THE EFFECT OF CHAFF COLLECTION ON THE COMBINE HARVESTER DISPERSAL OF WILD OAT (*Avena fatua* L.)

BY
STEVEN J. SHIRTLIFFE

A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfilment of the Requirements
of the Degree of

DOCTORATE OF PHILOSOPHY

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Abstract

The effect of chaff collection on the combine harvester dispersal of wild oat (*Avena fatua* L.)

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With herbicide resistant wild oat increasing in frequency, new weed management techniques must be explored which modify ecological processes to manage weed populations. The first objective of this research was to determine if chaff collection will reduce the dispersal of wild oat. Seed shed from wild oat was measured and the effect of chaff collection and seed shed was determined using a computer simulation model. Chaff collection results in a significant reduction in the dispersal distance of weed seeds by combine harvesters. Without chaff collection, combine harvesters can disperse wild oat seeds approximately 150 m. However, with chaff collection the dispersal is reduced to approximately 30 m. Wild oat and wheat display similar phenotypic development. The phyllochron interval is similar within locations. Plant development as measured by Zadoks plant development scale was different between wild oat and wheat but this difference was constant between years and locations. Seed shed occurs in wild oat during the ripening process of wheat. In an early harvest of wheat most of the weed seeds would still remain on the plant. A computer simulation model of harvest dispersal revealed that timing of harvest is the most important variable in wild oat patch expansion. A delayed harvest would occur when most of the weed seeds have been shed by the plant. Chaff collection and delayed harvest result in the least amount of wild oat patch expansion as determined through computer simulations. By delaying harvest most of the wild oat seeds

would fall to the ground in the original patch and would not be available to be taken into the combine and dispersed. An early harvest which attempts to maximize harvest export of wild oat seed is the most best strategy to manage a spatially uniform wild oat wild distribution. The second objective was to determine if a wild oat patch displays fractal geometry. A portion of a wild oat patch was determined to be highly fractal. This supports a fractal theory of dispersal which explains how a weed can be both highly dispersed and patchy.

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As part of my Doctoral thesis I attended classes and learned computer simulation modelling at the Montana State University in Dr. Bruce Maxwell's lab. Throughout this thesis Bruce has been an unofficial committee member. I wish to thank Bruce and his lab gang that were there in the winter of 95/96; Corey Colliver, Rob Davidson, Monica Brelsford, and Stephan Canner. My stay down at Bozeman, Montana was one of the most productive times in my life.

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Finally to my Dad and Mom, Jim and Janice Shirtliffe, Thanks for having the understanding to allow an old farm boy to pursue his goals.

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1.0 Introduction

The introduction of herbicides revolutionized weed control. The development of 2,4-D in 1942-1944 began the "Chemical Era of Agriculture" (Timmons, 1969). This "golden age" of weed control was short lived as herbicides have failed to control many weed problems. Since the first observation of herbicide resistant weeds in 1968 (Ryan, 1970), herbicide resistance has spread rapidly (Moss and Rubin, 1993). This had led to an interest in reduced reliance on herbicides and has launched research on alternatives to chemical weed control.

The change in focus away from herbicide-based research in weed science has resulted in the formation of the discipline of weed ecology. In weed ecology, one studies the biology and ecology of the weed-crop system, observing processes, and searching for ways to modify these processes in order to facilitate weed control. It was within this paradigm that this thesis was conducted.

Weeds often exist in patches. The observation that small patches of herbicide resistant weeds can be quickly spread by combine harvesters in a field suggested that trying to prevent the spread of weed seeds by combines may reduce weed patch expansion. Empirical studies suggested that weed seeds could be dispersed large distances by combines (McCanny and Cavers, 1988).

Although it would be of obvious benefit to farmers to reduce weed seed dispersal, there was no information in the literature on means to curtail combine dispersal of weed seeds. However, a translation of an old German paper reported that most of the weed seeds dispersed by combines were in the chaff portion of the refuse with little in the straw

(Petzold, 1955). At this point it also came to light that there was an unique piece of machinery that seemed to be promising. A chaff collector was being sold for the purpose of collecting chaff to feed to cattle. As the chaff probably contained many weed seeds, it was possible that collecting chaff may reduce weed seed dispersal.

Other questions on the nature of managing harvest dispersal of weeds followed. How far could wild oats be spread by a combine? How large an effect would this have over time? How many weed seeds would be shed at the time of harvest? If combines spread weed seeds a large distance, why are weeds still in patches? These questions formed the basis for this thesis.

The primary objective of this thesis was to quantify the dispersal of wild oat by combine harvesters and to determine if chaff collection reduced wild oat seed dispersal. As part of this objective, the rate of seed shed in wild oat was quantified. This empirical information was incorporated into a computer model which allowed for the movement of wild oat seeds across a field to be predicted. Simulations with this model determined the long term effect of weed seed dispersal and the effect of different management options on weed seed dispersal.

The secondary objective of this thesis was to determine if the spatial pattern exhibited by wild oat plants is fractal. If so, this may provide evidence of a theoretical link between the dispersal of weeds and the resulting fractal patch pattern.

The hypothesis of this dissertation is that limiting the mechanical dispersal of wild oat seeds can reduce the rate of wild oat patch expansion. Reduced mechanical dispersal can be accomplished through the collection of chaff as it is expelled from a combine during the harvest process. This should reduce weed seed return to the field as well as decrease weed seed dispersion. This in turn should result in less land being infested with wild oat, and reduced rates of wild oat patch expansion.

2.0 Literature Review

2.1 Introduction

This chapter is a review of the relevant literature on weed seed dispersal. The review is divided into four sections. As most of the work in this study was conducted on wild oat, a brief review of its biology is presented with a more detailed review on the phenological development and rate of seed shed. In the second section, dispersal of weed seeds is examined with a focus on the mechanical dispersal by combine harvesters. In the third section the use of computer simulation models in simulating weed control strategies and the use of spatially explicit models is reviewed. Ecological theory of fractal spatial patterns of plants, and its possible relationship to dispersal characteristics, is reviewed in the last section.

2.2 Biology of wild oat

Wild oat (*Avena fatua* L.) is the second most common weed in Manitoba as measured by relative abundance (Thomas et al. 1998); it occurs in 65% of all arable fields. Wild oat is a member of the Poaceae (grass) family. In Canada, wild oat has a spring annual life history. It is primarily self-pollinated and reproduces by seed (Sharma and Vanden Born, 1978).

Wild oat seed recently shed from the plant is usually dormant (Banting, 1974). After passing through primary dormancy it may germinate, but if conditions are not suitable it will enter a period of secondary dormancy. Wild oat seed can survive for intermediate lengths of time in the soil. Miller and Nalewaja (1990) placed wild oat seed in mesh bags and found that most seed viability is lost in the first seven months, after which the rate of viability loss remains relatively constant with a small proportion of seeds eventually surviving more than 14 years. Wild oat seed germinates primarily in the spring when soil temperatures are above 4.4 C (Friesen and Shebeski, 1961).

2.2.1 Wild oat Phenology

Phenological studies of weeds have been conducted to characterize the development of wild oat alone and to comparison it to other weed or crop species. Early studies (ie. Dew, 1980) generally related leaf or Haun stage (Haun, 1973) to the calender day. Dew (1980) found that wild oat (*Avena fatua* L.) had a slower rate of leaf appearance than barley (*Hordeum vulgare* L.) and tame oats (*Avena sativa* L) , but a faster rate than spring wheat (*Triticum aestivum* L.).

A more sophisticated approach is to relate the rate of leaf appearance, usually known as the phylochron interval, or Haun stage (Haun, 1973), to thermal time. Thermal time as expressed by growing degree days (GDD), is calculating by subtracting the mean daily temperature from the base temperature and summing the values for each day beginning at seedling emergence. By applying a linear regression to a plot of leaf stage versus GDD, the phylochron interval can be determined. As the concept of growing degree days takes into account differences in environment, phylochron intervals can be compared between locations and years.

Cousens et al. (1992) observed that the rate of leaf appearance in wild oat was similar to winter wheat and slower than barley. However, large differences in phylochron interval occurred between wild oat populations from two locations. The differences were attributed to possible differences in wild oat genotype or environmental variables. Cudney et al. (1989) found that in California wild oat and wheat had similar rates of leaf appearance. There have not been any studies on the Canadian prairies relating the development of wild oat in the field to GDD.

There have not been any studies comparing wild oat and field crop development using Zadoks stage (Zadoks et al. 1974). Such information would be useful to determine the time at which wild oat is ripe and susceptible to shattering.

2.2.2 Seed Shatter

Despite the information available on development of wild oat (including studies on the development of the inflorescence (Raju, 1990; Landes and Porter, 1990)), little information is available on the rate of seed shed in wild oat. Metz (1969) found that at barley harvest, 66% of wild oat seeds had already been shed. Further analysis of the data of Feldman and Reed (1974) indicates that at the first wheat harvest, 50% of seed shed had occurred compared to 70% and 73% at later harvest dates. Wilson (1970) investigated the rate of seed shed in wild oat growing in winter and summer cereals grown in England. In winter wheat 95% of the weed seeds had been shed before harvest compared to 44% in spring barley. This difference occurred even though both crops were harvested at a similar time. A reexamination of Wilson's (1970) experiment indicates that the rate of seed shed in wild oat displays a sigmoidal pattern in which the rate of seed shed begins slowly then progresses rapidly followed by a slow decline. In their experiments, Wilson and Cussans (1975) found that 90% of the wild oat seeds had been shed at the time of barley harvest. Naverette (1984, from Gonzalez-Andujar and Perry, (1995)) found that in Spain, there was greater than 99% seed shed in *Avena sterilis* L. at the time of harvest of winter wheat.

The proportion of seed shed in wild oat at grain crop harvest is not fixed. The rate of seed shed is a continuous function that should be related to the amount of thermal time accumulated between wild oat emergence and crop harvest. As different crops require different times to mature, one would expect different proportions of seed shed in wild oats at harvest time for each crop. Wild oats seedlings often emerge from the soil at a different time than the crop. It would be expected that a late emerging flush of wild oat would have less seed shed at harvest than an earlier emerging flush. Without information on the timing of seed shed it would not be possible to determine the proportion of weed seeds that have not been shed and are available for removal from the field or dispersal in the field. If the seed shed in wild oat were related to thermal time then the proportion of wild oat seed shed at time of harvest in various crops could be predicted.

2.3 Spatial Weed Distribution

Many weeds, including wild oat, have been observed to occur in patches (Colliver et al. 1996; Cardina et al. 1995). The patchy distribution of weeds can be described in many ways, ranging from the relatively simple negative binomial distribution to detailed kriged maps. The negative binomial distribution (Ross and Preece, 1985) has been employed to describe the frequency distribution of several weeds (Colliver and

Maxwell, 1995; Mortensen et al. 1993; Wiles et al. 1992; Marshall, 1988). However, describing a weed distribution with the negative binomial distribution only provides the frequency distribution of the weeds and does not provide any information about the spatial pattern. As a result, a species which fits a negative binominal distribution will usually be patchy but it is not an obligate requirement.

Mapping of weed patches within a field can give a more detailed picture of the distribution of the weeds at different spatial scales. Wilson and Brain (1991) mapped the occurrence of black grass (*Alopecurus myosroides*) in a 10 year single farm study. They observed a high degree of patchiness and noted that the patches were relatively stable over time.

Geostatistic analysis of spatial data is a recent development that have been used to describe the spatial variation of weeds. To produce a contour map of predicted weed densities, the population of the weeds at discrete sample points are kriged. This process consists of calculating the distance in which the density at one position varies with the density at another point (the semivariance). A weighted average of weed densities is calculated in all directions on the two-dimensional map. This information is used to develop a map of weed densities. Geostatistics have been used to map weed patches of Canada thistle (*Cirsium arvense*) (Donald, 1994), lambsquarters (*Chenopodium album*) (Cardina et al. 1995), grassy and broadleaf weeds (Johnson et al. 1995) and *Setaria* species (Mortensen et al. 1993).

Wild oat has been mapped and has in all cases been found to be a patchy species. Thornton et al. (1990) mapped wild oat in a wheat field by piecing together photographs taken from an unmanned balloon. Even though the field appeared to be completely infested from the ground, only 18% of the field was actually infested. Most of the wild oats occurred within small patches which sometimes coalesced into larger patches. Davidson et al. (1996) mapped the position of triallate resistant wild oat within wild oat patches and found that the proportion of resistance was also variable within the patch. Ground based perimeter mapping of weeds using a global positioning system (GPS) is a relatively quick means of mapping and it can give producers accurate weed maps on which to base herbicide applications. Colliver et al. (1996) found that wild oat was a highly patchy weed and that perimeter ground mapping could provide accurate maps of the area infested.

It is advantageous to the farmer to maintain weeds within patches. Thornton et al. (1990) demonstrated that a weed can be tolerated at a higher average density if it has a patchy distribution. This is true because of the rectangular hyperbolic relationship that exists between weed density and yield loss (Cousens, 1985). As weed density within a patch increases, the intra-specific weed competition increases relative to the interspecific competition between the weed and the crop, and subsequently, crop yield loss caused by an individual weed decreases. Brain and Cousens (1990) employed the negative binomial distribution in a statistical model of the effect of a clustering on yield loss and came to a similar conclusion. Therefore, practices which maintain weeds within patches will result in less yield loss for a given average density of weeds in the field.

A patchy distribution of weeds may also be desirable if herbicides are applied. A large reduction in herbicide use and subsequent cost could occur if only the portion of the field that contained weeds needed to be sprayed with herbicides (Johnson et al. 1995). Techniques that allow a combine operator to mark the position of wild oats using GPS technology have been found to be capable of providing adequate maps of that years weed patches (Colliver et al. 1996). Combined with information on dispersal, such maps could be employed to produce a prescriptive map for herbicide application in the following year. Sensors to detect weeds and turn on individual nozzles have also been used. The sensors can differentiate between large green weeds and soil (Ahrens, 1994) but are not able to distinguish between crops and weeds.

2.4 Weed Seed Dispersal

The management of weed seed dispersal has been recognized as an important process in managing weed populations. By reducing weed seed dispersal, weed populations can be reduced within a field (Maxwell and Ghersa, 1992). Ghersa and Roush (1993) argued that reducing dispersal of weeds is more profitable than trying to improve the competitive ability of the crop.

2.4.1 Natural dispersal

Natural dispersal in annual arable weed seeds without specialized dispersal structures is often confined to areas close to the parent plant. As annual plants cannot reproduce vegetatively, the seeds are quite large and do not usually have attachments to aid in wind dispersal. As a result, natural dispersal in annual plants occurs by seeds falling from the plant. Verkaar et al. (1983) observed dispersal in four herbaceous plants growing in a grassland and found that natural dispersal was limited to 3.5 m with most seeds falling within 1 m of the parent plant. A model was developed using the terminal velocity of the weed seed and the wind speed above and within the canopy to predict natural dispersal. The model, however, did not take into account the lean of the inflorescence away from the parent plant. Howard et al. (1991) observed that natural dispersal of two species of *Bromus* was less than 0.50 m when these species were grown in wheat. O'Toole and Cavers (1983) found that proso millet (*Panicum miliaceum* L.) rarely dispersed seed further than the height of the plant when it was grown in crops. Auld (1988) introduced seeds of three species into a pasture and monitored the spread of the weeds over time as influenced by grazing or mowing. After two years, most wild oat plants were confined to within 7 m of the origin with the exception of one plant that was 14 m away. As this study measured the combined effects of natural dispersal and dispersal by mowing or grazing, it probably overestimated natural seed dispersal. Ghersa et al. (1993) found that only 5% of the *Sorghum halepense* L. seed fell further than 1.4 m away from a patch. This study assessed natural dispersal of the weed into a mown area. As existing vegetation can reduce seed dispersal (Cousens and Mortimer, 1995; Verkaar et al. 1983), natural dispersal in *Sorghum halepense* was probably overestimated.

2.4.2 Mechanical Dispersal

2.4.2.1 Tillage Dispersal

The horizontal distance that weed seeds are moved by tillage is usually quite short. Howard et al. (1991) found that a rotary harrow spread two *Bromus* species less than 2 m with most of the dispersal being within 1 m of the source. Rew and Cussans (1997) investigated the effect of various tillage implements on the tillage dispersal of barley, field bean and oilseed rape. Seeds on the surface were moved farther than buried seeds. Flexible tined harrows and cultivators moved seeds further than power harrows or straight tine harrows. However, there was no difference in the mean seed difference between the tine implements and a plough. Most weed seeds were moved less than 1 m, but some seeds were moved up to 4.8 m. Distance of movement was inversely related to seed size with oilseed rape being moved further than barley which was in turn moved further than bean.

There is potential for long distance tillage movement of weed seeds caused by weed seeds being imbedded in soil that adheres to the tillage implements (Schippers et al. 1993). Although relatively few seeds are transported in this way, this mechanism could result in seeds moving a very large distance.

An important factor in recognizing the significance of tillage dispersal is that many tillage operations can be performed each year. For example, land within the Red River valley of Manitoba is typically tilled between five and eight times per year, and many of the operations are conducted in the same direction. Therefore, while natural dispersal only occurs once in the life cycle of the plant, tillage dispersal can act on the seed many times while the seed remains viable in the seed bank.

Although the amount of movement by tillage and natural dispersal may be small, it may be important for "phalanx spread " (Wilson and Lee, 1989, adapted from Lovett-Doust, 1981). In this type of invasion, the area that a plant species occupies expands by an advancing front of seeds. As all of the seeds in or on the soil may be dispersed by a tillage implement, this type of dispersal may be important in moving large amounts of seeds away from the epicentre of the patch. In this way the patch may expand while still remaining a distinctive patch.

2.4.2.2 Harvest Dispersal

Mechanical dispersal by a combine harvester has the potential to disperse weed seeds the farthest of any dispersal vectors within an arable farming system (Cousens and Mortimer, 1995). There have been several studies on the dispersal of weed seeds by combine harvesters. There is some discrepancy in the amount of dispersal by the combine. This is probably due to differences in combine type and weed species. The studies conducted with commercial combines, and with weed seeds still on the inflorescence often show weed seed dispersal that exceeds the maximum assayed distance in the experiment.

McCanny and Cavers (1988) measured the combine harvester dispersal distance of two biotypes of an invading weed, proso millet. Seed traps were laid out in commercial fields of corn for a distance of 50 metres in the area following natural patches of proso millet. The combine harvester seed dispersal exceeded the maximum distance of the experiment for 3.3% of the smaller black seed biotype and 0.9% of the golden seed biotype.

The dispersal of *Bromus interruptus* L. and *B. sterilis* L. by a small field scale combine harvester was assessed by Howard et al. (1991). Threshed, painted weed seeds were introduced into a combine while it was combining a barley field. A roll of polyethylene was unrolled while the combine moved ahead at a velocity of 1.75 km h^{-1}. More than 40% of the seeds were carried forward by the combine, and seeds of both species were spread up to 20 m by the combine harvester. Howard et al. (1991) also observed that most of the weed seeds were moved backwards from the point of introduction. This anomalous result and the short distance of dispersal may be due to flaws in the experimental design. The threshed weed seeds that were introduced into the machine probably travel through the machine more quickly than seeds which are still attached to the plants; dispersal distance is thus probably underestimated. In addition, the slow velocity of the combine would have contributed to an underestimation of dispersal distance since combine would have only travelled a short distance during the processing of the weed-crop mixture.

The dispersal of *Sorghum halepense* L. by a commercial maize combine was assessed by placing seed traps up to 50 m past a small patch of weeds (Ghersa et al. 1993). Weed seeds were spread past the maximum distance of the traps. Following a brief peak in weed seed dispersal past the weed clump, there was relatively little decline in the rate of seed spread from 7 m to 50 m.

Rew and Cussans (1995) assessed combine harvester dispersal of blackgrass (*Alopecurus myosuroides* L.) by counting the number of seedlings emerged in and following a 10 m wide plot of weeds. The harvester dispersed 24 % of the seeds beyond the original patch and some seedlings were found as far away as 50 m. Because the seed dispersal distance was estimated by seedling counts rather than by direct measurement of seeds, it must be recognized that the dispersal reported may be underestimated as it is a composite measurement of seed dispersal and seedling recruitment. Insects and rodents eat weed seeds and can exhibit density dependent foraging (Rew and Cussans, 1995), as well as predator satiation. These factors could affect dispersal distance estimates. Seedling recruitment may also be limited by the absence of safe sites for emergence (Crawley, 1990). Even under typical field conditions, not all weed seeds will germinate as some will become dormant. Because of these factors, assessing seed dispersal by counting seedlings instead of seeds will likely underestimate seed dispersal.

Ballaré et al. (1987 a) assessed the effect of three combine designs on the seed dispersal of *Datura ferox* L. directly, by measuring seeds in traps placed between rows of corn. Two slightly different conventional combines types spread weed seeds up to 21 m. A third combine harvester with an additional cleaning fan spread seeds of *D. ferox* up to 98 m. This study demonstrated the potential for machine design to influence the dispersal distance of weed seeds. In this case, the most complex machine dispersed weed seeds the furthest.

If a weed species is invasive, combine harvester dispersal can cause patch spread throughout the field. McCanny and Cavers (1988) reported that isolated patches of the black seeded biotype of *P. miliaceum* can be dispersed to the point of almost complete coverage of a field within two years. If one assumes that invading weed species begin as point sources within a field, then reducing the mechanical dispersal of weed seeds will slow the rate of weed patch spread.

Long distance dispersal by combine harvesters may be analogous to "guerilla type" plant invasion (Wilson and Lee, 1989, adapted from Lovett-Doust, 1981). Combine dispersal may result in individual plants emerging far from the original patch, as observed by Rew and Cussans (1995). If these plants are not killed by herbicides, they may create a new patch. The new patch, in turn, will produce seeds that may be dispersed long distances to form other patches. Combine dispersal differs from short distance natural and tillage dispersal, which would be expected to result in weeds invading as an advancing front. Weeds using both short and long distance dispersal strategies should be able to maintain an area of high density in the original patch while still expanding at a fast rate by long distance dispersal. Wilson and Lee (1989) named this invasion strategy "infiltrative invasion".

2.4.2.2.1 Combine weed seed dispersal

Combine harvesters disperse seeds because the mechanical separation of grain from material other than grain (MOG) occurs in a moving machine (Figure 2.1). Weeds are taken into the combine with unthreshed crop and during the time that it takes to thresh and clean the grain, the combine moves across the field. As weed and crop seeds differ in size, shape, mass, density and shape, some are ejected from the combine with the chaff and straw a distance beyond the point at which they were picked up. The three factors will determine how far a combine harvester will disperse weed seeds: 1) the number of weed seeds that are taken into the combine, 2) the number of weed seeds that are ejected from the combine harvester and 3) the distance that the combine harvester travels down the field before the seeds are ejected.

The number of weed seeds that the combine ingests affects dispersal distance by determining the number of seeds that are available for the combine to disperse in the field. The greater the number of weed seeds entering the combine, the greater the probability that some weed seeds will be carried down the field and dispersed. The seed yield of the weed, the effectiveness of the combine bringing the weeds into the thresher and the amount of seed shed that takes place prior to harvest, determine the number of weed seeds that enter the combine. Weeds often have seeds that shed before harvest (Naverette, 1984, from Gonzalez-Andujar and Perry, 1995) limiting the ingestion of weeds by the combine.

The number of weed seeds that are ejected by the combine is inversely related to the number of weed seeds that are retained by the combine. Weed seeds that are threshed in the combine can end up in either the clean grain tank, the chaff portion, the straw portion or exit the combine through a screened auger tube. The proportion of weed seeds that ends up in each pool is determined by the combine type and the adjustment of the threshing and cleaning mechanisms. The pneumatic wind cleaner separates the MOG and grain based on the aerodynamic properties of the particles (Shellard and Macmillan, 1978). The chaffer and shoe separates particles based on size of the particles and the width of the chaffer and shoe (Hunt, 1977).

The distance that a combine travels before dislodging weed seeds is the most obvious mechanism of combine harvester weed seed dispersal. Weed seeds are spread by combines predominantly in the direction of combine travel (Ballaré et al. 1987 a). The distance that the combine will have moved down the field is determined by the velocity of the combine and the length of time that the weed spends inside the combine (processing time). The velocity of the combine simply determines how far the combine will travel in a given processing time. The processing time of the material is determined by how long it takes the combine harvester to mechanically separate and clean the grain/weed mixture. As there are different designs of combine (rotary, conventional, special crop) the processing time and dispersal distance may vary (Ballaré et al. 1987 a). Within a combine there are also numerous places for weed seeds to get caught only to be ejected later (Howard et al. 1991). The return augers bring unthreshed heads and MOG back into the combine cylinder to be reprocessed (Figure 2.1). This mechanism may allow weed seeds to be recirculated in the combine several times, resulting in longer processing times.

2.5 Managing Weed Seed Dispersal

2.5.1 Timing of Harvest

The timing of harvest can affect the combine dispersal of weed seeds. If weed seeds fall off the plant before harvest they will not be available for dispersal or possible removal from the field in the clean grain or chaff, if it is collected. If the timing of crop harvest can be altered, then the number of weed seeds that enter the combine can be managed. It may be possible, for example, to allow all of the weed seeds to shed before harvest and reduce the number dispersed.

2.5.2 Chaff Collection

The ability of self-propelled combine harvesters to dissemination weed seeds was reported in Germany in the 1920's by the Reichskuratorium für Teknik in der Landwirtschaft (cited in Petzold, 1955). It was observed that where combine harvesters were used, the land became weed infested. Petzold (1955) found that for all weed species tested, 11% of the weed seeds were in the chaff while 86% were in the clean grain. These proportions were species specific as the proportion of weed seeds in the chaff and straw ranged from 3% to 93%. Feldman and Reed (1974) investigated the fate of wild oat seeds during swathing and combine harvesting. They found that most wild oats seeds which entering the combine were retained with the clean grain in the grain tank. Of the proportion of wild oats seeds which left the combine, approximately 70% were in the chaff.

Metz (1969) recommended that chaff collection be performed in conjunction with an early harvest to help control wild oat. Fogelfors (1982) found that in Sweden the collection of chaff and awn had a negligible effect on the subsequent occurrence of broadleaf weeds. However, this study was conducted using a direct cut combine which may have resulted in many weeds shattering before harvesting. Fogelfors (1982) conceded that if the combining could be done when there was a lower percentage of weed seed shed, the results would have been different. Furthermore, this study only considered average weed density and did not examine their spatial distribution. Matthews et al. (1996) reported that seed catching reduced the numbers of Rye grass (*Lolium rigidum* (Gaud.)) seeds and seedlings that occurred within crop rotations.

Chaff collection can also affect weed population dynamics by reducing the dispersal distance of weed seeds. By collecting chaff, the weed seeds which are in the grain chaff are prevented from being dispersed far from the original patch. If most of the weed seeds that leave the combine are in the chaff fraction, then chaff collection should reduce weed seed dispersal distance. There have been no studies conducted to assess the effect of chaff collection on the dispersal distance of weed seeds. A reduction in dispersal in general may allow less of the field to be affected by the weed in question, and it may slow the invasion of new species.

2.5.3 Weed Seeds in Manure

Chaff collected in fields may be ammoniated with anhydrous NH_3 and fed to cattle as an economical feed source (Olfert et al. 1991). Producers have found that when chaff is hydrated to approximately 25% moisture content, and then ammoniated at a rate of 3%, the resulting chaff has 13% crude protein and 50% total digestible nutrients (Thomas and Newton, 1996).

A concern that many cattle producers have is that the weed seeds that were originally present in the chaff will be returned to the field in the manure. This concern may be well justified as some weed seeds can remain viable even after being digested by cattle. Mt. Pleasant and Schlather (1994) surveyed 20 dairy farms and found viable weed seeds in the manure on 16 of the farms.

Most historical studies have focussed on the viability of weed seeds after they have passed through the digestive system of farm animals. In a non replicated study (Atkeson et al. 1934), weed seeds were mixed with feed and fed to cattle. The germination percentage of the weed seeds was measured in the manure after they passed through the animal. Weed seeds with hard seed coats, such as lambsquarters (*Chenopodium album* L.) and pigweed (*Amaranthus retroflexus* L.), survived digestion and manure storage much better than seeds of graminoid weeds. Wild oat or green foxtail seed did not survive both digestion and manure storage. In general, the manure ensilage process kills most soft coated weed seeds.

Harmon and Keim (1934) obtained similar results in a study of weed seed viability after the seed were digested through various farm animals. Digestion by chickens resulted in the greatest loss of seed viability with only 0.2 % of the weed seeds being viable after digestion. The viability of seeds passing through other animals ranged from 6.4 % to 9.6 %. Burial of seeds in manure for four months resulted in complete loss of viability in all seeds. This study did not include weeds that typically survive in manure such as pigweed and lambsquarters.

Blackshaw and Rode (1991) initiated a study to determine the effect of silage fermentation and rumen digestion on the viability of the seeds of several grass and broadleaf weed species. Seeds were placed in mesh bags and ensiled for eight weeks and/or placed in the rumen for 25 hours. Grass seeds, in general, did not survive the ensilage process and most were killed by the digestion. The exceptions to this were wild oat, which had viability of between 0 and 88%, and green foxtail (*Setaria viridus)* which had 17% viability. Broad leafed weeds with hard seedcoats survived best, with many weed seeds surviving both ensiling and digestion. It was found that seed survivability in the rumen over time exhibited a lag phase followed by a rapid decline in embryo viability.

Blackshaw and Rode's (1991) study probably overestimated the viability of wild oat after digestion because the seeds were placed directly in the rumen in mesh bags and were therefore not damaged by mastication. Harmon and Keim (1934) believed that the viability of weed seeds passing through different animals was correlated with the degree of mastication. Atkeson et al.(1934) noted that many wild oat seeds recovered in manure, following feeding to cattle, were broken, rendering them non-viable. Thurston (1963) obtained similar results, finding that of 2,000 wild oat seeds fed to a calf, only 10 were viable on recovery in the manure.

Weed seeds that are not killed by animal digestion can be killed if the manure is properly composted. Atkeson et al. (1934) observed that manure storage for three months reduced the germination of weed seeds by 62 to 100%. This study also included many hard seeded weed seeds such as pigweed and lambsquarters. Modern manure handling techniques may not always allow for a proper manure fermentation period and, therefore, may allow many weed seeds to return to the field (Mt. Pleasant and Schlather, 1994).

2.5.4 Burning Straw

If the straw and chaff exiting the combine contain weed seeds, then burning it may destroy some of these seeds. A re-analysis of data from Whybrew (1964) revealed that burning the straw of a previous barley crop reduced the average density of wild oat at harvest by 39% (averaged over all years and treatments) compared to treatments where the straw was removed by baling. Wilson and Cussans (1975) found that burning barley straw swaths resulted in a 27% decrease in wild oat seedling numbers the following year. However, even greater seed losses were reported when the plots were left unburnt and uncultivated in the fall. In a computer model of wild oat control in winter wheat, Cousens et al. (1986) estimated that 33% of that seasons wild oat seeds were killed by burning.

In addition to destroying seeds through desiccation and rapid oxidation of embryonic tissue, burning can stimulate some weed seeds to germinate in autumn. Burning resulted in a 600% increase in fall germination of weeds in untilled treatments, a 100% increase in the rotary cultivated treatments, and an 80% increase in the mouldboard ploughed treatments (Whybrew, 1964). Similarly, Wilson and Cussans (1975) reported a 200% to 300% increase in fall germination of wild oats after straw burning.

All of the previous studies compared straw burning with removal of straw by bailing. As it is a common practice in western Canada to return crop residues to the soil, it would be of benefit to have studies comparing burning with other treatments. Although the burning or removal of straw does not provide complete wild oat control (Whybrew, 1964; Wilson and Cussans, 1975), this method could be an important tool when managing herbicide resistant wild oat. Combine attachments which collect the chaff and place it on top of the straw row are now available. This process may result in greater wild oat seed destruction if the swaths are burned and more wild oat seeds being removed if the swathes are baled.

2.6 Modelling Weed Control Strategies

Computer simulation models can aid in our understanding of the weed crop system and can simulate the effect of potential control strategies over several years (Doyle, 1991). Life cycle models (Figure 2.2) divide the life of a weed into individual development stages (state variables). The state variables are connected by rate variables which determine the proportion or relationship between consecutive state variables. Difference equations are used to describe the change in population density from one state variable to the next. The parameter values for these difference equations are then determined by fitting linear or nonlinear regressions to data sets of censuses of the relevant life cycle stages. By arranging these equations together in a computer program, the plants life cycle (Figure 2.2) can be simulated mathematically. Viewed in this manner a mathematical model is an extension of regression analysis.

A simulation using a mathematical model can be used to predict what should happen but not necessarily what will happen (Cousens and Mortimer, 1995). Variation between sites, lack of good data for life cycle parameters, and the variability associated with environment can lower the predictive power of models (Cousens and Mortimer, 1995). Despite this caveat, mathematical models are useful tools for illustrating the effects of different management strategies over a longer time or larger space than would be economical to do experimentally. If the differences in a control strategy are large and consistent, then one can expect the model to predict the differences in weed population density between the control strategies reasonably well. There will be a difference between the predicted and observed density of weeds present, but the relative differences between the management strategies will be predicted to some degree.

Mathematical models of weed population dynamics can also help identify gaps in knowledge of the plant's life cycle, set research priorities based on these gaps, and devise possible novel methods of control (Maxwell et al. 1988). When paramaterizing models, the lack of data for a relationship usually indicates a knowledge gap in that area. Experiments then need to be conducted to fill that the knowledge gap. Parameter values may be changed to reflect different management practices, and simulation for several years may be done to ascertain the effectiveness of these management practices in reducing weed populations. The values that have a large effect on the outcome of the model indicate areas for possible weed control strategies. Using this logic, Maxwell and Ghersa (1992) identified seed dispersal as one of the most important processes affecting weed population dynamics.

Cousens et al. (1986) used a life cycle model to predict the long term effects of different wild oat control strategies in winter wheat. Their model predicted that it was most economically profitable to spray for wild oat when the density exceeded 2 - 3 plants m^{-2}. This was a considerably lower density than the one year threshold of 8 -10 plants m^{-2} predicted by only considering the returns for that year. Based on this model, a farmer spraying weeds only when they exceeded the one year economic threshold would make less money than if they would spray at the economic optimal threshold of 2 - 3 wild oat plants m^{-2}. The outcome of this model illustrated that one year economic returns when managing weeds can result in reduced profits in the long term from increased weed infestations.

Life cycle models which include a spatial component can more accurately simulate weed dynamics. By using a spatial model, important spatial ecological processes such as weed seed dispersal can be simulated. As weeds are spatially heterogenous in a field (Mortensen et al. 1993; Rew and Cussans, 1995; Cardina et al. 1995; Colliver et al.

1996) it would be unrealistic to use nonspatial models.

Ballaré et al. (1987 b) constructed a computer simulation of life cycle and dispersal of *Datura ferox* in soybeans. They found that combine harvester dispersal caused an exponential growth of weed seed production after a simulation of five years. Without this dispersal, weed seed production levelled off after three years. They concluded that this weed could be controlled only if dispersal was prevented and if a large proportion of the seeds were exported with the harvested grain.

Maxwell and Ghersa (1992) developed a theoretical model of the spread of green foxtail in spring wheat. They identified combine harvesters as a major source of weed seed dispersion and suggested that the combine could be used as a tool for reducing weed seed dispersal. It was concluded that a highly dispersed weed with low competitive ability had a greater impact on crop yield than a highly competitive weed with low dispersal.

Spatial models of weed life cycle dynamics revealed that weed seed dispersal is one of the most important processes in the weed-crop competition. Limiting the mechanical dispersal of wild oat seeds can reduce the rate of wild oat patch expansion. Reduced mechanical dispersal can be accomplished through the collection of chaff, as it is expelled from a combine during the harvest process. This should reduce weed seed return to the field as well as decrease weed seed dispersal resulting in less economic damage from wild oat.

2.7 Fractal Geometry

Mandelbrot (1975, 1982) synthesized many mathematical concepts in the discovery of fractal geometry. He described a fractal as "a shape made of parts similar to the whole in some way" (Mandelbrot, 1982). In an attempt to develop a more concise definition of fractals, other authors (Falconer, 1990; Baveye and Boast, 1998) have expanded this definition. However, the results only cloud the essential property of fractals, which is the self similarity of parts of the whole to the whole. Mathematically, a fractal is usually defined as a series in which the Hausdorff dimension (equivalent to the fractal dimension, *D*) exceeds the topological dimension (the topological dimension of a two dimensional plane would be one) (Mandelbrot, 1982).

The self similarity inherit in fractals can be either mathematical (true) or statistical (natural). Mathematical fractals have exact self similarity when viewed at any spacial scale. The self similarity of a Seirpinski triangle (Liebovich, 1998) is an example of a true fractal, a portion of the square is a reduced but identical part of the whole triangle. Statistical fractals which can be described using fractal geometry, have a statistically similar pattern of points when viewed over a limited spatial scale. Thus, the pattern of the objects viewed at different spatial scales will not be similar, but the distribution of the objects relative to each other will be (Mandelbrot, 1982).

Fractal geometry can be used to mathematically represent complex natural patterns (Milne, 1992). Many natural objects have been described using fractals including length of a coastline (Richardson, 1961, Mandelbrot, 1975, 1982), the pattern of branching in plant roots (Tatsumi et al. 1989) and the pattern of weeds within a weed patch (Wallinga, 1995). Natural objects are not true fractals as the processes and objects that define the fractal all have a finite spatial scale. This finite scale results in a limited scale of self similarity. As a result, the fractal nature of a weed patch could never be smaller than the description of a small cluster of individual weeds or larger then the distribution of weeds at a geographic scale. Similarly, natural objects never display the exact same pattern at different spatial scales. Because of these limitations, natural fractals are often referred to as statistical fractals or prefractals (Baveye and Boast, 1998).

A power law relationship between selected parameters is a consequence of the fractal geometry (Baveye and Boast, 1998). This distribution, also referred to as a Pareto distribution, was originally used by Pareto (1897) (Persky, 1992) to characterize the distribution of income over a population, and it takes the form:

$$N=Ax^{-\Upsilon} \qquad [1]$$

where N is the number of persons having income greater than or equal to x. A and a are fitted parameters. A power law function can be fitted to natural and mathematical objects that are fractal.

To determine if objects exhibit fractal properties, the fractal dimension D can be measured using the box counting method (Hastings and Sugihara, 1993). To calculate the fractal dimension of points on a two dimensional plane, a grid is placed over the area and the number of boxes that contain points are counted. This process is repeated for boxes of different sizes. If the distribution of points on the plane is fractal then the number of covering boxes will increase in a power law relationship (equation 1) as the size of the box increases. This relationship can be written as:

$$C=K\delta^{-D} \qquad [2]$$

where C is the number of boxes that are occupied by at least one point, K is a constant, δ is the length of one side of the box, and D is the fractal dimension. This equation is equivalent to equation 1 and describes a power function. To determine D, the negative slope of a linear regression of a plot of log number of covered squares versus log box is calculated.

The fractal dimension D describes the space filling properties of an object. An object or series of points on a two dimensional plane will have a fractal dimension of between one and two. A series of points, such as a line, will have a fractal dimension of one, which is equal to the topographical dimension (one) and is therefore not fractal. As D approaches two the series begins to fill the two dimension space in which the fractal occurs, and when D equals two completely fills it, producing a two dimensional plane. Therefore, for $1 < D < 2$ a series of points can be considered fractal.

As D increases, the complexity of the shape increases (Sugihara and May, 1990). When viewed as points on a two dimensional plane, as in a Lévy dust model, an increase in fractal dimension results in more uniform clumps of points (Mandelbrot, 1982; Kenkel, and Irwin, 1994). Therefore, the lower the fractal dimension is for point patterns the more clumped the distribution is.

The reported fractal dimensions for patterns of vegetation vary widely. Wallinga (1995) found that the spatial pattern of *Galium aparine* L. in an agricultural field was fractal and had a fractal dimension of $D = 1.51$ as measured using the correlation dimension. Other studies have measured the complexity of the border of a patch using the area - perimeter method. This method calculates the complexity of the border of the patch. Using the area - perimeter method, the patch complexity of a deciduous forest was calculated to have a value of $D = 1.20 - 1.52$ (Krummel et al. 1987). Haslett (1994) used the same method to determine that plant species distributions within mountain meadows have an extremely high fractal dimension of $D = 1.90 - 1.99$. A high fractal dimension would indicate a vegetative patch that has a very spatially complex surface. As it is fractal the apparent length of the perimeter would increase in a power law fashion as the scale of the measurement was decreased. As a result, a patch with a high fractal dimension calculated using this method will have a convoluted perimeter that is very complex. This may indicate that there is more surface area for small organisms to occupy.

A multifractal approach can be used to characterize a series in which the fractal dimension varies when the clustering of points within individual boxes is considered. By using multifractals, it is possible to distinguish between a series of points that are evenly spread over occupied boxes and a more clustered pattern of points (Appleby, 1996). The box count method considers whether or not a square contains objects, whereas a multifractal approach weights boxes based on the number of objects that are contained within the box (Scheuring and Riedi, 1994; Kenkel and Walker, 1996). By incorporating information on the proportion of points within a given box, the dispersion of points within the plane can be calculated. This approach allows the fractal dimension to be calculated with differing emphasis on the dispersion, or entropy of the pattern.

The entropy of a series of points is a measure of the disorder in a system. In a two dimensional plane it is a measure of the dispersion of the points within the plane. A system which has many points in one box and very few in all the others will have a lower degree of entropy than a system where the points are evenly dispersed through all the boxes. The entropy is described by the generalized entropy function (Rényi, 1970).

$$I_q(\delta) = 1/(1-q)\log\sum_{i=1}^{N\delta} p_i^q \qquad [3]$$

By varying the value of q in the generalized entropy function a series of entropy measures can be made which place more emphasis on areas that are more clustered. Using this method, D can be calculated for different vales of q. If a plot of $D(q)$ versus q results in a nonlinear relationship then the point pattern is considered to be multifractal.

Multifractal objects have been formed by a process, or multiple processes that operate at different scales (Sugihara and May, 1990). Because many natural processes can only operate over a finite scale (the length of a coastline is limited by the size of a grain of sand and the size of the earth) it would be expected that many natural objects are multifractal. Multifractals have been used to describe the formation of landscapes (Krummel et al. 1987) and the distribution of habitats for invertebrates (Gunnarsson, 1992). However, Appleby (1996) found that the spatial distribution of populations in England and the United States was not multifractal, indicating that the processes that created the pattern of populations was scale invariant.

2.7.1 Relationship of Dispersal to Patchiness

The fractal properties exhibited by patches of annual plants can be related to seed dispersal (Kenkel and Irwin, 1994). The natural dispersal pattern of seeds typically exhibits characteristics of the inverse power law (Harper, 1977). The inverse power law (equation 1) is a form of the equation used to determine fractal properties of point patterns (equation 2).

Kenkel and Irwin (1994) constructed a Lévy dust model of dispersion. It was found that the slope of the power law relationship between seed dispersal and distance was related to the fractal dimension of a point pattern map of the dispersing organisms. The calculated relationship was that the slope of the power law dispersal was equal to one minus the fractal dimensions of the spatial pattern (Kenkel and Irwin, 1995). The Lévy dust model is analogous to the dispersal of seed from an annual plant. If the dispersal has a high slope (a long tail) then the resultant pattern of patches will be more clumped.

Wallinga (1995) proposed a model for weed patch population dynamics that related the clumped distribution of weed patches to the low density that occurs in an arable agricultural field. The main premise is that within agricultural fields weeds are at a very low population near extinction where "critical phenomena" (Grassberger, 1983) are expected. By adjusting the removal rate of weeds in a spatial population model to maintain a constant population density, it was possible to create clusters of weeds that exhibited fractal dimensions. The fractal dimensions of these simulations were considered to be similar to those observed in *Galium aparine* L. in a field of winter wheat (1.17 versus 1.51). However, since D is the slope of a log-log relationship, and D for a pattern on a two dimensional plane is limited to $1 < D < 2$, these values are considered to be quite different. In addition, this model makes no provisions for long distance seed dispersal as all seeds are assumed to fall in the original cell or bordering cells. As Levy dust models that mimic seed dispersal characteristics can also generate fractals (Kenkel and Irwin, 1994), one would assume that ignoring this phenomena would alter the estimated fractal dimension of the modelled plant pattern. Wallinga (1995) did concede that this model may not be mechanistically perfect but asserts that it does illustrate that the aggregated pattern of weeds observed in the field need not be a function of soil factors.

Several distribution functions have been used to fit the dispersal pattern of seeds. The choice of dispersal function of the seed will also affect the spatial pattern that resulting plants exhibit. The mechanical dispersal of weeds may be analogous to the spread of plant pathogens because the spread of plant pathogens is often modelled using the power law (Mollison, 1977).

Shaw (1994, 1995) used a Cauchy distribution to describe the theoretical dispersion of a plant disease. The Cauchy distribution exhibits a similar curve to an exponential distribution at short dispersal distances, but the probability of being dispersed very large distances does not decrease exponentially. The spatial pattern of the Cauchy distribution results in the appearance of islands of disease that are separated from the initial foci and are fractal in nature over a finite spatial scale. Although the Cauchy distribution has not been commonly used it has been employed in the description of biological data such as the movement of screwworm flies (Mayer and Atzeni, 1993).

The relationship between dispersal data and the spread of organisms often depends on the shape of the tail of the dispersal. Kot et al. (1996) investigated this effect on the rate of spread for invading organisms. Using a data set of insect dispersal, they found that dispersal curves with long fat tails resulted in an invasion that accelerates with time.

The dispersal pattern of weed seeds can be theoretically related to the general spatial pattern of plants. Wallinga (1998) investigated this phenomena by analysing data that Rew had previously collected (Rew and Cussans, 1995). Using a similar approach as Kot et al. (1996), it was found that if the tail of the dispersal curve declines at less than an exponential rate, the invasion pattern of plants will not expand as an advancing front but will advance by establishing new colonies beyond the original patch. It would be expected that the resulting spatial pattern would be fractal.

The dispersal of weed seeds by combines may result in a fractal pattern of patches. McCanny and Cavers (1988), and Ghersa et al. (1993) found that the weed seeds were spread in excess of the maximum distance of the experiment (45 m, and 50 m, respectively). If the distribution curve exhibits a dispersal distribution that results in a fractal dispersal of seeds then this may provide a theoretical link between weed seed dispersal and weed patchiness. This theoretical relationship would address the apparent contradiction that exists between long distance weed seed dispersal and weed patchiness.

A mechanical weed seed dispersal pattern which results in a fractal pattern of weed patches may explain several aspects of weed distribution. The general and persistent patchy nature of weeds in fields (Wilson and Brain, 1991) has been previously discussed and may be related to mechanical dispersal which results in a long dispersal tail. Initial weed infestations of an invading species often appear initially as isolated patches within a field (McCanny and Cavers, 1988). The spread of herbicide resistant weeds both within a field and within a geographic area may also be explained by long distance dispersal resulting in a fractal pattern of patches.

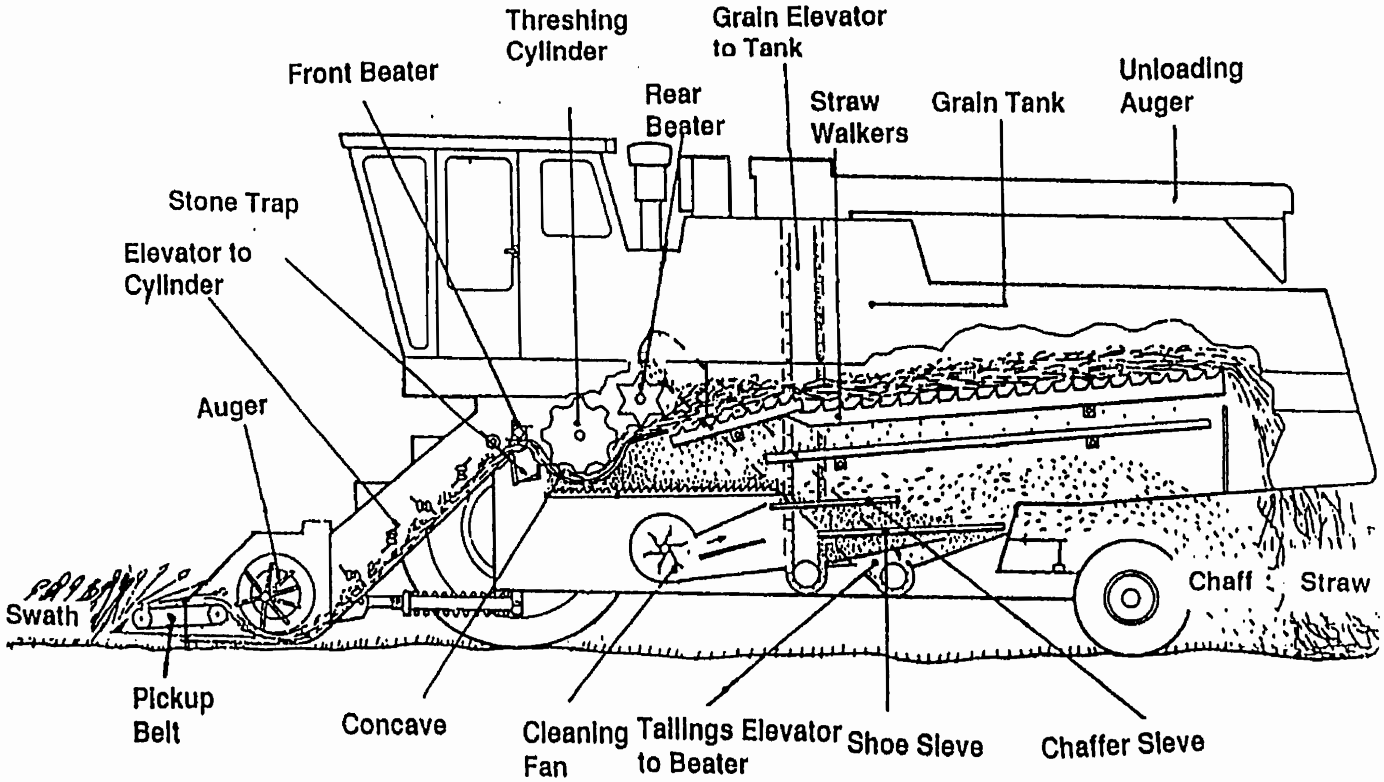


Figure 2.1. View of the flow of material through a self propelled combine harvester equipped with a pickup header for swaths. Small dots represent grain kernels. Adapted from Culpin, (1981).

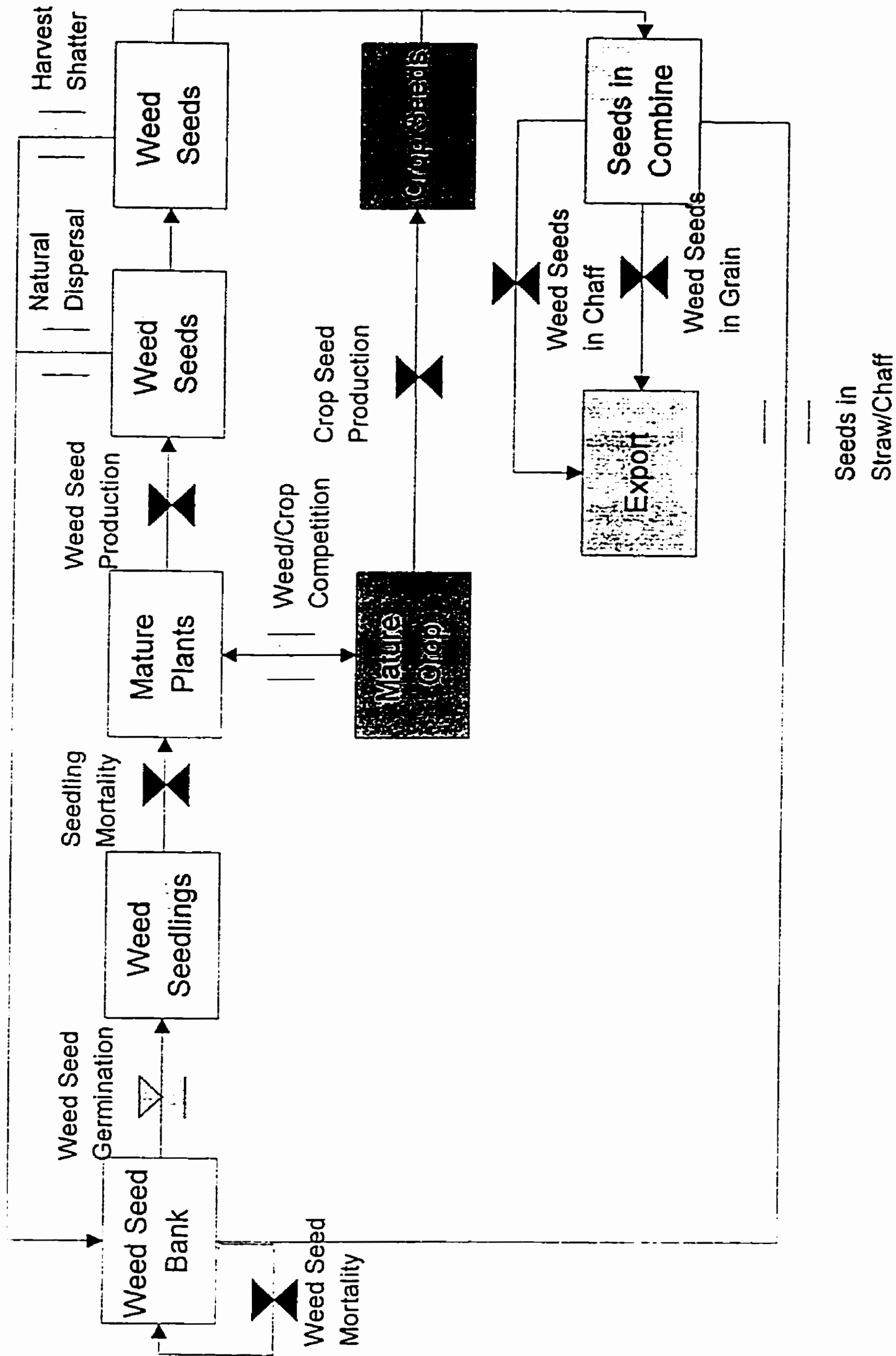


Figure 2.2. Life cycle diagram of wild oat.

3.0 The Effect of Chaff Collection on the Dispersal of Grassy Weed Seeds

3.1 Introduction

Combine harvesters have the potential to disperse weed seeds the furthest of any dispersal vectors within an arable farming system (Cousens and Mortimer, 1995). The ability of self-propelled combine harvesters to disseminate weed seeds was first reported in Germany in the 1920's (Petzold, 1955), where it was observed that land where combine harvesters were used became weed infested. The maximum observed distance of weed seed dispersal with a combine harvester ranges from approximately 20 metres for *Datura ferox* L.(Ballaré et al. 1987 a), poverty brome (*Bromus interruptus* L.) and *Bromus sterilis* L.(Howard et al. 1991), to greater than 45 metres for wild-proso millet (McCanny and Cavers, 1988), johnsongrass (*Sorghum halepense* L. (Pers.)) (Ghersa et al. 1993), and blackgrass (*Alopecurus myosuroides* L.) (Rew and Cussans, 1995). McCanny and Cavers (1988) reported that isolated patches of the black seeded biotype of wild-proso millet (*Panicum miliaceum* L.) could be dispersed by combine harvesters to almost completely cover a field within two years.

As wild oat is usually considered to be a patchy weed (Colliver et al. 1996), methods which reduce its dispersal should maintain the weed within patches and reduce its negative economic impact (Thornton et al. 1990). Bourgeois and Morrison (1997) observed that herbicide resistant wild oat infestations begin as small patches within a field. Therefore, any methods which prevent the spread of herbicide resistant wild oat should be a valuable integrated weed management technique for use in the absence of herbicidal control.

Combine harvesters disperse weed seeds because the mechanical separation of grain from material other than grain (MOG), takes place in a moving machine. Weeds are taken into the combine with the unthreshed crop, and during the time that it takes to thresh and clean the grain the combine carries the weed seed some distance in the field. A portion of the weed seeds are then returned to the field along with the MOG some distance past where the weed seeds were originally picked up.

The combine returns more weed seeds to the field in the chaff portion of the MOG than in the straw portion of the MOG (Petzold, 1955; Feldman and Reed, 1974). To reduce the dispersal of weed seeds, Metz (1969) recommended that the chaff portion of MOG be collected in conjunction with an early harvest. Matthews et al. (1996) reported that seed catching reduced the numbers of rye grass (*Lolium rigidum* Gaud.) seeds and plants that occurred within crop rotations. However, Fogelfors (1982) found that chaff collection had a negligible effect on the occurrence of broadleaf weeds. To determine the potential of chaff collection as a weed control method, mechanistic studies must be done to determine how effectively it works with different weeds.

The objectives of this study were to; 1) determine the distance that wild oat and green foxtail seeds would be dispersed by a combine harvester, 2) the effect of chaff collection on this dispersal and 3) assess the effect of combine separator adjustment on the harvest dispersal of wild oat.

3.2 Materials and Methods

3.2.1 Combine Seed Dispersal

The field weed seed dispersal experiments followed a randomized complete block design with four replicates in 1995 and three in 1996. The weed species evaluated was wild oat in 1995 and 1996 and wild oat with green foxtail in 1995. The weed seed dispersal of these species were compared with and without chaff collection. Prior to the experimental year, alfalfa had been grown in the experimental areas for at least four years. The length of the alfalfa stand had reduced the indigenous wild oat population to a very low level (Ominski et al. 1998). All the wild oat plants that emerged outside of the created weed patches were hand rouged from the experimental area prior to swathing.

3.2.1.1 Experiment Management 1995

UM5 wild oat (*Avena fatua* L.) (Heap et al. 1993) and UM7 green foxtail (*Setaria viridus* (L.) Beauv.) (Heap and Morrison, 1996) were seeded in discreet strips 7.6 m wide perpendicular to the plots (Figure 3.1). These weed populations were originally collected from Portage la Prairie, Manitoba, located approximately 50 km from the experimental site. These populations were used as they had been confirmed to be herbicide susceptible. Two experiments were conducted, the first with wild oat and green foxtail in separate strips (WOGF) and the second with only wild oat (WO). The weeds were seeded by spreading them on the soil surface with a Valmar Airflo pneumatic broadcaster (Elie, MB) and incorporating the seeds by cultivating and then packing the strips with packing harrows. The wild oat and green foxtail were seeded at 370 seeds m^{-2} and 2270 seeds m^{-2}, respectively. The entire experimental area including the weed strips was then sown to spring wheat (*Triticum aestivum* L. cv. Katepawa) at 75 kg ha^{-1}. The density of emerged plants was 98 m^{-2} for wheat, 45 m^{-2} for wild oat and 682 m^{-2} for green foxtail. The field was swathed with a 3.16 m wide self propelled swather at approximately 50% wheat head moisture concentration (Bauer and Black, 1989) which would have corresponded to 50% of the wild oat remaining on the plant (see Chapter 4). All the swathes ran from north to south. The height of the stubble following swathing was approximately 15 cm.

Weed seeds expelled from the rear of the combine in the chaff or straw were sampled with seed traps consisting of plastic garbage bags (90 cm by 125 cm) that were held to the ground with 5 cm roofing nails. Before harvest, 1 m sections of the windrow were moved 1.25 m to the side at 10 m intervals to accommodate the seed traps. The seed traps were placed perpendicular to the swath with two traps at each interval assessed. As the chaff falls directly behind the combine harvester, one trap was placed in the centre line of the swath to catch both the chaff and straw directly behind the combine. The straw is spread in a wider area than the chaff and to therefore collect straw without chaff, another trap was placed 0.62 m to the side of the centre line of the swather. The trap series collected the weed seeds for a total distance of 120 m past the wild oat patch. The placement of the traps began 5 m before the wild oat patch and ended with one set of traps that were placed 10 m past the termination of the swath.

The windrows were harvested with a New Holland model 1400, field scale, self-propelled, conventional combine (New Holland North America, 500 Diller Ave., New Holland, PA). The combine settings were; cylinder speed of 950 rpm, concave set at setting number 3, fan at setting number 5, chaffer at 9.5 mm and the shoe set at 3.18 mm. The velocity of the combine was 1.08 m s^{-1}. The wheat yielded 1 900 kg ha^{-1} and was harvested at approximately 12% grain moisture. The combine was equipped with a removable Redekop chaff collection system consisting of a model 925 chaff blower and a model 301 chaff wagon (Redekop Industries, Hwy 16 W, Saskatoon, SK). This chaff collection system was capable of collecting the chaff, but allowed the straw to be chopped and spread on the ground. Before harvesting the experimental area, the externally accessible areas of the combine harvester were cleaned and a weed free buffer area was harvested to aid in cleaning any weed seeds remaining inside of the harvester. The combine was not cleaned before individual swaths but was allowed to run empty as it moved the 140 m distance from the end of one swath to the start of the next swath. During the harvest the air temperature was between 19 C and 24 C, the relative humidity from 56% to 76%, and the two minute mean wind velocity (at 10 m) was between 2.6 m s^{-1} and 5.1 m s^{-1}. The environmental data was collected at an Environment Canada weather station located within 500 m of the experimental area.

The chaff and straw samples containing the weed seeds and grain were separated following harvest by cleaning the sample in mechanical seed cleaners and sorting by hand. The samples were initially pre-cleaned by separating the straw from the chaff and seeds using a commercial seed cleaner. The samples were then processed in a dockage tester (Carter Day Industries, Winnipeg, MB) with a wild oat riddle and having a 1.98 by 19 mm top sieve, a 1.98 mm centre sieve and a 1.41 mm bottom sieve. All samples containing wild oat or green foxtail seeds were then hand sorted and the weed seeds were counted.

The experimental area was cultivated following harvest. In the year following the chaff collection experiment the experimental area was seeded to flax (*Linum usitatissimum* L.), following a shallow cultivation with a field cultivator and packing. The distribution of the wild oat and green foxtail in the area where the combine had passed the year before was assessed by counting weed seedlings in 0.25 m^{-2} quadrats in similar but not identical locations as the centre seed traps the previous year.

3.2.1.2 Experiment Management 1996

The protocol for the 1996 experiment was the same as 1995 with the following exceptions. Green foxtail was not included in this study. Wild oat was seeded at 114 seeds m^{-2}, which resulted in a seedling density of 41.2 wild oat m^{-2}. The wheat was swathed at approximately 35% head moisture content which would have corresponded to the time when 40 % of the wild oat would remain on the plant (see Chapter 4). The placement of the plastic traps differed from the 1995 experiment. In 1999 the trap series began 10 m before the wild oat patch and continuing to 250 m past the wild oat patch. The traps were spaced at 5 m intervals for the first 40 m, 10 m intervals between 40 and 100 m, and 20 m intervals between 100 m and 260 m. Four additional traps were placed after the termination of the swath at 5 m intervals. The traps were constructed of the same material and were of the same size as those used in 1995 with the exception of the traps between 100 m and 260 m. These consisted of two garbage bags placed in the centre of the swath and two garbage bags placed at the side of each interval. These traps were therefore double the size of the other traps (180 by 125 cm). In 1996 the combine travelled at 0.60 m s^{-1}. The yield of the wheat was 2 600 kg ha^{-1} and it was harvested at 12% moisture. During the time of harvest the air temperature ranged from 23 C to 29 C, the relative humidity from 29% to 57%, and the two minute mean wind velocity (at 10 m) from 2.3 m s^{-1} to 4.2 m s^{-1}.

3.2.1.3 Data Analysis

Nonlinear regression analysis was performed on the wild oat seed numbers in the traps that followed the trailing edge of the patch using the SAS (Statistical Analysis Systems Institute, 1986) NLIN procedure. The parameters of the nonlinear regressions were compared using a F-test performed on the residual sums of squares (Ratkowsky, 1983). All seed dispersal graphs present the dispersal of weed seeds related to the time in seconds that weed seeds were first ejected from the combine after it left the trailing edge of the patch. By presenting the data in this way it was possible to compare treatments in which the combine was travelling at different velocities. To convert the dispersal time to distance, the dispersal time can be multiplied by the velocity of the combine. The following modified negative exponential regression (Auld, 1988) was fitted to each of the dispersal treatments;

$$Y=a*e(-x^{b}) \qquad [1]$$

Where Y is the predicted amount of wild oat seeds m^{-2} that are on the ground at x time past the patch in seconds, a is a regression parameter that describes the maximum seed output at the y intercept, and *b* is a regression parameter describing the slope of the exponential decline. This equation was fitted to the seed trap collection data from the trailing edge of the patch to the last trap where there was crop present.

3.2.2 Natural Wild Oat Seed Dispersal

This experiment follows a completely random design with six replicates. The experiment was conducted in 1996 at the Carman site. The wheat was seeded in the manner described in the chaff collection study. A short row of wild oat was hand seeded in each of the plots, and following emergence, one plant was selected and the others terminated. The distance wild oat seeds disperse naturally was assessed by placing seed traps in a hexagonal array around six individual wild oat plants growing in a crop of wheat (Figure 3.2). The placement of the traps was modelled after Murray (1996) and the trap design was modified from Werner (1975) and consisted of 15 cm plastic petri dishes glued onto 15 cm plastic tent pegs. Sheets of 12.5 cm filter paper were placed in the dishes and sprayed with Tanglefoot (Tanglefoot Co., Grand Rapids Mich.) so that the wild oat seeds would adhere to the trap. Six 3.18 mm holes were drilled around the periphery of each petri dish to allow water to drain from the trap. The seeds in the trap were sampled periodically after the initiation of seed shed and until the termination of seed shed. The height of the wild oat and wheat was approximately 1.4 m and 1.1 m, respectively. The direction and velocity of the wind is presented in appendix 1.

3.3 Results and Discussion

3.3.1 Combine Seed Dispersal

The dispersal of wild oat seeds in the centre row (directly behind the combine body) differed substantially between treatments for wild oat in both experiments in 1995 (Figure 3.3). The centre row consisted of the chaff portion of the MOG which falls directly behind the combine and a portion of the straw fraction. The straw fraction of the MOG was chopped and spread in the area behind and to both sides of the combine for both the chaff collection and chaff return treatments. Therefore, the dispersal of wild oat in the row to the side of the combine which only received straw of the MOG was similar in all treatments and, is not presented.

In both experiments chaff collection resulted in much reduced maximum dispersal distance of wild oat seed than chaff return (Figure 3.3). With chaff collection, there were very few seeds ejected beyond 20 seconds past the patch. However, in the chaff return treatment, wild oat seeds continued to be ejected from the combine for the entire measurement period, in excess of 100 seconds past the patch. This corresponded to a dispersal distance greater than 110 m (Figure 3.3). There was a predictable peak in wild oat seed output as the combine passed through the patch, followed by a steady decline as the combine continued past the patch. The last seed trap was in an area without crop, where the combine machinery was still running and presumably dislodging weed seeds that were present inside the machine (Figure 3.3). This increase in wild oat seed number past the crop area in the chaff return treatment indicated that there were still weed seeds in the combine that would have presumably been further away from the source patch had the assay distance been greater.

Although not compared statistically, the presence of green foxtail did not appear to affect the dispersal of wild oat (Figure 3.3). The small differences in the two experiments were probably due to the density of wild oat seed being approximately twice as high in the wild oat and green foxtail experiment as compared to the wild oat experiment. Thus it can be concluded that the wild oat seed dispersal would be similar in a mixed population of weeds.

The 1996 dispersal data (Figure 3.4) shows similar trends as the 1995 data. Chaff collection again resulted in a reduction in maximum dispersal distance and the amount of wild oat seed dispersed, with few seeds being dispersed after 20 seconds. The experiment in 1996 was conducted over a much longer distance (260 m versus 115 m) and with a reduced combine velocity (0.60 m s^{-1} versus 1.08 m s^{-1}) providing a much longer time to assess wild oat dispersal (430 s versus 100 s). As a result, there was sufficient time for the combine to virtually empty itself of weed seeds in both treatments. The traps at the end of the experiment, where no crop was present, did not contain more seeds than the traps preceding them, as they did in 1995 (Figure 3.3). This indicated that the maximum dispersal distance for wild oat was more accurately assessed in 1996 versus 1995.

The chaff collection treatment in 1996 greatly reduced the combine dispersal of wild oat seed. In the chaff return treatments wild oat seed was dispersed for 250 seconds past the wild oat patch (150 m), whereas in the chaff collection treatments most wild oat seeds were dispersed for approximately 50 s (30 m). However, in both treatments there were small amounts of wild oat seed that were still being expelled from the combine even as far as the maximum distance. This long dispersal tail may indicate that the dispersal continues at a very low level for a long distance.

The green foxtail seed dispersal is shown in Figure 3.5. It was not possible to fit equation 1 to the green foxtail data. The means of green foxtail seed density with standard errors are, therefore, presented instead. The effect of chaff collection with this weed species is more pronounced than with wild oat. There was over a tenfold difference in green foxtail seed dispersed at any given time between the chaff return and chaff collection treatments. Unlike wild oat, the green foxtail seeds dispersed by the chaff collection treatment never did level off. This may have been due to the low indigenous infestation of green foxtail over the entire experimental or it may simply reflect the tendency of green foxtail to be dispersed further than wild oat.

The values of the parameters for the fitted regressions shown in Figures 3.3 and 3.5 are given in Table 3.1 with the coefficient of determination. Chaff collection was always significantly ($P < 0.05$) different from chaff return for both parameters in all experiments. However, the slope of the decline (*b*) was inconsistent from 1995 to 1996. In 1996 the slope of the decline for chaff collection was greater than chaff return whereas in 1996 the slope for chaff collection was lower than the slope for chaff return. This could have been due to the imperfect fit of equation 1 to the data. In using equation 1 the *a* parameter often overestimated, in order in order to fit the curve properly (Figure 3.3). Another reason for the discrepancy between years could be the much longer sampling period in 1996.

The reason for the difference in wild oat dispersal between the two experiments in

1995 is not fully known (Table 3.1). It could have been due to the difference in wild oat plant population density within the patch at harvest. In the WO experiment there were 1 600 wild oat seeds m^{-2} at swathing, while in the WOGF experiment there were 2 800 wild oat seeds m^{-2}. This higher density of seeds in the WOGF experiment probably accounts for the differences ($P < 0.05$) between experiments in the parameter estimates for both a and b. Similarly, in 1996 there was a much higher density of wild oat seed in the patch at swathing (approximately 5000 m^{-2}) versus 1995. Because of this increase in wild oat seed density the peak of wild oats discharged in the chaff return treatment increased, causing the value of parameter a to be greater. However, the slope (b) remained relatively consistent between years in the chaff return treatment.

The values for dispersal in these experiment indicate weed seeds may be dispersed much further by combine harvesters than earlier reported. Based on reported operating velocities of the combines (Howard et al. 1991) or estimates of field combine velocity, most other studies have only reported seed dispersal by combine up to 40 seconds past the weed patch (Ballaré et al. 1987 a; McCanny and Cavers, 1988; Ghersa et al. 1993; Rew and Cussans, 1995). The greater seed dispersal observed in this study may be due to differences in machine design. Ballaré et al. (1987 a) assessed the effect of combine design on the seed dispersal of *Datura ferox* L. Two slightly different conventional combines spread weed seeds up to the maximum experimental distance of 21 m. A combine harvester with an additional cleaning fan spread seeds of *D. ferox* up to 98 m. These results suggest that a more complex machine disperses weed seeds further because seeds spend more time inside the machine.

Chaff collection resulted in fewer wild oat seedlings the following year than did chaff return (Figure 3.6), although the difference in seedling numbers was not as great as the difference in seed return (Compare Figure 3.4 with Figure 3.6). The seedlings that preceded the patch and those found in the patch were not shown as they did not differ between treatments. These seedlings were the result of wild oat seeds shed prior to harvest.

3.3.2 Natural Wild Oat Seed Dispersal

Figure 3.2 shows the total number of naturally dispersed wild oat seeds for all six replications collected in each trap location. There were a total of 159 wild oat seeds collected during seed shed. There was a large directional component of natural seed dispersal with 69% of the wild oat seeds trapped falling in the north east portion of the assay area. This was probably the result of a permanent lean that developed in the panicles because of the prevailing SSW wind during the period from panicle extension to early kernel development in wild oat (Appendix 1). Wild oat plants lean over from the wind and the seeds fall directly to the ground. Marshall and Butler (1991) observed that seeds of broad-leaved dock (*Rumex obtusifolius* L.) and orchard grass (*Dactylis glomerata* L.) both had a directional component to seed dispersal which was influenced by prevailing wind direction. Nadeau and King, (1991) noted that most of the seeds of *Linaria vulgaris* L. were dispersed to the south and west of the parent plant. Auld (1988) found that *Cardus tenuiflorus* Curt. had a wind-influenced seed dispersal directionality that resulted in seed spread greater than 4 m by the prevailing wind. This study also confounded natural dispersal with dispersal by mowing and grazing, and therefore may have masked any directionality that occurred from natural dispersal.

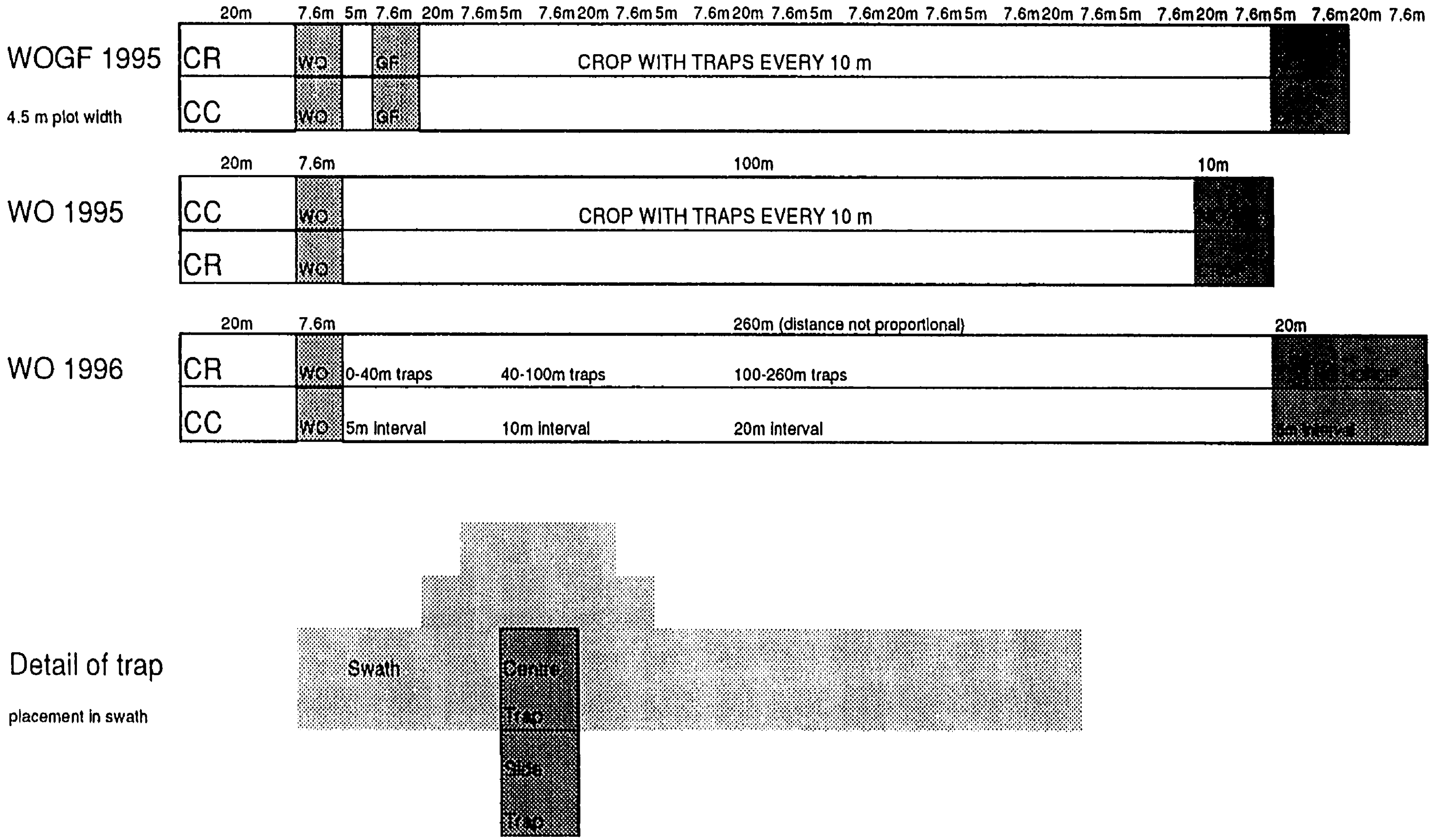
More than one half (53%) of the wild oat seeds were trapped in the six traps positioned 0.866 m from the wild oat plant. Based on calculated seed densities, 85% of the wild oat seed fell within a 0.866 m radius around the wild oat plant. The natural dispersal distance for wild oat in this study is slightly greater than that observed in other large seeded annual weeds. For example, Howard et al. (1991) observed that natural dispersal of two species of *Bromus* was less than 0.50 m when grown with wheat. The furthest assayed natural dispersal distance in this experiment was 1.5 m. At this distance four seeds were trapped and this raised the possibility that the experiment did not assay the total natural dispersal distance of wild oat. However, it is doubtful that natural dispersion would have carried the seeds much further as the wild oat plants did not exceed 1.4 m in height. O'Toole and Cavers (1983) found that proso millet rarely dispersed seed further than the height of the plant. Results of the present study suggest that relative to combine dispersal, natural seed dispersal of wild oat is short distanced.

3.4 Summary and Conclusions

The combine dispersal of wild oat has the potential to move wild oat seeds in excess of 150m in the field. The maximum natural dispersal distance of 1.5m appears to be insignificant when compared with combine dispersal. However, the proportion of seeds that are dispersed with each vector must be considered. As most of the wild oat seeds will usually be shed from the seed at harvest, natural dispersal may be important in phalanx (Lovett-Doust, 1981) patch expansion. By expanding in a slow wave there will always be a dense patch for the population to fall back on if a series of unfavourable growing conditions are encountered.

In contrast to natural dispersal, long distance dispersal of a small proportion of the weed seeds (ie. Combine dispersal) is more analogous to a guerilla (Lovett-Doust, 1981) type invasion. The combine carries weed seeds to areas which are far from the original patch. If recruitment is successful then a new patch may be established. These two types of dispersal in tandem comprise a strategy termed infiltrative invasion (Wilson and Lee, 1989). In this strategy occasional long distance dispersal results in the establishment of new patches beyond the expanding wave of the original patch. Short distance natural dispersal serves to consolidate areas around the patch and to maintain an expanding high density front.

This study demonstrated that chaff collection can greatly reduce the dispersal of wild oat and green foxtail. It appears that the utility of chaff collection in wild oat occurs mostly because of a reduction in weed seed dispersal distance and not through an increase in net export of seeds from the field though export of weed seeds was not calculated. The proportion of weed seeds that are brought into the combine using chaff collection can greatly reduce the dispersal of wild oat and green foxtail. However, the year to year variation in seedling recruitment may mask the effect of mechanical dispersal.



WOGF 1995
4.5 m plot width
20m 7.6m 5m 7.6m 20m 7.6m 5m 7.6m 20m 7.6m 5m 7.6m 20m 7.6m 5m 7.6m 20m 7.6m 5m 7.6m 20m 7.6m 5m 7.6m 20m 7.6m 5m 7.6m 20m 7.6m
CR
WO
GF
CROP WITH TRAPS EVERY 10 m
CC
WO
GF
WO 1995
20m 7.6m 100m 10m
CC
WO
CROP WITH TRAPS EVERY 10 m
CR
WO
WO 1996
20m 7.6m 260m (distance not proportional) 20m
CR
WO
0-40m traps
40-100m traps
100-260m traps
CC
WO
5m interval
10m interval
20m interval
Detail of trap
placement in swath
Swath
Centre
Trap
Side
Trap

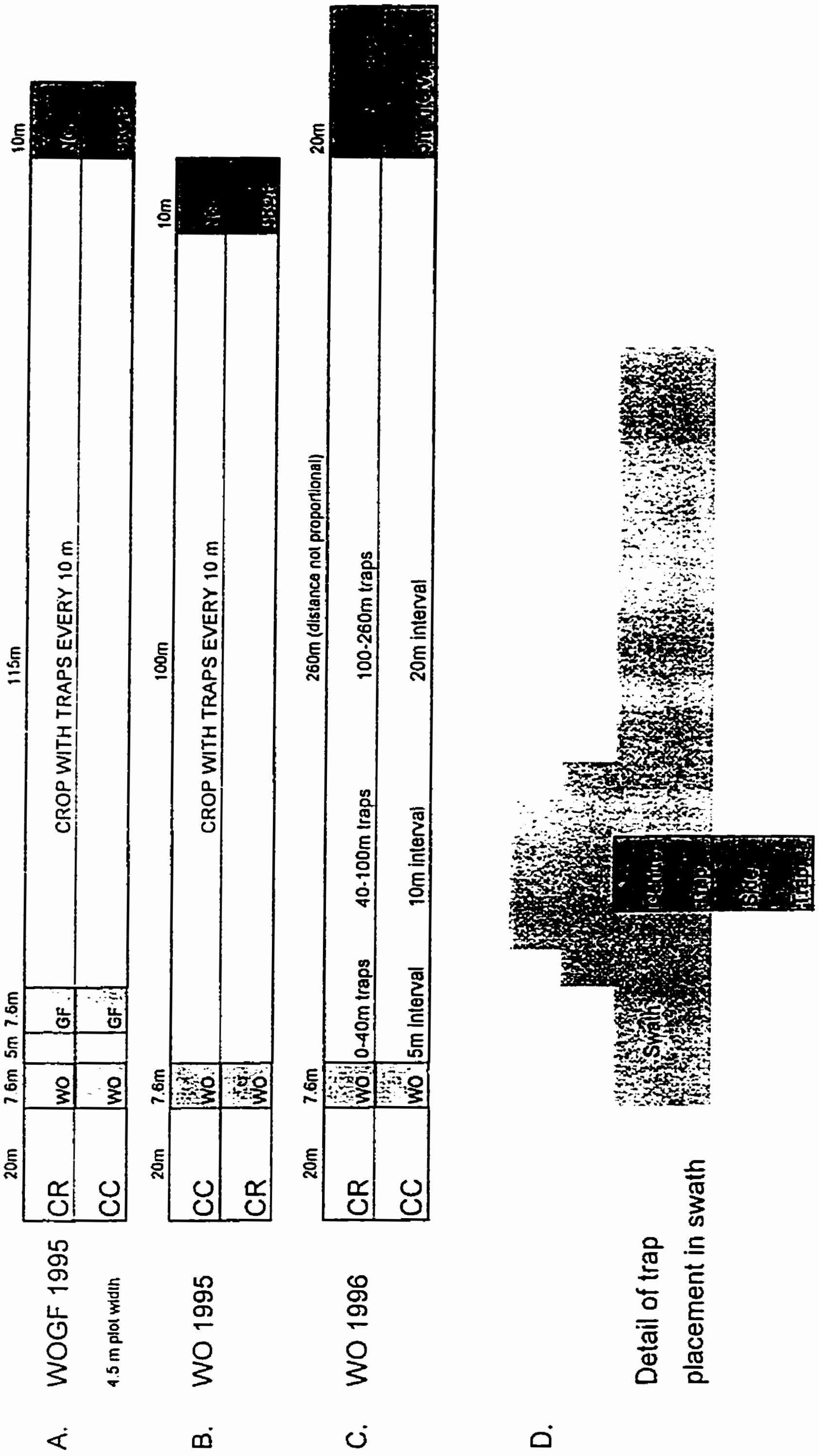


Figure 3.1. Chaff collection experiment plot layout for WOGF 1995 experiment (A), WO 1995 experiment (B), WO 1996 experiment (C) and detail of trap placement in swathes (D). CC - chaff collection, CR - chaff return.

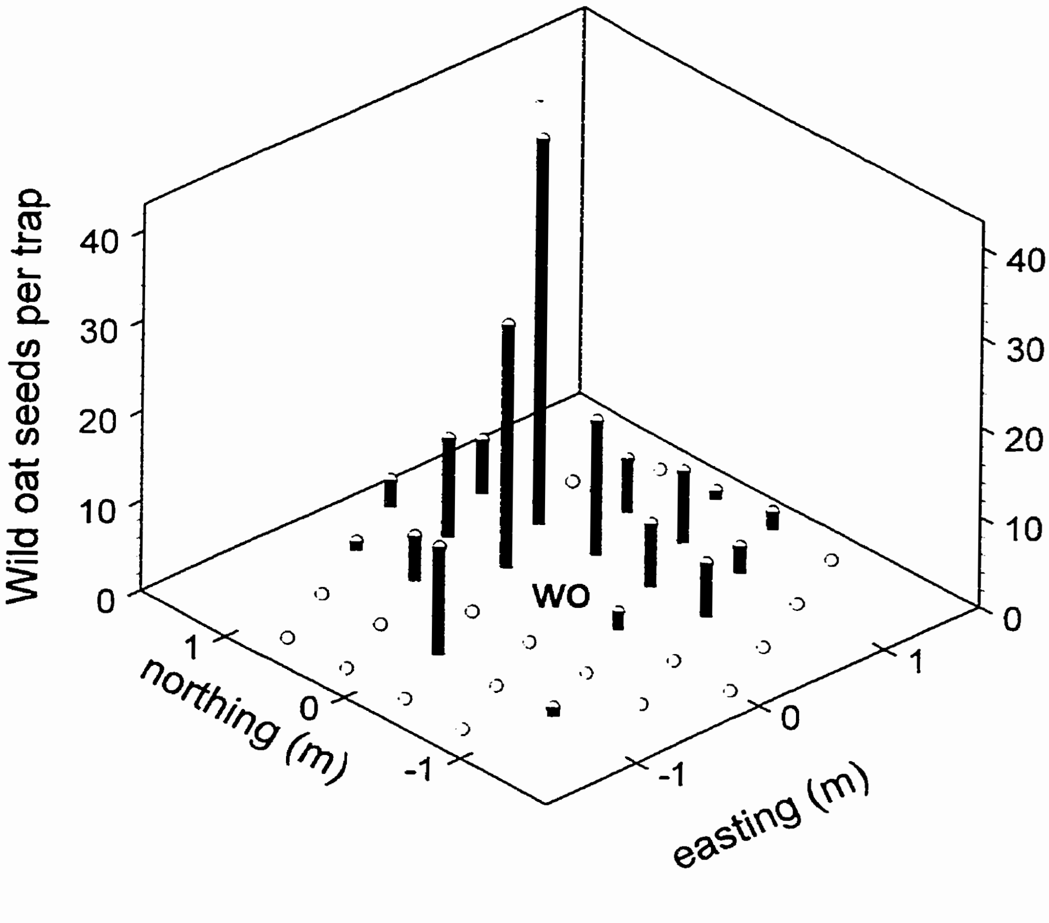


Figure 3.2. Natural seed dispersal of wild oat from six individual plants (position designated by wo) collected at trap locations in a hexagonal array.

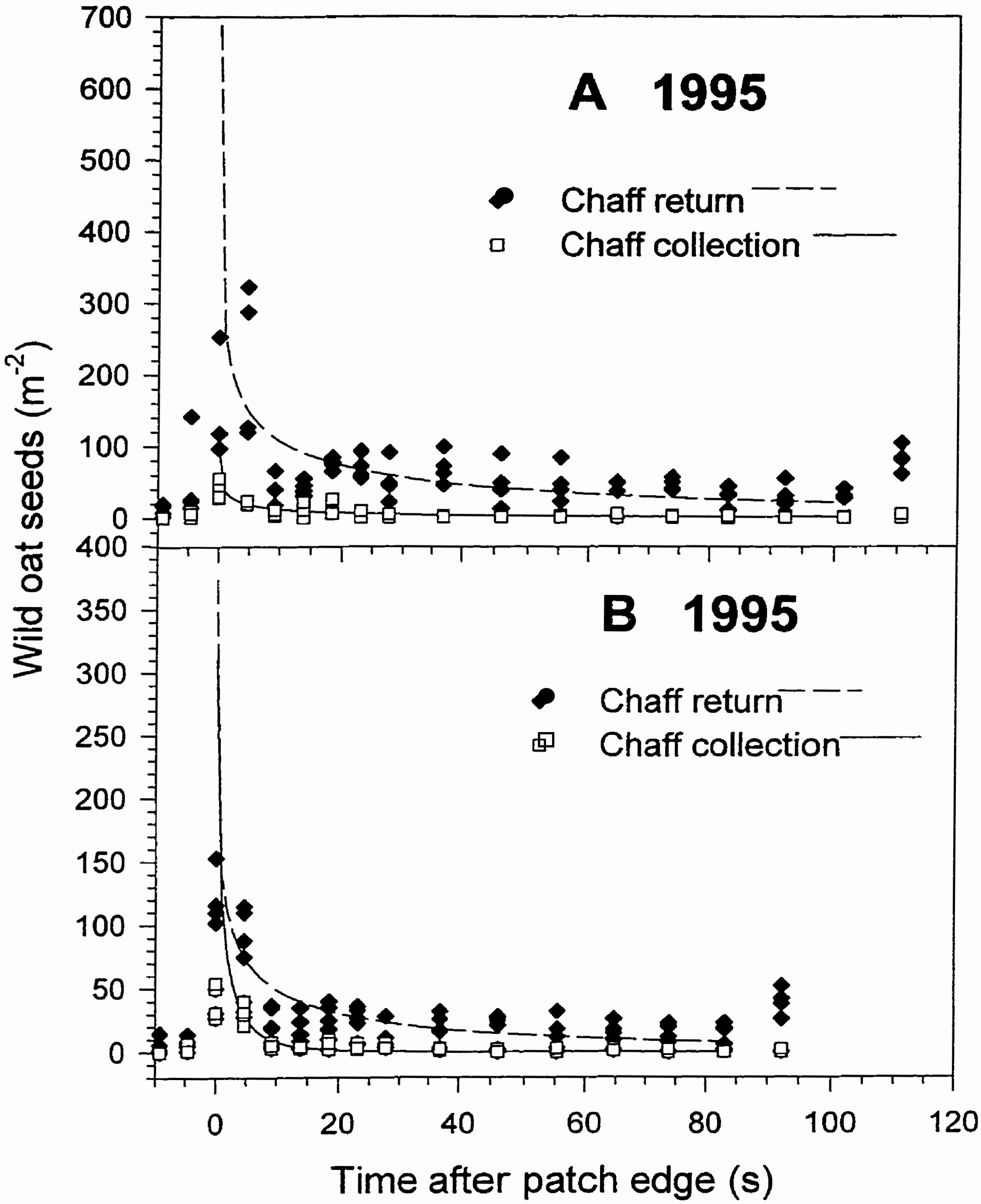


Figure 3.3. Dispersal of wild oat in 1995 for the WOGF experiment (A) and WO experiment (B). Symbols indicate seed density and lines represent fitted regressions.

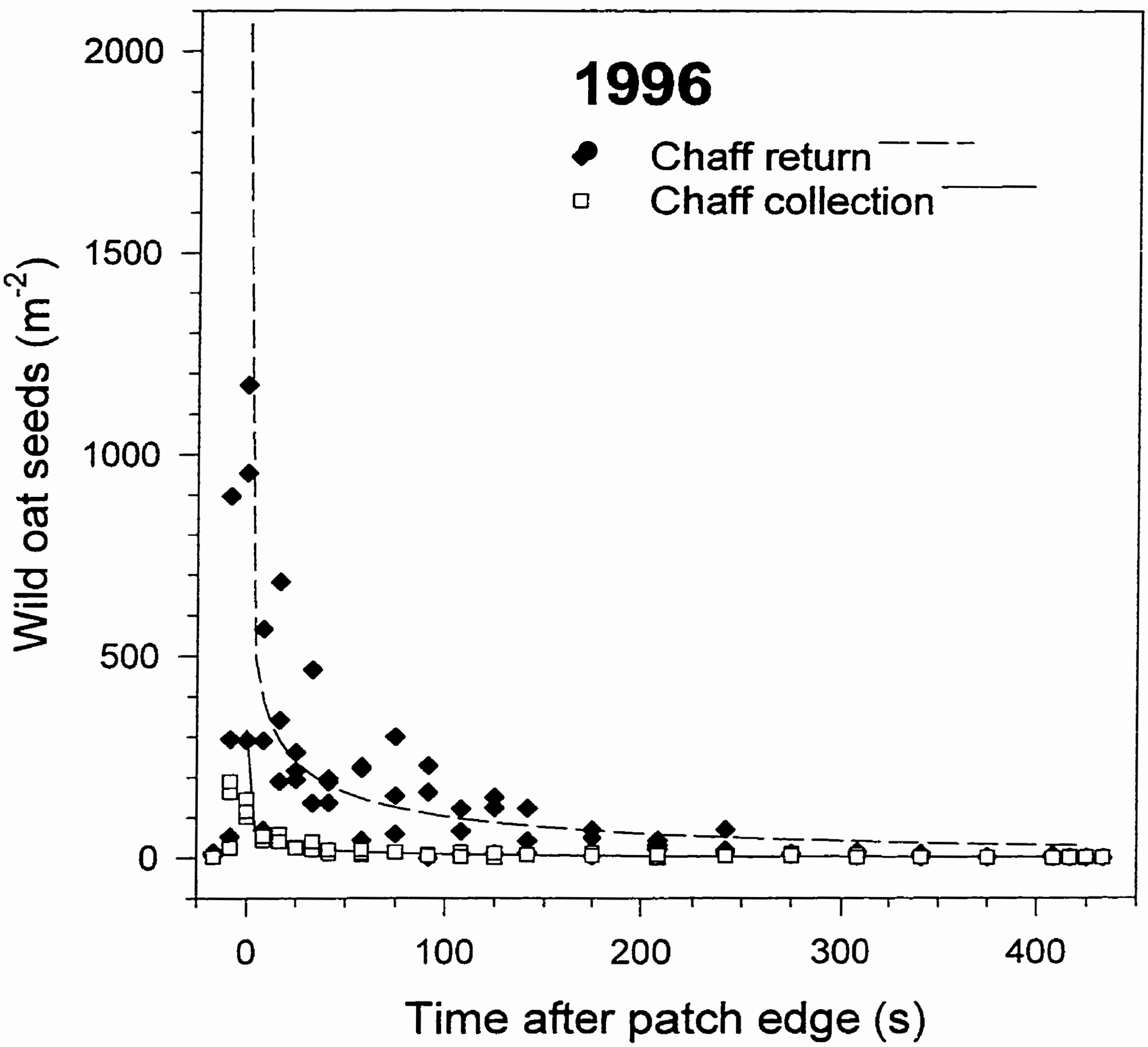


Figure 3.4. Dispersal of wild oat in 1996. Symbols indicate seed density and lines represent fitted regressions.

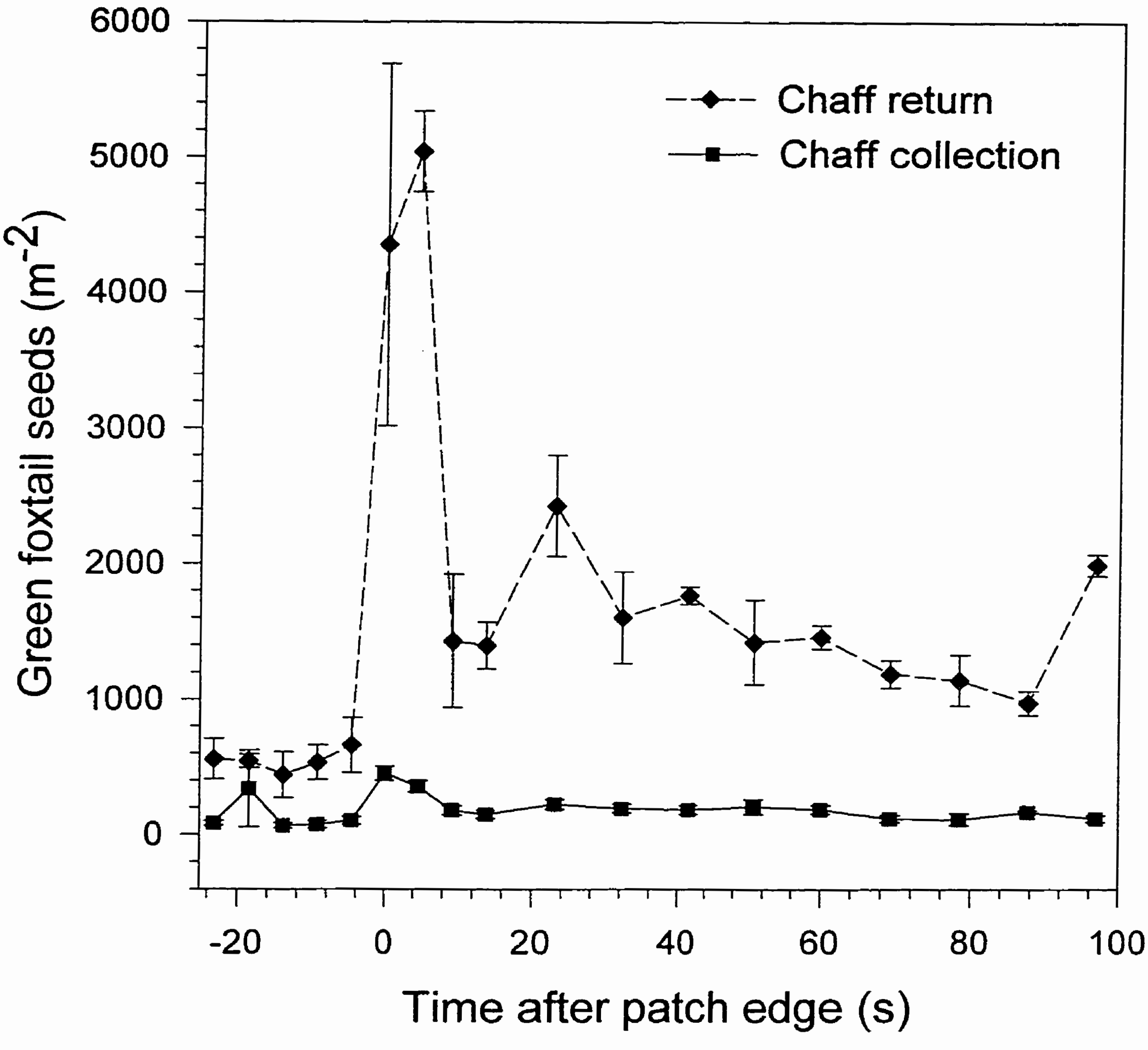


Figure 3.5. Dispersal of green foxtail in 1995 for the WOGF experiment. Data points are for means ± standard error of four replicates.

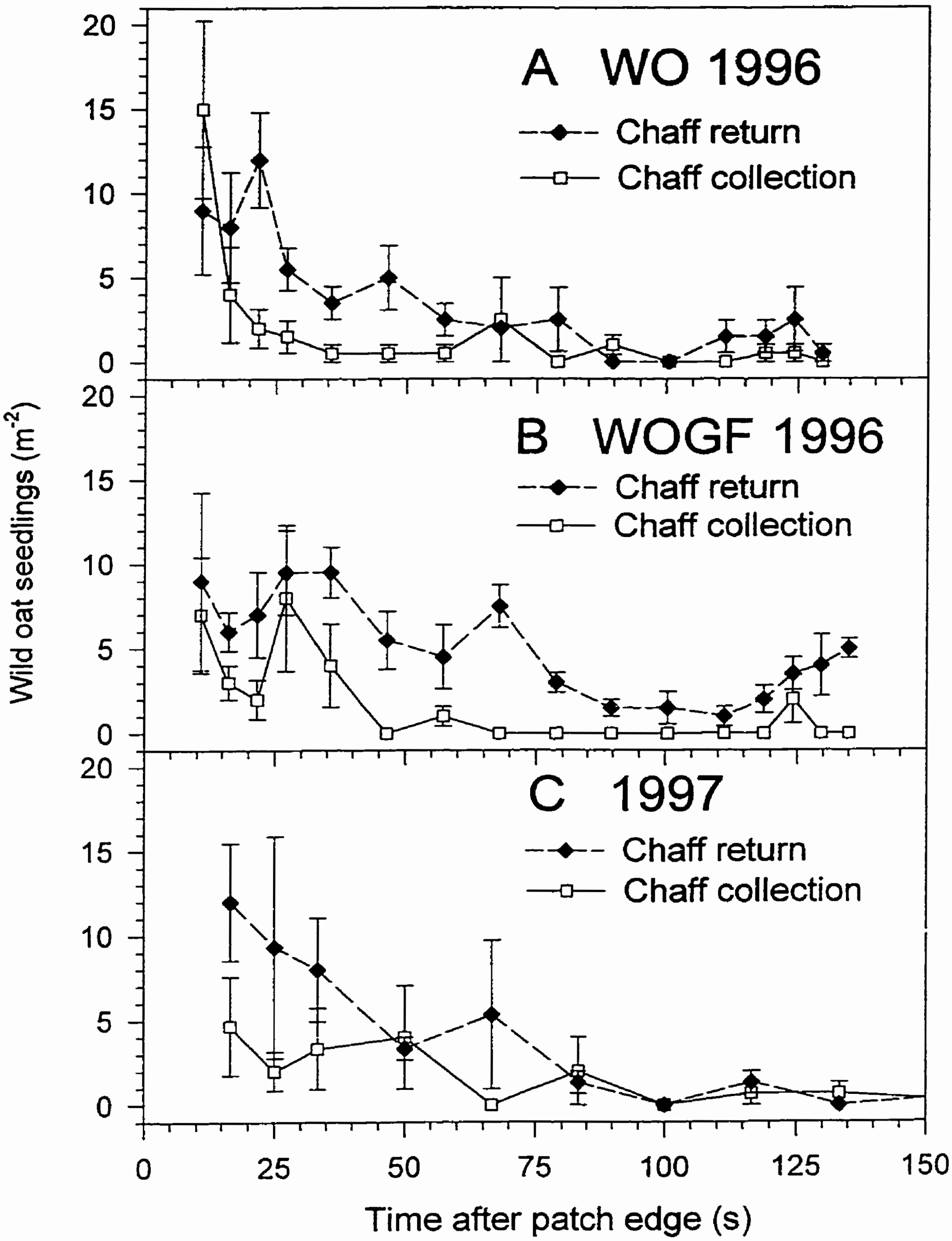


Figure 3.6. Seedling recruitment of wild oat in 1996 and 1997 in area where previous years experiment was performed. Data points are for means ± standard error of four replicates.

Table 3.1. Parameter estimates[a], standard errors (S.E.) and coefficient of determination (R^2), describing the effect of chaff collection on the mechanical dispersal of wild oat by a combine harvester. WO refers to the wild oat experiment and WOGF refers to the experiment with both wild oat and green foxtail (although only the dispersal of wild oat was fitted).

Year	Treatment	*a*	S.E.	*b*	S.E.	R^2
1995	Chaff collection WO	310.3	47.35	0.5618	0.0338	0.8112
	Chaff return WO	373.6	46.93	0.3070	0.0215	0.5785
	Chaff collection WOGF	100.0	14.46	0.3227	0.0246	0.7507
	Chaff return WOGF	688.5	108.9	0.2701	0.0254	0.3960
1996	Chaff collection	318.1	27.45	0.2010	0.010	0.8424
	Chaff return	2067	344.7	0.3239	0.0199	0.5277

[a] Refer to Results and Discussions section for a description of the model fitted.

4.0 The Development and Seed Shatter of Wild Oat (*Avena fatua*) in Relation to the Development of Spring Wheat (*Triticum Aestivum* L.)

4.1 Introduction

Wild oat (*Avena fatua* L.) is the second most common weed in Manitoba (Thomas et al. 1998) and occurs in 65% of all arable fields. Wild oat is a competitive weed that significantly reduces the yield of the crop and contaminates the commercial seed. Despite the importance of this weed, little information is known about its phenological development in the Canadian prairies.

In the previous chapter the potential of combine harvesters to disperse wild oat seeds long distances was established (see Chapter 3). For wild oat to be dispersed it has to be taken into the combine. As wild oat has a tendency to shed its seeds before or at harvest (Sharma and Vanden Born, 1978), the amount of seeds that are brought into the combine in production agriculture may be minimal. To determine the proportion of seeds that are taken into a combine, Cousens and Mortimer (1995) recommended that the phenological development of weeds be characterized in relation to farming operations.

The phenological development of grasses can be compared using the phyllochron interval. A phyllochron interval is the amount of thermal time that occurs between successive Haun leaf stages (Haun, 1973) in the vegetative life stage of grasses. The concept of thermal time allows precise estimates of a plant's phenology in varied environments. By relating plant development to thermal time, the effect of temperature on development is accounted for. Temperature is assumed to have a linear effect on the rate of leaf development above the base temperature of growth for the plant (Kirby, 1995). This relationship is often linear for the entire vegetative stage of the plant.

Previous studies that have compared the phyllochron interval in wild oat to wheat have produced conflicting results. Cousens et al. (1992) found that wild oat and wheat had a similar phyllochron interval. However, Ball et al. (1995) found that the phyllochron interval was shorter in wild oat than in wheat and Cudney et al. (1989) found that the phyllochron interval of wild oat was longer than wheat. All of these studies were done with a different base temperature used in the calculation of thermal time thereby making comparisons between studies impossible.

Other methods of measuring plant development include the Zadoks (Zadoks et al. 1974) developmental scale. The Zadoks (1974) scale divides the life cycle of the plant into successive development stages such as tillering and anthesis, and is therefore more descriptive through the life cycle of the plant. However, it has the disadvantage of not having an easily defined mathematical relationship to thermal time.

In studies where wild oat seed shed has been measured, it has never been related it to thermal time and only one study has included sequential harvests (Wilson, 1970). As a result, estimates of seed shed in wild oat at crop maturity vary from 44% to 99% (Wilson 1970; Metz 1969; Feldman and Reed 1974; Naverette 1984 from Gonzalez-Andujar and Perry, 1995).

The objective of this study was to characterize the development of wild oat in comparison to the development of spring wheat. As part of this objective the rate of seed shed in wild oat relative to the development of wheat was characterized. All development measures were related to thermal time to allow comparisons between years and locations.

4.2Materials and Methods

4.2.1 Phenological Development

4.2.1.1 1995

A field experiment consisted of staging wheat within nine plots of a completely randomized design. It was conducted at Carman, (lat. 49° 30' N, long. 98° 2' W) in 1995. Wild oat seed was spread on the soil surface at a rate of 250 viable seeds m^{-2} with a Valmar Airflo pneumatic broadcaster (Elie, MB) on May 17, 1995. The seed was incorporated by cultivating and then packing the strips with packing harrows. The following day the experimental area was sown to spring wheat (*Triticum aestivum* L. cv. Katepawa) at 75 kg ha^{-1} with a hoe-drill. Two wheat and wild oat plants were ringed in each of the nine plots as they emerged in order to track plants that emerged on the same day. The development of these plants was measured twice weekly using Zadoks plant development scale (Zadoks et al. 1974) and the initiation of seed shed in wild oat was noted. Daily maximum, minimum and mean air temperatures were recorded at both locations at Stevenson screen height (1.5 m) by the Environment Canada station located on the experimental farm at Carman, Manitoba.

4.2.1.2 1996

An experiment consisted of a field experiment with ten replications conducted at two locations; Winnipeg (lat. 49° 49' N, long. 97° 7' W) and Carman. In 1996 wild oat was seeded prior to planting the experimental area to spring wheat cv. Katepawa. Individual wheat and wild oat plants were ringed as they emerged in order to track plants of similar age. The development of these plants were tracked twice weekly using the Haun (1973) and Zadoks scales (Zadoks et al. 1974). One wild oat and one wheat plant were tracked daily within each of ten replications at each location. Daily maximum, minimum and mean air temperatures were recorded at both locations at Stevenson screen height (1.5 m), and were measured at Carman by the Environment Canada station, and at Winnipeg by a Campbell Scientific model CR21X micrologger (Campbell Scientific Inc., 815 West 1800 North, Logan, UT).

Prior to the onset of, and during seed shed, plants were harvested weekly in individual plots within each replication to determine the amount of seed shed. The number of wild oat florets was recorded as well as the number of glumes from which seeds had been shed. The percentage seed shed was recorded directly for the first three harvests at each location. Following the third harvest, the panicles of the plants began to break down, thereby making it impossible to determine the initial floret number. In order to estimate the total floret number that was present on these plants prior to panicle breakage, a regression on total floret number versus number of tillers was performed for the first three harvests at each location. These regressions were significant and the slopes were used to determine the potential seed output for plants harvested on the last three harvest dates.

4.2.2 Analysis

Thermal time was used so the differential effect of temperature at different locations could be accounted for. Growing degree days (GDD), were calculating using the following equation:

$$GDD = \sum_{s1}^{s2} (T_m - b_o) \qquad [1]$$

where *Tm* is the mean daily temperature, *bo* is the base temperature and *S1* and *S2* are development stages 1 and 2. GDD is a summation measurement incorporating the accumulated degree days for every day from development stage 1 to 2. The base temperature used was 0 C (Gallagher, 1979; Baker et al. 1980; Bauer et al. 1984; Cao and Moss, 1989)

The relationship between percent seed remaining on the panicle and GDD had a sigmoidal shape and the following log-logistic equation was fit to it:

$$Y = a + \frac{(100 - a)}{1 + e^{b \cdot (GDD - c)}} \qquad [2]$$

In equation 2, *Y* is the estimated percentage wild oat seed that is remaining on the plant, *a* is the lower asymptote of seed shed, 100 is the upper asymptote, *b* is the slope of the exponential decline, *c* is the point at which one half seed shed occurs and *GDD* is the growing degree days since emergence, base temperature 0 C. Linear and nonlinear regression analysis was performed on the data using either the GLM and NLIN procedure of SAS (Statistical Analysis Systems Institute 1986). The slopes of the linear regressions were compared using an extra sum of squares F-test (Ratkowsky, 1983).

4.2.3 Base Temperature Selection

The base temperature that is used to calculate accumulated GDD is usually determined by comparing the coefficients of variation of the regressions of development versus GDD for various base temperatures. This process was employed and there was little difference in base temperatures between -5 C to 5 C. Cousens et al. (1992) noted this phenomena and chose a base temperature for leaf appearance of -5 C. A base temperature of -5 C appears illogical as plant development usually ceases below 0 C. The choice of -5 C as a base temperature was defended by explaining that a base temperature is essentially an extrapolation and that a base temperature below 0 C does not presume that development occurs below 0 C. A base temperature of 0 C allows easy comparison to other studies (Gallagher, 1979; Baker et al. 1980; Bauer et al. 1984; Cao and Moss, 1989) and in the absence of a significantly better option, would seem to be the proper choice.

There can be additional problems in the calculation of GDD. The response of phyllochron interval to average temperature is typically sigmoidal and not linear (Shaykewich, 1995). The average temperature used in the calculation GDD is usually calculated by averaging the maximum and minimum daily temperature and subtracting the base temperature. However, this may not be equivalent to a mathematical average of the daily temperature. To alleviate this problem, Shaykewich (1995) recommends that average temperatures over a three hour time period be used instead of daily averages.

A more significant problem is that a daily average may not estimate the true base temperature when the average temperature for the day is close to 0 C. This happens because on a day when the average daily temperature is under the physiological base temperature for development, there may be a portion of the day when the temperature is higher than the physiological base temperature and as a result, the plant will still undergo some development during this portion of the day. Therefore, a daily average may underestimate the base temperature when the temperature is close to 0 C. As a result, growth and development may appear to continue even on days when the average temperature is below physiological base temperature.

4.3 Results and Discussion

In 1996 wild oat and wheat, accumulated 155.6 and 146.8 GDD at Carman and Winnipeg respectively, from time of seeding to emergence. Although individual plants of identical age were tracked, it was observed that most of the other wild oat plants emerged later than the wheat. Bauer et al. (1984) observed that emergence in spring wheat required from 94 and 138 GDD.

The rate of leaf appearance, as expressed by the Haun growth stage (Haun 1973), had a strong linear relationship to thermal time for wild oat and wheat, at both locations (Figure 4.1). The phyllochron interval was determined by the slope of the linear regression relating Haun leaf stage (Haun, 1973) to GDD. The phyllochron interval at Carman was 77.0 GDD for wild oat and 85.0 GDD for wheat. At Winnipeg the phyllochron interval was 99.0 GDD for wild oat and 105.1 GDD for wheat. The average rate of leaf appearance for wild oat and wheat was 25% higher at Carman than at Winnipeg. This difference between the locations was highly significant ($P < 0.01$). However, within locations, the phyllochron intervals of wheat and wild oat were consistent in relation to each other and did not differ significantly ($P < 0.05$).

The phyllochron interval for wild oat and wheat observed in this study were similar to those reported by others. Ball et al. (1995) used a base temperature of 0 C for development and found that wild oat had a lower phyllochron interval than winter wheat for two locations in Oregon. The phyllochron interval for winter wheat averaged 106.1 GDD and for wild oat it was 76.2 GDD. The higher phyllochron interval observed for wheat may be related to the winter annual habit of the wheat crop. The phyllochron interval reported for wild oat by Ball et al. (1995) is similar to that observed in the present study. However, unlike their results, where the development rate of wheat and wild oat differed, the present study showed similar phyllochron intervals within locations for wheat and wild oat.

Adjusting the base temperature used in the calculation of GDD allows the comparison of the phyllochron intervals observed in this study to other studies with different base temperatures. Using this approach the phyllochron intervals observed in this study were similar to others observed for wild oat and wheat. For example, Cousens et al. (1992) found that wild oat and wheat each had an average phyllochron interval of 99.0 when a base temperature of -5 C was used. Adjusting the base temperature to -5 C in the calculations for GDD in the present study yielded a phyllochron interval for wild oat of 96.1 GDD and 124.7 GDD at Carman and Winnipeg. For wheat the phyllochron interval at a base temperature of -5 C was 108 GDD and 129 GDD at Carman and Winnipeg, respectively. Cousens et al. (1992) also observed variability between locations for phyllochron interval (wheat ranged from 83.7 to 108.7 GDD and wild oat 85.5 to 101 GDD). Using a base temperature of 5 C, Cudney et al. (1989) calculated a phyllochron interval of 81 GDD for wheat and 84.5 GDD for wild oat. When results of the present study were calculated using a 5 C base temperature, the phyllochron interval for wild oat was 55 GDD and 75 GDD at Carman and Winnipeg, respectively. For wheat the phyllochron interval based on a base temperature of 5 C was 44 GDD and 78 GDD at Carman and Winnipeg, respectively. In summary, when results from the present study were compared with previously published results using common base temperatures the phyllochron intervals in the present experiment for both wheat and wild oat were higher than those found by Cousens et al. (1992) and lower than those found by Cudney et al. (1989). These differences in phyllochron interval may be attributed to differences in environmental conditions such as day length, as the Cousens et al. (1992) study was conducted in England and the Cudney et al. (1989) study was conducted in California.

Genetic differences may also be responsible for the differences in phyllochron interval (Miller et al. 1982). In the present study the same wild oat population was used at both locations. This wild oat population was originally collected at a third site, Portage la Prairie, MB, approximately 50 km from either site. Therefore the differences between locations in phyllochron development observed in the present study are not caused by genetic differences and therefore may be caused by environmental differences.

The phyllochron interval in monocots is determined mainly by thermal time, as expressed by GDD (Kirby, 1995). However, other environmental factors such as nutrient availability, water availability (Wilhelm and McMaster, 1995), day length (Cao and Moss, 1989) and soil strength (Masle and Passioura 1987) can also affect the phyllochron interval. Because of differing environmental conditions at the two locations in the present study, it is not surprising to see differences in average phyllochron interval between locations. The previous crop at the Carman site was alfalfa which can provide nitrogen to the following crop (Hesterman et al. 1987). As well, the seed bed in Winnipeg was very hard and dry resulting in spindly seedlings that never fully recovered from the early season stress.

Wild oat and wheat development, as measured by Zadoks plant developmental scale, was consistent between years and locations (Figure 4.2). There was a difference between the development of wild oat and wheat that remained consistent between location and year. As Zadoks scale measures the transition between different development stages, one of the controlling factors would be the initiation of anthesis. In long day plants such as wheat, anthesis is controlled by day length. Major (1980) found that wheat, barley and oats had an optimum photoperiod for flowering of approximately 17 hours. Increasing the photoperiod beyond 17 hours did not increase the rate of development. Because of the photoperiod effect it may have been expected that there would be a varying amount of vegetative development before anthesis. However, in western Canada day length is relatively consistent during the time of vegetative development in cereals. At Winnipeg, the day length peaks on June 23 at 16.1 hours. The period from May 28th to

July 15th has greater than 15.5 hours of daylight. This period would comprise most of the vegetative growth of cereal grains and may explain why it is that within the narrow seeding interval that is typically occurs in western Canada, the effect of day length is relatively unimportant in determining the timing of flowering in cereals. As a result it should be assumed that development into different growth stages is controlled mainly by thermal time.

Wild oat and wheat both proceeded through developmental stages at a similar rate even though the phyllochron interval was different between locations. In 1996 this occurred because the plants at Carman accumulated more leaves before heading than the plants at Winnipeg. The average number of leaves for wild oat and wheat at Carman was 9.8 and 8.9 respectively. The average number of leaves for wild oat and wheat at Winnipeg were 7.8 and 7.2 respectively. This large difference in leaf accumulation between sites may reflect the stress that the Winnipeg site experienced. Based on the present study, it would appear that phyllochron interval is more variable than Zadoks plant growth stages (Zadoks et al. 1974). Between locations the phyllochron interval varied while the Zadoks stage did not.

A three parameter sigmoidal function (equation 2) was fitted to measurements of the percentage seed remaining on the wild oat panicles (Figure 4.3) was fitted with. The fit of the equation was very good with a coefficient of determination of 0.9916. The seed shed began slowly but progressed very rapidly with most of the seeds falling off the panicles within a two week period between 1 470 and 1 680 GDD. The good fit of the sigmoidal equation suggests that seed shed should level off at approximately 1 850 GDD when 9% of the seed still remaining on the plant. However, the lower asymptote may be an anomaly caused by the last harvest date at Winnipeg, as the Carman data shows a steeper rate of seed shed between 1 750 GDD and 2 100 GDD than does the Winnipeg data. The initiation of seed shed was noted in 1995 and is indicated by an arrow on Figure 4.3. The timing of the beginning of seed shed in 1995 is very similar to that for both locations in 1996 and suggests that the relationship between seed shed and thermal time is consistent across years. A reexamination of Wilson's (1970) data reveals a general sigmoidal pattern of wild oat seed shed. Other studies have found similar amounts of wild oat seed remaining on the panicles at harvest in spring grown crops. Estimates have varied from 34% to 56% wild oat seed remaining at barley harvest (Wilson 1970; Metz 1969), and from 27% to 50% in spring wheat (Feldman and Reed 1974). In winter wheat, however, only 1 to 5% the wild oat seeds is remaining on the panicles by the time of harvest (Wilson 1970; Naverette 1984 from Gonzalez-Andujar and Perry 1995).

The period of seed shed observed in a production agriculture situation will be longer than that observed in the present study. Wheat and wild oat of similar age were tracked in the present study. In production agriculture wild oat may emerge before with and after the crop. Because of the multiple cohorts of seedlings emerging, the period of seed shed would be longer. This may allow the producer more flexibility in attempting to manage the proportion of seed shed in wild oat.

Percentage wild oat seed shed closely follows wheat head water content (Figure 4.4). Wheat is usually harvested when head moisture content is below 20%, a point where most of the wild oat seed would be shed. However, wheat can be windrowed at 60%

head moisture content without a loss in yield (Bauer and Black 1989), providing an opportunity to manage the percentage seed shed of wild oat at harvest.

As there is no direct mechanistic relationship between seed shed in wild oat and head water content in wheat, it may be argued that the correlation in Figure 4.4 is artifactual. However, the relationship may be a result of coevolution between wild oat and wheat based cropping system. Harvest usually takes place during the period of seed shed in wild oat (Wilson 1970; Metz 1969; Feldman and Reed 1974). This occurs even in diverse geographic and climatic regions. As grain varieties are bred for environmental conditions of that area and have varying maturity times, it could be that wild oat has evolved to synchronize seed shed with crop harvest. This strategy would allow wild oat to maximize seed output by having as long a growing period as possible throughout the crops growth. As seed shed would begin before harvest, most of the seeds would remain in the field to maximize evolutionary fitness. However, a portion would be exported from the field in the harvested grain which could allow wild oat to be dispersed through contaminated seed.

Genetic variation in the development of wild oat from different locations has been reported (Miller et al.1982). The morphological and developmental differences in 200 single plant accessions from the Red River Valley of Minnesota and North Dakota as well as 30 from western North Dakota was assessed. Heading date averaged 57 days but ranged from 47 to 67 days. The initiation of seed shed was not measured but could be presumed to correlate with heading date.

The sampling of genetic material in the study by Miller et al. (1982) may accentuate the observed genetic differences between the wild oat lines. As the single plant accessions were selected based on morphological differences, they may reflect the extremes that exist within a population of wild oats. As wild oat exists in the wild as a population, one would expect variation in morphological and developmental characteristics within a population. Sampling the extremes of individual populations would overestimate the variation that occurs between populations. However, these results do indicate that there are genetic differences in the development of wild oat within a geographic region.

Phyllochron interval in cereals is also under genetic control. Bauer et al. (1984) observed that the phyllochron interval of hard red spring wheat fell into two groups, with phyllochron intervals of 73 and 81 GDD. Differences in the phyllochron interval of wild oat between this study and studies in England (Cousens et al. 1992) and California (Cudney et al. 1989) indicate that there may be a genetic as well as an environmental difference in wild oat development.

The lack of a difference between the development of wild oat and wheat within location as measured by both the Haun scale (Haun, 1973) and Zadoks scale (Zadoks et al. 1974), indicates that these plants respond in a similar way to environmental variables. Therefore a developmental model may not describe the development of wild oat or wheat absolutely, but the difference from the predicted values will be similar for both wild oat and wheat. The relative leaf stage of wild oat should remain constant with that of wheat.

The timing of harvest will determine the proportion of wild oat seeds that remain on the plant and can be taken into the combine at harvest. If the crop were swathed early, at 60% head water content, then over half of the wild oat seeds could still be on the panicles of the plant at harvest. If the crop were straight combined (harvesting without a windrowing operation) when the wheat head moisture content was 10%, most of the wild oat seeds would have fallen from the plant. It is difficult to predict which strategy would be best for wild oat control. An early harvest would maximize the wild oat seed export from the field, and if done in conjunction with chaff collection, could prevent significant dispersal. A later harvest would allow most of the wild oat seed to fall on the ground, and little weed seed would be taken into the combine and spread in the field. As wild oat has a patchy spatial distribution (Colliver et al. 1996), the latter strategy may be preferred in the absence of chaff collection. The wild oat seed would remain in the field but most of it would fall into the weed patch where, presumably, there are already many seeds in the seed bank. As a result, the seed spread of wild oat would be minimized as most wild oat seed would remain in the patch in which it was produced.

By measuring the development of wild oat relative to thermal time it is possible to predict the proportion of wild oat seed shed that would occur at harvest in different crops. It would be expected that crops that are swathed early, such as barley or canola (*Brassica napus* L.), would have a greater proportion of wild oat still on the plant at swathing time, as compared to wheat. Many barley varieties mature approximately nine calender days earlier that wheat. Assuming that this would represent a difference of 150 GDD, then one could interpret from Figure 4.3 that there would still be approximately 80% of the wild oat seed still on the panicle of wild oat at barley harvest. Morrison et al. (1989) related the development of canola cultivar Westar) to thermal time. It was determined that for a base temperature of 5 C, 1 060 GDD accumulated from canola emergence to physiological maturity. Physiological maturity was determined to be when seeds in the lower pods were green-brown mottled. This corresponded to the earliest stage at which producers would swath canola. Using a base temperature of 5 C in calculating the seed shed of wild oat, 85% of the wild oat seeds would remain on the panicle at this time.

4.4 Summary and Conclusions

By relating plant development to thermal time it is possible to determine if plants develop in a consistent way across different environments. Wild oat and wheat development, as measured by the phyllochron interval, were similar within locations, but differed between locations. The differences between locations are probably the result of other unmeasured environmental factors. Progression through different development stages as measured by Zadoks (Zadoks et al. 1974), was different between wild oat and wheat. However, within each plant species the development was consistent between locations and years. As a result the Zadoks scale should be useful in relating plant development to thermal time in wild oat and wheat. There could be variation in the development of different genotypes of wild oat across a region. Further experiments must be conducted in order to determine the genetic variability within and between wild oat populations.

The seed shed in wild oat was synchronous with the maturation of wheat. By altering the type of crop, the harvest method or harvest timing, it would be possible to manage the proportion of wild oat seed shed at harvest. This would allow a producer to attempt to maximize export of wild oat seeds in the grain in the case of an early harvest or to minimize the amount of seeds that are dispersed by harvest machinery in a late harvest. The choice of the most advantageous management technique would depend on many factors including the extent of the wild oat infestation and the type of harvest machinery used.

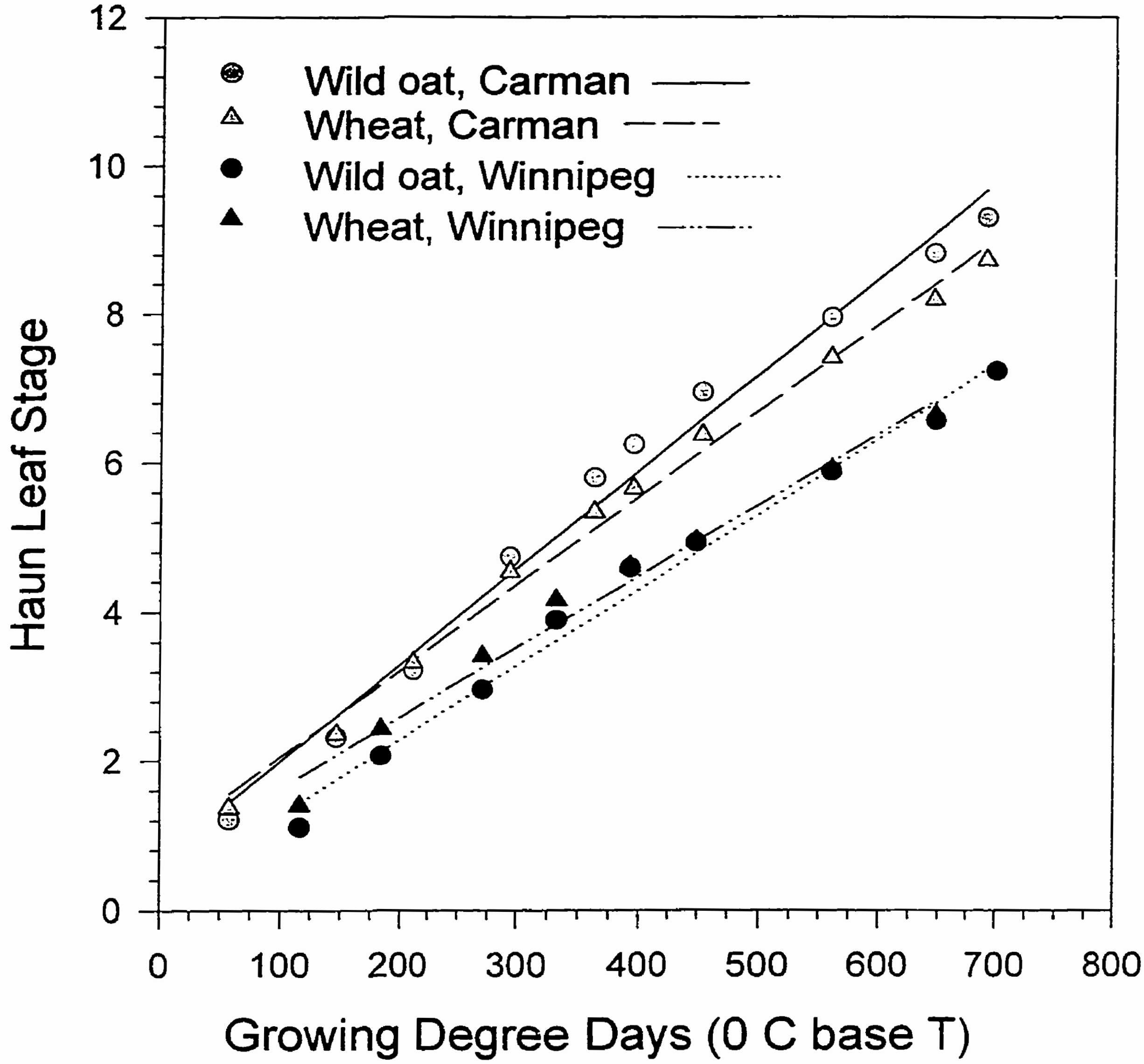


Figure 4.1.Haun (Haun 1973) leaf stage of wild oat and green foxtail at Winnipeg and Carman, 1996. Data points are for means of ten replicates. Lines represent fitted linear regressions. Values for the slopes of the lines are presented in the text as phylochron intervals.

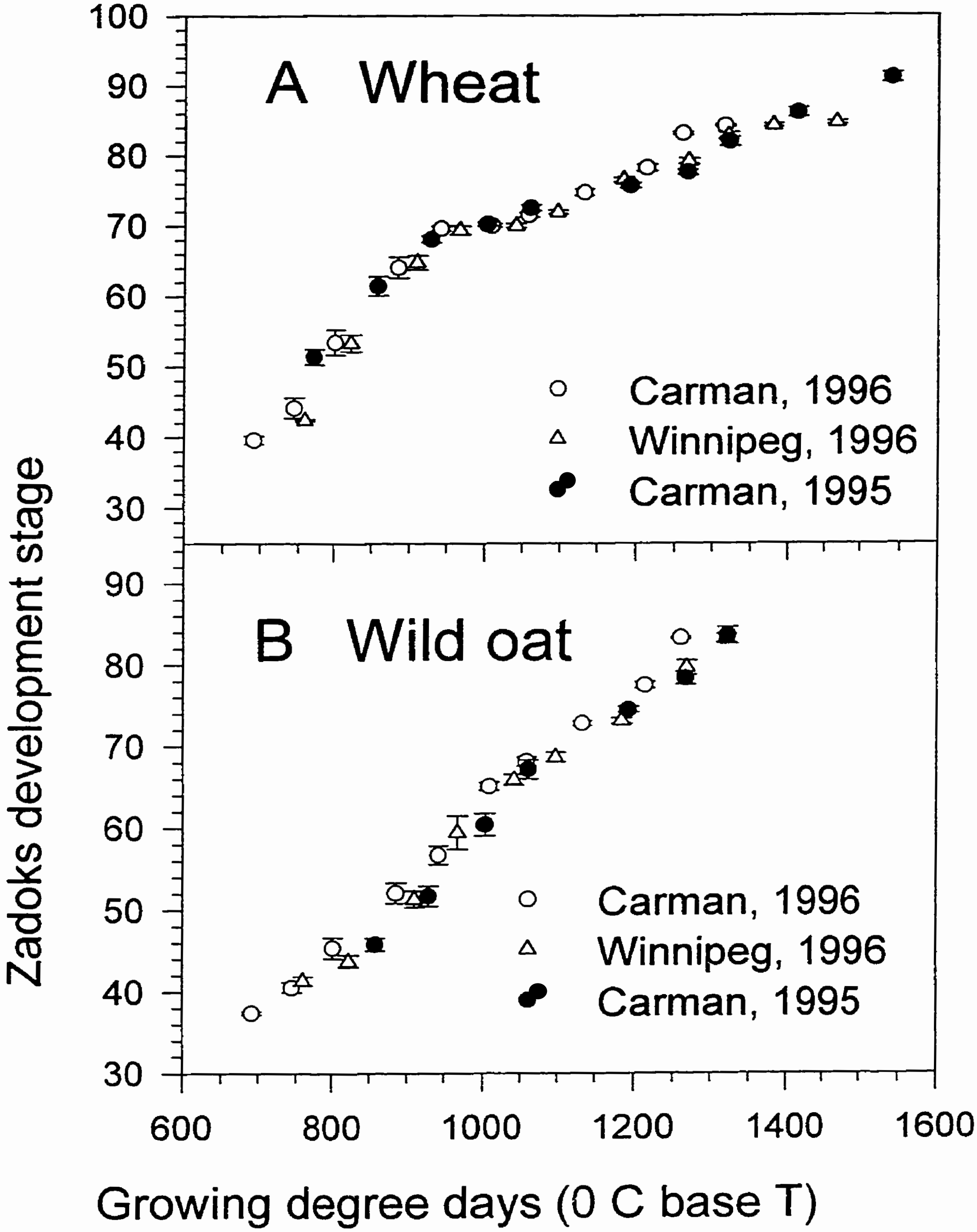


Figure 4.2. Zadoks (Zadoks et al. 1974) developmental stage of wild oat and green foxtail at Winnipeg and Carman, 1996 and Carman in 1995. Data points are for means plus and minus standard error of ten replicates in 1996 and 18 replicates in 1995.

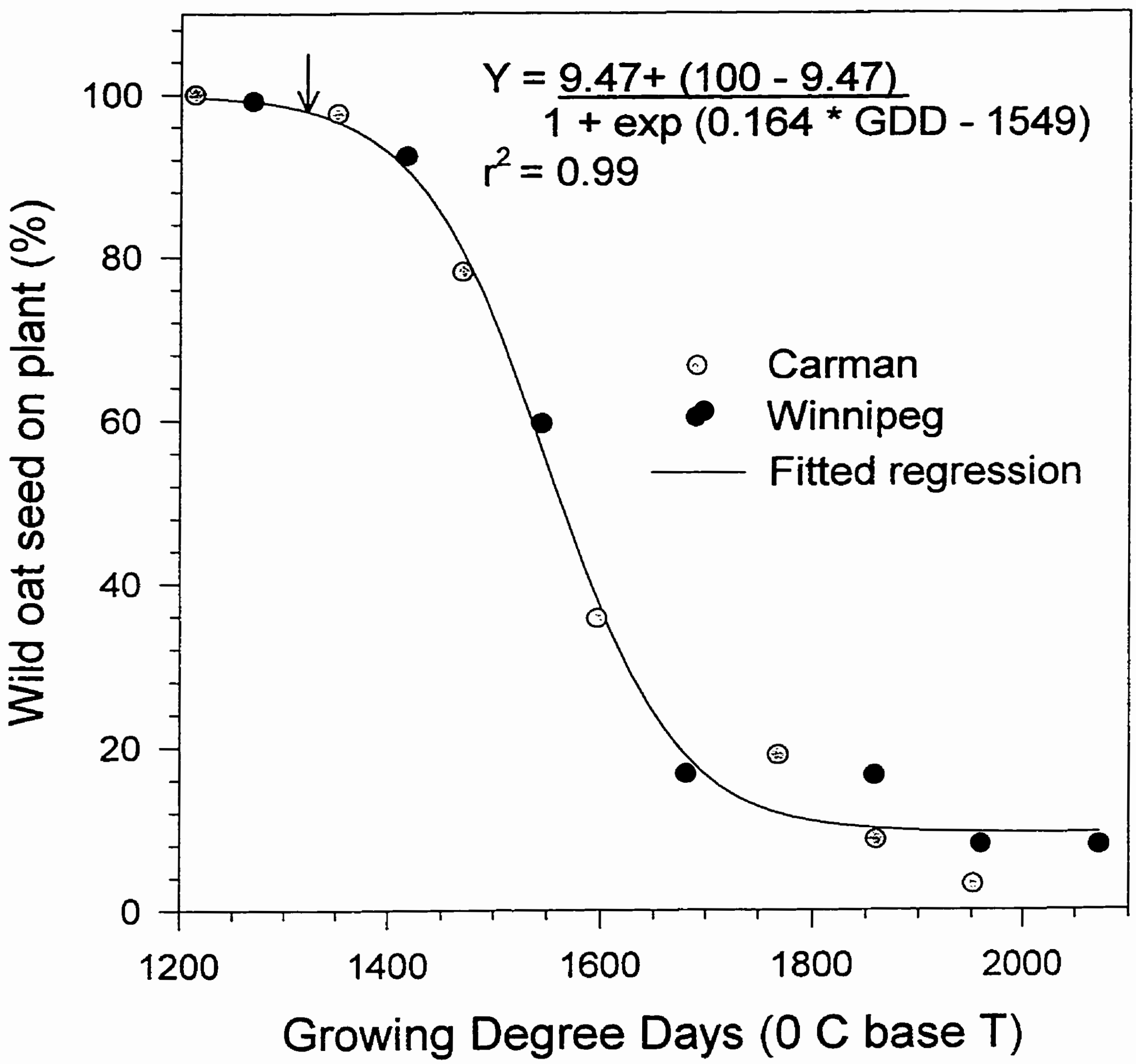


Figure 4.3. Percent wild oat seed shed and precent wheat head moisture at Winnipeg and Carman, 1996. The arrow indicates the initiation of seed shed in 1995. Lines represent fitted regressions.

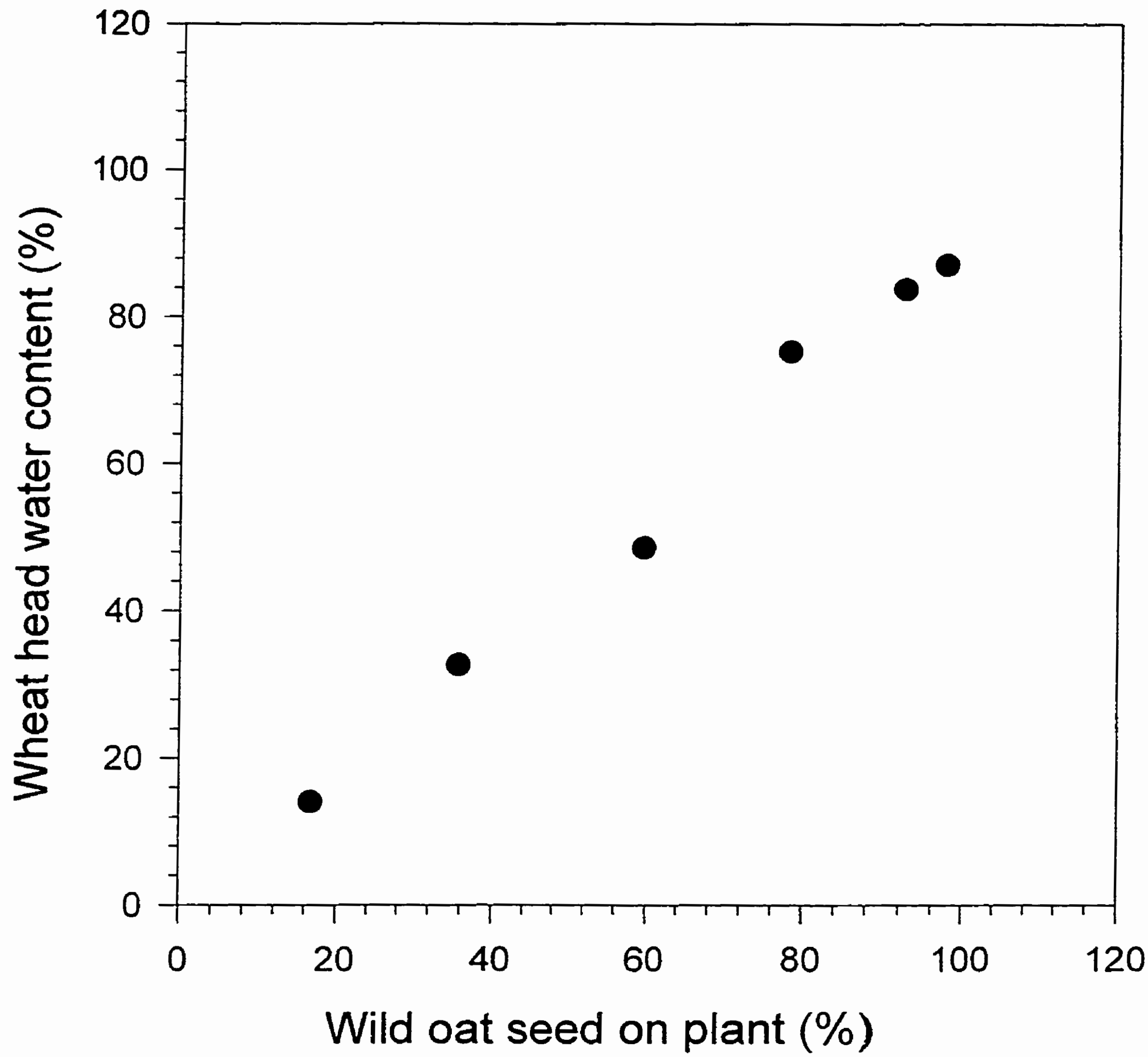


Figure 4.4. Correlation between wheat head moisture content and percentage seed shed in wild oat (inverse of percent remaining on panicle).

5.0 Modelling the Effect of Harvest Management on Wild Oat Seed Dispersal

5.1 Introduction

Herbicide resistance and multiple herbicide resistance are weeds are becoming common in wild oat (Bourgeois and Morrison, 1997) reducing and in the case of multiple herbicide resistance, eliminating herbicidal control options (Beckie et al. 1998). As a result, alternative methods of weed control must be explored.

Managing weed seed dispersal has the potential to reduce weed patch expansion (see Chapter 3). Combine harvesters have the greatest potential to disperse weed seeds within annual small grain cropping systems (Cousens and Mortimer, 1995). A combine harvester can disperse wild oat seed greater than 150 m from a wild oat patch (Chapter 3). However, if the chaff portion of the crop residue is collected as it is expelled from the combine, seed dispersal can be reduced to approximately 30 m.

The effectiveness of chaff collection may be limited by the amount of wild oat seed that is shed prior to harvest. In the previous chapter it was observed that seed shed of wild oat occurs during the ripening process of wheat. The rate of seed shed displayed a sigmoidal pattern which corresponded to the head moisture content of the wheat. If wheat is swathed early, most wild oat seed would not have been shed. However, if harvest was delayed until the wheat was dry enough to straight combine, then most of the wild oat seed would be shed.

It is not known if it would be more advantageous to harvest when few wild oat seeds have been shed or to wait and harvest the crop when most wild oat seeds have been shed from the plant. Both an early and a delayed harvest have benefits related to the management of wild oat. With an early harvest one attempts to capture as many wild oat seeds as possible in the harvest operation. This strategy maximizes the export of weed seeds from the field in the grain and collected chaff. With a delayed harvest one attempts to minimize combine wild oat seed dispersal. With the latter the strategy is to delay harvest until most of the wild oat seed had been shed, thereby limiting the amount of wild oat seed that is taken into the combine harvester. This results in less seed being available for dispersal by the combine harvester. These management strategies have not been explored experimentally.

In order for weed seed dispersal management to become a weed control strategy, the weeds must be spatially aggregated. Numerous studies have found that spatial aggregation in weeds is common, if not ubiquitous (Marshall, 1988; Wiles et al. 1992; Mortensen et al. 1993; Cardina et al. 1995; Johnson et al. 1995; Colliver et al. 1996). Surveys of wild oat have reported it to be a patchy weed species (Thornton et al. 1990; Colliver et al. 1996).

A computer simulation model approach was chosen to evaluate weed control options involving chaff collection and harvest timing. As the process of weed patch expansion occurs over a large area and takes several years to develop, the study of this phenomena was not amenable to small plot research. Therefore, a computer simulation model allowed for the simulation of the effect of different management techniques on wild oat dispersal. Computer simulations have been used previously to study weed seed dispersal (Ballaré et al. 1987 b; Maxwell and Ghersa, 1992).

The objective of this study was to identify harvest managements practices that reduce wild oat patch expansion. A spatial computer model of wild oat dispersal was constructed using dispersal and seed shed data from chapters three and four and wild oat life cycle data from a complimentary study.

5.2 Materials and Methods

5.2.1 Cropping Systems Experiment

The parameters for the model were obtained from a cropping systems experiment in which the population dynamics of wild oat were measured in wheat. The experiment was conducted at Carman, Manitoba, (lat. 49° 30′ N, long. 98° 2′ W) from 1994 to 1996. Wild oat was grown with flax in 1994 in order to establish a wild oat seedbank.

1994: UM-5 wild oats were mixed with fertilizer and spread on the entire experiment at a rate of 200 viable seeds m^2 on May 12. Fertilizer in the form of 30 kg ha^{-1} of P_2O_5 and 56 kg ha^{-1} of N was applied with the wild oats. The field was then cultivated to incorporate the seed on May 16. Flax was sown in all plots at a rate of 45 kg ha^{-1} on May 18. The experiment was sprayed with 1 L ha^{-1} of 280 g l^{-1} MCPA ester / 280 g l^{-1} Bromoxynil on June 13. The plots were harvested on Aug. 29. The conventional tilled annual plots were cultivated Sept. 1 and the zero-till annual plots were sprayed with 5 L ha^{-1} of 360 g l^{-1} glyphosate and 2 L ha^{-1} of 500 g l^{-1} 2, 4-D .

1995: The zero-till plots were sprayed with 5 L ha^{-1} of 360 g l^{-1} glyphosate on May 11, as a spring burn off. The conventional tillage annual crop plots were cultivated and packed on May 11. 60 kg ha^{-1} of N was banded with a double disk drill at a depth of 5 cm. 30 kg

ha^{-1} of P_2O_5 was applied with the seed. Following tillage or burn off, spring wheat cultivar Katepawa was seeded at 135 kg ha^{-1}. Broad-leaved weeds were controlled with in-crop herbicides throughout the experiment. The wheat was harvested on August 21 with a plot combine.

Data collection 1995: The weed seed bank was sampled within the plots with 16 samples per plot prior to weed seed germination. Four 0.25 m^2 permanent quadrats were established in each plot. Weed population counts were taken before seeding, after weed seedling emergence, before crop harvest and after crop harvest. Before the crop harvest, four 0.25 m^2 biomass samples were taken from each plot. The weeds were separated from the crop and the oven dry weight recorded.

5.2.1 Model and Assumptions

The model was used to calculate the spread of wild oat by combine harvesters during a six year period. A life cycle model was developed based on the life cycle of the wild oat in competition with wheat (Figure 5.1). A screen capture of the input screen of the model is shown in Figure 5.2. The size of the simulation field was 12.9 ha, which was subdivided into 4 m^2 cells. A seed production sub-model was used to calculate the seed output of each cell and a dispersal sub-model was used to calculate the combine dispersal of the seeds.

5.2.2 Seed Production Sub-model

The demographic parameters for the wild oat seed production sub-model were determined from data collected as a part of a cropping systems experiment and scientific literature. The experiment was initiated in 1994 with the seeding of flax and wild oat in the experimental area. In 1995 wheat was grown. Prior to seeding the seed bank was sampled in selected plots.

5.2.2.1 Seedling Recruitment

Seedling recruitment was assumed to occur in one cohort and was calculated as follows:

$$sdl = SBs * emrg$$

where *SBs* is the seed bank density, *emrg* is the emergence rate and *sdl* is the seedling population density. The amount of viable wild oat seed in the seedbank was estimated by using three cycles of tray germination of samples taken from the field. The germination cycles were conducted in a greenhouse (Gross, 1990).

5.2.2.2 Spring Pre-seeding Recruitment

Pre-seeding wild oat recruitment (*pssdl*) was calculated as follows:

$$pssdl = psemrg * emrg$$

where *psemrg* is the proportion of wild oats that germinated prior to seeding as related to the proportion of wild oats that germinated at or after seeding. The proportion of seeds germinating before seeding was based on observations from the cropping systems experiment.

5.2.2.3 Seedling Survivorship

Density dependent seedling survivorship to mature plants (*mp*) was assumed to occur and was described by a relationship proposed by Watkinson (1980) where:

$$mp = sdl / (1 + ddmort * sdl)$$

where *ddmort* is a density dependent coefficient describing plant mortality.

5.2.2.4 Seed Production

Seed production in wild oat was assumed to be density dependent and a function of total plant biomass. Plant biomass (Mpw) was described by the equation proposed by Watkinson (1980) where:

$$Mpw = womax * mp * (1 + woa * mp)^{-1}$$

where *womax* is the maximum weight of wild oat, *woa* is a density dependent parameter. Wild oat biomass was converted to wild oat seed density (*sds*) by the following:

$$sds = Mpw * spg * HI * spc$$

where *spg* is the seeds per gram, *HI* is the harvest index (calculated from data collected in chapter 4) and *spc* is a constant relating the remaining proportion of seeds on the plant to the total amount of seeds produced per plant.

5.2.2.5 Seed Shed

Seed shed (*Srain*) was calculated by:

$$Srain = sds * (1 - sr)$$

where *sds* is the total seeds produced and *sr* is the proportion of seeds removed from the field. The proportion of seeds that were still on the plant at harvest was based on data from chapter 4. Two scenarios were used for the simulations. In the first, the wheat crop was swathed early (*srearly*) and 50% of the wild oat seed still remained on the plant. In the second scenario it was assumed that the wheat harvest was delayed (*srlate*) and that 5% of the wild oat seeds still remained on the plant at time of harvest.

5.2.2.7 Seed Bank Mortality

Seed bank survival through the winter was assumed to be density independent and was described by the following:

$$Sbs = (Srain + SBf) * (1 - sbmort)$$

where *Srain* is the seed rain, *SBf* is the seed bank following spring emergence and *sbmort* is the seed mortality. Data from Miller and Nalewaja (1990) was used to estimate this parameter.

5.2.3 Seed Dispersal Sub-Model

Seeds produced by wild oat plants in each cell may be shed before harvest, taken into the combine harvester and exported from the field, or taken into the combine harvester and dispersed in the field. The seeds that were redistributed in the field were assumed to have a dispersal function which could be described using the following equation:

$$Y=a*e(-\frac{x}{c}^{b})$$

Where Y is the predicted amount of wild oat seeds m^{-2} that are on the ground at x distance beyond the original cell, a is a regression parameter that describes the proportion of maximum seed output at the y intercept, b and c are regression parameters describing the slope of the exponential decline of seed dispersal. This equation is similar to that used by Shirtliffe (Chapter 3) but differs in that an additional parameter is used. This results in the regression in a better fit of the tail of the regression equation. This three parameter function has the disadvantage of not allowing statistical comparison between parameter as the regression parameters are correlated. If the seed dispersal to a cell at a given distance was less than one, the probability of a wild oat seed landing in that cell was determined by a probability function. The maximum distance of mechanical dispersal was assumed to be 200 m.

The combine was assumed to cut an area of the field 10 m wide. The chaff portion of the crop residue was distributed into a 2 m wide area behind the combine or removed from the field with chaff collection, while the straw was distributed into an area 6 m wide behind the centre-line of the combine. The combine dispersal was in the direction that the combine travelled. For each simulated season the combine could travel either in a north-south or an east-west direction and the decision to travel in a particular direction was determined randomly.

5.2.3.1 Natural and Tillage Dispersal

The spatial resolution of this model was 2 m and the distance that wild oat seeds are naturally dispersed is usually less than 1 m (Shirtliffe, Chapter 3), therefore the mechanism of natural dispersal was not included in this model. Similarly tillage dispersal is usually less than 1 m (Howard et al. 1991; Rew and Cussans, 1997) and for this reason it was not included in this model.

The above equations were fitted to the data by using either the NLIN procedure or the REG procedure of SAS (Statistical Analysis Systems Institute, 1986). The values of all model parameters are shown in Table 5.1.

5.2.4 Simulations

For simplicity it was assumed that wheat was grown every year of the six year simulation. Three initial weed spatial simulations were considered for the model simulations. An irregular shaped area representing a field containing a small weed infestation and was referred to as the patch simulation (Figure 5.2a). A point pattern in which five cells within the field have wild oat seeds in them was chosen to represent a field in the initial stage of a herbicide resistant wild oat invasion. This was referred to as the point simulation (Figure 5.2b). A uniform distribution of the simulation area had wild oats in every cell and is not presented. For all simulations the starting seed bank for the cells containing wild oat was 500 seeds m^{-2}. For each of these starting wild oat patterns the timing of harvest or the collection of weed seeds in chaff could be varied. The field could be either swathed while 50% of the wild oats were still on the panicles or it could be harvested later, when only 5 % of the wild oats were still on the plants. The combine could either return the chaff to the ground or it could collect it in a chaff wagon and remove it from the simulated field. There were a total of 12 combinations of simulations (Table 2). Each simulation was run for six simulated years. For each simulation scenario 25 separate runs were conducted and the mean of the results is presented.

5.3 Results

5.3.1 Patch Simulation

In the patch simulations, chaff collection resulted in a 63% reduction in patch expansion compared to chaff return (Figure 5.3). Chaff collection prevented the spread of the wild oat patch to most areas of the simulated field, whereas chaff return allowed the patch to spread over much of the field area (Figure 5.4). A delayed harvest resulted in reduced dispersal of wild oat by a greater amount than did chaff collection (Figure 5.3). In the patch simulation study an early harvest dispersed wild oat seed to 874 % more area than a delayed harvest.

5.3.2 Point Source Simulation

Chaff collection also reduced dispersal in the point source simulations. The greatest increase in area occupied by wild oat occurred in the early harvested chaff return treatment in which the wild oat area increased by 6520 % after 6 years (Figure 5.5). The effect of chaff collection was most pronounced with an early harvest as chaff return resulted in a 4630 % greater increase in wild oat area infested than when chaff was collected with a delayed harvest. However, when the delayed harvest was practised in the point source simulation there was no wild oat dispersal outside of the original cells whether or not chaff was collected or returned. This resulted in a final distribution which was identical to the original distribution (Figure 5.2b).

5.3.3 Uniform Distribution Simulation

Wild oat dispersal responded differently to the treatments in the uniform distribution simulations compared to the patchy and point source simulations. As all of the area had wild oat present there was no possibility of patch expansion. Chaff collection and an early harvest resulted in a reduction in wild oat population (Fig 5.6). The average density from an early harvest was 51 % lower for chaff collection and 45 % lower for chaff return. Chaff collection had a relatively minor effect on reducing wild oat population only 1% with a delayed harvest and 6.7 % with an early harvest, for example.

5.4 Discussion

The results of the present study are similar to those observed by Ballaré et al. (1987 b). Using a spatial computer simulation of the life cycle and dispersal of *Datura ferox* in soybeans they found combine harvester dispersal resulted in a rapid spread of this weed. It was concluded that *Datura ferox* could only be controlled if a large proportion of the seed was exported with the grain. With *Datura ferox*, 99 % of the weed seeds were still on the plant at harvest. The only option to reduce dispersal in the study conducted by

Ballaré et al. (1987 b) was to use a combine of a different design. The present study illustrates that simple and inexpensive changes can reduce harvest dispersal. It also confirms the results of a simulation by Maxwell and Ghersa (1992), who suggested that combine harvesters could be used as a tool in reducing weed seed dispersal.

A delayed harvest eliminated wild oat patch expansion in the point source simulation (Table 2). With both chaff collection and chaff return there was no dispersal of wild oat outside of the original cells containing wild oat. Chaff collection and an early harvest resulted in only a 40% increase in area occupied by the wild oat. However, an early harvest without chaff collection resulted in a 6 600 % increase in the area occupied by wild oat (Figure 5.5).

A delayed harvest was more effective at reducing wild oat dispersal than was chaff collection. By delaying the harvest, only 5 % of the wild oat seeds were assumed to enter the combine at harvest. As 69 % of the wild oat seeds that enter a combine end up in the grain tank (woex, Table 5.1) the effect of chaff collection is reduced with a delayed harvest as there are few seeds available for dispersal. It is this mechanism that was responsible for the reduction in dispersal associated with a delayed harvest (Figure 5.3).

The point infestation was analogous to the beginning stages of a herbicide resistant weed infestation. From the simulation presented in this study, it can be inferred that herbicide resistant wild oat spreads in the field from harvest dispersal. As harvest dispersal was extremely limited with a delayed harvest it can also be inferred that for herbicide resistant weeds to completely cover a field they must have been dispersed with an early harvest with many wild oat seeds still on the panicle. Current models assume that herbicide resistance occurs at a low level in the population and is selected for by herbicides (Jasieniuk et al.1996). There is also the assumption that the mutation conferring resistance to wild oat is not inducible, but is selected for in the field by repeated herbicide application (Cousens and Mortimer, 1995). As a result it appears that seed dispersal is required for resistant wild oat to infest an entire field. However, herbicide resistant genes can move with pollen flow. Murray (1996) found that pollen from herbicide resistant wild oat could outcross with nonresistant wild oat at 60 cm, when the wild oat was grown in wheat or flax. As the model in the present study does not consider pollen flow it must be assumed that it will underestimate the spread of the herbicide resistant wild oat gene within a field.

The results of simulation runs of the computer model suggest wild oat management options for farmers. As simulations in which the area occupied by wild oat was small resulted in the largest increase in area occupied by wild oat it can be inferred that chaff collection would be most effective under circumstances when the crop does not receive an application of herbicides. For example, a situation in which a few small patches of wild oat may go unnoticed by a producer. Even if the patches were detected during field scouting it would not be economic to spray the entire field. Patch spraying could allow spot treatment but as wild oat is difficult to detect at the seedling stage in cereal crops such as wheat, it is likely that some small patches would still go undetected. Therefore, using a delayed harvest and chaff collection is a prophylactic and effective wild oat management tool. These two practices should reduce dispersal to such an extent that wild oat patches are kept as discrete units that later facilitate patch treatments. The use of other chemical and cultural weed control measures would ensure that wild oat populations are kept to a minimum.

Assuming one had a field with a uniform density of wild oat an early harvest would be preferential as dispersal had no effect on this simulation (Figure 5.6). However, many fields have been observed to have a patchy distribution of wild oat. For example Colliver et al. (1996) found that, at harvest, wild oat infested only 9% of one field. Even fields that appear to be uniformly infested may still have a patchy distribution of wild oat. For example, Thornton et al. (1990) reported that a field which from the ground appeared uniformly infested with wild oat was found to have only 18% of the area occupied by wild oat as assessed by low-level aerial photography. Given the patchy distribution of wild oat, a delayed harvest would be recommended in most circumstances. In circumstances where wild oat has been observed to cover a large portion of the field an early harvest may be considered to maximize seed export. However, under these circumstances the population of wild oat would be high and chaff collection or early harvest would not be expected to have a substantial effect on the population (Figure 5.6). This can occur because the vast quantities of seeds in the seed back act as a buffer to annual changes in seed return.

Producers with low populations of patchy wild oats should delay harvest as long as practical to reduce wild oat dispersal. Chaff collection can further reduce the dispersal but it may not be necessary if most of the wild oat are shed before harvest. As some crops such as barley and canola can mature earlier than wheat and germination of wild oat can occur over an extended period (Agenbag and de Villiers, 1989), there will be cases when the crop is ripe and many wild oat seeds remain on the plant. As an extended harvest delay could threaten crop quality, a chaff collection system may be necessary to reduce wild oat dispersal under these circumstances.

The direction that the combine travels in relation to the patch had an effect on dispersal distance. Although this phenomenon was not explored formally in this model it was observed during simulations that if the simulated combine ran in the same direction of the longest axis of the patch then the dispersal distance was greater than if the simulated combine ran perpendicular to the longest axis of the patch (Figure 5.4b). This occurred because more wild oat seeds are taken into the combine during the extended time it takes time to travel along the long axis of the patch. A greater number of seed in the combine results in a greater probability that some will be dispersed a long distance. Because of this relationship it would be recommended that producers combine perpendicular to the longest axis of the wild oat patch. However, this would be difficult to apply in practice, so a policy of alternating combine directions biannually would reduce dispersal when compared to combining the same direction every year. Unfortunately, this practice may be impractical in elongated or irregularity shaped fields.

Computer simulations are useful for predicting the effects of different variables and combinations of variables on systems which cannot be studied experimentally. In the present study, the length of time necessary to observe the long term harvest management effects would have been excessive and the size of the area would have occupied several research farms. Under these circumstances the best approach was to model the system. However, it must be recognized that there are effects that could change the outcome of these simulations. Although dispersal by combine was similar between years (see Chapter 3), life cycle parameters can vary greatly. Density dependent seedling recruitment has been observed (see Chapter 3) which suggested that seed predation satiation may have been a factor in one year of a two year study. If predator satiation of weed seeds occurred regularly, it would reduce the effect of chaff collection but it would not eliminate it. However, beyond all the variance and inability to predict the exact quantitative effect, it can be concluded that a delayed harvest and chaff collection will result in less wild oat patch expansion versus early harvest and chaff return.

5.5 Conclusions

Chaff collection with a late harvest can be an effective method to reduce the dispersal of wild oat. Computer simulations reveal that of the two techniques, a delayed harvest is most effective at reducing the expansion of isolated wild oat patches. There is potential for utilizing a late harvest or chaff collection in managing herbicide resistant wild oat management program. These harvest management techniques appear to reduce the amount of the field that has an infestation of herbicide resistant wild oats. Cultural control of weeds is rarely achieved through one single method. Chaff collection and the timing of harvest will not on their own control wild oat. They can, however, be a powerful tool of weed management within an integrated weed management program.

Table 5.1. Parameter definitions and values used in the model for the relationships used in the model and references where the data for calculating the parameter was obtained. (CC - chaff collection, CR - chaff return).

Parameter Definition	Parameter	Parameter value	Source
Spring recruitment	emrg	0.175	Cropping systems exp.
Pre-seeding recruitment	psemerg	0.4239	Cropping systems exp.
Seedling survivorship	ddmort	0.00329	Cropping systems exp.
Seed production	womax	2.344	Cropping systems exp.
	woa	0.0287	
Seed conversion	sds	38	Cropping systems exp.
Seed rain, early harvest	srearly	0.5	Chapter 4
Seed rain, delayed harvest	srlate	0.05	Chapter 4
Wild oat exported in grain	woex	0.687	Chapter 3
Wild oat exported in chaff	woex	0.264	Chapter 3
Chaff collection dispersal	cca	0.1858	Chapter 3
	ccb	1.037	
	ccc	0.3386	
CC seeds in centre row	cccen	0.33	Chapter 3
Chaff return dispersal	cra	0.0425	Chapter 3
	crb	12.89	
	crc	0.825	
CR seeds in centre row	crcen	0.9	Chapter 3
Maximum dispersal dist.	maxdisp	200	Shirtliffe et al. (1999)
Seed bank mortality	sbmort	0.62	Miller and Nalewaja (1990)

Table 2. Wild oat density and percentage increase in area covered after six years of modelled combine dispersal for all model simulations. (CC - chaff collection, CR - chaff return).

Simulation	Harvest timing	Residue management	Wild oat seedling density (m^{-2})	Percent increase in area occupied by wild oat
Patch	early	CC	1.00	653
	late	CC	2.00	0.03
	early	CR	1.42	1840
	late	CR	2.07	62.6
Point source	early	CC	n/a	40
	late	CC	n/a	0
	early	CR	n/a	6520
	late	CR	n/a	0
Solid	early	CC	215	n/a
	late	CC	442	n/a
	early	CR	246	n/a
	late	CR	446	n/a

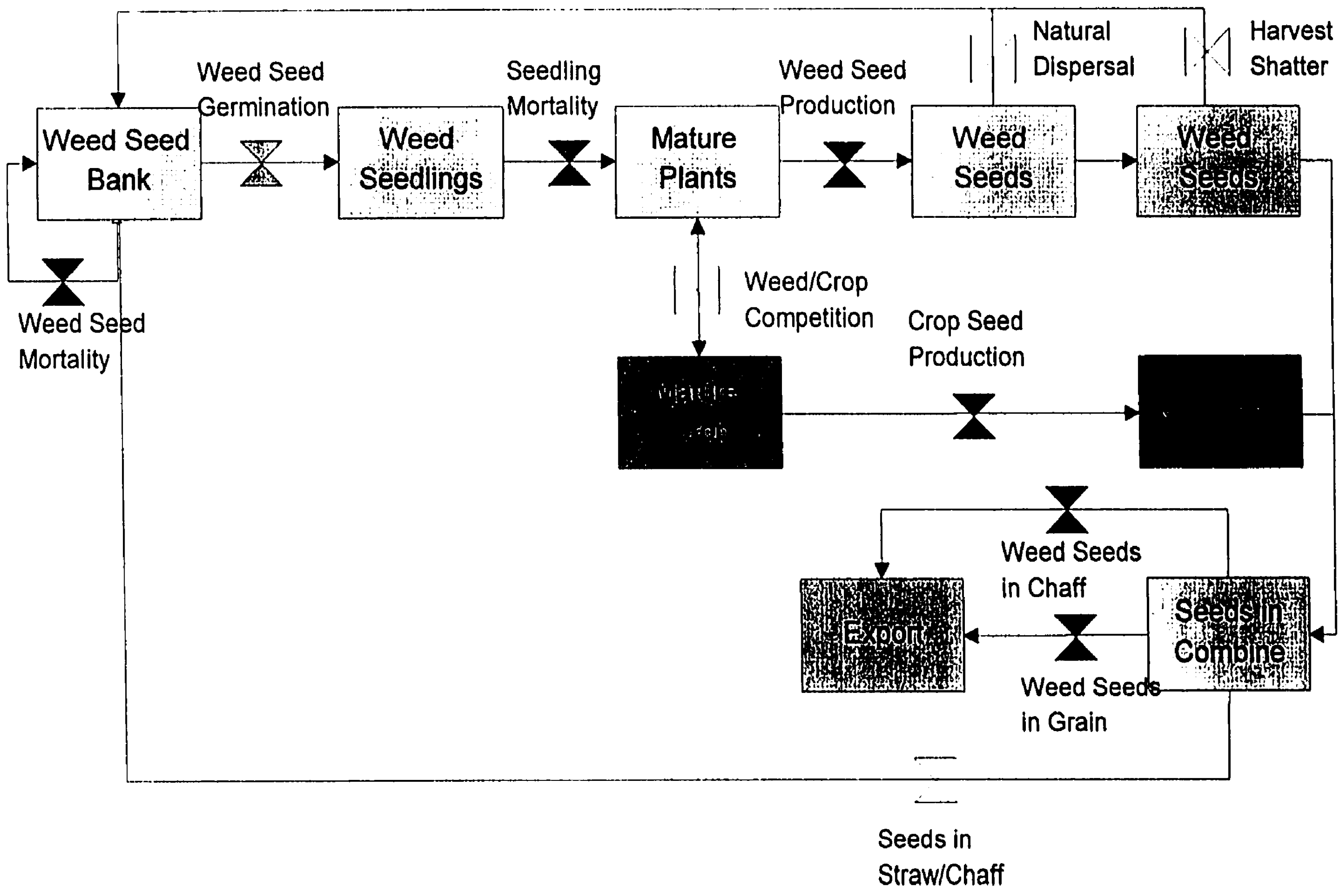


Figure 5.1. Life cycle flow chart illustrating construction of computer simulation model.

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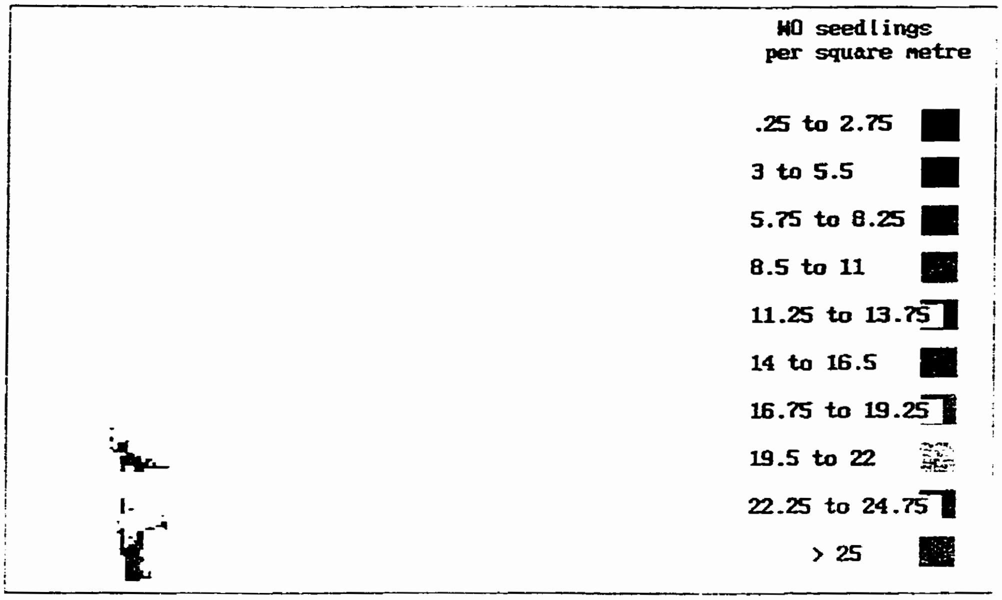


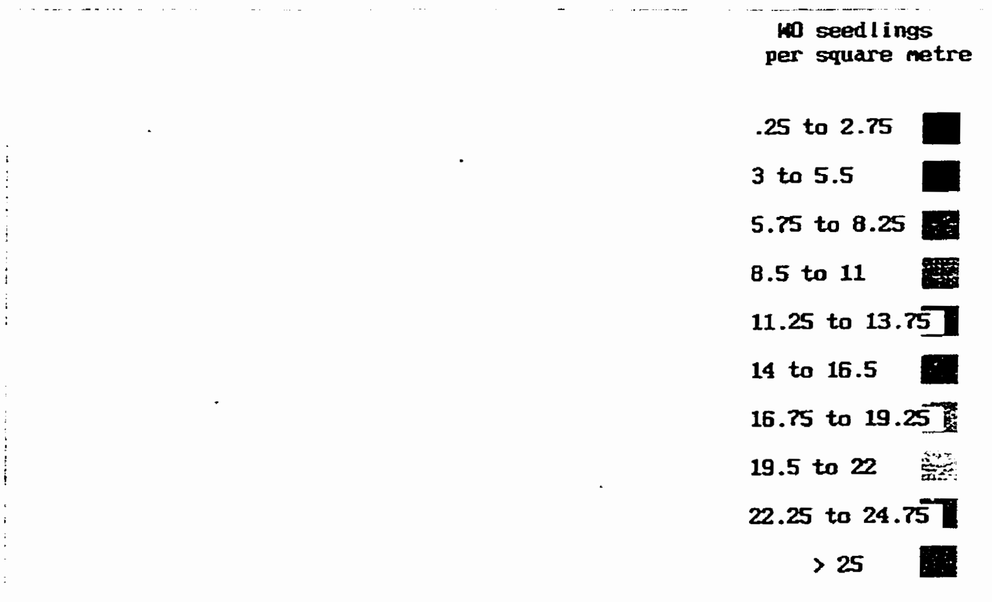


Figure 5.2. Initial input screen showing (upper) patch simulation and (lower) point source simulation. Simulation area was 13 ha.

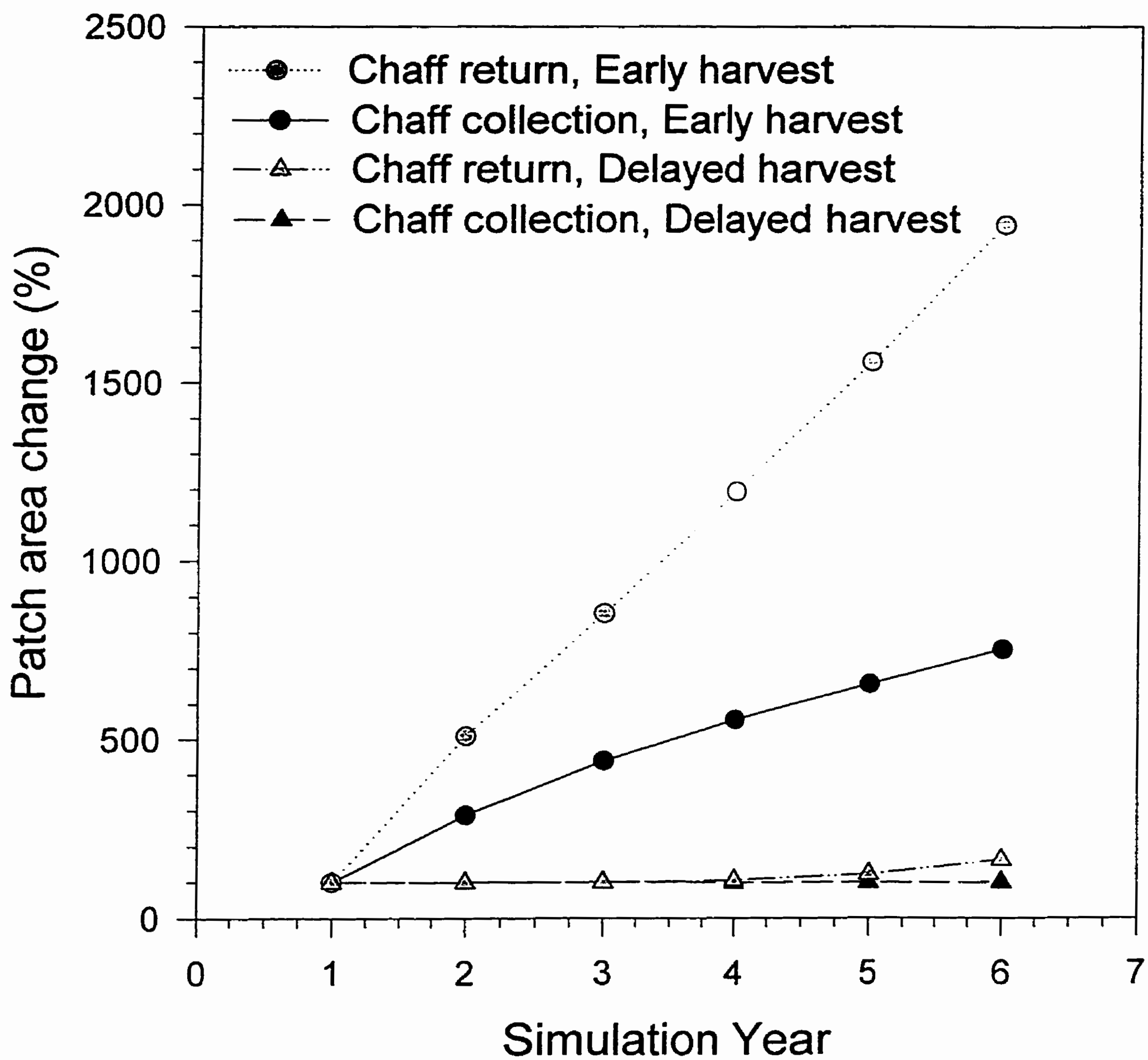


Figure 5.3. Simulated effect of chaff collection and timing of harvest on the increase in area occupied by wild oat in six years with a simulated patch as the initial wild oat distribution.

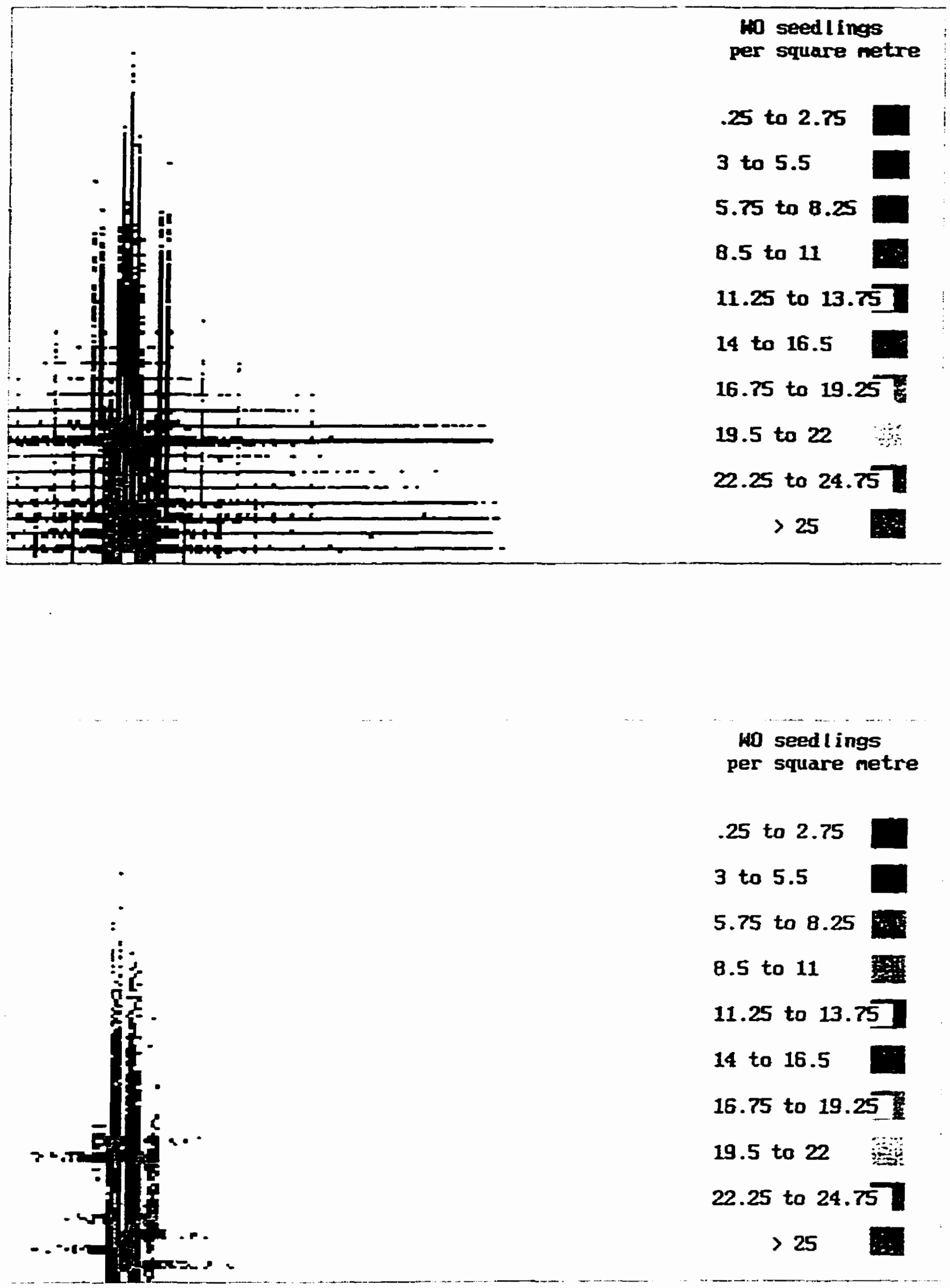
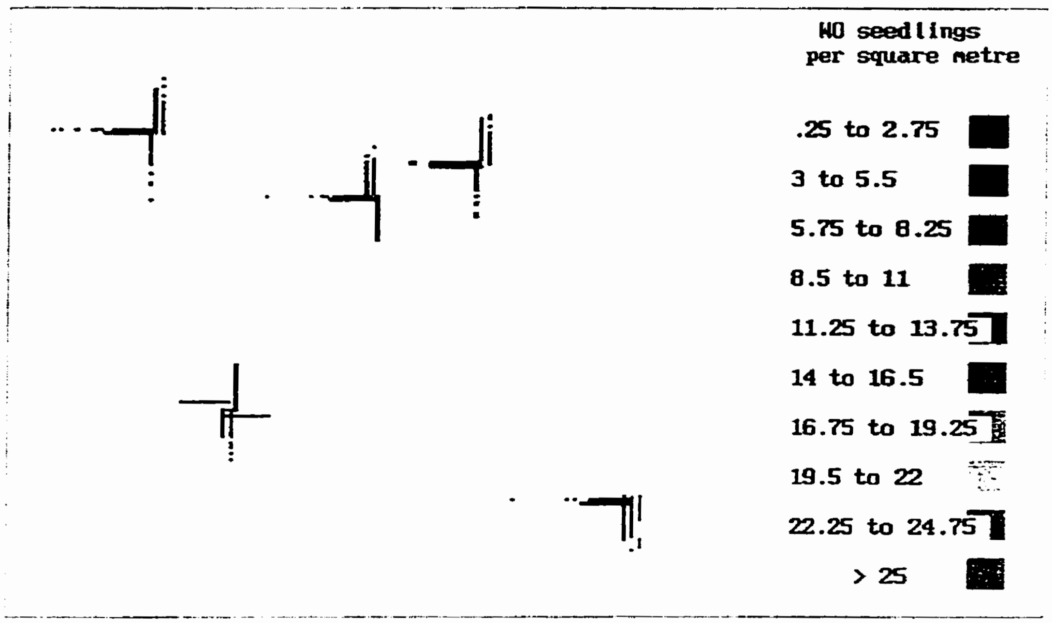


Figure 5.4. Patch source simulation of wild oat dispersal after six years that was harvested early (upper) with chaff return or (lower) with chaff collection. Simulation area was 13 ha.



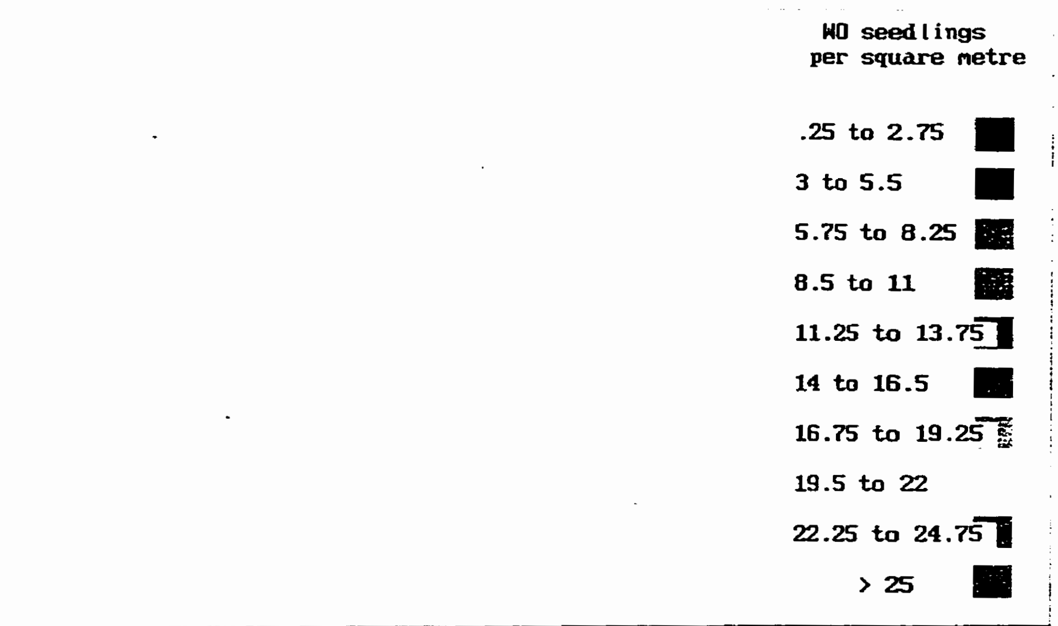


Figure 5.5. Point source simulation of wild oat dispersal after six years that was harvested early (upper) with chaff return or (lower) with chaff collection. Simulation area was 13 ha.

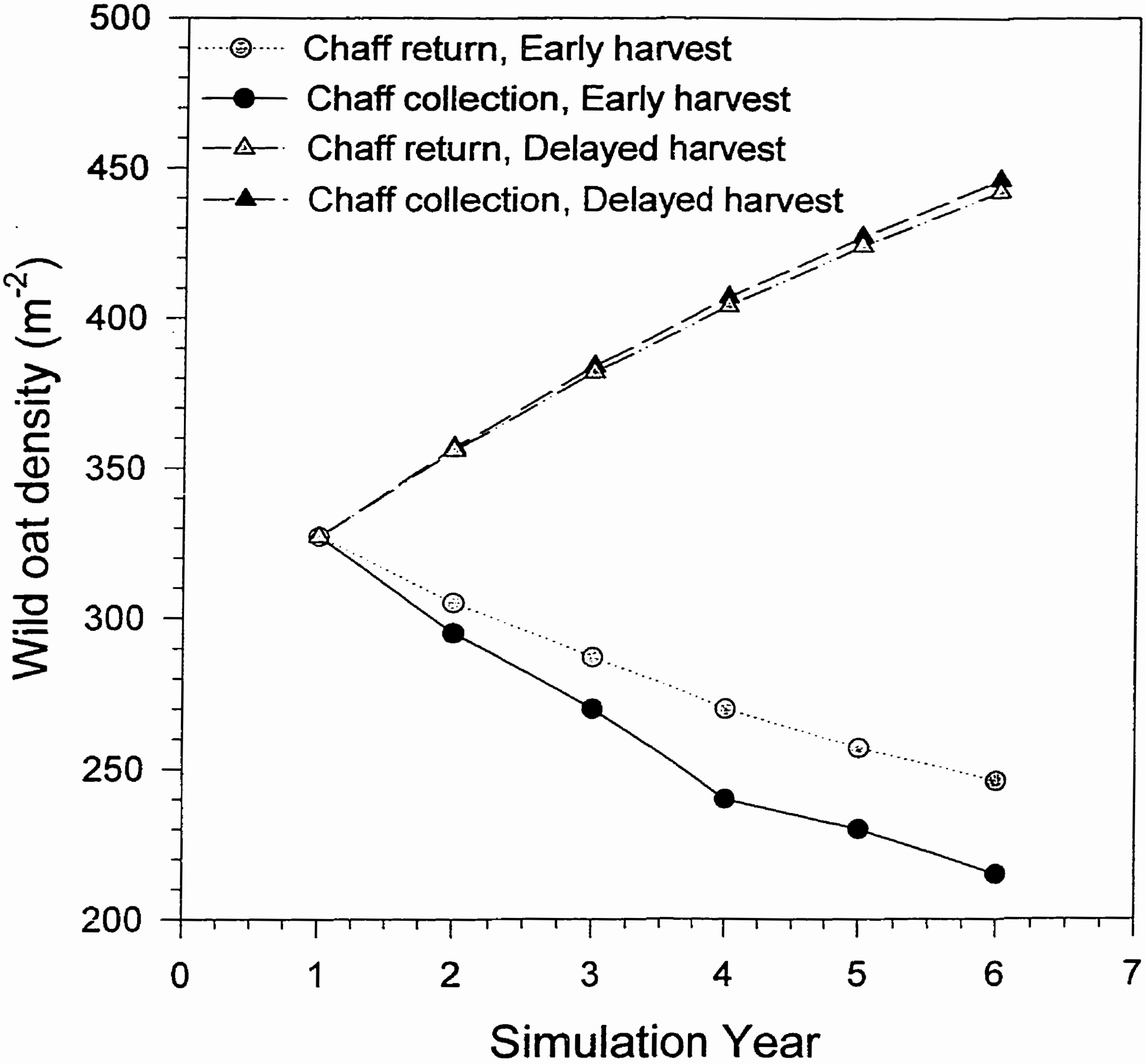


Figure 5.6. Simulated wild oat density change over time as affected by chaff collection and timing of harvest with a uniform distribution as the initial wild oat distribution.

6.0 The Fractal Geometry of an *Avena fatua* Patch

6.1 Introduction

An intuitive relationship exists between seed dispersal of an annual weed species and its spatial pattern. If seeds are dispersed a sufficient distance, the species should eventually spread and completely cover a suitable area. However, observed weed populations display highly aggregated spatial patterns (Marshall 1988; Wiles et al. 1992; Mortensen et al. 1993; Cardina et al. 1995; Johnson et al. 1995; Colliver et al. 1996), suggesting that environmental variation and disturbance factors may control the recruitment and establishment of arable weeds.

Aggregated spatial patterns of weeds may also result from characteristics of the seed dispersal curve. Kenkel and Irwin (1994) simulated seed dispersal using a Lévy flight model (Mandelbrot, 1982), in which dispersal distances are randomly selected from a probability distribution with a power-law tail. They proposed a theoretical relationship between spatial aggregation and dispersal characteristics. Species with the capacity for long-distance seed dispersal expand by establishing small patches far away ('guerilla' strategy; Lovett-Doust 1981; Wilson and Lee 1989), whereas organisms which disperse most of their seeds close to the origin will expand as an expanding front ('phalanx' strategy; Lovett-Doust 1981; Wilson and Lee 1989). Species capable of long-distance dispersal are thus expected to be more spatially aggregated than species having only limited dispersal capacity. Simulations using the Lévy flight model resulted in aggregated spatial distributions that were similar when viewed at variation spatial scales, implying statistical self-similarity and fractal characteristics (Mandelbrot, 1982). An alternative model of weed population dynamics that results in spatially fractal patches was proposed by Wallinga (1995). The main premise is that herbicide use in arable fields keeps weed populations at such low densities that "critical phenomena" are expected (Grassberger 1983). By adjusting the removal rate of weeds in a spatial population model to maintain a constant population density, aggregated spatial patterns were produced that were spatially fractal.

Theoretical models suggest that the type of species invasion is a function of the dispersal curve of the species (Harper, 1977). The shape of the tail of the dispersal curve is of particular importance (van der Plank, 1960). If the tail declines at less then an exponential rate, the species expands by establishing new colonies establishing beyond the original patch, rather than as advancing front (Kenkel and Irwin 1994; Wallinga, 1998). The dispersal curve of wild oat seeds has characteristics that may result in such an invasion pattern, since the seeds can be spread 150 m or more by a combine harvester (Shirtliffe, Chapter 3). This long-tailed dispersal curve may affect the invasion characteristics and spatial dispersion of wild oat, thus providing a theoretical link between weed seed dispersal and patchiness. This theoretical relationship would address the apparent contradiction that exists between long-distance weed seed dispersal and weed patchiness.

The objective of this study is to examine the relationship between seed dispersal and spatial patchiness in a population of wild oat (*Avena fatua* L.), a common annual weed of arable fields in Manitoba. To accomplish this, the population was mapped and examined for evidence of self-similarity using fractal analysis. The relationship between spatial pattern (fractal dimension D) and seed dispersal is discussed, and the connection between dispersal and invasion strategy of a species is summarized.

6.2 Materials and Methods

A wild oat patch located within a large experimental plot sown to wheat was mapped in 1996. The plot is part of a crop rotation experiment initiated in 1992, and had a rotation of wheat, pea, flax, wheat and pea (*Pisum sativum* L.). The experimental area received inorganic fertilizer, but herbicides have not been applied since the initiation of the experiment. Beginning in 1994, the crops were harvested with a New Holland model 1400 conventional combine (New Holland North America, 500 Diller Ave., New Holland, PA) and the chaff was collected with Redekop chaff collection system consisting of a model 925 chaff blower and a model 301 chaff wagon (Redekop Industries, Hwy 16 W, Saskatoon, SK). The same combine harvester and chaff collector was used to quantify mechanical wild oat dispersal (see Chapter 3).

The wild oat patch was first noted in 1994, and has been expanding ever since. A 10 x 10 m plot positioned within the patch was divided into one hundred 1 x 1 m grid units. Each grid unit was in turn divided into 16 squares, and the spatial coordinates of all wild oat plants in each square were carefully mapped. A total of 6896 plants were located in this way.

A fractal analysis of the resulting spatial point pattern was undertaken, using the grid or box-counting method to estimate the 'cluster dimension' D (Hastings and Sugihara

1993).

In this method, a regular grid of boxes of width δ is placed over the map and the total number of grid units containing at least one wild oat plant is determined. This step is repeated at various integer multiples of δ. Beginning with a grid of 60 x 60 boxes ($\delta = 1$), adjacent boxes were combined to obtain counts at $\delta = 1, 2, 3, 4, 5$ and 6. The defining power-law relationship is:

$$C_{\delta} \propto \delta^{-D} \qquad [1]$$

where C_{δ} is the number of boxes of width δ that are occupied by at least one wild oat plant, and D is the fractal dimension. The spatial pattern has fractal, self-similar properties if the log-log plot of C_{δ} vs. δ is linear. The fractal dimension D is determined as the slope of the principal component of the log-log plot.

The fractal dimension D describes the space-filling properties of a point pattern on the plane (Mandelbrot, 1982). A random point pattern is completely space-filling since all regions of the plane have an equal chance of being occupied, giving a fractal dimension D = 2. Values of D < 2 implies some degree of spatial aggregation, with smaller values of D indicating greater clustering or aggregation (i.e. less space-filling). The fractal dimension is thus interpretable as a scale-invariant measure of the degree of spatial aggregation.

6.3 Results and Discussion

The spatial pattern of the mapped wild oat population is strongly self-similar (log-

log plot $R^2 = 0.99$, $p < 0.001$; Figure 6.1). Statistical self similarity implies that the degree of aggregation of plants is similar when viewed at different scales, although the actual patterns need not be identical. The measured fractal dimension is $D = 1.69$, indicating deviation from a random pattern (i.e. $D < 2$) toward some degree of spatial aggregation. Wallinga (1995) obtained similar results for a patch of the annual weed cleavers (*Galium aparine* L.) in a winter wheat field in the Netherlands, although the degree of clustering in cleavers was greater then that observed in the present study ($D = 1.51$, vs. 1.69 in this study).

The degree of spatial aggregation (fractal dimension) of weed species in arable fields may be a function of both weed species biology and the cropping system used. For example, cleavers has small barbs on the seeds and foliage that assist in dispersal (Malik and Vanden Born 1988). By contrast, wild oat seeds have no special adaptations to assist in their natural dispersal. It is also possible that differences in cropping systems contributed to the observed difference between wild oat and cleavers, although the cropping system used in the Netherlands was not reported (Wallinga 1995).

Fractal self-similarity often indicates an underlying iterative process. In weeds, population processes such as germination, establishment and seed production potentially result in a multiplicative increase in population size. Seeds are dispersed at various distances from the parent plant, but most will fall close to the parent. As a result, most newly-established individuals occur in clusters around parent plants. However, a small proportion of seeds are moved a greater distance from the parent, spreading the population and establishing new clusters. These longer-distance dispersed plants follow the same iterative cycle of seed production and dispersal, resulting in different sized weed clusters ranging in size from a small cluster produced by a single panicle to large, long-established patches.

6.3.1 The Relationship Between Seed Dispersal and Spatial Aggregation

The fractal dimension of the spatial pattern of a plant species may be related to characteristics of its seed dispersal curve. Using the Lévy flight model, Kenkel and Irwin (1994) proposed a functional relationship between the dispersal curve of a species and spatial aggregation (as measured by the fractal dimension). The log-log plot of seed dispersal in natural wild oat populations is approximately linear, with a slope of -5.77 (Figure 6.2). This indicates that most seed are shed very close to the parent plant and that long-distance dispersal is very rare (Harper, 1977). According to Kenkel and Irwin (1994), such a steep log-log dispersal curve should result in the wild oat population producing a statistically random spatial pattern ($D = 2$). The observed pattern ($D = 1.69$) indicates greater spatial clustering than that predicted by the Lévy flight model, suggesting that long-distance dispersal in wild oat has been underestimated.

Combine harvesting may result in long-distance (combine harvester) seed dispersal, and could account for the discrepancy between the predicted and observed fractal dimension of wild oat. The log-log plot of seed dispersal resulting from combine harvesting is some what sigmoidal, and it is far less steep than the natural dispersal curve (Figure 6.3). Mechanical dispersal thus modifies the natural dispersal curve in two important ways: (a) it enhances long-distance seed dispersal (a less steep dispersal curve), resulting in greater spatial aggregation; (b) it results in a curvilinear log-log dispersal curve, implying that seeds are spread more evenly over the field which results in less spatial aggregation of individuals. A complex picture emerges, in which natural and mechanical weed seed dispersal act in concert to create a characteristic pattern of spatial aggregation. In the case of wild oat, the pattern deviates from random and is somewhat spatially aggregated. It is interesting to note that the observed spatial pattern of wild oat is fractal (i.e. statistically self-similar), despite the fact that the dispersal curve from mechanical combining is curvilinear.

It should be noted that only a small proportion of wild oat seed were mechanically dispersed, because chaff collection was performed in this study and many wild oat seeds were removed from the field with the chaff. It has been estimated that only 5% of wild oat seeds taken into the combine are mechanically dispersed (see Chapter 3). Depending on the time of harvest, between 5% and 40% of all seed produced by the wild oat population are brought into the combine. As a result, only 0.25% to 2% of all seeds produced are mechanically dispersed in a given year. Although this value is small, most of these seeds are dispersed over much greater distances than would occur with natural dispersal, resulting in a higher rate of spread and greater spatial aggregation of the weed population.

The harvest management strategy used may also affect the spatial aggregation and rate of spread of wild oat populations. If most wild oat plants shed their seed prior to harvesting, natural dispersal will predominate and long-distance dispersal will rarely occur. Under this scenario, the rate of spread will be low and the population is expected to display low levels of spatial aggregation (high fractal dimension), since the patch would expand as a moving front. Conversely, if a large proportion of wild oat seeds are mechanically dispersed, the rate of spread will increase and a greater degree of spatial aggregation (lower fractal dimension) is expected, since new patches are continuously being created.

In practice, seed dispersal may not be the only factor influencing the degree of spatial aggregation in a weed population. For example, seed germination and seedling establishment may be affected by natural environmental heterogeneity in arable fields, such as variation in soil clay content (Andreasen et al. 1991). In addition, interspecific competition may affect the distribution and abundance of weeds (Lehman and Tilman 1997). Finally, tillage equipment may disperse weed seeds over short distances (generally < 1 m, see Rew and Cussans 1997; Howard et al. 1991). In practice, tillage dispersal probably reduces spatial aggregation in weed populations.

6.3.2 Dispersal and Rate of Spread

The shape of a species dispersal curve is a strong determinant of its rate of spread. Since different dispersal models can be fitted to the same data, the selection of a function that properly models long-distance dispersal is of critical importance. Dispersal curves that describe long-distance dispersal (so-called "fat tailed" curves) often result in rates of spread that accelerate with time (Kot et al. 1996). In a simulation of seed dispersal in black grass (*Alopecurus myosuroides* Huds.), Wallinga et al. (1998) found that species invasion expands at an accelerated rate if the dispersal curve declines at less than an exponential rate. This is true of wild oat dispersal by combine harvesters (Figure 6.3).

Pollen records from the end of the Pleistocene era support this conclusion: tree species having "fat tailed" dispersal curves spread the most rapidly, even if they their mean seed dispersal distances are short (Clark, 1998).

Shaw (1995) reported similar results to Wallinga (1998) in a model simulation of plant disease spread using two different dispersal curves. A negative exponential curve resulted in invasion as an expanding front, whereas a model based on the Cauchy distribution resulted in an invasion characterized by the continuous formation of new 'daughter' patches. Although the spatial aggregation patterns resulting from the Cauchy distribution showed evidence of statistical self-similarity, the log-log plots were not linear so that the patterns were not truly fractal (Shaw, 1995).

6.4 Conclusion

Although fractal scaling of the wild oat patch was evident over the scales assessed, the 10 x 10 m plot was not large enough to determine large-scale interpatch spatial relationships. Natural fractals typically have a limited scale over which self-similarity is evident (Kenkel and Walker, 1996). For example, an individual plant requires a finite space for growth, so that fractal scaling is impossible at finer spatial scales. Since only a portion of a larger population was considered in this study, it is not known, with certainty, whether coarser spatial scales will have the same fractal dimension as the 10 x 10 m plot.

While the theoretical relationship between seed dispersal and plant spatial aggregation was not proven by this study, it is noteworthy that the empirical pattern of the mapped wild oat patch proved to be fractal and statistically self-similar. While a strict numerical relationship between dispersal and fractal spatial pattern is expected (Kenkel and Irwin, 1994), in practice, both the dispersal and spatial patterning in wild oat populations is a complex function of natural and mechanical (combine and tillage) seed dispersal, together with factors such as environmental variation and interspecific competition. Furthermore, it is impossible to know what proportion of the seed was spread in previous years or germinated from the seed bank. On balance, it is apparent that a multitude of factors control the demographics, dispersal and spatial patterning of wild oat populations in arable fields.

Computer simulation models are useful in demonstrating how dispersal curve shape can affect the invasion rates and aggregation patterns of weed populations. However, in practice a number of factors may determine the observed invasion and aggregation patterns of weeds in arable fields. Despite this, the present study has demonstrated that wild oat has a spatially aggregated spatial pattern that displays fractal, self-similar properties. Similar conclusions were reached by Wallinga (1995) for cleavers, another common weed species of arable fields. Further research should be directed toward determining the mechanism by which such patterns arise. For example, experiments in which the invasion dynamics of a species under controlled conditions (no initial seed bank, homogeneous substrate, no interspecific competition) should be undertaken, to determine the link between seed dispersal and spatial aggregation.

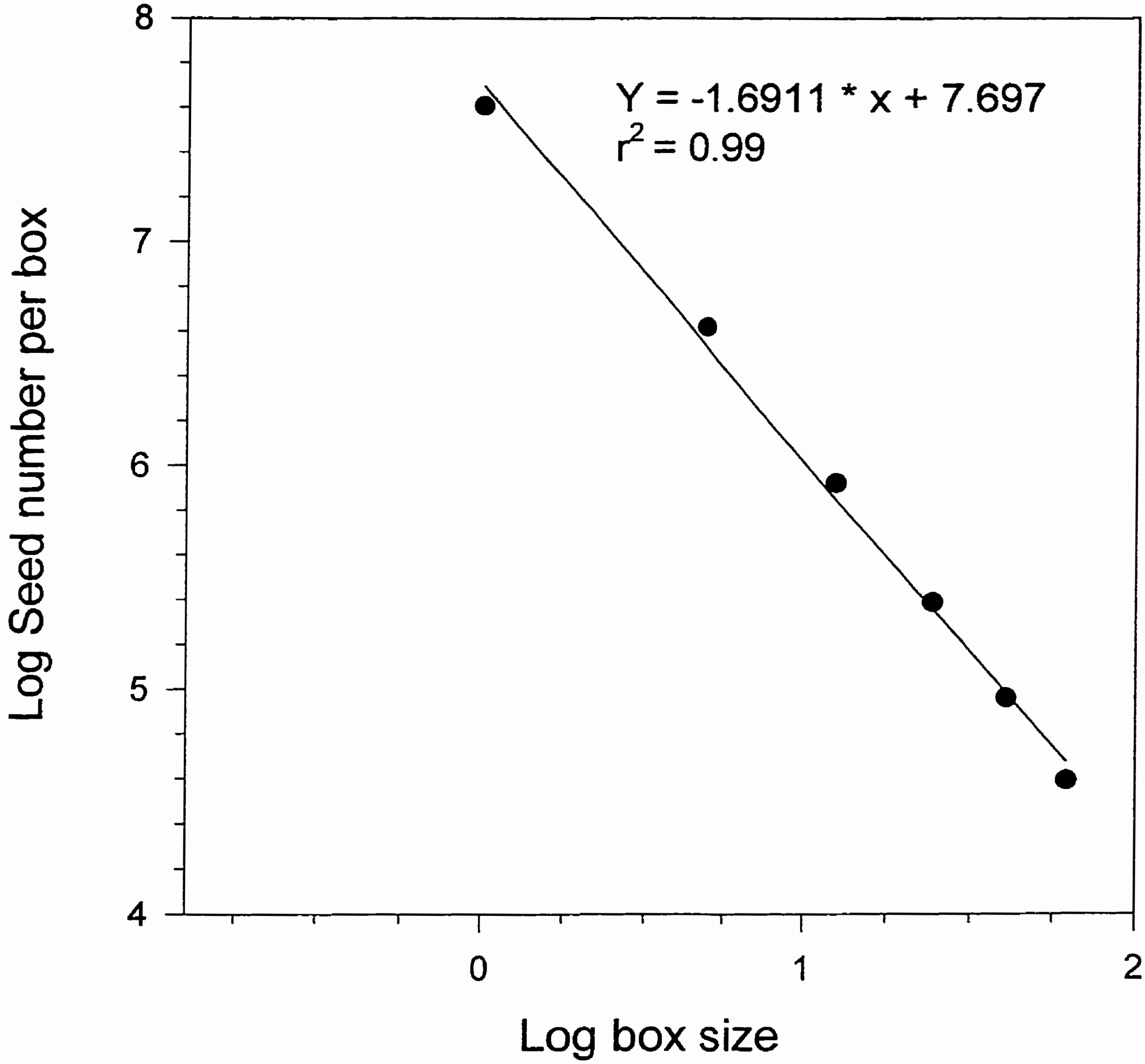


Figure 6.1. The scaling of wild oat seedlings per box with box size. The slope of the log-log plot gives the fractal dimension D.

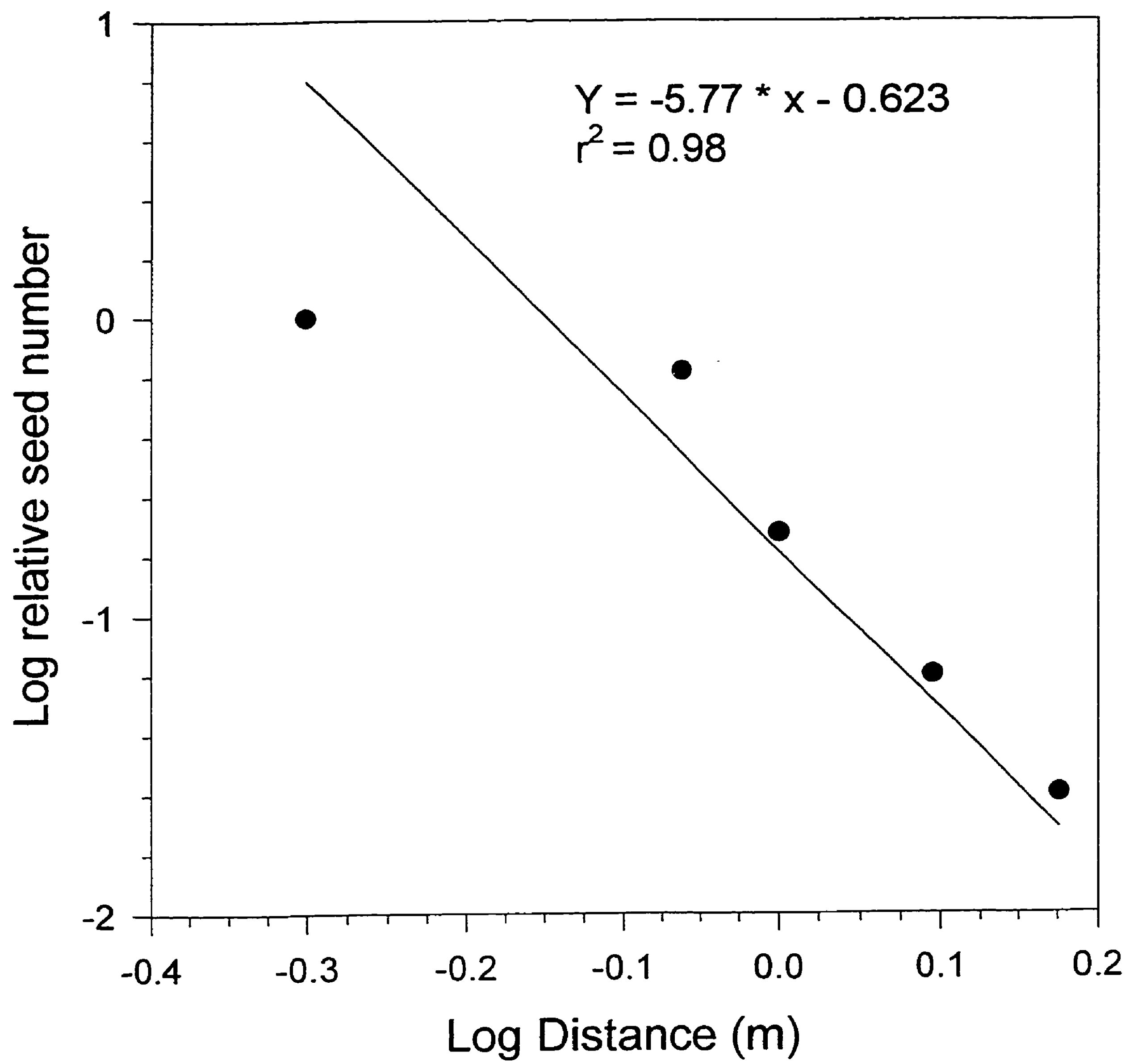


Figure 6.2. Relative wild oat natural seed dispersal. Note that seed number and distance are log transformed (base 10). The slope of the function is theoretically related to the fractal dimension D.

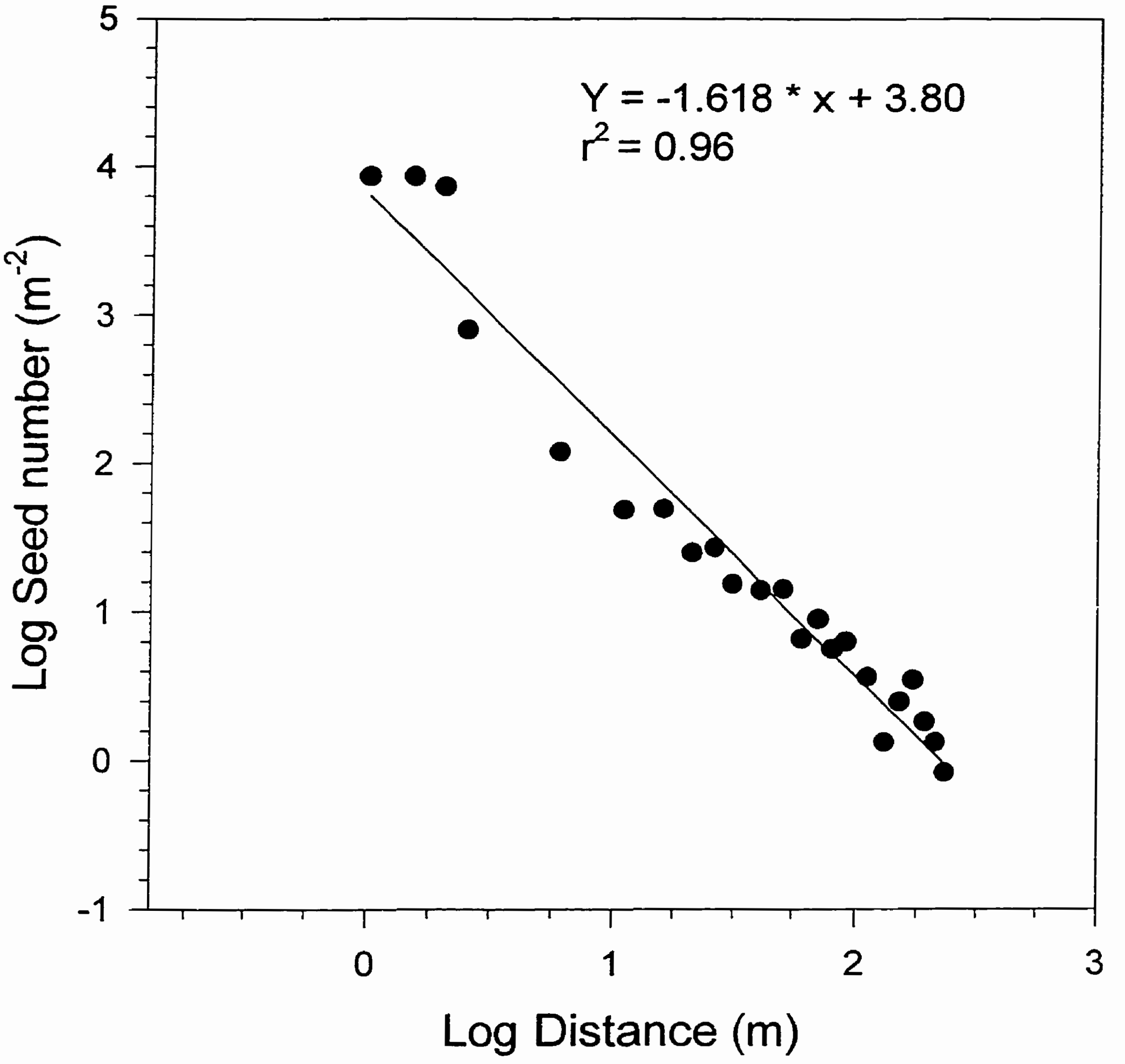


Figure 6.3. Wild oat seed dispersal by combine with chaff collection. Note that seed number and distance are log (base 10) transformed. The slope of the function is theoretically related to the fractal dimension D.

7.0 Summary and Conclusions

This thesis investigated the effect of combine harvester dispersal on the spread of wild oat patches. The intent was to provide a way of slowing the spread of herbicide resistant wild oat within a field. The research was conducted with the belief that to study processes one must observe and quantify ecological mechanisms.

The first step in the research into the effect of combine harvest dispersal was to measure the distance that wild oat are dispersed and the effect of chaff collection on this dispersal. It was found that combines could disperse wild oat and green foxtail long distances, much further than had been previously reported in the scientific literature. The distance was so great that in the first year the length of the experimental assay was not long enough to observe the end of the dispersal, even though a distance twice as long (100 m) as previously reported was used for the dispersal calculation. The next year the experiment was repeated with an assay distance of 250 m. This was a long enough distance to observe most seed dispersal as most combine dispersal had occurred by approximately 150 m.

Despite the convincing results from the first experiment, the utility of chaff collection for wild oat was still questioned by some farmers and researchers. The perception was that wild oat plants shed all of its seed before harvest. Although the observation that samples of harvested grain often contained large amounts of wild oat seed refuted this assertion, a detailed investigation of seed shed in wild oat was necessary.

An investigation to quantify the rate of development of wild oat relative to spring wheat was conducted. The first year it was conducted at one location and the attempts to measure seed shed were fraught with technical difficulty. Nonetheless, the season did provide good measures of the development and the initiation of seed shed of wild oat. The following year, a detailed study in plant development and seed shed of wild oat was conducted at two locations. Analysis of phyllochron interval relative to thermal time revealed that the phyllochron interval wild oat and wheat were similar within location but differed between locations. However, the development as measured by the Zadoks plant development scale revealed a consistent development of wild oat and wheat between locations and years. A detailed measure of seed shed in wild oat confirmed the consistency in development of wild oat. As this study revealed, seed shed between location was very consistent.

The timing of this seed shed raised an interesting management question. How would harvest timing effect wild oat seed dispersal? An early swathing would take place while there were still a substantial portion of will oat seeds that had not been shed. An early harvest would have the advantage of capturing more wild oat seed and exporting them from the seed. However, since more wild oat seed would be taken into the combine it could be presumed that harvest dispersal would also be further. A delayed harvest, such as would happen with straight combining, would result in the majority of wild oat seeds being shed before harvest. A later harvest would presumably reduce harvest dispersal as there would be less wild oat seed taken into the combine, but there would be less wild oat seed removed from the field. Without further investigation into the interaction of harvest timing, chaff collection and wild oat spatial arrangement, a management recommendation could not be made.

To conduct field scale experiments to test all combinations of harvest management options for wild oat dispersal would have been impossible. Even a simple study on the dispersal of wild oat seed occupies approximately 2 ha per year, so a multi-year investigation would have been prohibitive based on resource and time requirements. Therefore it was decided to use computer simulation model to determine the effect of different harvest management techniques on the dispersal of wild oat. A winter spent at Montana State University under the supervision of Doctor Bruce Maxwell provided the necessary instruction in order to develop a computer model of this process.

Simulations of management options run on a computer model revealed that chaff collection was effective at reducing the expansion of wild oat patches over a six year simulation period. An interesting observation from the a model simulation was that a delayed harvest substantially reduced wild oat patch expansion. A combination of a late harvest and chaff collection and a late harvest eliminated weed patch expansion. However, the results were different if the simulations were conducted on a field which was uniformly covered with wild oat. Under these circumstances an early harvest was more advantageous, as it resulted in a greater export of wild oat seed. The utility of this management approach may be limited, as all studies in which the spatial pattern of wild oat was measured have shown a patchy spatial distribution.

One nagging question remained: If combines can disperse wild oat seeds a great distance, why does wild oat still occur in patches? To answer this question it was necessary to investigate the ecological theory of organism invasion and the relationship between seed dispersal and resultant spatial patterns. A fractal theory of dispersal provided an explanation of how a species could be both highly dispersed and spatially aggregated. Fractals are objects with self similarity when viewed at different spatial scales. The iterative process which forms a fractal was analogous to the iterative process of weed seed production and dispersal. When a plant produces seeds, most of them will be dispersed very close to the parent plant. Some, however, will be carried a distance away where they may geminate and produce a daughter patch. Thus a weed species may have the ability to be dispersed far but will still produce a patchy, fractal spatial pattern. A partial validation of the fractal model of seed dispersal and spatial pattern was provided by the observation that a portion of a wild oat patch was fractal and that the fractal dimension was very similar to a log-log slop of combine dispersal.

Overall, this thesis answered most of the initial objectives. However, some questions still remain unanswered and other questions have arisen. The effect of different types and designs of combine harvesters on harvest dispersal was not evaluated in this study. Ballaré (1987 a) found that different combine designs have an effect on harvest dispersal, but he did not test any rotary type combines

The phenological development of wild oat was quite consistent in relation to environment in this study. However, this study only assessed one population of wild oat. As there are undoubtably many different populations, it would be interesting to assess this variability in a similar manner as was done in North Dakota by Miller et al. (1982).

The computer model allowed the simulation of different management studies over a large spatial and temporal scale. However, the often used adage, "All models are wrong but they can teach us something" would apply here. Even though the model was never (and one could argue, could never) formally validated, the results seem robust enough for us to have confidence in them. Because of the difficulty in validating large scale models, the utility of further research and refinement in this area is debatable.

Finally, the fractal analysis of the spatial pattern of a wild oat patch provided some interesting insights into ecological mechanisms linking dispersal and plant spatial pattern. However, only a portion of one patch was mapped. To understand the spatial dynamics of wild oat as it occurs in the field it would be necessary to map in detail several fields of wild oat and calculate the fractal dimension. The impracticality of this endeavour may prevent it form ever being done. A better way may be to introduce a weed invasion on a homogeneous soil and follow the development of a patch and the invasion process over time.

This thesis was based on a research project which was both theoretical and applied. I believe that this goal has been accomplished. Recommendations can now be made to producers telling them under which circumstances chaff collection will reduce weed seed dispersal. I am also confident in making general recommendations such as using delayed harvest as a management tool to reduce dispersal of small patches of herbicide resistant wild oat. The theoretically work of this thesis was an attempt to relate the processes of seed dispersal and plant spatial arrangement. Although the relationship between these ecological processes is not conclusively proven in this thesis, the observation that a wild oat patch has a fractal geometry suggests that the two may be related. Given the practical and theoretical implication of this thesis I would have to say that I am satisfied with the results and can only hope that future research programs provide me as much satisfaction as this one did.

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9.0 Appendix 1: Wind Speed 1996

Hourly wind speed and direction for Carman, Manitoba 1996, for the period from panicle extension to early kernel development in wild oat.

Date	Time	2m mean wind speed ($m\ s^{-1}$)	2m mean Vector magnitude ($m\ s^{-1}$)	2m mean Vector direction (degrees)
19-Jul	0	3.22	3.09	8.71
19-Jul	100	2.74	2.67	13.87
19-Jul	200	1.97	1.92	9.96
19-Jul	300	1.84	1.74	17.26
19-Jul	400	1.72	1.68	28.49
19-Jul	500	1.31	1.28	50.34
19-Jul	600	1.46	1.41	81.30
19-Jul	700	1.73	1.67	86.30
19-Jul	800	1.82	1.73	94.70
19-Jul	900	2.04	1.91	127.20
19-Jul	1000	2.32	2.26	134.70
19-Jul	1100	2.87	2.76	132.90
19-Jul	1200	2.94	2.84	122.10
19-Jul	1300	3.23	3.15	144.60
19-Jul	1400	3.13	3.07	148.60
19-Jul	1500	2.42	2.35	131.70
19-Jul	1600	2.91	2.79	122.70
19-Jul	1700	3.74	3.63	126.30
19-Jul	1800	3.40	3.32	123.50
19-Jul	1900	3.37	3.25	115.80
19-Jul	2000	2.99	2.93	120.80
19-Jul	2100	2.57	2.53	124.30
19-Jul	2200	2.48	2.43	125.10
19-Jul	2300	2.51	2.45	127.90
20-Jul	0	2.31	2.27	128.80
20-Jul	100	2.97	2.89	138.80
20-Jul	200	3.87	3.82	153.70
20-Jul	300	4.22	4.15	152.90
20-Jul	400	4.86	4.79	149.90
20-Jul	500	5.10	4.97	167.60
20-Jul	600	4.42	4.35	164.20
20-Jul	700	4.62	4.49	148.00
20-Jul	800	5.85	5.63	150.70
20-Jul	900	6.18	5.86	148.00
20-Jul	1000	5.26	5.08	181.20
20-Jul	1100	3.51	3.41	200.90
20-Jul	1200	2.81	2.75	218.10
20-Jul	1300	2.82	2.65	238.50
20-Jul	1400	4.78	4.70	252.80

20-Jul	1500	4.19	4.05	280.60
20-Jul	1600	3.46	3.37	301.40
20-Jul	1700	2.90	2.77	299.80
20-Jul	1800	1.87	1.82	297.60
20-Jul	1900	1.26	1.22	244.70
20-Jul	2000	0.33	0.30	221.20
20-Jul	2100	0.87	0.85	178.40
20-Jul	2200	0.27	0.27	201.00
20-Jul	2300	0.51	0.50	223.50
21-Jul	0	2.80	2.71	218.30
21-Jul	100	1.62	1.59	240.50
21-Jul	200	0.39	0.39	233.50
21-Jul	300	0.60	0.59	210.70
21-Jul	400	0.59	0.54	183.20
21-Jul	500	0.29	0.26	172.00
21-Jul	600	0.55	0.49	148.60
21-Jul	700	1.50	1.46	194.50
21-Jul	800	2.46	2.42	219.10
21-Jul	900	2.72	2.69	221.20
21-Jul	1000	4.70	4.62	224.70
21-Jul	1100	4.94	4.81	236.60
21-Jul	1200	4.86	4.70	261.40
21-Jul	1300	4.80	4.65	275.50
21-Jul	1400	5.24	5.08	273.10
21-Jul	1500	6.05	5.89	267.30
21-Jul	1600	5.92	5.69	288.40
21-Jul	1700	5.42	5.25	294.50
21-Jul	1800	3.95	3.78	273.00
21-Jul	1900	3.94	3.86	297.00
21-Jul	2000	4.61	4.48	293.90
21-Jul	2100	3.79	3.73	280.90
21-Jul	2200	3.44	3.38	281.80
21-Jul	2300	3.58	3.53	281.10
22-Jul	0	3.48	3.41	276.80
22-Jul	100	2.90	2.84	278.70
22-Jul	200	2.85	2.77	282.70
22-Jul	300	2.50	2.45	274.70
22-Jul	400	2.62	2.59	264.80
22-Jul	500	2.50	2.46	278.00
22-Jul	600	2.77	2.72	283.80
22-Jul	700	3.38	3.32	283.40
22-Jul	800	4.01	3.92	287.80
22-Jul	900	4.40	4.30	296.00
22-Jul	1000	4.47	4.32	293.30
22-Jul	1100	4.53	4.38	300.70
22-Jul	1200	5.27	5.12	293.00
22-Jul	1300	5.38	5.19	292.70
22-Jul	1400	5.49	5.34	296.70
22-Jul	1500	6.35	6.16	299.20
22-Jul	1600	5.86	5.69	301.10
22-Jul	1700	4.48	4.34	309.90
22-Jul	1800	2.99	2.85	324.60

22-Jul	1900	2.56	2.50	299.30
22-Jul	2000	1.86	1.83	289.30
22-Jul	2100	1.74	1.72	252.60
22-Jul	2200	0.61	0.59	247.00
22-Jul	2300	1.45	1.37	272.50
23-Jul	0	1.27	1.21	278.40
23-Jul	100	1.67	1.63	285.10
23-Jul	200	2.29	2.25	296.60
23-Jul	300	2.54	2.50	291.60
23-Jul	400	2.37	2.33	297.70
23-Jul	500	2.28	2.25	294.60
23-Jul	600	2.27	2.23	296.00
23-Jul	700	2.99	2.94	294.80
23-Jul	800	3.51	3.42	302.80
23-Jul	900	3.14	3.00	313.00
23-Jul	1000	3.32	3.21	301.50
23-Jul	1100	3.65	3.53	303.00
23-Jul	1200	4.20	4.04	295.00
23-Jul	1300	3.51	3.34	321.90
23-Jul	1400	2.79	2.72	315.80
23-Jul	1500	3.27	3.18	325.60
23-Jul	1600	2.53	2.43	317.20
23-Jul	1700	3.70	3.54	329.80
23-Jul	1800	4.58	4.45	339.70
23-Jul	1900	4.26	4.12	345.70
23-Jul	2000	3.04	2.96	340.90
23-Jul	2100	1.55	1.51	324.70
23-Jul	2200	2.06	1.99	319.40
23-Jul	2300	2.36	2.29	327.70
24-Jul	0	2.38	2.26	339.90
24-Jul	100	2.75	2.65	337.60
24-Jul	200	2.68	2.61	340.80
24-Jul	300	2.33	2.23	326.90
24-Jul	400	3.06	2.98	313.20
24-Jul	500	3.12	3.04	326.60
24-Jul	600	3.13	3.04	317.00
24-Jul	700	3.58	3.49	315.10
24-Jul	800	3.52	3.44	324.00
24-Jul	900	4.01	3.88	331.60
24-Jul	1000	4.65	4.48	332.70
24-Jul	1100	4.87	4.66	334.30
24-Jul	1200	4.62	4.42	343.10
24-Jul	1300	4.34	4.15	348.50
24-Jul	1400	4.79	4.59	343.40
24-Jul	1500	4.91	4.69	346.90
24-Jul	1600	4.40	4.23	343.30
24-Jul	1700	3.98	3.80	338.60
24-Jul	1800	3.72	3.60	340.70
24-Jul	1900	2.52	2.46	338.40
24-Jul	2000	2.33	2.28	332.60
24-Jul	2100	1.65	1.63	307.90
24-Jul	2200	1.71	1.70	295.90

24-Jul	2300	1.62	1.62	295.50
25-Jul	0	1.71	1.70	297.90
25-Jul	100	1.51	1.50	300.30
25-Jul	200	1.78	1.76	310.40
25-Jul	300	1.88	1.86	310.10
25-Jul	400	2.37	2.35	304.80
25-Jul	500	2.55	2.53	306.00
25-Jul	600	2.56	2.53	309.90
25-Jul	700	2.45	2.42	311.10
25-Jul	800	2.48	2.40	303.50
25-Jul	900	2.24	2.16	313.60
25-Jul	1000	2.27	2.09	343.20
25-Jul	1100	2.25	2.06	353.60
25-Jul	1200	2.09	1.87	359.80
25-Jul	1300	1.55	1.35	24.31
25-Jul	1400	1.63	1.41	36.08
25-Jul	1500	1.89	1.58	31.49
25-Jul	1600	1.83	1.54	34.04
25-Jul	1700	1.74	1.66	36.41
25-Jul	1800	1.10	1.07	37.98
25-Jul	1900	0.87	0.85	32.10
25-Jul	2000	0.59	0.56	4.98
25-Jul	2100	0.45	0.45	352.90
25-Jul	2200	0.69	0.69	344.20
25-Jul	2300	0.60	0.59	4.61
26-Jul	0	0.77	0.72	8.04
26-Jul	100	0.58	0.58	5.63
26-Jul	200	0.03	0.03	326.10
26-Jul	300	0.04	0.04	319.80
26-Jul	400	0.35	0.34	270.30
26-Jul	500	0.22	0.22	265.00
26-Jul	600	0.08	0.08	265.00
26-Jul	700	0.06	0.06	265.00
26-Jul	800	0.17	0.16	343.10
26-Jul	900	0.42	0.33	97.30
26-Jul	1000	0.66	0.61	101.70
26-Jul	1100	0.83	0.78	53.16
26-Jul	1200	0.96	0.65	120.30
26-Jul	1300	2.09	2.06	211.00
26-Jul	1400	2.37	2.35	229.50
26-Jul	1500	1.20	1.18	207.30
26-Jul	1600	1.11	1.10	207.30
26-Jul	1700	1.30	0.88	86.00
26-Jul	1800	1.23	1.20	58.81
26-Jul	1900	0.87	0.76	111.30
26-Jul	2000	0.52	0.52	157.50
26-Jul	2100	0.03	0.03	161.60
26-Jul	2200	0.61	0.34	28.00
26-Jul	2300	0.30	0.26	40.48
27-Jul	0	1.30	1.20	112.30
27-Jul	100	1.60	1.51	82.70
27-Jul	200	1.44	1.30	97.90

27-Jul	300	1.23	1.19	84.50
27-Jul	400	1.71	1.66	60.74
27-Jul	500	1.43	1.36	71.50
27-Jul	600	1.20	1.15	79.40
27-Jul	700	0.53	0.52	83.20
27-Jul	800	1.28	1.23	129.60
27-Jul	900	0.56	0.48	114.40
27-Jul	1000	1.58	1.43	104.90
27-Jul	1100	1.01	0.85	145.60
27-Jul	1200	0.68	0.43	85.30
27-Jul	1300	1.13	0.95	114.50
27-Jul	1400	2.03	1.77	75.10
27-Jul	1500	2.36	2.21	98.90
27-Jul	1600	2.65	2.53	90.90
27-Jul	1700	2.59	2.46	106.00
27-Jul	1800	2.25	2.16	110.90
27-Jul	1900	1.42	1.38	113.80
27-Jul	2000	0.91	0.88	100.20
27-Jul	2100	0.45	0.44	91.10
27-Jul	2200	0.20	0.18	78.10
27-Jul	2300	0.11	0.06	0.40
28-Jul	0	0.71	0.67	127.60
28-Jul	100	1.34	1.28	129.90
28-Jul	200	1.54	1.52	138.70
28-Jul	300	1.48	1.45	134.30
28-Jul	400	1.33	1.30	126.60
28-Jul	500	0.97	0.96	135.20
28-Jul	600	0.46	0.43	103.80
28-Jul	700	1.46	1.39	140.10
28-Jul	800	2.36	2.30	150.40
28-Jul	900	2.10	1.99	144.60
28-Jul	1000	2.04	1.92	147.10
28-Jul	1100	1.76	1.61	141.00
28-Jul	1200	2.23	2.11	121.30
28-Jul	1300	2.77	2.67	140.00
28-Jul	1400	2.48	2.40	136.30
28-Jul	1500	2.52	2.41	140.00
28-Jul	1600	2.46	2.37	116.60
28-Jul	1700	2.15	2.04	127.00
28-Jul	1800	1.93	1.85	110.90
28-Jul	1900	1.72	1.66	110.50
28-Jul	2000	1.30	1.27	88.20
28-Jul	2100	0.31	0.23	86.50
28-Jul	2200	0.25	0.25	12.75
28-Jul	2300	0.41	0.40	31.96
29-Jul	0	0.40	0.38	22.79
29-Jul	100	0.52	0.50	6.86
29-Jul	200	0.79	0.78	19.06
29-Jul	300	0.69	0.66	34.46
29-Jul	400	0.77	0.74	355.50
29-Jul	500	1.55	1.52	24.66
29-Jul	600	1.49	1.47	19.70

29-Jul	700	1.37	1.32	26.08
29-Jul	800	1.37	1.29	49.72
29-Jul	900	1.34	1.19	47.09
29-Jul	1000	1.77	1.66	102.70
29-Jul	1100	1.63	1.39	81.00
29-Jul	1200	1.32	1.16	313.70
29-Jul	1300	1.93	1.15	207.90
29-Jul	1400	1.80	1.68	208.50
29-Jul	1500	0.97	0.76	234.50
29-Jul	1600	1.06	0.46	206.00
29-Jul	1700	1.48	1.14	250.00
29-Jul	1800	1.21	0.97	317.30
29-Jul	1900	0.99	0.96	15.40
29-Jul	2000	0.41	0.40	341.80
29-Jul	2100	1.03	1.00	341.70
29-Jul	2200	0.80	0.61	6.21
29-Jul	2300	0.51	0.50	279.50
30-Jul	0	0.53	0.09	150.60
30-Jul	100	0.46	0.31	254.50
30-Jul	200	1.45	1.42	298.30
30-Jul	300	2.00	1.94	335.10
30-Jul	400	1.32	1.25	348.60
30-Jul	500	1.65	1.62	320.10
30-Jul	600	1.89	1.85	327.40
30-Jul	700	2.07	2.02	327.90
30-Jul	800	1.95	1.86	329.40
30-Jul	900	2.46	2.34	348.00
30-Jul	1000	2.77	2.64	340.40
30-Jul	1100	2.96	2.84	353.40
30-Jul	1200	3.05	2.90	7.80
30-Jul	1300	3.12	2.96	12.57
30-Jul	1400	2.76	2.63	7.36
30-Jul	1500	2.63	2.49	26.85
30-Jul	1600	2.29	2.17	21.27
30-Jul	1700	2.06	1.96	19.68
30-Jul	1800	1.70	1.67	15.31
30-Jul	1900	1.95	1.86	1.00
30-Jul	2000	1.37	1.36	334.50
30-Jul	2100	0.93	0.90	347.40
30-Jul	2200	0.85	0.59	146.60
30-Jul	2300	0.28	0.26	313.50
31-Jul	0	0.15	0.15	305.50
31-Jul	100	0.26	0.26	299.70
31-Jul	200	0.40	0.40	281.40
31-Jul	300	0.34	0.34	282.10
31-Jul	400	0.29	0.29	282.40
31-Jul	500	0.10	0.10	282.10
31-Jul	600	0.11	0.11	282.10
31-Jul	700	0.15	0.15	279.40
31-Jul	800	0.10	0.10	253.70
31-Jul	900	0.39	0.27	141.40
31-Jul	1000	1.16	0.98	168.10

31-Jul	1100	1.16	0.97	168.20
31-Jul	1200	1.95	1.79	153.80
31-Jul	1300	2.50	2.38	167.20
31-Jul	1400	2.62	2.49	155.40
31-Jul	1500	2.77	2.66	152.20
31-Jul	1600	2.89	2.75	161.90
31-Jul	1700	2.72	2.64	156.90
31-Jul	1800	2.54	2.49	150.30
31-Jul	1900	1.79	1.77	148.70
31-Jul	2000	0.96	0.96	144.00
31-Jul	2100	0.34	0.34	138.20
31-Jul	2200	0.51	0.51	123.40
31-Jul	2300	0.37	0.36	117.40
01-Aug	0	0.07	0.07	108.60
01-Aug	100	0.04	0.04	108.70
01-Aug	200	0.16	0.16	101.80
01-Aug	300	0.27	0.27	111.50
01-Aug	400	0.45	0.45	111.00
01-Aug	500	0.64	0.63	116.20
01-Aug	600	0.76	0.75	117.70
01-Aug	700	1.41	1.38	142.30
01-Aug	800	2.56	2.53	147.80
01-Aug	900	2.52	2.46	147.80
01-Aug	1000	2.85	2.81	155.10
01-Aug	1100	3.02	2.97	149.20
01-Aug	1200	3.84	3.68	162.50
01-Aug	1300	4.93	4.79	168.80
01-Aug	1400	4.71	4.62	158.00
01-Aug	1500	4.73	4.63	153.90
01-Aug	1600	4.79	4.69	161.80
01-Aug	1700	4.76	4.67	154.90
01-Aug	1800	4.45	4.37	152.80
01-Aug	1900	3.52	3.48	159.50
01-Aug	2000	1.97	1.95	160.30
01-Aug	2100	1.30	1.30	155.30
01-Aug	2200	1.37	1.36	156.10
01-Aug	2300	1.41	1.40	159.20

10.0 Appendix 2: Computer Simulation Program

QuickBASIC Source code for spatial wild oat dispersal model.

```
'COMBINE SIMULATION v 1.0
'This program is designed to simulate the combine dispersal of wild oat
'as described by Shirtliffe Chapter 5

OPEN "C:\comb1y.OUT" FOR OUTPUT AS #1
OPEN "C:\Combtot.OUT" FOR OUTPUT AS #2
OPEN "C:\seedbank.OUT" FOR OUTPUT AS #3

OPEN "C:\year1.OUT" FOR OUTPUT AS #5
OPEN "C:\year2.OUT" FOR OUTPUT AS #6
OPEN "C:\year3.OUT" FOR OUTPUT AS #7
OPEN "C:\year4.OUT" FOR OUTPUT AS #8
OPEN "C:\year5.OUT" FOR OUTPUT AS #9
OPEN "C:\year6.OUT" FOR OUTPUT AS #10

CLS
INPUT "Number of simulations to run", simtot
'simtot = 1
INPUT "Field length and width in metres (less than 180)  ", cellnu
'cellnu = 60
INPUT "Do you want to use chaff collection, 1 for yes 0 for no ", ccswitch
'ccswitch = 0
'INPUT "Number of years for model to run", generations
generations = 6
'INPUT "Do you want to spray? (every 0,1,2,3,4,5 years or based on ET(37))", spray
spray = 0
IF spray = 37 THEN
INPUT "What is the Economic threshold in WO plants per m^2?", ET
END IF
'INPUT "What is the efficacy of the herbicide? (% seed return of unsprayed)", spraykill%
'This can range between 62% and 98% based on interpolated 87.5% application (with full the
and 2% overlap it is probabley close to 92%)
'and usually between 75% and 99% when 100% application rate is chosen (unrealistic)
'spraykill = spraykill% / 100
spraykill = .95
'INPUT "Combine direction, 0 for y dir, 1 for both, 2 for x ", cdirswitch
cdirswitch = 1
'INPUT "Do you wish to import a map of WO seedbank? 1 = yes, 2 = no", womap
'womap = 2
'INPUT "Do you wish to change the weed patch parametres? 1 = yes, 0 = No", wppage
```

```
wppage = 1
INPUT "Do you wish to use early swath (1) or late strait combine (0)?", swath
'swath = 1
IF wppage = 1 THEN
CLS
INPUT "Rand patchs 1, strips 0=x, 2=y, herb res 3, map 4, solid 5", patchstrip
'patchstrip = 5

END IF


vl = cellnu + 5
DIM SHARED sp(vl, vl) AS LONG
DIM SHARED sb(vl, vl)  AS LONG
DIM SHARED cs(vl, vl) AS INTEGER
DIM SHARED mp(vl, vl) AS INTEGER
DIM SHARED ay(10)
DIM SHARED np(10)
DIM SHARED asd(10)  AS INTEGER
DIM SHARED spraycounter(10)  AS INTEGER

'*************************NUMBER OF SIMMULATIONS TO RUN*******************

'simtot = 1
DIM SHARED st(simtot)
FOR simmulation = 1 TO simtot  'SIMTOT = Number of simulations

RANDOMIZE TIMER
SCREEN 12
VIEW (10, 10)-(630, 400), , 6
WINDOW (0, 0)-(560, 400)
cn = cellnu 'cell number ie (x by x)
ss = 400 / cn   'square size  (do not change)
dcs = 10 'density classification size number
initcol = 13 'initial colour
x = 0
FOR N = ss TO 400 STEP ss
 x = 1 + x
 y = 0
 FOR Z = ss TO 400 STEP ss
  y = 1 + y
  LINE (N - ss, Z - ss)-(N, Z), 7, B
  sb(x, y) = 0
```

```
 NEXT Z
NEXT N

'routine to put legend on side of map
wodn = 2  'location for legend title (wild oat density)
LOCATE wodn, 63
 '?X PRINT "WO seedlings"
LOCATE wodn + 1, 62
 '?X PRINT "per square metre"
pd = 0 'density colour ploting  (begins at zero)
hd = 110 'highest density class
fl = 362.5  'first location for  Index
col = initcol - 2' - dcs + 1
FOR dds = 1 TO dcs
 fl = fl - 32.5
 LINE (520, fl - 20)-(540, fl), col, BF
  col = col - 1
  wodn = wodn + 2
LOCATE wodn + 2, 60
IF dds = 1 THEN
'?X PRINT (pd + 1) / 4; "to"; (pd + (hd / dcs)) / 4
pd = pd + (hd / dcs)
ELSE
IF dds = dcs THEN
'?X PRINT "      >"; (pd + 1) / 4
ELSE
IF dds >= 0 AND dds < dcs THEN
'?X PRINT (pd + 1) / 4; "to"; (pd + (hd / dcs)) / 4
pd = pd + (hd / dcs)
END IF
END IF
END IF
NEXT dds


'*************************** Herbicide resistant patch drawing **************
IF patchstrip = 3 THEN
FOR x = 1 TO cn
 FOR y = 1 TO cn
 ssb = 2000
  IF x = INT(cn * .2) AND y = INT(cn * .8) THEN
    sb(x, y) = ssb
     END IF
```

```
    IF x = INT(cn * .3) AND y = INT(cn * .35) THEN
      sb(x, y) = ssb
       END IF
    IF x = INT(cn * .5) AND y = INT(cn * .7) THEN
      sb(x, y) = ssb
       END IF
    IF x = INT(cn * .65) AND y = INT(cn * .75) THEN
      sb(x, y) = ssb
       END IF
    IF x = INT(cn * .85) AND y = INT(cn * .2) THEN
      sb(x, y) = ssb
       END IF


 NEXT y
NEXT x
END IF

'************************ Normal patch drawing ***************************
IF patchstrip = 4 THEN
FOR x = 1 TO cn
 FOR y = 1 TO cn
 ssb = 2000
  IF (x >= 31 AND x <= 34) AND (y >= 4 AND y <= 14) THEN
    sb(x, y) = ssb
     END IF
  IF (x >= 34 AND x <= 35) AND (y >= 5 AND y <= 6) THEN
    sb(x, y) = ssb
     END IF
  IF (x >= 33 AND x <= 35) AND (y >= 15 AND y <= 16) THEN
    sb(x, y) = ssb
     END IF
  IF (x >= 34 AND x <= 35) AND (y >= 17 AND y <= 19) THEN
    sb(x, y) = ssb
     END IF
  IF (x >= 40 AND x <= 41) AND (y >= 21 AND y <= 22) THEN
    sb(x, y) = ssb
     END IF
  IF (x >= 29 AND x <= 31) AND (y >= 44 AND y <= 46) THEN
    sb(x, y) = ssb
     END IF
  IF (x >= 30 AND x <= 34) AND (y >= 40 AND y <= 42) THEN
    sb(x, y) = ssb
     END IF
```

```
IF (x >= 33 AND x <= 35) AND (y >= 38 AND y <= 39) THEN
  sb(x, y) = ssb
   END IF

'ssb = 20

IF (x = 30) AND (y >= 12 AND y <= 20) THEN
  sb(x, y) = ssb
   END IF
IF (x = 37) AND (y >= 5 AND y <= 7) THEN
  sb(x, y) = ssb
   END IF
IF (x = 35) AND (y >= 10 AND y <= 11) THEN
  sb(x, y) = ssb
   END IF
IF (x = 30) AND (y >= 25 AND y <= 29) THEN
  sb(x, y) = ssb
   END IF
IF (x = 30) AND (y >= 38 AND y <= 39) THEN
  sb(x, y) = ssb
   END IF
IF (x = 27) AND (y >= 47 AND y <= 48) THEN
  sb(x, y) = ssb
   END IF
IF (x >= 36 AND x <= 38) AND (y = 20) THEN
  sb(x, y) = ssb
   END IF
IF (x >= 36 AND x <= 41) AND (y = 39) THEN
  sb(x, y) = ssb
   END IF
IF (x >= 35 AND x <= 36) AND (y = 40) THEN
  sb(x, y) = ssb
   END IF
IF (x >= 36 AND x <= 37) AND (y = 41) THEN
  sb(x, y) = ssb
   END IF
IF (x >= 32 AND x <= 33) AND (y = 42) THEN
  sb(x, y) = ssb
   END IF
IF (x >= 31 AND x <= 32) AND (y = 43) THEN
  sb(x, y) = ssb
   END IF

'ssb = 5
```

```
IF x = 33 AND y = 6 THEN
  sb(x, y) = ssb
    END IF
IF x = 36 AND y = 5 THEN
  sb(x, y) = ssb
    END IF
IF x = 35 AND y = 7 THEN
  sb(x, y) = ssb
    END IF
IF x = 35 AND y = 14 THEN
  sb(x, y) = ssb
    END IF
IF x = 32 AND y = 15 THEN
  sb(x, y) = ssb
    END IF
IF x = 32 AND y = 17 THEN
  sb(x, y) = ssb
    END IF
IF x = 29 AND y = 19 THEN
  sb(x, y) = ssb
    END IF
IF x = 29 AND y = 22 THEN
  sb(x, y) = ssb
    END IF
IF x = 37 AND y = 21 THEN
  sb(x, y) = ssb
    END IF
IF x = 39 AND y = 21 THEN
  sb(x, y) = ssb
    END IF
IF x = 41 AND y = 20 THEN
  sb(x, y) = ssb
    END IF
IF x = 40 AND y = 24 THEN
  sb(x, y) = ssb
    END IF
IF x = 32 AND y = 26 THEN
  sb(x, y) = ssb
    END IF
IF x = 40 AND y = 39 THEN
  sb(x, y) = ssb
    END IF
IF x = 38 AND y = 40 THEN
  sb(x, y) = ssb
```

```
      END IF
   IF x = 28 AND y = 44 THEN
     sb(x, y) = ssb
      END IF
   IF x = 27 AND y = 45 THEN
     sb(x, y) = ssb
      END IF
   IF x = 31 AND y = 47 THEN
     sb(x, y) = ssb
      END IF
   IF x = 27 AND y = 51 THEN
     sb(x, y) = ssb
      END IF

 NEXT y
NEXT x
END IF

'******************************** WO everywhere ****************************
IF patchstrip = 5 THEN
FOR x = 1 TO cn
 FOR y = 1 TO cn
 ssb = 2000
 sb(x, y) = ssb
 NEXT y
NEXT x
END IF



x = 0
FOR N = ss TO 400 STEP ss
 x = 1 + x
  y = 0
   FOR Z = ss TO 400 STEP ss
    y = 1 + y
     pa = sb(x, y) 'plot array to indicate which array to plot
     col = initcol '14 - dcs'initial colour
    ' pd = 0 'density colour ploting  (begins at zero)
    ' hd = 400 'highest density class
    ' PRINT #1, , x, y, sb(x, y)
     IF pa >= hd THEN
        LINE (N - ss, Z - ss)-(N, Z), col - dcs - 1, BF
      END IF
```

```
        ps = 0
        FOR ps = 1 TO dcs
          col = col - 1
            IF pa > pd AND pa <= pd + (hd / dcs) THEN
              LINE (N - ss, Z - ss)-(N, Z), col - 1, BF
            END IF
          pd = pd + (hd / dcs)
        NEXT ps
    NEXT Z
NEXT N



sdlrcrt = .175  ' the proportion of seeds germinating each year
woddmort = .003285 'density dependent mortality for WO seedlings

'WO seed production data*******************

scale = 38 'factor to convert WO biomass at 65% seed shed to seed number for 4 m^2
womax = 2.344 'wild oat biomass coefficient
ddwoseed = .0287  'density dependent wild oat seed production coeficient

'
'Combine seed proportion paramatres****************************************

woex = .687 'proportion of weed seeds ingested by combine that are exported with grain
ccolcc = .264 'proportion of weed seed ingested by combine that are exported in the  chaff
fraction
IF swath = 1 THEN woph = .5 ELSE woph = .05
pcrcc = .33 ' the proportion of weed seeds in centre row chaff collection
pcrcr = .9 ' the proportion of weed seeds in centre row chaff return
pharvmort = .2  'postharvest seed mortality

'Dispersal functions from 1996 data******************************************

maxdd = 100 'maximum dispersal distance (100 * 2m = 200 m) I think I meant 2m
dispacr = .04247  ' scaling factor for chaff return dispersal function 'check to see if these
functions are for the 2m or the one m reersion
dispbcr = 12.89 'regression for chaff return
dispccr = .82544   'regression for chaff return
dispacc = .1858 ' scaling factor for chaff colection dispersal function
dispbcc = 1.03663  'regression for chaff colection
dispccc = .33866   'regression for chaff colection
```

```
IF ccswitch = 1 THEN
pwoex = ccolcc + woex
md = mdcc
pcr = pcrcc
dispa = dispacc
dispb = dispbcc
dispc = dispccc

ELSE
pwoex = woex
md = mdcr
pcr = pcrcr
dispa = dispacr
dispb = dispbcr
dispc = dispccr

END IF



'******************BEGINNING OF LIFE CYCLE MODEL******************


spraycount = 0
patchsize = 0
t = generations    'time in generations for model to run
FOR g = 1 TO t  'g = generation in years
wyld = 0
 totsd = 0
 totwyld = 0
 avgyld = 0
 perwo = 0
 totperwo = 0
 wosquare = 0
 FOR x = 1 TO cn
    FOR y = 1 TO cn
   'x and y are are the coordiantes
     IF g > 1 THEN
     'post harvest (winter) seed mortality
     sb(x, y) = ((1 - pharvmort) * sb(x, y))
     IF sb(x, y) >= 1 THEN
     sb(x, y) = CINT(sb(x, y))
     ELSE
```

```
IF sb(x, y) < 1 AND sb(x, y) > RND THEN sb(x, y) = 1 ELSE sb(x, y) = 0
' the previous statement is a stochasitc less than one statement that determines
'the probability of a seed still existing in that area
END IF
END IF
sp(x, y) = sb(x, y) * sdlrcrt 'seedling recruitment
IF sp(x, y) >= 1 THEN
sp(x, y) = CINT(sp(x, y))
ELSE
IF sp(x, y) < 1 AND sp(x, y) > RND THEN sp(x, y) = 1 ELSE sp(x, y) = 0
' the previous statement is a stochasitc less than one statement that determines
'the probability of a seed still existing in that area
END IF


'PRINT #3, sb(x, y)


 sb(x, y) = sb(x, y) - sp(x, y)  'revised spring seed bank
sp(x, y) = sp(x, y) / 16 / (1 + woddmort * sp(x, y) / 16) * 16
'spring seedling mortality
IF sp(x, y) >= 1 THEN
sp(x, y) = CINT(sp(x, y))
ELSE
IF sp(x, y) < 1 AND sp(x, y) > RND THEN sp(x, y) = 1 ELSE sp(x, y) = 0
' the previous statement is a stochasitc less than one statement that determines
'the probability of a seed still existing in that area
 END IF


mp(x, y) = sp(x, y) 'stores the plant pop for mapping

wyld = cropdns / (1 / maxwyld * (cropdns - 1 + C * sp(x, y)))
totwyld = totwyld + wyld
'wyld wheat yield function
maxwfwyld = (cropdns / (1 / maxwyld * ((cropdns - 1))))

sp(x, y) = scale * (womax * sp(x, y) / 16) * (1 + ddwoseed * sp(x, y) / 16) ^ -1
'WO seed production equation based on CS 95 data


'natural dispersal of seeds inside of patch (seeds that fall off the plant before harvest
are returned to the same square that they originated
sb(x, y) = sp(x, y) * (1 - woph) + sb(x, y)
```

```
        'original dispersal all to original cell
        sp(x, y) = (sp(x, y) * woph) 'seeds remaining for mech disp

        IF g = 1 AND sp(x, y) >= 1 THEN patchcount = 1
        IF g = 1 THEN patchsize = patchsize + patchcount
        patchcount = 0
        IF sp(x, y) > 1 THEN perwo = 1 / (cn * cn) * 100 ELSE perwo = 0
        IF sp(x, y) > 1 THEN wosquare = wosquare + 1 ELSE wosquare = wosquare

        totperwo = totperwo + perwo


      NEXT y
  NEXT x


  'calculates the percentage increase of the patch size post spraying
avgyld = totwyld / (cn * cn)   'average yield function
totavgyld = avgyld + totavgyld
avgsd = totsd / (cn * cn) 'average seedling density calculation (prespraying)
asd(g) = avgsd
ay(g) = avgyld

'****************REDISTRIBUTION AND DISPERSAL MODEL*******

  'routine for spreading in y axis direction


'***********Y DIRECTION REDISTRIBUTION*****************************

  'subroutine that determines the amount of seeds that are
  'in the combine, the row they are in for a combine that is three rows wide
  ' this moves the patches in the y direction
'combdir = 1
RANDOMIZE TIMER
'IF g / 2 = INT(g / 2) THEN
IF CINT(RND) >= cdirswitch THEN 'an even odds yes or no function for either x or y
direction
combrand = INT(RND * 4)
 'combrand = 2
  FOR x = 1 TO cn
     FOR y = 1 TO cn
       IF ((x + 4) / 5) + combrand = INT(((x + 4) / 5) + combrand) THEN
       cs(x + combrand, y) = 0
```

```
        END IF
        IF ((x + 3) / 5) + combrand = INT(((x + 3) / 5) + combrand) THEN
        cs(x + combrand, y) = (1 - pwoex) * ((1 - pcr) / 2) * (sp(x + combrand + 3, y) + sp(x
+ combrand + 2, y) + sp(x + combrand + 1, y) + sp(x + combrand, y) + sp(x + combrand -
1, y))
        END IF
        IF ((x + 2) / 5) + combrand = INT(((x + 2) / 5) + combrand) THEN
       cs(x + combrand, y) = (1 - pwoex) * pcr * (sp(x + combrand - 2, y) + sp(x + combrand
- 1, y) + sp(x + combrand, y) + sp(x + combrand + 1, y) + sp(x + combrand + 2, y))
        END IF
        IF ((x + 1) / 5 + combrand) = INT(((x + 1) / 5) + combrand) THEN
        cs(x + combrand, y) = (1 - pwoex) * ((1 - pcr) / 2) * (sp(x + combrand - 3, y) + sp(x
+ combrand - 2, y) + sp(x + combrand - 1, y) + sp(x + combrand, y) + sp(x + combrand + 1,
y))
        END IF
        IF (x / 5) + combrand = INT((x / 5) + combrand) THEN
        cs(x + combrand, y) = 0
        END IF
        'cs(x, y) = CINT(cs(x, y))
      NEXT y
  NEXT x


'**************Y DIRECTION COMBINE DISPERSAL**********************

  'subroutine that moves the seeds that are in the combine down the field
  'assumes opposide directions for every second three row group
RANDOMIZE TIMER
IF CINT(RND) = 1 THEN  'even odds for direction
 FOR x = combrand + 1 TO cn
      xr = x
       DO WHILE x <= xr + 4
         FOR y = 1 TO cn
'dispersal funtion for patch mediun and long dist dipersal
'does not always give exact number of seeds that were in original cell it is based on a
probability function
IF cn - y < maxdd THEN actdd = cn - y ELSE actdd = maxdd
IF cs(x, y) > 0 THEN
FOR dd = 0 TO actdd
seedrem = cs(x, y) * (dispa * (2.718282 ^ (-1 * (dd ^ dispc / dispb))))
IF seedrem >= 1 THEN
sb(x, y + dd) = CINT(seedrem) + sb(x, y + dd)
ELSE
```

```
IF seedrem > RND THEN sb(x, y + dd) = sb(x, y + dd) + 1 ELSE sb(x, y + dd) = sb(x, y +
dd)
END IF
NEXT dd
END IF


            NEXT y
          x = x + 1
          LOOP
          xr = x
         ' xr2 = xr + 4
          DO WHILE x <= xr + 4
            FOR y = cn TO 1 STEP -1
'dispersal funtion for patch seed dipersal
'does not always give exact number of seeds that were in original cell it is based on a
probability function
IF y < maxdd THEN actdd = y ELSE actdd = maxdd
IF cs(x, y) > 0 THEN
FOR dd = 0 TO actdd
seedrem = cs(x, y) * (dispa * (2.718282 ^ (-1 * (dd ^ dispc / dispb))))
IF seedrem >= 1 THEN
sb(x, y - dd) = CINT(seedrem) + sb(x, y - dd)
ELSE
IF seedrem > RND THEN sb(x, y - dd) = sb(x, y - dd) + 1 ELSE sb(x, y - dd) = sb(x, y - dd)
END IF
NEXT dd
END IF

            NEXT y
           x = x + 1
          LOOP
          x = x - 1
 NEXT x

ELSE

FOR x = combrand + 1 TO cn
   xr = x
     DO WHILE x <= xr + 4
         FOR y = cn TO 1 STEP -1
'dispersal funtion for patch mediun and long dist dipersal
'moves weed seeds down
```

```
'does not always give exact number of seeds that were in original cell it is based on a
probability function
IF y < maxdd THEN actdd = y ELSE actdd = maxdd
IF cs(x, y) > 0 THEN
FOR dd = 0 TO actdd
seedrem = cs(x, y) * (dispa * (2.718282 ^ (-1 * (dd ^ dispc / dispb))))
IF seedrem >= 1 THEN
sb(x, y - dd) = CINT(seedrem) + sb(x, y - dd)
ELSE IF seedrem > RND THEN sb(x, y - dd) = sb(x, y - dd) + 1 ELSE sb(x, y - dd) = sb(x,
y - dd)
END IF
NEXT dd
END IF


        NEXT y
       x = x + 1
    LOOP
  xr = x
     DO WHILE x <= xr + 4
         FOR y = 1 TO cn
'dispersal funtion for patch mediun and long dist dipersal
'does not always give exact number of seeds that were in original cell it is based on a
probability function
'moves weeds down
IF cn - y < maxdd THEN actdd = cn - y ELSE actdd = maxdd
IF cs(x, y) > 0 THEN
FOR dd = 0 TO actdd
seedrem = cs(x, y) * (dispa * (2.718282 ^ (-1 * (dd ^ dispc / dispb))))
IF seedrem >= 1 THEN
sb(x, y + dd) = CINT(seedrem) + sb(x, y + dd)
ELSE
IF seedrem > RND THEN sb(x, y + dd) = sb(x, y + dd) + 1 ELSE sb(x, y + dd) = sb(x, y +
dd)
END IF
NEXT dd
END IF


         NEXT y
      x = x + 1
    LOOP
  x = x - 1
NEXT x
```

```
END IF

'************X DIRECTION REDISTRIBUTION**************************

  'subroutine that determines the amount of seeds that are
  'in the combine, the row thex are in for a combine that is three rows wide
  'this is for spreading in the x direction
 ELSE
 RANDOMIZE TIMER
 combrand = INT(RND * 4)
' combrand = 0
 FOR y = 1 TO cn
   FOR x = 1 TO cn
     IF ((y + 4) / 5) + combrand = INT(((y + 4) / 5) + combrand) THEN
     cs(x, y + combrand) = 0
     END IF
     IF ((y + 3) / 5) + combrand = INT(((y + 3) / 5) + combrand) THEN
     cs(x, y + combrand) = (1 - pwoex) * ((1 - pcr) / 2) * (sp(x, y + combrand + 3) + sp(x,
y + combrand + 2) + sp(x, y + combrand + 1) + sp(x, y + combrand) + sp(x, y + combrand
- 1))
     END IF
     IF ((y + 2) / 5) + combrand = INT(((y + 2) / 5) + combrand) THEN
       cs(x, y + combrand) = (1 - pwoex) * pcr * (sp(x, y + combrand - 2) + sp(x, y +
combrand - 1) + sp(x, y + combrand) + sp(x, y + combrand + 1) + sp(x, y + combrand + 2))
     END IF
     IF ((y + 1) / 5 + combrand) = INT(((y + 1) / 5) + combrand) AND y >= 1 THEN
     cs(x, y + combrand) = (1 - pwoex) * ((1 - pcr) / 2) * (sp(x, y + combrand - 3) + sp(x,
y + combrand - 2) + sp(x, y + combrand - 1) + sp(x, y + combrand) + sp(x, y + combrand +
1))
     END IF
     IF (y / 5) + combrand = INT((y / 5) + combrand) THEN
     cs(x, y + combrand) = 0
     END IF
     'cs(x, y) = CINT(cs(x, y))
   NEXT x
 NEXT y

'***********X DIRECTION COMBINE DISPERSAL********************

  'subroutine that moves the seeds that are in the combine down the field
  'assumes opposide directions for every second three row group
IF CINT(RND) = 1 THEN
 FOR y = combrand + 1 TO cn
   yr = y
```

```
        DO WHILE y <= yr + 4
          FOR x = 1 TO cn

'dispersal funtion for patch mediun and long dist dipersal
'does not always give exact number of seeds that were in original cell it is based on a probability function
IF cn - x < maxdd THEN actdd = cn - x ELSE actdd = maxdd
IF cs(x, y) > 0 THEN
FOR dd = 0 TO actdd
seedrem = cs(x, y) * (dispa * (2.718282 ^ (-1 * (dd ^ dispc / dispb))))
IF seedrem >= 1 THEN
sb(x + dd, y) = CINT(seedrem) + sb(x + dd, y)
ELSE
IF seedrem > RND THEN sb(x + dd, y) = sb(x + dd, y) + 1 ELSE sb(x + dd, y) = sb(x + dd, y)
END IF
NEXT dd
END IF

            NEXT x
          y = y + 1
        LOOP
    yr = y
        DO WHILE y <= yr + 4
          FOR x = cn TO 1 STEP -1


'dispersal funtion for patch mediun and long dist dipersal
'does not always give exact number of seeds that were in original cell it is based on a probability function
IF x < maxdd THEN actdd = x ELSE actdd = maxdd
IF cs(x, y) > 0 THEN
FOR dd = 0 TO actdd
seedrem = cs(x, y) * (dispa * (2.718282 ^ (-1 * (dd ^ dispc / dispb))))
IF seedrem >= 1 THEN
sb(x - dd, y) = CINT(seedrem) + sb(x - dd, y)
ELSE
IF seedrem > RND THEN sb(x - dd, y) = sb(x - dd, y) + 1 ELSE sb(x - dd, y) = sb(x - dd, y)
END IF
NEXT dd
END IF
            NEXT x
          y = y + 1
        LOOP
```

```
        y = y - 1
  NEXT y

 ELSE
 FOR y = combrand + 1 TO cn
   yr = y
     DO WHILE y <= yr + 4
       FOR x = cn TO 1 STEP -1
'dispersal funtion for patch mediun and long dist dipersal
'does not always give exact number of seeds that were in original cell it is based on a
probability function
IF x < maxdd THEN actdd = x ELSE actdd = maxdd
IF cs(x, y) > 0 THEN
FOR dd = 0 TO actdd
seedrem = cs(x, y) * (dispa * (2.718282 ^ (-1 * (dd ^ dispc / dispb))))
IF seedrem >= 1 THEN
sb(x - dd, y) = CINT(seedrem) + sb(x - dd, y)

ELSE
IF seedrem > RND THEN sb(x - dd, y) = sb(x - dd, y) + 1 ELSE sb(x - dd, y) = sb(x - dd, y)
END IF
NEXT dd
END IF
      NEXT x
     y = y + 1
    LOOP
yr = y
 DO WHILE y <= yr + 4
   FOR x = 1 TO cn

'dispersal funtion for patch mediun and long dist dipersal
'does not always give exact number of seeds that were in original cell it is based on a
probability function
IF cn - x < maxdd THEN actdd = cn - x ELSE actdd = maxdd
IF cs(x, y) > 0 THEN
FOR dd = 0 TO actdd
seedrem = cs(x, y) * (dispa * (2.718282 ^ (-1 * (dd ^ dispc / dispb))))
IF seedrem >= 1 THEN
sb(x + dd, y) = CINT(seedrem) + sb(x + dd, y)
ELSE
IF seedrem > RND THEN sb(x + dd, y) = sb(x + dd, y) + 1 ELSE sb(x + dd, y) = sb(x + dd,
y)
END IF
NEXT dd
```

```
END IF

    NEXT x
   y = y + 1
  LOOP
 y = y - 1
NEXT y
END IF
END IF




mapswitch = 1
IF mapswitch = 1 THEN
x = 0
FOR N = ss TO 400 STEP ss
 x = 1 + x
  y = 0
   FOR Z = ss TO 400 STEP ss
    y = 1 + y
    pa = mp(x, y) 'plot array to indicate which array to plot
     col = initcol '14 - dcs initial colour
     pd = 0 'density class for color plots (begins at zero)
    ' hd = 400 'highest density class


      IF pa = 0 THEN
        LINE (N - ss, Z - ss)-(N, Z), 0, BF
        LINE (N - ss, Z - ss)-(N, Z), 7, B
      'comment the last line out if you wish "ghosts" of the larger patches to remain
      END IF


      IF pa >= hd THEN
        LINE (N - ss, Z - ss)-(N, Z), col - dcs - 1, BF
      END IF
        FOR ps = 1 TO dcs
          col = col - 1
            IF pa > pd AND pa <= pd + (hd / dcs) THEN
              LINE (N - ss, Z - ss)-(N, Z), col - 1, BF
            END IF
          pd = pd + (hd / dcs)
        NEXT ps
```

```
    NEXT Z
NEXT N
END IF
LOCATE 27, 1
PRINT #1, patchsize, g, simmulation, avgsd, TIME$
IF g = 1 THEN PRINT #5, wosquare, g, patchsize, avgsd ELSE
IF g = 2 THEN PRINT #6, wosquare, g, patchsize, avgsd ELSE
IF g = 3 THEN PRINT #7, wosquare, g, patchsize, avgsd ELSE
IF g = 4 THEN PRINT #8, wosquare, g, patchsize, avgsd ELSE
IF g = 5 THEN PRINT #9, wosquare, g, patchsize, avgsd ELSE
IF g = 6 THEN PRINT #10, wosquare, g, patchsize, avgsd ELSE


'DO UNTIL INKEY$ <> ""
'LOOP


'PRINT #1, g; patchsize; asd(g); totperwo


NEXT g 'starts another year

'******************END OF MAPPING SUBPROGRAM*****************

PRINT #2, g, , simmulation, wosquare, patchsize

NEXT simmulation
'*************************** end of simmulation loop ********************
SOUND 212, 1.5
LOCATE 14, 23
PRINT "END OF SIMMULATAION"
DO UNTIL INKEY$ <> ""
LOOP
```