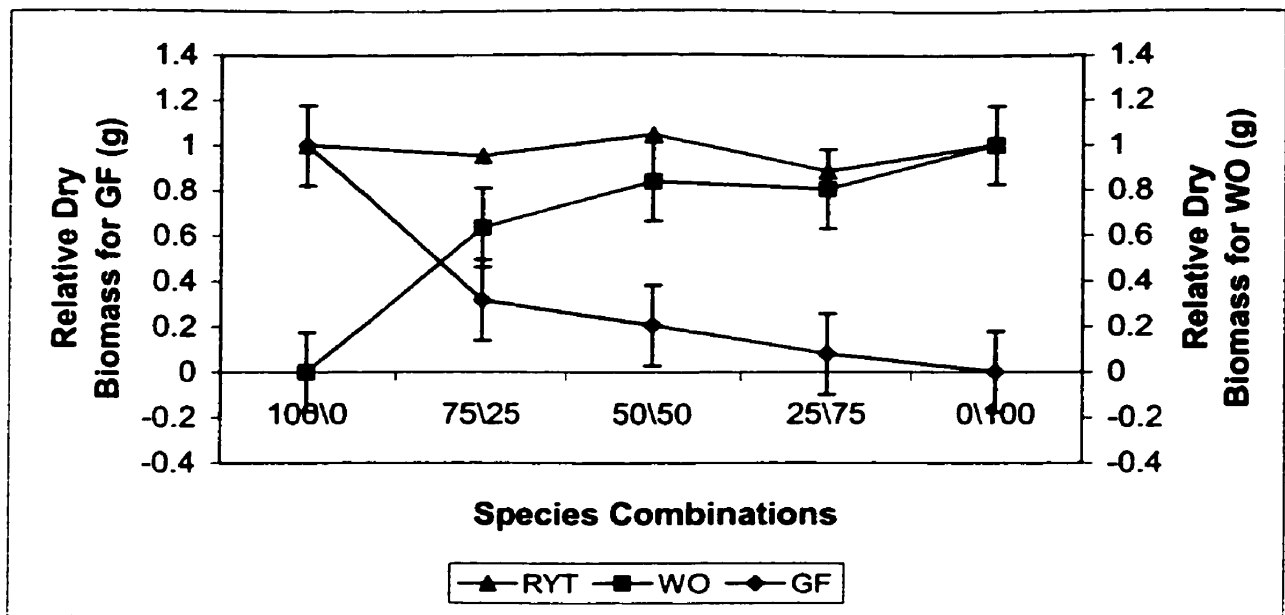


Figure 4.3. Results of replacement series experiment for green foxtail and wild oat showing relative dry biomass of green foxtail (GF) and wild oat (WO) and relative yield total (RYT). Experiment conducted at low total density (708 plants/ m²), and plants harvested at early reproductive stage.

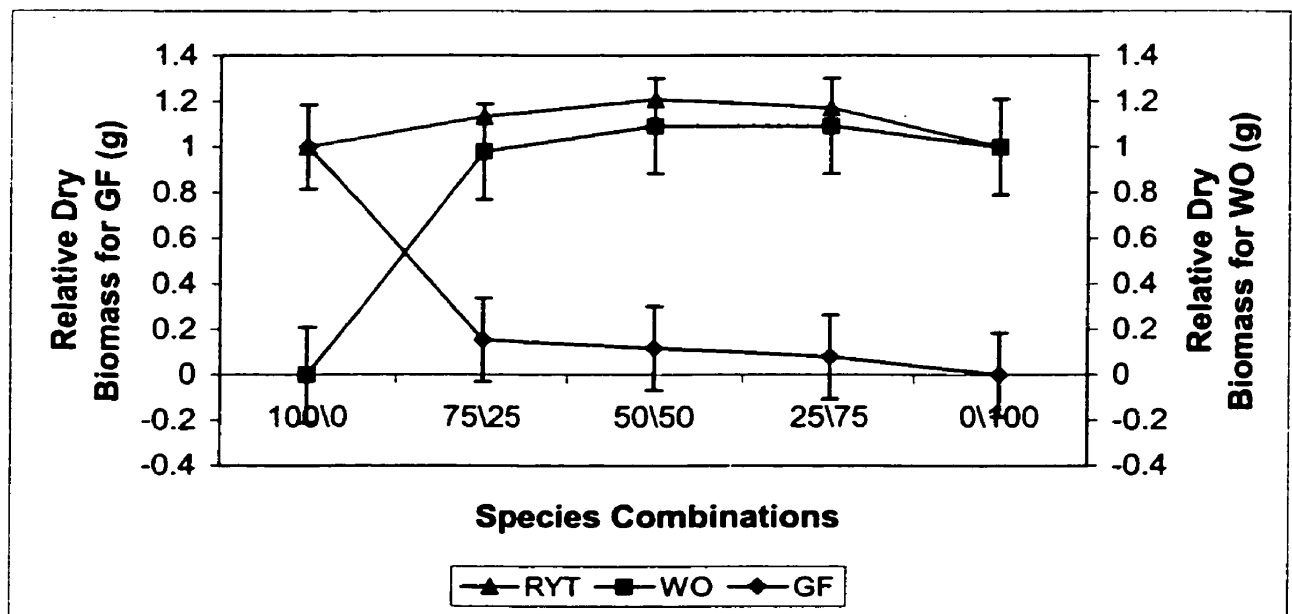


Figure 4.4. Results of replacement series experiment for green foxtail and wild oat showing relative dry biomass of green foxtail (GF) and wild oat (WO) and relative yield total (RYT). Experiment conducted at high total density (1416 plants/ m²), and plants harvested at early reproductive stage.

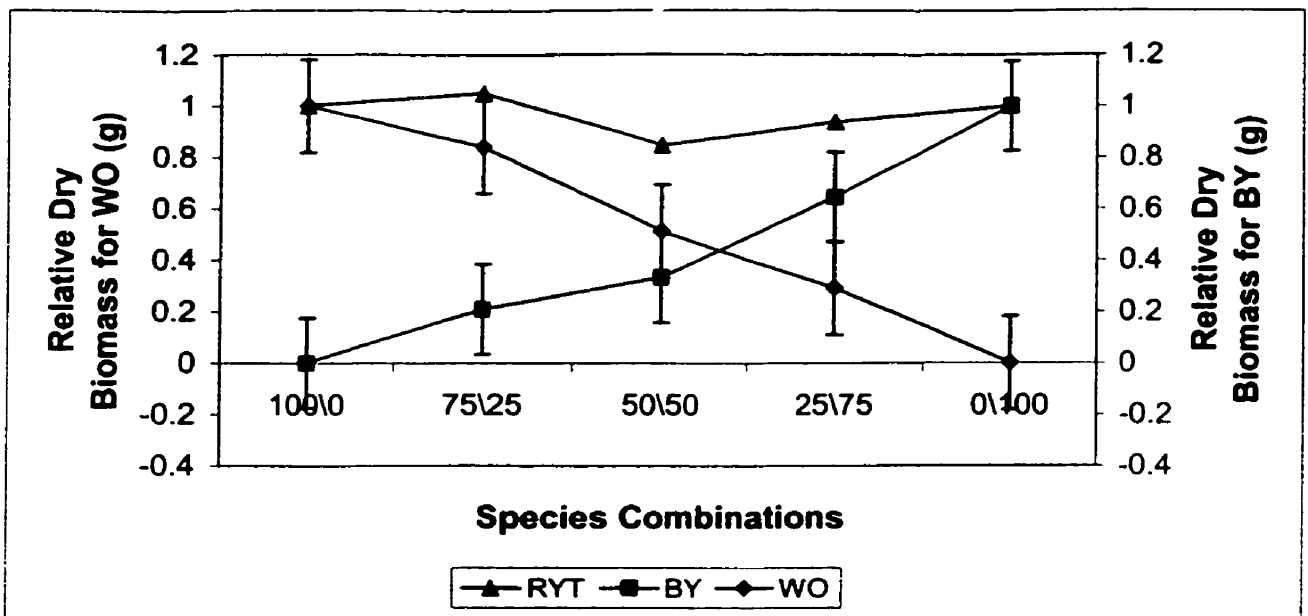


Figure 4.5. Results of replacement series experiment for wild oat and barnyardgrass showing relative dry biomass of wild oat (WO) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at low total density (708 plants/ m²), and plants harvested at early seedling stage. (4th leaf of wild oat).

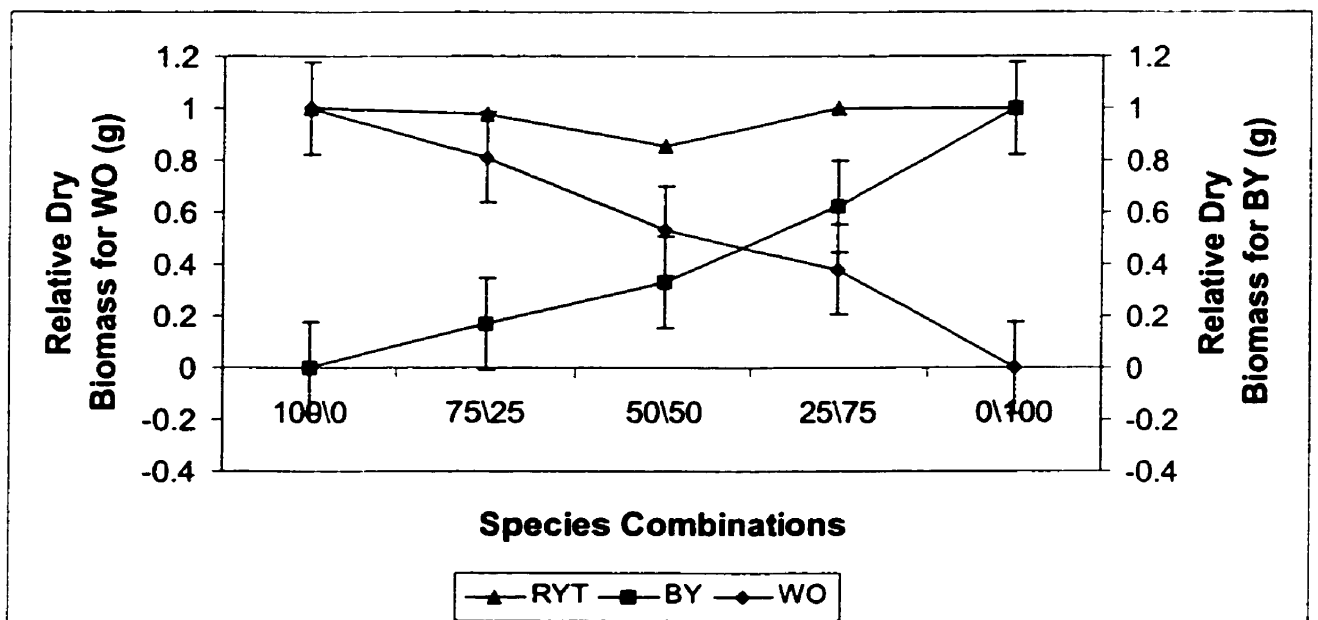


Figure 4.6. Results of replacement series experiment for wild oat and barnyardgrass showing relative dry biomass of wild oat (WO) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at high total density (1416 plants/ m²), and plants harvested at early seedling stage. (4th leaf of wild oat).

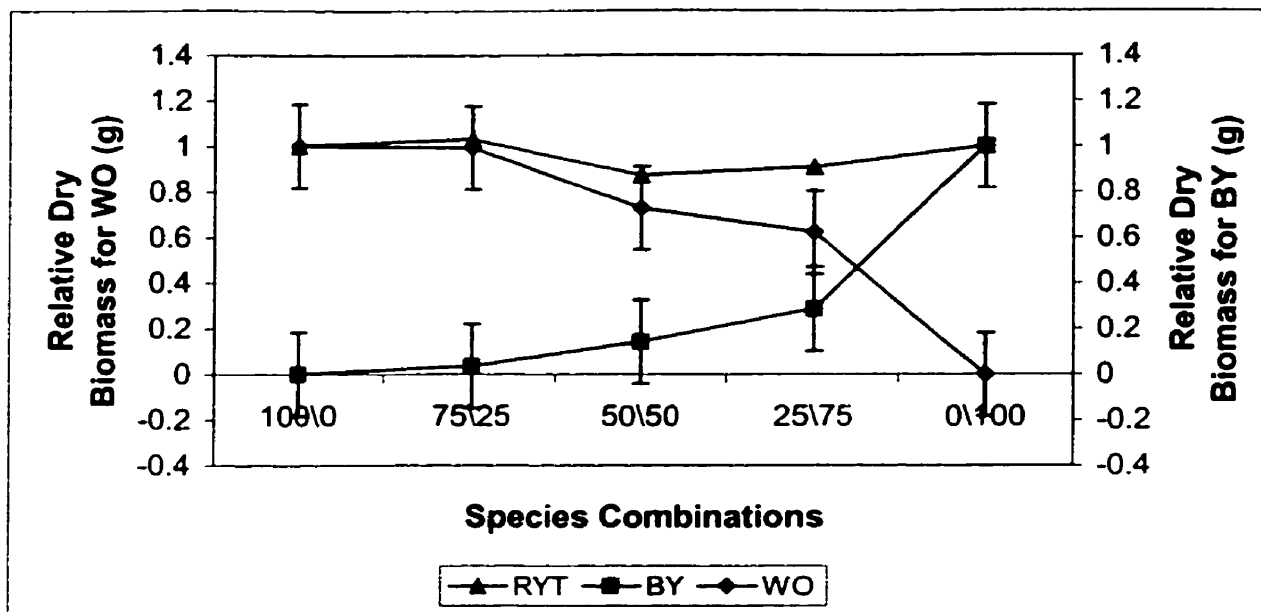


Figure 4.7. Results of replacement series experiment for wild oat and barnyardgrass showing relative dry biomass of wild oat (WO) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at low total density (708 plants/ m²), and plants harvested at early reproductive stage.

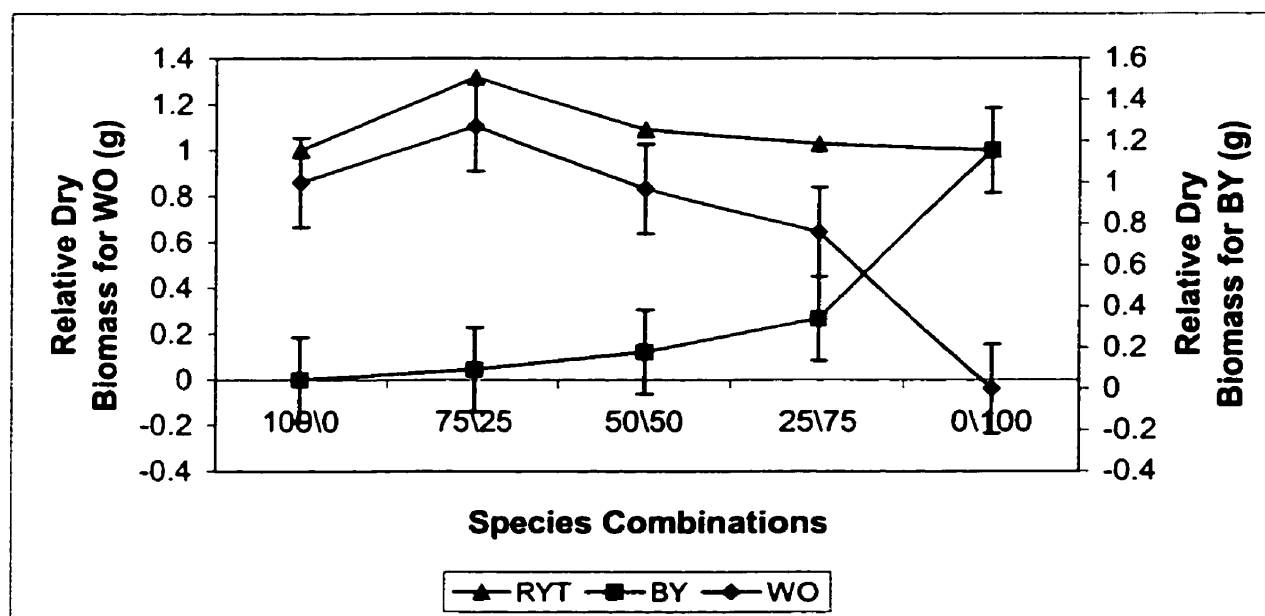


Figure 4.8. Results of replacement series experiment for wild oat and barnyardgrass showing relative dry biomass of wild oat (WO) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at high total density (1416 plants/ m²), and plants harvested at early reproductive stage.

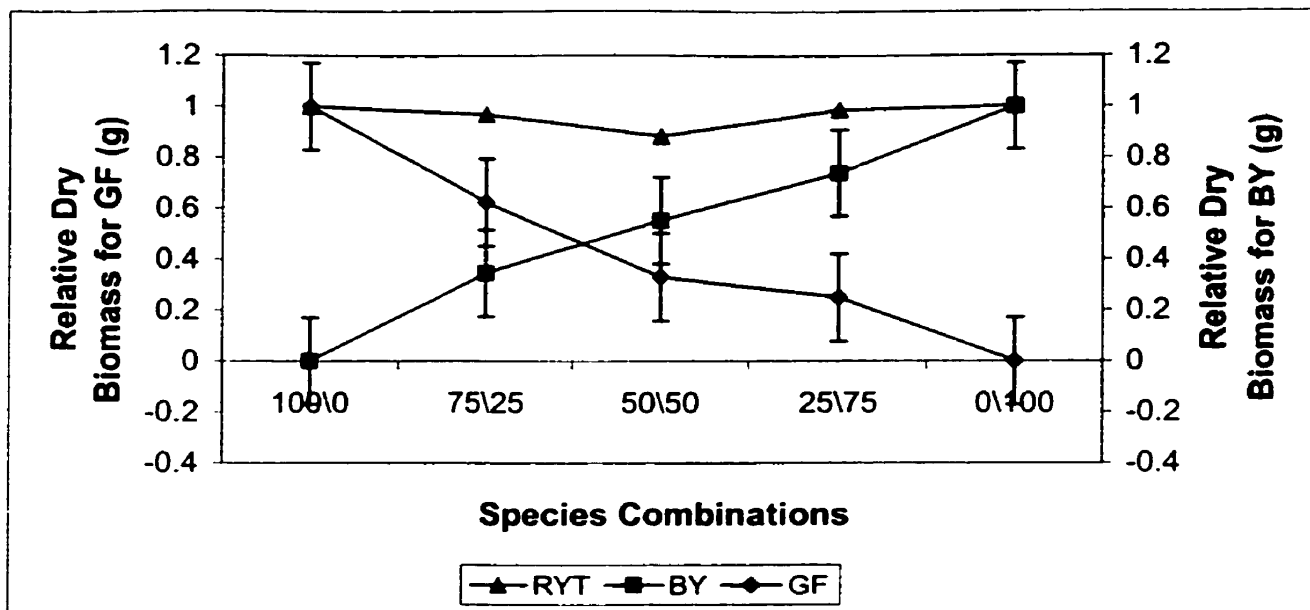


Figure 4.9. Results of replacement series experiment for green foxtail and barnyardgrass showing relative dry biomass of green foxtail (GF) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at low total density (708 plants/ m²), and plants harvested at early seedling stage. (4th leaf of wild oat).

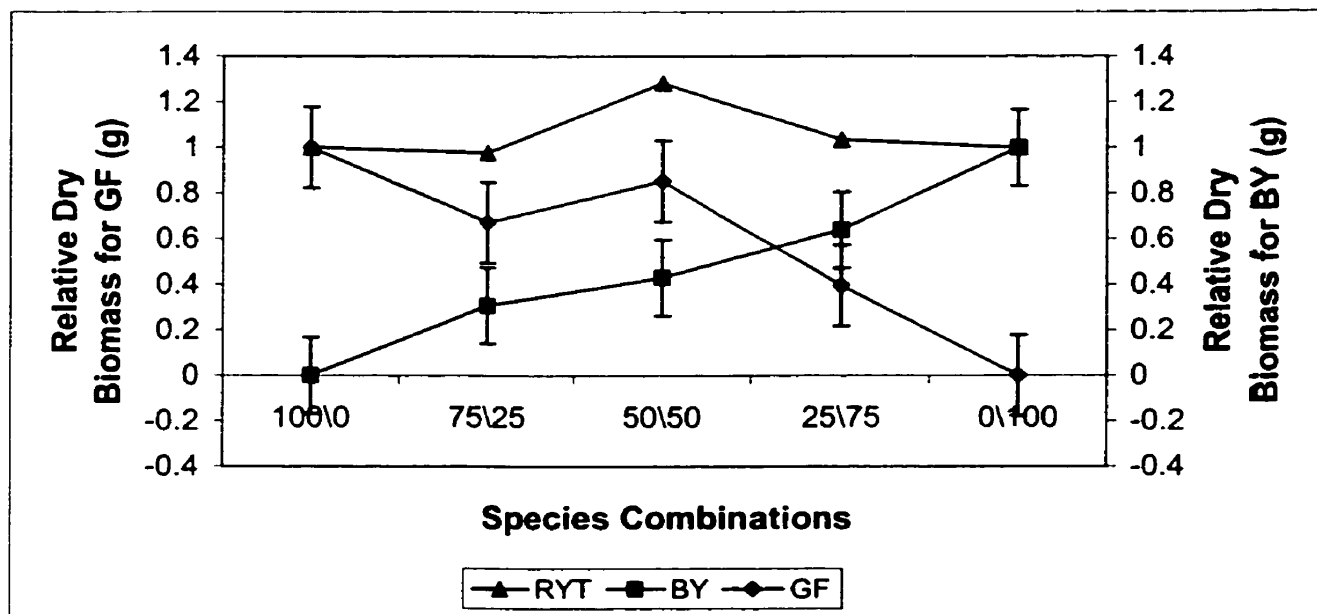


Figure 4.10. Results of replacement series experiment for green foxtail and barnyardgrass showing relative dry biomass of green foxtail (GF) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at high total density (1416 plants/ m²), and plants harvested at early seedling stage. (4th leaf of wild oat).

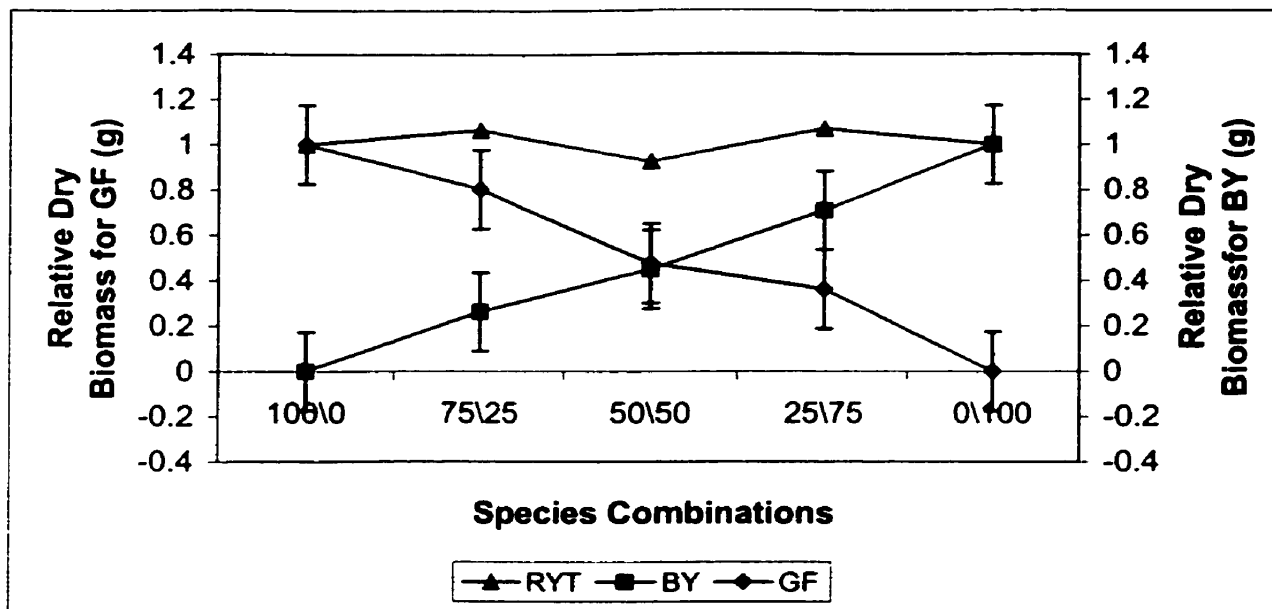


Figure 4.11. Results of replacement series experiment for green foxtail and barnyardgrass showing relative dry biomass of green foxtail (GF) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at low total density (708 plants/ m²), and plants harvested at early reproductive stage.

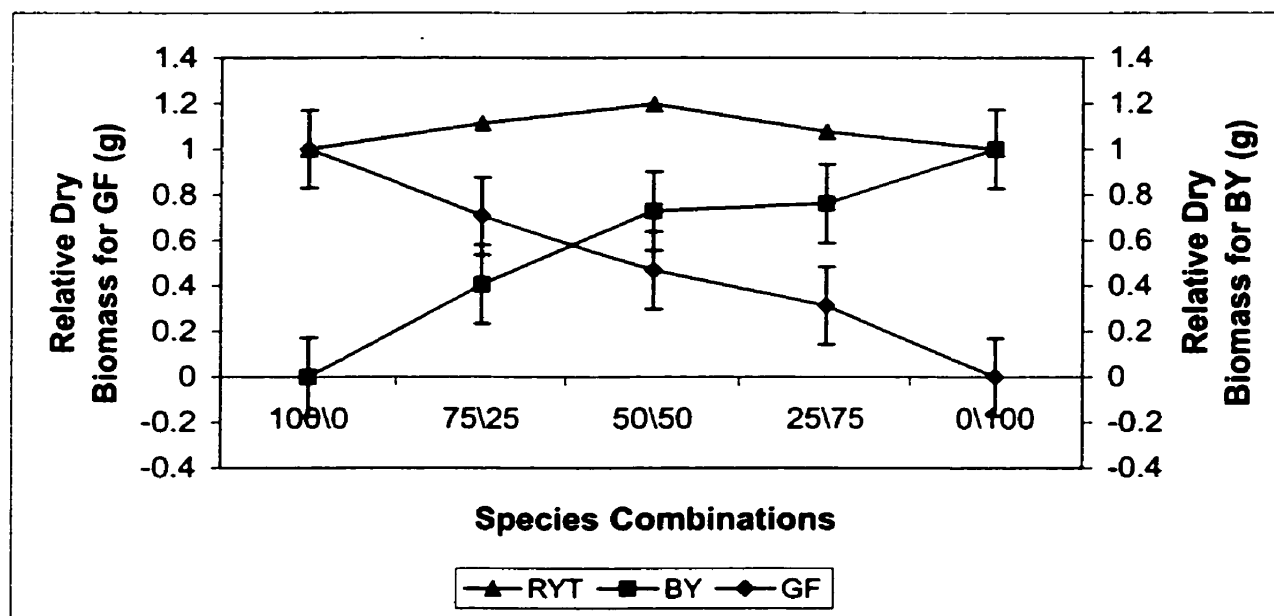


Figure 4.12. Results of replacement series experiment for green foxtail and barnyardgrass showing relative dry biomass of green foxtail (GF) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at high total density (1416 plants/ m²), and plants harvested at early reproductive stage.

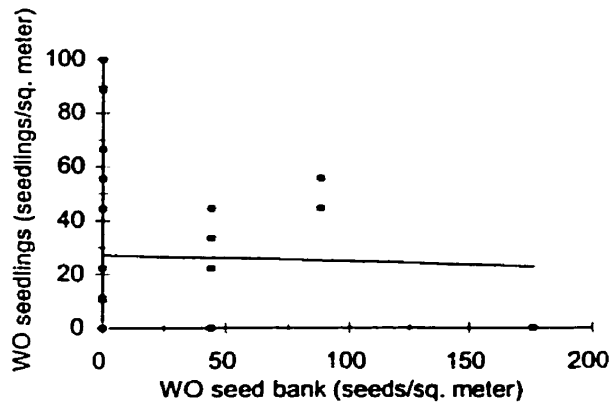


Figure 4.13. Relation of measured density of wild oat (WO) seeds in seed bank to density of wild oat (WO) seedlings (site 1, 1999 seed bank density taken in spring of 1999 prior to seeding of crop, and seedling densities taken in spring 1999 after seeding of crop). Wild oat seedling density = -0.024 (wild oat seed bank density) + 27.12 , $R^2 = 0.0011$.

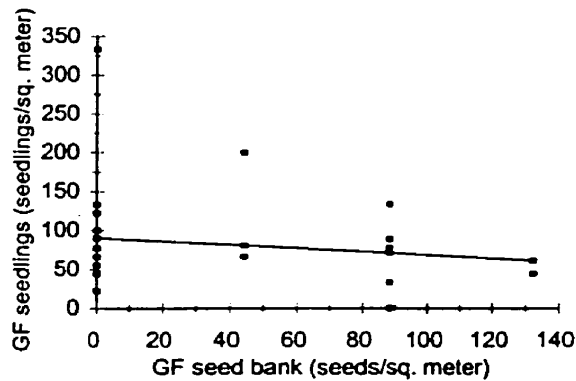


Figure 4.14. Relation of measured density of green foxtail (GF) seeds in seed bank to density of green foxtail (GF) seedlings (site 1, 1999 seed bank density taken in spring of 1999 prior to seeding of crop, and seedling densities taken in spring 1999 after seeding of crop). Green foxtail seedling density = -0.22 (green foxtail seed bank density) + 90.48 , $R^2 = 0.021$.

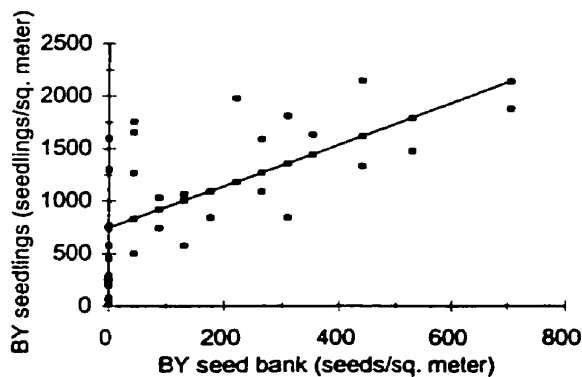


Figure 4.15. Relation of measured density of barnyard grass (BY) seeds in seed bank to density of barnyard grass (BY) seedlings (site 1, 1999 seed bank density taken in spring of 1999 prior to seeding of crop, and seedling densities taken in spring 1999 after seeding of crop). Barnyard grass seedling density = 1.98 (barnyard grass seed bank density) + 744.83 , $R^2 = 0.38$.

5.0 General Discussion

In this study, site 1 was surveyed and species associations were determined for two consecutive years. Studying this site over a longer period would provide greater insight into the stability of species associations. For example, will green foxtail and barnyardgrass still maintain a positive association with one another, even after 10 years? Several years of intensive surveying may be necessary to understand the long-term stability of species associations within weed patches.

Studying other sites, which contain wild oat, green foxtail, and barnyardgrass, would provide further confirmation of the associations determined for each species combination in this experiment. At site 1 from 1998 to 1999 green foxtail and wild oat changed from significantly associated to non significantly associated (table 3.10). In addition, from 1998 to 1999 wild oat and barnyardgrass changed from negatively associated to positively associated (table 3.10). Determining the level of significance and positive or negative association values of weed species from other locations, would allow one to understand if the values remained the same over a range of locations. This may have important implications for weed patch dynamics models and yield loss prediction models.

Understanding the association of weed species will provide important information for patch dynamics models. Association values may be indicative of the stability of patches over time. For example positively or negatively associated species may exist in relatively stable species associations. However,

a change from negative to positive association may result in a relatively unstable species association. Researchers creating patch dynamics models may want to consider the association values of weed species combinations as an important parameter.

In addition, quantifying the association of weed species may provide valuable insight for further development of yield loss prediction models. Stable positive or negative association values may lead to additive interference from multiple weed species infestations. However, changes in species associations from negative to positive may lead to non-additive yield loss. Investigating the mechanisms which affect association changes will be a challenging, but important contribution to weed science.

There are relatively few other studies which address the quantification of multiple weed species associations. Studying sites containing other associations of multiple weed species would serve to expand the breadth of knowledge concerning multiple weed species. Including other commonly occurring weed species from across the Canadian prairies in such studies would provide a significant contribution to weed association knowledge.

Establishing artificial weed populations in arable fields may also provide important insight for weed species associations. For example establishing quadrats with individual, or combinations of species, would allow the study of how species associations change relative to the original infestation. Determining the species associations within these quadrats after 1, 5, and 10 years would provide valuable information on how particular species associations change over

time. For example, would patches seeded to both green foxtail and barnyardgrass maintain a positive association even after 10 years, or would a negative association develop?

Experiments which are used to assess the effects of seasonal environmental variation on species dominance would provide valuable ecological data. Within this project, questions arose as to the level of influence the late seeding of 1999 compared to 1998 had on weed species associations. For example cool season species such as wild oat, may increase in presence under cool, early seeding conditions. In contrast, warm season species such as green foxtail and barnyardgrass may increase in presence under relatively warm, late seeding conditions. The level of influence of environmental conditions on species associations may be an important parameter in models of weed interactions.

Future studies into multiple weed species interactions may also include the effects of differential herbicide control on weed species associations. Differential herbicide control may cause association patterns to evolve. For example Accord (quinclorac) provides control of green foxtail and barnyardgrass, but no control of wild oats (Anonymous 2000). Seedlings of wild oat which survived herbicide application would have a distinct advantage over the other species present. These survivors may produce seed which would further shift the community composition of an area towards a particular species. In effect, seedling escapes might produce seed which would further fortify the areas in which the weed species had originally existed. The seed production from

seedling escapes may also increase the ability of these species to invade adjacent areas, effectively enlarging a patch area. Understanding the implications of these effects may lead to important insights into how agronomic decisions affect weed species associations, and weed patch movement.

The scale of experiments is often affected by the desired end result, and the logistical capabilities to complete these goals. Few experiments have been conducted in which the association of multiple weed species has been quantified, and those experiments that exist often used relatively small quadrates and sampled large-scale areas. This experiment focused on the survey of two 10 m x 10 m sites, at the scale of 10 cm x 10 cm, which balanced the area covered with logistical feasibility of completing the survey. It is important to examine weed species over a reasonably large area, and at a relatively fine scale, to gain an appropriate understanding of the spatial associations of multiple weed species. Future experiments in which weed species associations are examined, should focus on sampling areas relatively larger than performed in the past, and at relatively fine scales.

Studying fluctuations in species occupation of cells in the 10 m x 10 m site 1 from 1998 to 1999, may reveal important species association information. In site 1, from 1998 to 1999, for example, wild oat and green foxtail and wild oat and barnyardgrass combinations had a greater change in cells individually occupied by each species, than in cells mutually occupied or mutually unoccupied (tables 3.1-3.4). In contrast, from 1998 to 1999 green foxtail and barnyardgrass had a greater change in cells mutually occupied and mutually

unoccupied, than in cells individually occupied (tables 3.5-3.6). An interesting spatial consideration might be how many of the same cells at site 1 in 1999, contained the same species as in 1998. The fluctuation of species in cells between years may be another measure of species spatial stability. If no species for example consistently occupy any particular cells, then this may suggest that the interactions among these species is driven more by dispersal and micro site availability, than active competition mechanisms such as allelopathy. In addition, improving the understanding of the spatial stability of weed species will increase the knowledge of patch stability, which will facilitate site-specific weed management.

The frequency table for wild oat and barnyardgrass showed that, as the number of barnyardgrass per 10 cm x 10 cm cell increased, the number of wild oat per cell decreased (Appendix 1.1). As the number of barnyardgrass per cell increased from 0-12, the number of cells containing 1 wild oat per cell decreased from 644 to 0. From this data, hyperbolic curves could be produced showing that a high number of barnyardgrass per cell would coincide with a low number of wild oat per cell. These curves would have asymptotes. The asymptotes of the curves would indicate the density at which exclusion occurred between species, possibly due to competition or seed inundation.

The quantification of weed populations, and the resulting hyperbolic curves may provide a new method for in situ weed-weed interaction experiments. This could provide data from realistic field situations, allowing future ecological weed science experiments to partially move away from manipulated competition

experiments.

The results of the project, in general, suggest that for these species, dispersal was the overriding mechanism that determined association and species presence or absence in a cell. Whether this is true for weed species in general is not known, but it may be that for annual species in agricultural habitats, where the environment is relatively homogeneous and favorable for growth (high nutrient levels and good soil tilth), it is likely seed limitation and not micro site limitation that determines species associations.

The characterization of multiple weed species infestations provides a more realistic analysis of weed infestations than single species studies. Currently there is limited information available on the associations of multiple weed species infestations. Improving the understanding of multiple weed species infestations will allow researchers to use parameters based on more realistic situations for modeling both weed interactions, and the effects of weed interactions on crops. In the future, experiments, which address multiple weed species, will provide valuable contributions to understanding both weed communities, and their effects on crops.

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Appendix 1.1. Number of 10 cm x 10 cm cells within 10 m x 10 m site 1 in 1998 that contain wild oat and barnyardgrass at given densities

Species Densities Plants/10 cm ²		Barnyard grass												
		0	1	2	3	4	5	6	7	8	9	10	11	12
Wild oat	0	1255	1408	1316	1037	616	391	208	93	43	16	5	2	2
	1	711	644	434	223	104	40	19	9	1	2	1	0	0
	2	442	267	138	48	11	4	1	0	0	0	0	0	0
	3	234	98	41	15	1	2	0	0	0	0	0	0	0
	4	73	20	5	2	0	0	0	0	0	0	0	0	0
	5	15	1	0	0	0	0	0	0	0	0	0	0	0
	6	1	0	0	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0	0	0	0	0
	8	1	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2.1. Results of replacement series experiment for green foxtail and wild oat showing relative dry biomass of green foxtail (GF) and wild oat (WO) and relative yield total (RYT). Experiment conducted at low total density (708 plants/m²), and plants harvested at early seedling stage. (4th leaf of wild oat).

Density	Green foxtail	Wild oat	Relative yield total
100/0	1.0000	0.0000	1.0000
75/25	0.6160	0.3392	0.9552
50/50	0.4451	0.6073	1.0524
25/75	0.2739	1.0821	1.3560
0/100	0.0000	1.0000	1.0000

Appendix 2.2. Results of replacement series experiment for green foxtail and wild oat showing relative dry biomass of green foxtail (GF) and wild oat (WO) and relative yield total (RYT). Experiment conducted at high total density (1416 plants/ m²), and plants harvested at early seedling stage. (4th leaf of wild oat).

Density	Green foxtail	Wild oat	Wild oat and green foxtail
100/0	1.0000	0.0000	1.0000
75/25	0.7095	0.3511	1.0606
50/50	0.3582	0.5697	0.9279
25/75	0.2503	0.7695	1.0198
0/100	0.0000	1.0000	1.0000

Appendix 2.3. Results of replacement series experiment for green foxtail and wild oat showing relative dry biomass of green foxtail (GF) and wild oat (WO) and relative yield total (RYT). Experiment conducted at low total density (708 plants/ m²), and plants harvested at early reproductive stage.

Density	Green foxtail	Wild oat	Wild oat and green foxtail
100/0	1.0000	0.0000	1.0000
75/25	0.3153	0.6351	0.9504
50/50	0.2060	0.8404	1.0464
25/75	0.0793	0.8075	0.8868
0/100	0.0000	1.0000	1.0000

Appendix 2.4. Results of replacement series experiment for green foxtail and wild oat showing relative dry biomass of green foxtail (GF) and wild oat (WO) and relative yield total (RYT). Experiment conducted at high total density (1416 plants/ m²), and plants harvested at early reproductive stage.

Density	Green foxtail	Wild oat	Wild oat and green foxtail
100/0	1.0000	0.0000	1.0000
75/25	0.1533	0.9793	1.1326
50/50	0.1158	1.0924	1.2082
25/75	0.0788	1.0924	1.1712
0/100	0.0000	1.0000	1.0000

Appendix 2.5. Results of replacement series experiment for wild oat and barnyardgrass showing relative dry biomass of wild oat (WO) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at low total density (708 plants/ m²), and plants harvested at early seedling stage. (4th leaf of wild oat).

Density	Wild oat	Barnyardgrass	Wild oat and barnyardgrass
100/0	1.0000	0.0000	1.0000
75/25	0.8401	0.2090	1.0491
50/50	0.5120	0.3334	0.8454
25/75	0.2920	0.6464	0.9384
0/100	0.0000	1.0000	1.0000

Appendix 2.6. Results of replacement series experiment for wild oat and barnyardgrass showing relative dry biomass of wild oat (WO) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at high total density (1416 plants/ m²), and plants harvested at early seedling stage. (4th leaf of wild oat).

Density	Wild oat	Barnyardgrass	Wild oat and barnyardgrass
100/0	1.0000	0.0000	1.0000
75/25	0.8085	0.1715	0.9800
50/50	0.5281	0.3277	0.8558
25/75	0.3788	0.6224	1.0012
0/100	0.0000	1.0000	1.0000

Appendix 2.7. Results of replacement series experiment for wild oat and barnyardgrass showing relative dry biomass of wild oat (WO) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at low total density (708 plants/ m²), and plants harvested at early reproductive stage.

Density	Wild oat	Barnyardgrass	Wild oat and barnyardgrass
100/0	1.0000	0.0000	1.0000
75/25	0.9932	0.0359	1.0291
50/50	0.7287	0.1432	0.8719
25/75	0.6212	0.2864	0.9076
0/100	0.0000	1.0000	1.0000

Appendix 2.8. Results of replacement series experiment for wild oat and barnyardgrass showing relative dry biomass of wild oat (WO) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at high total density (1416 plants/ m²), and plants harvested at early reproductive stage.

Density	Wild oat	Barnyardgrass	Wild oat and barnyardgrass
100/0	1.0000	0.0000	1.0000
75/25	1.2723	0.0441	1.3164
50/50	0.9689	0.1205	1.0894
25/75	0.7607	0.2671	1.0278
0/100	0.0000	1.0000	1.0000

Appendix 2.9. Results of replacement series experiment for green foxtail and barnyardgrass showing relative dry biomass of green foxtail (GF) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at low total density (708 plants/ m²), and plants harvested at early seedling stage. (4th leaf of wild oat).

Density	Green foxtail	Barnyardgrass	Green foxtail and barnyardgrass
100/0	1.0000	0.0000	1.0000
75/25	0.6225	0.3450	0.9675
50/50	0.3295	0.5515	0.8810
25/75	0.2485	0.7377	0.9862
0/100	0.0000	1.0000	1.0000

Appendix 2.10. Results of replacement series experiment for green foxtail and barnyardgrass showing relative dry biomass of green foxtail (GF) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at high total density (1416 plants/ m²), and plants harvested at early seedling stage. (4th leaf of wild oat).

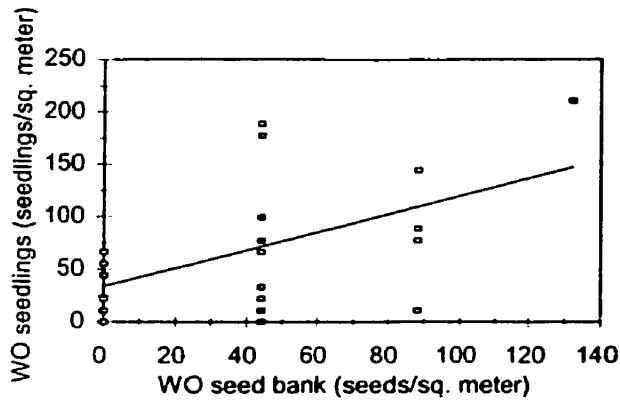
Density	Green foxtail	Barnyardgrass	Green foxtail and barnyardgrass
100/0	1.0000	0.0000	1.0000
75/25	0.6705	0.3062	0.9767
50/50	0.8534	0.4298	1.2832
25/75	0.3951	0.6391	1.0342
0/100	0.0000	1.0000	1.0000

Appendix 2.11. Results of replacement series experiment for green foxtail and barnyardgrass showing relative dry biomass of green foxtail (GF) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at low total density (708 plants/ m²), and plants harvested at early reproductive stage.

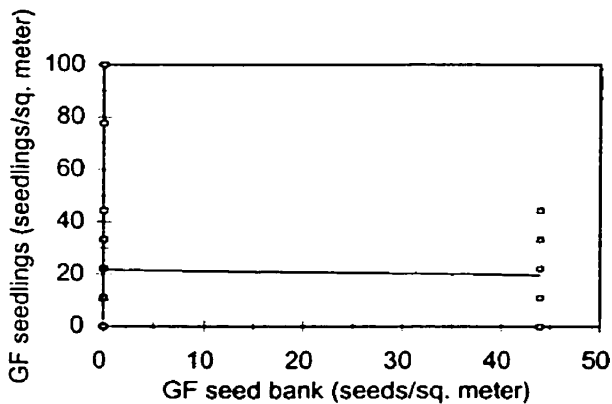
Density	Green foxtail	Barnyardgrass	Green foxtail and barnyardgrass
100/0	1.0000	0.0000	1.0000
75/25	0.8019	0.2615	1.0634
50/50	0.4756	0.4489	0.9245
25/75	0.3605	0.7078	1.0683
0/100	0.0000	1.0000	1.0000

Appendix 2.12. Results of replacement series experiment for green foxtail and barnyardgrass showing relative dry biomass of green foxtail (GF) and barnyardgrass (BY) and relative yield total (RYT). Experiment conducted at high total density (1416 plants/ m²), and plants harvested at early reproductive stage.

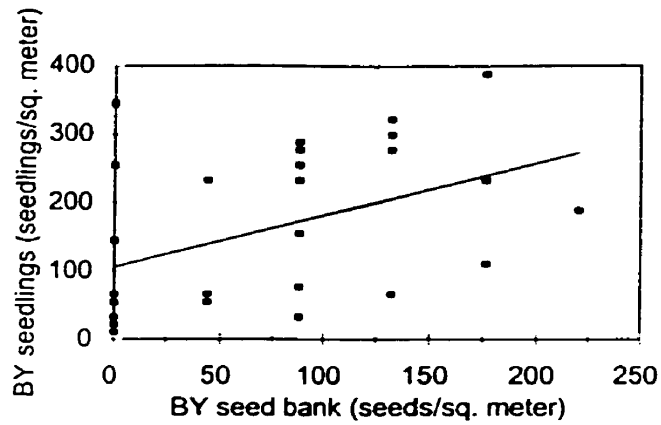
Density	Green foxtail	Barnyardgrass	Green foxtail and barnyardgrass
100/0	1.0000	0.0000	1.0000
75/25	0.7065	0.4068	1.1133
50/50	0.4687	0.7284	1.1971
25/75	0.3131	0.7616	1.0747
0/100	0.0000	1.0000	1.0000



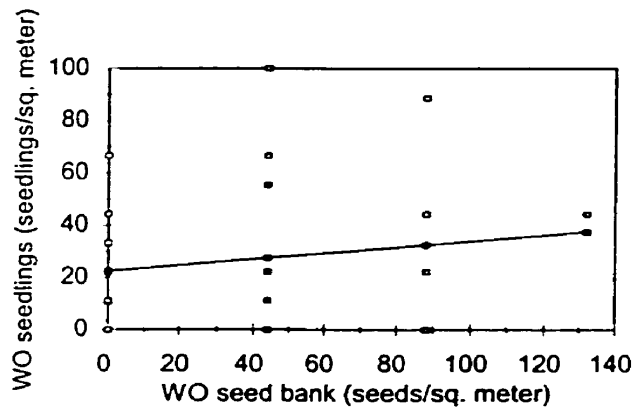
Appendix 3.1. Relation of measured density of wild oat (WO) seeds in seed bank to density of wild oat (WO) seedlings (site 1, 1998 seed bank density taken in fall of 1998 prior to harvest of crop, and seedling densities taken in spring 1998 after seeding of crop). Wild oat seedling density = 0.85 (wild oat seed bank density) + 34.01 , $R^2 = 0.33$.



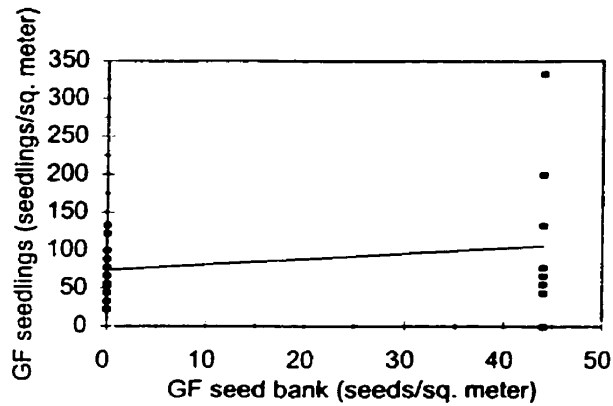
Appendix 3.2. Relation of measured density of green foxtail (GF) seeds in seed bank to density of green foxtail (GF) seedlings (site 1, 1998 seed bank density taken in fall of 1998 prior to harvest of crop, and seedling densities taken in spring 1998 after seeding of crop). Green foxtail seedling density = -0.044 (green foxtail seed bank density) + 21.69 , $R^2 = 0.0015$.



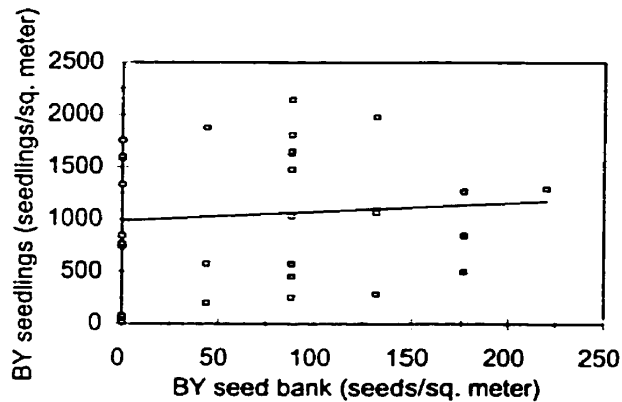
Appendix 3.3. Relation of measured density of barnyardgrass (BY) seeds in seed bank to density of barnyardgrass (BY) seedlings (site 1, 1998 seed bank density taken in fall of 1998 prior to harvest of crop, and seedling densities taken in spring 1998 after seeding of crop). Barnyardgrass seedling density = 0.76 (barnyardgrass seed bank density) + 106.39 , $R^2 = 0.194$.



Appendix 3.4. Relation of measured density of wild oat (WO) seeds in seed bank to density of wild oat (WO) seedlings (site 1, 1998 seed bank density taken in fall of 1998 prior to harvest of crop, and seedling densities taken in spring 1999 after seeding of crop). Wild oat seedling density = 0.11 (wild oat seed bank density) + 22.49 , $R^2 = 0.023$.



Appendix 3.5. Relation of measured density of green foxtail (GF) seeds in seed bank to density of green foxtail (GF) seedlings (site 1, 1998 seed bank density taken in fall of 1998 prior to harvest of crop, and seedling densities taken in spring 1999 after seeding of crop). Green foxtail seedling density = 0.71 (green foxtail seed bank density) + 74.60 , $R^2 = 0.058$.



Appendix 3.6. Relation of measured density of barnyardgrass (BY) seeds in seed bank to density of barnyardgrass (BY) seedlings (site 1, 1998 seed bank density taken in fall of 1998 prior to harvest of crop, and seedling densities taken in spring 1999 after seeding of crop). Barnyardgrass seedling density = 0.86 (barnyardgrass seed bank density) + 987.56 , $R^2 = 0.0084$.