

The Relative Importance of Seed and Microsite Limitation in

Annual and Perennial Weed Populations

BY

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A Thesis

Submitted to the Faculty of Graduate Studies

In Partial Fulfillment of the Requirements

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**of**

**Doctor of Philosophy**

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## ABSTRACT

Boyd, Nathan Shawn. Ph.D., The University of Manitoba, May, 2003. The relative importance of seed and microsite limitation for recruitment of annual and perennial weed populations. Major Professor; Rene C. Van Acker.

Seedling recruitment of annual and perennial weed species is dependant upon the number of seeds present in the soil and the biotic and abiotic conditions directly surrounding those seeds. Field and green house experiments were conducted to study the relative importance of soil physical properties and seed and microsite limitation on the emerging weed population. In the green house and in growth chambers a variety of experiments were conducted to determine the effects of seeding depth, soil moisture, gaseous environment, light and soil aggregate size on the emergence of a variety of weed species. The species were categorized as generalist, able to germinate and emerge under a wide range of conditions, or specialist, only able to emerge under a narrow range of conditions.

In field experiments three seed densities (200, 400, 1200 seeds  $m^{-2}$ ) of green foxtail, wild mustard, wild oat and canola were seeded in separate plots in a Winkler Soil Series and in a Hochfeld Soil Series in Manitoba, Canada in 2001 and 2002. Five treatments (control, irrigated, compacted, compacted and irrigated, and no crop) were applied to all weed seed densities of each weed species in a factorial design. Following weed seed placement in the top 6 cm the entire area was seeded to AC Barrie wheat. Weed counts as well as several soil physical parameters were measured throughout both seasons. Weed emergence increased with increasing seeding density for all species but proportional emergence decreased with increasing seed density for all species. We suggest that the emergence of weed species in these experiments was both seed and microsite limited. Increasing the number of seeds in the soil increased the probability of seeds landing within an appropriate microsite.

## **FORWARD**

All manuscripts contained within this thesis are formatted for publication within the Weed Science Journal produced by the Weed Science Society of America. The reference list is also formatted to adhere to the guidelines established for publication within Weed Science.

## NOMENCLATURE

Following is a list of the common names, latin names and Bayer codes for the weed and crop species used in the experiments discussed within this thesis.

barnyardgrass, *Echinochloa crus-galli* L. ECHCG  
catchweed bedstraw, *Galium aparine* L. GALAP  
common milkweed, *Asclepias syriaca* L. ASCSY  
curly dock, *Rumex crispus* L. RUMCR  
dandelion, *Taraxacum officinale* Weber in Wiggers TAROF  
field pennycress, *Thlaspi arvense* L. THLAR  
foxtail barley, *Hordeum jubatum* L. HORJU  
green foxtail, *Setaria viridis* (L.) Beauv. SETVI  
perennial sowthistle, *Sonchus arvensis* L. SONAR  
quackgrass, *Elytrigia repens* (L.) Nevski AGGRE  
round leaved mallow, *Malva pusilla* Sm. MALSU  
spring wheat, *Triticum aestivum* L., "AC Barrie".  
wild mustard, *Brassica kaber* (D.C.) L.C. Wheeler SINAR  
wild oat, *Avena fatua* L. AVEFA

## INTRODUCTION

Weed management is an important issue in all cropping systems. Crop losses due to uncontrolled weed populations are usually higher than losses caused by diseases or insect pests (Kropff and Walter 2000). Due to the significant impact that weed populations may have on crop yields the discipline of weed science evolved with a control mentality . The introduction of herbicides and their ability to control weed populations effectively promoted this mind set. In recent years, increasing incidence of herbicide resistant weeds, increased environmental awareness and public opinion have slowly altered weed management concepts within the agricultural sector. Weed Scientist have become aware of the importance of understanding the biology and ecology of weed populations to attain efficient management practices. A weed survey conducted between 1993 and 1994 and given to members of the Weed Science Society of America determined that over half of the respondents felt that contributions of weed biology to weed management had been high (Norris 1997).

A key aspect of weed biology in arable systems is seedling recruitment. In annual weeds, typically found in arable crops, recruitment biology may be one of the main factors controlling the weed population (Crawley 1990). Recruitment is determined by the number of seeds in the soil, the state of those seeds as well as the soil conditions around the seeds. The presence or absence of seeds within the soil profile is not usually a good indicator of the weed population that will emerge. Cardina and Sparrow (1996) tested several methods for predicting potential seedling densities from seed bank measurements and found all of the methods were relatively poor predictors of field population density. Seeds may be present in the soil but not until the microsite conditions around the seed are appropriate will dormancy be broken and seeds germinate and emerge. A better understanding of what range of conditions promote seedling emergence of different weed species and a better understanding of the relationship between the seed bank, microsite and the emerging weed seedlings will lead to better and more accurate weed emergence and population dynamics models as well as agronomic practices that effectively manage weed populations.

## **LITERATURE REVIEW**

### **Weed Biology in Weed Science**

#### **Herbicide Use and Reduction**

Within agriculture, weed populations reduce yield and quality of the crop and hinder harvesting operations. Just within the United States of America the economic impact of weeds on agricultural production is approximately 15 billion dollars per year (Bridges 1994). A large proportion of that amount is spent on herbicides. Herbicide use has many benefits including increased crop yield and quality by reducing or eliminating competition, eradication of hard to control weeds, reduction of reliance on cultivation and reduction in energy cost and management time (Zoschke 1994). Since the advent of herbicides in the late 1940's farm labour inputs have declined, machinery inputs have remained relatively constant and agricultural chemical inputs have increased (Bridges 1994). Due to the relatively cheap cost and reliability of herbicides, farms in North America appear to be replacing labour and machinery inputs with chemical inputs.

In recent years concerns about herbicide residues have risen. Environmentalist and the general public view agricultural chemicals as pollutants of the atmosphere, food, soil, surface water and groundwater (Bellinder et al. 1994). As well, documentation of herbicide resistant weeds around the world is on the rise. These concerns in combination with low commodity prices have led to increased interest in reducing herbicide application rates. As public and economic pressure increase there will be continually more incentive to find ways to reduce overall herbicide inputs while maintaining farm productivity. Several governments in the last few decades have implemented various policies or forms of legislation to attempt to promote reductions in chemical input use. In 1985, the Swedish government mandated a 50% reduction in agricultural pesticide use by 1990 (Bellinder et al. 1994). The United Kingdom government also implemented a policy on pesticide use aimed at minimizing chemical use rather than mandating a specific reduction level (Lawson 1994).

The Swedish model is especially interesting because it mandated a specific reduction target for pesticide use. The three areas of emphasis within their model were

risk reduction, use reduction and specific protection for health and the environment (Bellinder et al. 1994). Risk reduction measures were initiated by enforcing the re-registration of all herbicides. The new registration guidelines included greater requirements for toxicological and environmental fate data, reduction in mammalian toxicity of compounds and prevention of registration of compounds with broad biological activity, high leaching potential and chemicals with extended soil residues. As well, testing of the efficacy of lower dosage rates and the inclusion of this information on labels was required. The results of these measures was a reduction of registered products from 677 in 1986 to 322 in 1991. The number of registered active ingredients during the same time frame dropped from 201 to 122 (Bellinder et al. 1994).

The second emphasis within the Swedish model was use reduction. To reduce chemical usage policy makers suggested that pesticides could only be used when other economically equivalent control measures did not exist. As well, dosage levels were selected based on achieving an acceptable level of control rather than maximum effect. To attain this goal research funding for increasing crop competitiveness, improving crop rotation, weed biology and non-chemical control increased. Extension services also increased to help farmers improve their usage of herbicides. By 1991 Sweden announced that they had achieved their goal of reducing agricultural pesticide use by 47% (Bellinder et al. 1994). This overall decrease in chemical use was a result of dosage reduction and a shift to low dose materials not decrease in treated areas. Specific protections for health and environment included restriction on locations of cleaning and mixing herbicide tanks, mandatory certification of applicators and increased scrutinization of residues on food.

The United Kingdom purposed to minimize pesticide use rather than arbitrarily setting limits like the Swedish government. A government policy established that pesticide use should be limited to the minimum necessary for the effective control of pests compatible with the protection of human health and the environment (Lawson 1994). This policy was pursued by implementing such strategies as certification for all persons applying pesticides or providing advice when buying or selling pesticides, pesticide regulation and increased funding in such areas as alternative and sustainable farming practices and land management strategies. With this policy the United Kingdom achieved a 40% reduction in the tonnage of active ingredient applied and a 34% reduction



in the amount applied per hectare between 1982 and 1990 (Lawson 1994). This reduction is similar to what was seen in other countries and was attributed primarily to the introduction of new lower dose chemistry herbicides.

Within Canada, pesticide sales have fluctuated between \$600 and \$900 million from 1982 to 1992 with herbicides accounting for 70% of the sales (Hamill et al. 1994). As of 1994, only 3 out of 10 provinces had any policy for pesticide reduction. As public pressure increases there will probably be a greater demand for pesticide reduction within Canada. Ironically, with cutbacks in various support programs including research and extension while giving industry greater influence, Canada's ability to implement and regulate any pesticide reduction policy is unlikely. There are benefits to reducing pesticide applications in Canada both to the farmers and to the environment. Policies or programs aimed at reducing pesticide use need to combine increased regulation and increased research for alternative weed control options.

### **Weed Biology and Weed Management**

Due to the significant impact that weed populations have on crop yields, the discipline of weed science evolved to reflect a control mentality. The advent of herbicides enforced the idea that weeds should be viewed as a problem that may be controlled with herbicides rather than through non-herbicidal agronomic practices. Zimdahl (1991) stated that the, "how to control" mentality had dominated the discipline of weed science until recently. Early work in other disciplines, such as plant pathology and entomology, focused on taxonomy, disease description and the identification of causal agents (Mortensen et al. 2000). Over time the importance of understanding the biology and ecology of weeds has become more recognized. A survey of members of the Weed Science Society of America determined that over half of the respondents felt that contributions of weed biology to weed management had been high (Norris 1997).

The discipline of weed science is still herbicide dominated. The effectiveness of most herbicides in weed control is beyond question. Agricultural producers, like any other business managers, adopt practices which are effective, conserve time and are cost efficient. Therefore, weeds have been viewed as a problem that can be controlled with

herbicides rather than a component of an ecosystem that needs to be managed within an ecological framework. In recent years, increasing public concern about the side-effects of herbicides and increased herbicide resistance in many weed species has led to a growing interest in developing alternative weed management practices (Mortensen et al. 2000). Many agronomic alternatives require an understanding of basic weed biology and ecology to make them effective. For example, improving the timing of herbicide application requires understanding when and where weeds will emerge and the effective use of crop rotation to manage weed populations requires an understanding of how weed populations interact with various crop rotations.

## **The Weed Seed and Weed Seedling Recruitment**

### **The Seed**

The seed is the independent beginning of the next generation in plants. As such, angiosperms must expend tremendous energy in flowering and production of viable seeds to ensure a continuation of their genotype. A living seed contains a viable embryo that is a miniature plant with the beginnings of the shoot and root already formed. The embryo is typically surrounded by the endosperm which functions as a food source for the developing embryo before and after germination. The embryo and endosperm are protected by several different levels of tissue that provide protection for the developing embryo as well as aiding in distribution and regulation of dormancy and germination.

Germination begins with the uptake of water by the seed (imbibition) and ends with the emergence of the radicle. Properly defined, germination includes (1) imbibition (2) hydration of tissues (3) absorption of O<sub>2</sub> (4) activation of enzymes and digestion (5) transport of hydrolyzed molecules to the embryo axis (6) increase in respiration and assimilation (7) initiation of cell division and enlargement and (8) embryo emergence (Gardner 1985). With proper environmental conditions a viable seed will germinate unless it is dormant.

## Seed Dormancy

Dormancy is difficult to define and as a physical condition it is difficult to establish when it begins and when it ends. Frequently, a dormant seed may have completed almost all of the necessary metabolic steps to complete germination but the radicle does not elongate (Bewley 1997). Dormancy can be defined as the failure of a viable seed to germinate under environmental conditions that normally support germination of non dormant seeds of the same type (Gardner 1985). Benech-Arnold et al. (2000) suggest that dormancy be defined as, “an internal condition of the seed that impedes its germination under otherwise adequate hydric, thermal and gaseous conditions”. Dormancy may be a result of coat enhanced dormancy, which is when the embryo is constrained by the structures surrounding it, or embryo dormancy which occurs when the embryo itself is dormant (Bewley 1997). There are many different dormancy classes. Thermodormancy and photodormancy are initiated by high temperatures and high light intensities. Primary, innate, secondary or induced dormancy are classifications based on the timing of dormancy (Hilhorst and Toorop 1997).

When released from a plant, a seed may or may not exhibit primary dormancy. Seeds exhibiting primary dormancy will not germinate even under suitable environmental conditions. Due to extensive domestication and breeding most crop plants do not exhibit primary dormancy. However, under adverse conditions (drought, high temperature or other unfavourable environmental conditions) dormancy may reappear in these species (Hilhorst and Toorop 1997). One form of primary dormancy is displayed in seeds with hard or thick seed coats as is often seen in legumes. The seed coat may prevent non-dormant embryo growth by physically constraining the embryo. This restraint may be broken by microbial attack, high temperatures, extreme drought or passage through an animals digestive track. As well, the seed coat may prevent water from entering the seed with a densely compacted layer of scleroid cells or water repellent compounds (Gardner 1985; Hilhorst and Toorop 1997).

Abscisic acid (ABA) may regulate the onset of dormancy and maintain a seed in the dormant state (Bewley 1997). There is a strong correlation between exogenous ABA application and primary dormancy (Corbineau et al. 1991; Kawakami et al. 1996). The

germination response to ABA depends on the stage of development of the seed and environmental conditions such as temperature ( Hilhoorts and Toorop 1997; Corbineau et al. 1991). Although exogenous applications of ABA induce dormancy this does not prove that endogenous ABA levels regulate dormancy. To test the effects of endogenous ABA researchers have used mutant varieties of several different crops that are ABA deficient. Research using mutant plants that do not produce ABA shows that the embryo itself must produce the hormone in order to induce dormancy. The ABA content in seeds decreases after imbibition and appears to play a role in germination (Kawakami et al. 1996). Despite this evidence, a correlation between ABA content and germination is not always evident and this insensitivity casts doubt on the hypothesis that ABA is the primary regulator of dormancy (Hilhorst and Toorop 1997).

Seed becomes quiescent after dormancy release and will germinate if the environmental conditions are suitable. Different seeds require different variations in temperature, light, nitrogen and oxygen to begin germination. In some species, dry storage at high temperatures induces germination while in other species imbibition and low temperatures induces germination (Hilhorst and Downie 1996). If one or more of the germination variables are missing the quiescent seed may become dormant again and will not germinate even if the proper environmental conditions exist. This may be true even if the seed has already imbibed water. This phenomenon is referred to as secondary dormancy (Bulard 1986; Hilhorst and Toorop 1997). Reviewing the events of secondary dormancy Bewley (1997) concluded that our understanding of the processes required for dormancy are still incomplete but the following conclusion may be drawn: (1) imbibed dormant seeds and nondormant seeds have similar metabolisms. (2) Dormancy release may be at the level of transcription but there is little evidence of germination promoting proteins. (3) The respiration rate, pathway and enzymes involved do not appear to regulate dormancy. (4) The state or condition of membranes may affect dormancy regulation but the mechanism is not clearly understood.

There is a continuum between dormancy and germination with degrees of relative dormancy. Vegis (1964) reported that as dormancy is released the temperature range promoting seed germination widens to a maximum. The opposite occurs when dormancy is induced. Research conducted by Malik and Vanden Born (1987) supports this theory.

They found that the effects of light and temperature on catchweed bedstraw germination become less important as the seed ages and the species becomes more general in its germination requirements. Therefore, we can conclude that the species becomes less dormant with time. In many cases, once the degree of dormancy is sufficiently low it must be terminated by an environmental factor to allow the continuation of germination (Benech-Arnold et al. 2000). The sensitivity to dormancy breaking environmental factors is dependant upon the degree of dormancy (Benech-Arnold et al. 2000). The induction of dormancy, specifically secondary dormancy, is a process whereby the range of conditions required for germination narrows until the seed will no longer germinate. Seeds of some species may move one direction on this continuum over long periods of time or seeds may fluctuate in both directions on this continuum between or within seasons.

### **Seed Germination**

The point at which germination is initiated and dormancy is released is not distinct. It is difficult to measure the exact moment of germination. Germination commences when imbibition occurs and ends when the radicle protrudes from the seed coat.

Many seeds germinate in response to environment and hormonal cues (Dutta et al. 1994). For example, some species require dark and others light to initiate germination (Carpenter et al. 1993). The energy level, wavelength and photoperiod all affect germination (Gardner 1985). Frequently light and temperature interact to affect germination. Seeds of orchard grass (*Dactylis glomerata* L.) obtain maximum germination with light and alternating temperatures (Probert and Smith 1986). For broad-leaved dock (*Rumex obtusifolius* L.) germination remained at around 17.5 % in complete darkness but increased to 96.8% or 91.2% with a 10 minute exposure to red light or 60 minute exposure to elevated temperatures respectively.

Exposure to light or darkness affects giberellin (GA) levels in seeds. Giberellins have been found to stimulate germination. Tomato (*Lycopersicon esculentum* Mill.) and Arabidopsis spp. mutants that do not produce giberellins within the seed will not germinate without applied GA except when exposed to white light. Germination may

occur under these conditions because exposure to light may induce GA synthesis (Karssen et al. 1989). Germination in light is often dependant on the presence of nitrate in the growth medium. Although not well understood, the presence of nitrate is linked to the action of phytochrome. Without nitrates in the solution embryos often are not capable of germination after exposure to far red light even when exposed to red light afterwards. Hilhorst et al. (1986) reported that when nitrate was present, seeds germinated after exposure to far red light. Whenever either red light or nitrate were not present the seeds returned to secondary dormancy (Hilhorst and Downie 1996). Gibberellins are not the only compound that induces germination. Ethylene in full light, potassium nitrate, thiourea and hydrogen peroxide have all been shown to induce germination. Under some conditions these chemical compounds may replace the need for light or for particular temperatures in order to stimulate germination (Gardner 1995).

The first step towards seed germination is the uptake of water, often called imbibition. This essentially passive process is controlled by the difference in water potential between the seed and surrounding medium (Shaykewich and Williams 1971a; Vertucci 1989). The water potential in a dry seed may approach levels of  $-100$  MPa (Shaykewich and Williams 1971a) which is far lower than water potentials that exist in most soils during a growing season. Due to the extreme differences between initial water potentials in a seed and typical soil water potentials, small changes in soil water potential will have very little influence on early water uptake in seeds. As seeds imbibe water differences between water potential of the soil and the seed decrease. During later stages of imbibition soil and seed water potentials become similar enough that small changes in soil water potential influence the imbibition of water by the seed (Shaykewich and Williams 1971b). It is during this stage of late imbibition that dry soils may hinder or prevent seed germination.

Water uptake during germination is generally classified into three phases: rapid hydration, a lag period, and a second phase of rapid hydration (King and Oliver 1994; Vertucci 1989). The first phase of rapid water uptake typically occurs at seed water contents below 7-8% and is characterized by strongly bound moisture within the seed (Vertucci and Leopold 1984). Seeds of at least some species in this phase remain in primary dormancy (Esashi et al. 1993) with very little biochemical activity occurring

although light reactions and some oxidative processes are possible (Vertucci 1989). Gallagher and Cardina (1997) found that to reduce photoinduction of redroot pigweed (*Amaranthus retroflexus* L.) germination by 50% the water potential of the soil would have to be between  $-3.0$  and  $-4.0$  MPa. They concluded that complete inhibition of photoinduction of redroot pigweed germination would not be expected even under severe drought conditions.

The second phase typically occurs when seed moisture content is between 8 and 24% and water is loosely bound (Vertucci and Leopold 1984). Afterripening, the process undergone by most seeds to break dormancy, primarily occurs at seed water content levels between 7 and 14% moisture (on a dry weight basis) for a variety of species (Esashi et al. 1993; Leopold et al. 1988) and may be inhibited at moisture contents above or below this range. For wild oat (*Avena fatua* L.), afterripening primarily occurs when seeds are in the 5 to 20% moisture range (Foley 1994). Within the second phase enzymatic and nonenzymatic activity occurs but there is insufficient moisture to allow mitochondrial electron transport. The third phase typically occurs when seed moisture content is above 24% and the water is very loosely bound (Vertucci and Leopold 1984). It is during this phase that radicle emergence, respiration and mitochondrial activity occur in seeds of many species (Vertucci 1989).

The rapid increase in respiration shortly after imbibition is related to an increase in mitochondrial activities (Morohashi 1986). The dry tissues of the seed contain poorly differentiated mitochondria (Ehrenshaft and Brambl 1990). Despite structural and enzymatic damage that occurs during seed drying and development the mitochondria contain enough enzymes to provide adenosine triphosphate (ATP) to support metabolism for several hours after imbibition (Bewley 1997). During imbibition the mitochondria become enlarged and develop a complex inner membrane structure. In some seeds, mitochondrial repair is the main source of mitochondrial development. In pea (*Pisum sativum* L.) cotyledons the inhibition of protein synthesis did not prevent the increase of mitochondrial activity suggesting that the maintenance of respiration repair of the mitochondria is more important than the synthesis of new mitochondria (Morohashi 1986). The pattern of mitochondrial development and repair varies among species. Morohashi (1986) studied mitochondrial development in tissues of several different seed

pieces. They found that starch storing seeds of species such as soybeans (*Glycine max* L.) and kidney beans (*Phaseolus vulgaris* L.) depend primarily on improvement of pre-existing mitochondria. Lipid storing seeds of species such as pumpkins (*Cucurbita pepo* L.) and cucumbers (*Cucumis sativus* L.), depend on the synthesis of new mitochondrial proteins.

Once metabolism in a seed has begun, transcription of many different messenger RNAs and many different proteins necessary for normal cellular metabolism are produced. Bewley (1997) concluded that there are no specific protein markers exclusive to germination. Mullen et al. (1996) concluded that the embryo DNA remained constant at all stages of seed development but RNA contents increased following germination in the embryo and the megagametophyte. They found an accumulation and disappearance of a distinct group of synthesized protein sets. Li and Foley (1996) found approximately 20 translated polypeptides that were more abundant in dormant oat (*Avena sativa* L.) seeds than oats that had been exposed to dry warm temperature to induce germination (after ripened). Lalonde and Bewley (1986) reported a change in mRNA populations in the axis of pea seeds. While there may not be a specific protein marker indicating the start of germination, there appear to be patterns and groups of proteins that degrade and others that are formed after germination has begun. In fact, there may be specific genes that control individual germination processes. For example, some proteins are synthesized as imbibition progresses. If desiccation occurs during imbibition and interrupts the process a different set of proteins are formed. When the seeds are moistened the original set of proteins are synthesized again (Lalonde and Bewley 1986).

Research suggests that there is little relationship between seed water potential and the rate of seed imbibition (Vertucci 1989). Therefore, seed diffusivity or seed size plays an important role in determining the rate of imbibition while differences in water potential between the seed and the soil determine the extent of imbibition. If the physiological structure or the chemical composition of seeds alter the rate or extent of seed imbibition they may also affect the timing of seed germination. Under conditions of similar seed-soil contact and identical rates of diffusion, larger seeds will have a lower proportional water content than smaller seeds following a given time of absorption. The



smaller surface to area ratio of large seeds means that they require longer periods of time to imbibe adequate moisture for germination.

The last phase of germination is the extension of the radicle. This extension may be caused by cell division, cell expansion or a combination of both (Bewley 1997). Radicle extension is turgor driven. There must be enough pressure within the radicle to overcome testa, endosperm and embryo resistance. Testa resistance is the amount of pressure required for the radicle to push through the maternal integuments. This is the last step of germination and it controls whether or not the seed will complete germination. The surrounding sheath and locular tissue may provide enough resistance to prevent germination. Some authors hypothesize that the resistance provided by surrounding structures inhibit germination more than endogenous ABA (Berry and Bewley 1992). Endosperm resistance affects the speed at which germination occurs but it will not prevent it from occurring (Hilhorst and Downie 1996).

There are three hypotheses on the causes for radicle growth. One is that the water potential in the radicle decreases due to the import of solutes which causes an increase in water uptake (Bewley 1997). The second possibility is that the extensibility of the radicle cell walls allow the cells to elongate (Bewley 1997). Plant cells may enlarge 10-1000 fold in volume, a result of water uptake and cell wall relaxation. The cell wall may expand by synthesis and secretion of wall polymers (Cosgrove 1997). In the radicle, it is more probable that biochemical loosening allows turgor pressure to extend the wall polymer network. Expansins and xyloglucan endotransglycosylase have been implicated in cell wall expansion but neither protein has been reported in germinating seeds (Bewley 1997). The third hypothesis is that the seed tissues surrounding the radicle tip weaken allowing the tip to elongate. Applying gibberellins to seeds weakens the endosperm walls at the radicle tip and may promote radicle emergence. In lettuce (*Lactuca sativa* L.) seeds, the endosperm surrounds the embryo inhibiting germination. Weakening of the cell walls is necessary for radicle protrusion. The breakdown requires enzymes and is temperature and pH dependant (Dutta et al. 1994). Addition of gibberellins to a growth medium enhance germination and weakening of the cell walls of the endosperm, however, there is no direct proof that endogenous gibberellins function the same way that applied gibberellins do (Groot and Karssen 1987).

## **The Microsite**

### **Definition**

A 'safe site' is the combination of all biotic and abiotic variables directly surrounding the seed which allows for successful seedling recruitment (Harper 1977). Harper et al. (1965) first defined the 'safe site' as the combination of conditions directly surrounding the seeds that break dormancy and induce germination allowing seed germination and emergence. Seedling germination occurs when the conditions directly surrounding the seed are within the range of the germination requirements for a particular species. The term 'safe site' is currently used infrequently with most ecologists using the more general term microsite (Crawley 1990, Eriksson and Ehrlén 1992). Weed seedling recruitment is the successful germination of seed and establishment of seedlings at the soil surface. Weed seedling recruitment levels are determined by the number of seeds in the soil profile and the number of available microsites.

### **Components of the Microsite**

**Light, Seed Germination and Seedling Emergence.** Exposure to light breaks dormancy and promotes germination in many weed species (Gallagher and Cardina 1997; Bartley and Frankland 1985; Letchamo and Gosselin 1996). The light response in seeds is controlled by the photoreversible pigment phytochrome (Probert and Smith 1986; Noggle and Fritz 1983). Photoconversion of phytochrome from the red light absorbing form to the biologically active far-red absorbing form promotes germination in some species and inhibits it in others (Gallagher and Cardina 1997; Bartley and Frankland 1985). Sensitivity to light is dependant on many factors including the level of seed dormancy, seed burial and the gaseous environment directly surrounding the seed (Benvenuti and Macchia 1998; Gallagher and Cardina 1998a; Benvenuti and Macchia 1997). For some species, seed burial elevates seed sensitivity to incident radiation (Benvenuti and Macchia 1998; Gallagher and Cardina 1998a) with even brief exposures

to light (less than 1 second) promoting germination (Milberg et al. 1996; Woolley and Stoller 1978).

Although many weed seeds are highly sensitive to light very little light penetrates the soil. Woolley and Stoller (1978) reported that less than 1% of incident radiation penetrated 2.2 millimeters through a Drummer silty clay loam or a Broomfield sand. Benvenuti (1995) found that light penetration was strongly dependant on soil type and particle size. Despite the variation he reported that 0.01% of incident light penetrated all soil types tested at a depth of no more than 4 mm. Therefore, in non-disturbed soil, light exposure within the top few millimeters of soil may play an important role in weed population dynamics but it will have very little impact below these shallow depths.

Due to the high sensitivity to short exposures of incident light many authors have suggested that the brief exposure of weed seeds to light during disturbance is adequate to promote germination (Botto et al. 1998; Wesson and Wareing 1969). Gallagher and Cardina (1998b) reported a 30 to 55% increase in redroot pigweed and giant foxtail (*Setaria faberii* Herrm.) emergence following day cultivation compared to night cultivation. Night versus day cultivation had no impact on the germination and emergence of several other weed species. Buhler (1997) found that annual grass and large-seeded broadleaf species showed little response to light exposure during tillage while small-seeded annuals often displayed reduced emergence when the tillage was done in the dark. Milberg et al. (1996) found that for 24 of 44 species, germination was stimulated by a short duration of exposure to light. Buhler (1997) noted that the most consistent observation, concerning the impact of light exposure during disturbance on weed emergence, was the inconsistency of the response to light. The impact of day versus night cultivation on weed emergence is highly variable depending on the species present, the state of dormancy of seed and the type of cultivation equipment being used (Botto et al. 1998; Milberg et al. 1996; Benvenuti and Macchia 1998; Gallagher and Cardina 1998b). Due to the high variability in effect, night cultivation may not be an aid to weed management.

**Soil Moisture, Seed Germination and Seedling Emergence.** Soil moisture may limit seed germination and emergence (Roman et al. 1999; Martinez-Ghersa et al. 1997;

Roberts and Potter (1980). Weaver et al. (1988) reported that total weed emergence of four weed species decreased as soil moisture decreased and the time to 50% emergence increased slightly with decreasing soil moisture. Despite the general trend of decreasing emergence with a decrease in soil moisture, germination response to soil moisture is species dependant (Hoveland and Buchanan 1973). Martinez-Ghersa et al. (1997) found that barnyard grass (*Echinochloa crus-galli* (L.) Beauv.) and redroot pigweed germination at 20 and 30 °C was curtailed at soil moisture levels of 1/4 and 1/8 field capacity. Nuttall (1982) reported 74% emergence of canola (*Brassica napus* L.) at field capacity and only 15% emergence at 50% of field capacity. However, he also found that soil moisture did not affect dormancy release of lambsquarters (*Chenopodium album* L.) seeds. Osmotic potentials below -1.2 MPa only reduced wild oat and sterile oat (*Avena sterilis* L.) germination by 33% and 45%, respectively, while germination of stinking mayweed (*Anthemis cotula* L.) was reduced by 95% at -10 MPa (Fernandez-Quinantilla et al. 1990; Gealy et al. 1994). Roberts et al. (1980) reported that lack of soil moisture was the over-riding factor limiting emergence following disturbance. They hypothesized that soil moisture levels control seedling number by limiting germination initiation or causing the death of seedlings before they are established.

The impact of soil moisture on seed germination interacts with various other biotic and abiotic variables including temperature and incoming radiation. Photoconversion of phytochrome from the red light absorbing form to the biologically active far-red absorbing form requires hydration in most species (Gallagher and Cardina 1997). Gallagher and Cardina (1997) reported that seedling emergence of redroot pigweed in response to red light increased with volumetric soil water content. In the absence of adequate moisture, light may inhibit germination of some weed species (Hsiao and Simpson 1971).

Germination and emergence may also be determined by the strong interaction between temperature and moisture (Roman et al. 1999; Ghorbani et al. 1999; Martinez-Ghersa et al. 1997). In some weed species, dormancy breaking and germination does not occur unless soil water content is high enough for germination (Martinez-Ghersa et al. 1997). This moisture limitation may be overcome for some species if temperatures are high enough (Oryokot et al. 1997b). Conversely, germination may increase with

temperature once a certain water potential is achieved (Gealy et al. 1994). Weaver et al. (1988) concluded that temperature was the main factor affecting the relative time of emergence of green pigweed (*Amaranthus powellii* S. Wats.), green foxtail, lambsquarters and tomato with moisture modifying the response. It appears that moisture has a greater impact on the number of weeds emerging while temperature has a greater impact on the timing of weed emergence within a specific range.

**Soil Temperature, Seed Germination and Seedling Emergence.** The germination response of weeds to constant or fluctuating temperatures is species specific (Weaver et al. 1988; Fernandez-Quintilla et al. 1990). Most weed species obtain the highest percentage germination under alternating temperatures. Redroot pigweed and barnyard grass had higher germination rates at 20/30°C than at 20°C (Martinez-Ghersa et al. 1997). Baskin and Baskin (1977) reported high rates of germination of lambsquarters and redroot pigweed at 35/20 °C. Nishamoto and McCarty (1997) reported only 10% germination of goose grass (*Eleusine indica* (L.) Gaertn.) at constant temperatures and 99% emergence with fluctuating temperatures of 35/20 °C and light. While some plants germinate least when there is little alternation in temperature (Williams 1983), others, like downy brome (*Bromus tectorum* L.) may germinate best at constant temperatures (Thill et al. 1979).

The optimum germination temperature varies between species and between ecotypes within a species. Letchamo and Gosselin (1996) reported that dandelion (*Taraxacum officinale* L.) had higher germination rates with light and higher temperatures (25°C) than with light and lower temperatures (10°C), while, Washitani (1984) reported 90% emergence of dandelion at temperatures between 10 and 18°C. Some species, however, germinate well under a wide range of temperatures. Fernandez-Quintilla et al. (1990) reported that 70-80% of wild oat seeds germinated at temperatures ranging from 10 to 30°C. Conversely, sterile oat had optimum germination at 10°C with germination declining to 70% at 20°C and dropping to a low of 35% at 30°C.

There is a strong interaction between temperature and light with regard to species germination although the light requirement for some species may be overcome by high temperatures. For redroot pigweed the requirement of light for germination is more

pronounced at 20°C than at 30°C (Gallagher and Cardina 1998a). Differences between light and dark germination of white clover (*Trifolium repens* L.) only occurred at temperatures between 5-10°C (Niedzwiedz-Siegien and Lewak 1988). Taylorson and Dinola (1989) proposed that high temperatures may cause a transition from a light requiring to a light independent state in a seed. The temperature dependant light requirement may prevent seeds from germinating that were exposed to light during disturbance but then buried at depths where seedling emergence was unlikely. Conversely, seeds near the soil surface, where emergence is probable, germinate due to the high temperature even without exposure to light (Gallagher and Cardina 1998a).

Moisture and temperature also interact affecting weed germination. Temperature has the greater impact on the rate of emergence and moisture modifies the response (Blackshaw 1991; Weaver et al. 1988). The effects of temperature and moisture within species specific boundaries may be additive (Ghorbani et al. 1999). Gealy et al. (1994) reported less than 2% emergence of stinking mayweed at water potentials of -10 MPa. At water potentials greater than -0.6 MPa, germination increased with temperature. Oryokot et al. (1997b) reported that moisture limitation did not delay seed germination of green pigweed and redroot pigweed at temperatures above 23.8 and 27.9°C, respectively. Although temperature and moisture may interact to determine germination, the rate of shoot and radicle elongation may be determined by temperature alone (Roman et al. 1999).

**Soil Gaseous Environment, Seed Germination and Seedling Emergence.** Within agricultural fields in Western Canada most weeds emerge from the top 4 cm of the soil profile (du Croix Sissons et al. 2000). For many species deep burial within the soil appears to result in secondary dormancy rather than suicidal germination (Benvenuti et al. 2001a). Non-dormant seeds must be able to detect environmental cues that cause a transformation from non-dormancy to dormancy. To be effective, the environmental signals causing this transformation must change with increasing soil depth. Light, temperature fluctuations, soil moisture and the gaseous environment surrounding the seed may all provide signals of seed depth within the soil profile.

Most seeds require oxygen for germination (Benvenuti and Macchia 1999, Benvenuti and Macchia 1997) although some may germinate in the absence of oxygen (Rumpho and Kennedy 1981). Gutterman et al. (1992) reported that most seeds were able to germinate at 15% oxygen and that higher oxygen concentrations caused more rapid germination. Benvenuti and Macchia (1995) also found that hypoxia decreased seed germination and the rate of germination. Although germination seems to increase with increasing oxygen concentration some species may exhibit decreased germination in normoxic concentrations (21% oxygen) compared to hypoxic concentrations (between 5 and 10% oxygen) (Benvenuti and Macchia 1997).

Oxygen concentrations within the soil decline with depth (Topp et al. 2000). High soil moisture, soil compaction, soil texture, high microbial activity or poor soil structure may decrease soil oxygen concentration or inhibit gaseous movement within the soil (Benvenuti 2003; Drew 1992; Hodgson and Macleod 1989; Ishii and Kadoya 1991). Seeds buried in low oxygen concentration conditions switch from aerobic to anaerobic metabolism (Benvenuti 2003; Holm 1972). At low oxygen concentrations and under conditions of poor gas diffusion anaerobic metabolites build up around the seed and inhibit seed germination. These conditions may also induce secondary dormancy and a light requirement for germination (Holm 1972). The inhibitory effects of low oxygen concentration on seed germination can be alleviated in some cases by flushing the atmosphere around the seed with inert gases to remove anaerobic metabolites (Benvenuti and Macchia 1995). Therefore, oxygen concentration or the inability to remove fermentation products from the gaseous environment directly surrounding seeds may inhibit germination (Benvenuti 2003).

## **The Seed in the Microsite**

### **Seed Depth**

The position of seed within the soil profile affects weed seed population dynamics. The microsite requirements for some species are extremely specific. Curly dock (*Rumex crispus* L.) for example, will only emerge when seeds are at or near the

surface. Even burial at 1 cm can significantly reduce weed seedling emergence (Weaver and Cavers 1979). For other species, such as common milkweed (*Asclepias syriaca* L.) there is negligible emergence when seeds are on the surface or below 7 cm (Yenish et al. 1996). Wild oat can emerge from depths ranging from near the surface to 20 cm (Sharma and Vandeborn 1978). Despite the wide variation in depths from which weeds can emerge, in common arable fields most weeds emerge from seed located within the top 1-6 cm (Cousens and Moss 1990; du Croix Sissons et al. 2000).

The range of depths from which weeds emerge is dependant on the species, as well as on soil type, tillage practice, and a variety of soil physical properties (Buhler and Mester 1991; Mohler and Galford 1997; Yenish et al. 1996). When testing a variety of weed species Benvenuti et al. (2001a) found that depth mediated inhibition was significant with every species. With most weed species the number of seedling emerging decreases and the time to emergence increases with increasing seeding depth (Benvenuti et al. 2001a; Cussans et al. 1996). In most cases suicidal germination does not occur when seeds are placed deep within the soil profile. Instead seeds typically enter secondary dormancy (Benvenuti et al. 2001a; Benvenuti et al. 2001b). Cussans et al. (1996) also found decreased emergence with increasing depth. The response to depth varied depending on soil tilth. Benvenuti (2003) reported that germination inhibition due to burial depth was directly proportional to clay content and inversely proportional to sand content.

### **Seed Size**

Seed size and shape vary between species. One would anticipate that size and shape would affect seed dispersal, burial and perhaps survival. In conventional tillage fields seeds may be moved horizontally largely independent of seed size or shape. While burial may reduce seed predation and increase seed longevity it may also prevent seed germination. Benvenuti et al. (2001a) found a relation between seed size and emergence. The ability to emerge from deeper depths increased in a nonlinear fashion with seed size. Therefore, one would expect larger seeds to persist for shorter periods of time in the seedbank due to their ability to germinate over a larger range of depths. The



effect of seed depth within the soil profile depends on soil texture and aggregate size. Cussans et al. (1996) found that the emergence of large seeded species is less responsive to seeding depth and aggregate size. Smaller seeded species showed greater emergence when covered by larger clods. This suggest that the smaller seeds benefited from increased exposure to light, gas diffusion or lower germination energy was required to emerge from the soil. Large seeded species can exert greater emergence energy allowing them to break through soil crust at least when the soil is moist (Mohler and Galford 1997).

Seed persistence in the soil is determined by a variety of factors including seed size and shape (Thompson et al. 1993). The increased longevity of smaller seeds within the soil may be due to their ease of burial which then increases the probability of their survival or it may increase dormancy levels. Thompson et al. (1993) found a significant relationship between seed size and shape and soil persistence for a range of species from Europe.

Turnbull et al. (1999) suggests that seed size is part of a competition-colonization trade-off. When comparing large and smaller seeds within a species the larger seeds tended to be less dormant and the resulting seedlings more competitive (Peters 1985). Turnball et al. (1999) suggest that seeds compete for available microsites and large seeded species are the best competitors. As well, smaller seeded species are more dependent on disturbance for establishment than larger seeded species (Burke and Grime 1996). Burke and Grime (1996) reported that smaller seeded species tend to have a more rapid germination and growth rate enabling them to quickly colonize disturbed areas. Larger seeded species have slower growth rates but are more adapted to survive high competitive situations. Since species have a relatively constant reproductive biomass they must make a trade-off between seed size and number. Therefore, when seeds of large and small seeded species are present large seeded species are more competitive but smaller seeded species produce more seeds and reach a greater range of microsites. One would then expect larger seeded species to become more prominent under highly competitive situations whereas small seeded species may be more efficient colonizers.

## Temporal Variation of the Microsite and Seed Germination

### Seasonal Emergence Patterns

The microsite conditions directly surrounding the seed will depend on the time of year during which weed seedlings emerge. Spring emerging and fall emerging weeds will face very different conditions. Most species exhibit an emergence peak once during a season but some have two emergence peaks per season (typically spring and fall) or have no definite emergence peak during a season (Ogg and Dawson 1984; Håkansson 1983). Common ragweed (*Ambrosia artemisiifolia* L.) only germinates in early-to-mid spring while redroot pigweed reaches peak emergence in late spring or early summer and it may continue to emerge through the summer (Baskin and Baskin 1977). Emergence of dandelion and perennial sow-thistle (*Sonchus arvensis* L.) occurs mainly in the spring while chamomile (*Matricaria recutita*) shows no consistent pattern of emergence (Roberts and Neilson 1981). Generally, obligate winter annuals will only germinate in the autumn while facultative winter annuals may germinate in the spring as well. Summer annuals generally germinate in the spring or throughout the summer (Baskin and Baskin 1985).

Many different variables in combination may impact the seasonal emergence of weeds but temperature probably plays the most important role with other variables modifying the resultant emergence pattern (Blackshaw 1991; Weaver et al. 1988). Although emergence for some species is not limited by temperature and they emerge under a wide range of temperatures (Fernandez-Quintilla et al. 1990), many others are temperature limited emerging only during the season when the temperature is within the proper range (Washitani 1984; Baskin and Baskin 1977). The effects of temperature on weed seed germination and emergence appear to be additive (Ghorbani et al. 1999). Weed and crop seeds have different threshold temperatures below which no germination occurs (Wiese and Binning 1987; Vigil et al. 1997). The accumulated growing degree hours or growing degree days above this base threshold temperature can be a reliable predictor of emergence timing (Forcella 1992; Marshall and Squire 1996; Blackshaw and Harker 1997). The time to reach the required accumulated growing degree days will vary

with the season affecting the rate of emergence and the length of the weed emergence period.

Seasonal variation in dormancy may also play an important role in determining the timing of weed germination and emergence. Milberg and Andersson (1997) buried weed seeds from several annuals in November and exhumed them monthly from March of the following spring to April of the following year. They reported that all species showed substantial seasonal changes in dormancy level. Cardina and Sparrow (1997) noted that velvetleaf (*Abutilon theophrasti* Medic.) seeds exhibited a 30 to 70% decline in dormancy from maturity to winter with little change from winter through to summer and a further decline the following autumn. Seasonal variation in dormancy cycles ensures that seeds are able to germinate only during the season when seedlings have the greatest potential for successful establishment. Once the seed is non-dormant, germination can take place if the conditions are suitable. For seeds, the switch from dormant to non-dormant is not discrete but a continuum from total dormancy to complete non-dormancy (Baskin and Baskin 1985).

### **Impacts of Agronomy on Weed Emergence Patterns**

Weed population densities and weed biomass may be reduced in cropping systems where temporal diversification of management actions are used. Liebman et al. (1996) reported that weed biomass was lower in a potato (*Solanum tuberosum* L.) / oats rotation than in a potato / clover (*Trifolium spp.*) rotation. Liebman and Dyck (1993) reported that among crop rotation studies weed densities in fields with crop rotation had lower weed densities in 21 studies, higher in 1 study and equivalent in 5 studies when compared to monocultures.

Crop rotation enables a producer to include crops which are seeded and emerge at different times and in different seasons. Schreiber (1992) reported a reduced green foxtail population in a soybean-wheat-corn rotation when compared to monoculture corn. Chancellor (1985) found that spring germinating weeds were found more frequently in spring sown crops while fall germinating weeds occurred more often in fall germinating crops. Weed populations may also be controlled by varying the seeding date. Delaying

seeding and cultivating before planting destroys early emerging weeds (Liebman and Dyck 1993). Spandl et al. (1998) reported that an earlier planting of wheat generally resulted in increased green foxtail emergence while delayed planting increased the rate of emergence but resulted in lower densities. The more simultaneous green foxtail emergence and reduced density may facilitate control. In contrast, Melander (1995) found that planting date had an inconsistent effect on weed plant populations in the spring although emergence seemed to be delayed at later drilling dates compared to the early drilling dates. Seeding a crop early or late alters the temperature and moisture levels to which weed seeds are exposed. Late seeding allows early emerging weeds to be eliminated by pre-seeding tillage while early seeding may allow the crop to germinate and begin to grow before weeds emerge. Weed emergence models may allow producers to better determine the best seeding date that allows the crop to compete adequately with the weeds (Weaver et al. 1988). Using emergence conditions for weed control will only work when there is sufficient difference between the emergence requirements of the crop and the species within the given seed bank (Blackshaw 1991). Properly planned crop rotations will include crops with different planting dates and this will help to prevent any particular weed species from dominating.

### **Spatial Variation of the Microsite and Seed Germination**

Weed communities vary between environmental regions, fields and between areas within fields. This spatial variation in weed communities is due to spatial variation in the many factors that affect germination, growth and reproduction. The plant reproductive capability, seed dispersal, and soil microsite conditions determine the species and the density of weeds that emerge. The relative importance of seed and microsite limitation of weed populations varies with species and scale. Between ecoregions, environmental conditions may favor specific weed species over others. In this situation some weed populations may become seed limited due to poor emergence, survival and seed set of individuals within an ecoregion for which they are not well adapted. On a smaller scale (within an agricultural field), weed populations may also be seed or microsite limited. If seeds of all weed species that grow within that ecoregion are present within one field the

weed populations often are still aggregated with specific species dominating. This aggregation is primarily due to historical events, seed dispersal, and recruitment limitation.

### **Ecoregion Scale Variation**

Large-scale landforms, climate, natural vegetation, soils and land uses determine ecoregions (Van Acker et al. 2000). The size and the type of ecoregion varies depending on what is being measured. Weed families or species may predominate in different ecoregions. Fernandez-Quintilla et al. (1990) reported that 70-80% of wild oat seeds germinated at temperatures ranging from 10 to 30°C while sterile oat had optimum germination at 10°C. Consequently, wild oat predominates in cool moist areas while sterile oat predominates in Mediterranean regions.

The levels of light, temperature, moisture and frost-free period may vary between ecoregions (Dale and Thomas 1987). Day length varies as you move from south to north and this variation may impact weed populations. Thomas and Dale (1991) concluded that weed community structure in Manitoba was largely determined by climatic variables rather than agronomic variables or crop selection. This may have been largely due to the fact that the study was limited to spring seeded crops which are grown in an agronomically similar manner as well as the fact that farming activities tend to level any variation in ecological condition. Similar results were reported in Saskatchewan cereal and oilseed fields where weed community associations with ecoregions were determined mainly by the soil or associated climate rather than the crop and the cultural practices (Dale and Thomas 1987). The separation was not as strong in Manitoba regions, which may be due in part to a lack of as clear of a distinction in environmental variables between ecoregions as is found in Saskatchewan (Dale et al. 1992). However, Van Acker et al. (2000) reported variation in weed densities between crops in Manitoba. This difference was largely attributed to differences in herbicide use. Andreasen et al. (1991) also found that crop type and soil clay content were the variables that had the greatest influence on the occurrence of weed species in 316 Danish fields. It is important to remember that soil zones are due in part to historical climatic patterns (temperature and

moisture) and also determine the crop grown in the region (Dale et al. 1992). Consequently, geographic factors representing climate, crop and management factors all interact and are difficult to separate.

Environmental factors appear to have the overriding impact on weed species distribution at broad scales. Mack and Pyke (1983) reported that year to year variation in environment overrode any differences found between habitat types along a 200 km transect. Several studies have shown that crop rotation and other management factors affect weed populations. These studies generally compare weed populations within an ecoregion whereas surveys between ecoregions generally show environment as the overriding variable. Van Acker et al. (2000) found that climate and different agronomic practices between ecoregions affected weed populations. Few studies have compared similar management practices between ecoregions to determine their impact on weed populations.

### **Farm Scale Variation**

Within ecoregions and years weed populations may vary between farms due to differences in soil type, management practices, cropping sequence and soil fertility. Farm management plays a key role in determining the density and diversity of weed communities. Variables such as, tillage, fertility and ground cover all dramatically alter the microsite conditions directly surrounding seeds.

The shift from one tillage system to another or the presence of one tillage system or another should cause differences in weed population dynamics (Buhler 1995). Many authors have suggested that a switch from conventional to reduced tillage should result in increased populations of perennials, summer annual grasses, wind disseminated weeds, biennial and winter annual species and volunteer crop plants (Buhler 1995; Swanton et al. 1993; Froud-Williams et al. 1983). This change in species composition may be due more to management practices affecting seed rain and weed life span than to alterations of microsite. For example, the reduction of tillage favors perennials or taprooted species that rely upon vegetative reproduction (Froud-Williams et al. 1983). Volunteer crop species germinate best near the surface and the lack of fall cultivation allows winter

annuals and biennial species to become established (Swanton et al. 1993). As well, an increase in annual grasses in no-till fields may be due to the fact that most of these species have a light requirement for germination and consequently germinate most frequently near the surface (Froud-Williams et al. 1983). Although there may be general trends in weed population dynamics in conservation tillage fields it is important to note that location, environment, type of tillage and weed management inputs in individual fields can create tremendous variability around the mean (Buhler 1995). Buhler et al. (1994) noted that reduced tillage may result in greater populations of perennials but that this may be overcome by proper management techniques. Derksen et al. (1993) concluded that location and year effects had a greater impact than tillage system on weed population dynamics and resultant weed communities.

Conservation tillage usually involves a reduction of soil disturbance and a maintenance of crop residue cover (Swanton et al. 1993). When weed seeds are not incorporated with tillage, surface residue may provide the appropriate conditions allowing weed emergence (Buhler and Mester 1991). Tillage itself may not affect soil temperature (Oryokot et al. 1997b) but residue on the surface may alter soil temperature, moisture and light transmittance enough to impact weed microsite conditions and ultimately weed population dynamics. The increased organic matter content found in reduced tillage fields results in reduced diurnal temperature fluctuations when stubble mulch is present (Froud-Williams et al. 1981). Teasdale and Mohler (1993) found that hairy vetch (*Vicia hirsute* L.) and rye (*Secale cereale* L.) residue reduced daily maximum soil temperature as well as the daily soil temperature amplitude. They noted that the reduction in soil temperature was not enough to reduce weed emergence but the reduction in temperature amplitude was adequate to reduce germination of weed seeds that require temperature fluctuations to break dormancy. Yunusa et al. (1994) found that mulches reduced the soil temperature at 5 cm by 7 °C compared to unmulched soils. Standing wheat stubble may also reduce soil temperatures (Wilkins et al. 1988). Malhi and O'Sullivan (1990) reported that soil temperatures at 2.5 cm were 2.8 °C lower under zero tillage than conventional tillage. Lower soil temperatures in zero tillage fields may be a result of the high solar reflectivity and low thermal conductivity of crop residues in comparison to soil (Johnson and Lowery 1985). Crop residues may also reduce weed

emergence by reducing the amount of light reaching the soil surface. Teasdale (1993) reported that hairy vetch residue may suppress weed establishment of species with a light requirement but may not suppress several other species. However, Teasdale and Mohler (1993) found that light transmittance through hairy vetch and rye cover crops was adequate to stimulate germination. Therefore, although crop residue and tillage regime do impact the microsite it may not be adequate to prevent weed emergence of most weeds but might affect the germination of weeds that are on the threshold of germination.

Weed seed predation may also impact weed population dynamics. In reduced tillage fields the increase in ground cover may also result in an increase in predators. Reader (1991) concluded that the presence of ground cover provided a habitat for seed predators. Reader and Beisner (1991) reported greater species specific predation in areas where the ground cover was dense versus less dense areas. Both vertebrates and invertebrates eat weed seeds and this may affect the dynamics of the weed population via preferentially feeding on the seeds of certain species (Marino et al. 1997; Povey et al. 1993). The decrease of broadleaf weeds in reduced tillage fields (Buhler 1995; Froud-Williams et al. 1983; Froud-Williams et al. 1981) may be partially caused by preferential predation of broadleaf weed seeds by the increased predator populations in no-tillage fields (Brust 1994).

Tillage buries crop residue and alters the characteristics of the soil surface affecting weed seedling dynamics (Buhler 1995). The type and timing of tillage may also affect weed population dynamics by altering the vertical distribution of weed seeds. Yenish et al. (1996) found that 50 to 60% of the weed seeds were deposited at depths of 11-16 cm after tillage, which is well below the depth from which many weeds emerge (Du Croix Sissons et al. 2000). Therefore, weed seeds that have a short viability would remain within the soil long enough to die if further deep cultivation did not occur bringing them to the surface. Modeling emergence based on the maximum depth of emergence is valid for weed species whose seed viability rapidly declines (Yenish et al. 1996) but may be very difficult for species for which the weed seeds may last for extended periods within the soil profile (ie. species that tend not to be seed limited). Further cultivation will bring seeds back to the surface (Cousens and Moss 1990) allowing germination of seeds that may otherwise have died. Consequently, for seeds



that may last for extended periods in the seed bank, burial may induce secondary dormancy, reduce seed predation and seed death allowing a greater number of seeds to germinate over a longer period of time.

There is no doubt that disturbance also changes the soil environment and consequently the environmental conditions directly surrounding weed seeds independently of the effects of ground cover or position of seeds in the soil (Mohler and Galford 1997). Campbell et al. (1989) reported that zero-tillage plots on the Brown soil zone of Saskatchewan had increased organic matter, microbial biomass, nitrogen and phosphate activity in the top 7.5 cm of the soil. Conservation tillage generally has lower soil temperatures and higher soil moisture levels that may also affect weed emergence (Johnson and Lowery 1985; Malhi and O'Sullivan 1990). These conditions may impact weed populations but to isolate the cause of the variation in weed populations within fields is extremely difficult.

### **Tillage and Weed Populations**

**Tillage and Weed Seed Movement.** Tillage operations move weed seeds both horizontally and vertically. The type of implement used and the speed traveled affects the distance weed seeds move during tillage operations. Rew and Cussans (1997) found that 84% of weed seeds moved less than 1 m horizontally from the source during cultivation and no seeds moved more than 4.8 m. While only limited horizontal movement of seeds occurs impacting spatial dynamics, vertical movement of weeds seeds has a much greater impact on weed populations by affecting the timing, number and type of weeds emerging. The layer where the seed is deposited determines what environmental conditions directly surround the seed and thus determine the probability of germination.

Various tillage regimes affect the vertical movement of seeds within the soil profile. Buhler and Mester (1991) found that mean depths of weed emergence were shallowest in no-till, followed by chisel and conventional tillage. In a simulated seed dispersal experiment, Yenish et al. (1996) found that 90% of seeds remained within 2 cm of the surface with no-till while chisel plow and discing placed 40% of the seeds 4 cm

from the surface with nearly 100% of the seeds within the top 10 cm of the soil profile. Moldboard plowing placed 50 to 60% of the seeds at 11-16 cm with few seeds above 8 cm. With multiple cultivations, seeds that were buried during the initial cultivation may be moved back to the surface. Cousens and Moss (1990) reported that with a single simulated seed rain, plowing initially buried seeds deep within the profile but after 5 years with annual cultivation the distribution of weed seeds was similar between the surface and 20 cm depths changing little with additional tillage. With rigid tine cultivation it took approximately 10 years to reach a stable distribution which was approximately equal to the distribution of the moldboard plowed plots. Moldboard plowing tends to homogenize the soil seed bank horizontally and vertically while reduced tillage produces denser seed banks in the upper 5 cm (Feldman et al. 1998). Generally, as tillage decreases the number of weed seeds and weed seeds germinating near the surface increases (Spandl et al. 1998). Therefore, since reduced tillage generally has more weed seeds near the surface, no-tillage fields should have higher populations of seeds on or near the surface while conventional tillage should have fewer weed seeds on the surface but more seeds spread throughout the soil profile forming a persistent seed bank.

The depth of weed seeds within the soil profile also affects the timing of weed seedling emergence. The greater the depth the slower the emergence (Cussans et al. 1996). This trend is somewhat species specific with many weeds having optimum germination rates just below the surface of the soil. Some weed species have reduced emergence or reduced rates of emergence when seeds are placed directly on the soil surface (Boyd 2003). The timing of emergence is important since the competitive ability of a weed depends on whether it emerges before, after or during crop emergence. Weeds germinating after crop emergence will not have as large of an effect on yield nor will they produce as many weed seeds (Wall and Friesen 1990).

**Tillage and Soil Temperature.** Tillage not only moves seeds horizontally and vertically within the soil but also changes the soil physical environment directly around the seed. Soil temperature is one of the key parameters determining the timing of weed seedling emergence. It has generally been observed that no-tillage soils or reduced tillage soil have lower soil temperatures than conventionally tilled soils.

While tillage affects soil temperature in many ways the percent residue cover left on the soil following cultivation has the greatest impact on spring soil temperatures (Potter et al. 1985). During the day plant stubble or surface debris left on the surface acts as an insulator due to its low thermal conductivity. Since soil is typically darker in color than plant material and has a lower reflectivity it absorbs incoming radiation more rapidly than surface stubble which increases the soil reflection coefficient reducing the heat absorbed during the day (Johnson and Lowery 1985). During the night, surface debris reduces the emission of long wave radiation (Hay et al. 1978). Consequently, spring soils with high levels of material on the surface absorb less heat during the day and emit less heat during the night resulting in an overall decrease in soil temperatures as well as a decrease in temperature fluctuations.

Stubble or surface debris also affects winter and early spring soil temperatures in northern climates by holding more snow during the winter months which also acts as a soil insulator. Larsen et al. (1988) reported warmer soil temperatures and increased winter wheat survival in tall stubble systems. Benoit and Van Sickle (1991) found that soil temperatures were highest in no-till soils that had stubble during the winter months. The accumulation of snow had a greater impact on temperature than tillage regime or residue level alone. Although no-till soils generally have lower temperatures, Benoit and Van Sickle (1999) reported that the no-till residue treatment tended to have higher temperatures in early spring just before planting and became frost free 10 to 30 days before other tillage and residue combinations. A combination of the warmer winter temperatures, earlier warming of the soil and lower heat absorption and emission impacts the survival and timing of weed seedling emergence.

The second way that tillage affects soil temperatures is by altering soil bulk density, pore space and water content which affect the transmission of energy into and out of the soil. The movement of heat through the soil depends on the thermal conductivity and volumetric heat capacity (Hay et al. 1978). Thermal conductivity is a measure of the ease with which the soil conducts or transmits heat while soil volumetric heat capacity is the amount of heat the soil must absorb or lose to produce a one degree change in temperature. The ratio of these properties (thermal diffusivity) is a measure of the rate and depth of heat transfer through the soil (Hay et al. 1978). Potter et al. (1985)

reported a similar soil volumetric heat capacity for a variety of tillage treatments while thermal diffusivity was significantly greater in the no-till soil than in the conventional and chisel plow systems. Therefore they concluded that the thermal conductivity must also have been greater in the no-till system. Since thermal conductivity is affected by bulk density, pore volume and water content, any change in these factors should alter the transmission of heat. The impact of tillage on these variables is not consistent and it depends on many variables including conditions during cultivation and soil type. Blevins et al. (1983) reported no difference in bulk density between no-till and conventional till while Gantzer and Blake (1978) reported higher bulk density in no-till versus conventional till. Even in the absence of measurable differences in bulk density or soil water content, tillage may alter the pore size distribution and soil matrix affecting thermal conductivity (Potter et al. 1985). Also, higher moisture content and increased bulk density in no-till soils could increase soil diffusivity thus transferring heat more rapidly deeper into the soil resulting in cooler surface temperatures than conventional tillage even when similar amounts of heat were taken in (Johnson and Lowery 1985).

**Tillage and Soil Moisture.** Soil cultivation breaks surface crusts, alters soil porosity and buries surface residue. These factors or a combination of these factors affects water infiltration rates as well as the water holding capacity of the soil. Although infiltration rates may initially be higher following tillage (Blevins and Frye 1993) most studies have found increased soil water in no-till when compared to conventional tillage (Bidlake et al. 1992; Blevins et al. 1971; Malhi and O'Sullivan 1990). Consequently, no-till soils may provide a method for conserving water during dry years but may also lead to excessive moisture in wet years.

Increased residue levels typically apparent in no-till fields affect soil moisture in several different ways. First, surface stubble or debris may increase the amount of snow kept on a field during the winter months (Benoit and Van Sickle 1991). In spring the snow melt can greatly influence soil moisture levels. Second, soil surface debris slows evaporation from the soil surface by shading the soil from solar radiation, insulating the soil from heat and impeding the movement of water vapor from the soil to the air (Blevins and Frye 1993). It is difficult to determine if the difference in evaporation rates

is due solely to surface cover or if changes in the soil physical properties also alter evaporation rates (Steiner 1989). Teasdale and Mohler (1993) reported a decline in soil moisture content during droughty periods without residues compared to plots with crop residues left intact. Third, surface debris may hinder or prevent the run off of water during rainfall increasing infiltration levels. No-tillage plots with surface residues also have higher soil porosity and infiltration rates than tilled plots which may partially explain increased soil moisture levels in no-till fields. Therefore, lower soil temperatures found in reduced tillage plots with increased crop residue may reduce weed emergence while increased moisture during droughty periods may increase weed emergence (Teasdale and Mohler 1993).

Tillage alters soil physical parameters affecting soil moisture. Infiltration rates may be affected by the size and number of pores in the soil. In conventionally tilled systems the pores are created primarily by the tillage equipment while pores are created primarily by biological processes in no-till systems (Benjamin 1993). Logsdon et al. (1990) reported that the total number of pores was often greater for no-till than for plots that were moldboard plowed. Not only is the number of pores affected but also the continuity of the pores. It is generally acknowledged that higher bulk densities are found in no-till systems with less total pore volume. However, no-till soils tend to have a greater number of continuous earthworm channels that reach the surface (Benjamin 1993). The continuous pores contribute significantly to infiltration rates and hydraulic conductivity (Azooz and Arshad 1996). Blevins et al. (1983) reported that saturated hydraulic conductivity measurements suggest better water movement in no-tillage compared to conventional tillage. The increased water movement results in less runoff from the soil surface.

Increased levels of soil moisture may vary spatially. Oryokot et al. (1997b) reported no moisture differences at 2.5 cm between no-till, chisel till and moldboard plowing. Conversely, Malhi and O'Sullivan (1990) reported that soil moisture in the surface layer (0-15 cm) was 7.2% greater on zero-tillage plots than conventional tillage plots. Blevins et al. (1971) also found higher volumetric soil water contents in no-tillage soils to depths of 60 cm with the greatest differences occurring in the top 8 cm. Since

most weeds germinate from the top 7 cm of the soil profile (du Croix Sissons et al. 2000) the increased moisture levels in this area could dramatically affect the weed population.

Variation in moisture levels between tillage types also varies over time. Soil moisture is typically lost from the root zone by surface runoff, evaporation, transpiration and percolation to depths beyond the normal root zone (Blevins et al. 1971). In the early part of the season when the soil is not covered the greatest water loss occurs from evaporation. As the plant canopy develops and shades the soil, transpiration becomes the most important route of water loss (Blevins et al. 1971). Therefore, tillage impacts on crop growth and development will also affect soil water content indirectly.

**Timing of Tillage and Its Impact on Weed Populations.** The timing of tillage affects both the timing of plant kill and the timing of vertical seed movement in the seed bank. Early spring cultivation may kill early emerging weeds but also bring seeds to the surface that may germinate prior to the establishment of the crop canopy. Late cultivation just prior to seeding may allow some early emerging species to grow large enough to limit the effectiveness of cultivation. Plowing directly following plant harvest may restrict seed shedding by killing early fall germinating seeds (Bostrom 1999). However, early plowing may not kill weed species that germinate late in the fall forming plant rosettes. For example, perennial sow-thistle is better controlled by late plowing than early plowing which allows the seeds to germinate and form a rosette (Bostrom and Fogelfors 1999).

The timing of seed movement affects weed populations. Volunteer canola seed may be induced into secondary dormancy if buried thus forming a seedbank (Lopez-Granados and Lutman 1998). For this species, fall tillage should be avoided or delayed as long as possible to prevent the formation of a weed seedbank. For other weed species which germinate on or near the surface, seed burial may prevent germination and kill the seed. Foxtail barley (*Hordeum jubatum* L.) germinates best within the top two cm of the soil and seed viability may rapidly be reduced when buried below 7 cm (Best et al. 1978). Therefore, a single cultivation will bury weed seeds with a short viability causing seed mortality if further deep cultivation does not occur bringing them to the surface (Cousens and Moss 1990). Cultivation and the consequent seed burial of seeds that may last for extended periods in the seed bank may induce secondary dormancy, reduce seed

predation and seed death allowing a greater number of seeds to germinate over a longer period of time.

### **Crop Rotation and Weed Populations**

**Crop Selection.** Crop type may be one of the main factors determining the relative occurrence of weed species within a field or farm (Andreasen et al. 1991). Andersson and Milberg (1998) found that after site, crop species was the second most important variable determining weed flora. Diverse crop rotations typically include grains, smother crops, cultivated crops and sod crops which all function in different ways to help in the control of weed growth and emergence (Liebman and Dyck 1993). As well, different crops may dictate herbicide selection with different spectra and modes of action which impact the weed community (Légère and Samson 1999). The effectiveness of crop rotations is highly dependant on the crops selected and their order within the rotation (Doucet et al. 1999).

Row crops may be useful in weed management systems because they permit cultivation throughout the early part of the season killing emerging weeds (Liebman and Dyck 1993). Vangessel et al. (1998) found that in-row cultivation was effective for controlling weed populations but at least two weeding operations per season were needed in order to equal the effectiveness of chemical weed control. Cultivating the weeds prior to significant root growth was also important to obtain adequate control. Row crops allow a combination of chemical and mechanical control helping in the control of weed populations throughout the growing season as well as helping to deplete the weed seed bank for the following crops. This is accomplished both by limiting weed seed production and by stimulating the germination of seeds and then killing the resulting weed seedlings which emerge between the crop rows.

Incorporating forages into a cropping system may play an important role in integrated weed management systems. However, the effectiveness of a sod crop is dependant on the length of its existence, species composition and management (Liebman and Dyck 1993). Schoofs and Entz (2000) reported that forage systems were at least as effective as the sprayed wheat control at suppressing wild oat. Conversely, Stevenson et

al. (1998) found greater weed populations in barley-forage rotations than barley monocultures. The increase in weed species richness and diversity was attributed to reduced frequency of tillage and herbicide application, improved soil resource availability and forage management especially in terms of their termination (Stevenson et al. 1997). Despite the increased competition, barley rotated with forages had a dry weight 29% greater than the monoculture, illustrating the benefits of rotation on crop yields beyond crop-weed interactions. The ideal forage system for weed management would be a combination of species that combine the early season vigor of biennials, the strong mid season competitive ability of a C<sub>4</sub> crop and the continuous competition of a long season crop (Schoofs and Entz 2000).

**Monoculture and Crop Rotation.** Weed population densities and weed biomass may be reduced using crop rotation. Schreiber (1992) found that crop rotation significantly reduced giant foxtail densities in all tillage systems. Liebman et al. (1996) reported that weed biomass was lower in a potato/oats rotation than a potato/clover rotation. Kegode et al. (1999) reported that an increase in crop diversity while simultaneously reducing tillage resulted in fewer grass and broad-leaved weeds seeds being produced. Other papers have reported that crop rotation had very little influence on seedbank size, distribution or major species abundance (Barberi and Cascio 2001). Doucet et al. (1999) found that crop rotation accounted for only 5.5% of the variation in total weed density. Crop rotation may even increase weed populations and the weed seed bank if one crop within the rotation does not establish adequately (Singer et al. 2000). In fact, crop rotation may deleteriously affect soil properties if one aspect of the rotation is not managed properly (Lal et al. 1994). Liebman and Dyck (1993) reported that among crop rotation studies of the literature surveyed weed densities in fields with crop rotation had lower weed densities in 21 studies, higher in 1 study and equivalent in 5 studies when compared to monocultures.

Crop rotation may alter weed communities in several ways. Crop monocultures are thought to simplify weed communities resulting in a weed flora dominated by few species (Liebman and Dyck 1993). Continuous cropping results in higher weed densities of species that thrive in conditions similar to the growing conditions of the crop (Hume



1982). Derksen et al. (1994) reported that continuous cropping tended to result in greater total weed density as well as weed populations more similar in composition than crop-fallow rotations although the populations of some species seemed indifferent to cropping sequence. In monocultures, weed flora is closely related to crop type (Streibig 1979) with weed species with requirements near to those of the crop species being favored (Thomas and Dale 1991). Crop rotations prevent the simplification and domination of the weed community by utilizing diversity in planting dates, harvest date, competitive ability of crops, fertility requirements and other management variables (Liebman and Dyck 1993). This array of conditions favors evenness among several species of weeds instead of domination of one specific weed species (Légère and Samson 1999). Diverse crop rotations typically include grains, smother crops, cultivated crops and sod crops, which all function in different ways to help control weed growth and emergence (Liebman and Dyck 1993). Ominski et al. (1999) reported lower populations of some weed species when fields seeded to cereals had been planted to alfalfa (*Medicago sativa*) in the previous season. As well, different crops may dictate the herbicide selection with different spectra and modes of action which may impact the weed community (Légère and Samson 1999). The variation between weed communities seen in different crop rotations can be overcome or partially hidden by fertilizer applications or climate variation making it difficult to detect differences in the weed community. Hume (1982) reported that the addition of fertilizer reduced the variation between continuously cropped and short term rotations.

The length of the rotation may also determine its effectiveness in limiting weed populations. Daugovish et al. (1999) found 8 plants  $m^{-2}$  and 0.1 plants  $m^{-2}$  for two and three year rotations, respectively. They found that weed densities were reduced 100-fold after two cycles of a three year rotation compared with a 2-year rotation. Crop rotation in combination with reduced tillage is an effective way of limiting grass and broad-leaved weed seed production (Kegode et al. 1999).

**Timing of Seeding.** The microsite conditions directly surrounding the seed will depend on the time of year during which weed seedlings emerge. Crop rotation enables a producer to include crops which are seeded and emerge at different times and in different

seasons. Schreiber (1992) reported a reduced giant foxtail stand in a soybean-wheat-corn rotation when compared to monoculture. Chancellor (1985) found that spring germinating weeds were found more frequently in spring sown crops while fall germinating weeds occurred more often in fall germinating crops.

Delaying seeding and cultivating before planting destroys early emerging weeds (Liebman and Dyck 1993). Spandl et al. (1998) reported that earlier planting of wheat generally resulted in increased green foxtail emergence. Delayed planting increased the rate of emergence but decreased the density of weed emergence. The reduced and more simultaneous green foxtail emergence may simplify control measures. In contrast, Melander (1995) found that drilling date had an inconsistent effect on weed plant populations in the spring although emergence tended to be delayed at the later drilling date compared to the early drilling date. Seeding a crop early or late alters the temperature and moisture levels to which weed seeds are exposed. Late seeding allows cultivation to eliminate all of the early emerging weeds while early seeding may allow the crop to germinate and begin to grow before weed emergence. Using relative times of emergence of crop and weeds as controlled by temperature may allow producers to better determine the best seeding date that allows the crop to compete adequately with the weeds (Weaver et al. 1988). Properly planned crop rotations will include crops with different planting dates to prevent the domination of any particular weed species.

**Cover Crops.** Many different types of cover crops may be used in a rotation to help control weed populations. The type of cover crop used will depend on the growing conditions, crops preceding and following the cover crop, the presence or absence of animals on the farm, markets for hay or silage in the local area. Problem weeds should also be considered before selecting the cover crop to choose the crop most likely to have the strongest detrimental affect on weed emergence and growth for the problem species. When the appropriate cover crop species is selected and properly managed it may significantly reduce rising weed populations. Teasdale (1993) found that a live cover crop of hairy vetch reduced weed populations by 87%. Moyer et al. (2000) found that under favourable weather conditions fall rye was as effective at controlling weed populations as a combination of post-harvest herbicides and early spring tillage. They

also found that cover crops may reduce the emergence of some weeds while increasing the emergence of others. Zasada et al. (1997) found similar patterns with cover crops of rye adequately controlling low densities of lambsquarters but not adequately controlling high densities of lambsquarters or pigweed at any density.

Cover crops can affect weed populations by altering soil temperature conditions. Calkins and Swanson (1998) found that cover crops used in nursery field management increased winter soil temperatures and decreased summer soil temperatures. Teasdale and Daughtry (1993) also found that live and desiccated hairy vetch cover crops reduced the daily maximum temperature as well as the daily temperature amplitude when compared to bare soil.

Cover crops may also affect soil moisture conditions. While live cover crops use water they also reduce soil evaporation and increase soil water infiltration (Calkins and Swanson 1998). Under very hot and dry conditions soils with cover crops may have lower soil water contents than uncovered soils. Under many environmental conditions live cover crops will not reduce soil moisture to levels seen with bare ground (Teasdale and Daughtry 1993).

Weed seed germination may also be reduced by cover crops due to light interception by the cover crop or allelopathic affects. Since light levels of less than 0.1% transmittance are required to activate germination in species requiring light for germination, it is unlikely that cover crops reduce light levels below what is required for germination (Teasdale and Daughtry 1993). Allelopathic affects, however, can have a very strong impact on weed populations. Creamer et al. (1996) reported that Crimson Clover (*Trifolium incarnatum*) inhibited the emergence of Eastern nightshade (*Solanum ptycanthum* Dunal.) beyond what could be attributed to physical suppression alone.

**Effects of Fallowing on Weed Populations.** Weed communities in monocultures tend to be more homogeneous and have greater densities than weed communities in crop - fallow situations (Derksen et al. 1994). Fallow results in an increase in soil water content, mineralized nitrogen levels, and it provides an opportunity to control weeds. Conversely, if not properly managed fallow may also damage soil structure, lead to wind

and water erosion and increase the number of weed seeds in the seed bank. Weeds may be controlled during the fallow year with cultivation, herbicides or a combination of both.

Soil residues left on the surface following the crop help to prevent soil erosion, reduce soil water evaporation and affect weed seedbank dynamics (Blackshaw and Lindwall 1995a). The amount of residue left on the surface during the fallow year is partially dependant on the crop grown. Blackshaw and Lindwall (1995a) found that residue persistence was highest for flax, less for wheat, barley, rye, canola, and lowest for lentil. They concluded that crops with high rates of residue degradation such as lentil should not be followed by a fallow year.

Emerging weeds may be controlled during the fallow year with tillage. Unfortunately, tillage may also impact residue levels. Fenster and Wicks (1982) found that tillage reduced wheat residues by 42 to 78% as compared to no-till plots. Molberg and Hay (1962) found that chemical summer fallow maintained 91% of the original crop residue compared to 24% for cultivated summer fallow. Tillage is appropriate when residue levels are high enough to leave adequate cover on the surface preventing erosion following tillage (Blackshaw and Lindwall 1995a). The effectiveness of tillage depends on the timing, type of tillage and type of weeds present. Blackshaw and Lindwall (1995b) reported that cultivation during the fallow year controlled most spring emerging weeds but did not control some overwintering weeds such as flixweed (*Descurainia sophia* (L.) Webb) or downy brome. The best control was achieved when a combination of tillage and herbicides were used to control weeds.

Herbicide applications alone to control weeds during fallow periods may not produce complete weed control, herbicide persistence in the soil may affect crop emergence in the following season and plant herbicide resistance may impact the effectiveness of herbicides (Molberg and Hay 1968). Despite the negative effects, chemical fallow also leaves more residues intact affecting moisture retention and seedbank dynamics. Moisture retention is an important aspect of the fallow year in drier regions of the prairies. Blackshaw and Lindwall (1995b) reported soil water accumulation with a herbicide -tillage combination for weed control was similar to or greater than water conservation under herbicide only or tillage only control. Higher moisture levels are maintained when crop residues are left intact or at least left intact

during the winter (Pannkuk et al. 1997). Fenster and Wicks (1982) reported that plots treated with herbicides stored 24 and 21% more soil water at two locations than tillage treatments. In some cases, in fallow fields where weeds were not controlled, the weeds did not affect water storage capability (Pannkuk et al. 1997).

It would appear that the greatest weed control is obtained with a combination of herbicide and tillage. No-till farmers that rely solely on chemical fallow may have trouble controlling some types of weeds. Kettler et al. (2000) reported that one tillage operation with a moldboard plow during the fallow section of a rotation decreased downy brome populations in two of the three years tested. Smith et al. (1996) analysed a long term and a short term fallow-crop system in terms of economics. The short term experiment showed no differences between the conventional and reduced tillage fallow systems. The long term experiment showed a build-up of difficult to control weeds in the herbicide only treatment, lower average crop yield, higher herbicide costs resulting in lower net returns in the herbicide only system and higher net returns in the tillage only system. Therefore, an occasional tillage with a moldboard plow in no-tillage systems during the fallow part of the rotation may help control some weed species while maintaining many of the soil quality benefits of no-till.

The frequency of fallow in a rotation may affect the economic viability of a rotation. Zentner and Campbell (1988) found that the viability of including fallow in a rotation depends on the price being offered for the crop grown. At low wheat prices, a fallow-wheat rotation was the most profitable due to low production costs. At high wheat prices, a continuous wheat monoculture was most economically viable despite high production costs. Removing fallow altogether from a rotation may also be a viable alternative. Replacing fallow with a crop may increase the overall crop production within a rotation while increasing the amount of straw returned to the soil. It may also reduce the potential for leaching nitrate and improve the aggregate stability of a soil (Arshad et al. 1998).

## Field Scale Variation

Within individual fields weed populations may be aggregated. Population aggregation is caused by factors such as variation in weed dispersal and variations in soil physical properties, soil cover, drainage and canopy development within a field. Upon invasion, weed spatial patterns are due to dispersal processes and mechanisms (Dessaint et al. 1991). Following dispersal, seeds are generally distributed around the mother plant with the distance of dispersal depending on the seed size and shape, parent size and dispersal mechanisms of the seed. The level of aggregation depends on weed density (Mulugeta and Stoltenberg 1997). At low weed densities the level of aggregation tends to be greater. Peart (1989a) found that the density of the seed rain of different grasses in a grassland was patchy at all scales from cm to km, but was not significantly correlated with recruited seedling spatial patterns. Aggregation may be further modified by agronomic practices such as tillage and harvest techniques (Dessaint et al. 1991). Gerhards et al. (1997) found that seedling distribution was significantly aggregated and that weed patches were well conserved between years. Using quadrats of 1.8 by 0.6 m, Zhang and Hamill (1998) found that there was not always a close spatial relationship between the parent plants and weed seedling emergence. The emergence of the weeds was impacted by dispersal mechanisms and biotic and abiotic soil characteristics. In agriculture, the timing of weed seed shed, before or after combine harvesting, dramatically affects the extent of aggregation as well as the persistence of patches (Colbach et al. 2000).

Site properties and weed populations are known to vary within a given location and within a given time (Dieleman et al. 2000a). The aggregation of weed populations may be caused by soil abiotic or biotic characteristics. Variation in soil moisture caused by ground cover, soil type or compaction may impact weed germination (Bhatnagar et al. 1983; Jurik and Zhang 1999). A variety of factors which impact emergence may vary spatially and temporally with a field. Dieleman et al. (2000a) found that total nitrogen, phosphorus, percent organic carbon and soil texture varied spatially within a given field. Levels of soil compaction may reduce pore space and increase the rigidity of the soil

reducing surface microsites and creating a mechanical barrier to weed emergence (Sheldon 1974). Openings in the crop canopy may also impact weed emergence. Peart (1989b) found that the formation of canopy gaps in a bunchgrass sward strongly affected colonization. In contrast, Feldman et al. (1998) found that tillage system had a greater impact on weed emergence than the timing or the size of the opening in the crop canopy.

The impact of microtopography on seedling emergence is probably studied more than any other variable. Harper et al. (1965) concluded that at the scale of individual seeds the soil surface is highly heterogeneous. This variation in microtopography should provide a variety of conditions that may affect weed emergence. During moist warm periods germination may occur irregardless of the microtopography but during dry or cold periods microtopography may provide a safe zone for germination (Evans and Young 1972). Variations in emergence due to microtopography may be due to variations in soil moisture and temperature directly surrounding the seed (Harper et al. 1965). Evans and Young (1972) found that pitting the soil surface maintained soil temperatures and moisture within ranges required for seedling establishment of rangeland weeds.

Despite the evident spatial variation of soil conditions and weed populations in individual fields a mechanistic understanding of the causes of this variation is not available (Dieleman et al. 2000b). Kephart and Paladino (1997) concluded that abiotic factors like soil moisture, air temperature and soil temperature varied more temporally within a habitat than between habitats while variables such as light, soil depth and the surrounding vegetation significantly affected emergence. Conversely, Bratton (1976) found that microtopography, soil moisture gradients, canopy structure and seasonal change all influenced the distribution of species within an understory. Therefore, it is evident that spatial variation within small areas exists and the conditions directly surrounding the seed may vary greatly and this will affect weed emergence. The mechanisms and the extent of the interactions between microsite characteristics and seed germination and emergence processes is still poorly understood.

## Seed and Microsite Limitation of Weed Populations

All plant populations are to some extent seed and microsite limited (Eriksson and Ehrlen 1992). The plant population in a given area is determined by the number of seeds present in the soil and a combination of all soil biotic and abiotic conditions directly surrounding the seed. A plant species may not be present within a specific region because: (1) the environmental conditions are not normally within the range required for a sufficient proportion of the seeds to germinate forming a persistent population, (2) the environmental conditions are not within the required range for that species to grow, develop and shed new seeds to guarantee the continuation of its population or (3) seeds of that species have not been introduced to that region. On the extremes of a specific species habitat, the species becomes increasingly microsite limited until the point is reached where the species can no longer exist. Within the region where the plant normally successfully exists, the presence of seeds within the soil is necessary for recruitment to occur. However, the presence of seeds does not guarantee seedling recruitment. In this situation, a plant population must be partially microsite limited.

Recruitment in a plant community is limited by seed number, microsite conditions, plant to plant competition or seed predation (Crawley 1990). In low disturbance ecosystems with a high plant density plants appear to be predominately limited by microsite conditions or plant competition. Seed limitation will be more likely to occur in situations where there is a high proportion of bare ground (Crawley 1990). The removal of plant material may open appropriate microsites permitting further recruitment with high density stands. Burke and Grime (1996) found that the level of bare ground was consistently the most important factor determining the probability of successful recruitment in grassland systems. Bratton (1976) also found that the structure of a forest canopy including the size and position of openings, light passage through the canopy and distance from other trees affected understory recruitment. Therefore, it appears that recruitment in low disturbance ecosystems is largely dependant on disturbance to alter microsite conditions allowing seeds to establish at the soil surface. Recruitment of new individuals occurs in "empty sites" which suggests that lower



recruitment levels should be observed in species rich communities because there are fewer empty sites (Tilman 1997). In fact, germination in an appropriate microsite may be more important than the effects of competition between seedlings. Fowler (1988) found that seedlings within 2 cm of each other had higher rates of survival and growth than seedlings further apart. He concluded that the germination within the appropriate microsite had a stronger impact on seedling survival than competition amongst the seedlings.

The importance of different microsite variables depends on the ecosystem and the plant species involved. In some situations recruitment occurs in bare sites because of changes in soil moisture (Aguilera and Lauenroth 1995). In short term studies care should be taken before concluding which environmental parameters have the greatest impact on seedling recruitment. Kephart and Paladino (1997) found that variables such as soil moisture and temperature varied more seasonally within a habitat than between habitats. The same authors found that differences in light, soil depth and vegetation height were the variables most closely related to recruitment and growth of grasses in a grassland. Other authors have found that microtopography and seasonal change were the most important variables determining niche differentiation and thus species diversity (Bratton 1976).

Variation in weather patterns between regions or between years within regions plays a decisive role in determining the recruitment of new individuals. Mack and Pyke (1983) reported that year to year variation in environment along a 200 km transect overrode any intrinsic differences between habitat types along the transect in terms of population dynamics. Similar trends are noted in agricultural ecosystems where plant community structure is determined largely by climatic variables (Thomas and Dale 1991). It has been firmly established that accumulated temperature and moisture do impact the number and type of plants emerging in all ecosystems (Fernandez-Quintilla et al. 1990; Roman et al. 1999; Weaver et al. 1988). These two variables play important roles in determining the microsite to which the seed is exposed. Consequently, there has been a surge in the number of studies trying to estimate emerging weed populations based on temperature and moisture variables (Grundy and Mead 2000).

In many agricultural fields the majority of the biomass is removed on an annual basis and the soil is cultivated mixing plant seeds throughout the soil profile. Under these conditions one would not expect plant competition to play a major role in determining the species composition. As well, many weed species are short lived with recruitment determined almost entirely by germination and dormancy biology (Crawley 1990). Yet in agricultural fields where weed seed return often exceeds recruitment, there is little relationship between weed population densities and seed return from the previous year (Crawley 1990), and weed populations generally occur in patches (Peart 1990). These three points would suggest that variables other than seed number influence the recruitment of weed species within agricultural fields.

It is apparent that the initial patchiness of a weed populations is due to dispersal processes (Dessaint et al. 1991). Since seeds only move a small distance from the mother plant one would anticipate a greater increase in density around the mother plant over time than an increase in weed density further from the mother plant (Nadeau and King 1991). Agronomic practices such as tillage and harvest modify this initial spatial pattern depending on the time of seed shed. Colbach et al. (2000) determined that the strength and the persistence of a weed patch was dependant on whether the seeds were dispersed before or after combining. In many cases weed patches are relatively stable (Gerhards et al. 1997). Weed patches in fields may be caused by historical events allowing the initiation of the patch and continued seed rain maintaining its stability. Therefore, we could hypothesize that weed population spread is limited by the ability of the plants to disperse there seeds to new areas. Therefore, we can hypothesize that in agricultural fields weed populations are seed limited.

The above mentioned hypothesis is somewhat unsatisfying because we know that there is only a very poor relationship between seed rain and seedling recruitment the following year (Crawley 1990). As mentioned previously in this review several authors have tried to relate environmental or agronomic factors to weed populations. Other authors have suggested that weed patches occur and remain relatively stable within a field because microsite conditions favour their recruitment, growth and development within the area where the patch occurs. Dieleman et al. (2000a) suggest that site properties such as soil type, moisture and topography all affect weed species abundance.

Therefore, since both weed populations and site properties vary across agricultural fields this may lead to population aggregation (Dieleman et al. (2000b). Zhang and Hamill (1998) found that there was not always a close spatial relationship between parent plants and their offspring with velvet leaf. In fact, they suggest that biotic and abiotic environmental conditions may affect the spatial relationships. Under these conditions the weed populations appear to be more affected by the microsite than the number of seeds in the soil.

We can safely conclude that the timing of dispersal and the number of seeds dispersed affects the recruitment of weed populations at least to some extent the following year. We can also conclude that soil biotic and abiotic factors do impact the germination and emergence of weed populations. However, the relationship or the relative importance of seed and microsite limitation in plant populations is still poorly understood in agricultural ecosystems.

### **Research Rationale and Objectives**

Recruitment biology has been discussed since biblical times. Jesus explained in the parable of the sower how recruitment is determined by microsite (stony ground representing unfavourable conditions), competition (the thorns), predation (the fowls) and the presence of the seeds sown by the sower. Approximately two thousand years later we are still uncertain if plant recruitment is predominately seed or microsite limited (Crawley 1990). Many experiments have been conducted in low disturbance ecosystems to determine what variables affect plant recruitment and invasion. Surprisingly, within agricultural ecosystems little work has been done to determine what affects the recruitment and invasion of weed species. Crawley (1990) stated:

“The reluctance to carry out simple manipulative field experiments on recruitment has meant that the relative importance of seed, microsities, competition and herbivory remains unknown even in systems that have been studied over many years. The practice of sowing extra seeds and following their fate and the fate of any seedlings they may produce should be a routine element of any field study in plant dynamics. Seeds should be sown into a range of microhabitats, apparently

unsuitable as well as apparently suitable, so that we increase our understanding of why plants do not occur in certain places.”

With this statement in mind we set out with three main objectives. The first objective was to determine to what extent and how depth of seed placement within the soil profile affects weed seed germination and emergence. Only when we can identify and at least partially understand the variables that effect the germination and establishment of a weed seedling within agricultural fields will we be able to model population dynamics accurately. The second objective was to group weed species into functional groups based on germination and emergence characteristics. More specifically, attempt to group weed species as recruitment generalist (plants able to germinate and become established at the soil surface under a broad array of conditions) or specialist (plants only able to germinate and become established at the soil surface under a narrow array of conditions) or somewhere in between. Our third and final objective was to design a simple manipulative experiment where we sowed various densities of seeds within agricultural fields and adjusted the microsite and allowed the emerging seedlings to compete with the crop or removed the crop to eliminate competition. The purpose of this objective was to determine the relative importance of seed and microsite limitation for annual weed species.

**MANUSCRIPT #1****THE EFFECTS OF DEPTH AND FLUCTUATING SOIL MOISTURE ON THE EMERGENCE OF EIGHT ANNUAL AND SIX PERENNIAL PLANT SPECIES****ABSTRACT**

Weed seedling emergence is partially dependant on biotic and abiotic conditions directly surrounding the seed. When environmental conditions are appropriate, seed germination and emergence occurs. In a greenhouse we studied the impact of seeding depth (surface, 1-2, 3-4, 6-7 cm) and fluctuating soil moisture regimes (field capacity (FC) - 1/3 FC - FC; FC - 1/6FC - FC) on percent weed emergence. At field capacity, wild mustard and field pennycress had the greatest percent emergence when seeds were placed on or near the soil surface whereas percent emergence of barnyardgrass and round leaved mallow was unaffected by seeding depth. All perennials tested had the greatest percent emergence at field capacity when seeds were placed near or on the soil surface except for common milkweed which only emerged below the soil surface. When soil moisture levels fluctuated, surface seeds of barnyardgrass, catchweed bedstraw, green foxtail, wheat and wild oat resulted in less emergence than seeds below the soil surface, field pennycress had increased emergence when the seeds were placed on the surface and round leaved mallow and wild mustard emergence was unaffected by seeding depth. The emergence of curly dock, dandelion and perennial sowthistle was unaffected by seeding depth whereas foxtail barley and quackgrass emergence was reduced when seeds were placed on the surface and soil moisture fluctuated.

## INTRODUCTION

Weed seedling recruitment is the successful germination of seeds and subsequent seedling establishment. It is determined by the number of seeds in the soil profile and by environmental conditions directly surrounding the seed. The combination of all biotic and abiotic variables surrounding the seed is referred to as the microsite (Harper 1977). Seedling germination occurs when conditions directly surrounding non dormant seeds are within the range matching the germination requirements for that particular species.

The position of seed within the soil profile affects weed seedling recruitment. The microsite requirements for some species are extremely specific. Curly dock for example will only emerge when seeds are at or near the soil surface. Even burial at 1 cm significantly reduces emergence (Weaver and Cavers 1979). For other species, such as common milkweed there is negligible emergence when seeds are on the surface or below 7 cm (Yenish et al. 1996). Wild oat can emerge from depths ranging from near the surface to 20 cm (Sharma and Vandeborn 1978). The range of depths from which weeds emerge is dependant on the species, as well as on soil type, tillage practice, and a variety of soil physical properties (Buhler and Mester 1991; Mohler and Galford 1997; Yenish et al. 1996). Despite the wide variation in depths from which weeds can emerge, in common arable fields most weeds emerge from seed located within the top 1-4 cm (Cousens and Moss 1990; du Croix Sissons et al. 2000; Mohler 1996).

Soil moisture also affects weed seedling recruitment. Although wild oat tends to emerge in cool temperatures and moist soils (Sharma and Vandeborn 1978), Fernandez-Quinantilla et al. (1990) found that osmotic potentials below -1.2 MPa reduced germination of wild oat by only 33%. Green foxtail emergence was reported to decline at -0.65 MPa, whereas that of round leaved mallow declined at -0.28 MPa, with less than 20% emergence occurring at osmotic potentials of -1.03 to -1.53 Mpa (Blackshaw et al. 1981; Blackshaw 1990). The impact of soil moisture on germination and emergence is highly variable among weed species while moisture conditions within a field may vary considerably both horizontally and vertically. Although climatic variables such as rainfall and temperature play key roles in determining soil moisture, these vary seasonally and spatially. Within agricultural fields, soil moisture may be altered by many

variables including litter cover and tillage (Mahli and O'Sullivan 1990; Teasdale and Mohler 1993).

The timing and type of tillage changes the position of weed seeds within the soil profile and the microsite conditions to which seeds are exposed (Spandl et al. 1998; Yenish et al. 1996). Different tillage regimes may affect the fluctuation in soil temperature and moisture within the soil. Consequently, tillage affects the timing, type and number of weeds emerging within arable fields (Cousens and Moss 1990; Cussans et al. 1996). For many weed species, little information exists on how seed depth affects weed emergence. A better understanding of how seed depth within the soil profile and fluctuating moisture levels affect the emergence of common weed species would increase our ability to plan management strategies for these species and predict their response to significant changes in management practice.

The objectives of this study were to test the effect of depth and fluctuating moisture levels on the percent seedling emergence of a variety of annual and perennial weed species found on Northern Great Plains.

## MATERIALS AND METHODS

The emergence of six perennial and eight annual weed species representing a range of weed species found across the Northern Great Plains was evaluated in a soil depth experiment and a soil depth by soil moisture experiment. All seeds were stored in sealed containers at 4 °C or less from harvest until the beginning of the experiments. Two seed collections were used, one was collected in Southern Manitoba, Canada and one was collected in Alberta, Canada (Table 1-1). The seeds collected from various locations in Manitoba were combined as they were collected to create a single seed collection for each species. In two experiments, the number of plants emerging were counted and recorded three times per week until emergence ceased. A seedling was counted as emerged once any part of the radicle emerged from the seed for surface placed seeds or once any part of the shoot emerged from the soil when seeds were placed below the surface. There was no intention to explore the impact of seed source on emergence

**Table 1-1.** Harvest location in Manitoba or Alberta, harvest year and percentage of maximum emergence (maximum number of seeds out of fifteen emerging from the soil during these experiments) for seeds used in this study.

Species	Alberta Seed Lots			Manitoba Seed Lots		
	Harvest Location	Harvest Year	Max. Emerg	Harvest Location	Harvest Year	Max. Emerg.
barnyardgrass	- <sup>b</sup>	-	-	Winnipeg <sup>d</sup>	2000	13
catchweed bedstraw	- <sup>b</sup>	-	-	various <sup>a</sup>	2000	15
curly dock	Lethbridge	2001	13	various	1998	7
dandelion	- <sup>b</sup>	-	-	Carman <sup>d</sup>	1999	14
field pennycress	Leth/Lac	97/01	9	various	2000	10
foxtail barley	Lacombe	1999	9	various	1999	12
green foxtail	Leth/Lac <sup>c</sup>	97/01	12	Portage <sup>d</sup>	1997	15
milkweed	- <sup>b</sup>	-	-	Carman <sup>d</sup>	1998	12
perennial sowthistle	Lethbridge	2001	9	various	2000	9
quackgrass	- <sup>b</sup>	-	-	various	1986	9
round leaved mallow	Leth/Lac	99/01	2	various	1987	7
wheat	Leth/Lac	00/01	15	Carman <sup>d</sup>	1999	15
wild mustard	Leth/Lac	98/01	15	various	1986	12
wild oat	Leth/Lac	00/01	14	Carman <sup>d</sup>	1990	15

<sup>a</sup>Seeds were collected from multiples sites across Manitoba.

<sup>b</sup>Manitoba seed was used.

<sup>c</sup>Seeds collected from both Lethbridge and Lacombe

<sup>d</sup>Seeds were collected from discrete natural patches across the Carman, Winnipeg or Portage La Prairie regions.

emergence was used as a relative measure in this study. For each species in each experiment, it was calculated by dividing the number of emerged seedlings in each pot by the maximum number of seedlings that emerged in a pot in the same seed collection (Manitoba response to given treatments. We included seeds from more than one source



to obtain a relatively general emergence response for the species studied. Percent of maximum (seeds or Alberta seeds) and run. Therefore, the maximum emergence differed between runs and seed lots.

This relative measure was used to eliminate variation between species due to possible differences in seed dormancy levels between seed collections.

### **Soil Depth Experiment**

This experiment was run as a randomized block design replicated twice and repeated 3 times (3 runs) for a total of 6 replications with 4 seeding depths and 14 seeds placed at each depth. The first two runs were done with seeds from Manitoba and the last run with one replication of seeds from Lethbridge, Alberta and one replication with seeds from Lacombe, Alberta. If seeds of a particular species could not be obtained from Alberta, seeds from the Manitoba seed collection were used for the third run (Table 1-1). The experiment was seeded in 15.5 cm diameter by 14 cm deep pots in a potting mixture consisting of 1/3 each of sand, sterilized topsoil, and peat moss. Seeds were placed on the surface or at 1-2 cm, 3-4 cm, or 6-7 cm below the surface in each pot. All pots were kept in a greenhouse during the summer months where temperature fluctuated throughout the day. Minimum and maximum temperatures averaged 14 and 32 °C, respectively. Supplemental lighting with 450 W high pressure sodium lamps were on daily for a 14 hour photoperiod. The pots were watered daily to keep the soil moist at all times.

Data for each of the 14 weed species were analyzed separately using the repeated measures statement in SAS and a general linear model (SAS 1990). Least squares means were used to determine the effect of seeding depth and time on weed emergence. The experiment ended 19 days after planting when seedling emergence had stopped. Final emergence as well as emergence half way through the experiment are reported. Run and seed lot were not significantly different so each run and seed lot were treated as a replicate in the final analysis. All data were normally distributed with constant variance.

### Soil Depth by Moisture Experiment

This experiment was run as a factorial design with 3 seeding depths and 2 moisture levels. It was replicated twice and repeated 3 times (3 runs) for a total of 6 replications. The first two runs were done with seeds from the Manitoba seed collection and the last run with one replicate of each of Lethbridge, Alberta and Lacombe, Alberta seed collections. If seeds of a particular species could not be obtained from Alberta, seeds from the Manitoba seed collection were used for the third run (Table 1-1). Fifteen seeds were placed in each pot for a specific depth by soil moisture treatment. The experiment was seeded in 15.5 cm diameter by 14 cm deep pots in a potting mixture consisting of 1/3 each of sand, sterilized topsoil, and peat moss. Seeds were placed on the surface or 1-2 cm or 3-4 cm below the surface. For the first soil moisture treatment, soil moisture was allowed to fluctuate between field capacity and 1/3 field capacity. Soil moisture was allowed to fluctuate between field capacity and 1/6 field capacity for the second soil moisture treatment.

To measure field capacity eight pots containing the same amount of the same soil mixture used in the experiment were placed in an oven and dried for 48 hours at 80 °C. These pots were used to determine average dry weight of soil in pots in the experiment. All pots in the experiment were saturated with water directly following seeding. Two randomly chosen pots from each treatment combination were weighed one day after saturation. The amount of water within the soil 24 hours after saturation was considered the field capacity of the soil. The average dry weight of the soil was subtracted from the average wet weight of the soil to determine water content. The same pots were weighed daily and the average weight was determined for both moisture treatments. When the pots reached 1/3 or 1/6 of field capacity they were returned to field capacity by slow watering into the top of the pots until water exited the bottom of the pots. All pots were kept in a greenhouse where minimum and maximum temperatures averaged 14 and 32 °C, respectively. Supplemental lighting with 450 W high pressure sodium lamps were on for a 14 hour photoperiod throughout the experiment.

Data for each of the 14 weed species were analyzed separately using the repeated statement and a general linear model in SAS (SAS 1990). Least squares means were

used to determine the effect of seeding depth, soil moisture and their interactions on weed emergence. Run and seed lots did not differ significantly so runs and seed lots were simply treated as replications for final analysis. All data was normally distributed with constant variance.

## RESULTS AND DISCUSSION

The interaction between seeding depth and soil moisture fluctuation was not significant for any of the species included in the soil depth by moisture experiment. Only main effects are presented for this experiment. The interaction may not have been present because the design of the experiment confounded the effects of depth of seeding with the effects of soil drying from the surface downward. Deeply placed seeds would not have experienced as great a moisture fluctuation as seeds placed on the surface. Although this limits the explanatory power of our experiment it also mimics conditions which would occur in field situations where soils dry from the surface downward.

### Annual Weed Species

Seeding depths between 0 and 7 cm did not affect round leaved mallow emergence at field capacity and seeding depths between 0 and 4 cm did not affect round leaved mallow emergence with fluctuating soil moisture (Tables 1-2 and 1-3). Blackshaw (1990) reported that the greatest round leaved mallow emergence occurring at depths of 0.5 to 2 cm with emergence declining significantly from 3 through 6 cm and no emergence occurring at 8 cm. Although fluctuating soil moisture did not significantly affect emergence of this species in our experiment, Makowski and Morrison (1989) found that major infestations of this weed generally occur in regions of Western Canada where precipitation levels are high.

Barnyardgrass emergence was also unaffected by seeding depth when moisture did not fluctuate although surface seeds or seeds at 6-7 cm emerged more slowly than seeds between 1 and 4 cm (Table 1-2). Surface seeds of barnyardgrass had significantly less emergence than seeds between 1 and 4 cm when moisture levels fluctuated (Table 1-

3). Since barnyardgrass seeds require exposure to light for germination to occur (Taylorson and Dinola 1989) moisture or another variable that interacts with moisture must hinder surface germination for this species.

Surface seeds of catchweed bedstraw, wild oat, spring wheat and green foxtail had significantly less emergence than seeds between 1 to 4 cm both when moisture levels were constant and when they fluctuated (Tables 1-2 and 1-3). For catchweed bedstraw, emergence from 6-7 cm was also significantly lower than emergence from 1-4 cm when moisture levels were constant. Other authors have reported that the majority of catchweed bedstraw seedlings emerge from depths of 0 to 5 cm (Rottele 1980) with little or no establishment of seedlings from seeds on the soil surface (Froud-Williams et al. 1984). Surface germination for this species may be inhibited because it germinates best in darkness with adequate moisture (Sjostedt 1959). Even exposure to very low light intensities inhibits germination of catchweed bedstraw (Malik and VandenBorn 1987). These specific conditional requirements for emergence may help to explain the prevalence of catchweed bedstraw in the northern Aspen Parkland and Boreal Transition ecoregions of Manitoba compared to other eco-regions in the same Province. Both areas have a reliable rainfall pattern in the spring and a high proportion of the land is cultivated ensuring seed burial into a moist soil (Van Acker et al. 2000).

Green foxtail and wild oat emergence was generally unaffected by seeding depth or by fluctuating soil moisture conditions if seeds were placed below the soil surface. This may help to explain the relative ubiquity of these two species in cereal and oilseed fields in Manitoba (Van Acker et al. 2000). Since green foxtail and wild oat germinate better when seeds are slightly buried one would expect lower levels of emergence in no-tillage fields where the weed seeds are not incorporated. It has often been reported, however, that higher populations of annual grass weeds such as green foxtail are found in reduced tillage fields (Buhler 1992; Froud-Williams et al. 1983) or that there is no consistent association between annual grass population levels and tillage practice (Derksen et al. 1993). This illustrates the complexity of the interactions among variables that impact weed populations.

**Table 1-2.** Percent of maximum emergence 10 and 19 days after planting (DAP) of eight annual weed species seeded at four depths with the soil maintained at field capacity.

Species	Planting depth, 10 DAP				Planting depth, 19 DAP			
	surface	1-2 cm	3-4 cm	6-7 cm	surface	1-2 cm	3-4 cm	6-7 cm
	-----%-----							
barnyardgrass	18 b	40ab	51 a	24 b	41 a	44 a	54 a	31 a
catchweed bedstraw	3 b	51 a	43 a	10 b	9 b	73 a	58 a	20 b
green foxtail	51 b	82 a	89 a	74 a	50 b	85 a	88 a	72 ab
round leaved mallow	14 a	17 a	14 a	7 a	19 a	31 a	33 a	19 a
field pennycress	53 a	8 b	12 b	10 b	70 a	10 b	12 b	12 b
wheat	71 b	92 a	72 b	78 ab	71 b	93 a	76 b	78 ab
wild mustard	42 b	72 a	18 c	7 c	54 a	72 a	19 b	7 b
wild oat	45 b <sup>a</sup>	88 a	90 a	81 a	66 b	92 a	90 a	83 ab

<sup>a</sup>Percent maximum emergence within the same species and same time frame after planting (10 or 19 DAP) with different letters are significantly different least squares means at  $P < 0.05$ .

Wild mustard and field pennycress were the only annual weeds for which optimal emergence levels occurred when seed was placed on or just below the surface. Hazebroek and Metzger (1990) reported that moisture was the main factor limiting emergence of surface-placed seeds of field pennycress. In our study, percent emergence of field pennycress was significantly higher for seeds placed on the surface than for seeds placed just below the surface both when the soil was kept at field capacity and when soil moisture levels fluctuated between field capacity and 1/3 or 1/6 field capacity (Tables 1-2 and 1-3).

At 19 DAP, wild mustard emergence was significantly higher for seeds placed on the surface or at 1-2 cm than for seeds placed at deeper depths. Surface emergence of wild mustard was slower at field capacity compared to when seeds were placed just below the surface but by 19 DAP there was no difference in percent emergence. Wild

mustard emergence was not affected by depth when soil moisture levels fluctuated (Table 1-3).

**Table 1-3.** Percent of maximum emergence of eight annual weed species seeded at three depths 19 days after planting (DAP) with the soil fluctuating between field capacity (FC) and 1/3 FC or FC and 1/6 FC.

Species	Planting depth		
	surface	1-2 cm	3-4 cm
	-----%-----		
barnyardgrass	18 b <sup>a</sup>	50 a	58 a
catchweed bedstraw	2 b	54 a	40 a
green foxtail	50 b	77 a	82 a
round leaved mallow	11 a	15 a	17 a
field pennycress	52 a	19 b	10 b
wheat	55 b	89 a	85 a
wild mustard	28 a	31 a	15 a
wild oat	25 b	87 a	79 a

<sup>a</sup>Percent of maximum emergence within the same species with different letters are significantly different least squares means at  $P < 0.05$ .

### Perennial Weed Species.

Curly dock, perennial sowthistle and dandelion all had significantly greater percent emergence in soils at field capacity when seeds were placed on or near the soil surface (Table 1-4). Emergence of curly dock seeds placed on or near the surface occurred relatively slowly but by 19 DAP the emergence of seeds was significantly higher than seeds placed at deeper depths. Weaver and Cavers (1979) found similar results with even a shallow burial (1 cm) significantly reducing emergence of curly dock.

Percent emergence of perennial sowthistle was especially sensitive to depth in soils maintained at field capacity with almost no emergence occurring when seeds were placed below the surface. Zollinger and Kells (1991) reported that perennial sowthistle requires high soil moisture levels for surface germination and this may help explain why this species predominately occurs in poorly drained soils or in soils with a high water holding capacity.

Percent of maximum emergence of curly dock, perennial sowthistle and dandelion was not significantly affected by seeding depth when moisture levels fluctuated between field capacity and 1/3 or 1/6 field capacity (Table 1-5). Comparisons of the two

**Table 1-4.** Percent maximum emergence of six perennial weed species seeded at four depths 10 and 19 days after planting (DAP) with the soil maintained at field capacity.

Species	Planting depth, 10 DAP				Planting depth, 19 DAP			
	surface	1-2 cm	3-4 cm	6-7 cm	surface	1-2 cm	3-4 cm	6-7 cm
	-----%							
curly dock	5 a <sup>a</sup>	5 a	2 a	0 a	48 a	21 ab	10 b	5 b
dandelion	60 a	33 ab	2 b	8 b	62 a	62 a	7 b	11 b
foxtail barley	25 b	88 a	30 b	3 b	47 b	86 a	36 bc	8 c
milkweed	0 b	83 a	75 a	0 b	0 b	96 a	83 ac	40 bc
Perennial sowthistle	9 a	0 a	0 a	0 a	44 a	0 b	0 b	0 b
quackgrass	17 b	52 a	47 a	13 b	56 ab	69 a	70 a	22 b

<sup>a</sup> Percent maximum emergence within the same species and same time frame after planting (10 or 19 DAP) with different letters are significantly different least squares means at  $P < 0.05$ .

experiments suggest that when soil moisture levels fluctuated the percentage emergence for seeds closest to the surface generally declined as compared to when soil moisture

levels were kept at field capacity whereas emergence at deeper depths was less affected. It may be that seeds placed on the surface experience a much greater fluctuation in soil moisture levels than seeds below the surface where the soil dries at a much slower rate. Similar results would probably occur in agricultural fields and surface germinating species may be a greater problem in wet years.

Foxtail barley emergence was somewhat sensitive to depth with emergence being highest for seeds placed at 1-2 cm when soils were maintained at field capacity (Table 1-4). Quackgrass emergence was less sensitive to depth of seed placement than the other perennials (Table 1-4). At 10 DAP, surface placed seeds of quackgrass had significantly less emergence than seeds at depths of 1-4 cm but this difference had disappeared by 19 DAP. At field capacity quackgrass seeds at 6-7 cm had significantly less emergence than seeds between 1-4 cm.

**Table 1-5.** Percent maximum emergence of five perennial weed species seeded at three depths 19 days after planting (DAP) with the soil fluctuating between field capacity (FC) and 1/3 FC or FC and 1/6 FC.

Species	Planting depth		
	surface	1-2 cm	3-4 cm
	-----%-----		
curly dock	12 a	15 a	6 a
dandelion	24 a	28 a	8 a
foxtail barley	15 c	70 a	39 b
perennial sowthistle	20 a	27 a	8 a
quackgrass	23 b <sup>a</sup>	54 a	51 a

<sup>a</sup> Percent maximum emergence within the same species with different letters are significantly different least squares means at  $P < 0.05$ .

Foxtail barley and quackgrass were the only two perennials for which significantly less emergence occurred when seeds were placed on the surface and moisture levels fluctuated. Foxtail barley emergence was greater at 1-2 cm than surface seeds or for the 3-4 cm depth. When averaged over all seeding depths, percent



emergence of curly dock, perennial sowthistle and dandelion was not affected by fluctuating soil moisture (data not shown). Quackgrass and foxtail barley had significantly greater emergence when moisture levels fluctuated between FC and 1/3 FC than when they fluctuated between FC and 1/6 FC. This may help to explain why foxtail barley is more commonly found in wet, fertile soils (Best et al. 1978). Milkweed was not included in the depth by moisture experiment because of insufficient seed numbers.

### **Implications**

Weed control of surface germinating species may be accomplished in several ways. For weeds that do not have a long seed bank duration such as foxtail barley (Best et al. 1978), burial of seed by fall tillage may prevent germination the following spring. Fall tillage, however, should be avoided where species such as curly dock and wild mustard are a concern. The seeds of these species form long-lived seed banks allowing for re-infestations when seeds are brought to the surface by tillage (Baskin and Baskin 1985; Mulligan and Bailey 1975). For surface germinating species such as wild mustard and curly dock, seeds should be left on the surface after harvest allowing for predation, fall germination and subsequent winter kill (Marino et al. 1997; Povey et al. 1993). Spring emerging seedlings of these species could be controlled with shallow tillage or with pre-seeding herbicide applications. Species such as green foxtail and wild oat seem to be able to emerge from a broad range of depths and they may emerge under a wide range of moisture conditions. For these species, therefore, it is very difficult to recommend control methods related to altering microsite conditions.

**MANUSCRIPT #2****THE EFFECTS OF SEEDING DEPTH AND SOIL AGGREGATE SIZE ON THE  
EMERGENCE OF EIGHT ANNUAL AND THREE PERENNIAL PLANT  
SPECIES****ABSTRACT**

Seedling recruitment of annual and perennial weeds is partially dependant on microsite conditions. Soil aggregate size may affect soil light penetration, the gaseous environment and moisture levels directly surrounding the seed. Within this experiment we studied the impact of soil aggregate size (A1 < 2.0 mm; 2.0 mm < A2 < 12.7 mm; A3 > 12.7 mm) and seeding depth (1, 3, 5 and 7 cm depths) on weed emergence. Eight annual and three perennial weeds commonly found in Manitoba, Canada were seeded in all aggregate sizes and depths. At least 97.6 % of all photosynthetically active radiation was intercepted by the soil at 1 cm depths with all aggregate sizes. Emergence increased with aggregate size for five of the 11 species studied, five species were unaffected by aggregate size and one species had decreased emergence with large aggregate sizes. Percentage emergence decreased with increasing depth for eight of the 11 species. Emergence of wild oat, barnyard grass and wheat were not affected by seeding depth.

## INTRODUCTION

Tillage alters the horizontal and vertical distribution of weed seeds in the soil as well as the soil conditions directly surrounding the seed. Generally, as tillage decreases, the number of weed seeds near the surface increases (Spandl et al. 1998). Yenish et al. (1996) found that in no-till 90% of the seeds remained within 2 cm of the surface while moldboard plowing placed 50 to 60% of the seeds at 11 to 16 cm depths. However, during multiple tillage events seeds that were once buried may be brought back to the surface equalizing the distribution of weeds seeds between the surface and 20 cm depths (Cousens and Moss 1990). This vertical movement of weed seeds within the soil horizon impacts weed population dynamics. du Croix Sissons et al. (2000) reported that the majority of weeds in no-till and conventional-till fields emerged from depths between 0 and 4.2 cm. While some species may emerge from far greater depths (Sharma and Vanden Born 1978) the greater the depth the longer it takes for weeds to emerge (Cussans et al. 1996).

Tillage not only affects the vertical distribution of weed seeds within the soil profile but also changes the conditions directly surrounding the seed. In fact, Mohler and Galford (1997) concluded that weed emergence and seedling survival is affected by changes in soil conditions caused by disturbance independent of seed redistribution effects. The type and timing of tillage may affect soil aggregation, bulk density and porosity. Cussans et al. (1996) reported that weed emergence may be slower in smaller aggregate soils than in large aggregate soils especially for seeds emerging from deeper depths. The extent to which aggregate size affects weed emergence depends on the weed species. The emergence of species with larger seeds, such as wheat and catchweed bedstraw, have been reported to be less affected by clod size than species with smaller seeds (Cussans et al. 1996). Variation in soil texture and structure may impact weed population dynamics by influencing the depth of light penetration, the gaseous environment directly surrounding the seed, the range of temperature fluctuations or the energy required for the seedling to penetrate through the soil (Baskin et al. 1996; Benvenuti et al. 2001b; Benvenuti and Macchia 1997; Benvenuti 1995).

The objectives of this experiment were to determine the impact of soil aggregate

size and seeding depth on weed emergence when moisture was kept constant and non limiting.

## MATERIAL AND METHODS

Seeds of 11 weed species (three perennials and eight annuals) were collected from various locations in Manitoba, Canada (manuscript #1). All seeds had been kept in storage at 4 °C following harvest until the beginning of the experiment. The experiment was set up as a factorial with three soil aggregate sizes, three seeding depths and two replicates. The experiment was repeated once. Fifteen seeds of each species were seeded in 15.5 x 14 cm pots. A mixture of 1/3 sand, peat moss and topsoil (clay loam) was placed in the bottom of each pot and the weed seeds were placed on the surface of this soil. A clay loam soil was sieved into three aggregate size classes; small aggregates less than 2.0 mm, medium sized aggregates ranging between 2.0 mm to 12.7 mm, and large aggregates, larger than 12.7 mm. The sieved soil was placed on top of the weed seeds to depths of 1, 3 and 7 cm. All pots were watered every second day to keep the soil moist at all times in order to minimize any variation in moisture that might have been caused by the different aggregate sizes. All pots were kept in a green house with day / night temperatures of 24 and 18 °C, respectively.

The number of plants emerging were counted and recorded three times per week until emergence ceased. A seedling was counted once any part of the plant emerged from the soil. The percentage of maximum emergence was determined by dividing the number of seedlings of each species in each pot by the maximum number of seedlings that emerged of the same species from one pot in each run of this experiment. The pot with the greatest number of weeds emerging was not used if there were not other pots within the experiment with similar emergence levels. This was done to ensure that an outlier did not bias the results. This method was used to eliminate any variation between species due to different dormancy levels since we only desired to evaluate the germinable portion of the seeds used. Possible variation in embryo growth potential caused by stratification periods was not accounted for in this experiment.

The data were analyzed using a general linear model and repeated measures.

Least squares means were used for all comparisons (SAS institute Inc., 1990). All species were analyzed together and then individually. Only main effects are presented because the interaction between depth and aggregate size was not significant. Consequently, the model contains hidden replication where all aggregate sizes are used to estimate the effects of depth, and all depths are used to estimate the effects of aggregate size. Data from days evenly spaced throughout the experiment are presented to provide information on the rate of emergence.

### **Light transmittance**

Light (PAR) transmittance through the three soil aggregate sizes at the three depths was measured using a Li-Cor LI-188B integrating quantum, radiometer, photometer with a LI-190SA quantum sensor (Li-Cor, Lincoln, Ne.). Measurements were taken in the afternoon in the greenhouse. Sunlight was the only light source with intensities between 76 and 155  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The sensor was placed within a box with a black interior. All cracks were sealed to prevent light entry. A round opening with a diameter of 7.7 cm was left at the top of the box. The quantum sensor was placed in the box located just below the surface of the opening. Black plastic pipe with a 7.7 cm diameter was cut at 1, 3, and 7 cm lengths and one end closed off with clear plastic thus forming a black pot with a clear bottom. Soils of specific aggregate size classes were placed within individual black pots of each height. An empty black pot of a given height was placed on the black box and a PAR reading was taken. This pot was removed then another black pot of the same height but containing soil of a particular aggregate size class was placed directly on the black box and a second reading taken. From these two measurement the percent light interception by the particular soil aggregate size was determined. Light interception was measured both with dry soil and with soil that had been watered and left for three to four hours to determine if wetting the soil influenced light interception. Each measurement for soils in each aggregate class and for each pot height were replicated four times and the means compared using Duncan's means comparisons.

## RESULTS AND DISCUSSION

### Light interception

The amount of light intercepted was not affected by soil moisture. For all depths and soil aggregate sizes used in this experiment at least 97.6% of all incoming quantum energy was intercepted (Table 2-1). Light interception did not differ significantly with any soil aggregate size class. Light interception was 1.3% lower at 7 cm versus 3 cm when the soil was dry but under no other condition did soil depth significantly influence the level of light interception. There were no significant interactions between soil aggregate size and soil depth effects on light interception. These results agree with Wooley and Stoller (1978) who reported that less than 1% of incident radiation penetrates 2.2 millimetres through Drummer silty clay loam or a Broomfield sand. Although, Benvenuti (1995) found that light penetration was strongly dependant on soil type and particle size, he reported that regardless of soil type only 0.01% of incident light penetrated all soil types to depths of 4 mm. Therefore, it appears that light plays very little role in weed emergence when seeds are present at soil depths greater than a few mm regardless of soil type or aggregation.

**Table 2-1.** The effects of three soil aggregate sizes (A1<2.0 mm; 2.0mm<A2<12.7mm, A3>12.7mm) and three soil depths (1, 3, 7 cm) on percent light interception.

	Aggregate Size			Depth		
	A1	A2	A3	1 cm	3 cm	7 cm
	-----% light interception-----					
Dry	98.1 a <sup>a</sup>	98.6 a	98.1 a	98.9 a	98.2 ab	97.6 b
Wet	98.8 a	98.9 a	98.3 a	98.4 a	99.2 a	98.3 a

<sup>a</sup>Percentage of light interception within soil aggregate sizes or depth with different letters are significantly different at P<0.05.

### Soil aggregate size and seeding depth effects on emergence

Soil aggregate size and seeding depth were analyzed independently because the interaction between these two variables was not significant for all species except green foxtail. When averaged over all species, aggregate size did not influence emergence 9 days after planting (DAP) but by 16 DAP there was significantly more emergence in soils with large aggregates (>12.7 mm). This trend continued until the end of the experiment. Cussans et al. (1996) reported similar results with smaller seeded species showing greater emergence when seeds were covered with larger sized aggregates. Seedling depth had a greater impact on emergence than soil aggregate size. Overall emergence of seeds placed at 1 cm depth was significantly higher than seeds placed at 3 cm and emergence at the 3 cm depth was significantly higher than emergence from the 7 cm depth. When all species were averaged together the differences in emergence between depths was evident from 9 DAP until the end of the experiment.

Wild oat, canola, field pennycress and barnyardgrass emergence was not affected significantly by aggregate size. (Table 2-2). Wild oat and barnyard grass emergence was not affected by seeding depth although 16 DAP there was a greater percentage emergence of wild oat from the 1 cm than from the 7 cm depth (Table 2-3). The ability of wild oat to emerge under a wide range of conditions may help to explain its predominance in fields in Manitoba, Canada (Van Acker et al., 2000). Field pennycress and oilseed rape emergence from the 7 cm depth was significantly less than emergence from 1 cm. Other authors have also reported a reduction in canola emergence with increasing depth (Nuttall, 1982; Thomas et al., 1994).

Catchweed bedstraw and wild mustard emergence was significantly higher with aggregates greater than 12.7 mm than with aggregates less than 2.0 mm (Tables 2-2). There was no significant difference in percentage emergence between aggregates less than 2.0 mm and aggregates between 2.0 mm and 12.7 mm (Table 2-2). Catchweed bedstraw and wild mustard emergence also tended to decrease with increasing depth with significantly less emergence from 7 cm depths than from the 1 cm depth (Table 2-3). Rottele (1980) found that the greatest catchweed bedstraw emergence occurred from seeds placed at 0 to 5 cm depths. Wild mustard emergence increases with soil aeration

due to cultivation (Mulligan and Bailey, 1975) and it is very sensitive to depth with most seeds emerging near the surface (manuscript #1). Therefore, higher percentage emergence with larger aggregates may be partially due to increased aeration. Decreased emergence with increasing seed depth may be attributed to reduced gas exchange or a lack of oxygen at deeper depths (Benvenuti et al., 2001a). Percentage emergence of green foxtail was significantly higher with aggregates less than 2.0 mm than with aggregates between 2.0 and 12.7 mm. This difference was not significant until 23 DAP. Emergence tended to decrease with increasing seeding depth with percentage emergence significantly lower from the 7 cm than from the 1 cm depth 9 DAP. These results agree with Boyd and Van Acker (manuscript #1) who reported significantly less emergence of this species when seeds were placed on the surface or at 7 cm versus seeds placed at depths between 1-4 cm. du Croix Sissons et al. (2000) reported that field emergence of green foxtail occurred mainly from depths less than 4.2 cm. Green foxtail was the only species for which the effects of depth significantly interacted with aggregate size. Percentage emergence from the 7 cm depth was significantly lower with aggregates greater than 12.7 mm and between 2.0 mm and 12.7 mm than emergence with aggregates less than 2.0 mm. Poor emergence with larger aggregates may have been due to the inability of green foxtail to exert enough pressure to protrude through the large aggregates. When green foxtail seeds were placed at 1 cm depths emergence was significantly higher with aggregates less than 2.0 mm than with aggregates between 2.0 and 12.7 mm. In Saskatchewan and Alberta, Canada, green foxtail is most commonly found on medium textured or coarse soils and it is rarely found on fine textured soils. In Manitoba, where the seeds for these experiments originated, green foxtail is commonly found on all soil textures (Douglas et al. 1985).

Percentage emergence of volunteer spring wheat was significantly higher with aggregates between 2.0 and 12.7 mm than when aggregates were less than 2.0 mm (Table 2-2). Although deeper seeding may slow the rate of emergence it did not significantly affect the percentage emergence at 23 DAP (Table 2-3). Cussans et al. (1996) found that wheat was less responsive to sowing depth and aggregate size than other species with similar seed sizes.

Percentage emergence of foxtail barley was not affected by aggregate size.



**Table 2-2.** The effects of three soil aggregate sizes (A1 <2.0 mm; 2.0mm < A2 < 12.7 mm; A3 >12.7 mm) on least squares means of weed emergence 9, 16 and 23 days after planting (DAP).

Weed Species	9 DAP			16 DAP			23 DAP		
	A1	A2	A3	A1	A2	A3	A1	A2	A3
	-----% of maximum emergence-----								
barnyardgrass	29a <sup>a</sup>	36 a	22 a	46 a	42 a	26 a	50 a	42 a	26 a
catchweed bedstraw	32 a	38 a	45 a	44 b	49 ab	65 a	39 b	56 ab	68 a
green foxtail	58 a	56 a	55 a	71 a	60 a	63 a	77 a	60 b	66 ab
canola	58 a	55 a	52 a	58 a	57 a	57 a	58 a	57 a	56 a
field pennycress	16 a	17 a	26 a	20 a	20 a	30 a	21 a	20 a	33 a
wheat	67 b	83 a	76 ab	73 a	86 a	76 a	74 b	86 a	81 ab
wild mustard	23 a	30 a	38 a	24 b	32 ab	44 a	25 b	33 ab	46 a
wild oat	49 a	57 a	64 a	56 a	59 a	69 a	56 a	64 a	69 a
foxtail barley	43 a	41 a	28 a	52 a	48 a	44 a	53 a	51 a	39 a
perennial sowthistle	1 a	3 a	1 a	3 a	12 a	14 a	6 b	17 ab	25 a
dandelion	0 a	6 a	9 a	5 b	8 b	22 a	6 b	13 ab	24 a

<sup>a</sup>Percentage of maximum emergence within the same species and measurement time after planting (9, 16 or 23 DAP) with different letters are significantly different at  $P < 0.05$ .

**Table 2-3.** The effects of seeding depth (D1 = 1 cm; D2 = 3 cm; D3 = 7 cm) on least squares means of weed emergence 9, 16 and 23 days after planting (DAP).

Weed species	9 DAP			16 DAP			23 DAP		
	D1	D2	D3	D1	D2	D3	D1	D2	D3
	-----% of maximum emergence-----								
barnyard grass	29 a <sup>a</sup>	33 a	25 a	35 a	44 a	35 a	36 a	47 a	35 a
catchweed bedstraw	56 a	55 a	4 b	69 a	64 a	25 b	71 a	59 a	33 b
green foxtail	66 a	62 a	41 b	69 ab	72 a	52 b	75 a	73 a	54 b
canola	76 a	64 a	26 b	78 a	66 a	28 b	78 a	66 a	27 b
field pennycress	37 a	22 a	1 b	39 a	29 a	2 b	39 a	31 a	5 b
wheat	82 a	74 a	69 a	84 a	81 ab	70 b	84 a	81 a	76 a
wild mustard	45 a	43 a	3 b	49 a	45 a	7 b	50 a	46 a	8 b
wild oat	64 a	58 a	48 a	71 a	63 ab	49 b	71 a	64 a	54 a
foxtail barley	76 a	34 b	1 c	85 a	48 b	11 c	87 a	49 b	11 c
P. sow-thistle	3 a	2 a	0 a	19 a	7 a	4 a	30 a	15 ab	2 b
dandelion	12 a	3 ab	0 b	26 a	8 b	1 b	31 a	11 b	1 b

<sup>a</sup>Percentage of maximum emergence within the same species and measurement time after planting (9, 16 or 23 DAP) with different letters are significantly different at  $P < 0.05$ .

Perennial sow thistle and dandelion emergence increased with aggregate size (Table 2-2). In all three perennial species percentage emergence decreased with increasing depth (Table 2-2).

The results of this experiment are important for several reasons. First, since light appears only to penetrate the top few millimeters of the soil profile it probably does not play a large role in weed emergence in field situations except during cultivation when seeds can be briefly exposed to light. Second, most species in this study had substantially reduced emergence when seeded at 7 cm depths. Therefore, when sampling the seed bank or studying weed population dynamics only a shallow emergence zone needs to be taken into account. Third, conditions which lead to large aggregate formation in the field may result in increased weed emergence.

This study was not designed to determine which factors limited weed emergence as seeding depth or aggregate size were altered. However, potential limiting factors would include gas exchange, physical impedance of seedling emergence and temperature. In this experiment temperature probably did not affect weed emergence because relatively small pots were used and air circulated freely around them. It may be most likely that the results of this experiment were due to differences in physical impedance of the growing seedling or differences in the gaseous environment around the seed as a function of differences in seeding depth or soil aggregate size.

**MANUSCRIPT #3****INFLUENCE OF SHADING BY BARLEY STRAW ON THE EMERGENCE OF  
TEN ANNUAL AND FIVE PERENNIAL SURFACE SEEDED WEED SPECIES****ABSTRACT**

Reduced tillage typically results in greater weed seed populations and higher rates of surface debris on the soil surface. An experiment was conducted to determine the effect of various rates of ground cover (0, 20, and 90%) by barley straw on the germination of surface placed seeds. Fifteen seeds of 10 annual and 5 perennial weed species were placed on the soil surface and one of three ground cover treatments applied. All treatments were replicated 4 times and the number of emerging weeds counted every second day until emergence ceased. On average, 20 and 90% ground cover significantly increased percentage weed emergence when compared to zero cover. In 5 of the 10 annual species studied, canola, barnyardgrass, catchweed bedstraw, green foxtail and field pennycress, emergence was not affected significantly by soil cover. In the remaining 5 annual species, wild oat, wild mustard, round leaved mallow, white cockle and wheat, 90% ground cover significantly increased emergence. Ground cover had no had no significant impact on perennial weed emergence.

## INTRODUCTION

Shifting from conventional to reduced tillage may bring changes in weed population dynamics. This switch could result in increased populations of perennials, summer annual grasses, biennial and winter annual species and volunteer crop plants (Buhler 1995; Swanton et al. 1993; Froud-Williams et al. 1983). These changes in weed populations may be due to changes in vertical movement of seeds within the soil profile. Volunteer crop species germinate best near the surface and the lack of fall cultivation may allow winter annuals and biennials to become established (Swanton et al. 1993). Buhler and Mester (1991) reported that mean depths of weed emergence were shallowest in no-till, followed by chisel and conventional tillage. With continual seed rain the number of weed seeds germinating near the surface increases as tillage decreases (Spandl et al. 1998).

Conservation tillage may alter microsite conditions within the soil and consequently change the weed population dynamics by altering the soil physical characteristics and maintaining crop residue cover (Swanton et al. 1993). Campbell et al. (1989) reported that zero-tillage plots on the Brown soil zone of Saskatchewan had increased organic matter, microbial biomass, nitrogen and phosphate activity in the top 7.5 cm of the soil. Conservation tillage often has lower soil temperatures and higher soil moisture levels which may also affect weed emergence (Johnson and Lowery 1985; Malhi and O'Sullivan 1990). Reduced tillage can alter the environmental conditions directly surrounding the weed seeds independently of the effects of ground cover or seed position in the soil (Mohler and Galford 1997).

Greater levels of surface residue in no-till fields may alter soil temperature, moisture and light transmittance impacting weed microsite conditions and ultimately weed population dynamics. The increased organic matter content found in reduced tillage results in reduced temperature amplitude when stubble mulch is present (Froud-Williams et al. 1981). The germination response of weeds to constant or fluctuating temperatures is species specific (Weaver et al. 1988, Fernandez-Quinantilla et al. 1990) with most weed species obtaining the highest percentage germination under fluctuating temperatures (Martinez-Ghersa et al. 1997, Nishamoto and McCarty 1997). Teasdale and

Mohler (1993) found that hairy vetch and rye residue reduced daily soil maximum temperature and daily soil temperature amplitude. The reduction in temperature was probably not enough to reduce weed emergence but the reduction in amplitude could reduce germination of weed seeds that require temperature fluctuations to break dormancy. Nishamoto and McCarty (1997) reported only 10% germination of goose grass at constant temperatures and 99% emergence with fluctuating temperatures and light. Surface residue may provide the appropriate conditions for weed emergence when weed seeds are not incorporated with tillage (Buhler and Mester 1991).

Crop residues and tillage practice may also affect soil moisture levels. Oryokot and Swanton (1997) reported no moisture differences at 2.5 cm between no-till, chisel till and moldboard plowing. Conversely, Malhi and O'Sullivan (1990) reported that soil moisture in the surface layer (0-15 cm) was 7.2% greater on zero-tillage plots than conventional tillage plots. Maurya (1986) found that no-tillage plots with surface residues had a higher soil porosity and infiltration rate than tilled plots which may partially explain the increased soil moisture content of no-till fields. Crop residues on the surface may increase soil water storage and conservation (Doran et al. 1984, Bhatnagar et al. 1983). Teasdale and Mohler (1993) reported a decline in soil moisture content during droughty periods without residues compared to plots with crop residues left intact. Lower soil temperatures found in reduced tillage plots with increased crop residue may reduce weed emergence while increased moisture during dry periods may increase weed emergence (Teasdale and Mohler 1993).

Crop residues impact weed emergence by reducing the amount of light reaching the soil surface. Exposure to light breaks dormancy and promotes germination in many weed species (Gallagher and Cardina 1997; Bartley and Frankland 1985; Letchamo and Gosselin 1996). Photoconversion of phytochrome from the red light absorbing form to the biologically active far-red absorbing form promotes germination in some species and inhibits it in others (Gallagher and Cardina 1997; Bartley and Frankland 1985). Sensitivity to light is dependant on many factors including the level of seed dormancy, seed burial and the gaseous environment directly surrounding the seed (Benvenuti and Macchia 1998; Gallagher and Cardina 1998a; Benvenuti and Macchia 1997). Teasdale (1993) found that hairy vetch residue may suppress weed establishment of species with a

light requirement but may not suppress several other species. However, Teasdale and Mohler (1993) reported that light transmittance through hairy vetch and rye cover crops was adequate to stimulate germination.

The objectives of this experiment were to determine the effects of crop residue on the emergence of surface placed seeds. Soil was moist at all times and temperature was kept constant between treatments in an attempt to isolate the impact of light transmittance through crop residue on emergence.

## MATERIALS AND METHODS

Seeds from fifteen weed species were collected from various locations in Manitoba, Canada (Table 3-1). All seeds were stored at 4 °C prior to the beginning of the experiments in a sealed container. The experiment was seeded in a greenhouse on October 11 and the second run on November 6 with greenhouse day / night temperatures maintained at 24 °C / 18 °C.

The experiment was seeded in 10 cm x 12.5 cm x 5 cm trays. A sterilized clay loam top soil was firmly pressed into the trays creating a flat even surface. Fifteen seeds of each species were evenly distributed on the surface. Barley straw was chopped manually to various lengths and placed randomly on the surface. Three levels of ground cover were used. The three treatments were zero, 20%, or 90% ground cover. A small piece of paper matching the dimensions of the pots with 10 randomly placed 0.38 cm<sup>2</sup> holes was used to determine the percent ground cover by the barley straw. Holes at least 50% filled were counted to and used to estimate ground cover. Barley straw was added to each pot until the desired ground cover had been achieved. On average 20% and 90% cover was equivalent to 91 and 820 kg barley straw ha<sup>-1</sup>, respectively. All pots were watered every second day to keep the soil moist throughout the experiment.

The experiment was designed as a randomized complete block design with 3 treatments and two blocks. The experiment was repeated once. The two runs of the experiment did not differ significantly and were treated as replicates within the final analysis. All seedlings were counted and recorded 14 and 26 days after planting. Each species was analysed separately using a general linear model in SAS (SAS Institute Inc.

1990). Emergence means were compared in SAS using Duncan's means comparisons. All data were normally distributed with constant variance.

Light transmittance through the barley straw was measured using a Li-Cor LI-188B integrating quantum, radiometer, photometer with a LI-190SA quantum sensor. The sensor was placed within a box with a black interior. All cracks were sealed to prevent light entry.

**Table 3-1.** Harvest location in Manitoba, harvest year and maximum emergence (maximum number of seeds out of fifteen emerging from the soil during this experiment).

Species	Harvest location	Harvest year	Maximum emergence
Barnyardgrass	Winnipeg	2000	13
Canola	Carman	1997	15
Catchweed bedstraw	Western Manitoba	2000	15
Curly dock	Southern Manitoba	1998	7
Dandelion	Carman	1999	14
Field pennycress	Winnipeg area	2000	10
Foxtail barley	Southern Manitoba	1999	12
Green foxtail	Portage	1997	15
Perennial sowthistle	Southern Manitoba	2000	9
Quackgrass	Southern Manitoba	1986	9
Round leaved mallow	Southern Manitoba	1987	7
Spring wheat	Carman	1999	15
White cockle	Winnipeg area	2000	15
Wild mustard	Winnipeg area	1986	12
Wild oat	Carman	1990	15



A 10 x 12.5 cm opening was left at the top of the box and covered with glass. The quantum sensor was placed in the box located just below the surface of the opening. Ground cover levels equivalent to zero, 20 and 90% were placed on the glass. Light measurements were taken just before the straw was placed on the glass and directly after to determine the extent of light interception. Each measurement was replicated 10 times and the means compared using Duncan's means comparisons.

## RESULTS AND DISCUSSION

### Light interception

Exposure to light promotes germination in many species and inhibits it in others (Gallagher and Cardina 1997; Letchamo and Goselin 1996; Bartley and Frankland 1985). Surface debris may inhibit or promote weed germination. In this study, soil cover as low as 20% resulted in statistically significantly less light reaching the surface than zero cover (Table 3-2). Ninety percent soil cover intercepted significantly more light than 20% cover. The reduction in light transmittance appears to have increased the overall percentage weed emergence. When all species were averaged together 20 and 90% cover had significantly higher percentage weed emergence than pots without surface cover (Table 3-3). Typically, ground cover has been studied to determine its potential for weed control (Teasdale and Mohler 1993). The results of this greenhouse study suggest that ground cover, even as low as 20%, may promote the emergence of some weed seeds on the soil surface if soil moisture levels are not limiting.

Conservation tillage usually involves soil disturbance reduction and maintenance of crop residue cover (Swanton et al. 1993). The reduction in soil disturbance will increase the number of weed seeds near or on the surface (Yenish et al. 1996; Spandl et al. 1998). These conditions may promote the emergence of some species that germinate well on the surface but decrease the emergence of seeds that require burial to break dormancy and germinate. When seeds are not incorporated, surface residue may provide

the appropriate conditions allowing weed emergence of those species that emerge best if buried below the soil surface (Buhler and Mester 1991).

**Table 3-2.** Photosynthetically active radiation intercepted and reaching the soil surface at zero, low (20%) and high (90%) ground cover.

Measurement	Zero	Low	High
Light reaching soil surface ( $\mu\text{E m}^{-2} \text{s}^{-1}$ )	102.4 a <sup>a</sup>	91.7 b	20.0 c
Light intercepted by straw ( $\mu\text{E m}^{-2} \text{s}^{-1}$ )	0.0 c	10.7 b	77.1 a

<sup>a</sup>Light measurements at zero, low and high ground cover with different letters are significantly different at  $p < 0.05$ .

**Table 3-3.** The percentage emergence of annual and perennial weeds at 14 and 26 days after planting (DAP) with zero, low (20%) and high (90%) ground cover by barley straw.

Species	14 DAP			26 DAP		
	Zero	Low	High	Zero	Low	High
	-----% emergence-----					
Annuals	32.7 c (a) <sup>a</sup>	46.7 b (a)	64.8 a (a)	39.7 c (a)	55.9 b (a)	71.2 a (a)
Perennials	27.7 a (a)	38.1 a (a)	27.5 a (b)	35.5 a (a)	44.0 a (a)	36.6 a (b)
Average	31.0 b	43.8 a	52.3 a	38.3 b	51.9 a	59.7 a

<sup>a</sup>Percentage of maximum emergence within the same time frame after planting (14 or 26 DAP) and plant type (annual or perennial) with different letters are significantly different at  $p < 0.05$ . Percentage of maximum emergence within cover level (zero, low and high) and time frame after planting (14 or 26 DAP) with different letters in brackets are significantly different.

## Annuals

Significantly higher percentage emergence of annuals occurred at 90% soil cover 14 and 26 DAP than at low or zero cover (Table 3-3). Twenty percent soil cover had significantly higher annual weed emergence than no soil cover. This suggests that

emergence of the majority of annual species used in this experiment are either inhibited by exposure to light or the straw helps maintain higher levels of soil moisture and humidity around the seed.

For 5 of the 10 annuals studied, shading had no significant effect on emergence. Barnyardgrass, catchweed bedstraw, green foxtail, field pennycress and round leaved mallow emergence was not affected significantly by soil cover (Table 3-4). Taylorson and Dinola (1989) propose that high temperatures (20 / 30 °C) cause barnyardgrass to shift from a light requiring to a light independent state. This may explain why ground cover had no effect on this species in this experiment. In early spring when temperatures are cool, shading by ground cover may inhibit germination of barnyardgrass. Although not significant, round leaved mallow, catchweed bedstraw, green foxtail and field pennycress tended to have higher emergence with 90% cover than zero cover. Froud-Williams et al. (1984) reported that catchweed bedstraw seedlings do not establish on the surface and Sjostedt (1959) reported that they germinate best in darkness with adequate moisture. Since the soil was kept damp and catchweed bedstraw emergence tended to increase with cover we can hypothesize that light inhibits germination to a degree but does not prevent it. Field pennycress emergence also tended to increase with cover. Hazebroek and Metzger (1990) found that exposure to red light promoted field pennycress emergence and shading limited emergence. Other studies have reported that field pennycress seeds germinate best in weak light or darkness (Mulligan and Bailey 1975). In this study shading had no significant effect on emergence.

For all five species where shade significantly affected emergence, 90% ground cover resulted in significantly higher percentage emergence than lower ground cover levels (Table 3-4). Percentage emergence with 20% cover was only significantly higher than zero cover with wild oat. These results agree with Sawhney and Hsiao (1986) who reported that direct or diffused light inhibited germination of wild oat and that this inhibition was greater at greater light intensities. However, the effect of light on seed germination depends on moisture availability and the state of dormancy (Hou and Simpson 1991, Hsiao and Simpson 1971). Mulligan and Bailey (1975) reported that research thus far has given conflicting results on the effects of light on wild mustard germination. In this study shading significantly increased emergence. White cockle was

the only annual species where 20% cover had significantly lower emergence than 90% cover. Therefore, ground cover generally increases annual weed emergence with 90% cover not being significantly different from 20%.

**Table 3-4.** The percentage emergence of annual weeds at 14 and 26 days after planting (DAP) at zero, low (20%) and high (90%) soil cover by barley straw.

Species	14 DAP			26 DAP		
	Zero	Low	High	Zero	Low	High
	-----% of maximum emergence-----					
Barnyardgrass	47 a	36 a	44 a	61 a	42 a	50 a
Canola	45 a	47 a	82 a	47 b	70 ab	83 a
Catchweed bedstraw	13 a	31 a	56 a	25 a	38 a	56 a
Field pennycress	47 a	70 a	81 a	56 a	75 a	86 a
Green foxtail	57 a	55 a	79 a	59 a	57 a	80 a
Round leaved mallow	0 b	19 ab	31 a	0 a	38 a	50 a
Spring wheat	27 b	48 ab	60 a	35 b	58 ab	75 a
White cockle	42 b	57 b	90 a	52 b	62 b	92 a
Wild mustard	28 b	43 ab	70 a	30 b	48 ab	70 a
Wild oat	21 b <sup>a</sup>	62 a	55 a	34 b	73 a	70 a

<sup>a</sup>Percentage of maximum emergence within the same species and same time frame after planting (14 or 26 DAP) with different letters are significantly different at  $p < 0.05$ .

## Perennials

Percentage emergence of perennials on average was not significantly affected by ground cover (Table 3-5). This would be expected since most of the perennial species used in this study are surface germinators (manuscript #1). Light may increase germination of dandelion (Letchamo and Gosselin 1996) but may not have any impact under alternating temperatures (Williams 1983). Although curly dock requires light for

germination adequate light appears to have reached the surface with 20 and 90% cover to promote emergence (Baskin and Baskin 1985) (Table 3-5). It is important to note that exposure to light or shading did not reduce or increase percentage emergence. When analyzing species individually there were no significant differences between percentage emergence at different ground cover levels (Table 3-5). Although not significant, perennial sowthistle percentage emergence appeared to be reduced by 90% ground cover.

**Table 3-5.** The percentage emergence of perennial weeds 14 and 26 days after planting (DAP) at zero, low (20%) and high (90%) soil cover by barley straw.

Species	14 DAP			26 DAP		
	Zero	Low	High	Zero	Low	High
Quackgrass	19 a <sup>a</sup>	31 a	16 a	34 a	41 a	19 a
Foxtail barley	40 a	44 a	35 a	46 a	52 a	63 a
Curly dock	25 a	30 a	15 a	35 a	35 a	25 a
Perennial sowthistle	19 a	22 a	6 a	22 a	25 a	9 a
Dandelion	37 a	63 a	63 a	40 a	67 a	67 a

<sup>a</sup>Percentage of maximum emergence within the same species and same time frame after planting (14 or 26 DAP) with different letters are significantly different at  $p < 0.05$ .

Increased annual weed populations may occur in reduced tillage fields where moisture is not limiting. The maintenance of soil cover may improve microsite conditions directly surrounding a seed increasing annual weed seed emergence. However, perennial weed emergence did not appear to be impacted by surface debris. An increase in perennial weeds in no-till fields may be due to less soil disturbance in the fall and a change in the vertical distribution of weed seeds in the soil profile towards the surface. However, many variables such as seed predation and moisture fluctuations may counteract the effects of ground cover. Further field experiments need to be conducted to determine if results obtained indoors are similar to results obtained under field conditions.

**MANUSCRIPT #4****SEED GERMINATION OF COMMON PLANT SPECIES AS AFFECTED BY  
OXYGEN CONCENTRATION, LIGHT AND OSMOTIC POTENTIAL****ABSTRACT**

Three laboratory experiments were conducted to determine the effects of oxygen concentration (21, 10, 5 and 2.5%), exposure to light and osmotic potential on the germination of wheat, canola and a range of weed species. When all species were analysed together germination was only significantly reduced when oxygen concentrations dropped from 5% to 2.5% oxygen. Germination tended to increase as the osmotic potential of the solution increased. Seed germination for some species like barnyardgrass was inhibited by the combination of exposure to normoxic (21% oxygen) conditions and light. This combination of conditions may function as a signal to prevent soil surface germination. Wild mustard and field pennycress seed germination was not reduced by normoxic conditions when seeds were exposed to light but germination was significantly lower than seeds in normoxic conditions and darkness. Green foxtail seed germination was relatively insensitive to oxygen concentration but limited by osmotic potential. Wild oat seed germination increased with increasing osmotic potential with osmotic potential having a greater influence when the seeds were exposed to light. Dandelion, foxtail barley, curly dock and perennial sowthistle germination was affected more by osmotic potential and light exposure than oxygen concentration. Oxygen concentration may be a signal for depth detection limiting or promoting germination in some species.

## INTRODUCTION

Seed depth within the soil profile strongly influences the probability of emergence. Species like curly dock will only emerge when seeds are on or near the surface (Weaver and Cavers 1979). The emergence of other weed species like wild oat is not as strongly influenced by depth and seedlings can emerge from depths up to 20 cm (Sharma and Vanden born 1978). The range of depths from which weed species may emerge is dependant on the species and soil physical parameters.

Within agricultural fields in Western Canada most weeds emerge from the top 4 cm of the soil profile (du Croix Sissons et al. 2000). For many species deep burial within the soil appears to result in secondary dormancy rather than suicidal germination (Benvenuti et al. 2001a). Non-dormant seeds must be able to detect environmental cues that cause a transformation from non-dormancy to secondary dormancy. To be effective, the environmental signals causing this transformation must change with increasing soil depth. Light, temperature fluctuations, soil moisture and the gaseous environment surrounding the seed may all provide signals of seed depth within the soil profile.

For many species, exposure to light breaks dormancy and promotes germination (Gallagher and Cardina 1997, Letchamo and Gosselin 1996). For some species, light is only required to break dormancy after prolonged burial (Wesson and Wareing 1968). For other species, exposure to light inhibits germination (Malik and Vanden Born 1987). Since very little light penetrates below 2-4 mm in soil (Benvenuti 1995, Woolley and Stoller 1978) exposure to light can only occur when seeds are on or near the surface or during soil disturbance. Therefore, one might expect that the primary role of light in weed seedbank dynamics is to function as a signal preventing germination on the soil surface of seeds that require burial and as a dormancy breaking signal when deeply buried seeds are moved to shallower soil depths.

Soil moisture affects both the timing of weed emergence and the number of weed seedlings emerging (Roman et al. 1999; Weaver et al. 1988). Seed germination may be reduced when soil moisture potential is lower than water potentials within the seeds. Lack of water may be the overriding control for seed germination in very dry conditions (Roberts et al. 1980). Under high moisture conditions the lack of oxygen or the inability

to remove fermentation products may limit seed germination (Holm 1972). Excessive moisture fills soil pores preventing gaseous movement towards and away from seeds.

Most seeds require oxygen for germination (Benvenuti and Macchia 1995; Benvenuti and Macchia 1997) although some may germinate in the absence of oxygen (Rumpho and Kennedy 1981). Gutterman et al. (1992) reported that most seeds were able to germinate at 15% oxygen and that higher oxygen concentrations caused more rapid germination. Benvenuti and Macchia (1995) also found that hypoxia decreased seed germination and rate of germination. Although germination seems to increase with increasing oxygen concentration some species may exhibit decreased germination in normoxic concentrations (21% oxygen) compared to hypoxic concentrations (between 5 and 10% oxygen) (Benvenuti and Macchia 1997).

Oxygen concentrations within the soil decline with depth (Topp et al. 2000). High soil moisture, soil compaction, high microbial activity or poor soil structure may decrease soil oxygen concentration or inhibit gaseous movement within the soil (Drew 1992; Hodgson and Macleod 1989; Ishii and Kadoya 1991). Seeds buried in low oxygen concentration conditions switch from aerobic to anaerobic metabolism (Holm 1972). At low oxygen concentrations and under conditions of poor gas diffusion anaerobic metabolites build up around the seed and inhibit seed germination. These conditions may also induce secondary dormancy and a light requirement for germination (Holm 1972). The inhibitory effects of low oxygen concentration on seed germination can be alleviated in some cases by flushing the atmosphere around the seed with inert gases to remove anaerobic metabolites (Benvenuti and Macchia 1995). Therefore, oxygen concentration or the inability to remove fermentation products from the gaseous environment directly surrounding the seed may inhibit seed germination.

The objectives of these experiments were to test the effects of oxygen concentration, light and osmotic potential on the germination of various common weed species in western Canada. The weed species used in these experiments represent a range of weed types found on the Northern Great Plains of North America. Very little research has been conducted to examine the effects of oxygen concentration and its interaction with light and osmotic potential on weed seed germination. Studying the effects of these environmental variables on germination may lead to an increased understanding of the



mechanisms of depth detection for given species and consequently a better understanding of their recruitment biology. This information may help us to model the population dynamics and potential for invasion and proliferation of each species as well as devise means of management which reflect an understanding of their recruitment biology.

## MATERIALS AND METHODS

### Seed Source

All seeds used in the experiments were taken from a mixture of collections from Manitoba and Alberta, Canada (manuscript #1). The seeds were kept in a seed storage room at 4 °C until the beginning of the experiment. A mixed origin seed source (manuscript #1) was used because our objectives did not include an exploration of the impact of seed lot on germination response to given treatments.

### Oxygen Concentration

Pre-mixed oxygen concentrations of 21, 10, 5 and 2.5% oxygen balanced nitrogen were used in this study. The tanks were purchased from and the gas premixed by a private company (Welders Inc, Winnipeg, MB). Seeds were germinated in petri dishes on a double layer of filter paper. Holes drilled in the sides of each petri dish facilitated air movement. Petri dishes were placed in double clear plastic bags and flushed with given gas mixtures for at least three minutes at 10 L min<sup>-1</sup>. Gas flow from the tanks was measured using a single stage regulator. Bags were then slowly sealed while still being flushed allowing them to fully inflate and remain inflated throughout the experiment.

### Light and Dark Germination

For experiment 1 and 2 the petri dishes sealed within clear plastic bags were placed in a temperature controlled greenhouse with day / night temperatures of 24 °C and 18 °C, respectively. For experiment 3, the petri dishes sealed within clear plastic bags

were placed in a growth chamber with day / night temperatures of 24 °C and 14 °C, respectively. Cool white (215 W) and Grow lite fluorescent bulbs on a 16 hour photoperiod were used in the growth chamber. Light intensity ranged from 160 to 190  $\mu\text{mol m}^{-2}\text{s}^{-1}$  over the experimental area. Those germinated in lighted conditions remained within the clear plastic bags for the duration of the experiment. Those germinated in dark conditions were placed in black bags after being sealed within the clear plastic bags. The black bag was placed within a white bag to minimize potential affects of the black bags on temperature in the petri dishes. Four tidbits (Hoskin Scientific) were used to measure temperature inside the clear bags and the bags placed within the black plastic. The minimum, maximum and range of temperature within 24 hour periods did not differ between seeds kept in light or dark conditions.

### **Osmotic Potentials**

Various osmotic potentials were created within petri dishes using Polyethylene glycol 8000. Potentials were created using the equations described by Michel (1983). Five millilitres of given solutions were placed in each petri dish.

### **Experiment 1**

The purpose of this experiment was to test the effects of the interaction between oxygen concentration and light on the germination of various weed species. Germination of eight annual plant species (barnyardgrass, canola, catchweed bedstraw, green foxtail, field pennycress, wheat, wild mustard and wild oat) and four perennial weed species (curly dock, dandelion, foxtail barley and perennial sowthistle) under 21, 10, 5 and 2.5% oxygen concentrations in light and dark was tested. Twenty seeds of each species were placed on double layers of filter paper in each petri dish. All petri dishes were placed in a greenhouse with day / night temperatures of 24 and 18 °C, respectively. The experiment was analysed as a factorial design with four replicates in the first run. In the green house species were randomized within each sealed bag and the bags were randomly assigned as light or dark treatments. The experiment was repeated with two replicates in the second

runSeeds were sealed in bags for 14 days then removed and the number of germinated seeds counted. A seed was counted as germinated if any portion of the radicle had emerged from the seed.

## **Experiment 2**

The purpose of this experiment was to test the effect of the interaction between oxygen concentration and osmotic potential on the germination of several weed species. Germination was tested for five annual plant species (barnyardgrass, green foxtail, canola, wheat and wild oat) and four perennial plant species (curly dock, dandelion, foxtail barley and perennial sowthistle) under 21, 10, 5 and 2.5% oxygen concentrations and osmotic potentials of  $-0.01$ ,  $-0.5$  and  $-1$  MPa. Catchweed bedstraw, field pennycress and wild mustard were not included in experiment two because seeds of these species do not germinate well under light and this experiment was conducted only under light. Twenty seeds of each species were placed in petri dishes in a greenhouse with day / night temperatures of 24 and 18 °C, respectively. The experiment was analysed as a factorial design with two replicates. One replicate of all weed species in each of the osmotic potentials used in this experiment were randomly placed in each sealed bag with each oxygen concentration. The experiment was repeated twice for a total of three runs. Petri dishes containing seeds were left enclosed in plastic bags for 14 days and then removed and germination level counted. A seed was counted as germinated if any part of the radicle had emerged from the seed.

## **Experiment 3**

The purpose of this experiment was to test the effect of the interaction between oxygen concentration, light exposure and osmotic potential on the germination of four weed species. Germination was tested for catchweed bedstraw, barnyardgrass, wild mustard and wild oat in both light and dark; 21, 10, 5 and 2.5% oxygen concentrations and under osmotic potentials of 0,  $-0.1$  and  $-0.5$  MPa. These four weed species were

chosen for this experiment because in previous experiments we found that germination of cleaver seed was sensitive to oxygen concentration and light, germination of barnyardgrass seed was sensitive to light but not oxygen concentration, germination of wild mustard seed was sensitive to oxygen concentration but not light and germination of wild oat seed was not sensitive to either light or oxygen concentration. Twenty seeds of each species were placed in each petri dish in a growth chamber with day / night temperatures of 24 and 14 °C, respectively. The experiment was set up as a factorial design with three replicates and it was repeated once. One rep of each species in each osmotic potential solution was randomly placed in each sealed bag. The sealed bags with the four oxygen concentrations were randomly designated light or dark treatments. The petri dishes were sealed in bags for 14 days and then removed and germination level counted. A seed was counted as germinated if any part of the radicle had emerged from the seed.

### **Statistical Analysis**

Data were analysed as a Factorial model in SAS (SAS Institute Inc. 1990) using general linear models and least squares means comparisons. All differences were considered significant if  $P < 0.05$ . For each experiment all species were analysed together as well as individually. Runs were combined within each experiment and considered as replicates because they did not differ significantly when analysed separately. Data met all normality conditions, therefore, data transformation was not required. Main effects are presented unless interactions were significant.

Percent of maximum germination was used to represent treatment effects because it is a relative measure and it eliminates variation between species due to differences in dormancy levels. It was calculated by dividing the number of germinated seeds of each species in each pot by the maximum number of seeds that emerged for the same species and seed lot within an experiment.

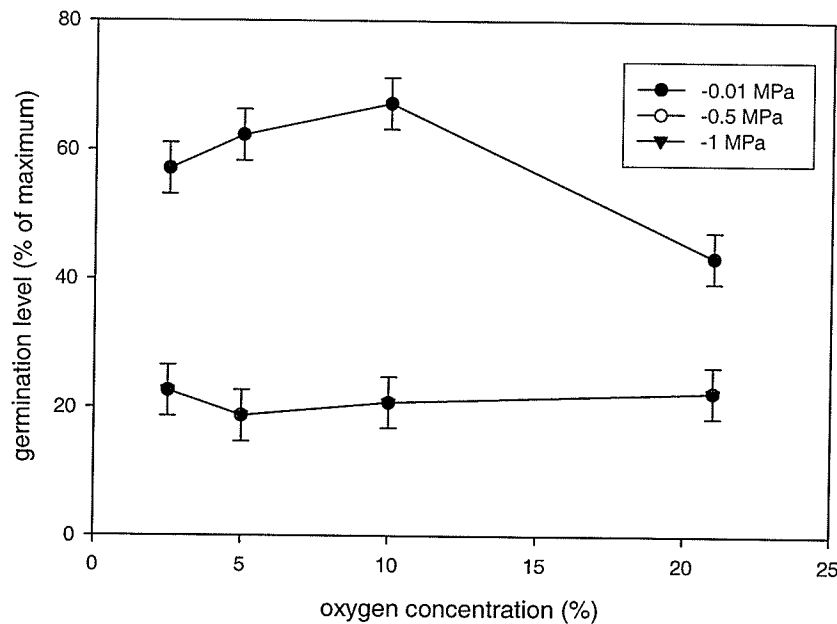
## RESULTS AND DISCUSSION

### Results for all species combined

In experiment one when all species were analysed together seed germination was only significantly reduced when oxygen concentrations reached 2.5%. At oxygen concentrations of 21, 10 and 5%, percent of maximum germination was 68, 64 and 62 %, respectively. Percent germination at oxygen concentrations of 2.5% was 53%. Benvenuti and Macchia (1995) noted a much larger effect of oxygen concentration on jimsonweed (*Datura stramonium*) where oxygen concentrations of 10 and 5% oxygen reduced germination by 2/3 and 1/3, respectively relative to normoxic conditions. Al-Ani et al. (1985) reported a more gradual impact of oxygen concentration on crop seed germination. Benvenuti and Macchia (1997) reported that bur beggarticks had significantly less germination at 21% oxygen concentrations than at 5 and 10% oxygen concentration. Therefore, it appears that seed germination response to oxygen concentration varies between species. Species were analysed individually because they respond differently to oxygen concentration and a combined analysis provides limited information.

In experiment two, the interaction between oxygen concentration and osmotic potential was significant ( $p=0.0008$ ) (Figure 4-1). At  $-0.5$  and  $-1$  MPa germination remained low and increased slightly at oxygen concentrations of 21%. At  $-0.01$  MPa seed germination increased with increasing oxygen concentration up to 10% oxygen. Germination then decreased significantly at oxygen concentrations of 21%. A similar trend was also reported with bur beggarticks where seed germination was significantly lower at oxygen concentrations of 21% versus oxygen concentrations of 5 and 10% (Benvenuti and Macchia 1997). Exposure to light and normoxia (21% oxygen) with adequate moisture may function as a signal that the seed is not below the soil surface and

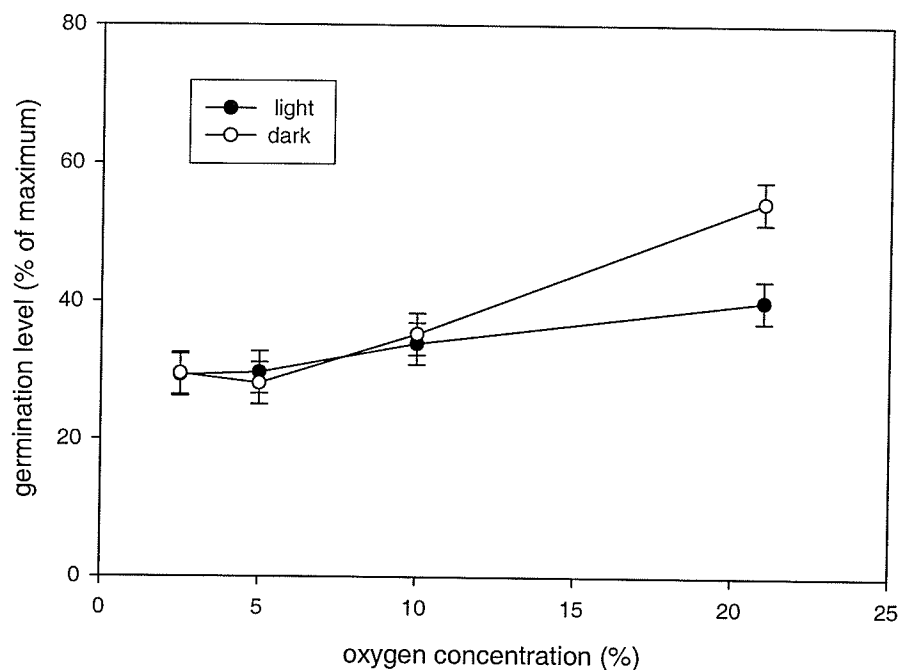
thus inhibit seed germination.



**Figure 4-1.** The effect of oxygen concentration and osmotic potential on seed germination for all species combined.

In experiment three, seeds exposed to light had slight increases in germination with increasing oxygen concentrations (Figure 4-2). When seeds were kept in the dark, germination increased significantly from 5 to 21% oxygen, rising significantly higher than germination levels obtained when seeds were exposed to light. This experiment supports the theory that light exposure and high oxygen concentrations interact to limit seed germination for some species.

There was also a significant interaction between exposure to light and osmotic potential in experiment three. At low osmotic potentials (-0.5 MPa) seeds kept in the dark had significantly higher germination levels than seeds exposed to light. At high osmotic potentials the presence of light did not significantly affect germination. Light may inhibit germination of



**Figure 4-2.** The effect of oxygen concentration and osmotic potential on seed germination for all species combined.

some species when seeds are exposed to relatively dry conditions. Therefore, weed flushes following tillage should occur predominately when the soil has a high moisture content (Roberts and Potter 1980). Weed flushes may be delayed until rainfall or irrigation following tillage if the soil is dry.

### Annual Weed Species

**Barnyardgrass.** In experiment one, barnyardgrass seed germination was significantly reduced when seeds were kept in the dark compared to when they were exposed to light (Table 4-1). The effects of light interacted significantly with osmotic potential ( $p=0.0001$ ) for barnyardgrass seed germination in experiment three. Exposure to light allowed a significant increase in seed germination with increasing osmotic potential (Figure 4-3). For seeds in darkness, increasing osmotic potential did not lead to increasing germination. Taylorson and Dinola (1989) also reported a light requirement

for barnyardgrass seed germination. They found that exposure to very low light intensities was sufficient to induce germination.

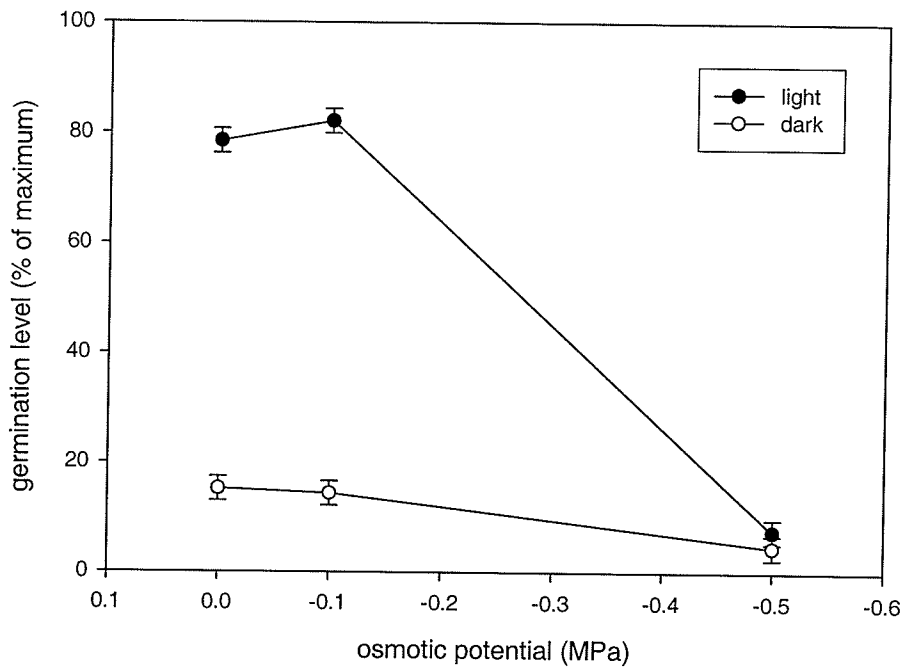
**Table 4-1.** The effect of light exposure on percent of maximum weed seed germination in experiment 1.

Species	light	dark
	-----% germination-----	
Barnyardgrass	69 a <sup>a</sup>	24 b
Canola	91 a	84 b
Curly dock	47 a	32 a
Dandelion	68 a	57 a
Field pennycress	62 a	62 a
Foxtail barley	84 a	78 a
Green foxtail	81 a	84 a
Perennial Sowthistle	33 a	28 a
Spring wheat	86 a	88 a
Wild mustard	44 a	45 a
Wild oat	74 a	72 a

<sup>a</sup>Within species least squares means followed by different letters are significantly different according to LSD at P=0.05.

When osmotic potential was not a limiting factor (seeds placed in water) and seeds were exposed to light, barnyardgrass seed germination was not affected by oxygen concentration (Table 4-2). This is not surprising since barnyardgrass has the rare ability to germinate in the complete absence of oxygen (Rumpho and Kennedy 1981). In experiment two, when the seeds were exposed to light, the effects of oxygen concentration interacted significantly with osmotic potential (Figure 4-4). Very little germination occurred at -1 MPa. At an osmotic potential of -0.01 MPa, germination increased when oxygen concentration increased from 2.5 to 10% oxygen. Germination then declined when oxygen concentration increased from 10 to 21%.





**Figure 4-3.** The effect of osmotic potential and light exposure on barnyardgrass seed germination.

A similar pattern was noted when osmotic potential was  $-0.5$  MPa where germination increased with oxygen concentrations between 2.5 and 5% and declined when oxygen concentration was raised above 5%. Yoshioka et al. (1998) reported that carbon dioxide levels in the soil increased following rainfall and that this increase was sufficient to promote barnyardgrass germination. They hypothesized that low oxygen concentrations and high carbon dioxide levels in the soil may be used as a signal in barnyardgrass seeds to detect high moisture levels. Our results may support this hypothesis. It appears that when barnyardgrass seeds are exposed to light and have sufficient moisture, oxygen concentration above 5-10% limit seed germination. When exposed to light and moisture stress germination is inhibited and sensitivity to oxygen concentration increases with germination being inhibited at oxygen concentrations above 5%. High oxygen concentrations and exposure to light inhibit barnyardgrass seed germination and may act as a signal preventing soil surface germination or germination during very dry periods. Elevated carbon dioxide concentrations combined with low oxygen concentrations may

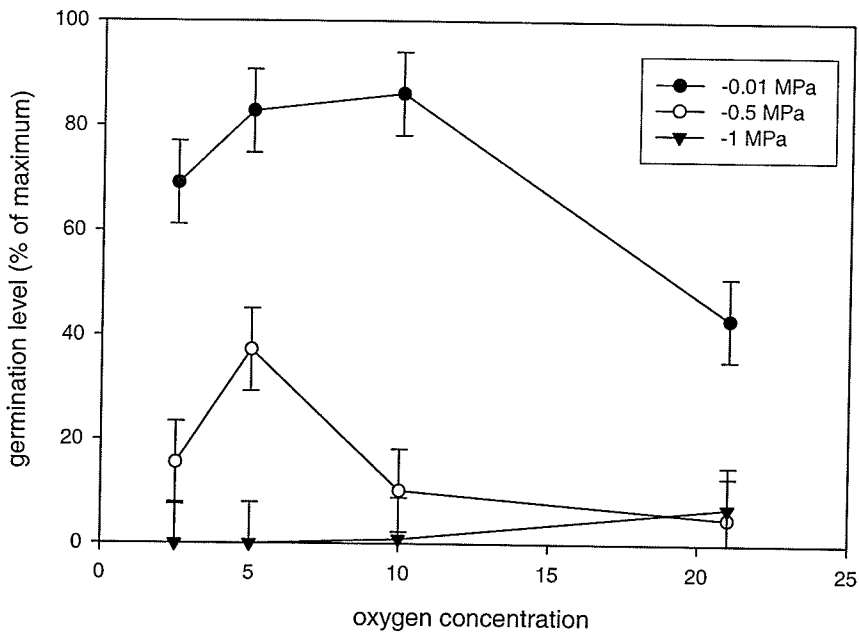
further strengthen the signal to germinate and promote germination below the surface during periods of high soil moisture content (Yoshioka et al. 1998).

**Catchweed bedstraw.** In experiment one there was no significant interaction between oxygen concentration and light conditions for any species except catchweed bedstraw. Catchweed bedstraw seed germination increased significantly with increasing oxygen concentration when seeds were kept in the dark but there was much less of an effect when seeds were exposed to light (Figure 4-5). In experiment three, the effects of light interacted significantly with oxygen concentration ( $p=0.0006$ ). Catchweed bedstraw seed germination generally increased with increasing oxygen concentration and this increase was greater when the seeds were not exposed to light (Figure 4-6).

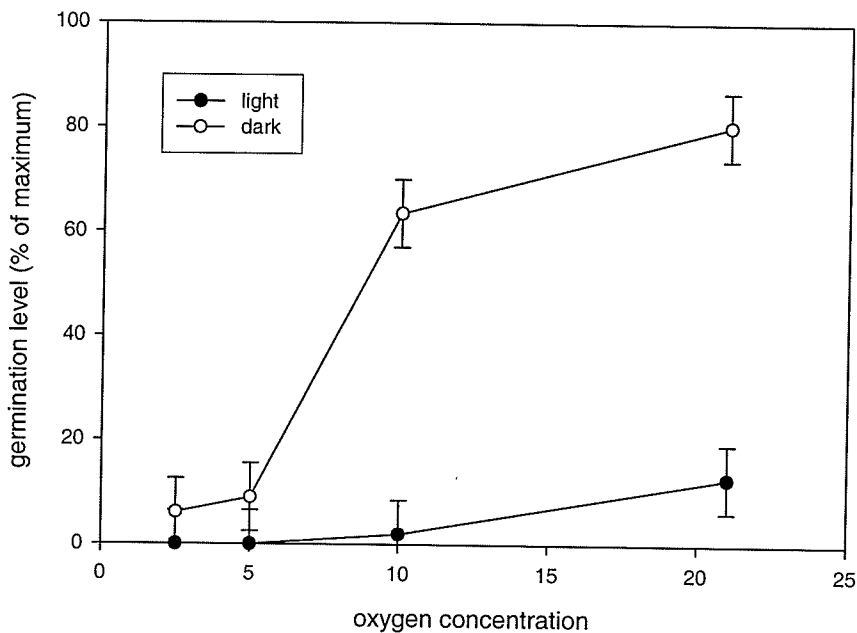
**Table 4-2.** The effect of oxygen concentration on plant seed germination averaged across light and dark conditions. Data from experiment 1.

Species	Oxygen concentration (%)			
	2.5	5	10	21
	----- % of maximum -----			
Barnyardgrass	44 a <sup>a</sup>	44 a	52 a	48 a
Canola	84 b	85 b	90 ab	92 a
Curly dock	47 a	42 a	36 a	32a
Dandelion	56 a	67 a	67 a	62 a
Field pennycress	43 c	63 b	62 b	78 a
Foxtail barley	82 a	83 a	81 a	77 a
Green foxtail	70 b	86 a	84 a	90 a
Perennial Sowthistle	14 b	36 a	34 a	38 a
Spring wheat	80 a	91 a	90 a	88 a
Wild mustard	19 c	35 bc	48 b	75 a
Wild Oat	66 a	76 a	74 a	76 a

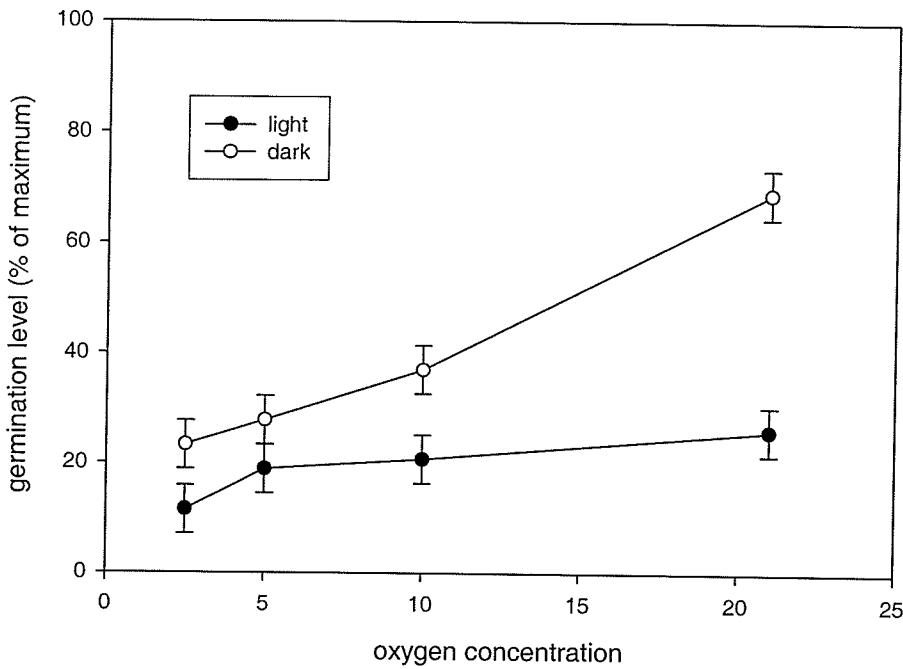
<sup>a</sup>Within species least squares means followed by different letters are significantly different according to LSD at  $P=0.05$ .



**Figure 4-4.** The effect of oxygen concentration and osmotic potential on barnyardgrass seed germination.



**Figure 4-5.** The effect of oxygen concentration and light exposure on catchweed bedstraw seed germination. Data from experiment 1.



**Figure 4-6.** The effect of oxygen concentration and light exposure on catchweed bedstraw seed germination. Data from experiment 3.

Seeds of catchweed bedstraw do not readily germinate on the soil surface and germinate best when they are buried at depths between 0 and 5 cm (Froud-Willaims et al. 1984, Rottele 1980). Poor surface germination may be due to light inhibition at even low light intensities (Malik and Vanden Born 1987). Poor germination at depths below 5 cm may be caused by a lack of sufficient gas diffusion rates to or away from the seed.

**Field pennycress.** Oxygen concentration had a large impact on field pennycress seed germination (Table 4-2). The highest level of germination was obtained at an oxygen concentration of 21%. Seed germination levels at oxygen concentrations of 10 and 5% were significantly lower than germination levels at 21% and significantly higher than germination levels at 2.5%. Field pennycress seed germinates best on or near the soil surface (manuscript #1) and lack of oxygen may act as a trigger initiating secondary dormancy when seed is buried at deeper soil depths. Freshly harvested field pennycress seed is dormant but dormancy is lost after a relatively short period of afterripening (Hazebroek and Metzger 1990). In our experiments, light had no significant impact on

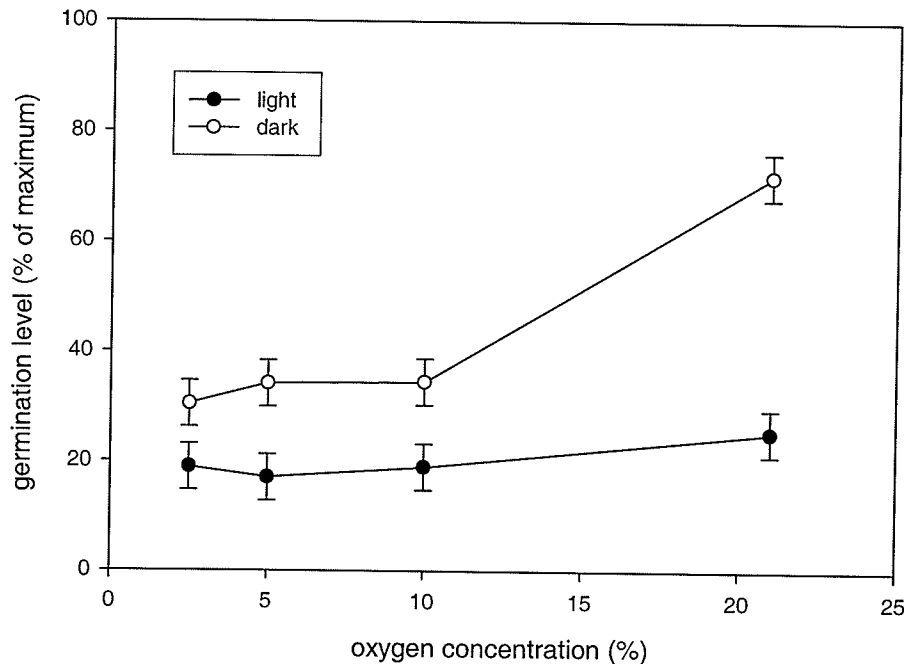
field pennycress seed germination, but other studies have reported that light promotes germination of this species (Hazebroek and Metzger 1990).

**Green foxtail.** In experiment one, green foxtail was not affected significantly by exposure to light (Table 4-1). Freshly harvested green foxtail seeds are nearly completely dormant but relatively short storage periods (3-4 weeks) at low temperatures (6 °C) will break dormancy (Vanden Born 1971). The green foxtail seeds used in these experiments had been stored at 4 °C for extended periods of time and may not have had a light requirement to break dormancy. Green foxtail seed germination was significantly lower at oxygen concentrations of 2.5% than at all other oxygen concentrations in experiment one (Table 4-2). In experiment two and three, oxygen concentration had no significant impact on germination of green foxtail seed. Green foxtail germination can occur from soil depths up to 12 cm (Vanden Born 1971) although du Croix Sissons et al. (2000) reported that most green foxtail seedlings in agricultural fields recruited from depths between 1.2 and 4.2 cm. Our results suggest that green foxtail seed germination is relatively insensitive to oxygen concentration and there must be other environmental factors which prevent germination when oxygen concentrations are above 2.5%.

Germination of green foxtail was significantly higher at -0.01 MPa than -0.5 MPa and significantly higher at -0.5 MPa than at -1 MPa. Blackshaw et al. (1981) reported even stronger inhibition of green foxtail germination with germination completely inhibited at -0.78 and -1.5 MPa. Dry soil may limit green foxtail germination by inducing dormancy (Forcella and Decker 1997).

**Wild mustard.** In experiment one, exposure to light did not significantly affect wild mustard seed germination (Table 4-1). Holm (1972) found that freshly harvested wild mustard seeds germinated equally well in light or dark. After burial in soil for six months the seeds required light for germination. Wild mustard seeds used in this experiment had been kept at a constant temperature in a relatively humid environment and may never have developed a light requirement for germination. In experiment three the effect of light on wild mustard seed germination interacted significantly with oxygen concentration ( $p=0.0002$ ). Wild mustard germination remained consistently low at all

oxygen concentrations when seeds were exposed to light (Figure 4-7). When seeds were not exposed to light, germination increased significantly when oxygen concentration increased from 10 to 21%. This suggests that germination may be optimal for seeds placed near but not on the soil surface. Deep burial of seeds in the soil and exposure to low oxygen concentrations and anaerobic metabolites may result in conversion of seeds from primary to secondary dormancy and this may cause the induction of a light requirement for germination (Holm 1972). Dormancy and longevity of buried wild mustard seeds may be a result of low oxygen concentrations (Mulligan and Bailey 1975). In experiment one and three, wild mustard seed germination consistently increased with increasing oxygen concentration (Table 4-2).

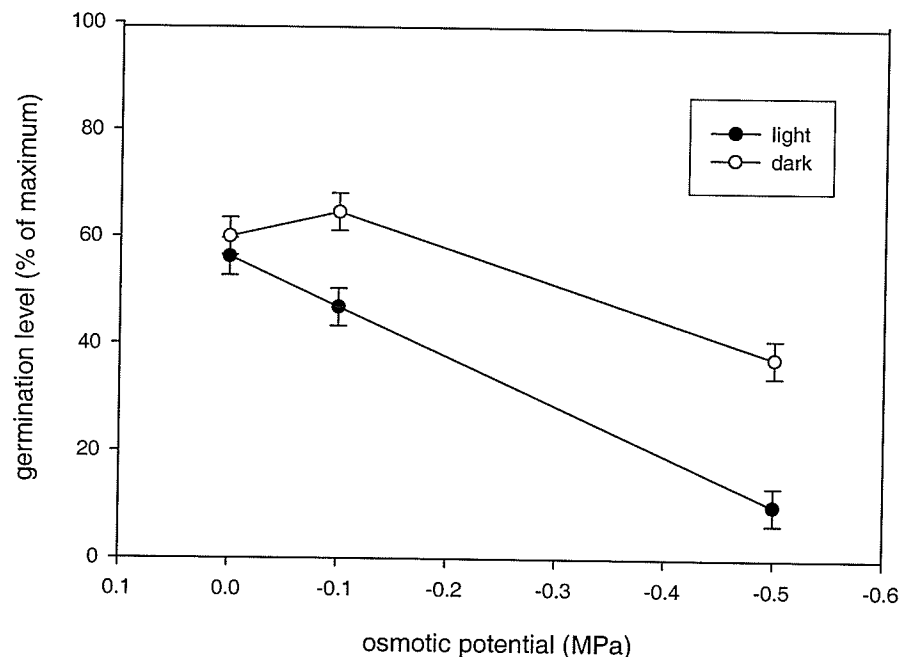


**Figure 4-7.** The effect of oxygen concentration and light exposure on wild mustard seed germination.

**Wild Oat.** In experiment one, wild oat seed germination was not affected significantly by exposure to light (Table 4-1). Wild oat seed germination was not affected by oxygen concentration in either experiment one or two (Table 4-2 and 4-3). In experiment three,

wild oat seed germination was 59% when oxygen concentration was 21%, which was a significantly higher germination level than at all other oxygen concentrations.

There was a significant interaction between the effects of light and osmotic potential ( $p=0.0034$ ) on wild oat seed germination in experiment three. As osmotic potential of the solution increased, wild oat germination generally increased (Figure 4-8). Osmotic potential had



**Figure 4-8.** The effect of osmotic potential and light exposure on wild oat seed germination.

a greater impact on seed germination in the presence of light suggesting that exposure to light may break dormancy in these wild oat seeds allowing increased germination. Hou and Simpson (1990) also reported an interactive effect between light and water deficit on wild oat seed germination. In their experiment seed germination was only inhibited by far-red light when seeds were exposed to water deficit. They concluded that the effects of light on dormancy level depended on the dormancy state of the seed. The results of our experiment differ from those of Hsiao and Simpson (1971) in that conditions of low water availability germination of wild oat seeds are inhibited by exposure to light and in conditions of high water availability germination of wild oat seed is promoted by light.

Many other studies have shown that light inhibits wild oat germination (Sharma and Vanden Born 1978). Differences in results between authors is not surprising because wild oat seed response to light is dependent on the dormancy state of the seed (Hou and Simpson 1993). Hou and Simpson (1991) suggest that germination of freshly harvested non-dormant seeds of wild oat may be inhibited by exposure to light thus preventing the germination of seeds in the fall when they mature and fall to the surface. The response of dormant wild oat seeds to light depends on the manipulation of dormancy states. Since there appears to be a wide range of dormancy states within a population of wild oat seeds in their natural environment (Hou and Simpson 1990) the effect of light on a wild oat population is likely to be highly variable.

**Table 4-3.** The effect of oxygen concentration on weed seed germination. Results from experiment 2.

Species	oxygen concentration (%)			
	2.5	5	10	21
	----- % of maximum-----			
Canola	39 b	41 b	49 ab	58 a
Dandelion	16 a <sup>a</sup>	17 a	16 a	24 a
Foxtail barley	27 a	29 a	33 a	31 a
Green foxtail	37 a	28 a	34 a	30 a
Perennial sowthistle	8 a	12 a	8 a	6 a
Spring wheat	73 a	63 ab	74 a	47 b
Wild oat	17 ab	8 b	26 a	20 ab

<sup>a</sup>Within species least squares means followed by different letters are significantly different according to LSD at P=0.05.

**Crop Species.** Wheat seed germination levels were not affected by exposure of seeds to light. Wheat seed germination was not affected by oxygen concentration in experiment one but slightly lower germination occurred at oxygen concentrations of 21% versus all other oxygen concentrations in experiment two (Table 4-3). Al-Ani et al. (1985) also



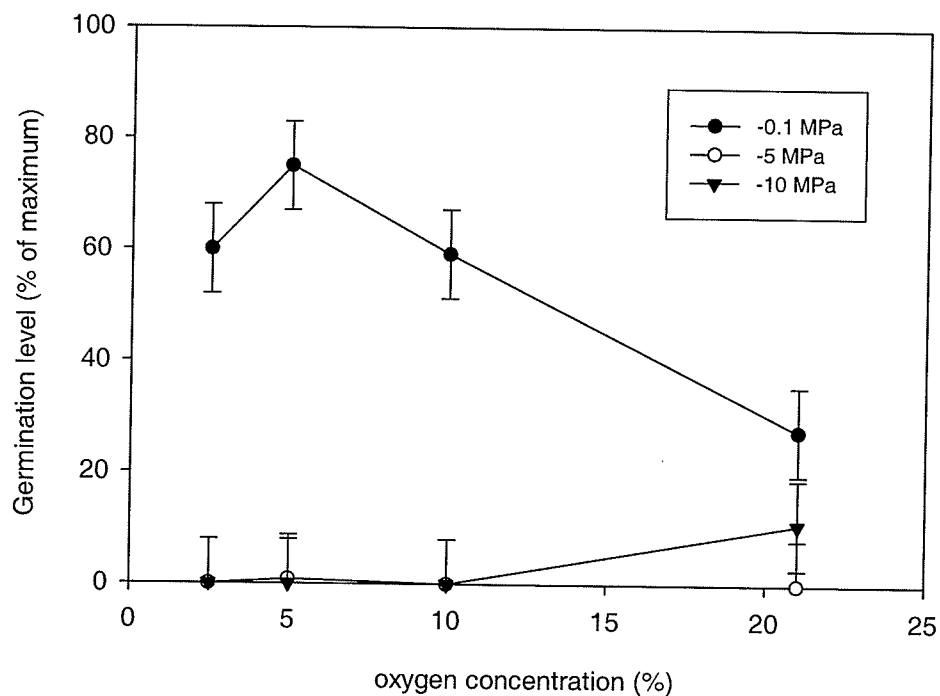
found that wheat germinated relatively well at all oxygen concentrations below 21% with germination of wheat even occurring at oxygen concentrations as low as 0.1%. Wheat was the only species for which seed germination was not significantly different between osmotic potentials of  $-0.01$  and  $-0.5$  MPa. Based on these results, one might expect volunteer wheat to become a problem volunteer weed in no-till situations due to its ability to germinate successfully on the surface even in drier conditions.

In experiment one canola seed germination was significantly reduced in the absence of light. López-Granados and Lutman (1998) found that nearly 100% of freshly harvested canola seed germinated in light or in dark. They also found that secondary dormancy could be induced in a proportion of the seeds by exposing them to low osmotic potentials in the dark. In our experiment, increased canola seed germination with exposure to light suggests that at least a proportion of the seed lot we used had developed a light requirement for germination. Germination was also significantly reduced at oxygen concentrations of 2.5 and 5% when compared to germination at oxygen concentrations of 21% (Table 4-2). A similar effect of oxygen concentration on canola seed germination was found in experiment two when germination was averaged over all osmotic potentials. Canola seed germination was significantly affected by osmotic potential with higher seed germination at  $-0.01$  MPa than at  $-0.5$  MPa and significantly higher germination at  $-0.5$  MPa than at  $-1$  MPa (Table 4-4). To control volunteers López-Granados and Lutman (1998) suggested avoiding fall tillage which will bury freshly harvested non-dormant seeds exposing them to darkness and typically dry soil conditions. Seeds exposed to these conditions might enter dormancy creating future volunteer problems.

### **Perennial weed species**

Light did not inhibit seed germination for any of the four perennial weed species used in these experiments (Table 4-1). Seeds of all four perennial weed species have been shown to germinate best on or near the soil surface (Best et al. 1978; manuscript #1; Letchamo and Gosselin 1996, Weaver and Cavers 1979) with light often promoting seed germination (Letchamo and Gosselin 1996). When osmotic potential was not a limiting

factor, curly dock, dandelion and foxtail barley seed germination was not affected by oxygen concentration (Table 4-2). Perennial sowthistle seed germination was significantly lower at oxygen concentrations of 2.5% than at all other oxygen concentrations. In experiment two, there was a significant interaction between oxygen concentration and osmotic potential for curly dock seed germination levels (Figure 4-9). Very little germination occurred at osmotic potentials of  $-0.5$  and  $-1$  MPa.



**Figure 4-9.** The effect of oxygen concentration and osmotic potential on curly dock seed germination.

At  $-0.01$  MPa germination increased when oxygen concentrations were decreased from 21 to 5%. Germination at oxygen concentrations of 2.5% was significantly lower than at oxygen concentrations of 5%. Dandelion, foxtail barley and perennial sowthistle seed germination was not affected by oxygen concentration even when exposed to various osmotic potentials. Osmotic potential also impacted perennial sowthistle seed germination where germination levels at  $-0.5$  and  $-1$  MPa were significantly lower than germination levels at  $-0.01$  MPa. Germination of dandelion and foxtail barley seed was not as sensitive to osmotic potential as curly dock seed. Seed germination for the former

two species was significantly higher at  $-0.01$  MPa than at  $-0.5$  MPa and significantly higher at  $-0.5$  MPa than at  $-1$  MPa (Table 4-4). Osmotic potential had a greater impact than oxygen concentration on seed germination for all three of these species. However, at osmotic potentials below 0, germination levels of curly dock seed decreased with increasing oxygen concentration. For the few perennial species included in this study, oxygen concentration did not play a large role in inhibiting seed germination. Light and osmotic potential, both deterministic variables for surface germination capability, had a more significant impact on seed germination for these species.

On the basis of our results using a range of weed species with different life cycles we conclude that the impact of light, osmotic potential and oxygen concentration on seed germination is species specific. Exposure to light and high oxygen concentration may inhibit barnyardgrass germination and act as a signal preventing germination in dry soils or on the soil surface. Light exposure may inhibit soil surface germination of catchweed bedstraw while low oxygen concentrations may inhibit deep germination. Light inhibition and promotion of germination in oxygen concentrations between 10 and 21% may favour wild mustard germination on or near the surface. Wild oat appears to express a range of dormancy states and reactions to light within a single population. Burial of annual weed species, such as wild mustard and canola, for which seed germination is sensitive to oxygen concentration may induce secondary dormancy in seeds and increase the probability of future weed or volunteer problems. Seed germination of wheat was less sensitive to osmotic potential and light than canola in these experiments, suggesting that volunteer wheat may have a greater potential than canola to become a volunteer weed in no-till fields.

Seed germination of the perennial weed species studied in this experiment was not generally affected by oxygen concentration but appeared to be somewhat sensitive to light and osmotic potential. Seed germination for many perennials may occur in the fall if adequate moisture exists and if seeds are left on the soil surface. Fall tillage may bury seeds of these species and cause secondary dormancy, leading to future weed problems.

**Table 4-4.** The effect of osmotic potential (MPa) on weed seed germination.

Species	Osmotic Potential (MPa)		
	-0.01	-0.5	-1
	-----% of maximum-----		
Canola	84 a	42 b	15 c
Dandelion	46 a <sup>a</sup>	7 b	1 c
Foxtail barley	56 a	29 b	5 c
Green foxtail	67 a	22 b	9 c
Perennial sowthistle	21 a	1 b	4 b
Spring wheat	83 a	69 a	40 b
Wild oat	42 a	11 b	1b

<sup>a</sup>Within species least squares means followed by different letters are significantly different according to LSD at P=0.05.

For the species we tested, microenvironmental cues signalling depth within the soil profile varied broadly among species. Agronomic practices that limit seed germination and encourage seed death for a particular weed species may help control a specific weed invasion. However, in mixed weed populations, altering agronomic practices to control the recruitment of one weed species may favour the recruitment of another. More work needs to be done to relate the results of controlled experiments on germination, such as those we have conducted, to the actual conditions experienced by seeds in the field and how these field conditions vary with depth and agronomic practice. In this manner, the information we have presented can then be used to predict the relative recruitment level of given species under certain agronomic practices and used to model approaches to limit their recruitment.

**MANUSCRIPT #5**  
**IMBIBITION RESPONSE OF GREEN FOXTAIL, CANOLA, WILD MUSTARD**  
**AND WILD OAT TO DIFFERENT OSMOTIC POTENTIALS**

**ABSTRACT**

The ability of seeds to imbibe water is dependant on the difference in water potentials between the seed and the surrounding medium as well as seed diffusivity. Differences in imbibition rates at various osmotic potentials may impact the timing or the number of seeds germinating. The proportional moisture content and imbibition rate of canola, green foxtail, wild mustard and wild oat was examined over time in osmotic solutions of 0, -0.5 and -1 MPa. Average wild oat imbibition rate was significantly higher than all other species studied while the average green foxtail imbibition rate was significantly lower than all other species studied. Differences between imbibition rates may have been caused by differences in seed size or seed diffusivity. Wild mustard and canola had the highest proportional moisture content at 25 hours and were the only two species to achieve greater than 80% germination within this time frame. Germination levels were reduced in osmotic solutions of -0.5 and -1 MPa compared to 0 MPa for all species. Species differ in their ability to imbibe water as well as their ability to germinate at lower seed moisture contents.

## INTRODUCTION

Seed germination is partially controlled by water potential and temperature (Roman et al. 1999). The first step towards seed germination is the uptake of water, often called imbibition. This essentially passive process is controlled by the difference in water potential between the seed and surrounding medium (Shaykewich and Williams 1971a, Vertucci 1989). The water potential in a dry seed may approach levels of  $-100$  MPa (Shaykewich and Williams 1971a) which is far lower than water potentials that exist in most soils during a growing season. Small changes in soil water potential will have very little influence on early water uptake in seeds due to the extreme differences between initial water potentials in a seed and typical soil water potentials. As the seed imbibes water, differences between water potential of the soil and the seed decrease. During later stages of imbibition, soil and seed water potentials are similar enough that small changes in soil water potential influence the imbibition of water by the seed (Shaykewich and Williams 1971a). It is during this stage of late imbibition that dry soils may hinder or prevent seed germination.

Water uptake during germination is generally classified into three phases: rapid hydration, a lag period, and a second phase of rapid hydration (King and Oliver 1994, Vertucci 1989). The first phase of rapid water uptake typically occurs at seed water contents below 7-8% (Vertucci and Leopold 1984). For at least some species, seeds in this phase remain in primary dormancy (Esashi et al. 1993) with very little biochemical activity occurring, although light reactions and some oxidative processes are possible (Vertucci 1989). Gallagher and Cardina (1997) found that to reduce photoinduction of redroot pigweed by 50% the water potential of the soil would have to be between  $-3.0$  and  $-4.0$  MPa. They concluded that complete inhibition of photoinduction of redroot pigweed germination would not be expected even under severe drought conditions.

The second phase typically occurs when seed moisture contents is between 8 and 24% (Vertucci and Leopold 1984). Afterripening primarily occurs at seed water content levels between 7 and 14% moisture (on a dry weight basis) for a variety of species (Esashi et al. 1993; Leopold et al. 1988) and may be inhibited at moisture contents above or below this range. In wild oat, afterripening primarily occurs when seeds are in the 5 to

20% moisture range (Foley 1994). Within this second phase, enzymatic and nonenzymatic activity occurs but there is insufficient moisture to allow mitochondrial electron transport to proceed. The third phase typically occurs when seed moisture content is above 24% (Vertucci and Leopold 1984). It is during this third phase that radicle emergence, respiration and mitochondrial activity occur in seeds of many species (Vertucci 1989).

Results from the literature suggests that there is little relationship between seed water potential and the rate of seed imbibition (Vertucci 1989). Therefore, seed diffusivity or seed size plays an important role in determining the rate of imbibition, while differences in water potential between the seed and the soil determine the extent of imbibition. If the physiological structure, chemical composition or the seed size alter the rate or extent of seed imbibition (proportional water content) they may also affect the timing of seed germination. When seed solution contact is guaranteed over a specified period of imbibition, larger seeds should have a higher rate of imbibition but a lower proportional water content than smaller seeds. The smaller surface to volume ratio of large seeds may mean that larger seeds will require a longer period of time to imbibe an adequate proportional moisture content for germination to occur. Consequently, where seed soil contact is guaranteed smaller seeds should germinate more rapidly than larger seeds.

The objective of this experiment was to compare the seed imbibition characteristics of four plant species at various osmotic potentials over time.

## MATERIALS AND METHODS

Canola, green foxtail, wild mustard and wild oat seeds collected in Manitoba, Canada were used in this experiment. All seeds were kept in a seed storage room at 4 °C until the beginning of the experiment. These species were selected because they are common weeds on the Northern Great Plains, they represent a range of seed sizes and because they differ in their germination response to osmotic potential (manuscript #4).

In previous experiments using the same seed collections, average seed weight had been calculated for each of these species. Approximately fifty seeds, as determined by

weight, of each species were placed between two filter papers in individual petri dishes. The filter paper in each petri dish was soaked with six millimetres of an osmotic solution. All species were tested in osmotic solutions of 0, -0.5 or -1 MPa. Osmotic solutions were made with Polyethylene glycol 6000 and distilled water using the equations described by Michel (1983). Additional solution was added to the petri dishes throughout the experiment if the paper did not remain completely saturated. Petri dishes were kept in a lighted room with fluorescent bulbs with an average light intensity of  $19 \text{ } \mu\text{mol m}^{-2}\text{s}^{-1}$  at  $24 \text{ } ^\circ\text{C}$ . The experiment was set up in a completely randomized design with four replicates. The experiment was repeated once. The effect of run was not significant so data was combined for the final analysis. Eight replicates of fifty seeds of the same seed collection for each species were weighed and placed in the oven at  $80 \text{ } ^\circ\text{C}$  for 48 hours to determine the dry weight of the seeds. This information was used to calculate the initial moisture content of the seeds when they were placed in the solution.

At 1, 2, 4, 6, 13, 25 and 48 hours seeds were removed from the petri dishes and gently pressed between paper towels to remove external moisture. The seeds were weighed and immediately placed back in the petri dishes. Proportional moisture was determined by subtracting the oven dry seed weight from the wet seed weight and dividing by the oven dry seed weight. Rate of uptake was calculated by subtracting the seed weight of two consecutive measurements and dividing by the elapsed time. The data was analysed as a randomized block design in SAS (SAS institute Inc. 1990) using a general linear model and the repeated statement. Means were compared using least squares means comparisons. The data was normally distributed with a constant variance.

## RESULTS AND DISCUSSION

### Rate of Seed Imbibition

The initial moisture content of the seeds was 3, 7, 11 and 13% (dry weight basis) for green foxtail, canola, wild mustard and wild oat, respectively. Vertucci (1989) stated that seeds with a higher initial moisture content imbibe faster than seeds with a low initial



moisture content. The results of our experiment generally support this statement. For example, wild oat, the seed with the highest initial moisture content, had a significantly higher average imbibition rate than the other three species at all osmotic potentials when averaged over time (Table 5-1). As well, the average rate of imbibition for wild oat remained relatively constant between the three osmotic potential treatments. The imbibition rate for canola seed also remained relatively constant across all osmotic potentials. Imbibition rates for wild mustard were not significantly different than for canola at 0 and -0.5 MPa but declined and were significantly lower than canola at -1 MPa (Table 5-1). Green foxtail seed had the lowest initial moisture content and had a significantly lower average rate of imbibition than either wild oat or canola. On average, imbibition rates for wild mustard seed were more responsive to differences in osmotic potential compared to the other three species tested.

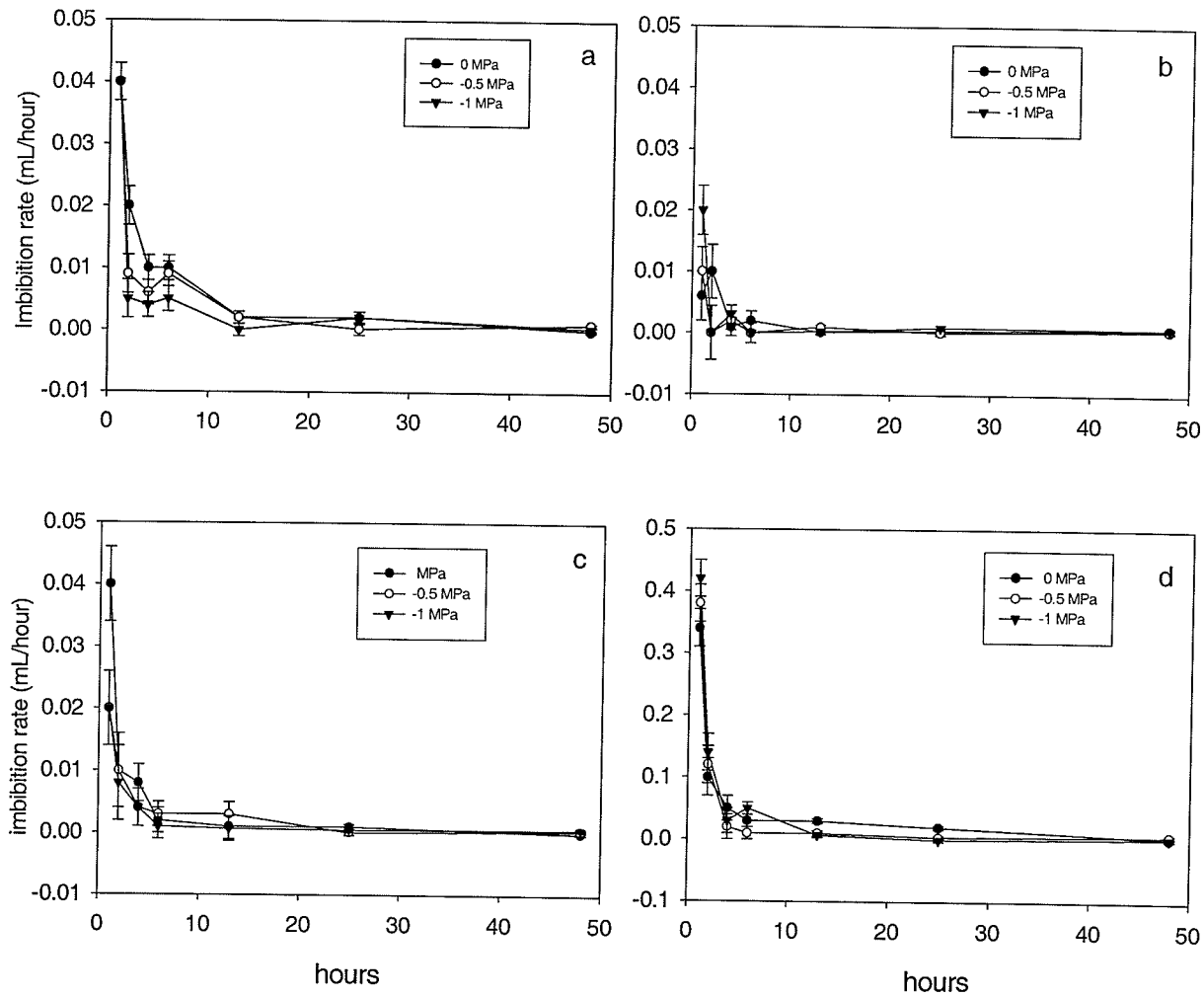
**Table 5-1.** Average imbibition rate ( $\text{mL hour}^{-1}$ ) over time for canola, green foxtail, wild mustard and wild oat seeds exposed to solutions producing osmotic potentials of either 0, -0.5 or -1 MPa.

Species	0 MPa	-0.5 MPa	-1 MPa
	-----mL min <sup>-1</sup> -----		
Canola	0.012 b <sup>a</sup>	0.010 b	0.010 b
Green foxtail	0.003 c	0.002 c	0.004 c
Wild mustard	0.009 b	0.006 bc	0.005 c
Wild oat	0.083 a	0.079 a	0.094 a

<sup>a</sup>Least squares means of imbibition rates within the same osmotic potential with different letters are significantly different  $P < 0.05$ .

Using an average rate of seed imbibition to estimate water uptake may not be the most appropriate way to compare imbibition response among species because imbibition rates changed over time ( $p \leq 0.0002$ ). The rate of imbibition for all species declined exponentially and approached zero as the water potential of the seeds increased (Figure 5-1). Rates of wild oat seed imbibition generally remained significantly higher than rates of imbibition for all other species throughout the experiment at all osmotic potentials ( $p < 0.05$ ), (Figure 5-1). There were no significant differences in imbibition rate over time among any of the remaining three species except during the first hour of imbibition at 0 MPa when green foxtail seed had a significantly lower rate of imbibition than canola or wild mustard seed (data not shown). Green foxtail seed had limited ability to take

advantage of the large difference in seed and solution water potentials early in the experiment and imbibition rates remained low. This suggests that differences in



**Figure 5-1.** Imbibition rate over time of (a) canola seed, (b) green foxtail seed, (c) wild mustard seed, and (d) wild oat seed in solutions producing osmotic potentials of 0, -0.5 and -1 MPa.

diffusivity between seeds of green foxtail, wild mustard and canola may be small and only evident when the difference between the seed and the soil osmotic potential is large. Differences between rates of imbibition among species may have been due to differences in seed size or diffusivity. In this experiment it was not possible to differentiate between

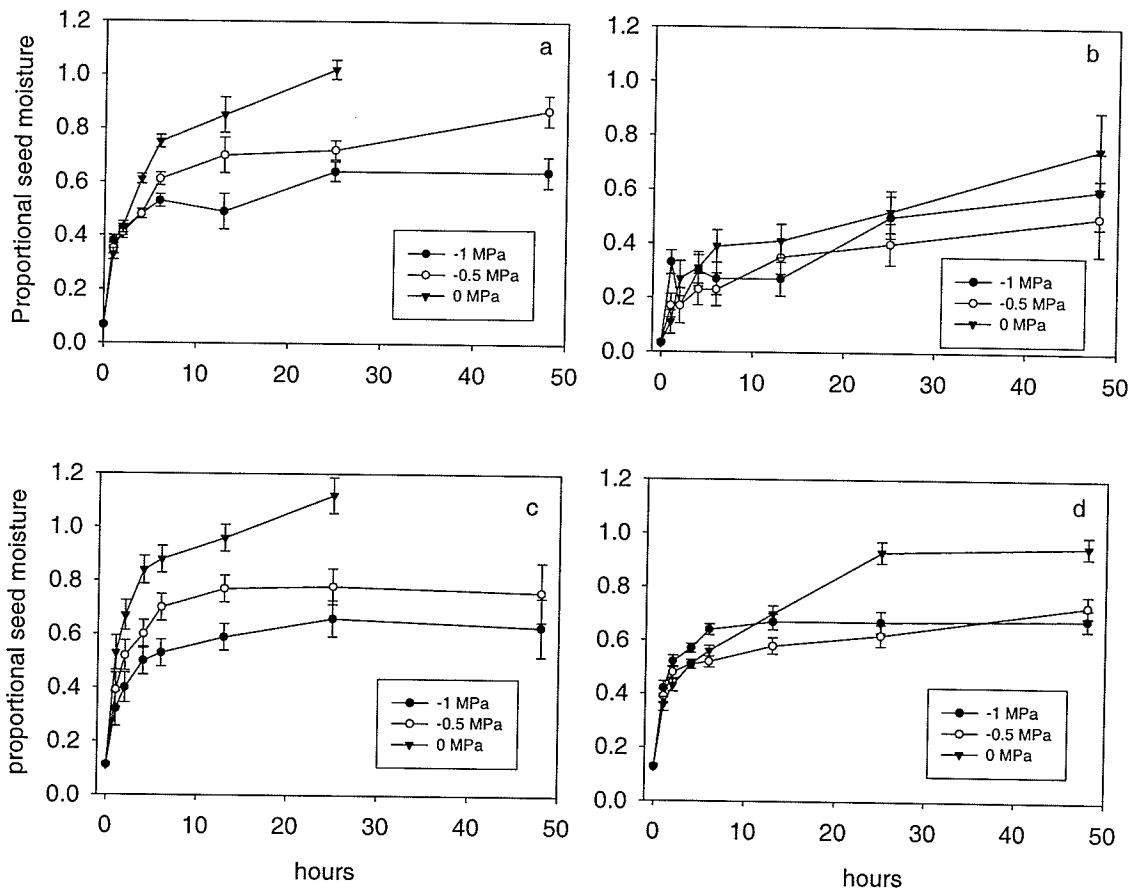
the two. Wild oat seeds were the largest seed used in this experiment and wild oat had the highest rate of imbibition over time. In petri dishes where seed-solution contact is high, larger seeds have a greater area of contact and are able to imbibe water at a greater rate. However, the larger the seed the lower the area to volume ratio and the smaller the rate of imbibition per unit volume of seed. Consequently, wild oat absorbed water at a greater rate than other seeds but took longer to reach moisture levels high enough to allow germination. In soil, the seed to soil contact plays an important role in water absorption especially as the water content of the seed increases (Shaykewich and Williams 1971a).

Water imbibition rates for wild oat did not differ significantly between osmotic potentials early in the experiment, but imbibition rates in 0 MPa remained significantly higher than imbibition rates in  $-0.5$  and  $-1$  MPa between 13 and 25 hours (Figure 5-1d). At 48 hours, the rate of uptake was not significantly different between osmotic potentials. Canola seed imbibition rate in 0 MPa was significantly higher than for seeds in  $-0.5$  or  $-1$  MPa at two hours and tended to be higher until 12 hours (Figure 5-1a). The rate of imbibition for wild mustard seed was significantly higher in 0 MPa compared to  $-5$  and  $-10$  MPa at one hour but from 2 through 48 hours, the imbibition rate did not differ significantly between osmotic potentials (Figure 5-1c). Increased proportional moisture content of wild mustard and canola seeds in 0 MPa compared to  $-0.5$  and  $-1$  MPa was due to the higher rate of imbibition that occurred during the early stages of the experiment. While imbibition rates were highest for wild oat seeds, the time required to attain similar proportional moisture contents as the smaller seeds used in this experiment, was greater due to the decreased surface to area ratio of the large wild oat seed. Rate of imbibition by green foxtail seeds was highly variable during the first 6 hours but was generally very low and it did not vary significantly after 13 hours (Figure 5-1b).

### **Proportional seed moisture and germination**

Due to the low initial proportional moisture content of green foxtail seeds, the initial water potential within the seeds would have been well below the water potential treatments used in this experiment. As a result, green foxtail was the only species in this

experiment for which proportional moisture content of the seeds did not differ significantly between the three osmotic treatments over time (Figure 5-2b). However, at 48 hours greater than 80% germination was observed for green foxtail seeds in water and no germination was observed for seeds in osmotic solutions of  $-0.5$  and  $-1$  MPa. Therefore, the proportional moisture content must not be the sole trigger influencing seed germination. These results are similar to those of Blackshaw et al. (1981) who reported a complete inhibition of green foxtail germination at  $-0.78$  and  $-1.53$  MPa. Douglas et al. (1985) referenced a study by Manthey and Nalewaja who found 75% germination of green foxtail seeds at 0 MPa and 3% germination at  $-0.8$  MPa. In previous experiments



**Figure 5-2.** Proportional seed moisture content over time of (a) canola seed, (b) green foxtail seed, (c) wild mustard seed, and (d) wild oat seed in solutions producing osmotic potentials of 0,  $-0.5$  and  $-1$  MPa.

using the same seed lots we found 67, 22 and 9% germination levels of green foxtail after 14 days in osmotic solutions of 0,  $-0.5$  and  $-1$  MPa (manuscript #4). In the 0 MPa

treatment, proportional moisture content of green foxtail seed at 48 hours was significantly lower than all other species tested and yet greater than 80% of this seed germinated. The ability of green foxtail to imbibe water at low water potentials and germinate at relatively low proportional seed moisture content may be an adaptation allowing seeds of this species to germinate near the soil surface (du Croix Sissons et al. 2000) in warm microsites (Douglas et al. 1985).

Using moisture characteristic data from Shaykewich and Williams (1971a) we can see why canola seeds are able to imbibe water at very low osmotic potentials. Using their equation we calculated the osmotic potential of the canola seeds used in this experiment before imbibition to be  $-113$  MPa. Following one hour of imbibition in water the seeds would have had an osmotic potential of  $-2$  MPa, which is still less than the lowest osmotic potential used in this experiment. This helps to explain why we do not find large differences between different osmotic potential treatments in the rate of canola seed imbibition. According to the model of Shaykewich and Williams (1971a), by 13 hours, the osmotic potential of canola seed begins to approach zero and at this stage drier soils may hinder germination.

The proportional quantity of water imbibed by seeds of canola, wild mustard and wild oat was affected significantly by osmotic potential (Figures 5-2). Between 1 and 25 hours the proportional moisture content of wild mustard seed in the 0 MPa treatment was significantly higher than for all other species (Figure 5-2). At 25 hours, the proportional moisture content of canola and wild mustard seeds were not significantly different at 101 and 102%, respectively (Figures 5-2a and c). In the 0 MPa treatment greater than 80% germination occurred for both of these species when proportional moisture content reached these levels and as a result no further weighing of the seed in 0 MPa treatment was done after 25 hours. Wild mustard and canola seeds in the  $-0.5$  or  $-1$  MPa treatments never reached proportional moisture levels this high and after 25 hours no seed germination occurred for these two species at these osmotic potentials. By 48 hours, 25 and 10% germination occurred for wild mustard and canola, respectively, in the  $-0.5$  MPa treatment, while no germination occurred for either of these species in the  $-1$  MPa treatment. As the proportional seed moisture content of wild oat and canola increased the percentage germination and the time to reach maximum germination increased. In this

respect, seed imbibition appears to have had an additive effect on seed germination for these two species.

The proportional moisture content of wild mustard and canola seeds in either the  $-0.5$  MPa or  $-1$  MPa treatments was not significantly different between the two species (data not shown). However, these two species did react differently to the changes in osmotic potential. Proportional seed moisture content of wild mustard was significantly higher in the  $-0.5$  MPa versus the  $-1$  MPa treatments at 2 to 12 hours but not significantly different from 12 to 48 hours. For canola seed, the proportional moisture content did not differ significantly between the  $-0.5$  and the  $-1$  MPa treatments until after 6 hours. The proportional seed moisture content remained significantly different between osmotic potential treatments for the remainder of the experiment. Wild mustard seeds appeared to respond more strongly than canola seeds to a difference in osmotic potential early in the experiment. As well, during the first 25 hours of imbibition, wild mustard seeds achieved a slightly higher proportional moisture content than the other species used in this experiment (data not shown). Since seed diffusivity, not osmotic potential, affects the rate of imbibition (Vertucci 1989), wild mustard seed structure or the greater initial moisture content of the seeds used in this experiment must have allowed for a more rapid uptake of water during the early stages of imbibition compared to the other species. An ability to imbibe rapidly is essential for species that germinate on the soil surface where moisture levels rapidly fluctuate. For some species, germination occurs more rapidly when seeds are exposed to wetting and drying cycles. In these cases the effects of previous imbibition cycles are additive (Baskin and Baskin 1982).

Exposure to low osmotic potentials may induce secondary dormancy in some species (Khan and Karssen 1980; Staniforth and Cavers 1979). Lopez-Granados and Lutman (1998) reported imbibition with osmotic potentials of  $-1.5$  MPa in canola with far red light or dark induced secondary dormancy. They found that a greater proportion of seeds entered secondary dormancy the longer they were exposed to these conditions. Khan and Karssen (1980) reported similar results with osmotic potentials of  $-0.86$  MPa inducing secondary dormancy in *Chenopodium bonus-henricus* L. The drop in seed germination for all species observed in this experiment under low osmotic potentials may have been caused by an induction of secondary dormancy.

No wild oat germination occurred until 48 hours when wild oat seeds had reached a proportional moisture content of 95% (Figure 5-2d). Proportional moisture content of wild oat seeds in the  $-1$  MPa treatment was significantly higher than wild oat seeds in the  $-0.5$  and  $0$  MPa treatments early in the experiment (2-6 hours), but it remained constant at 67% from 13 through 48 hours. During the same time, the proportional moisture content of wild oat seeds in the remaining osmotic potential treatments increased. Proportional moisture content of wild oat seeds in the  $-0.5$  MPa treatment was not significantly different than seeds in the  $-1$  MPa treatment between 25 and 48 hours (Figure 5-2d), and no germination of wild oat seed was observed under either osmotic potential treatment. The proportional moisture content of wild oat seed increased slightly from 93 to 95% from 25 to 48 hours for seeds in the  $0$  MPa treatment. In a previous experiment using the same seed lot, 42, 11, and 1% percent germination of wild oat seed was observed after 14 days in osmotic potential treatments of  $-0.01$ ,  $-0.5$  and  $-1$  MPa, respectively (manuscript #4). Fernandez-Quinantilla et al. (1990) only found a 33% reduction in wild oat seed germination when seeds were placed into treatments with osmotic potentials of  $-1.2$  MPa. It is important to note that germination of wild oat seeds in the field does not ensure recruitment because seeds germinating under low osmotic potentials may not be able to continue their development (Fernandez-Quinantilla et al. 1990).

Dormant seeds requiring cold stratification to become non-dormant must be partially imbibed while they are exposed to low temperatures to break dormancy (Baskin and Baskin 1998). Afterripening of many species typically occurs at proportional moisture contents between 7 and 14% (Esashi et al. 1993 Leopold et al. 1988). At the beginning of our experiment seeds of all species except canola (which typically does not require afterripening for germination) had a proportional moisture content within this range. Afterripening of wild oat occurs primarily between 5 and 22% seed moisture (Foley 1994). At the beginning of our experiment the wild oat seeds had a proportional moisture content of 12%. All of the species studied within this experiment can readily imbibe substantial amounts of moisture even at very low soil water potentials. This suggests that for these species, imbibition resistance does not limit afterripening in field situations except perhaps in a dry soil crust or for seeds placed very near the surface of an

extremely dry soil. After one hour in osmotic solutions as low as  $-1$  MPa proportional seed moisture contents were 33, 38, 32 and 42% for green foxtail, canola, wild mustard and wild oat seed, respectively. Germination at various osmotic potentials for the species included in this experiment does not appear to be an all or nothing event. It is reasonable to assume that there exists an osmotic potential below which seeds will not germinate. Water potentials above that level may have an additive effect on germination with increasing osmotic potential resulting in increasing levels of seed germination (Ghorbani et al. 1999).

Plant seeds imbibe water even at very low osmotic potentials. Rate of imbibition declined in an exponential manner over time for all species studied. Wild oat, the species with the largest seed in this study, had the highest rate of imbibition over time but took longer to reach proportional moisture contents sufficient for germination when compared to wild mustard or canola. Wild mustard imbibed water rapidly at high osmotic potentials but its ability to germinate and imbibe water declined in reduced osmotic potential solutions. Green foxtail, the smallest seeded species in this study did not germinate more rapidly than wild oat and took longer to achieve similar proportional moisture contents. Green foxtail imbibed water at a much slower rate in high osmotic potentials than all other species while imbibition levels, but not the number of seeds germinating, appeared to be impacted less by drops in osmotic potential than other species. Therefore, proportional seed moisture content influences seed germination but is not the sole determinant of seed germination.



**MANUSCRIPT #6****REDROOT PIGWEED AND WILD OAT RECRUITMENT AND GROWTH IN FALLOW, ESTABLISHING FORAGE AND WHEAT CROPS IN SOUTHERN, MANITOBA****ABSTRACT**

Weed recruitment is dependant on the number of seeds in the soil and the biotic and abiotic conditions directly surrounding the seed. Crop species may compete with weed species affecting weed growth and development as well as weed recruitment. To examine the effect of crop species and seed bank size on wild oat and redroot pigweed an experiment was conducted where seeds of redroot pigweed and wild oat were seeded separately at high (1000 seeds plot<sup>-1</sup>) and low (100 seeds plot<sup>-1</sup>) densities and together at high (500 seeds of each species plot<sup>-1</sup>) and low (50 seeds of each species plot<sup>-1</sup>) densities in fallow, forage or wheat plots. The location, timing, and number of emerging weed seedlings was monitored throughout the growing season. Dry biomass production of crop and weeds was also measured. Wild oat recruitment was highly dependant on the number of seeds in the seed bank. The wheat crop decreased the number and the size of wild oat plants emerging when compared to fallow or forage. Wild oat emergence was aggregated on a fine scale with 55 and 64% of wild oat seedlings emerging within 2 or 3 cm of another seedling, respectively. Redroot pigweed recruitment occurred later in the season than wild oat. Pigweed emergence was microsite limited with no recruitment increase with increasing seed number. The presence of the forage or wheat crop or the presence of wild oat decreased the number and size of redroot pigweed plants.

## INTRODUCTION

Germination biology, not weed seed banks, may be one of the main factors controlling annual weed populations in arable crops (Crawley 1990). The presence of seeds within the soil profile is not usually a good indicator of the weed population that will be present in the following year. Cardina and Sparrow (1996) tested several methods for predicting potential seedling densities from seed bank measurements and found all of the methods were relatively poor predictors of field population density. The emergence of weeds is largely dependant on seeds being present in the soil and the conditions directly surrounding those seeds. When the conditions around the seed are within the appropriate range dormancy is broken and seed germination and emergence occurs.

Microsite conditions may vary within a given location and within a given time (Dieleman et al. 2000a). In low disturbance ecosystems, disturbance or openings in the canopy strongly affect colonization (Peart 1989B). Plant recruitment is largely limited by the availability of safe sites (Penet 1985; Tilman 1997). The level of bare ground may be one of the most important factors limiting recruitment in high plant density ecosystems (Burke and Grime 1996). In agricultural ecosystems most of the biomass is removed on a regular basis. Under these conditions one would expect weed populations to be limited by the number of seeds in the soil rather than the availability of safe sites (Crawley 1990). Crops emerging with or following weed emergence may not limit or affect weed recruitment but may affect weed growth and development.

Weed population aggregation is caused by variation in weed dispersal and variations in soil physical properties, soil cover, drainage and canopy development within a field. Initially weed spatial patterns are due to dispersal processes and mechanisms (Dessaint et al. 1991). Following dispersal, seeds are generally distributed around the mother plant with the distance of dispersal depending on the seed size and shape, parent size and dispersal mechanisms of the seed. The spatial pattern or aggregation is further modified by agronomic practices such as tillage and harvest techniques (Dessaint et al. 1991). Gerhards et al. (1997) found that seedling distribution was aggregated and that weed patches are often persistent between years.

Weed recruitment may be aggregated on a large or a fine scale. Fowler (1988) found that seedlings with neighbour seedlings within 2 cm had higher rates of survival than those without neighbouring seedlings. They suggest that microscale aggregation may occur because germination in favorable microsites outweighs the effects of seedling competition. Turnbull et al. (1999) suggests that seeds may even compete for appropriate microsites.

A combination of the number of seeds in the soil profile and the number of available microsites may determine weed seedling recruitment (Eriksson and Ehrlén 1992). Crawley (1990) hypothesized that plant populations in areas with high proportions of bare ground are more probable to be seed limited while competition or microsite limited populations would be more likely in grasslands or forests. The relative importance of seed and microsite limitation in plant ecosystems is still poorly understood. Crawley (1990) states that the lack of simple seed addition and microsite manipulation experiments studying recruitment limits our understanding of the importance of seeds and microsites in determining weed population dynamics.

The objectives of this experiment were to study the effects of various levels of competition, using no competition (fallow), weak competition (establishing forage crop) and strong competition (wheat crop), and different weed seed densities on wild oat and redroot pigweed recruitment. These species were chosen because wild oat is a large seeded species that germinates early in the spring in Manitoba over a wide range of conditions while pigweed is a much smaller seed that generally germinates later in the season and is more specific in its germination requirements. We attempted to determine if wild oat and redroot pigweed were seed or microsite limited in the presence or absence of crop competition.

## MATERIALS AND METHODS

A weed emergence experiment was conducted at the University of Manitoba's research station in Carman, Manitoba and on the research farm on campus in Winnipeg, Manitoba during the summer of 2000. At each site the plots were cultivated prior to sowing. The Carman research station had been sown to wheat the previous season while

the Winnipeg site had been fallow in the season preceding. At each site a 3 x 3 x 2 factorial experiment was replicated two times. Three weed seeding combinations, three crops and two weed densities were sown in 2m x 1m plots with guard rows between each plot sown with barley. All plots received the equivalent of 100 kg N ha<sup>-1</sup> of 23-10-5-5 applied to the surface in early May and incorporated with a rake. Two different crops or a fallow treatment were assigned to each plot and were seeded in early May, 2000. Wheat (*Triticum aestivum* 'AC Barrie') was sown by hand at 100 kg ha<sup>-1</sup> with 18 cm row spacings and 5-6 cm deep. Second, a forage crop was sown consisting of 20% alfalfa (*Medicago sativa*), 45% meadow brome (*Bromus spp.*), 30% orchard grass (*Dactylis glomerata*) and 5% timothy (*Phleum pratense* L). The mixture was seeded at 16.8 kg ha<sup>-1</sup> on the surface and then lightly raked to incorporate the seed. The third plot was left fallow. Within each plot wild oat, redroot pigweed or both were seeded by hand and incorporated in the top 5 cm of the soil profile before crop seeding. Both species were seeded at two densities (Table 6-1). When one weed species was planted individually the high seed density consisted of 1000 seeds plot<sup>-1</sup> and the low seed density consisted of 100 seeds plot<sup>-1</sup>. When both weed species were seeded together the total number of seeds remained the same in the high and low density treatments with each species having one half the number of seeds as when they were seeded individually (Table 6-1).

On May 30 and June 6 two 13 cm by 13 cm quadrats divided into 1 cm grids were placed directly above each plot. Weed emergence was marked on clear plastic sheets to determine the fine scale spatial emergence pattern of wild oat. Following June 6, spatial measurements were discontinued due to crop growth. On June 6 all weeds were counted and the height of two weeds per plot of each species was measured. On July 13, when the wheat was near maturity all redroot pigweed plants were counted. Wild oat panicles were counted and two plants per plot were harvested to estimate the number of panicles per plant. The average number of panicles per plot was used to estimate the number of mature wild oat plants in each plot. On July 20-21 two 0.16 m<sup>2</sup> quadrats were randomly placed within each plot and all plant material was harvested. The sample was separated into crop and weed species, then dried and weighed to determine dry biomass.

**Table 6-1.** Crops and weed seed densities seeded in this experiment in 2 m x 1 m plots.

Weed Species Seeded	Crop	Density	Wild oat seeds plot <sup>-1</sup>	Pigweed seeds plot <sup>-1</sup>	Crop g seed m <sup>-2</sup>
Wild oat + Pigweed	Fallow	high	500	500	0
		low	50	50	0
	Forage	high	500	500	1.7
		low	50	50	1.7
	Wheat	high	500	500	10
		low	50	50	10
Pigweed	Fallow	high	0	1000	0
		low	0	100	0
	Forage	high	0	1000	1.7
		low	0	100	1.7
	Wheat	high	0	1000	10
		low	0	100	10
Wild oat	Fallow	high	1000	0	0
		low	100	0	0
	Forage	high	1000	0	1.7
		low	100	0	1.7
	Wheat	high	1000	0	10
		low	100	0	10

Small scale patchiness of wild oat weed emergence was determined by measuring the distance between each wild oat plant and its closest neighbor. The proportion of seedlings with neighbouring seedlings emerging less than 1 cm, 2 cm or 3 cm away compared to the proportion of seedlings without a neighbor within 3 cm was calculated by determining the percentage of plants with a neighbour less than 1 cm, 2 cm or 3 cm away. The probability of having a seedling emerging with 1, 2 or 3 cm was compared using Duncan's means comparison.

The experiment was analyzed as a factorial experiment with two replications at two sites. Means were analyzed using the least squares means function of SAS (SAS institute Inc. 1990). All means were considered significantly different if  $p < 0.05$ . Pearson's correlation coefficients were used to determine the extent of the relationship between crop biomass and weed dry biomass.

## RESULTS AND DISCUSSION

Redroot pigweed emergence occurred much later than wild oat emergence. Emergence of this species typically occurs in late spring, early summer or may continue throughout the summer (Roberts 1986; Baskin and Baskin 1977) while wild oat emergence typically occurs in early spring or late fall in Canada (Sharma and Vanden Born 1978). Wild oat emerges in cool moist conditions allowing them to compete early in the season with the crop (Sharma and Vanden Born 1978). The later date of redroot pigweed emergence is probably due to the higher temperature requirement for germination (Gallagher and Cardina 1998a). By June 6 not enough redroot pigweed plants had emerged in this experiment to analyze emergence data.

### **Seed Density Effects on Weed Emergence and Biomass.**

Wild oat recruitment increased with seeding density ( $p=0.0025$ ) (Table 6-2). Seed density also affected the growth of wild oat plants in the three crops. At high weed seed densities wild oat plant height was significantly shorter in the fallow plots than in the wheat or forage plots ( $p < 0.05$ ). At low weed densities, wild oat height in the fallow and forage was significantly shorter than plants growing with the wheat. Taller wild oat plants in plots with high levels of competition may have been a result of shade avoidance mechanisms (Smith and Whitelam 1997) such as stem elongation (Ballaré et al. 1990).

Redroot pigweed recruitment was unaffected by seed density (Table 6-2). Seeding both species together at high densities reduced redroot pigweed emergence. Redroot pigweed emergence was significantly lower when seeded with wild oat at high seed densities (500 pigweed seeds  $\text{plot}^{-1}$ ) than when seeded alone at low density (100

pigweed seeds plot<sup>-1</sup>). Therefore, redroot pigweed emergence was limited by plant competition not seed number. Redroot pigweed germinates best when exposed to light and at high temperatures (Gallagher and Cardina 1998a; Chu et al. 1978). The early emergence of wild oat and subsequent canopy development prior to redroot pigweed emergence may have altered the soil microsite reducing the ability of redroot pigweed to emerge

Pigweed seeding density did not significantly affect redroot pigweed dry biomass (Table 6-3). Pigweed dry biomass was significantly lower at high and low seeding densities when seeded with wild oat versus dry biomass of pigweed seeded without wild oat. Therefore, wild oat recruitment and growth hindered pigweed recruitment and plant growth in this experiment.

**Table 6-2.** Number of redroot pigweed and wild oat plants and wild oat panicles at different weed seeding densities averaged across crops and sites in 2 m<sup>2</sup> on July 13.

Species Seeded	Density	Redroot pigweed	Wild oat (panicles)	Wild oat
Wild oat + pigweed	high	5.5 c <sup>a</sup>	211.3 a	85.1 a
Pigweed	high	15.5 a	4.8 b	1.8 b
Wild oat	high	5.4 c	182.2 a	79.8 a
<i>Average</i>	<i>high</i>	8.8 A	132.8 A	55.5 A
Wild oat + pigweed	low	6.8 bc	39.3 b	16.1 b
Pigweed	low	11.2 ab	4.4 b	2.5 b
Wild oat	low	4.3 c	50.7 b	13.3 b
<i>Average</i>	<i>low</i>	7.4 A	31.5 B	10.6 A

<sup>a</sup>Means within columns with the same letter are not significantly different (p<0.05). Numbers in italics are the average of all treatments within one density level. Averages within a column with the same uppercase letter are not significantly different (p<0.05).

**Table 6-3.** Weed dry biomass per area ( $\text{g m}^{-2}$ ) and per plant ( $\text{g plant}^{-1}$ ) and panicle (pan.) number per wild oat plant at different weed seeding densities averaged across crops and sites.

Species Seeded	Density	Redroot pigweed		Wild oat		
		$\text{g m}^{-2}$	$\text{g plant}^{-1}$	$\text{g m}^{-2}$	$\text{g plant}^{-1}$	Pan. $\text{pl}^{-1}$
Wild oat + pigweed	high	1.6 b <sup>a</sup>	0.02 b	230.5 b	0.5 b	2.8 a
Pigweed	high	71.5 a	0.34 b	9.9 c	---	0.8 b
Wild oat	high	5.3 b	---	329.3 a	0.7 b	2.5 a
<i>Average</i>	<i>high</i>	<i>26.1 A</i>	<i>0.27 A</i>	<i>189.9 A</i>	<i>0.4 B</i>	<i>2.0 A</i>
Wild oat + pigweed	low	6.6 b	0.96 ab	192.1 b	3.8 a	2.6 a
Pigweed	low	53.6 a	1.60 a	4.9 c	---	0.6 b
Wild oat	low	1.3 b	---	159.6 b	2.3 ab	3.3 a
<i>Average</i>	<i>low</i>	<i>20.5 A</i>	<i>0.85 A</i>	<i>118.9 B</i>	<i>2.0 A</i>	<i>2.2 A</i>

<sup>a</sup>Least squares means within columns with the same letter are not significantly different ( $p < 0.05$ ).

Numbers in italics are the average of all treatments within one density level. Averages within a column with the same uppercase letter are not significantly different ( $p < 0.05$ ).

Wild oat had a significantly greater number of panicles and plants at the high seeding density than the low seeding density (Table 6-2). The number of wild oats emerging when seeded with redroot pigweed was not significantly different than when wild oat was seeded alone although the seed number was doubled when one species was planted alone. Therefore, it appears that wild oat was seed limited originally but above a particular seed concentration other variables appear to have limited recruitment. Redroot pigweed did not appear to affect wild oat emergence at these sites which would be expected since they emerge later in the season. Unfortunately, the seeding densities used in this experiment were not adequate to determine at what threshold the wild oat population went from seed to microsite limitation.

Wild oat dry biomass was significantly greater in high seeding densities compared to low seeding densities and significantly greater when planted alone than when planted with pigweed at high seeding densities (Table 6-3). The average dry biomass per plant



was significantly greater at low seeding densities than at high seeding density suggesting that competition between wild oat plants hindered weed growth but the total biomass produced with high seeding densities was greater because of the increased number of plants. The average number of panicles per plant did not differ between seeding density treatments suggesting that the difference in dry biomass between seeding density treatments was probably due to leaf production and perhaps individual panicle size.

### **Crop Effects on Weed Recruitment and Weed Biomass Production**

Total crop dry biomass production levels varied significantly. Wheat had the highest average biomass production at  $69 \text{ g m}^{-2}$ . The forage crop did not establish well and had significantly lower average dry biomass production at  $13.4 \text{ g m}^{-2}$ . In the fallow plots some weeds did survive but biomass production was significantly lower than either forages or wheat at  $2.9 \text{ g m}^{-2}$ .

Redroot pigweed recruitment and dry biomass were significantly higher in fallow plots than forage or wheat (Tables 6-4 and 5). When seeded with wild oat there was no significant difference between the effects of different crops on redroot pigweed recruitment. Less competitive crops had greater wild oat growth which masked the crop effects by maintaining a dense canopy. A dense crop canopy may reduce redroot pigweed recruitment by altering microsite conditions (Urwin et al. 1996). Temperature changes and light interception may affect pigweed emergence and growth (McLachlan et al. 1993; Urwin et al. 1996). McLachlan et al. (1993) reported that the rate of leaf appearance in redroot pigweed is substantially reduced by canopy density. Knezevic and Horak (1998) reported a reduction in dry matter and seed production when redroot pigweed grew with sorghum. In this experiment, individual seedling dry biomass was significantly higher in fallow than wheat suggesting that the crop not only reduces the number of plants emerging by altering the microsite but also reduced the dry biomass of the weed by competing for resources. This competition may also affect the number of weed seeds produced within a season. McLachlan et al. (1995) reported that increased light interception caused by an increasing corn (*Zea mays*) canopy delayed reproductive

initiation, seed number per plant and the ratio of reproductive biomass to vegetative biomass in redroot pigweed.

Since redroot pigweed populations appear to be susceptible to crop shading (Urwin et al. 1996; Knezevic and Horak 1998) and germinate in late spring or throughout the summer (Roberts 1986; Baskin and Baskin 1977) early crop seeding may be an effective alternative to obtain adequate control of this species. Environmental conditions and the time of weed emergence will partially determine the extent of competition between the crop and weeds (Cowan et al. 1998). Seeding the crop before redroot pigweed emergence may allow a thick canopy to establish before temperatures are warm enough for this species to germinate thus preventing its emergence and slowing its growth. Selecting crops or varieties known to form a thick early canopy may also aid in weed control where redroot pigweed is known to be a problem (Urwin et al. 1996).

A significantly greater number of wild oat panicles and wild oat seedlings were always found in the fallow and forage treatments versus the wheat treatment (Table 6-4). Wild oat dry biomass was also significantly impacted by competition from the wheat crop. Wild oat dry biomass per plot and dry biomass per plant was significantly higher in fallow followed by forage followed by wheat plots when wild oat and pigweed were seeded together (Table 6-5). A similar trend was noted when wild oat was planted by itself. As well, the number of panicles per wild oat plant tended to be higher in fallow than in wheat. Therefore, we can conclude that the presence of a competitive crop reduces the number of seedlings emerging and hinders wild oat growth and consequently wild oat seed production.

Wild oat germinates under a wide range of conditions although it preferentially emerges early in the spring under cool wet conditions in Manitoba (Sharma and Vanden Born 1978). Peters and Wilson (1983) reported that the majority of wild oat seeds were shed by early emerging plants. Plants emerging before the crop produced five times as many seeds per plant as those that emerged at the 2 or 3 leaf stage of the crop. Consequently, soil disturbance in early spring to promote germination of wild oat followed by adequate weed control and delayed seeding may be one method to manage wild oat populations.

**Table 6-4.** Number of redroot pigweed and wild oat plants and wild oat panicles within different crop selections averaged over site and seeding density.

Species Seeded	Crop	Pigweed (plants plot <sup>-1</sup> )	Wild oat (pan. plot <sup>-1</sup> )	Wild oat (plants plot <sup>-1</sup> )
Wild oat + pigweed	fallow	6.8 b	181.5 a	45.9 ac
Wild oat + pigweed	forage	5.2 b	142.9 a	73.2 a
Wild oat + pigweed	wheat	6.4 b	51.6 b	32.6 bc
Pigweed	fallow	24.9 a	5.9 b	1.7 d
Pigweed	forage	8.8 b	6.1 b	3.6 d
Pigweed	wheat	6.4 b	1.9 b	1.1 d
Wild oat	fallow	8.2 b	151.8 a	53.4 ab
Wild oat	forage	3.0 b	154.1 a	62.5 a
Wild oat	wheat	3.4 b	43.5 b	23.7 cd

<sup>a</sup>Least squares means within columns with the same letter are not significantly different ( $p < 0.05$ ).

**Table 6-5.** The effects of crop on weed dry biomass production per plot and per plant averaged over site and weed seed densities.

Species Seeded	Crop	Pigweed		Wild oat		
		g m <sup>-2</sup>	g plant <sup>-1</sup>	g m <sup>-2</sup>	g plant <sup>-1</sup>	Pan. pl <sup>-1</sup>
Wild oat + pigweed	fallow	2.7 b <sup>a</sup>	0.02 b	368.9 a	4.61 a	4.1 a
Wild oat + pigweed	forage	9.5 b	1.45 ab	229.9 b	1.61 b	2.2 bc
Wild oat + pigweed	wheat	0.0 b	0.00 b	35.1 c	0.18 b	1.8 c
Pigweed	fallow	147.8 a	1.91 a	14.4 c	---	---
Pigweed	forage	39.4 b	0.98 ab	7.4 c	---	---
Pigweed	wheat	0.5 b	0.03 b	0.4 c	---	---
Wild oat	fallow	4.7 b	---	385.2 a	2.28 ab	3.4 ab
Wild oat	forage	5.2 b	---	301.5 ab	1.63 b	3.1 ab
Wild oat	wheat	0.0 b	---	46.6 c	0.46 b	2.2 bc

<sup>a</sup>Least squares means within columns with the same letter are not significantly different ( $p < 0.05$ ).

### **Small Scale Weed Patches**

The extent of patchiness was only determined for wild oat. There was a 55 and 64% chance that if one weed emerged another one would emerge within 2 or 3 cm, respectively. There was a 35% chance that wild oat seedlings would emerge further than 3 cm from any other emerging wild oat seedling. There was a 28% chance that one wild oat seedling would emerge within 1 cm of another wild oat seedling. These results agree with Fowler (1988) who reported that seedlings with neighboring seedlings within 2 cm had a greater chance of survival. He suggests that the importance of microsite plays a more important role than competition between individuals. Our results suggest that wild oat recruitment is aggregated on a very fine scale.

### **Seed or Microsite Limitation of Weed Populations**

Weed populations may be seed, microsite or seed and microsite limited (Crawley 1990, Eriksson and Ehrlén 1992). The relative importance of each variable may be species specific as well as varying spatially and temporally. The results of this experiment suggest that redroot pigweed is predominately microsite limited while wild oat is predominately seed limited within a range of seed densities and then becomes microsite limited as seed density increased. Wild oat only remains viable within the seed bank for two to six years (Sharma and Vanden Born 1978). Consequently, a large proportion of the seeds present in the soil germinate each year. Barralis et al. (1988) reported that wild oat seed populations in the soil decreased by about 80% each year with approximately 15% of the seeds emerging annually. To maintain a weed population wild oat must be able to germinate under a wide range of soil depths, moistures and temperatures (Fernandez-Quinantilla et al. 1990; Sharma and Vanden Born 1978). Therefore, a population of germination generalists, like wild oat, should be mostly seed limited. Microsite limitation may only occur under extreme conditions, at the periphery of the habitat where this species can survive or with different levels of dormancy typically found within a population. Conversely, redroot pigweed may last from 5 to 40 years within the seed bank (Egley and Chandler 1983, Weaver and McWilliams 1980). Since the seeds last for extended periods germination percentage of the seed bank is

relatively low each year (Roberts 1986, Barralis et al. 1988). Under these conditions the seeds do not need to emerge within one year and the population may be more microsite limited. Williams (1983) supported this theory by reporting that species which tend to form a more persistent seed bank, such as redroot pigweed, show a larger response to altering conditions while species that only last for short periods in the seed bank, such as wild oat, were less specific in their germination requirements.

**MANUSCRIPT #7****SOIL COMPACTION AND WEED EMERGENCE IN A HOCHFELD AND  
WINKLER SOIL SERIES****ABSTRACT**

Soil compaction may alter soil physical, chemical and biological conditions and consequently alter weed seed recruitment. Weed recruitment may increase or decrease with compaction depending on the level of compaction and various environmental variables. Weed and wheat emergence data were collected on a compacted and non compacted Hochfeld and Winkler soil series in Manitoba, Canada. Both soil types were compacted with wheel traffic following the seeding of a wheat crop. Weed emergence and soil moisture levels were measured throughout the season. Wheat emergence was significantly lower in compacted versus non compacted soils. Total weed emergence as well as emergence of individual species (green foxtail, redroot pigweed, lamb's-quarters and lady's thumb) was generally unaffected by compaction in the Winkler soil series. Total weed emergence was significantly higher in the compacted Hochfeld soil versus the non compacted Hochfeld soil. Lady's thumb had significantly greater emergence levels on the Winkler versus the Hochfeld soil in 2002 while green foxtail, redroot pigweed and lamb's-quarters had significantly greater emergence on the Hochfeld soil series versus the Winkler soil series in 2002.

## INTRODUCTION

Most agricultural fields are subjected to wheel traffic at least three times during a growing season (Voorhees et al. 1978). Soil compaction by wheel traffic alters the arrangement of soil particles within the soil (Jurik and Zhang 1999) which may in turn alter plant emergence, growth and development. Wheel traffic has been reported to increase the density, strength and size of soil clods and increase soil bulk density, soil strength and aggregate mean weight diameter in the top 15 cm of the soil profile (Voorhees et al. 1978, Liebig et al. 1993). These alterations in soil structure reduce pore space and alter pore size limiting water storage and gas exchange within the soil (Sheldon 1974). Non compacted soils have a higher water storage capacity, higher saturated water contents and higher gravimetric water contents (Liebig et al. 1993).

Plant germination and emergence generally decreases with decreasing soil moisture content but the germination response to soil moisture is species specific (Hoveland and Buchanan 1973). While compaction may decrease the water storage capabilities of the soil it also increases seed soil contact. Therefore, compaction may either inhibit (Thill et al. 1979) or stimulate weed germination (Jurik and Zhang 1999) depending on seasonal rainfall and the severity of the compaction.

High soil moisture, soil compaction, high microbial activity or poor soil structure may decrease soil oxygen concentration or inhibit gaseous movement within the soil (Drew 1992; Hodgson and Macleod 1989, Ishii and Kadoya 1991). At low oxygen concentrations and under conditions of poor gas diffusion anaerobic metabolites build up around the seed and inhibit seed germination or induce secondary dormancy and a light requirement for germination (Holm 1972). Therefore, oxygen concentration or the inability to remove fermentation products from the gaseous environment directly surrounding the seed may inhibit seed germination in compacted soils especially under high soil moisture contents.

An experiment was conducted on two soil types to determine the effects of soil compaction on wheat and weed seed germination and emergence.

## MATERIALS AND METHODS

Field experiments were conducted at the University of Manitoba's Carman research station in 2001 and 2002. In both years, the experiment was conducted on both a Winkler and a Hochfeld Soil series. The Winkler soil series on the research farm has an average pH of 5.8 with a 6.5% organic matter content. The particle size distribution is approximately 60% sand, 15% silt and 25% clay. The Hochfeld soil series has an average pH of 5.2 and a 4.7% organic matter content. The particle size distribution is approximately 76% sand, 10% silt and 14% clay (Mills and Haluschak 1993). The experiment was conducted on both soil series in 2001 and 2002 with different plot locations each year. Shallow cultivation (10 cm) occurred at both sites 2 days prior to seeding.

The experiment was seeded on May 14 (Julian day 134) in 2001 and May 18 (Julian day 138) in 2002. AC Barrie wheat was seeded in 15 cm rows at 104 kg ha<sup>-1</sup>. Fertilizer (23-24-0) was applied with the seed at a rate of 180 kg ha<sup>-1</sup>. To compact the soil, a ½ ton truck was driven back and forth 5 times across the soil after seeding to form two compacted strips each 60 cm wide. Three quadrats (50 X 50 cm) were randomly placed in each strip and three quadrats were placed in a straight line beside each strip in the non compacted soil giving two replicates with 3 experimental units per treatment. Soil volumetric moisture was measured weekly with a TDR probe (Hoskin Scientific, Vancouver, B.C.) in the top 6 cm of the soil in both the compacted and non compacted treatments. Soil bulk density was determined from 5.2 cm diameter soil cores taken once from the top 4 cm of the soil profile following soil compaction and dried in an oven for 48 hours at 80 °C.

Soil moisture characteristic curves were determined in order to estimate the soil water potential of the two soil types at various soil moisture contents. Saturated soil samples made from a random bulked sample from each site were placed within pressure plates at pressures of -0.001, -0.002, -0.2, -0.6 and -1.5 MPa. When no further moisture was removed from the soil at the given pressure the samples were removed from the apparatus weighed, then dried, and weighed again to determine the moisture content (Klute 1998). A non-linear inverse second order polynomial curve was fitted to the data.



This curve was used to estimate the osmotic potential of the soil at various moisture contents.

All weather data were collected from a weather station on the research station. Growing degree days (GDD) were calculated using the following formula:

$$\text{GDD} = (T_{\text{max}} + T_{\text{min}}/2) - T_{\text{base}} \quad 7.2$$

Where  $T_{\text{max}}$  was the daily maximum temperature,  $T_{\text{min}}$  was the daily minimum temperature and  $T_{\text{base}}$  equalled 0 °C.

Emerging wheat and weed species were counted within each 50 X 50 cm quadrat on June 4 and June 20 in 2001 and May 30 and June 18 in 2002. The data were sorted into total weed emergence, emergence of monocots (primarily green foxtail), emergence of dicots as well as emergence of individual species. The data were analysed in SAS (SAS Institute Inc. 1990) as a randomized complete block design using general linear models and the repeated measures statement. All variables were considered fixed. Least squares means were used to compare the treatment effects. The experiments were terminated in early July in 2001 and 2002 when weed emergence had practically ceased.

## RESULTS AND DISCUSSION

Year had the greatest impact on wheat and weed emergence level with site and treatment altering it's impact. 2001 was warmer than 2002 with 165 and 92 accumulated growing degree days between May 1 and seeding in 2001 and 2002, respectively. Therefore, a greater proportion of weeds may have emerged prior to seeding in 2001 versus 2002 and been killed by cultivation (which occurred 7 and 2 days prior to seeding in 2001 and 2002, respectively). In 2001 698 and 875 growing degree days accumulated between May 1 and weed counts 1 (June 5) and 2 (June 20), respectively. In 2002, only 366 and 511 growing degree days accumulated between May 1 and weed counts 1 (May 30) and 2 (June 18), respectively. Despite the greater amount of accumulated heat by

time of seeding in 2001 versus 2002 there was a significant increase in the density of warm season weeds in 2002 versus 2001 (Table 7-1). This difference was probably due to differences in the seedbank between sites in 2001 and 2002.

**Table 7-1.** Soil bulk density ( $\text{g cm}^{-3}$ ), wheat emergence level (plants  $\text{m}^{-2}$ ), total weed emergence level (plants  $\text{m}^{-2}$ ) 33 and 43 days after planting (DAP), and individual species emergence level (plants  $\text{m}^{-2}$ ) 43 days after planting averaged across compaction treatments in 2001 and 2002.

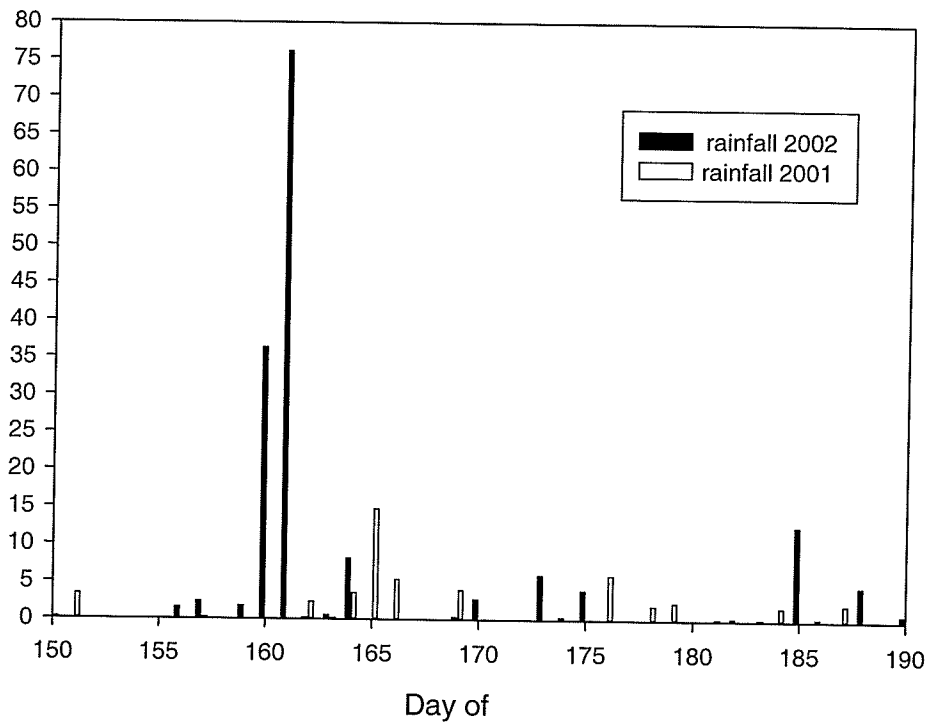
	Winkler Soil Series		Hochfeld Soil Series	
	2001	2002	2001	2002
Bulk density	0.99 c <sup>a</sup>	1.10 b	1.09 b	1.28 a
Wheat	763 a	560 b	801 a	581 b
Total weed (33 DAP)	195 b	189 b	204 b	513 a
Total weed (43 DAP)	157 b	417 b	212 b	2085 a
Total dicot	189 b	141 b	160 b	771 a
Green foxtail	4 b	276 b	40 b	1315 a
Redroot pigweed	185 b	11 c	143 bc	663 a
Lamb's-quarter	1 b	7 b	11 b	32 a
Lady's thumb	3 b	33 a	0 b	0 b

<sup>a</sup>Least squares means with different letters within rows are significantly different at  $p < 0.05$ .

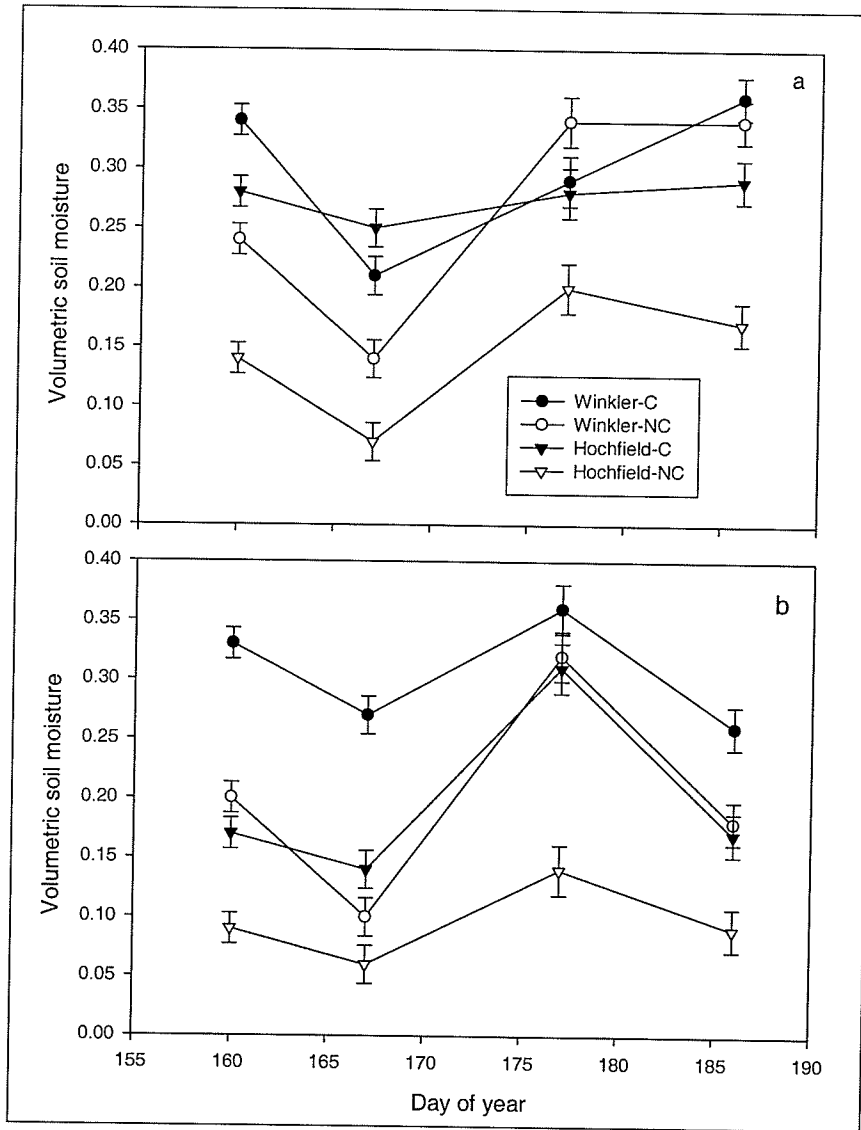
Total rainfall between May 1 and seeding was similar between years with 22 and 29 mm of rain falling in 2001 and 2002, respectively. Total rainfall between seeding and the final weed counts was 72 and 140 mm in 2001 and 2002, respectively. The greater amount of rainfall after seeding in 2002 versus 2001 was largely due to two large rainfall events that occurred in early June 2002 between the two weed counts. Due to the large volume of water that fell over a short period of time during this period in 2002 much of the moisture was not absorbed by the soil (Figure 7-2). Bulk density was significantly higher in 2002 than 2001 in both soil series. As well, bulk density of the Hochfield soil series was significantly higher than the bulk density of the Winkler soil series in both years when averaged across compaction treatments (Table 7-1).

A.C Barrie wheat emergence was generally reduced in 2002 versus 2001. The difference in bulk densities between years may have caused the significant increase in wheat emergence in 2001 versus 2002 with an average of 782 wheat plants  $\text{m}^{-2}$  emerging in 2001 and 570 wheat plants  $\text{m}^{-2}$  emerging in 2002. The effect of year interacted significantly with treatment ( $p=0.022$ ), (Table 7-2). In both years compaction

significantly reduced wheat seedling emergence but compaction had a far greater impact in 2001 than in 2002. Despite the difference in bulk density between soil series wheat emergence was not significantly different between the Hochfeld and Winkler soil series.



**Figure 7-1.** Rainfall (mm) in 2001 and 2002 at the Carman research station.



**Figure 7-2.** Volumetric soil moisture in the top 6 cm of the soil in both compacted (C) and non compacted (NC) Winkler and Hochfeld soils in (a) 2001 and (b) 2002.

**Table 7-2.** Soil bulk density ( $\text{g cm}^{-3}$ ), wheat emergence (plants  $\text{m}^{-2}$ ) 43 days after planting, total weed emergence levels (plants  $\text{m}^{-2}$ ) 33 and 43 days after planting (DAP), and individual species emergence level (plants  $\text{m}^{-2}$ ) 43 days after planting averaged across years in two soil series and compacted (C) or non-compacted (NC) treatments.

	Winkler Soil Series		Hochfeld Soil Series	
	C	NC	C	NC
Bulk density	1.13 b <sup>a</sup>	0.99 c	1.29 a	1.07 b
Wheat	505 b	817 a	557 b	825 a
Total weed (33 DAP)	144 b	240 b	449 a	268 b
Total weed (43 DAP)	207 c	368 c	1305 a	992 b
Total dicot	125 b	205 b	493 a	437 a
Green foxtail	81 b	199 b	811 a	544 a
Redroot pigweed	80 b	116 b	448 a	357 a
Lamb's-quarter	4 b	4 b	16 ab	27 a
Lady's thumb	15 ab	21 a	0 b	0 b

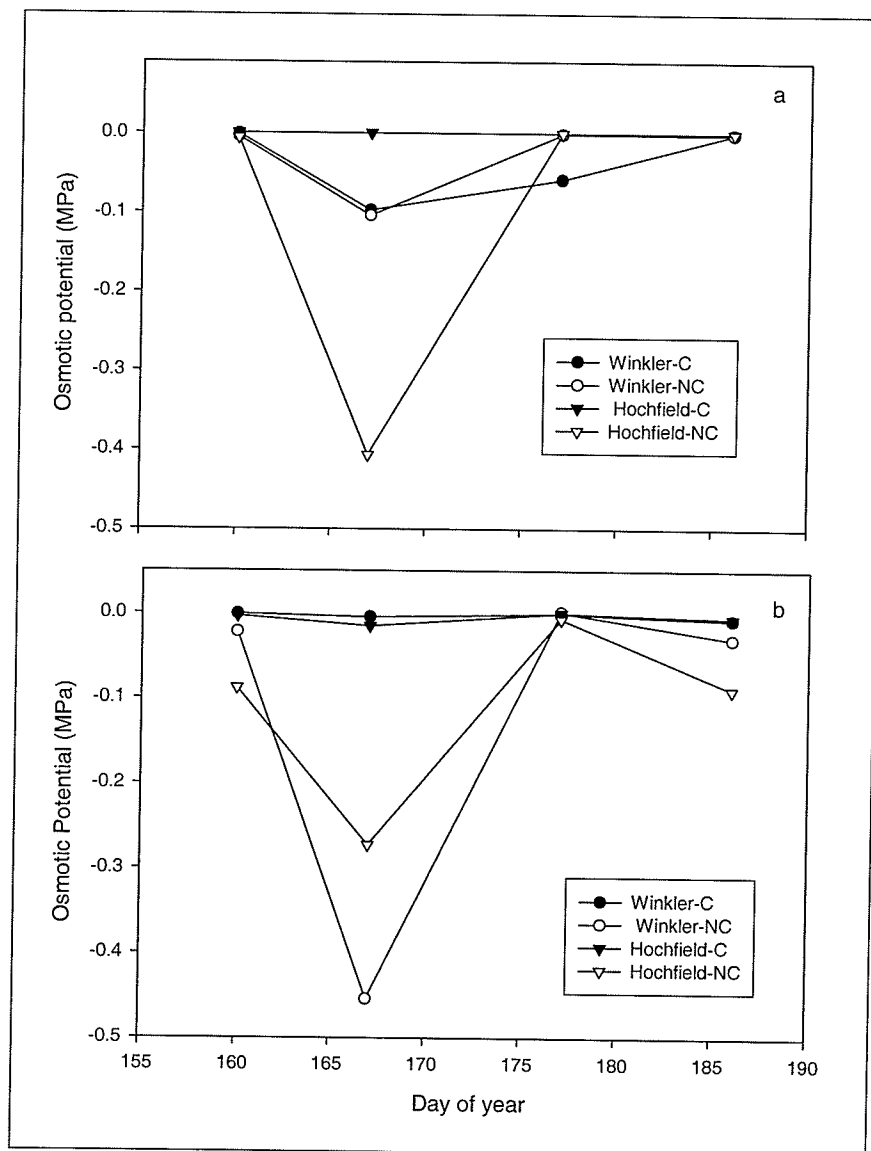
<sup>a</sup>Least squares means with different letters within rows are significantly different at  $p < 0.05$ .

Total weed emergence at both sampling times was significantly higher in 2002 than in 2001 on the Hochfeld soil series. There was a significant interaction between year and soil series ( $p=0.034$ ) with weed emergence in 2002 in the Hochfeld soil series significantly higher than for any other site year (Table 7-1). The increase in overall weed emergence was not due to an increase in emergence level for any one individual weed species but was due to a significant increase in emergence level of all weed species. Soil series and treatment also interacted significantly affecting total weed emergence ( $p=0.024$ ). In this experiment compaction appears to have affected the emergence of wheat differently than it has affected the emergence of weeds. Compaction did not affect weed emergence in the Winkler soil series at either sampling date. At 33 DAP total weed emergence in the compacted Hochfeld soil was significantly higher than in the non-compacted Hochfeld soil. At 43 DAP there was significantly greater weed emergence in the compacted Hochfeld soils than in the non compacted Hochfeld soils and weed emergence in both treatments in the Hochfeld soil was significantly higher than weed emergence in the Winkler soils (Table 7-2). It appears that increased bulk density in the Hochfeld soil series allowed increased weed emergence and compacting the soil further increased seed germination. Increased bulk density may have increased weed emergence

by altering the microsite around the seed (Jurik and Zhang 1999). However, differences in weed emergence between sites may also have been due to differences in seedbanks between the two sites which was not measured.

The difference in weed emergence level between years may have been due to changes in accumulated temperature or moisture. Differences in weed emergence level between sites within a year may have been due to differences in soil moisture or soil moisture availability due to differences in seed soil contact. In 2001, the Hochfeld soil series had significantly lower soil moisture levels when not compacted than either the Winkler soil series or the compacted Hochfeld soils (Figure 7-2). In 2001, the non-compacted Winkler soil also had significantly lower soil moisture levels than the compacted soils early in the season. Following rainfall the soil moisture levels of the non-compacted Winkler soil rose to levels similar or higher than levels in the compacted Winkler and Hochfeld soils and this did not occur in the non-compacted Hochfeld soil. This may explain why compaction affected weed emergence levels in the Hochfeld soil but not in the Winkler soil series. This is further emphasized by the dramatic drop in the osmotic potential of the non-compacted Hochfeld soils in 2001 and 2002 when compared to all other treatments (Figure 7-3). In 2002 the soil moisture levels of the Winkler soils remained as high or significantly higher than the Hochfeld soil series but weed emergence levels were significantly lower than in the Hochfeld soil series (Figure 7-2).

Green foxtail had significantly greater emergence in the Hochfeld series compared to the Winkler series in 2002. No significant differences in green foxtail emergence were found between sites in 2001 although there was a general trend of increased green foxtail emergence in the Hochfeld soil. Douglas et al. (1985) also reported greater green foxtail emergence on medium or coarse textured soils in Saskatchewan and Alberta, Canada with little emergence occurring on fine textured soils. Soil osmotic potentials dropped significantly in 2002 but may not have dropped low enough to inhibit green foxtail germination (Blackshaw et al. 1981; Douglas et al. 1985). The drop in wheat emergence in 2002 may have allowed an increase in green foxtail germination and emergence despite the dry conditions due to an increase in the number of available microsites.



**Figure 7-3.** The osmotic potential of compacted (C) and non compacted (NC) Hochfeld and Winkler soils in (a) 2001 and (b) 2002.

Redroot pigweed and lamb's-quarter emergence levels were unaffected by compaction (Table 7-2). However, both species tended to have greater emergence in the Hochfeld versus the Winkler soil series especially in 2002. Roman et al. (1999) reported that lambsquarters emergence drops rapidly below  $-0.1$  MPa. In this experiment osmotic

potential did drop as low as  $-0.5$  MPa but only for a brief period of time (Figure 7-3). Redroot pigweed had significantly greater emergence levels in 2001 versus 2002 in the Winkler soil series. This may have been due to the greater accumulation of growing degree days. Lady's-thumb was the only species which had significantly greater emergence in the Winkler soil series than the Hochfeld soil series. Ladies thumb may preferentially grow in heavier soils (ie. Winkler soil series) because the moisture levels tend to remain higher throughout the season (Figure 7-2). Hot or dry soils can induce secondary dormancy in lady's-thumb with weed flushes only occurring during rainy spells (Staniforth and Cavers 1979).

Differences in the emergence levels of individual weed species between years and sites may be partially attributed to differences in the seed bank. However, in this experiment, variation between years appeared to be affected by meteorological variables. Preferential emergence of particular species within a particular soil series may be due to particular germination and emergence requirements for a given species. For example, lady's-thumb densities may be greater in the Winkler soil because a higher soil moisture level is maintained in this soil contents throughout the growing season when compared to the Hochfeld soil (Figure 7-2).



**MANUSCRIPT #8****SEED AND MICROSITE LIMITATION OF CANOLA, GREEN FOXTAIL,  
WILD MUSTARD AND WILD OAT IN A WHEAT FIELD IN SOUTHERN  
MANITOBA****ABSTRACT**

Seedling recruitment of annual weed species is dependant upon the number of seeds present and the biotic and abiotic conditions directly surrounding those seeds. A field experiment was conducted to study the relative importance of these variables in determining the emerging weed population. Three seed densities (200, 400, 1200 seeds  $m^{-2}$ ) of green foxtail, wild mustard, wild oat and canola were seeded in separate plots in a Hochfeld and Winkler soil series in Manitoba, Canada in 2001 and 2002. Five treatments (control, irrigated, compacted, compacted and irrigated, and no crop) were applied to all weed seed densities of each weed species in a factorial design. Following weed seed incorporation in the top 6 cm the entire area was seeded to AC Barrie wheat. Weed counts as well as several soil physical parameters were measured throughout both seasons. Irrigation or compaction increased wild oat emergence when averaged over both years. Green foxtail emergence tended to increase with compaction in 2001 but not in 2002. Weed emergence levels increased with increasing seeding density for all species but proportional emergence decreased with increasing seed density for all species. We suggest that the emergence of weed species in this experiment was both seed and microsite limited. Increasing the number of seeds in the soil increased the probability of seeds landing within an appropriate microsite. Therefore, weed spread and weed patch formation may be determined both by seed dispersal and variability of soil microsite conditions. Management practices should be followed which limit seed dispersal of all species and disfavor the emergence of hard to control species during critical periods.

## INTRODUCTION

Seedling recruitment in a plant community is limited by seed number, microsite conditions, plant to plant competition or seed predation (Crawley 1990). Plants appear to be predominately limited by microsite conditions or plant competition in low disturbance ecosystems with a high plant density. The removal of plant material opens appropriate microsities in these high density stands. Seedling recruitment of new individuals then occurs in the "empty sites" (Tilman 1997). Burke and Grime (1996) found that the level of bare ground was consistently the most important factor determining the probability of successful recruitment in grassland systems. Bratton (1976) reported similar results within a forest ecosystem where the structure of the forest canopy including the size and position of openings, light passage through the canopy, and distance from other trees affected under story recruitment. Recruitment probably occurs in "empty sites" because of changes in microsite conditions such as soil moisture (Aguilera and Lauenroth 1995) and light (Kephart and Paladino 1997).

One would expect seed limitation to be the dominant limiter of seedling recruitment in situations where there is a high proportion of bare ground (Crawley 1990). In annually cropped fields a majority of biomass is removed on an annual basis and the soil is cultivated, mixing plant seeds throughout the soil profile. As well, the life cycle of many weed species is short with recruitment determined almost entirely by germination and dormancy biology (Crawley 1990). Under these conditions, one would not expect plant competition to play a major role in determining species composition in a given area. Instead, one would anticipate seed limitation limiting the prominence of particular species within a given area. Yet in agricultural fields, weed seed return most often exceeds recruitment, there is usually little relationship between weed population densities in a given year and seed return from the previous year (Crawley 1990), and weed populations generally occur in patches. The characteristics of weed infestations in agricultural fields suggest that variables other than seed number influence the recruitment of weed species.

Based on the assumption that the spatial arrangement of individuals of weedy species is influenced by biotic and abiotic variables, several authors have tried to relate

environmental or agronomic factors to weed presence in space. Dieleman et al. (2000a) suggests that site properties such as soil type, moisture and topography all affect weed species abundance. Therefore, since weed populations and site properties both vary across agricultural fields, variation in site properties may lead to spatial aggregation of weed infestations (Dieleman et al. (2000b). However, Dessaint et al. (1991) reported that the initial patchiness of a weed population is due to dispersal processes. Since seeds move only a small distance from the mother plant one would anticipate greatest densities around mother plants over time (Nadeau and King 1991). Colbach et al. (2000) reported that the density and the persistence of a weed patch was not dependant on soil variables but on whether or not seeds for a given weed species were dispersed before or after combining. Weed patches may be initiated by historical events and seed rain may maintain the patch. It may be, therefore, that weed patch or infestation spread is limited by the ability of weed species to disperse seeds to new areas. If this were true, we would conclude that weed population spread is seed limited. However, Zhang and Hamill (1998) reported that there was not always a close spatial relationship between parent plants and their offspring. This result would suggest that weed patch or infestation spread is limited by the presence of suitable microsite conditions.

Growth for all plant populations in all ecosystems is to some extent both seed and microsite limited (Eriksson and Ehrlén 1992) and evidence in weed science literature supports this conclusion. There would be, however, a continuum from greater to lesser seed and microsite limitation of population growth for a given weed species in agricultural fields. Knowing whether the population growth of a given weed species is more or less seed or microsite limited would prove useful when devising management strategies. We suggest that the population of a given weed species in an agricultural field is microsite limited if the following conditions are met (1) if small changes in soil biotic or abiotic conditions alter the proportion of the seed bank that emerges within a season, and (2) if the relationship between cumulative emergence and seed number is non-linear. The objective of this study was to explore, on the basis of our hypothesis, whether the field emergence of canola, green foxtail, wild mustard and wild oat was more or less limited by either seed number or microsite conditions.

## MATERIALS AND METHODS

Field experiments were conducted at the University of Manitoba's Carman research station in 2001 and 2002. In both years, the experiment was conducted on a Winkler and a Hochfeld Soil series. The Winkler soil series on the research farm has an average pH of 5.8 with a 6.5% organic matter content. The particle size distribution is approximately 60% sand, 15% silt and 25% clay. The Hochfeld soil series has an average pH of 5.2 and a 4.7% organic matter content. The particle size distribution is approximately 76% sand, 10% silt and 14% clay. The experiment was conducted on both soil series in 2001 and 2002 with different plot locations each year.

Seeds of green foxtail, wild mustard and wild oat were collected from various discrete patches in southern, Manitoba, Canada (manuscript #1). The seed collections for each species were combined at the time of collection and stored in a seed storage room at 4 °C until the initiation of the experiment. Canola seeds were also collected from one seed lot and stored in the same seed storage room. Seeds were seeded by species into separate 50 by 50 cm plots at densities of 50, 100, or 300 the day before the wheat was seeded. In each plot seeds were incorporated into the top 6 cm of the soil with a hoe. The entire experimental area was seeded to wheat (c.v. AC Barrie) in 15 cm rows at a rate of 104 kg ha<sup>-1</sup> using a double disc press drill on May 14 (day of year 134) in 2001 and May 18 (day of year 138) in 2002. 23-24-0 fertilizer was spread with the seed at a rate of 180 kg ha<sup>-1</sup>.

Five treatments were applied to each plot to determine the effect of crop competition, soil moisture and compaction on the emergence of the weed populations. The treatments included a control, an irrigated treatment, a compacted treatment, an irrigated and compacted treatment and a control with no crop. For the irrigated treatments a small dike was constructed around the 50 by 50 cm plots and the equivalent of 2.54 cm of rain was added once per week with a garden watering can. For the compacted treatments a roller was run over the 50 by 50 cm following seeding to increase the bulk density of the near surface soil layers.

## Data collection

Weed emergence was counted once per week in each plot from crop seeding until the time when new weeds were no longer emerging. After each count, weed seedlings were clipped at the soil surface to prevent miscounts and to remove potential seedling competition effects on emergence. To account for weeds emerging from the natural seed bank, four quadrats were randomly placed within each rep. The number of canola, green foxtail, wild mustard and wild oat seedlings that emerged within these four quadrats were also counted each week and the average emergence for a given rep, at a given site in a given year was subtracted from weed counts for the same species from the plots where seeds of a given species had been added. In 2002, green foxtail emergence was not counted on one of the reps in the Hochfeld soil series site due to high green foxtail emergence from the natural seedbank which made accurate weed counts at this test site impossible in one of the two replicates.

Soil volumetric moisture in each plot was measured once or more per week using a Theta probe (Hoskin Scientific, Vancouver, BC) which provides an integrated measure of soil moisture in the top 6 cm of the soil profile. Soil bulk density in the top 4 cm of the soil profile was measured once (after compaction treatments were applied) in all plots just prior to wheat emergence. An integrated measure of penetration resistance in the top 6 cm of the soil profile was measured in each plot using a penetrometer (Hoskin Scientific, Vancouver BC). Three measurements per plot were taken between the wheat rows and averaged to determine the average penetration resistance in each plot. Soil temperature was measured hourly using stowaway tidbits (Onset computer corporation, Pocasset, MA) buried at 2.5 cm. Minimum, maximum and mean soil temperatures as well as ranges were recorded at each site and in each replicate. Tidbits were placed in each of the microsite modification treatments where wild oat was sown at the lowest density. Growing degree days (GDD) were calculated using these data and using the following formula:

$$\text{GDD} = (T_{\max} + T_{\min}/2) - T_{\text{base}}$$

Where  $T_{\max}$  was the daily maximum temperature,  $T_{\min}$  was the daily minimum temperature and  $T_{\text{base}}$  equalled zero. Air temperature and rainfall was also monitored by an on-sight weather station.

Soil moisture characteristic curves were determined in order to relate measures of gravimetric soil moisture to osmotic potential for the two soil series in this experiment. For each soil series, soil samples from the top 4 cm were taken randomly and were placed within pressure plates at pressures of  $-0.001$ ,  $-0.002$ ,  $-0.2$ ,  $-0.6$  and  $-1.5$  MPa. When moisture was no longer being removed from a soil at a given pressure, the sample was removed from the apparatus, weighed, then dried at  $80$  C for 48 hours, and weighed again to determine the moisture content. A non-linear inverse second order polynomial curve was fitted to the resulting data. This curve was used to estimate the osmotic potential of the soil at various moisture contents.

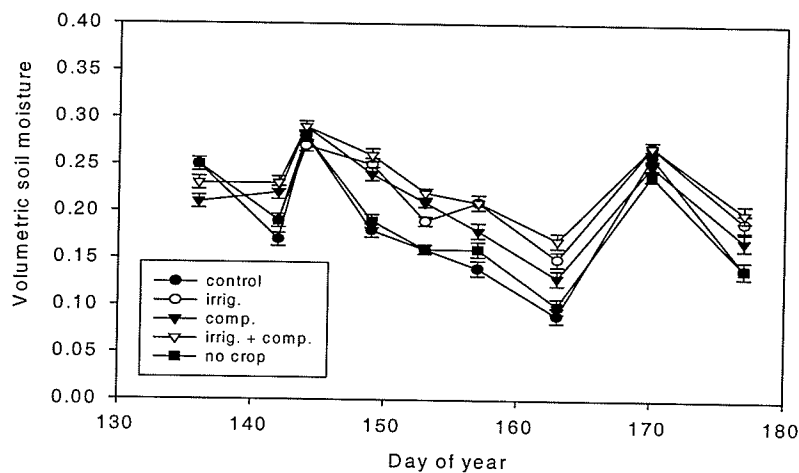
### **Experimental design and set up**

The experiment was set up as a factorial design with three seeding densities, five treatments and two sites (the Winkler and Hochfeld soil series) with two replicates per site over two years. All variables in the model were considered fixed. Weed emergence, proportional weed emergence and soil moisture were analysed using a general linear model and the repeated statement in SAS (SAS Institute Inc. 1990). Soil temperature was analysed using a general linear model with time included as one of the fixed dependant variables in the model. The strength of the relationship between seed number and seedling emergence was determined by calculating the R-square values for a general linear model where the independent variable was seed number and the dependant variable was seedling emergence. All data was normally distributed with constant variance. Main effects are reported except where interactions were significant.

## RESULTS AND DISCUSSION

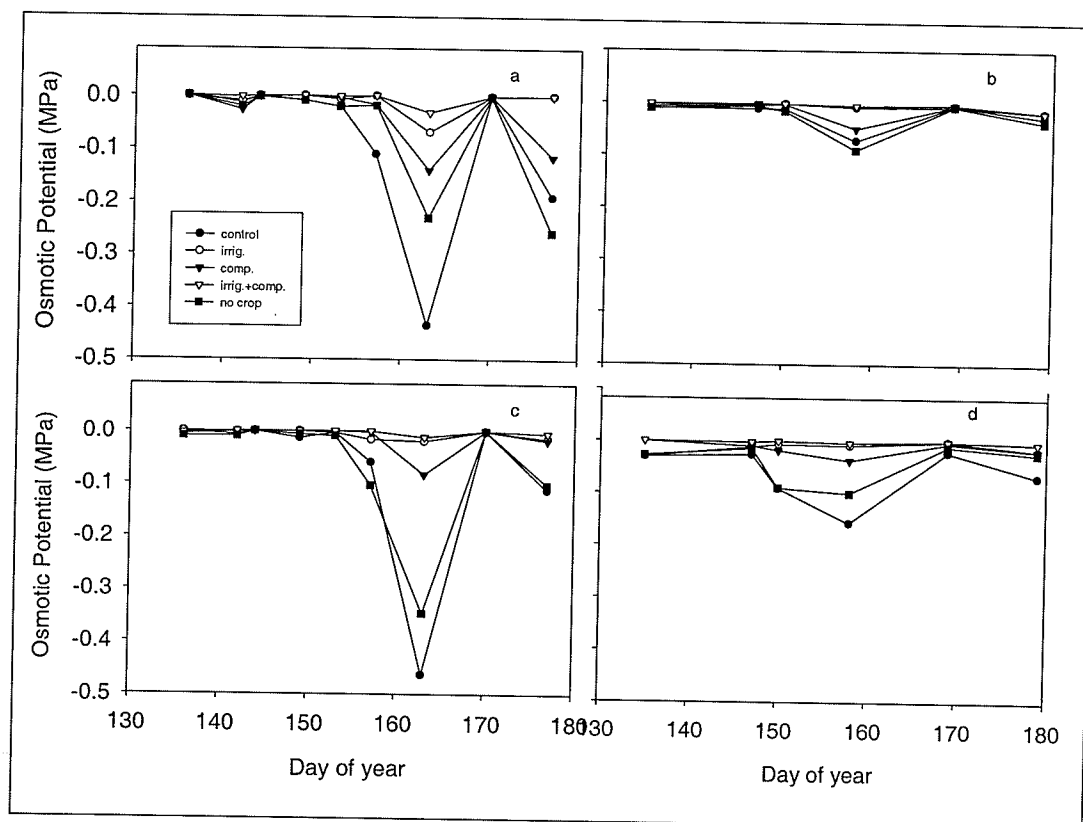
### Treatment Effects on Microsite Condition

Several authors have reported that in common arable fields most weeds emerge from seeds located within the top 6 cm of the soil profile ( Cousens and Moss 1990; du Croix Sissons et al. 2000; Mohler 1996). To characterize this recruitment zone the microsite conditions were measured within the top 6 cm of the soil profile. Soil volumetric moisture in the top 6 cm of the soil profile differed significantly between years, among treatments and over time but not between soil types (sites). Irrigation, compaction or a combination of these two treatments generally resulted in higher volumetric soil moisture levels throughout the season when compared to the control and the no crop treatments (Figure 8-1). Some authors have reported no relationship between soil compaction and soil moisture levels (Voorhees et al. 1978) while others have reported an increase in soil moisture levels under compacted conditions (Liebig et al. 1993). The effects of compaction on soil moisture levels are variable depending on soil type, degree of compaction, weather and initial soil moisture levels (Jurik and Zhang 1999).



**Figure 8-1.** Volumetric soil moisture of the top 6 cm of the soil profilee in the control, irrigated (irrig.), compacted (comp.), irrigated and compacted (irrig.+comp.) and no crop treatments in 2001 averaged over two soil types.

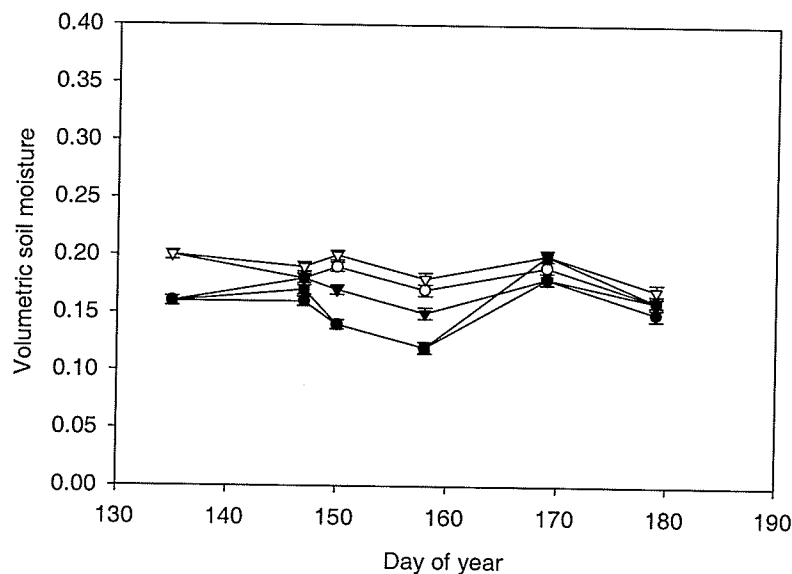
Osmotic potential differed significantly between years and soil types (sites) over time, and among treatments. At the driest point of the season (day of year 163) large differences in soil osmotic potentials were noted between treatments (Figure 8-2). Differences in soil osmotic potential or soil volumetric moisture between treatments followed similar trends. Soil osmotic potential was lowest in the control treatment followed by the no crop treatment, suggesting that the crop used more moisture from the top 6 cm of the soil profile than had evaporated when no crop was present. Soil osmotic potential was greater in the compacted treatment versus the control or no crop treatments but it was lower in the compacted treatment than in the irrigated or the irrigated plus compacted treatment. Trends in treatment effects were similar between soil series although smaller differences were found in soil osmotic potential between the compacted, irrigated and irrigated plus compacted treatments in the Hochfeld versus the Winkler soil series (Figure 8-2).



**Figure 8-2.** Soil osmotic potential for control, irrigated (irrig.), compacted (comp.), irrigated and compacted (irrig.+comp.) and no crop treatments in (a) Winkler soil series 2001, (b) Winkler soil series 2002, (c) Hochfeld soil series 2001, and (d) Hochfeld soil series 2002.



In 2002 less fluctuation in volumetric soil moisture occurred over time within a season compared to 2001 (Figure 8-3). Similar trends in treatment effects on volumetric soil moisture content were found between years. In general, soil volumetric moisture levels were lowest in the control and no crop treatments. The reduction in variability in soil volumetric moisture levels in 2002 versus 2001 resulted in smaller differences in osmotic potential between treatments in 2002 versus 2001. This was reflected in the lack of significant treatment effects on cumulative weed emergence in 2002 versus 2001 for all species except wild oat. In the Winkler soil series the compacted, control and no crop treatments tended to have lower osmotic potentials but these levels did not drop below  $-0.1$  MPa at any time in any of the treatments in 2002 (Figure 8-2). There was greater variation in osmotic potential in the Hochfeld versus the Winkler soil series. This difference was expected because soil moisture content has a greater influence on osmotic potential at relatively high osmotic potential levels (0 to  $-0.2$  Mpa) in the Hochfeld versus the Winkler series soils (data not shown). Osmotic potentials were lowest in the control treatments followed by the no crop and compacted treatment.



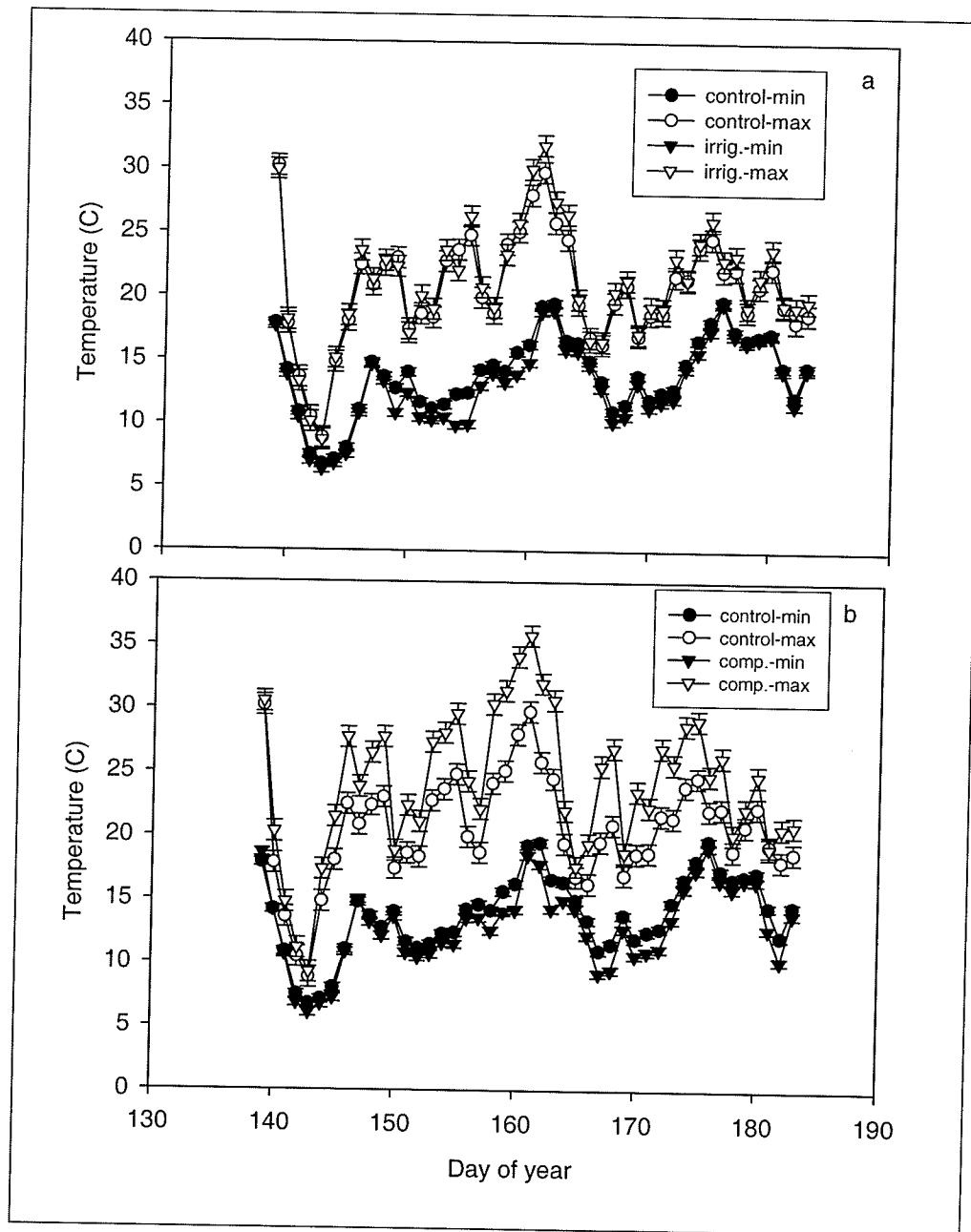
**Figure 8-3.** Volumetric soil moisture of the top 6 cm of the soil profile in the control, irrigated (irrig.), compacted (comp.), irrigated and compacted (irrig.+comp.) and no crop treatments in 2002 averaged over two soil types.

Soil temperature was affected by treatment. In 2001, soil maximum temperature at 2.5 cm was significantly greater in the compacted versus the control treatment (Figure 8-4). Irrigation of the compacted treatments reduced the effect but it remained significant (Figure 8-5). Jurik and Zhang (1999) reported no differences in soil temperature between compacted and non-compacted soils. The same authors did reference a study by Voorhees (1977) who reported that wheel traffic increased soil mean temperatures by 1.1 to 1.7 °C. Similar trends in treatment effects on soil temperature were observed in 2002 but the differences were not as large (Figures 8-6 and 7). In 2001 and 2002 the presence or the absence of the crop had little effect on soil temperature (Figure 8-5 and 7).

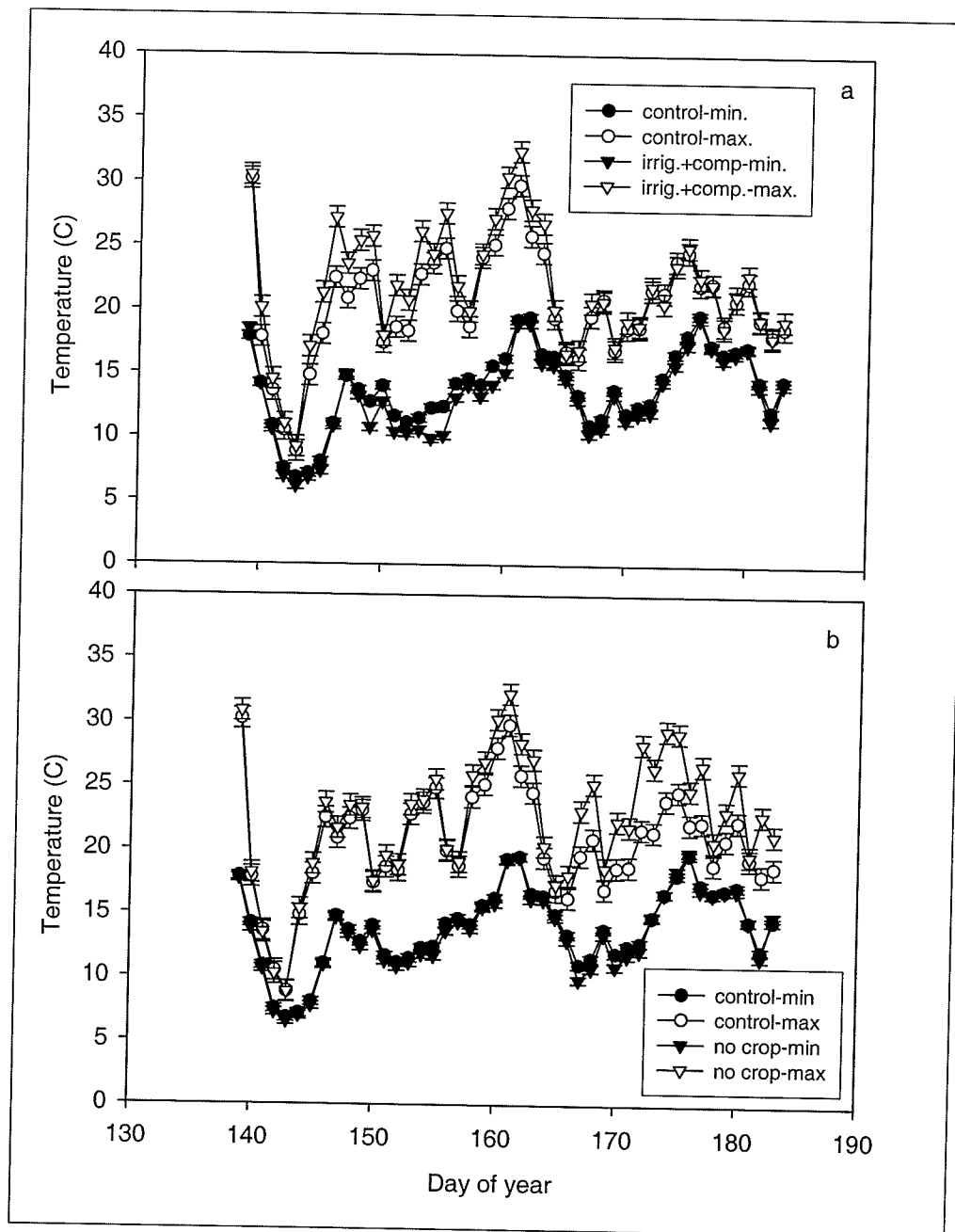
Differences between treatments in maximum temperature affected the amount of soil growing degree days accumulated over the emergence period (Table 8-1). In 2001, near the end of the emergence period (day of year 178) accumulated growing degree days (GDD) were higher in the compacted treatment than in all other treatments. The no crop treatment had the second highest accumulation followed by the irrigated and compacted treatment. By the end of the emergence period significantly fewer GDD's were accumulated in the control and the irrigated treatments than all other treatments. In 2002, the trend was similar and by the end of the emergence period more GDD's had accumulated in the compacted treatment compared to the control, irrigated, and irrigated and compacted treatments (Table 8-1).

In 2001, bulk density was generally higher in the Hochfeld versus the Winkler soil series (Table 8-2). The compacted and the compacted plus irrigated treatments had significantly higher bulk densities than all other treatments in both soil series. In 2002, little difference in bulk density was observed between the two soil series. In 2002, the compacted and compacted plus irrigated treatments had significantly higher bulk densities than all other treatments in the Hochfeld soil series but not in the Winkler soil series.

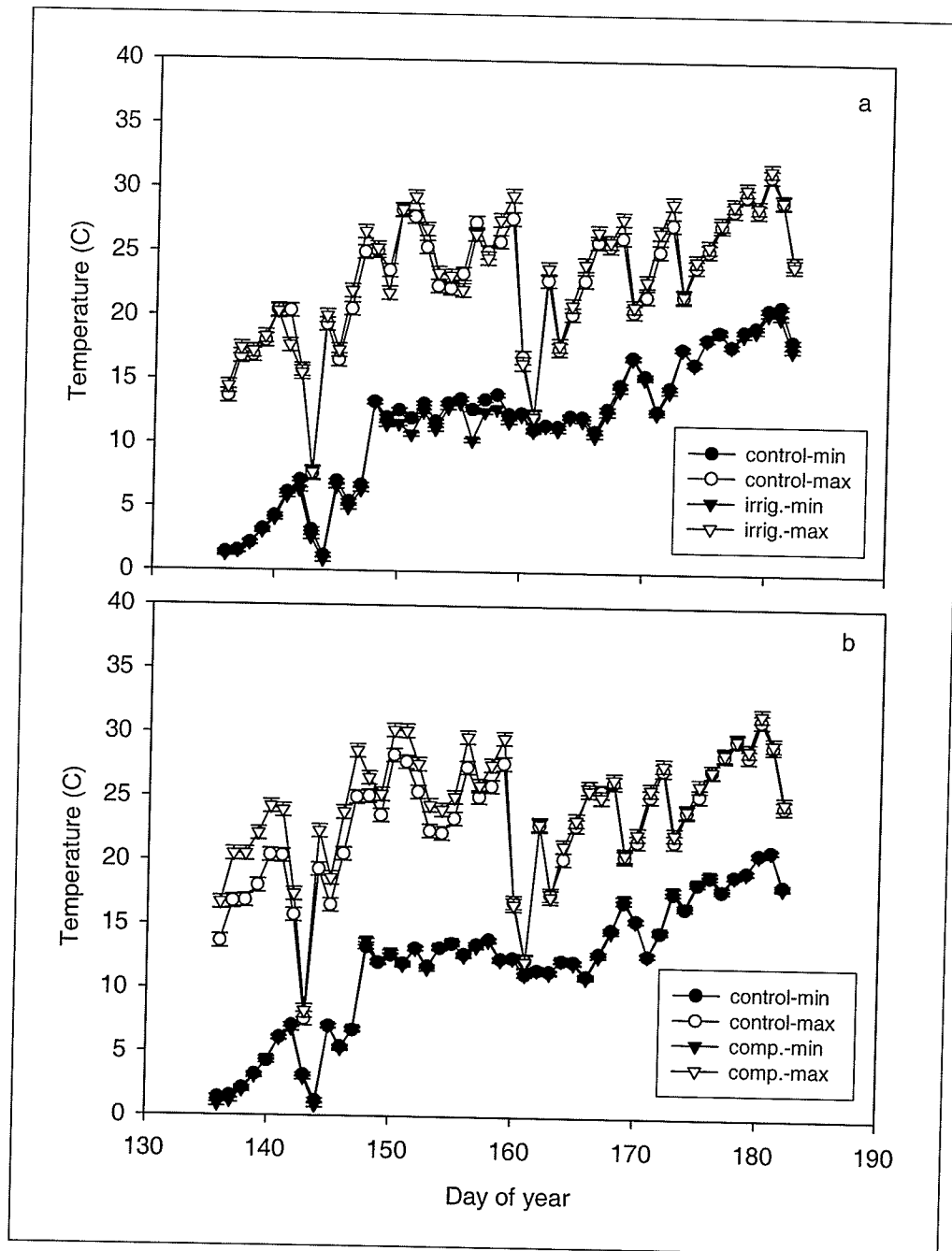
In 2001, penetration resistance tended to be higher in the Winkler soil series than the Hochfeld soil series (Table 8-2). In 2001 in the Winkler series soils penetration resistance was highest in the compacted treatment followed by the irrigated plus compacted treatment. It was lowest in the no crop treatment. In 2001, a similar trend of treatment effects on penetration resistance occurred in the Hochfeld soil series. In 2002,



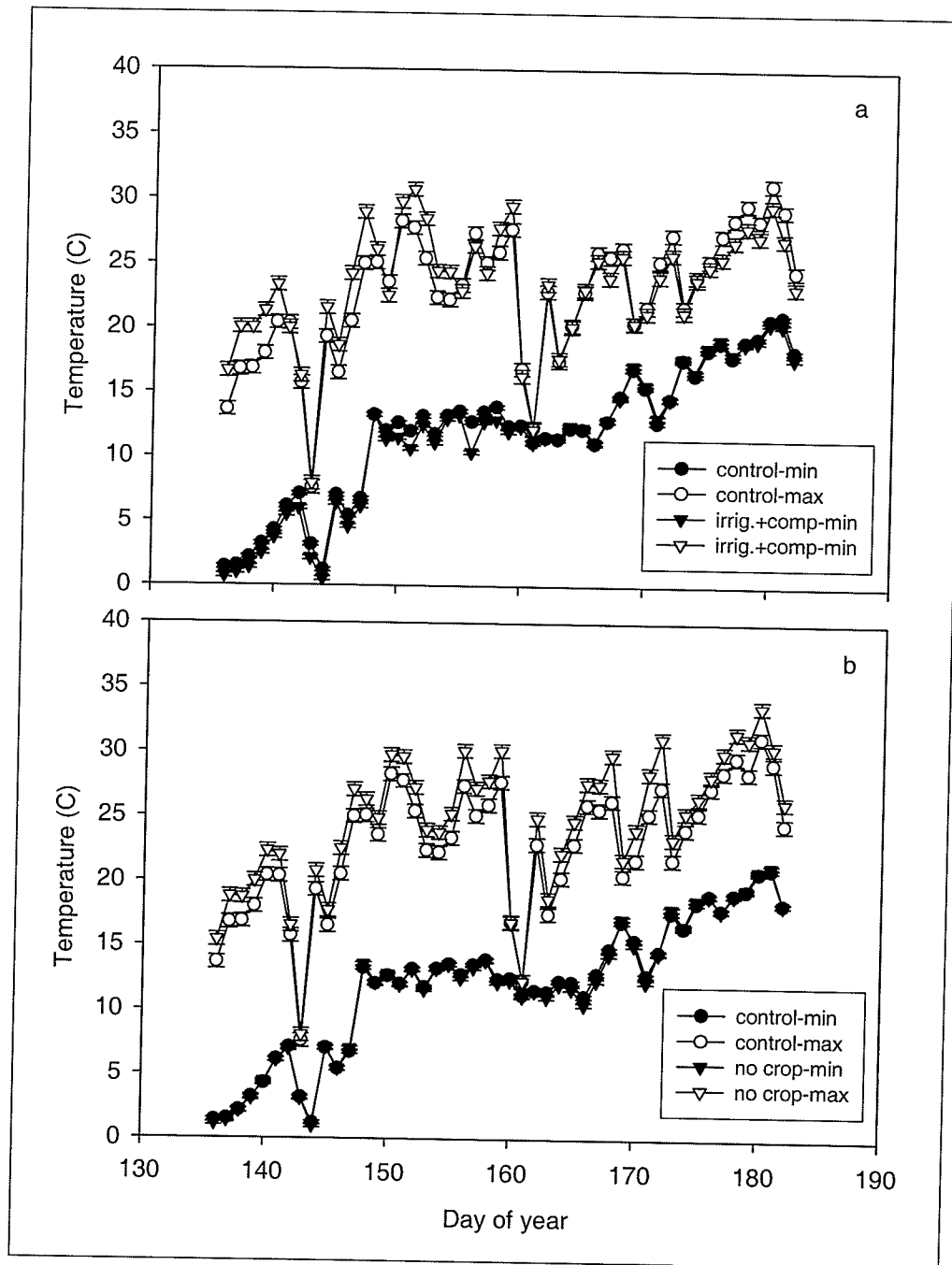
**Figure 8-4.** Maximum (max) and minimum (min) soil temperature at 2.5 cm as affected by (a) irrigation (irrig.) and (b) compaction (comp.) in 2001.



**Figure 8-5.** Maximum (max) and minimum (min) soil temperature at 2.5 cm as affected by (a) compaction and irrigation (irrig.+comp) and (b) crop removal (no crop) in 2001.



**Figure 8-6.** Maximum (max) and minimum (min) soil temperatures at 2.5 cm as affected by (a) irrigation (irrig.) and (b) compaction (comp.) in 2002.



**Figure 8-7.** Maximum (max) and minimum (min) soil temperature at 2.5 cm as affected by (a) irrigation and compaction (irrig.+comp) and crop removal (no crop) in 2002.

**Table 8-1.** The accumulated growing degree days (base 0 °C) (GDD) in 2001 and 2002 at day of year 149, 155 and 178 in control, irrigated, compacted, irrigated and compacted (irrig.+comp) and no crop treatments averaged over sites.

Treatment	2001			2002		
	149	155	178	149	155	178
	-----gdd-----					
Control	164 c <sup>a</sup>	263 c	689 d	167 c	280 c	719 b
Irrigated	162 c	258 c	683 d	166 c	279 c	721 b
Compacted	176 a	285 a	746 a	186 a	305 a	750 a
Irrig.+comp	173 ab	275 b	702 c	177 b	293 b	726 b
No crop	165 bc	265 c	718 b	178 b	296 b	754 a

<sup>a</sup>Least squares means of growing degree days within the same day of year with different letters are significantly different at  $P < 0.05$  using least squares means comparisons.

**Table 8-2.** Penetration resistance and bulk density of Hochfeld and Winkler series soils as affected by control, irrigated, compacted, irrigated and compacted (irrig.+comp) and no crop treatments in 2001 and 2002.

Treatment	Penetration Resistance				Bulk Density			
	2001		2002		2001		2002	
	Hoch.	Wink.	Hoch.	Wink.	Hoch.	Wink.	Hoch.	Wink.
	-----MPa-----				-----g cm <sup>-3</sup> -----			
Control	0.6 fg <sup>a</sup>	1.16 c	1.50 a	1.30 b	1.21 b	1.07 c	1.20 b	1.22 ab
Irrigated	0.72 ef	1.19 c	1.4 ab	1.38 ab	1.21 b	1.12 c	1.20 b	1.23 ab
Compacted	0.9 de	1.75 a	1.50 a	1.35 ab	1.38 a	1.24 b	1.24 a	1.26 a
Irrig.+comp	0.96 d	1.39 b	1.48 a	1.40 ab	1.39 a	1.22 b	1.23 a	1.24 a
No crop	0.49 g	0.94 d	1.4 ab	1.27 b	1.19 b	1.10 c	1.19 b	1.23 ab

<sup>a</sup>Penetration resistance and bulk densities in both soil series within each year followed by different letters are significantly different at  $P < 0.05$  using least squares means comparisons.

there was very little difference in penetration resistance between soil series. In 2002, treatment had no effect on penetration resistance in either soil series.

The absence of crop cover in Manitoba fields resulted in higher osmotic potentials during dry periods and a greater cumulation of growing degree days by the middle of the growing season compared to the control treatment. These differences combined with the increased light levels reaching the soil in areas with no crop cover may impact the growth

and emergence of some weed species explaining the bloom of weed growth often observed by producers in crop canopy gaps. Slight soil compaction increased soil moisture levels and accumulated growing degree days throughout the entire growing season. In some situations slight compaction of soil surface layers may lead to increased and more rapid weed emergence in the spring.

### **Microsite Modification Treatment Effects on Weed Emergence**

The effect of microsite modification treatments on weed emergence differed significantly between years but not soil series. Microsite modification treatments had no effect on canola emergence in 2001 and 2002 (Table 8-3). In 2001, green foxtail emergence was significantly higher in the compacted treatments versus other treatments except the irrigated and compacted treatment (Table 8-3). Green foxtail emergence in the compacted treatment was 66% higher than in the irrigated non-compacted treatment. Based on empirical emergence models for green foxtail in this region of the Northern Great Plains (Bullied et al. 2003) the differences in growing degree days between treatments should have accounted for a maximum difference in emergence of 15 %. The dramatically lower soil osmotic potential in the control plots versus the compacted plots combined with the decrease in accumulated growing degree days may explain the much lower level of green foxtail emergence in the control treatment (Figure 8-2). In 2001, green foxtail emergence was significantly higher in the soil compaction treatment versus all other treatments except for the combined irrigation and soil compaction treatment. This effect may be attributed to a greater accumulation of GDD's in the soil compaction treatment since green foxtail preferentially germinates in warmer temperatures (Douglas et al. 1985).

Wild mustard emergence was affected by treatment in 2001 but not in 2002. In 2001, wild mustard emergence was significantly higher in the irrigated treatment than in the irrigated and compacted treatment but not significantly higher than in any of the other treatments (Table 8-3). Empirical emergence models for wild mustard emergence in the northern great plains (Bullied et al. 2003) would suggest that differences in accumulated growing degree days between these two treatments should have accounted for a



difference in emergence of only 1%. Wild mustard emergence is responds to increased moisture (manuscript #1) but emergence may be limited when increased moisture and compaction combine to limit gas diffusion into the soil (manuscript #4).

**Table 8-3.** Total cumulative emergence in 2001 and 2002 of canola, green foxtail and wild mustard seedlings in the control, irrigated, compacted, irrigated and compacted (irrig.+comp) and no crop treatments averaged across seeding densities and sites. Wild oat emergence in 2001 and 2002 are averaged because year was not significant.

Treatment	01/02	2001			2002		
	Wild oat	Canola	Green foxtail	Wild mustard	Canola	Green foxtail	Wild mustard
	-----Cumulative Emergence-----						
Control	40 b	83 a <sup>a</sup>	63 b	59 ab	38 a	46 a	28 a
Irrigated	56 a	77 a	58 b	70 a	38 a	45 a	26 a
Compacted	60 a	73 a	96 a	55 ab	46 a	51 a	28 a
Irrig.+comp	64 a	73 a	78 ab	48 b	42 a	44 a	36 a
No crop	39 b	85 a	70 b	62 ab	50 a	45 a	24 a

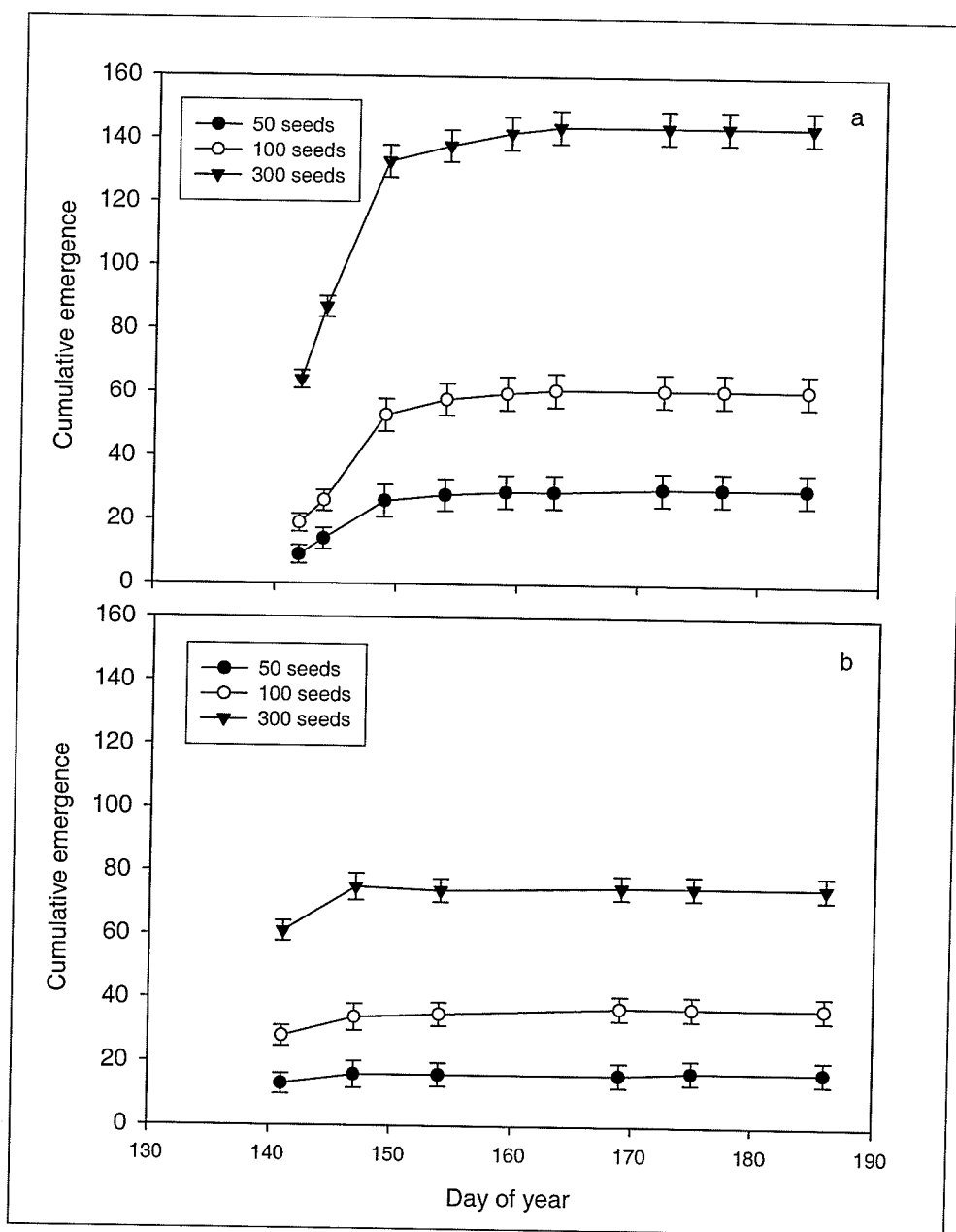
<sup>a</sup> Emergence counts within the same species and year followed by different letters are significantly different at  $P < 0.05$  using least squares means comparisons.

Wild oat emergence was not significantly different between years so the data were combined for analysis. Wild oat emergence was significantly lower in the control and no crop treatments versus all other treatments. The positive effect of the compacted and irrigated treatments on wild oat emergence does not appear to be related to effects of these treatments on soil temperature and accumulated growing degree days. The irrigated and compacted treatments resulted in a significant increase in osmotic potential. Since wild oat preferentially survives in cool and moist habitats (Sharma and Vanden Born 1978) the higher osmotic potential may have caused the increase in wild oat emergence.

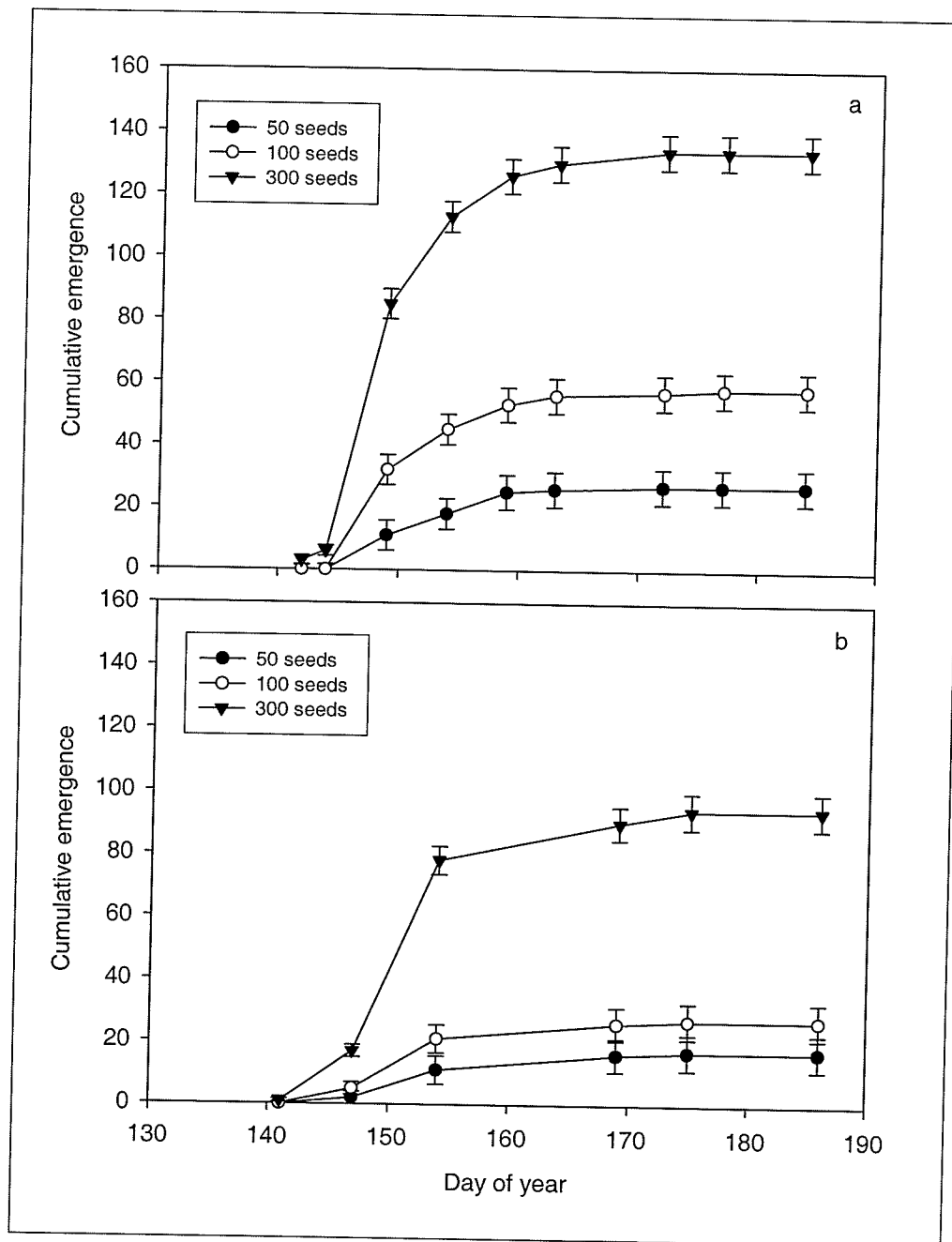
### Seeding Density Effects on Weed Emergence

The number of plants emerging increased with seeding density for all four plant species (Figures 8-8 through 8-11). When testing the correlation between seedling emergence and seeding density 80 and 60% of the variation (R-squared values) in the

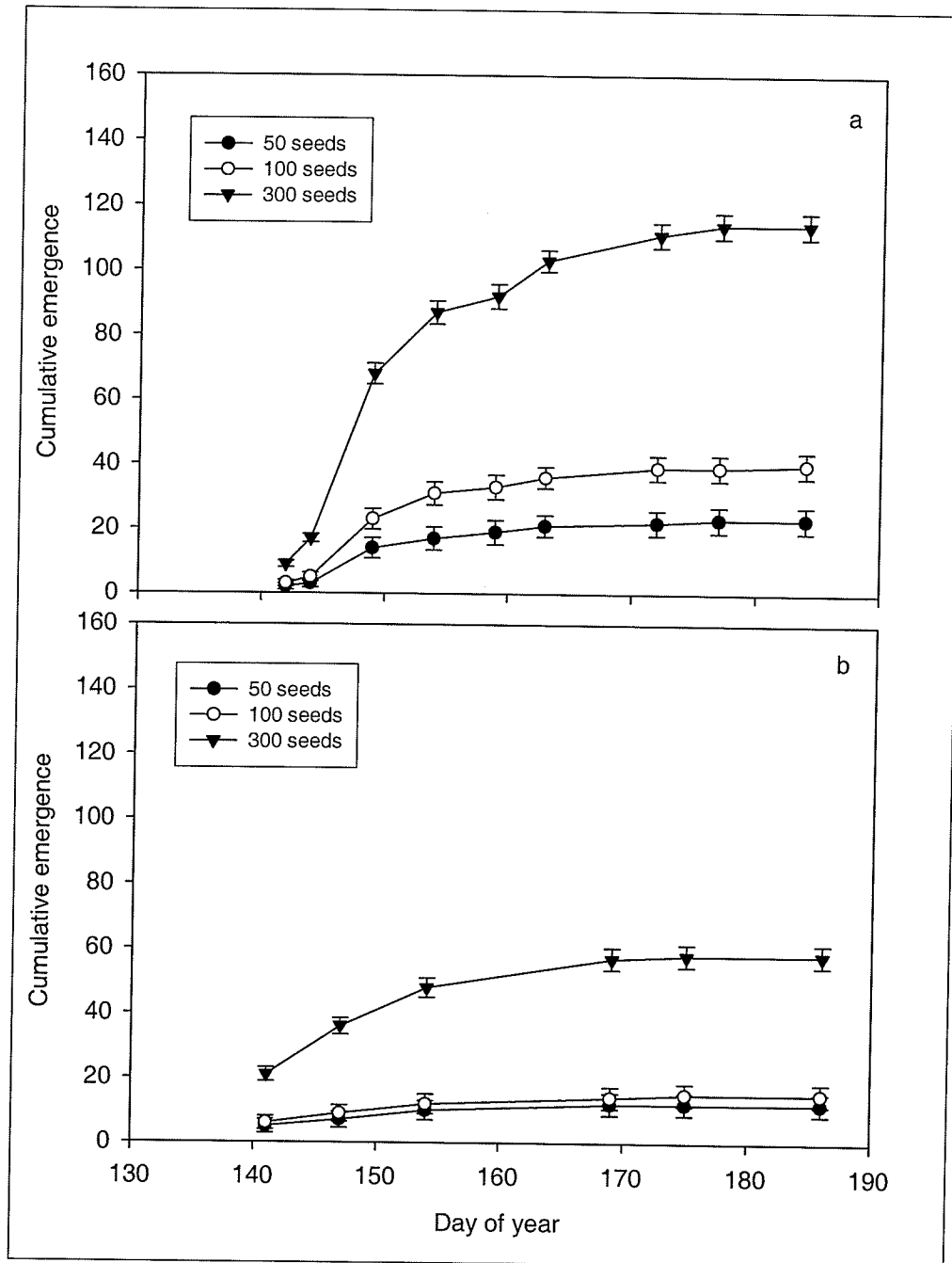
final canola emergence could be explained by the seed number in 2001 and 2002, respectively. In 2001 and 2002, 75 and 83% of the variation in final green foxtail emergence could be explained by the variation in seeding density. Seeding density explained 77% and 60% of the variation in wild mustard seedling final emergence in 2001 and 2002, respectively.



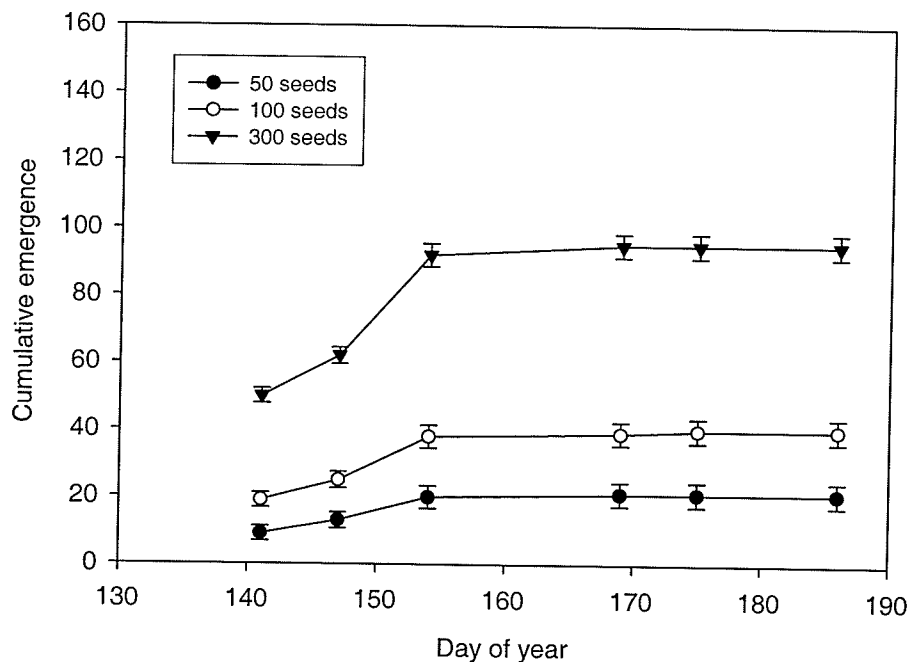
**Figure 8-8.** Cumulative emergence of canola in a 50 by 50 cm quadrat over time in plots seeded with 50, 100 and 300 seeds plot<sup>-1</sup> in (a) 2001 and (b) 2002 averaged over sites.



**Figure 8-9.** Cumulative emergence of green foxtail in 50 by 50 cm quadrats over time in plots seeded with 50, 100 and 300 seeds plot<sup>-1</sup> in (a) 2001 and (b) 2002 averaged over sites.



**Figure 8-10.** Cumulative emergence of wild mustard in a 50 by 50 cm quadrat over time in plots seeded with 50, 100 and 300 seeds plot<sup>-1</sup> in (a) 2001 and (b) 2002 averaged over sites.



**Figure 8-11.** Cumulative emergence of wild oat in 50 by 50 cm quadrats over time in plots seeded with 50, 100 and 300 seeds plot<sup>-1</sup> in 2001 and 2002 averaged across sites.

When averaged over both years 58% of the variation in final wild oat emergence could be explained by differences in seeding density.

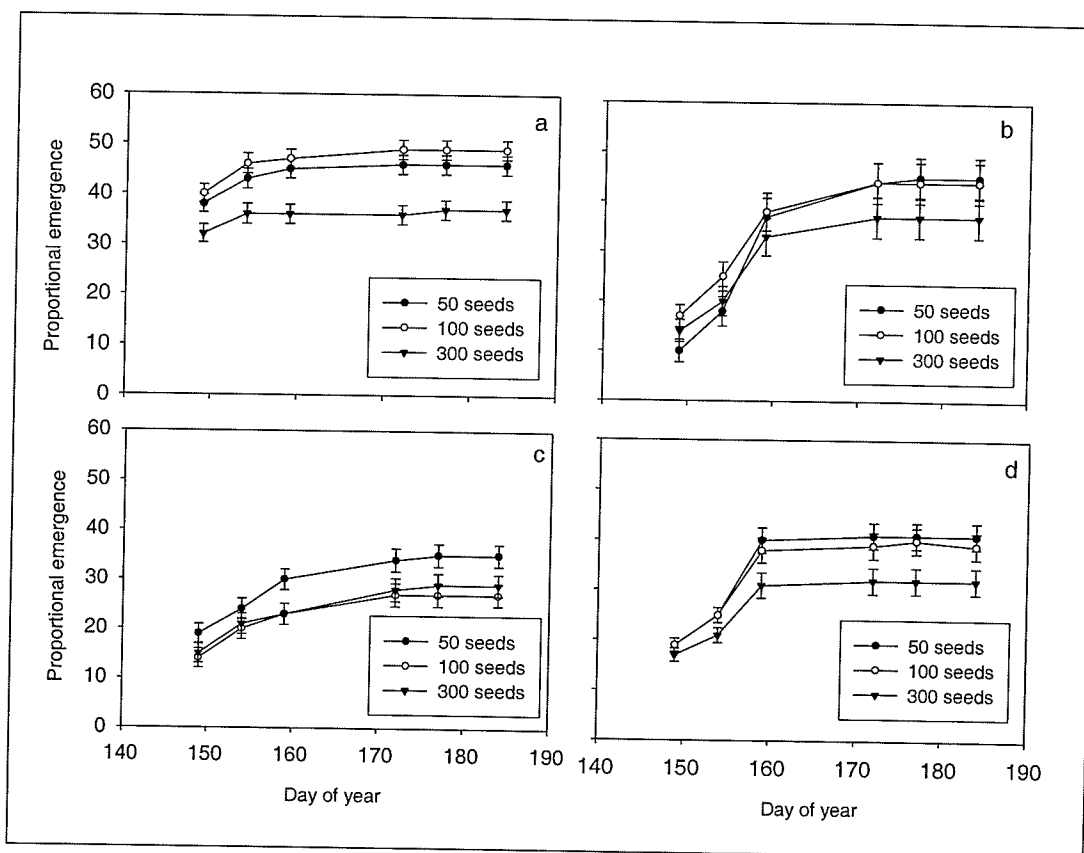
Emergence levels in the field were lower than germination levels in petri dishes for all species (Table 8-4). This suggests that for canola, wild mustard, green foxtail and wild oat a significant proportion of non-dormant seeds are not germinating and emerging in the field. Predation may have removed a proportion of the seeds. Seeds may have landed where conditions were not within the range required for germination. Seeds may also have landed where conditions caused the seed to enter secondary dormancy. As seeding density increased, proportional emergence declined in some cases. At seed densities of 300 seeds plot<sup>-1</sup> proportional emergence of canola, green foxtail and wild oat was significantly lower than in plots where seed density was 50 or 100 seeds plot<sup>-1</sup> (Figure 8-12).

**Table 8-4.** Percentage germination of seeds following standard germination test in petri dishes versus final percentage emergence of seedlings from field experiments when seeds were incorporated in the top 6 cm of the soil in 2001 and 2002. Field emergence is averaged across treatments, sites and seed densities.

Test	Canola	Green foxtail	Wild mustard	Wild oat
	-----% germination-----			
Germination test	95±2.6 <sup>a</sup>	90±4.2	74±7.9	76±6.2
Field emergence 2001	56±1.6 <sup>b</sup>	52±2.7	41±1.9	39±2.1
Field emergence 2002	32±1.6	32±4.7	20±1.9	36±2.1

<sup>a</sup> Germination mean plus or minus the standard error.

<sup>b</sup> Emergence mean plus or minus the standard error.



**Figure 8-12.** Proportional emergence of (a) canola, (b) green foxtail, (c) wild mustard and (d) wild oat from plots seeded with 50, 100 and 300 seeds plot<sup>-1</sup>. Data represent mean of results from 2001 and 2002 averaged across soil series.

Proportional emergence of wild mustard in plots with seed densities of 100 or 300 seeds plot<sup>-1</sup> was significantly lower than proportional emergence in plots with a seed density of

50 seeds  $m^{-2}$  (Figure 8-12). The decline in proportional emergence with increasing seed density may have been caused by microsite saturation at higher seed densities or increased preferential predation at higher seeding densities

Crawley (1990) suggested that recruitment in a plant community is limited by seed number, microsite conditions, plant to plant competition and seed predation. In this experiment we did not determine the effect of predation on seedling recruitment. We can, however, estimate the effect of crop competition, microsite condition and seed number on seedling recruitment. The presence or the absence of the crop did not affect the number of seedlings emerging in this experiment. Removal of plant material is necessary for recruitment to occur in native grasslands and forests (Bratton 1976; Burke and Grime 1996). In annual cropping systems most biomass is removed at some time during the growing season. Spring emerging weeds may emerge prior to the crop or during the early stages of crop growth when the crop is only weakly competitive. We conclude that crop competition did not affect weed emergence in this experiment. The absence of canopy effect is not surprising since most weeds in annual cropping systems germinate and emerge prior to canopy closure. In addition, a large proportion of canola, wild mustard and wild oat seedlings emerged prior to or at the same time as the crop. In our experiment therefore, differences in recruitment must be due to differences in seed number, microsite conditions or predation effects.

The number of emerged seedlings increased with the number of seeds present in the soil. However, the annual weed populations in this experiment cannot be considered solely seed limited for a number of reasons. First, changing microsite conditions affected the number of weed seedlings emerging in wild oat in both years and green foxtail and wild mustard in one out of two years. Second, the number of seedlings emerging in the field was lower than the number of seeds germinating in petri dishes. Third, the number of seedlings emerging in the field was far lower than the seed density in the soil. Fourth, proportional emergence declined with increasing seedling density. This would suggest that in our experiment the recruitment of these four weed species was primarily microsite limited.

We suggest that a specified volume of soil contains a specific number of potential microsities. A potential microsite is defined as a microsite composed of the necessary

conditions to promote germination and emergence of a specific plant species. The switch from a potential to an actual microsite occurs upon the arrival of the seed. Therefore, a weed population is limited by the number of potential microsites within a field. A weed population is secondarily seed limited because increasing the number of seeds within the seed bank increases the probability that a seed will land within a potential microsite. Limiting seed dispersal or altering the number of potential microsites within an arable field will dramatically alter the annual recruitment of a weed species.

Weed patch initiation and weed population spread is determined both by seed dispersal and microsite conditions. Effective weed management will always include limiting seed return because increasing the number of weed seeds increases the probability that the seeds will land in an appropriate microsite. In some cases altering the microsite via management may also play an important role. Altering the microsite with management will favor emergence of some species while disfavoring the emergence of others. Management practices should be followed which limit seed dispersal of all species and disfavor the emergence of hard to control species, such as herbicide resistant weeds, during critical periods.



## GENERAL DISCUSSION

### GERMINATION AND EMERGENCE CHARACTERISTICS OF SPECIFIC ANNUAL AND PERENNIAL PLANT SPECIES

#### Annual Species

**Barnyardgrass.** Barnyardgrass emergence is largely unaffected by seed depth or soil aggregate size within the top 7 cm of the soil profile when the soil is maintained at field capacity. The depth within the soil profile may impact the rate of emergence with seeds on the soil surface and seeds at depths of 7 cm or greater taking longer to emerge. Some authors have reported barnyardgrass emergence up to depths of 10 cm in the soil profile with maximum emergence occurring at 1 to 2 cm (Dawson and Bruns 1962 in Maun and Barrett 1986). Barnyardgrass germinates and grows best in high moisture conditions. Seedling establishment from surface germinating seeds may be hindered by a lack of moisture. In fact, barnyardgrass is able to continue growth in saturated soils or soils submerged by water (Maun and Barrett 1986). Consequently, one would anticipate barnyardgrass infestations in high moisture areas.

The ability of barnyardgrass to germinate over a relatively wide range of depths and moisture levels may partially be due to its ability to germinate over a wide range of oxygen levels. Barnyardgrass is one of the few species that has the rare ability to germinate in the complete absence of oxygen (Rumpho and Kennedy 1981). The effects of oxygen on seed germination vary depending on the osmotic potential of the germination media and if seeds are exposed to light. Germination of barnyardgrass seeds exposed to light increases with oxygen levels up to 10% oxygen when the soils are relatively moist (osmotic potentials between  $-0.01$  and  $-0.5$  MPa) and decreases when oxygen levels rise above 10%. High oxygen concentrations and exposure to light in combination inhibit germination and may act as a signal preventing soil surface germination or germination during very dry periods. Elevated carbon dioxide concentrations combined with low oxygen concentrations may promote germination below the surface during periods of high soil moisture content (Yoshioka et al. 1998).

Freshly collected seeds of barnyardgrass exhibit innate dormancy (Maun and Barrett 1986) and may require exposure to light for germination to occur (Taylorson and Dinola 1989). Exposure to even very low light intensities is sufficient to induce germination. The only exception is the apparent inhibition of germination in light with 21% oxygen concentrations. It is unlikely that surface debris would intercept sufficient incoming radiation to prevent the germination of this species. I found that 90% ground cover by straw did not affect barnyardgrass germination. The effects of light mediate the response of barnyardgrass seeds to osmotic potential as well. Germination only increases with increasing osmotic potential when the seeds are exposed to light. Osmotic potentials between 0 and  $-0.5$  MPa have little influence on seed germination when the seeds are kept in dark conditions.

This species exhibits preferential germination, growth and development on high moisture soils. Early emerging seedlings produce the most seeds which may remain viable in the soil for several years. A small proportion of barnyardgrass seeds may remain viable up to 13 years (Dawson and Bruns 1975). This weed may be controlled by shallow tillage at monthly intervals (Ogg and Dawson 1984). Due to its ability to germinate over a wide range of conditions, barnyardgrass seedlings need to be controlled early in the season preventing seedling dispersal.

**Canola.** Canola seeds in soils maintained at field capacity germinated equally well on the surface and at all depths up to 4 cm. We found reduced emergence at soil depths of 7 cm. Other authors have reported a general decrease in canola seed emergence with increasing depth (Nuttall 1982; Thomas et al. 1994). Fluctuating moisture only reduced surface germination of canola in our experiments. Germination was not affected by aggregate size.

Lopez-Granados and Lutman (1998) reported that exposure to light or dark conditions had no effect on the germination of recently harvested canola seeds in moist conditions. In our experiments canola seed germination was significantly reduced when seeds were not exposed to light. Increased canola seed germination with exposure to light suggests that at least a proportion of the seed lot used had developed a light requirement for germination.

Low oxygen concentration (less than 5%) and low osmotic potentials (less than – 0.5 MPa) may trigger secondary dormancy in canola. The imbibition rate for canola seed remains relatively constant across a range of osmotic potentials (0 to –1.5 MPa) while germination decreases with decreasing osmotic potential. Lopez-Granados and Lutman (1998) reported imbibition with osmotic potentials of –1.5 MPa in canola with far red light or dark induced secondary dormancy. They found that a greater proportion of seeds entered secondary dormancy the longer they were exposed to these conditions. Osmotic potential of the solution, not the rate or extent of imbibition, appears to trigger secondary dormancy. To control volunteers Lopez-Granados and Lutman (1998) suggested avoiding fall tillage which will bury freshly harvested non-dormant seeds exposing them to darkness, typically dry soil conditions and perhaps low oxygen concentrations. Seeds exposed to these conditions may enter dormancy creating future volunteer problems.

**Catchweed Bedstraw.** Catchweed bedstraw has poor germination at the soil surface and below 4 cm depths in the soil profile. Rottele (1980) and Froud-Williams et al. (1984) reported that the majority of catchweed bedstraw seedlings emerge from depths between 0 and 5 cm with little or no establishment of seedlings from seeds on the soil surface. Surface germination for this species may be inhibited because it germinates best in darkness with (Sjostedt 1959) exposure to even very low light intensities inhibiting germination (Malik and VandenBorn 1987).

Greater catchweed bedstraw germination and emergence was observed with larger aggregates (greater than 12.7 mm diameter) than with smaller aggregates (less than 2.0 mm diameter). As well, catchweed bedstraw seed germination increased significantly with increasing oxygen concentration when seeds were kept in the dark but there was much less of an effect when seeds were exposed to light. Therefore, greater percentage emergence when seeds are buried by larger aggregates may partially be due to increased aeration. Decreased emergence with increasing seed depth may be attributed to reduced gas exchange or a lack of oxygen at deeper depths (Benvenuti et al. 2001a). Catchweed bedstraw is a specialist with very specific germination requirements. Seed burial is necessary for germination to occur since light inhibits germination. Burial cannot exceed 5 cm or few seeds will germinate. The seeds germinate best with adequate moisture but

excessive moisture may limit gas diffusion inhibiting seed germination. The species is quite sensitive to changes in moisture availability with germination reduced at  $-0.25$  MPa and completely inhibited at  $-0.75$  MPa (Malik and Vanden Born 1988). The effects of light and temperature become less important as the seed ages and the species becomes more general in its germination requirements (Malik and Vanden Born 1988). The change from specific to general germination requirements probably occurs because the seeds only remain viable within the seed bank for 2 to 3 years.

Catchweed bedstraw (cleavers) thrives in moist environments while false cleavers thrives in relatively dry and sunny habitats (Malik and Vanden Born 1988). Shallow fall or spring tillage may incorporate seeds and increase aeration leading to increased seedling emergence. Deep cultivation every 3 to 4 years in heavily infested areas may bury seeds beyond the recruitment zone and seed viability may be lost before additional deep tillage returns the seeds to the recruitment zone. Alternatively, no-till fields may have reduced emergence due to poor surface germination of this species.

**Green Foxtail.** Green foxtail emergence was generally unaffected by seeding depth or by fluctuating soil moisture conditions if seeds were placed below the soil surface. Germination can occur from soil depths up to 12 cm (Vanden Born 1971) although du Croix Sissons et al. (2000) reported that most green foxtail seedlings in agricultural fields recruited from depths between 1.2 and 4.2 cm. Since green foxtail germinates better when seeds are slightly buried one would expect lower levels of emergence in no-till fields where the weed seeds are not incorporated. It has often been reported, however, that higher populations of annual grass weeds such as green foxtail are found in reduced tillage fields (Buhler 1992, Froud-Williams et al. 1983). Increased residue cover may affect surface germination of green foxtail seeds but in our experiments cover levels between 0 and 90% had no effect on the number of seedlings emerging.

The effects of depth on seed germination varied with aggregate size. Large aggregate sizes decreased emergence at all depths compared to smaller aggregate sizes. Green foxtail germination was relatively insensitive to oxygen concentration which may partially explain its ability to germinate from a broad range of depths over a broad range of textures (Douglas et al., 1985). Although, freshly harvested green foxtail seeds are

nearly completely dormant, relatively short periods (3-4 weeks) at low temperatures (6 °C) will break dormancy (Vanden Born 1971). Green foxtail was not affected significantly by exposure to light in any of our experiments suggesting that light does not play a large role in the population dynamics on non dormant green foxtail seeds.

Green foxtail imbibition rates remain relatively low over a range of osmotic potentials. Green foxtail germination but not imbibition declines with declining osmotic potential. Blackshaw et al. (1981) reported a complete inhibition of green foxtail germination at  $-0.78$  and  $-1.53$  MPa. Douglas et al. (1985) referenced a study by Manthey and Nalewaja who found 75% germination of green foxtail seeds at 0 MPa and 3% germination at  $-0.8$  MPa. Osmotic potential has a much greater impact on germination level than would be expected based on imbibition levels. Green foxtail imbibes water at relatively low water potentials and also germinates at relatively low proportional seed moisture contents. This may be an adaptation to allow seeds of this species to germinate near the soil surface in warm microsites (Douglas et al. 1985).

Green foxtail seeds can germinate and emerge over a wide range of environmental conditions. Seeds of this species can also form a persistent seed bank that remains viable for an extended period of time (Douglas et al. 1985). Green foxtail is a  $C_4$  species that germinates later in the growing season in Western Canada during warmer temperatures. Early seeding may lead to increased foxtail emergence (Spandl et al. 1998) especially if emergence occurs prior to canopy establishment. Delayed seeding decreases the density of seedlings and increases the rate of emergence (Spandl et al. 1998, Spandl et al. 1999). Delayed seeding may lead to better green foxtail control via reduced plant densities and more simultaneous emergence patterns.

**Field Pennycress.** Optimal field pennycress emergence occurs on or just below the soil surface. Oxygen concentration has a large impact on field pennycress seed germination with germination decreasing with decreasing oxygen level. Low oxygen concentrations or high carbon dioxide concentrations may act as a trigger initiating secondary dormancy when seeds are buried at deeper soil depths (Bibbey 1948) although changes in dormancy level can occur independent of depth of burial (Courtney 1966 in Best and McIntyre 1975). Aggregate size has no significant impact on germination and emergence levels.

In our experiments field pennycress emergence was relatively insensitive to moisture level. Hazebroek and Metzger (1990) reported that moisture was the main factor limiting emergence of surface-placed seeds of field pennycress. Seeds on the surface would be exposed to greater fluctuations in soil moisture which in turn may impact emergence in some situations. Hazebroek and Metzger (1990) found that exposure to red light promoted emergence and shading limited field pennycress emergence. Other studies have shown that seeds germinate best in weak light or darkness (Mulligan and Bailey 1975) or that light stimulates seed germination (Best and McIntyre 1975). In our experiments the presence or the absence of light in adequate moisture conditions did not affect seed germination. Ground cover ranging from 0 to 90% cover also had no impact on seed germination.

Field pennycress is adapted to a wide range of conditions and grows in both wet and dry habitats (Best and McIntyre 1975). This species may also survive for extended periods in the seed bank (up to 20 years) (Best and McIntyre 1975). To manage the population, limiting seed dispersal is very important. Cultivation following seed dispersal should be avoided since buried field pennycress seeds will become dormant causing problems in future years. Seeds left on the surface may germinate in the spring or the fall and be controlled with tillage or herbicides prior to crop seeding. Delayed crop seeding may control a large proportion of the plant population (Best and McIntyre 1975).

**Round Leaved Mallow.** Germination of round leaved mallow is relatively insensitive to depth. Blackshaw (1990) found that this species emerges over a range of depths with the greatest round leaved mallow emergence occurring at depths of 0.5 to 2 cm with emergence declining significantly from 3 through 6 cm and no emergence occurring at 8 cm. Although fluctuating soil moisture did not significantly affect emergence of this species in our experiment, Makowski and Morrison (1989) found that major infestations of this weed generally occur in regions of Western Canada where relative precipitation levels are high. Emergence tended to increase with increased crop cover.

Round leaved mallow germinates and emerges over a wide range of environmental conditions and seeds remain viable for extended periods of time in the seed bank. To prevent long term problems with this species steps should be taken to limit

seed dispersal. This species is a poor competitor and cannot generally survive under grass cover except in high nutrient situations (Makowski and Morrison 1989). Crop rotation that incorporates competitive crops should help control this species.

**Wheat.** Wheat seedlings can emerge over a wide range of depths although seeds on the soil surface generally do not germinate quite as well as seeds below the surface. Since wheat germination is not affected by exposure to light it is unclear why germination of seeds on the soil surface is somewhat inhibited. Surface inhibition may not occur in fields with high levels of surface debris. Wheat can germinate over a fairly wide range of osmotic potentials and is less responsive to sowing depth and aggregate size than other species with similar seed sizes (Cussans et al. 1996).

Since wheat can emerge over a wide range of depth it is not surprising that germination was not affected by oxygen concentration except for a slight decrease in germination levels at oxygen concentrations of 21%. Al-Ani et al. (1985) also found that wheat germinated relatively well at all oxygen concentrations below 21% with germination of wheat even occurring at oxygen concentrations as low as 0.1%. Compaction can reduce wheat germination but the reasons for this reduction are unclear.

Based on these results, one might expect wheat to become a problem volunteer weed in no-till situations due to its ability to germinate relatively successfully on the surface even in drier conditions. Wheat could also cause volunteer problems in conventional tillage fields due to its ability to germinate from a wide range of depths. The apparent lack of dormancy in this species facilitates management.

**Wild Mustard.** Wild mustard has optimal emergence levels when seed are placed on or just below the surface. Preferential surface germination of this species may be due to a light requirement or sensitivity to gas diffusion. Wild mustard seeds imbibe water rapidly at high osmotic potentials but imbibition rates drop when moisture becomes limiting. This may be an adaptation to surface germination where it would be an advantage to rapidly imbibe moisture when it is available. Research thus far has given conflicting results on the effects of light on wild mustard germination (Mulligan and Bailey 1975). Holm (1972) found that freshly harvested wild mustard seeds germinated

equally well in light or dark conditions. After burial in soil for six months the seeds required light for germination. In our experiments, wild mustard seeds on the soil surface had increased germination with increasing ground cover.

The effect of light on wild mustard seed germination varies with oxygen concentration. Seed germination generally increases with increasing oxygen concentration in light and in dark conditions with oxygen concentration having the greatest impact when the seeds were kept in the dark. Germination of wild mustard seeds at high oxygen concentrations in dark conditions may help ensure germination of seeds near the soil surface that have not been exposed to light. Deep burial of seeds in the soil and exposure to low oxygen concentrations and anaerobic metabolites may result in the induction of secondary dormancy and this may cause the induction of a light requirement for germination (Holm 1972). Dormancy and the ability to remain viable for an extended period of time in the seed bank may depend somewhat on low oxygen concentrations in the soil (Mulligan and Bailey 1975).

Wild mustard seeds germinate more rapidly with large aggregates. As well, wild mustard emergence increases with soil aeration due to cultivation (Mulligan and Bailey 1975). Therefore, higher percentage emergence with larger aggregates may be partially due to increased aeration. Decreased emergence with increasing seed depth, especially with smaller aggregates, may be attributed to reduced gas exchange or a lack of oxygen at deeper depths (Benvenuti et al., 2001a).

Wild mustard seeds can survive for extended periods within the seed bank (Mulligan and Bailey 1975). Cultivation following seed dispersal in the fall may bury freshly dispersed seeds inducing secondary dormancy causing future infestations and long term problems with this species. Seeds should be left on the surface in the fall to encourage seed death, predation or early spring germination. Shallow spring cultivation combined with applications of nitrogen fertilizer may expose dormant seeds to light and promote germination (Goudey et al. 1987). The early emerging weeds may be controlled with tillage or herbicides.

**Wild Oat.** Wild oat emergence is generally unaffected by seeding depth within the top 7 cm of the soil profile or by fluctuating soil moisture conditions if seeds are below the soil



surface. Since wild oat seeds germinate better when seeds are slightly buried one would expect lower levels of emergence in no-till fields where the weed seeds are not incorporated. However, higher populations of annual grass weeds such as wild oat are often found in reduced tillage fields (Buhler 1992; Froud-Williams et al. 1983). Many variables including the increased stubble of no-till fields may remove the inhibitory effects of surface germination and affect plant survival. The ability to germinate under a wide range of conditions may help explain the relative ubiquity of this species in cereal and oilseed fields in Manitoba (Van Acker et al. 2000).

The effects of light on wild oat seed germination vary with osmotic potential, oxygen concentration and the dormancy state of the seed. In our experiments, wild oat seed germination was not affected significantly by exposure to light in most cases. Sawhney and Hsiao (1986) reported that direct or diffused light inhibited germination of wild oat and that this inhibition was greater at greater light intensities. Other authors have found that the effect of light on seed germination depends on moisture availability and the state of dormancy (Hou and Simpson 1991; Hsiao and Simpson 1971). Wild oat germination is generally greater in higher osmotic potential solutions. In fact, our experiments suggest that osmotic potential has an even greater impact on seed germination in the presence of light which suggests that exposure to light may break dormancy in dormant wild oat seeds allowing increased germination. Differences in results between authors is not surprising because wild oat seed response to light is dependent on the dormancy state of the seed (Hou and Simpson 1993). Hou and Simpson (1991) suggest that germination of freshly harvested non-dormant seeds of wild oat may be inhibited by exposure to light thus preventing the germination of seeds in the fall when they mature and fall to the surface. Since there appears to be a wide range of dormancy states within a population of wild oat seeds in their natural environment (Hou and Simpson 1990) the effect of light on a wild oat population is likely to be highly variable.

Oxygen concentration has little impact on wild oat seed germination. This result was anticipated because this species can germinate over a wide range of depths and moisture contents. Fernandez-Quinantilla et al. (1990) found that osmotic potentials of -1.2 MPa only reduced germination by 33%. Wild oat seeds can imbibe water at very low osmotic potentials and have a higher average imbibition rate than many other

species. As well, the average imbibition rate remains relatively constant across osmotic potentials. However, the larger the seed the lower the area to volume ratio and the smaller the rate of imbibition per unit volume of seed. Consequently, wild oat absorbs water at a greater rate than other seeds but takes longer to reach moisture levels high enough to allow germination.

Wild oat can germinate and emerge in a wide array of environmental conditions but prefers cool climates with moist soils (Sharma and Vanden Born 1978). The seeds of this species only remain viable for a short period of time in the soil. Broad germination requirements may ensure survival. Given that the seeds germinate under a wide array of environmental conditions and that the seeds have short dispersal distances limiting seed dispersal should localize populations and facilitate control. Soil disturbance in early spring to promote germination of wild oats followed by an adequate control and a delayed crop seeding may be one method to manage a wild oat population.

### **Perennial Species**

**Curly Dock.** Maximum emergence occurs when seeds are on the surface and soils are at or near field capacity. Weaver and Cavers (1979) found that even a shallow burial (1 cm) significantly reduced emergence of curly dock. In our experiments, seed depths between the surface and 4 cm had no effect on the number of seedlings emerging when moisture levels fluctuated. Ground cover did not affect the number of seeds on the soil surface that germinated suggesting that surface germination is only advantageous under conditions of adequate moisture. Baskin and Baskin (1985) found that curly dock seeds do not exhibit dormancy but require light for germination to occur. Osmotic potential and light exposure had a greater impact than oxygen concentration on seed germination. When osmotic potentials were below 0, germination levels of curly dock seed decreased with increasing oxygen concentration. These two variables may interact preventing surface germination when moisture levels are not adequate for growth and development.

Curly dock seeds may survive for extended periods in the seed bank (Baskin and Baskin 1985; Roberts and Neilson 1981). Seed burial by fall cultivation may bury seeds preventing germination in the short term but future cultivations may return the seeds to

the soil surface allowing germination. No single non-herbicidal control method has been proven to be an effective means of obtaining sufficient curly dock control (Foster 1989).

**Dandelion.** Maximum emergence occurs when seeds are on the soil surface and when soils are at field capacity. The effect of depth is not as apparent when soil moisture levels fluctuate. Light exposure triggers dandelion germination (Lechamo and Gosselin 1996) but alternating temperatures may overcome the need for light exposure (Williams 1983). Dandelion emergence increases with increasing aggregate size and is unaffected by oxygen concentration. Dandelion seeds probably detect proximity to the soil surface via light and temperature fluctuations.

Seeds of dandelion exhibit no primary dormancy and may germinate shortly after dispersal (Stewart-Wade et al. 2002). Deep cultivation may bury seeds preventing emergence. Since seeds remain viable for up to 5 years in the seed bank additional cultivation within that time frame may return viable seeds to the recruitment zone. Seedlings should be controlled when they are small in the spring or the fall with cultivation or herbicides. Repeated shallow cultivation may reduce populations over time and prevent the establishment of rosettes (Stewart-Wade et al. 2002).

**Foxtail Barley.** Foxtail barley emergence was somewhat sensitive to depth with emergence being highest for seeds placed at 1-2 cm when soils were maintained at field capacity. Exposure to light inhibits germination which may explain the germination decrease of seeds on the soil surface (Banting 1979). Ground cover and soil aggregate size did not affect the number of foxtail barley seeds emerging. Emergence is impacted by fluctuating moisture levels which may help explain why foxtail barley is more commonly found in wet, fertile soils (Best et al. 1978). Oxygen concentration does not affect foxtail barley germination.

Foxtail barley seeds only remain viable in the seed bank for a short period of time (2 years or less) (Best et al. 1978). Depletion of the seed bank should occur fairly rapidly if newly emerged seedling are controlled prior to seed development. Deep cultivation ever 3 or 4 years may bury weed seeds beyond the recruitment zone. Seed death should occur within 2 years.

**Perennial Sowthistle.** Maximum emergence occurs when seeds are on the soil surface and when soils are at field capacity. Almost no emergence of seeds occurred when seeds were below the surface. Seed depths between the surface and 4 cm had no effect on emergence when moisture levels fluctuated suggesting that a high proportion of seeds only germinate on the surface when moisture is not limiting. Zollinger and Kells (1991) reported that perennial sowthistle requires high soil moisture levels for surface germination and this may help explain why this species predominately occurs in poorly drained soils or in soils with a high water holding capacity. Perennial sowthistle emergence increased with aggregate size but was not affected by oxygen concentration except at 2.5% oxygen. I found that ground cover did not affect germination. Lemna and Messersmith (1990) reference Pegtel (1974) who reported that seedlings survive best in areas with protective plant cover or litter and high moisture as compared with open, cultivated soil. The level of surface cover may impact the amount of moisture absorbed by the seed.

Perennial sowthistle seeds do not require light for germination but light may stimulate germination (Lemna and Messersmith 1990). The combination of light, soil moisture and temperature fluctuations may interact to ensure surface germination of this species in an appropriate habitat. Deep cultivation may bury weed seeds beyond the recruitment zone. Seeds may only remain viable for 3 years within the seed bank. Cultivation tends to reduce perennial sow-thistle populations depending on the type and timing of tillage (Lemna and Messersmith 1990).

**Quackgrass.** Quackgrass emergence is less sensitive to depth of seed placement than other perennial weed species. Emergence decreases with increasing depth in moist soils. Ground cover had no significant affect on weed emergence.

## WEED SPECIES RECRUITMENT BASED CATEGORIZATION

Grouping species according to form or functional characteristics may assist in understanding plant population dynamics (McIntyre et al. 1995). In agricultural ecosystems plant recruitment is determined almost entirely by germination and dormancy biology (Crawley 1990). We also know that the environmental variables that trigger seed germination and emergence vary between weed species. Grouping weed species according to germination and emergence characteristics may allow agronomic recommendation based on weed biology and ecology principles that are applicable across a range of species. As well, classification based on recruitment characteristics may lead to recruitment models, which are applicable to groups of species rather than individuals. Previous work has attempted to group species by a variety of plant characteristics including seed size (Benvenuti et al. 2001a), seed bank characteristics (Thompson and Grime 1979) and plant life-history attributes (McIntyre et al. 1995).

At the beginning of this experiment we suggested that weed species could be classified as germination and emergence generalists or germination and emergence specialists. A germination and emergence generalist was defined as a species that can germinate and emerge under a wide array of environmental conditions. A germination and emergence specialist was defined as a species which could only germinate and emerge under a very narrow array of environmental conditions. I speculated that a germination and emergence generalist should have seed limited populations with seeds that only remain viable for short periods of time in the seed bank. Conversely, a germination and emergence specialist should only germinate and emerge under very specific conditions and seeds may remain viable in the seed bank for extended periods of time until those conditions are present in the environment directly surrounding the seed. This hypothesis was partially based upon work conducted by Barralis et al. (1988). They found that species with a high annual rate of decrease in the seed bank had an average of 15% emergence each year. Species with a low annual rate of decrease had an average of 8% emergence each year.

A series of green house experiments were conducted to determine the effects of seed depth, aggregate size, light, moisture and oxygen concentrations on seed

germination and emergence. A plant species was described as a generalist if germination or emergence was unaffected by treatment or if there was no consistent pattern in the majority of experiments. When a particular species was affected by treatment in the majority of experiments it was labeled as a germination and emergence specialist. Using this system of classification barnyardgrass, canola, green foxtail, round leaved mallow, wheat, wild oat and quackgrass were labeled as generalist. Catchweed bedstraw, field pennycress, foxtail barley, wild mustard, curled dock, dandelion and perennial sow-thistle were labeled as specialist.

The experiments conducted throughout this process measured the effects of seeding depth or variables that change with seeding depth. The label generalist or specialist as applied to specific species, consequently, reflected how the species responded to seed depth. For example, all species labeled as specialist were soil surface germinators or, in one case, germinated within a specified range below the soil surface. Species labeled as generalist were relatively insensitive to seed depths between 0 and 7 cm within the soil profile. Based on scientific studies by other authors of weed seed duration within the seed bank, I found no relationship between the duration of viable seeds of each species within the seedbank and this classification system. I also found no relationship between this classification system and the species that disperse dormant seeds and those whose seeds are not initially dormant. Classifying a weed species solely on its response to depth may not be particularly useful. I suggest that it may be more useful to group species based on their response to depth and based on the average length of time their seeds remain viable within the seed bank.

Using a depth – duration classification system field pennycress, wild mustard and curled dock were classified as surface germinators which remain viable for extended periods of time in the seed bank (Baskin and Baskin 1985; Best and McIntyre 1975; Mulligan and Bailey 1975). Fall tillage will bury seeds inducing secondary dormancy in these species. Subsequent tillage events will cause new infestations when seeds are returned to the recruitment zone. Shallow pre-seeding tillage in the spring may promote germination allowing control before crop emergence. Dandelion and perennial sow-thistle were classified as surface germinators with a short seed bank duration (Stewart-Wade et al. 2002). Fall tillage and subsequent seed incorporation may not lead to future

infestations as long as the seeds are left buried for several years to ensure that they are not viable when returned to the recruitment zone. Barnyardgrass, green foxtail and round leaved mallow are relatively insensitive to depth and remain viable for extended periods of time within the seed bank (Dawson and Bruns 1975; Douglas et al. 1985; Makowski and Morrison 1989). For these species it is imperative that seed dispersal and seed production be limited to prevent significant growth in their population. Canola, wild oat and foxtail barley are relatively insensitive to depth but only remain viable for a short time period in the seedbank (Best et al. 1978; Sharma and Vanden Born 1978). Deep tillage may bury seeds of weeds within this group to depths below the recruitment zone. If no additional tillage is done for several years the seeds may die before they are brought back to the recruitment zone. Catchweed bedstraw germinates within a very specific depth range (between depths of 1 and 4 cm) and seeds of this species have a short life span within the seed bank. Species that fit into this category may be controlled by deep tillage or no-till to ensure that a large proportion of the seeds remain above or below the recruitment zone.

Weed species are not easily classified into form or functional groups. The depth – duration classification system previously described may not accurately reflect the weed population dynamics that occurs in agricultural ecosystems. For example, round leaved mallow occurs in the same classification group as green foxtail but occurs with far less frequency in most agricultural ecosystems in the Northern Great Plains. The predominance of a particular weed species within an ecosystem is determined by its entire life cycle, not just recruitment. Susceptibility to herbicides, seed production, timing of emergence and many other variables all interact to determine the success of a specific species within a cropping system. To group weed species accurately will require a classification system that incorporates characteristics of the entire life cycle.

Current studies in weed biology and ecology focus on species specific responses to environmental variables. Weed populations in agricultural fields, however, are rarely composed of one species. As a result, it is very difficult to apply the current weed biology knowledge base to control weeds within a multi-species population. Grouping weed species into functional groups is appealing because agronomic practices could be applied based on the response of a group of weed species rather than individuals. There

are situations, however, where understanding the biology of a specific species is of importance. For example, when one species becomes a predominant problem within a specific crop or field, when a particular species has become resistant to readily available herbicides and when an additional herbicide must be added to a tank mix to control one particular weed species.

The ultimate goal of research in weed biology must be to understand how an agricultural ecosystem functions and how a weed population interacts within this system. Weed biology research is still in the early stages of understanding the basic life cycle of individual weed species. It is not surprising that it remains difficult to classify weed species into functional groups. Understanding the individual components of a weed population should lead to understanding how these component interact and how each component fits within the agricultural system. Our ability to manage, not control, a weed population should increase as our understanding of the entire system increases. A successful weed management system will not focus on eliminating weeds at all costs, but instead will focus on creating a system where crop growth and development is favored more than weed growth and development.

## **WEED SEEDS AND MICROSITES AND THEIR ROLE IN DETERMINING WEED POPULATIONS**

### **Microsite Variability**

Within the soil profile microsite conditions will vary temporally and spatially. The importance of these limiting factors are dependant on the temporal and spatial scale studied (Eriksson and Ehrlén 1992). A plant species may be microsite limited at the extremes of the spatial or temporal scale within which it normally exists and seed limited within the time or space it normally occupies. It is also important to specify at which scale the population is being studied. A plant population may differ within a season between regions and also between seasons within a region (Mack and Pyke 1983, Thomas and Dale 1991). It has been firmly established that accumulated temperature and



moisture do impact the number and type of plants emerging in all ecosystems (Fernandez-Quintilla et al. 1990; Roman et al. 1999; Weaver et al. 1988). These two variables play important roles in determining the microsite to which the seed is exposed. In this field research we are interested in the seed and microsite limitation of four weed species over two seasons within a region where they normally occur.

### **Seed and Microsite Limitation**

Plant recruitment in all ecosystems is limited by seed number, microsite conditions, plant to plant competition or seed predation (Crawley 1990). In low disturbance ecosystems with a high plant density recruitment appears to be predominately limited by microsite conditions or plant competition. The removal of plant material may open appropriate microsites permitting further recruitment with high density stands. The level of bare ground or the size and position of openings within a canopy consistently play a large role in determining recruitment in low disturbance ecosystems (Bratton 1976; Burke and Grime 1996). In many agricultural fields, the majority of the biomass is removed on an annual basis and the soil is cultivated mixing plant seeds throughout the soil profile. In this situation there will be little or no soil cover by plants during a substantial proportion of the year. During these time periods plant competition will have no effect on weed recruitment.

In most cropping systems only minimal crop growth and soil cover by crop canopies is maintained in the fall or in the spring. Most weed species exhibit peak emergence during this period with some species emerging throughout the growing season (Ogg and Dawson 1984, Håkansson 1983). Therefore, crop competition probably affects the growth and development of weed species (Knezevic and Horak 1998, McLachlan et al. 1993), inhibits germination of species which germinate throughout the season or late in the season (Urwin et al. 1996) but exhibits minimal inhibitory ability on early germinating weeds. This may explain why the presence or absence of the crop in our experiment never had a significant impact on weed emergence. Canola, wild mustard and wild oat all germinate relatively early in the season. Green foxtail may germinate later in the season but emergence in plots with and without the wheat crop stopped at the

same time with no effect of crop presence on the number of seedlings emerging. We therefore conclude that weed recruitment in our experiments was unaffected by crop competition.

In low disturbance ecosystems the availability of appropriate microsites appears to be the primary determining factor in recruitment biology (Gross 1980). The importance of different microsite variables depends on the ecosystem and the plant species involved. In some situations recruitment occurs in bare sites because of changes in soil moisture (Aguilera and Lauenroth 1995). In other situations changes in temperature or light quantity or quality may affect recruitment (McLachlan et al. 1993, Urwin et al. 1996). In short term studies care should be taken before specifying which environmental parameters have the greatest impact on seedling recruitment. Kephart and Paladino (1997) found that variables such as soil moisture and temperature varied more seasonally within a habitat than between habitats while differences in light, soil depth and vegetation height were closely correlated with recruitment and growth of grasses in a grassland. Other authors have found that microtopography and seasonal change were the most important variables determining niche differentiation and thus species diversity (Bratton 1976).

Some authors have suggested that the importance of seed limitation in plant population dynamics has been underestimated (Eriksson and Ehrlén 1992). Tilman (1997) found that total plant community cover increased significantly with the number of species added as seed. In fact, they found that many species which had been absent from a site were able to germinate, emerge, survive and reproduce once the seed limitation was overcome. Reader and Buck (1991) studied the recruitment of new plant species on soil mounds within a field. They found that recruitment on the soil mounds was largely dependant on the presence of a seed producing plant of the same species. They concluded that the population in these low competitive situations was seed limited.

In our experiments the addition of seeds increased the number of weed species emerging in wheat fields in the early spring. These results appear to support the suggestion of Crawley (1990) who said that in situations where there is a high proportion of bare ground during the emergence period seed limitation should be more likely to occur. However, the weed populations in our experiments cannot be entirely seed limited

because microsite alterations affected recruitment. Altering the microsite had no effect on canola emergence and only affected wild mustard and green foxtail emergence in one out of two years. Wild oat emergence was significantly affected by microsite in both years. Based on these observations canola germination may be solely seed limited while the remaining species may be seed and microsite limited.

Harper (1977) developed the "safe-site hypothesis" suggesting that a finite number of appropriate microsites exist within a given volume of soil and that these appropriate microsites become saturated at high seed densities. Therefore, if this theory is correct it follows that proportional emergence should decline as the number of seeds sown within a given volume of soil increases. Shaw and Antonovics (1986) reported that sowing seeds of *Salvia lyrata* even at densities 100-fold greater than naturally occurring densities did not change the proportional emergence. They concluded that the number of microsites suitable for germination is virtually unlimited and that a negative response of seedling emergence to seed density has not been demonstrated under natural conditions. Our results contradict Shaw and Antonovics (1986) and support Harper's theory. The proportional emergence of three out of four species in our experiments declined with increasing seed density. This decline cannot be attributed to seedling competition because seedlings were removed upon emergence. We suggest that a finite number of microsites does exist within a specific time period and that it is possible to saturate that number of "safe sites".

The concept of a "safe site" is not static. The location of appropriate microsites which allows germination and emergence may vary depending upon seasonal and daily environmental fluctuations. For example, following a rainfall event enough moisture may exist near the surface to promote germination resulting in multiple safe sites. Following several warm dry days the soil surface may be relatively dry with only a few safe sites within pitted or covered areas (Evans and Young 1972, Harper et al. 1965). Since the number and location of microsites varies temporally the relative importance of microsite limitation will also vary temporally. During years where soil conditions generally promote seed germination and emergence altering the microsite will have little effect on the number of emerging seedlings (Evans and Young 1972). Conversely, during years where conditions in the soil do not favour germination and emergence,

fewer microsites will exist and fewer seeds will germinate. This may partially explain the increased germination and increased effects of treatment found in 2001 with green foxtail and wild mustard versus 2002. In 2002, fewer seeds germinated and treatment had no effect suggesting that slight compaction or irrigation or a combination of both did not alter the microsites sufficiently to increase germination. In 2001, more appropriate microsites existed within the soil and small changes significantly increased the number of appropriate microsites.

Recruitment is dependant upon the number of appropriate microsites and the number of seeds. If a microsite is defined as the combination of all variables directly surrounding a seed then the number of potential microsites for a small seeded species is greater than the number of potential microsites for a large seeded species if they both require identical conditions for germination to occur. Based on this principle alone there is a greater number of appropriate microsites for smaller seeds than larger seeded species. Since species have a relatively constant reproductive biomass they must make a trade-off between seed size and number. Smaller seeded species tend to produce more seeds (Turnbull et al. 1999) that last longer in the seed bank (Thompson et al. 1993) with a more rapid growth and germination rate (Burke and Grime 1996) and have a greater number of potential microsites. Large seeded species, on the other hand, are able to germinate under a wider range of conditions (Leishman et al. 2000, Sheldon 1974) and are more competitive for safe sites (Turnbull et al. 1999). Based on this information large seeded species should typically be more seed limited while small seeded species should be more microsite limited. The results of our research do not necessarily support this hypothesis because we did not find a strong tendency for large seeded species (wild oat) to be more seed limited than small seeded species (green foxtail, wild mustard).

### **A Conceptual Framework for Seed and Microsite Limitation**

It is unlikely that any plant population is entirely seed limited or entirely microsite limited (Eriksson and Ehrlén 1992). It is more likely that a continuum exists between no seed limitation/all microsite limitation and all seed limitation/no microsite limitation and species lie somewhere on that continuum (Eriksson and Ehrlén 1992). Roughgarden et

al. (1985) developed a recruitment limitation model for sessile marine organisms which may also work for plant recruitment predictions. In their model they assume that the rate of settlement is proportional to the space available for settlement. The magnitude of the slope of this parameter, the settlement parameter, provides a measure of recruitment limitation. Large settlement parameter values suggest space or microsite limitation whereas a small value suggests recruitment or seed limitation. A similar model could be developed where the rate of seedling recruitment is proportional to the number of available microsites. The slope of this relationship would provide a measure of seed or microsite limitation. Although the above mentioned model makes intuitive sense it may be impossible to construct. The model requires a measure of the number of available microsites and assumes a finite number of microsites exist within the soil. As previously discussed, the number and location of microsites varies over time in agricultural fields.

As a conceptual framework I propose that a field is composed of potential and actual microsites. A potential microsite is defined as a given area slightly larger than the volume of a specific seed that possesses a range of physical, chemical and biological components that may initiate seed germination. The potential microsite converts to an actual microsite when a seed arrives within the specified area. Consequently, seedling recruitment of a specific species is determined by the number of potential microsites that exist within the soil (microsite limitation). Increasing the number of seeds dispersed increases the probability that a seed will land within a potential microsite (seed limitation). The relative importance of seed or microsite limitation will depend upon the range of conditions which promote germination within a plant species with germination and emergence generalist being less microsite limited than germination and emergence specialist.

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## APPENDIX 1

## Anova Tables for Manuscript #1

## Experiment 1 from Manuscript #1

**Barnyardgrass**

Dependent Variable: d10

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	8	12440.01667	1555.00208	4.07	0.0094
Error	15	5735.62167	382.37478		
Corrected Total	23	18175.63833			

R-Square	Coeff Var	Root MSE	d10 Mean
0.684434	58.64855	19.55441	33.34167

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	8356.188333	1671.237667	4.37	0.0118
depth	3	4083.828333	1361.276111	3.56	0.0399

Dependent Variable: d19

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	8	9804.31167	1225.53896	2.32	0.0765
Error	15	7933.46167	528.89744		
Corrected Total	23	17737.77333			

R-Square	Coeff Var	Root MSE	d19 Mean
0.552736	54.34684	22.99777	42.31667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	8187.818333	1637.563667	3.10	0.0407
depth	3	1616.493333	538.831111	1.02	0.4120

**Curly Dock**

Dependent Variable: d10

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	93.724583	31.241528	0.56	0.6504
Error	20	1124.695000	56.234750		
Corrected Total	23	1218.419583			

R-Square	Coeff Var	Root MSE	d10 Mean
0.076923	251.7141	7.498983	2.979167

Source	DF	Type I SS	Mean Square	F Value	Pr > F
depth	3	93.72458333	31.24152778	0.56	0.6504

Dependent Variable: d19

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	6621.20792	2207.06931	3.03	0.0536
Error	20	14591.02833	729.55142		
Corrected Total	23	21212.23625			

R-Square    Coeff Var    Root MSE    d19 Mean  
0.312141    129.6231    27.01021    20.83750

Source	DF	Type I SS	Mean Square	F Value	Pr > F
depth	3	6621.207917	2207.069306	3.03	0.0536

**Catchweed bedstraw**

Dependent Variable: d10

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	8	20011.99344	2501.49918	4.32	0.0083
Error	14	8097.40656	578.38618		
Corrected Total	22	28109.40000			

R-Square    Coeff Var    Root MSE    d10 Mean  
0.711932    93.21574    24.04966    25.80000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	10071.94833	2014.38967	3.48	0.0297
depth	3	9940.04511	3313.34837	5.73	0.0090

Dependent Variable: d19

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	8	19593.79004	2449.22375	4.08	0.0107
Error	14	8410.04822	600.71773		
Corrected Total	22	28003.83826			

R-Square    Coeff Var    Root MSE    d19 Mean  
0.699682    60.83085    24.50954    40.29130

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	3455.49409	691.09882	1.15	0.3803
depth	3	16138.29594	5379.43198	8.96	0.0015

**Field Pennycress**

Dependent Variable: d10

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	8	11166.66667	1395.83333	3.60	0.0157

Error	15	5816.66667	387.77778
Corrected Total	23	16983.33333	

R-Square	Coeff Var	Root MSE	d10 Mean
0.657507	94.52196	19.69207	20.83333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	2683.333333	536.666667	1.38	0.2853
depth	3	8483.333333	2827.777778	7.29	0.0030

Dependent Variable: d19

Sum of					
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	8	19850.00000	2481.25000	5.08	0.0034
Error	15	7333.333333	488.88889		
Corrected Total	23	27183.33333			

R-Square	Coeff Var	Root MSE	d19 Mean
0.730227	85.59032	22.11083	25.83333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	4233.333333	846.66667	1.73	0.1880
depth	3	15616.66667	5205.55556	10.65	0.0005

**Wheat - CRD to make model significant**

Dependent Variable: d10

Sum of					
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	3	1696.484583	565.494861	3.52	0.0339
Error	20	3213.425000	160.671250		
Corrected Total	23	4909.909583			

R-Square	Coeff Var	Root MSE	d10 Mean
0.345523	16.18250	12.67562	78.32917

Source	DF	Type I SS	Mean Square	F Value	Pr > F
depth	3	1696.484583	565.494861	3.52	0.0339

pendent Variable: d19

Sum of					
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	3	1681.074583	560.358194	3.00	0.0546
Error	20	3730.685000	186.534250		
Corrected Total	23	5411.759583			

R-Square	Coeff Var	Root MSE	d19 Mean
0.310634	17.19128	13.65775	79.44583

Source	DF	Type I SS	Mean Square	F Value	Pr > F
depth	3	1681.074583	560.358194	3.00	0.0546

**Wild oat**

Dependent Variable: d10

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	8	11636.16167	1454.52021	8.43	0.0002
Error	15	2586.72792	172.44853		
Corrected Total	23	14222.88958			

R-Square	Coeff Var	Root MSE	d10 Mean
0.818129	17.25714	13.13197	76.09583

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	3706.107083	741.221417	4.30	0.0126
depth	3	7930.054583	2643.351528	15.33	<.0001

Dependent Variable: d19

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	8	6633.40333	829.17542	2.46	0.0637
Error	15	5065.83292	337.72219		
Corrected Total	23	11699.23625			

R-Square	Coeff Var	Root MSE	d19 Mean
0.566995	22.25855	18.37722	82.56250

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	4208.938750	841.787750	2.49	0.0781
depth	3	2424.464583	808.154861	2.39	0.1092

**Experiment 2 From Manuscript #1****Barnyardgrass**

Dependent Variable: d19

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	14270.98611	1427.09861	2.69	0.0218
Error	25	13270.78361	530.83134		
Corrected Total	35	27541.76972			

R-Square	Coeff Var	Root MSE	d19 Mean
0.518158	54.72270	23.03978	42.10278

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	889.44472	177.88894	0.34	0.8868
depth	2	10812.27722	5406.13861	10.18	0.0006
moisture	1	1955.11361	1955.11361	3.68	0.0665
depth*moisture	2	614.15056	307.07528	0.58	0.5681



**Curly dock**

Dependent Variable: d19

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	4692.51699	469.25170	1.04	0.4404
Error	25	11277.22424	451.08897		
Corrected Total	35	15969.74123			

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	3166.407014	633.281403	1.40	0.2570
depth	2	516.125606	258.062803	0.57	0.5716
moisture	1	992.775069	992.775069	2.20	0.1504
depth*moisture	2	17.209306	8.604653	0.02	0.9811

**Catchweed bedstraw**

Dependent Variable: d19

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	29164.24708	2916.42471	4.27	0.0015
Error	25	17069.56464	682.78259		
Corrected Total	35	46233.81172			

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	7311.38392	1462.27678	2.14	0.0934
depth	2	17588.94891	8794.47445	12.88	0.0001
moisture	1	1280.92410	1280.92410	1.88	0.1830
depth*moisture	2	2982.99015	1491.49508	2.18	0.1336

**Dandelion**

Dependent Variable: d19

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	6597.61111	659.76111	0.80	0.6341
Error	25	20739.75778	829.59031		
Corrected Total	35	27337.36889			

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	1590.012222	318.002444	0.38	0.8554
depth	2	2572.037222	1286.018611	1.55	0.2319
moisture	1	1938.934444	1938.934444	2.34	0.1389
depth*moisture	2	496.627222	248.313611	0.30	0.7439

**Foxtail barley**

Dependent Variable: d19

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	21699.12143	2169.91214	8.71	<.0001
Error	25	6228.41780	249.13671		
Corrected Total	35	27927.53923			

R-Square	Coeff Var	Root MSE	d19 Mean
0.776979	38.17981	15.78407	41.34139

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	2196.34208	439.26842	1.76	0.1572
depth	2	17976.94621	8988.47310	36.08	<.0001
moisture	1	1474.17603	1474.17603	5.92	0.0225
depth*moisture	2	51.65712	25.82856	0.10	0.9019

**Green foxtail**

Dependent Variable: d19

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	17002.13736	1700.21374	4.10	0.0020
Error	25	10371.15040	414.84602		
Corrected Total	35	27373.28776			

R-Square	Coeff Var	Root MSE	d19 Mean
0.621121	28.54706	20.36777	71.34806

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	8017.390347	1603.478069	3.87	0.0099
depth	2	8162.343606	4081.171803	9.84	0.0007
moisture	1	411.616469	411.616469	0.99	0.3287
depth*moisture	2	410.786939	205.393469	0.50	0.6154

**Perennial sowthistle**

Dependent Variable: d19

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	11498.31038	1149.83104	1.27	0.2998
Error	25	22672.90129	906.91605		
Corrected Total	35	34171.21167			

R-Square	Coeff Var	Root MSE	d19 Mean
0.336491	163.3654	30.11505	18.43417

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	7228.996792	1445.799358	1.59	0.1982
depth	2	2343.590450	1171.795225	1.29	0.2924
moisture	1	449.934803	449.934803	0.50	0.4877
depth*moisture	2	1475.788339	737.894169	0.81	0.4546

**Quackgrass**

Dependent Variable: d19

	Sum of					
Source	DF	Squares	Mean Square	F Value	Pr > F	
Model	10	17106.34111	1710.63411	1.91	0.0928	
Error	25	22443.97111	897.75884			
Corrected Total	35	39550.31222				

R-Square	Coeff Var	Root MSE	d19 Mean
0.432521	69.96073	29.96262	42.82778

Source	DF	Type I SS	Mean Square	F Value	Pr > F	
bl	5	3178.392222	635.678444	0.71	0.6229	
depth	2	7024.470556	3512.235278	3.91	0.0332	
moisture	1	6125.671111	6125.671111	6.82	0.0150	
depth*moisture	2	777.807222	388.903611	0.43	0.6532	
		Standard	LSMEAN			

**Roundleaved mallow**

Dependent Variable: d19

	Sum of					
Source	DF	Squares	Mean Square	F Value	Pr > F	
Model	10	4506.66944	450.66694	1.22	0.3250	
Error	25	9223.08028	368.92321			
Corrected Total	35	13729.74972				

R-Square	Coeff Var	Root MSE	d19 Mean
0.328241	136.2494	19.20737	14.09722

Source	DF	Type I SS	Mean Square	F Value	Pr > F	
bl	5	2423.624722	484.724944	1.31	0.2902	
depth	2	223.775556	111.887778	0.30	0.7411	
moisture	1	887.046944	887.046944	2.40	0.1336	
depth*moisture	2	972.222222	486.111111	1.32	0.2857	

**Field pennycress**

Model	10	18461.89586	1846.18959	2.19	0.0543	
Error	25	21051.40090	842.05604			
Corrected Total	35	39513.29676				

R-Square	Coeff Var	Root MSE	d19 Mean
0.467232	107.6665	29.01820	26.95194

Source	DF	Type I SS	Mean Square	F Value	Pr > F	
bl	5	6604.90735	1320.98147	1.57	0.2053	
depth	2	11396.06269	5698.03134	6.77	0.0045	
moisture	1	285.55367	285.55367	0.34	0.5656	
depth*moisture	2	175.37216	87.68608	0.10	0.9015	

**Canola**

Dependent Variable: d19

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	10	14721.45062	1472.14506	4.45	0.0012
Error	25	8270.01186	330.80047		
Corrected Total	35	22991.46248			

R-Square	Coeff Var	Root MSE	d19 Mean
0.640301	21.82485	18.18792	83.33583

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	11128.34146	2225.66829	6.73	0.0004
depth	2	2692.71995	1346.35998	4.07	0.0295
moisture	1	223.15380	223.15380	0.67	0.4192
depth*moisture	2	677.23541	338.61770	1.02	0.3739

**Wheat**

Dependent Variable: d19

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	10	11500.63908	1150.06391	2.66	0.0231
Error	25	10816.61819	432.66473		
Corrected Total	35	22317.25728			

R-Square	Coeff Var	Root MSE	d19 Mean
0.515325	26.67341	20.80059	77.98250

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	1819.622058	363.924412	0.84	0.5334
depth	2	9179.340800	4589.670400	10.61	0.0005
moisture	1	69.361136	69.361136	0.16	0.6923
depth*moisture	2	432.315089	216.157544	0.50	0.6127

**Wild mustard**

pendent Variable: d19

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	10	6227.84644	622.78464	0.98	0.4823
Error	25	15838.03041	633.52122		
Corrected Total	35	22065.87686			

R-Square	Coeff Var	Root MSE	d19 Mean
0.282239	90.46128	25.16985	27.82389

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	1126.636422	225.327284	0.36	0.8737
depth	2	2236.759772	1118.379886	1.77	0.1918
moisture	1	1623.284100	1623.284100	2.56	0.1220
depth*moisture	2	1241.166150	620.583075	0.98	0.3894

**Wild oat**

Dependent Variable: d19

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	34371.99701	3437.19970	10.79	<.0001
Error	25	7961.52594	318.46104		
Corrected Total	35	42333.52296			

R-Square	Coeff Var	Root MSE	d19 Mean
0.811933	26.82275	17.84548	66.53111

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	1954.81622	390.96324	1.23	0.3256
depth	2	31596.52969	15798.26484	49.61	<.0001
moisture	1	429.73290	429.73290	1.35	0.2564
depth*moisture	2	390.91820	195.45910	0.61	0.5493

## APPENDIX 2

## Anova Tables for Manuscript #4

## Experiment 1 in Manuscript #1

## Barnyardgrass

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	20639.05410	2063.90541	6.93	0.0001
Error	21	6257.21469	297.96260		
Corrected Total	31	26896.26879			

R-Square	Coeff Var	Root MSE	pemerg Mean
0.767358	39.45563	17.26159	43.74938

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	3	2260.60036	753.53345	2.53	0.0849
gas	3	61.77161	20.59054	0.07	0.9758
light	1	17317.53551	17317.53551	58.12	<.0001
gas*light	3	999.14661	333.04887	1.12	0.3643

## Curly dock

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	10637.50000	1063.75000	2.48	0.0382
Error	21	9009.37500	429.01786		
Corrected Total	31	19646.87500			

R-Square	Coeff Var	Root MSE	pemerg Mean
0.541435	68.33071	20.71275	30.31250

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	3	1140.625000	380.208333	0.89	0.4643
gas	3	4790.625000	1596.875000	3.72	0.0273
light	1	3403.125000	3403.125000	7.93	0.0103
gas*light	3	1303.125000	434.375000	1.01	0.4069

## Catchweed bedstraw

Dependent Variable: permeg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	30303.34958	3030.33496	43.53	<.0001
Error	21	1461.82702	69.61081		
Corrected Total	31	31765.17660			

R-Square	Coeff Var	Root MSE	pemerg Mean
0.953980	40.52609	8.343309	20.58750

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	3	199.00868	66.33623	0.95	0.4331
gas	3	13624.12373	4541.37457	65.24	<.0001
light	1	8758.92301	8758.92301	125.83	<.0001
gas*light	3	7721.29416	2573.76472	36.97	<.0001

**Dandelion, Foxtail barley, Green foxtail, Perennial sowthistle, round leaved mallow, wheat and wild oat**

Original ANOVA non significant

**Quackgrass**

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	9775.39063	977.53906	2.19	0.0622
Error	21	9360.35156	445.73103		
Corrected Total	31	19135.74219			

R-Square 0.510845    Coeff Var 35.79311    Root MSE 21.11234    pemerg Mean 58.98438

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	3	2475.585938	825.195313	1.85	0.1688
gas	3	6811.523438	2270.507813	5.09	0.0083
light	1	4.882813	4.882813	0.01	0.9176
gas*light	3	483.398438	161.132813	0.36	0.7814

**Round leaved mallow**

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	2856.89293	285.68929	0.41	0.9239
Error	21	14463.91082	688.75766		
Corrected Total	31	17320.80375			

R-Square 0.164940    Coeff Var 55.45854    Root MSE 26.24419    pemerg Mean 47.32219

**Field pennycress**

Dependent Variable: pemerg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	5175.781250	517.578125	4.26	0.0025
Error	21	2553.710938	121.605283		
Corrected Total	31	7729.492188			

R-Square 0.669615    Coeff Var 14.62712    Root MSE 11.02748    pemerg Mean 75.39063

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	3	727.539063	242.513021	1.99	0.1457
gas	3	4008.789063	1336.263021	10.99	0.0002
light	1	4.882813	4.882813	0.04	0.8431
gas*light	3	434.570313	144.856771	1.19	0.3372

**Canola**

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	10	2276.562500	227.656250	2.30	0.0519
Error	21	2078.906250	98.995536		
Corrected Total	31	4355.468750			

R-Square    Coeff Var    Root MSE    pemerg Mean  
0.522691    11.81406    9.949650    84.21875

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	3	439.843750	146.614583	1.48	0.2485
gas	3	402.343750	134.114583	1.35	0.2838
light	1	1188.281250	1188.281250	12.00	0.0023
gas*light	3	246.093750	82.031250	0.83	0.4929

**Wild mustard**

Source	DF	Squares	Mean Square	F Value	Pr > F
Model	10	12304.68750	1230.46875	1.37	0.2600
Error	21	18867.18750	898.43750		
Corrected Total	31	31171.87500			

R-Square    Coeff Var    Root MSE    pemerg Mean  
0.394737    71.04936    29.97395    42.18750

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	3	1054.687500	351.562500	0.39	0.7605
gas	3	9414.062500	3138.020833	3.49	0.0337
light	1	312.500000	312.500000	0.35	0.5616
gas*light	3	1523.437500	507.812500	0.57	0.6440

**Experiment 2 in Manuscript #4****Barnyardgrass**

Dependent Variable: pemerg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
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Model	16	73810.67167	4613.16698	12.20	<.0001
Error	55	20798.70333	378.15824		
Corrected Total	71	94609.37500			

R-Square	Coeff Var	Root MSE	pemerg Mean
0.780162	65.38400	19.44629	29.74167

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	1207.03333	241.40667	0.64	0.6713
gas	3	4390.01833	1463.33944	3.87	0.0139
moisture	2	61920.90083	30960.45042	81.87	<.0001
gas*moisture	6	6292.71917	1048.78653	2.77	0.0199

**Curly dock**

Dependent Variable: permeg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	56009.72222	3500.60764	9.14	<.0001
Error	55	21068.05556	383.05556		
Corrected Total	71	77077.77778			

R-Square	Coeff Var	Root MSE	pemerg Mean
0.726665	100.6550	19.57181	19.44444

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	1631.94444	326.38889	0.85	0.5191
gas	3	1419.44444	473.14815	1.24	0.3057
moisture	2	46659.02778	23329.51389	60.90	<.0001
gas*moisture	6	6299.30556	1049.88426	2.74	0.0211

**Dandelion**

Dependent Variable: permeg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	38804.78389	2425.29899	6.38	<.0001
Error	55	20906.30597	380.11465		
Corrected Total	71	59711.08986			

R-Square	Coeff Var	Root MSE	pemerg Mean
0.649876	106.4011	19.49653	18.32361

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	9211.90569	1842.38114	4.85	0.0010
gas	3	820.81486	273.60495	0.72	0.5444
moisture	2	28538.04361	14269.02181	37.54	<.0001
gas*moisture	6	234.01972	39.00329	0.10	0.9958

**Foxtail barley**

Dependent Variable: permeg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	50133.57722	3133.34858	4.92	<.0001
Error	55	35031.26722	636.93213		

Corrected Total 71 85164.84444

R-Square Coeff Var Root MSE pemerg Mean  
0.588665 83.90751 25.23751 30.07778

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	14958.21278	2991.64256	4.70	0.0012
gas	3	397.68778	132.56259	0.21	0.8903
moisture	2	31104.80528	15552.40264	24.42	<.0001
gas*moisture	6	3672.87139	612.14523	0.96	0.4601

### Green foxtail

Dependent Variable: pemerg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	58952.63722	3684.53983	8.65	<.0001
Error	55	23433.11389	426.05662		
Corrected Total	71	82385.75111			

R-Square Coeff Var Root MSE pemerg Mean  
0.715568 63.63084 20.64114 32.43889

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	9646.95611	1929.39122	4.53	0.0016
gas	3	762.05222	254.01741	0.60	0.6202
moisture	2	44165.34778	22082.67389	51.83	<.0001
gas*moisture	6	4378.28111	729.71352	1.71	0.1354

### Perennial sowthistle

Dependent Variable: pemerg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	16119.79056	1007.48691	1.91	0.0396
Error	55	29062.16222	528.40295		
Corrected Total	71	45181.95278			

R-Square Coeff Var Root MSE pemerg Mean  
0.356775 269.8183 22.98702 8.519444

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	5428.98778	1085.797556	2.05	0.0851
gas	3	265.271667	88.423889	0.17	0.9180
moisture	2	5482.080278	2741.040139	5.19	0.0086
gas*moisture	6	4943.450833	823.908472	1.56	0.1766

### Canola

Dependent Variable: pemerg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	82380.5556	5148.7847	7.01	<.0001
Error	55	40384.7222	734.2677		

Corrected Total 71 122765.2778

R-Square 0.671041  
Coeff Var 57.89350  
Root MSE 27.09737  
pemerg Mean 46.80556

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	13565.27778	2713.05556	3.69	0.0059
gas	3	3818.05556	1272.68519	1.73	0.1708
moisture	2	57669.44444	28834.72222	39.27	<.0001
gas*moisture	6	7327.77778	1221.29630	1.66	0.1476

### Wheat

Dependent Variable: pemerg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	42693.05556	2668.31597	3.59	0.0002
Error	55	40873.26389	743.15025		
Corrected Total	71	83566.31944			

R-Square 0.510888  
Coeff Var 42.53036  
Root MSE 27.26078  
pemerg Mean 64.09722

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	9439.23611	1887.84722	2.54	0.0387
gas	3	8409.37500	2803.12500	3.77	0.0156
moisture	2	23104.86111	11552.43056	15.55	<.0001
gas*moisture	6	1739.58333	289.93056	0.39	0.8822

### Wild oat

Dependent Variable: pemerg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	36542.28222	2283.89264	4.99	<.0001
Error	55	25159.69722	457.44904		
Corrected Total	71	61701.97944			

R-Square 0.592238  
Coeff Var 119.4678  
Root MSE 21.38806  
pemerg Mean 17.90278

Source	DF	Type I SS	Mean Square	F Value	Pr > F
bl	5	7985.39944	1597.07989	3.49	0.0082
gas	3	3005.84056	1001.94685	2.19	0.0995
moisture	2	21791.66778	10895.83389	23.82	<.0001
gas*moisture	6	3759.37444	626.56241	1.37	0.2432

## Experiment 3 in Manuscript #4

### Barnyard grass

Dependent Variable: pemerg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	28	161823.6111	5779.4147	50.30	<.0001

Error	115	13213.7153	114.9019
Corrected Total	143	175037.3264	

R-Square	Coeff Var	Root MSE	pemerg Mean
0.924509	31.79339	10.71923	33.71528

Source	DF	Type I SS	Mean Square	F Value	Pr > F
block	5	490.45139	98.09028	0.85	0.5147
gas	3	929.68750	309.89583	2.70	0.0492
moist	2	55183.68056	27591.84028	240.13	<.0001
light	1	71779.34028	71779.34028	624.70	<.0001
gas*light	3	776.90972	258.96991	2.25	0.0859
gas*moist	6	196.87500	32.81250	0.29	0.9428
moist*light	2	31469.09722	15734.54861	136.94	<.0001
gas*moist*light	6	997.56944	166.26157	1.45	0.2028

**Cleavers**

Dependent Variable: permeg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	28	79716.5544	2847.0198	8.01	<.0001
Error	115	40851.2578	355.2283		
Corrected Total	143	120567.8122			

R-Square	Coeff Var	Root MSE	pemerg Mean
0.661176	64.40532	18.84750	29.26389

Source	DF	Type I SS	Mean Square	F Value	Pr > F
block	5	22909.30889	4581.86178	12.90	<.0001
gas	3	18173.36056	6057.78685	17.05	<.0001
moist	2	11019.64431	5509.82215	15.51	<.0001
light	1	14408.00111	14408.00111	40.56	<.0001
gas*light	3	6577.03722	2192.34574	6.17	0.0006
gas*moist	6	2937.01403	489.50234	1.38	0.2293
moist*light	2	363.09347	181.54674	0.51	0.6012
gas*moist*light	6	3329.09486	554.84914	1.56	0.1646

**Wild Mustard**

Dependent Variable: permeg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	28	91648.6728	3273.1669	10.10	<.0001
Error	115	37250.7603	323.9197		
Corrected Total	143	128899.4331			

R-Square	Coeff Var	Root MSE	pemerg Mean
0.711009	57.42187	17.99777	31.34306

Source	DF	Type I SS	Mean Square	F Value	Pr > F
block	5	43915.66306	8783.13261	27.12	<.0001
gas	3	14241.37806	4747.12602	14.66	<.0001
moist	2	4788.82764	2394.41382	7.39	0.0010
light	1	18518.67361	18518.67361	57.17	<.0001
gas*light	3	7047.04472	2349.01491	7.25	0.0002

gas*moist	6	1707.94403	284.65734	0.88	0.5129
moist*light	2	418.18097	209.09049	0.65	0.5263
gas*moist*light	6	1010.96069	168.49345	0.52	0.7920

**Wild Oats**

Dependent Variable: pemerg

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	28	63878.76778	2281.38456	7.92	<.0001
Error	115	33111.56715	287.92667		
Corrected Total	143	96990.33493			

R-Square	Coeff Var	Root MSE	pemerg Mean
0.658610	37.01916	16.96840	45.83681

Source	DF	Type I SS	Mean Square	F Value	Pr > F
block	5	1213.10118	242.62024	0.84	0.5222
gas	3	9719.96576	3239.98859	11.25	<.0001
moist	2	35318.43431	17659.21715	61.33	<.0001
light	1	9631.78674	9631.78674	33.45	<.0001
gas*light	3	841.25965	280.41988	0.97	0.4077
gas*moist	6	2339.95236	389.99206	1.35	0.2390
moist*light	2	3444.79764	1722.39882	5.98	0.0034
gas*moist*light	6	1369.47014	228.24502	0.79	0.5774

## APPENDIX 3

## ANOVA tables for Manuscript #8

## Cumulative Weed Emergence

## Green foxtail 2001

Dependent Variable: m22

Source	DF	Sum of			
		Squares	Mean Square	F Value	Pr > F
Model	22	893.833333	40.628788	1.01	0.4758
Error	37	1487.016667	40.189640		
Corrected Total	59	2380.850000			

R-Square	Coeff Var	Root MSE	m22 Mean
0.375426	667.3189	6.339530	0.950000

Dependent Variable: m24

Source	DF	Sum of			
		Squares	Mean Square	F Value	Pr > F
Model	22	1994.466667	90.657576	1.52	0.1268
Error	37	2203.866667	59.563964		
Corrected Total	59	4198.333333			

Dependent Variable: m29

Source	DF	Sum of			
		Squares	Mean Square	F Value	Pr > F
Model	22	70391.06667	3199.59394	6.97	<.0001
Error	37	16993.26667	459.27748		
Corrected Total	59	87384.33333			

R-Square	Coeff Var	Root MSE	m29 Mean
0.805534	50.03290	21.43076	42.83333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	106.66667	106.66667	0.23	0.6327
block	1	123.26667	123.26667	0.27	0.6075
density	2	58111.43333	29055.71667	63.26	<.0001
trt	4	5677.50000	1419.37500	3.09	0.0272
site*density	2	817.63333	408.81667	0.89	0.4192
site*trt	4	3057.16667	764.29167	1.66	0.1791
density*trt	8	2497.40000	312.17500	0.68	0.7062

Dependent Variable: j3

Source	DF	Sum of			
		Squares	Mean Square	F Value	Pr > F
Model	22	114113.7667	5186.9894	10.68	<.0001
Error	37	17970.8167	485.6977		
Corrected Total	59	132084.5833			

R-Square	Coeff Var	Root MSE	j3 Mean
0.863945	37.72648	22.03855	58.41667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	109.35000	109.35000	0.23	0.6379
block	1	312.81667	312.81667	0.64	0.4274
density	2	96316.03333	48158.01667	99.15	<.0001
trt	4	9398.16667	2349.54167	4.84	0.0031
site*density	2	57.70000	28.85000	0.06	0.9424
site*trt	4	3339.56667	834.89167	1.72	0.1665
density*trt	8	4580.13333	572.51667	1.18	0.3378

Dependent Variable: j8

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	128745.4667	5852.0667	9.59	<.0001
Error	37	22578.4667	610.2288		
Corrected Total	59	151323.9333			

R-Square	Coeff Var	Root MSE	j8 Mean
0.850794	36.30986	24.70281	68.03333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	6.6667	6.6667	0.01	0.9173
block	1	194.4000	194.4000	0.32	0.5759
density	2	108386.4333	54193.2167	88.81	<.0001
trt	4	12477.6000	3119.4000	5.11	0.0022
site*density	2	152.6333	76.3167	0.13	0.8828
site*trt	4	3213.3333	803.3333	1.32	0.2819
density*trt	8	4314.4000	539.3000	0.88	0.5392

Dependent Variable: j12

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	132160.4000	6007.2909	9.67	<.0001
Error	37	22992.5833	621.4212		
Corrected Total	59	155152.9833			

R-Square	Coeff Var	Root MSE	j12 Mean
0.851807	35.35096	24.92832	70.51667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	14.0167	14.0167	0.02	0.8814
block	1	176.8167	176.8167	0.28	0.5969
density	2	113074.4333	56537.2167	90.98	<.0001
trt	4	11805.2333	2951.3083	4.75	0.0034
site*density	2	290.4333	145.2167	0.23	0.7928
site*trt	4	2892.9000	723.2250	1.16	0.3425
density*trt	8	3906.5667	488.3208	0.79	0.6180

Dependent Variable: j21

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	138875.2333	6312.5106	10.22	<.0001
Error	37	22852.7000	617.6405		
Corrected Total	59	161727.9333			

R-Square	0.858697	Coeff Var	34.21621	Root MSE	24.85237	j21 Mean	72.63333
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Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	6.6667	6.6667	0.01	0.9178
block	1	77.0667	77.0667	0.12	0.7259
density	2	121361.2333	60680.6167	98.25	<.0001
trt	4	10711.7667	2677.9417	4.34	0.0056
site*density	2	553.2333	276.6167	0.45	0.6424
site*trt	4	2679.8333	669.9583	1.08	0.3782
density*trt	8	3485.4333	435.6792	0.71	0.6848

Dependent Variable: j26

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	139531.5000	6342.3409	10.10	<.0001
Error	37	23228.1500	627.7878		
Corrected Total	59	162759.6500			

R-Square	0.857286	Coeff Var	34.25249	Root MSE	25.05569	j26 Mean	73.15000
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Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	25.3500	25.3500	0.04	0.8418
block	1	74.8167	74.8167	0.12	0.7319
density	2	122340.4000	61170.2000	97.44	<.0001
trt	4	10467.9000	2616.9750	4.17	0.0069
site*density	2	569.2000	284.6000	0.45	0.6390
site*trt	4	2633.2333	658.3083	1.05	0.3955
density*trt	8	3420.6000	427.5750	0.68	0.7051

Dependent Variable: j13

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	139531.5000	6342.3409	10.10	<.0001
Error	37	23228.1500	627.7878		
Corrected Total	59	162759.6500			

R-Square	0.857286	Coeff Var	34.25249	Root MSE	25.05569	j13 Mean	73.15000
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Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	25.3500	25.3500	0.04	0.8418
block	1	74.8167	74.8167	0.12	0.7319
density	2	122340.4000	61170.2000	97.44	<.0001



trt	4	10467.9000	2616.9750	4.17	0.0069
site*density	2	569.2000	284.6000	0.45	0.6390
site*trt	4	2633.2333	658.3083	1.05	0.3955
density*trt	8	3420.6000	427.5750	0.68	0.7051

## The GLM Procedure

## Repeated Measures Analysis of Variance

## Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
site	1	17.4241	17.4241	0.01	0.9406
block	1	90.4463	90.4463	0.03	0.8653
density	2	585810.0333	292905.0167	94.52	<.0001
trt	4	52687.2852	13171.8213	4.25	0.0063
site*density	2	154.0037	77.0019	0.02	0.9755
site*trt	4	14071.0852	3517.7713	1.14	0.3550
density*trt	8	18029.0593	2253.6324	0.73	0.6666
Error	37	114658.8463	3098.8877		

## The GLM Procedure

## Repeated Measures Analysis of Variance

## Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	Adj Pr > F			
				F Value	Pr > F	G - G	H - F
time	8	427846.6000	53480.8250	407.20	<.0001	<.0001	<.0001
time*site	8	612.4593	76.5574	0.58	0.7918	0.5388	0.6227
time*block	8	973.2370	121.6546	0.93	0.4949	0.3898	0.4286
time*density	16	156716.7667	9794.7979	74.58	<.0001	<.0001	<.0001
time*trt	32	18656.2148	583.0067	4.44	<.0001	0.0004	<.0001
time*site*density	16	3452.4630	215.7789	1.64	0.0573	0.1812	0.1443
time*site*trt	32	6715.6148	209.8630	1.60	0.0249	0.1522	0.1050
time*density*trt	64	8251.1407	128.9241	0.98	0.5211	0.4816	0.4950
Error(time)	296	38876.1704	131.3384				

**Canola 2001**

Dependent Variable: m22

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	36720.23333	1669.10152	10.41	<.0001
Error	37	5934.75000	160.39865		
Corrected Total	59	42654.98333			

R-Square	Coeff Var	Root MSE	m22 Mean
0.860866	41.27602	12.66486	30.68333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	176.81667	176.81667	1.10	0.3006
block	1	1152.81667	1152.81667	7.19	0.0109
density	2	33506.53333	16753.26667	104.45	<.0001
trt	4	325.06667	81.26667	0.51	0.7311
site*density	2	124.93333	62.46667	0.39	0.6802

site*trt	4	604.93333	151.23333	0.94	0.4501
density*trt	8	829.13333	103.64167	0.65	0.7340

Dependent Variable: m24

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	63254.93333	2875.22424	13.15	<.0001
Error	37	8092.00000	218.70270		
Corrected Total	59	71346.93333			

R-Square	Coeff Var	Root MSE	m24 Mean
0.886582	34.82402	14.78860	42.46667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	135.00000	135.00000	0.62	0.4371
block	1	851.26667	851.26667	3.89	0.0560
density	2	60331.03333	30165.51667	137.93	<.0001
trt	4	438.43333	109.60833	0.50	0.7350
site*density	2	133.90000	66.95000	0.31	0.7381
site*trt	4	438.83333	109.70833	0.50	0.7347
density*trt	8	926.46667	115.80833	0.53	0.8266

Dependent Variable: m29

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	141157.9667	6416.2712	12.32	<.0001
Error	37	19266.8833	520.7266		
Corrected Total	59	160424.8500			

R-Square	Coeff Var	Root MSE	m29 Mean
0.879901	32.34505	22.81943	70.55000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	2926.0167	2926.0167	5.62	0.0231
block	1	126.1500	126.1500	0.24	0.6255
density	2	124477.5000	62238.7500	119.52	<.0001
trt	4	2237.7667	559.4417	1.07	0.3831
site*density	2	1040.6333	520.3167	1.00	0.3779
site*trt	4	3102.5667	775.6417	1.49	0.2252
density*trt	8	7247.3333	905.9167	1.74	0.1216

Dependent Variable: j3

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	145330.9333	6605.9515	13.08	<.0001
Error	37	18689.6500	505.1257		
Corrected Total	59	164020.5833			

R-Square	Coeff Var	Root MSE	j3 Mean
0.886053	30.13408	22.47500	74.58333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	2870.4167	2870.4167	5.68	0.0224

block	1	220.4167	220.4167	0.44	0.5130
density	2	129407.6333	64703.8167	128.09	<.0001
trt	4	1839.6667	459.9167	0.91	0.4680
site*density	2	1423.4333	711.7167	1.41	0.2572
site*trt	4	2977.3333	744.3333	1.47	0.2299
density*trt	8	6592.0333	824.0042	1.63	0.1493

Dependent Variable: j8

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	148706.0667	6759.3667	12.39	<.0001
Error	37	20187.5833	545.6104		
Corrected Total	59	168893.6500			

R-Square	Coeff Var	Root MSE	j8 Mean
0.880472	30.39467	23.35830	76.85000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	1960.8167	1960.8167	3.59	0.0658
block	1	104.0167	104.0167	0.19	0.6649
density	2	135621.3000	67810.6500	124.28	<.0001
trt	4	1456.7333	364.1833	0.67	0.6186
site*density	2	902.2333	451.1167	0.83	0.4454
site*trt	4	3196.6000	799.1500	1.46	0.2326
density*trt	8	5464.3667	683.0458	1.25	0.2978

Dependent Variable: j12

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	154150.1000	7006.8227	12.87	<.0001
Error	37	20144.0833	544.4347		
Corrected Total	59	174294.1833			

R-Square	Coeff Var	Root MSE	j12 Mean
0.884425	29.86959	23.33312	78.11667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	2870.4167	2870.4167	5.27	0.0274
block	1	132.0167	132.0167	0.24	0.6253
density	2	140379.6333	70189.8167	128.92	<.0001
trt	4	1392.2667	348.0667	0.64	0.6378
site*density	2	1302.2333	651.1167	1.20	0.3138
site*trt	4	2954.0000	738.5000	1.36	0.2677
density*trt	8	5119.5333	639.9417	1.18	0.3397

Dependent Variable: j21

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	153914.5333	6996.1152	12.85	<.0001
Error	37	20150.4500	544.6068		
Corrected Total	59	174064.9833			

R-Square	Coeff Var	Root MSE	j21 Mean
0.884236	29.84883	23.33681	78.18333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
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site	1	2926.0167	2926.0167	5.37	0.0261
block	1	144.1500	144.1500	0.26	0.6100
density	2	140053.4333	70026.7167	128.58	<.0001
trt	4	1430.2333	357.5583	0.66	0.6260
site*density	2	1275.2333	637.6167	1.17	0.3213
site*trt	4	2935.9000	733.9750	1.35	0.2708
density*trt	8	5149.5667	643.6958	1.18	0.3359

Dependent Variable: j26

Sum of					
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	22	153914.5333	6996.1152	12.85	<.0001
Error	37	20150.4500	544.6068		
Corrected Total	59	174064.9833			

R-Square	Coeff Var	Root MSE	j26 Mean
0.884236	29.84883	23.33681	78.18333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	2926.0167	2926.0167	5.37	0.0261
block	1	144.1500	144.1500	0.26	0.6100
density	2	140053.4333	70026.7167	128.58	<.0001
trt	4	1430.2333	357.5583	0.66	0.6260
site*density	2	1275.2333	637.6167	1.17	0.3213
site*trt	4	2935.9000	733.9750	1.35	0.2708
density*trt	8	5149.5667	643.6958	1.18	0.3359

Dependent Variable: j13

Sum of					
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	22	153914.5333	6996.1152	12.85	<.0001
Error	37	20150.4500	544.6068		
Corrected Total	59	174064.9833			

R-Square	Coeff Var	Root MSE	j13 Mean
0.884236	29.84883	23.33681	78.18333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	2926.0167	2926.0167	5.37	0.0261
block	1	144.1500	144.1500	0.26	0.6100
density	2	140053.4333	70026.7167	128.58	<.0001
trt	4	1430.2333	357.5583	0.66	0.6260
site*density	2	1275.2333	637.6167	1.17	0.3213
site*trt	4	2935.9000	733.9750	1.35	0.2708
density*trt	8	5149.5667	643.6958	1.18	0.3359

Repeated Measures Analysis of Variance  
Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
site	1	13063.585	13063.585	3.79	0.0593
block	1	2398.230	2398.230	0.70	0.4097
density	2	1003205.233	501602.617	145.44	<.0001
trt	4	9413.900	2353.475	0.68	0.6086

site*density	2	6794.159	3397.080	0.98	0.3830
site*trt	4	19312.470	4828.118	1.40	0.2531
density*trt	8	35879.822	4484.978	1.30	0.2735
Error	37	127607.222	3448.844		

Repeated Measures Analysis of Variance  
Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	Adj Pr > F			
				F Value	Pr > F	G - G	H - F
time	8	155048.2667	19381.0333	228.02	<.0001	<.0001	<.0001
time*site	8	6653.9481	831.7435	9.79	<.0001	0.0022	0.0003
time*block	8	620.9037	77.6130	0.91	0.5058	0.3581	0.4000
time*density	16	40678.7000	2542.4188	29.91	<.0001	<.0001	<.0001
time*trt	32	2566.7333	80.2104	0.94	0.5585	0.4573	0.4828
time*site*density	16	1958.9074	122.4317	1.44	0.1216	0.2478	0.2324
time*site*trt	32	2769.4963	86.5468	1.02	0.4446	0.4152	0.4285
time*density*trt	64	5747.7444	89.8085	1.06	0.3724	0.4138	0.4117
Error(time)	296	25159.0778	84.9969				

**Wild Mustard 2001**

Dependent Variable: m22

Source	DF	Sum of			
		Squares	Mean Square	F Value	Pr > F
Model	22	2218.000000	100.818182	4.89	<.0001
Error	37	763.250000	20.628378		
Corrected Total	59	2981.250000			

R-Square	Coeff Var	Root MSE	m22 Mean
0.743983	95.61784	4.541847	4.750000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	498.8166667	498.8166667	24.18	<.0001
block	1	176.8166667	176.8166667	8.57	0.0058
density	2	672.7000000	336.3500000	16.31	<.0001
trt	4	86.8333333	21.7083333	1.05	0.3937
site*density	2	259.4333333	129.7166667	6.29	0.0045
site*trt	4	145.4333333	36.3583333	1.76	0.1572
density*trt	8	377.9666667	47.2458333	2.29	0.0420

Dependent Variable: m24

Source	DF	Sum of			
		Squares	Mean Square	F Value	Pr > F
Model	22	4806.533333	218.478788	6.37	<.0001
Error	37	1268.400000	34.281081		
Corrected Total	59	6074.933333			

R-Square	Coeff Var	Root MSE	m24 Mean
0.791208	69.15360	5.855005	8.466667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
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site	1	976.066667	976.066667	28.47	<.0001
block	1	166.666667	166.666667	4.86	0.0338
density	2	2284.433333	1142.216667	33.32	<.0001
trt	4	254.933333	63.733333	1.86	0.1383
site*density	2	358.433333	179.216667	5.23	0.0100
site*trt	4	278.933333	69.733333	2.03	0.1096
density*trt	8	487.066667	60.883333	1.78	0.1135

Dependent Variable: m29

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	37824.16667	1719.28030	8.40	<.0001
Error	37	7569.23333	204.57387		
Corrected Total	59	45393.40000			

R-Square	Coeff Var	Root MSE	m29 Mean
0.833253	40.74910	14.30293	35.10000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	540.00000	540.00000	2.64	0.1127
block	1	17.06667	17.06667	0.08	0.7743
density	2	34278.70000	17139.35000	83.78	<.0001
trt	4	272.56667	68.14167	0.33	0.8539
site*density	2	24.70000	12.35000	0.06	0.9415
site*trt	4	1474.50000	368.62500	1.80	0.1492
density*trt	8	1216.63333	152.07917	0.74	0.6531

Dependent Variable: j3

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	61758.30000	2807.19545	10.94	<.0001
Error	37	9497.30000	256.68378		
Corrected Total	59	71255.60000			

R-Square	Coeff Var	Root MSE	j3 Mean
0.866715	35.76195	16.02135	44.80000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	2232.60000	2232.60000	8.70	0.0055
block	1	68.26667	68.26667	0.27	0.6091
density	2	54517.90000	27258.95000	106.20	<.0001
trt	4	1250.26667	312.56667	1.22	0.3199
site*density	2	228.10000	114.05000	0.44	0.6446
site*trt	4	1031.73333	257.93333	1.00	0.4174
density*trt	8	2429.43333	303.67917	1.18	0.3353

Dependent Variable: j8

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	68112.86667	3096.03939	10.69	<.0001
Error	37	10711.46667	289.49910		

Corrected Total 59 78824.33333

R-Square 0.864110  
 Coeff Var 35.32458  
 Root MSE 17.01467  
 j8 Mean 48.16667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	1949.40000	1949.40000	6.73	0.0135
block	1	15.00000	15.00000	0.05	0.8212
density	2	60274.23333	30137.11667	104.10	<.0001
trt	4	1815.66667	453.91667	1.57	0.2032
site*density	2	336.70000	168.35000	0.58	0.5641
site*trt	4	1417.93333	354.48333	1.22	0.3171
density*trt	8	2303.93333	287.99167	0.99	0.4561

Dependent Variable: j12

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	90553.36667	4116.06212	19.23	<.0001
Error	37	7919.88333	214.05090		
Corrected Total	59	98473.25000			

R-Square 0.919573  
 Coeff Var 27.47508  
 Root MSE 14.63048  
 j12 Mean 53.25000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	6678.15000	6678.15000	31.20	<.0001
block	1	14.01667	14.01667	0.07	0.7994
density	2	75644.40000	37822.20000	176.70	<.0001
trt	4	2138.66667	534.66667	2.50	0.0592
site*density	2	1615.60000	807.80000	3.77	0.0322
site*trt	4	1787.60000	446.90000	2.09	0.1021
density*trt	8	2674.93333	334.36667	1.56	0.1700

Dependent Variable: j21

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	105506.1333	4795.7333	16.68	<.0001
Error	37	10638.8667	287.5369		
Corrected Total	59	116145.0000			

R-Square 0.908400  
 Coeff Var 29.49029  
 Root MSE 16.95691  
 j21 Mean 57.50000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	7348.26667	7348.26667	25.56	<.0001
block	1	77.06667	77.06667	0.27	0.6077
density	2	89522.80000	44761.40000	155.67	<.0001
trt	4	2627.16667	656.79167	2.28	0.0786
site*density	2	1233.73333	616.86667	2.15	0.1314
site*trt	4	2258.56667	564.64167	1.96	0.1204
density*trt	8	2438.53333	304.81667	1.06	0.4112

Dependent Variable: j26

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	111127.7667	5051.2621	16.73	<.0001
Error	37	11170.4167	301.9032		
Corrected Total	59	122298.1833			

R-Square	Coeff Var	Root MSE	j26 Mean
0.908662	29.55831	17.37536	58.78333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	7774.81667	7774.81667	25.75	<.0001
block	1	84.01667	84.01667	0.28	0.6010
density	2	93725.73333	46862.86667	155.22	<.0001
trt	4	3107.76667	776.94167	2.57	0.0536
site*density	2	1537.73333	768.86667	2.55	0.0920
site*trt	4	2405.76667	601.44167	1.99	0.1159
density*trt	8	2491.93333	311.49167	1.03	0.4303

Dependent Variable: j13

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	111295.7667	5058.8985	16.73	<.0001
Error	37	11185.8333	302.3198		
Corrected Total	59	122481.6000			

R-Square	Coeff Var	Root MSE	j13 Mean
0.908673	29.57032	17.38735	58.80000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	7797.60000	7797.60000	25.79	<.0001
block	1	86.40000	86.40000	0.29	0.5961
density	2	93835.90000	46917.95000	155.19	<.0001
trt	4	3108.76667	777.19167	2.57	0.0538
site*density	2	1550.10000	775.05000	2.56	0.0906
site*trt	4	2422.56667	605.64167	2.00	0.1142
density*trt	8	2494.43333	311.80417	1.03	0.4306

Repeated Measures Analysis of Variance  
Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
site	1	18223.6463	18223.6463	13.63	0.0007
block	1	370.0167	370.0167	0.28	0.6019
density	2	411534.6926	205767.3463	153.93	<.0001
trt	4	11296.0481	2824.0120	2.11	0.0988
site*density	2	2456.4704	1228.2352	0.92	0.4079
site*trt	4	9489.3815	2372.3454	1.77	0.1547
density*trt	8	14324.2519	1790.5315	1.34	0.2552
Error	37	49459.2907	1336.7376		



Repeated Measures Analysis of Variance  
Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	Adj Pr > F		
				F Value	Pr > F	G - G H - F
time	8	211706.9148	26463.3644	368.35	<.0001	<.0001 <.0001
time*site	8	17572.0704	2196.5088	30.57	<.0001	<.0001 <.0001
time*block	8	335.3000	41.9125	0.58	0.7914	0.5130 0.5944
time*density	16	93222.1074	5826.3817	81.10	<.0001	<.0001 <.0001
time*trt	32	3366.5852	105.2058	1.46	0.0557	0.2079 0.1669
time*site*density	16	4688.0630	293.0039	4.08	<.0001	0.0111 0.0023
time*site*trt	32	3733.6519	116.6766	1.62	0.0211	0.1583 0.1133
time*density*trt	64	2590.6148	40.4784	0.56	0.9967	0.8607 0.9261
Error(time)	296	21265.3593	71.8424			

**Green Foxtail 2002-Hochfeld soil series removed**

Dependent Variable: m21

Sum of					
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	15	39.10000000	2.60666667	0.92	0.5681
Error	14	39.86666667	2.84761905		
Corrected Total	29	78.96666667			
	R-Square	Coeff Var	Root MSE	m21 Mean	
	0.495146	460.2243	1.687489	0.366667	

Source	DF	Type I SS	Mean Square	F Value	Pr > F
block	1	1.63333333	1.63333333	0.57	0.4614
density	2	4.26666667	2.13333333	0.75	0.4908
trt	4	12.80000000	3.20000000	1.12	0.3847
density*trt	8	20.40000000	2.55000000	0.90	0.5452

Dependent Variable: m27

Sum of					
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	15	2029.200000	135.280000	3.35	0.0146
Error	14	564.666667	40.333333		
Corrected Total	29	2593.866667			
	R-Square	Coeff Var	Root MSE	m27 Mean	
	0.782307	78.72958	6.350853	8.066667	

Source	DF	Type I SS	Mean Square	F Value	Pr > F
block	1	13.333333	13.333333	0.33	0.5744
density	2	1290.466667	645.233333	16.00	0.0002
trt	4	301.533333	75.383333	1.87	0.1719
density*trt	8	423.866667	52.983333	1.31	0.3130

Dependent Variable: j3

Sum of					
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	15	27489.50000	1832.63333	8.90	<.0001
Error	14	2881.46667	205.81905		
Corrected Total	29	30370.96667			

R-Square	Coeff Var	Root MSE	j3 Mean
0.905124	39.16213	14.34639	36.63333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
block	1	864.03333	864.03333	4.20	0.0597
density	2	25967.26667	12983.63333	63.08	<.0001
trt	4	114.46667	28.61667	0.14	0.9649
density*trt	8	543.73333	67.96667	0.33	0.9401

Dependent Variable: j18

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	15	33679.60000	2245.30667	8.03	0.0002
Error	14	3915.86667	279.70476		
Corrected Total	29	37595.46667			

R-Square	Coeff Var	Root MSE	j18 Mean
0.895842	37.89511	16.72438	44.13333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
block	1	418.13333	418.13333	1.49	0.2416
density	2	31761.86667	15880.93333	56.78	<.0001
trt	4	50.13333	12.53333	0.04	0.9957
density*trt	8	1449.46667	181.18333	0.65	0.7270

Dependent Variable: j24

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	15	37920.66667	2528.04444	7.84	0.0002
Error	14	4515.20000	322.51429		
Corrected Total	29	42435.86667			

R-Square	Coeff Var	Root MSE	j24 Mean
0.893599	38.98412	17.95868	46.06667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
block	1	580.80000	580.80000	1.80	0.2010
density	2	35098.06667	17549.03333	54.41	<.0001
trt	4	190.20000	47.55000	0.15	0.9611
density*trt	8	2051.60000	256.45000	0.80	0.6162

Dependent Variable: j14

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	15	37920.66667	2528.04444	7.84	0.0002
Error	14	4515.20000	322.51429		
Corrected Total	29	42435.86667			

R-Square	Coeff Var	Root MSE	j14 Mean
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0.893599 38.98412 17.95868 46.06667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
block	1	580.80000	580.80000	1.80	0.2010
density	2	35098.06667	17549.03333	54.41	<.0001
trt	4	190.20000	47.55000	0.15	0.9611
density*trt	8	2051.60000	256.45000	0.80	0.6162

Source	DF	Type III SS	Mean Square	F Value	Pr > F
block	1	580.80000	580.80000	1.80	0.2010
density	2	35098.06667	17549.03333	54.41	<.0001
trt	4	190.20000	47.55000	0.15	0.9611
density*trt	8	2051.60000	256.45000	0.80	0.6162

Repeated Measures Analysis of Variance  
Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
block	1	1767.20000	1767.20000	2.25	0.1555
density	2	94243.24444	47121.62222	60.08	<.0001
trt	4	380.27778	95.06944	0.12	0.9726
density*trt	8	3090.42222	386.30278	0.49	0.8420
Error	14	10979.63333	784.25952		

Repeated Measures Analysis of Variance  
Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	Adj Pr > F			
				F Value	Pr > F	G - G	H - F
time	5	63568.11111	12713.62222	163.22	<.0001	<.0001	<.0001
time*block	5	691.53333	138.30667	1.78	0.1292	0.2022	0.1730
time*density	10	34976.75556	3497.67556	44.90	<.0001	<.0001	<.0001
time*trt	20	479.05556	23.95278	0.31	0.9977	0.8978	0.9788
time*density*trt	40	3450.24444	86.25611	1.11	0.3486	0.4095	0.3818
Error(time)	70	5452.63333	77.89476				

Greenhouse-Geisser Epsilon 0.2430

Huynh-Feldt Epsilon 0.5389

Standard LSMEAN

**Canola 2002**

Dependent Variable: m21

Source	DF	Sum of			
		Squares	Mean Square	F Value	Pr > F
Model	22	40965.46667	1862.06667	9.05	<.0001
Error	37	7615.46667	205.82342		
Corrected Total	59	48580.93333			

R-Square 0.843242  
Coeff Var 42.36185  
Root MSE 14.34655  
m21 Mean 33.86667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	6283.26667	6283.26667	30.53	<.0001
block	1	81.66667	81.66667	0.40	0.5326
density	2	24586.03333	12293.01667	59.73	<.0001
trt	4	2545.60000	636.40000	3.09	0.0272
site*density	2	1222.03333	611.01667	2.97	0.0637
site*trt	4	1777.06667	444.26667	2.16	0.0929
density*trt	8	4469.80000	558.72500	2.71	0.0185

Dependent Variable: m27

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	50424.16667	2292.00758	6.37	<.0001
Error	37	13319.76667	359.99369		
Corrected Total	59	63743.93333			

R-Square	Coeff Var	Root MSE	m27 Mean
0.791043	45.57286	18.97350	41.63333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	4968.60000	4968.60000	13.80	0.0007
block	1	64.06667	64.06667	0.18	0.6756
density	2	37233.03333	18616.51667	51.71	<.0001
trt	4	1492.76667	373.19167	1.04	0.4014
site*density	2	647.50000	323.75000	0.90	0.4156
site*trt	4	2626.56667	656.64167	1.82	0.1449
density*trt	8	3391.63333	423.95417	1.18	0.3384

Dependent Variable: j3

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	46815.03333	2127.95606	7.61	<.0001
Error	37	10339.90000	279.45676		
Corrected Total	59	57154.93333			

R-Square	Coeff Var	Root MSE	j3 Mean
0.819090	40.24950	16.71696	41.53333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	4646.40000	4646.40000	16.63	0.0002
block	1	147.26667	147.26667	0.53	0.4724
density	2	34381.03333	17190.51667	61.51	<.0001
trt	4	1204.93333	301.23333	1.08	0.3814
site*density	2	967.50000	483.75000	1.73	0.1911
site*trt	4	2298.93333	574.73333	2.06	0.1064
density*trt	8	3168.96667	396.12083	1.42	0.2218

Dependent Variable: j18

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	48259.36667	2193.60758	7.59	<.0001
Error	37	10691.48333	288.95901		
Corrected Total	59	58950.85000			

R-Square	Coeff Var	Root MSE	j18 Mean

0.818637 39.95016 16.99879 42.55000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	5208.01667	5208.01667	18.02	0.0001
block	1	156.81667	156.81667	0.54	0.4660
density	2	35033.20000	17516.60000	60.62	<.0001
trt	4	1269.76667	317.44167	1.10	0.3717
site*density	2	1070.53333	535.26667	1.85	0.1711
site*trt	4	2296.90000	574.22500	1.99	0.1167
density*trt	8	3224.13333	403.01667	1.39	0.2311

Dependent Variable: j24

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	48337.66667	2197.16667	7.48	<.0001
Error	37	10872.51667	293.85180		
Corrected Total	59	59210.18333			

R-Square 0.816374  
 Coeff Var 40.12978  
 Root MSE 17.14211  
 j24 Mean 42.71667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	5245.35000	5245.35000	17.85	0.0001
block	1	183.75000	183.75000	0.63	0.4341
density	2	35209.73333	17604.86667	59.91	<.0001
trt	4	1269.10000	317.27500	1.08	0.3805
site*density	2	1134.40000	567.20000	1.93	0.1594
site*trt	4	2194.23333	548.55833	1.87	0.1369
density*trt	8	3101.10000	387.63750	1.32	0.2646

Dependent Variable: j14

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	48377.36667	2198.97121	7.42	<.0001
Error	37	10965.88333	296.37523		
Corrected Total	59	59343.25000			

R-Square 0.815213  
 Coeff Var 40.27030  
 Root MSE 17.21555  
 j14 Mean 42.75000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	5208.01667	5208.01667	17.57	0.0002
block	1	190.81667	190.81667	0.64	0.4274
density	2	35338.80000	17669.40000	59.62	<.0001
trt	4	1249.83333	312.45833	1.05	0.3928
site*density	2	1112.13333	556.06667	1.88	0.1675
site*trt	4	2205.90000	551.47500	1.86	0.1380
density*trt	8	3071.86667	383.98333	1.30	0.2759

Source	DF	Type III SS	Mean Square	F Value	Pr > F
site	1	31490.8028	31490.8028	19.00	<.0001
block	1	795.0694	795.0694	0.48	0.4928
density	2	200870.2167	100435.1083	60.61	<.0001
trt	4	8563.6833	2140.9208	1.29	0.2909
site*density	2	6000.0389	3000.0194	1.81	0.1778
site*trt	4	13144.2389	3286.0597	1.98	0.1173
density*trt	8	19700.6167	2462.5771	1.49	0.1957
Error	37	61314.1417	1657.1390		

Repeated Measures Analysis of Variance  
Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	Adj Pr > F			
				F Value	Pr > F	G - G	H - F
time	5	3589.891667	717.978333	53.33	<.0001	<.0001	<.0001
time*site	5	68.847222	13.769444	1.02	0.4056	0.3634	0.3897
time*block	5	29.313889	5.862778	0.44	0.8234	0.6443	0.7460
time*density	10	911.616667	91.161667	6.77	<.0001	0.0001	<.0001
time*trt	20	468.316667	23.415833	1.74	0.0306	0.1054	0.0601
time*site*density	10	154.061111	15.406111	1.14	0.3317	0.3424	0.3406
time*site*trt	20	255.361111	12.768056	0.95	0.5271	0.4817	0.5068
time*density*trt	40	726.883333	18.172083	1.35	0.0961	0.1937	0.1402
Error(time)	185	2490.875000	13.464189				

**Wild Mustard 2002**

Dependent Variable: m21

Source	DF	Sum of			
		Squares	Mean Square	F Value	Pr > F
Model	22	9593.23333	436.05606	4.82	<.0001
Error	37	3349.35000	90.52297		
Corrected Total	59	12942.58333			

R-Square    Coeff Var    Root MSE    m21 Mean  
0.741215    91.33782    9.514356    10.41667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	3010.416667	3010.416667	33.26	<.0001
block	1	150.416667	150.416667	1.66	0.2054
density	2	3112.233333	1556.116667	17.19	<.0001
trt	4	598.166667	149.541667	1.65	0.1819
site*density	2	1052.233333	526.116667	5.81	0.0064
site*trt	4	732.833333	183.208333	2.02	0.1111
density*trt	8	936.933333	117.116667	1.29	0.2768

Dependent Variable: m27

Source	DF	Sum of			
		Squares	Mean Square	F Value	Pr > F
Model	22	22206.63333	1009.39242	7.81	<.0001
Error	37	4780.35000	129.19865		
Corrected Total	59	26986.98333			

R-Square    Coeff Var    Root MSE    m27 Mean  
0.822865    65.01368    11.36656    17.48333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	5940.15000	5940.15000	45.98	<.0001
block	1	109.35000	109.35000	0.85	0.3635
density	2	10649.23333	5324.61667	41.21	<.0001
trt	4	787.23333	196.80833	1.52	0.2155
site*density	2	2970.30000	1485.15000	11.50	0.0001
site*trt	4	849.10000	212.27500	1.64	0.1841
density*trt	8	901.26667	112.65833	0.87	0.5485

Dependent Variable: j3

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	27119.50000	1232.70455	6.65	<.0001
Error	37	6858.90000	185.37568		
Corrected Total	59	33978.40000			

R-Square    Coeff Var    Root MSE    j3 Mean  
0.798139    58.18493    13.61527    23.40000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	3557.40000	3557.40000	19.19	<.0001
block	1	160.06667	160.06667	0.86	0.3588
density	2	17527.30000	8763.65000	47.28	<.0001
trt	4	950.06667	237.51667	1.28	0.2949
site*density	2	1848.70000	924.35000	4.99	0.0121
site*trt	4	1419.93333	354.98333	1.91	0.1284
density*trt	8	1656.03333	207.00417	1.12	0.3748

Dependent Variable: j18

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	34607.96667	1573.08939	6.91	<.0001
Error	37	8422.76667	227.64234		
Corrected Total	59	43030.73333			

R-Square    Coeff Var    Root MSE    j18 Mean  
0.804262    54.33789    15.08782    27.76667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	3345.06667	3345.06667	14.69	0.0005
block	1	299.26667	299.26667	1.31	0.2589
density	2	25261.03333	12630.51667	55.48	<.0001
trt	4	965.06667	241.26667	1.06	0.3901
site*density	2	1226.63333	613.31667	2.69	0.0808
site*trt	4	1740.26667	435.06667	1.91	0.1291
density*trt	8	1770.63333	221.32917	0.97	0.4724

Dependent Variable: j24

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	22	35404.20000	1609.28182	6.93	<.0001
Error	37	8596.78333	232.34550		
Corrected Total	59	44000.98333			

R-Square	Coeff Var	Root MSE	j24 Mean
0.804623	53.83008	15.24288	28.31667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	3212.01667	3212.01667	13.82	0.0007
block	1	303.75000	303.75000	1.31	0.2602
density	2	26401.63333	13200.81667	56.82	<.0001
trt	4	910.06667	227.51667	0.98	0.4307
site*density	2	1136.63333	568.31667	2.45	0.1005
site*trt	4	1668.06667	417.01667	1.79	0.1506
density*trt	8	1772.03333	221.50417	0.95	0.4862

Dependent Variable: j14

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	22	35564.36667	1616.56212	6.90	<.0001
Error	37	8668.63333	234.28739		
Corrected Total	59	44233.00000			

R-Square	Coeff Var	Root MSE	j14 Mean
0.804023	53.70684	15.30645	28.50000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	3053.06667	3053.06667	13.03	0.0009
block	1	299.26667	299.26667	1.28	0.2657
density	2	26708.80000	13354.40000	57.00	<.0001
trt	4	911.33333	227.83333	0.97	0.4343
site*density	2	1072.93333	536.46667	2.29	0.1155
site*trt	4	1688.60000	422.15000	1.80	0.1492
density*trt	8	1830.36667	228.79583	0.98	0.4692

Repeated Measures Analysis of Variance  
Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
site	1	21762.2250	21762.2250	22.24	<.0001
block	1	1273.1361	1273.1361	1.30	0.2614
density	2	100414.6722	50207.3361	51.30	<.0001
trt	4	4492.5722	1123.1431	1.15	0.3495
site*density	2	8909.0167	4454.5083	4.55	0.0171
site*trt	4	7706.4833	1926.6208	1.97	0.1196
density*trt	8	7937.7444	992.2181	1.01	0.4427
Error	37	36211.5139	978.6896		



Repeated Measures Analysis of Variance  
Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	Adj Pr > F			
				F Value	Pr > F	G - G	H - F
time	5	16165.51389	3233.10278	133.95	<.0001	<.0001	<.0001
time*site	5	355.89167	71.17833	2.95	0.0138	0.0795	0.0518
time*block	5	48.98056	9.79611	0.41	0.8443	0.5912	0.6919
time*density	10	9245.56111	924.55611	38.31	<.0001	<.0001	<.0001
time*trt	20	629.36111	31.46806	1.30	0.1810	0.2750	0.2474
time*site*density	10	398.41667	39.84167	1.65	0.0954	0.1929	0.1623
time*site*trt	20	392.31667	19.61583	0.81	0.6963	0.5557	0.6060
time*density*trt	40	929.52222	23.23806	0.96	0.5397	0.4910	0.5091

**Wild Oat 2001-2002**

Dependent Variable: m21

Source	DF	Sum of			
		Squares	Mean Square	F Value	Pr > F
Model	22	50273.76667	2285.17121	12.07	<.0001
Error	97	18364.82500	189.32809		
Corrected Total	119	68638.59167			

R-Square    Coeff Var    Root MSE    m21 Mean  
0.732442    52.13636    13.75965    26.39167

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	147.40833	147.40833	0.78	0.3798
block	1	130.20833	130.20833	0.69	0.4090
density	2	36368.26667	18184.13333	96.05	<.0001
trt	4	8221.71667	2055.42917	10.86	<.0001
site*density	2	564.46667	282.23333	1.49	0.2303
site*trt	4	477.71667	119.42917	0.63	0.6417
density*trt	8	4363.98333	545.49792	2.88	0.0064

Dependent Variable: m27

Source	DF	Sum of			
		Squares	Mean Square	F Value	Pr > F
Model	22	65168.71667	2962.21439	13.15	<.0001
Error	97	21849.15000	225.24897		
Corrected Total	119	87017.86667			

R-Square    Coeff Var    Root MSE    m27 Mean  
0.748912    45.52567    15.00830    32.96667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	14.70000	14.70000	0.07	0.7989
block	1	48.13333	48.13333	0.21	0.6449
density	2	51777.26667	25888.63333	114.93	<.0001
trt	4	7633.86667	1908.46667	8.47	<.0001
site*density	2	801.80000	400.90000	1.78	0.1741
site*trt	4	552.46667	138.11667	0.61	0.6542
density*trt	8	4340.48333	542.56042	2.41	0.0204

Dependent Variable: j3

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	147408.7500	6700.3977	14.02	<.0001
Error	97	46361.2417	477.9509		
Corrected Total	119	193769.9917			

R-Square	Coeff Var	Root MSE	j3 Mean
0.760741	43.51386	21.86209	50.24167

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	9451.8750	9451.8750	19.78	<.0001
block	1	621.0750	621.0750	1.30	0.2571
density	2	112885.2167	56442.6083	118.09	<.0001
trt	4	12843.3667	3210.8417	6.72	<.0001
site*density	2	4645.3500	2322.6750	4.86	0.0097
site*trt	4	2240.8333	560.2083	1.17	0.3279
density*trt	8	4721.0333	590.1292	1.23	0.2873

Dependent Variable: j18

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	153280.9833	6967.3174	13.90	<.0001
Error	97	48628.8083	501.3279		
Corrected Total	119	201909.7917			

R-Square	Coeff Var	Root MSE	j18 Mean
0.759156	43.51162	22.39035	51.45833

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	9275.2083	9275.2083	18.50	<.0001
block	1	525.0083	525.0083	1.05	0.3087
density	2	118683.7167	59341.8583	118.37	<.0001
trt	4	13007.5833	3251.8958	6.49	0.0001
site*density	2	4888.0167	2444.0083	4.88	0.0096
site*trt	4	2173.5833	543.3958	1.08	0.3688
density*trt	8	4727.8667	590.9833	1.18	0.3197

Dependent Variable: j24

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	156022.5333	7091.9333	13.68	<.0001
Error	97	50279.8333	518.3488		
Corrected Total	119	206302.3667			

R-Square	Coeff Var	Root MSE	j24 Mean
0.756281	43.88167	22.76727	51.88333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	9720.0000	9720.0000	18.75	<.0001
block	1	512.5333	512.5333	0.99	0.3225
density	2	120541.5167	60270.7583	116.27	<.0001
trt	4	13019.6167	3254.9042	6.28	0.0002
site*density	2	5172.0500	2586.0250	4.99	0.0087
site*trt	4	2341.5833	585.3958	1.13	0.3473

density*trt	8	4715.2333	589.4042	1.14	0.3457
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Dependent Variable: jl4

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	22	156022.5333	7091.9333	13.68	<.0001
Error	97	50279.8333	518.3488		
Corrected Total	119	206302.3667			

	R-Square	Coeff Var	Root MSE	jl4 Mean
	0.756281	43.88167	22.76727	51.88333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
site	1	9720.0000	9720.0000	18.75	<.0001
block	1	512.5333	512.5333	0.99	0.3225
density	2	120541.5167	60270.7583	116.27	<.0001
trt	4	13019.6167	3254.9042	6.28	0.0002
site*density	2	5172.0500	2586.0250	4.99	0.0087
site*trt	4	2341.5833	585.3958	1.13	0.3473
density*trt	8	4715.2333	589.4042	1.14	0.3457

Repeated Measures Analysis of Variance  
Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
site	1	27565.3125	27565.3125	13.53	0.0004
block	1	931.6125	931.6125	0.46	0.5005
density	2	535877.4333	267938.7167	131.51	<.0001
trt	4	64117.5750	16029.3937	7.87	<.0001
site*density	2	18405.7333	9202.8667	4.52	0.0133
site*trt	4	8237.2083	2059.3021	1.01	0.4058
density*trt	8	26952.9833	3369.1229	1.65	0.1197
Error	97	197635.0292	2037.4745		

Repeated Measures Analysis of Variance  
Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	Adj Pr > F			
				F Value	Pr > F	G - G	H - F
time	5	78066.41250	15613.28250	198.60	<.0001	<.0001	<.0001
time*site	5	10763.87917	2152.77583	27.38	<.0001	<.0001	<.0001
time*block	5	1417.87917	283.57583	3.61	0.0033	0.0562	0.0466
time*density	10	24920.06667	2492.00667	31.70	<.0001	<.0001	<.0001
time*trt	20	3628.19167	181.40958	2.31	0.0011	0.0567	0.0430
time*site*density	10	2838.00000	283.80000	3.61	0.0001	0.0264	0.0182
time*site*trt	20	1890.55833	94.52792	1.20	0.2467	0.3139	0.3106
time*density*trt	40	630.85000	15.77125	0.20	1.0000	0.9932	0.9972
Error(time)	485	38128.66250	78.61580				

**Test to determine the importance of Density in determining Weed Population in 2001 and 2002.**  
**Model1: emergence = density**

**Green foxtail 2001**

Dependent Variable: m22

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	108.300000	54.150000	1.36	0.2653
Error	57	2272.550000	39.869298		
Corrected Total	59	2380.850000			

R-Square	Coeff Var	Root MSE	m22 Mean
0.045488	664.6541	6.314214	0.950000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	108.3000000	54.1500000	1.36	0.2653

Dependent Variable: m24

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	488.133333	244.066667	3.75	0.0295
Error	57	3710.200000	65.091228		
Corrected Total	59	4198.333333			

R-Square	Coeff Var	Root MSE	m24 Mean
0.116268	372.3652	8.067913	2.166667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	488.1333333	244.0666667	3.75	0.0295

Dependent Variable: m29

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	58111.43333	29055.71667	56.58	<.0001
Error	57	29272.90000	513.55965		
Corrected Total	59	87384.33333			

R-Square	Coeff Var	Root MSE	m29 Mean
0.665010	52.90705	22.66185	42.83333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	58111.43333	29055.71667	56.58	<.0001

Dependent Variable: j3

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	96316.0333	48158.0167	76.74	<.0001
Error	57	35768.5500	627.5184		
Corrected Total	59	132084.5833			

R-Square	Coeff Var	Root MSE	j3 Mean
0.729200	42.88214	25.05032	58.41667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	96316.03333	48158.01667	76.74	<.0001

Dependent Variable: j8

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	108386.4333	54193.2167	71.94	<.0001
Error	57	42937.5000	753.2895		
Corrected Total	59	151323.9333			

R-Square	Coeff Var	Root MSE	j8 Mean
0.716254	40.34216	27.44612	68.03333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	108386.4333	54193.2167	71.94	<.0001

Dependent Variable: j12

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	113074.4333	56537.2167	76.59	<.0001
Error	57	42078.5500	738.2202		
Corrected Total	59	155152.9833			

R-Square	Coeff Var	Root MSE	j12 Mean
0.728793	38.53019	27.17021	70.51667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	113074.4333	56537.2167	76.59	<.0001

Dependent Variable: j21

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	121361.2333	60680.6167	85.68	<.0001
Error	57	40366.7000	708.1877		
Corrected Total	59	161727.9333			

R-Square	Coeff Var	Root MSE	j21 Mean
0.750404	36.63855	26.61180	72.63333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	121361.2333	60680.6167	85.68	<.0001

Dependent Variable: j26

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	122340.4000	61170.2000	86.26	<.0001
Error	57	40419.2500	709.1096		
Corrected Total	59	162759.6500			

R-Square	Coeff Var	Root MSE	j26 Mean
0.751663	36.40344	26.62911	73.15000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	122340.4000	61170.2000	86.26	<.0001

Dependent Variable: j13

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F

Model	2	122340.4000	61170.2000	86.26	<.0001
Error	57	40419.2500	709.1096		
Corrected Total	59	162759.6500			

R-Square	Coeff Var	Root MSE	j13 Mean
0.751663	36.40344	26.62911	73.15000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	122340.4000	61170.2000	86.26	<.0001

Repeated Measures Analysis of Variance  
Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
density	2	585810.0333	292905.0167	83.60	<.0001
Error	57	199708.1500	3503.6518		

Source	DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
time	8	427846.6000	53480.8250	314.52	<.0001	<.0001	<.0001
time*density	16	156716.7667	9794.7979	57.60	<.0001	<.0001	<.0001
Error(time)	456	77537.3000	170.0379				

**Volunteer Canola 2001**

Dependent Variable: m22

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	33506.53333	16753.26667	104.38	<.0001
Error	57	9148.45000	160.49912		
Corrected Total	59	42654.98333			

R-Square	Coeff Var	Root MSE	m22 Mean
0.785524	41.28895	12.66882	30.68333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	33506.53333	16753.26667	104.38	<.0001

Dependent Variable: m24

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	60331.03333	30165.51667	156.09	<.0001
Error	57	11015.90000	193.26140		
Corrected Total	59	71346.93333			

R-Square	Coeff Var	Root MSE	m24 Mean
0.845601	32.73591	13.90185	42.46667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	60331.03333	30165.51667	156.09	<.0001

## The GLM Procedure

Dependent Variable: m29

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	124477.5000	62238.7500	98.69	<.0001
Error	57	35947.3500	630.6553		
Corrected Total	59	160424.8500			

R-Square	Coeff Var	Root MSE	m29 Mean
0.775924	35.59582	25.11285	70.55000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	124477.5000	62238.7500	98.69	<.0001

Dependent Variable: j3

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	129407.6333	64703.8167	106.55	<.0001
Error	57	34612.9500	607.2447		
Corrected Total	59	164020.5833			

R-Square	Coeff Var	Root MSE	j3 Mean
0.788972	33.04000	24.64234	74.58333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	129407.6333	64703.8167	106.55	<.0001

Dependent Variable: j8

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	135621.3000	67810.6500	116.17	<.0001
Error	57	33272.3500	583.7254		
Corrected Total	59	168893.6500			

R-Square	Coeff Var	Root MSE	j8 Mean
0.802998	31.43840	24.16041	76.85000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	135621.3000	67810.6500	116.17	<.0001

Dependent Variable: j12

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	140379.6333	70189.8167	117.97	<.0001
Error	57	33914.5500	594.9921		
Corrected Total	59	174294.1833			

R-Square	Coeff Var	Root MSE	j12 Mean
0.805418	31.22568	24.39246	78.11667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	140379.6333	70189.8167	117.97	<.0001

Dependent Variable: j21

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	140053.4333	70026.7167	117.36	<.0001
Error	57	34011.5500	596.6939		
Corrected Total	59	174064.9833			

R-Square	Coeff Var	Root MSE	j21 Mean
0.804604	31.24364	24.42732	78.18333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	140053.4333	70026.7167	117.36	<.0001

Dependent Variable: j26

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	140053.4333	70026.7167	117.36	<.0001
Error	57	34011.5500	596.6939		
Corrected Total	59	174064.9833			

R-Square	Coeff Var	Root MSE	j26 Mean
0.804604	31.24364	24.42732	78.18333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	140053.4333	70026.7167	117.36	<.0001

Dependent Variable: j13

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	140053.4333	70026.7167	117.36	<.0001
Error	57	34011.5500	596.6939		
Corrected Total	59	174064.9833			

R-Square	Coeff Var	Root MSE	j13 Mean
0.804604	31.24364	24.42732	78.18333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	140053.4333	70026.7167	117.36	<.0001

Source	DF	Type III SS	Mean Square	F Value	Pr > F
density	2	1003205.233	501602.617	133.31	<.0001
Error	57	214469.389	3762.621		



Source	DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
time	8	155048.2667	19381.0333	194.34	<.0001	<.0001	<.0001
time*density	16	40678.7000	2542.4188	25.49	<.0001	<.0001	<.0001
Error(time)	456	45476.8111	99.7298				

Greenhouse-Geisser Epsilon 0.1451  
Huynh-Feldt Epsilon 0.1514

**Wild Mustard 2001**

Dependent Variable: m22

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	672.700000	336.350000	8.30	0.0007
Error	57	2308.550000	40.500877		
Corrected Total	59	2981.250000			

R-Square 0.225644    Coeff Var 133.9796    Root MSE 6.364030    m22 Mean 4.750000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	672.7000000	336.3500000	8.30	0.0007

Dependent Variable: m24

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	2284.433333	1142.216667	17.18	<.0001
Error	57	3790.500000	66.500000		
Corrected Total	59	6074.933333			

R-Square 0.376043    Coeff Var 96.31598    Root MSE 8.154753    m24 Mean 8.466667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	2284.433333	1142.216667	17.18	<.0001

Dependent Variable: m29

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	34278.70000	17139.35000	87.90	<.0001
Error	57	11114.70000	194.99474		
Corrected Total	59	45393.40000			

R-Square 0.755147    Coeff Var 39.78362    Root MSE 13.96405    m29 Mean 35.10000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	34278.70000	17139.35000	87.90	<.0001

Dependent Variable: j3

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	54517.90000	27258.95000	92.83	<.0001

Error	57	16737.70000	293.64386
Corrected Total	59	71255.60000	

R-Square	Coeff Var	Root MSE	j3 Mean
0.765103	38.25009	17.13604	44.80000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	54517.90000	27258.95000	92.83	<.0001

Dependent Variable: j8

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	60274.23333	30137.11667	92.60	<.0001
Error	57	18550.10000	325.44035		
Corrected Total	59	78824.33333			

R-Square	Coeff Var	Root MSE	j8 Mean
0.764665	37.45322	18.03997	48.16667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	60274.23333	30137.11667	92.60	<.0001

Dependent Variable: j12

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	75644.40000	37822.20000	94.44	<.0001
Error	57	22828.85000	400.50614		
Corrected Total	59	98473.25000			

R-Square	Coeff Var	Root MSE	j12 Mean
0.768172	37.58244	20.01265	53.25000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	75644.40000	37822.20000	94.44	<.0001

Dependent Variable: j21

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	89522.8000	44761.4000	95.84	<.0001
Error	57	26622.2000	467.0561		
Corrected Total	59	116145.0000			

R-Square	Coeff Var	Root MSE	j21 Mean
0.770785	37.58519	21.61148	57.50000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	89522.80000	44761.40000	95.84	<.0001

Dependent Variable: j26

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F

Model	2	93725.7333	46862.8667	93.49	<.0001
Error	57	28572.4500	501.2711		
Corrected Total	59	122298.1833			

R-Square	Coeff Var	Root MSE	j26 Mean
0.766371	38.08747	22.38908	58.78333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	93725.73333	46862.86667	93.49	<.0001

Dependent Variable: j13

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	93835.9000	46917.9500	93.36	<.0001
Error	57	28645.7000	502.5561		
Corrected Total	59	122481.6000			

R-Square	Coeff Var	Root MSE	j13 Mean
0.766122	38.12545	22.41776	58.80000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	93835.90000	46917.95000	93.36	<.0001

Source	DF	Type III SS	Mean Square	F Value	Pr > F
density	2	411534.6926	205767.3463	111.05	<.0001
Error	57	105619.1056	1852.9668		

Source	DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
time	8	211706.9148	26463.3644	225.34	<.0001	<.0001	<.0001
time*density	16	93222.1074	5826.3817	49.61	<.0001	<.0001	<.0001
Error(time)	456	53551.6444	117.4378				

### Green foxtail 2002

Dependent Variable: m21

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	4.26666667	2.13333333	0.77	0.4724
Error	27	74.70000000	2.76666667		
Corrected Total	29	78.96666667			

R-Square	Coeff Var	Root MSE	m21 Mean
0.054031	453.6355	1.663330	0.366667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	4.26666667	2.13333333	0.77	0.4724

Dependent Variable: m27

Sum of

Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	1290.466667	645.233333	13.37	<.0001
Error	27	1303.400000	48.274074		
Corrected Total	29	2593.866667			

R-Square	Coeff Var	Root MSE	m27 Mean
0.497507	86.13167	6.947955	8.066667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	1290.466667	645.233333	13.37	<.0001

Dependent Variable: j3

Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	25967.26667	12983.63333	79.61	<.0001
Error	27	4403.70000	163.10000		
Corrected Total	29	30370.96667			

R-Square	Coeff Var	Root MSE	j3 Mean
0.855003	34.86186	12.77106	36.63333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	25967.26667	12983.63333	79.61	<.0001

Dependent Variable: j18

Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	31761.86667	15880.93333	73.50	<.0001
Error	27	5833.60000	216.05926		
Corrected Total	29	37595.46667			

R-Square	Coeff Var	Root MSE	j18 Mean
0.844832	33.30579	14.69895	44.13333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	31761.86667	15880.93333	73.50	<.0001

Dependent Variable: j24

Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	35098.06667	17549.03333	64.57	<.0001
Error	27	7337.80000	271.77037		
Corrected Total	29	42435.86667			

R-Square	Coeff Var	Root MSE	j24 Mean
0.827085	35.78609	16.48546	46.06667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	35098.06667	17549.03333	64.57	<.0001

Source            DF   Type III SS   Mean Square   F Value   Pr > F  
Dependent Variable: jl4

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	35098.06667	17549.03333	64.57	<.0001
Error	27	7337.80000	271.77037		
Corrected Total	29	42435.86667			

R-Square	0.827085	Coeff Var	35.78609	Root MSE	16.48546	jl4 Mean	46.06667
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Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	35098.06667	17549.03333	64.57	<.0001

Source	DF	Type III SS	Mean Square	F Value	Pr > F
density	2	94243.24444	47121.62222	78.45	<.0001
Error	27	16217.53333	600.64938		

Source	DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
time	5	63568.11111	12713.62222	170.38	<.0001	<.0001	<.0001
time*density	10	34976.75556	3497.67556	46.87	<.0001	<.0001	<.0001
Error(time)	135	10073.46667	74.61827				

### Canola

Dependent Variable: m21

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	24586.03333	12293.01667	29.20	<.0001
Error	57	23994.90000	420.96316		
Corrected Total	59	48580.93333			

R-Square	0.506084	Coeff Var	60.58283	Root MSE	20.51739	m21 Mean	33.86667
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Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	24586.03333	12293.01667	29.20	<.0001

Dependent Variable: m27

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	37233.03333	18616.51667	40.03	<.0001
Error	57	26510.90000	465.10351		
Corrected Total	59	63743.93333			

R-Square	0.584103	Coeff Var	51.80046	Root MSE	21.56626	m27 Mean	41.63333
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Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	37233.03333	18616.51667	40.03	<.0001

Dependent Variable: j3

Source	Sum of				
	DF	Squares	Mean Square	F Value	Pr > F
Model	2	34381.03333	17190.51667	43.03	<.0001
Error	57	22773.90000	399.54211		
Corrected Total	59	57154.93333			

R-Square	Coeff Var	Root MSE	j3 Mean
0.601541	48.12652	19.98855	41.53333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	34381.03333	17190.51667	43.03	<.0001

Dependent Variable: j18

Source	Sum of				
	DF	Squares	Mean Square	F Value	Pr > F
Model	2	35033.20000	17516.60000	41.75	<.0001
Error	57	23917.65000	419.60789		
Corrected Total	59	58950.85000			

R-Square	Coeff Var	Root MSE	j18 Mean
0.594278	48.14179	20.48433	42.55000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	35033.20000	17516.60000	41.75	<.0001

Dependent Variable: j24

Source	Sum of				
	DF	Squares	Mean Square	F Value	Pr > F
Model	2	35209.73333	17604.86667	41.81	<.0001
Error	57	24000.45000	421.06053		
Corrected Total	59	59210.18333			

R-Square	Coeff Var	Root MSE	j24 Mean
0.594657	48.03689	20.51976	42.71667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	35209.73333	17604.86667	41.81	<.0001

Source	DF	Type III SS	Mean Square	F Value	Pr > F
density	2	35209.73333	17604.86667	41.81	<.0001

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The GLM Procedure

Dependent Variable: j14

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	35338.80000	17669.40000	41.96	<.0001
Error	57	24004.45000	421.13070		
Corrected Total	59	59343.25000			

R-Square	Coeff Var	Root MSE	j14 Mean
0.595498	48.00344	20.52147	42.75000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	35338.80000	17669.40000	41.96	<.0001

Repeated Measures Analysis of Variance  
Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
density	2	200870.2167	100435.1083	40.60	<.0001
Error	57	141008.5917	2473.8349		

Source	DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
time	5	3589.891667	717.978333	48.79	<.0001	<.0001	<.0001
time*density	10	911.616667	91.161667	6.20	<.0001	0.0001	<.0001
Error(time)	285	4193.658333	14.714591				

**Wild Mustard 2002**

Dependent Variable: m21

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	3112.23333	1556.11667	9.02	0.0004
Error	57	9830.35000	172.46228		
Corrected Total	59	12942.58333			

R-Square	Coeff Var	Root MSE	m21 Mean
0.240465	126.0719	13.13249	10.41667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	3112.23333	1556.11667	9.02	0.0004

Dependent Variable: m27

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	10649.23333	5324.61667	18.58	<.0001
Error	57	16337.75000	286.62719		
Corrected Total	59	26986.98333			

R-Square	Coeff Var	Root MSE	m27 Mean
0.394606	96.83547	16.93007	17.48333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	10649.23333	5324.61667	18.58	<.0001

Dependent Variable: j3

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	17527.30000	8763.65000	30.36	<.0001
Error	57	16451.10000	288.61579		
Corrected Total	59	33978.40000			

R-Square	0.515837	Coeff Var	72.60126	Root MSE	16.98870	j3 Mean	23.40000
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Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	17527.30000	8763.65000	30.36	<.0001

Dependent Variable: j18

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	25261.03333	12630.51667	40.52	<.0001
Error	57	17769.70000	311.74912		
Corrected Total	59	43030.73333			

R-Square	0.587046	Coeff Var	63.58854	Root MSE	17.65642	j18 Mean	27.76667
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Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	25261.03333	12630.51667	40.52	<.0001

Dependent Variable: j24

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	26401.63333	13200.81667	42.75	<.0001
Error	57	17599.35000	308.76053		
Corrected Total	59	44000.98333			

R-Square	0.600024	Coeff Var	62.05385	Root MSE	17.57158	j24 Mean	28.31667
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Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	26401.63333	13200.81667	42.75	<.0001

Dependent Variable: j14

	Sum of				
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	26708.80000	13354.40000	43.44	<.0001
Error	57	17524.20000	307.44211		
Corrected Total	59	44233.00000			

R-Square	0.603821	Coeff Var	61.52290	Root MSE	17.53403	j14 Mean	28.50000
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Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	26708.80000	13354.40000	43.44	<.0001

Source	DF	Type III SS	Mean Square	F Value	Pr > F
density	2	100414.6722	50207.3361	32.41	<.0001
Error	57	88292.6917	1548.9946		

Repeated Measures Analysis of Variance  
Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F	Adj Pr > F	G - G	H - F
time	5	16165.51389	3233.10278	127.63	<.0001	<.0001	<.0001	<.0001
time*density	10	9245.56111	924.55611	36.50	<.0001	<.0001	<.0001	<.0001
Error(time)	285	7219.75833	25.33249					

Greenhouse-Geisser Epsilon 0.3122  
Huynh-Feldt Epsilon 0.3307

**Wild Oat 2001-2002**

Dependent Variable: m29

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	36368.26667	18184.13333	65.93	<.0001
Error	117	32270.32500	275.81474		
Corrected Total	119	68638.59167			

R-Square 0.529852  
Coeff Var 62.92771  
Root MSE 16.60767  
m29 Mean 26.39167

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	36368.26667	18184.13333	65.93	<.0001

Dependent Variable: j3

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	51777.26667	25888.63333	85.95	<.0001
Error	117	35240.60000	301.20171		
Corrected Total	119	87017.86667			

R-Square 0.595019  
Coeff Var 52.64458  
Root MSE 17.35516  
j3 Mean 32.96667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	51777.26667	25888.63333	85.95	<.0001

Dependent Variable: j8

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	51777.26667	25888.63333	85.95	<.0001
Error	117	35240.60000	301.20171		
Corrected Total	119	87017.86667			

Model	2	112885.2167	56442.6083	81.64	<.0001
Error	117	80884.7750	691.3229		
Corrected Total	119	193769.9917			

R-Square	Coeff Var	Root MSE	j8 Mean
0.582573	52.33310	26.29302	50.24167

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	112885.2167	56442.6083	81.64	<.0001

Dependent Variable: j21

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	118683.7167	59341.8583	83.42	<.0001
Error	117	83226.0750	711.3340		
Corrected Total	119	201909.7917			

R-Square	Coeff Var	Root MSE	j21 Mean
0.587806	51.82998	26.67085	51.45833

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	118683.7167	59341.8583	83.42	<.0001

Dependent Variable: j26

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	120541.5167	60270.7583	82.22	<.0001
Error	117	85760.8500	732.9987		
Corrected Total	119	206302.3667			

R-Square	Coeff Var	Root MSE	j26 Mean
0.584295	52.18236	27.07395	51.88333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	120541.5167	60270.7583	82.22	<.0001

Dependent Variable: j13

		Sum of			
Source	DF	Squares	Mean Square	F Value	Pr > F
Model	2	120541.5167	60270.7583	82.22	<.0001
Error	117	85760.8500	732.9987		
Corrected Total	119	206302.3667			

R-Square	Coeff Var	Root MSE	j13 Mean
0.584295	52.18236	27.07395	51.88333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
density	2	120541.5167	60270.7583	82.22	<.0001

Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
density	2	535877.4333	267938.7167	91.17	<.0001
Error	117	343845.4542	2938.8500		

Repeated Measures Analysis of Variance  
Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	Adj Pr > F		
				F Value	Pr > F	G - G H - F
time	5	78066.41250	15613.28250	154.03	<.0001	<.0001 <.0001
time*density	10	24920.06667	2492.00667	24.58	<.0001	<.0001 <.0001
Error(time)	585	59298.02083	101.36414			

Greenhouse-Geisser Epsilon 0.2172  
Huynh-Feldt Epsilon 0.2214

### Proportional Weed Emergence

#### Green Foxtail

Dependent Variable: m29

Source	DF	Sum of		F Value	Pr > F
		Squares	Mean Square		
Model	16	20787.86667	1299.24167	10.16	<.0001
Error	73	9338.53333	127.92511		
Corrected Total	89	30126.40000			

R-Square 0.690022    Coeff Var 61.24765    Root MSE 11.31040    m29 Mean 18.46667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	15015.20000	15015.20000	117.37	<.0001
site	1	21.60000	21.60000	0.17	0.6823
density	2	756.46667	378.23333	2.96	0.0582
trt	4	2550.06667	637.51667	4.98	0.0013
year*trt	4	1191.30000	297.82500	2.33	0.0641
site*trt	4	1253.23333	313.30833	2.45	0.0537

Dependent Variable: j3

Source	DF	Sum of		F Value	Pr > F
		Squares	Mean Square		
Model	16	32552.64444	2034.54028	9.12	<.0001
Error	73	16278.34444	222.99102		
Corrected Total	89	48830.98889			

R-Square 0.666639    Coeff Var 53.73689    Root MSE 14.93288    j3 Mean 27.78889

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	23506.93889	23506.93889	105.42	<.0001
site	1	260.41667	260.41667	1.17	0.2834
density	2	644.82222	322.41111	1.45	0.2422
trt	4	4664.93333	1166.23333	5.23	0.0009
year*trt	4	1525.70000	381.42500	1.71	0.1569

site*trt	4	1949.83333	487.45833	2.19	0.0789
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Dependent Variable: j8

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	28716.91111	1794.80694	4.83	<.0001
Error	73	27120.07778	371.50791		
Corrected Total	89	55836.98889			

R-Square	Coeff Var	Root MSE	j8 Mean
0.514299	48.17297	19.27454	40.01111

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	12818.67222	12818.67222	34.50	<.0001
site	1	28.01667	28.01667	0.08	0.7844
density	2	510.42222	255.21111	0.69	0.5063
trt	4	8170.82222	2042.70556	5.50	0.0006
year*trt	4	3195.07778	798.76944	2.15	0.0832
site*trt	4	3993.90000	998.47500	2.69	0.0378

Dependent Variable: j21

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	27377.91111	1711.11944	3.93	<.0001
Error	73	31750.54444	434.93896		
Corrected Total	89	59128.45556			

R-Square	Coeff Var	Root MSE	j21 Mean
0.463024	46.88901	20.85519	44.47778

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	9916.088889	9916.088889	22.80	<.0001
site	1	147.266667	147.266667	0.34	0.5624
density	2	1012.955556	506.477778	1.16	0.3178
trt	4	8367.288889	2091.822222	4.81	0.0017
year*trt	4	3690.077778	922.519444	2.12	0.0868
site*trt	4	4244.233333	1061.058333	2.44	0.0544

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Dependent Variable: j26

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	26529.44444	1658.09028	3.75	<.0001
Error	73	32298.37778	442.44353		
Corrected Total	89	58827.82222			

R-Square	Coeff Var	Root MSE	j26 Mean
0.450968	46.58196	21.03434	45.15556

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	9187.755556	9187.755556	20.77	<.0001

site	1	96.266667	96.266667	0.22	0.6423
density	2	1062.288889	531.144444	1.20	0.3069
trt	4	8393.488889	2098.372222	4.74	0.0019
year*trt	4	3455.077778	863.769444	1.95	0.1109
site*trt	4	4334.566667	1083.641667	2.45	0.0537

Dependent Variable: jl3

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	26529.44444	1658.09028	3.75	<.0001
Error	73	32298.37778	442.44353		
Corrected Total	89	58827.82222			

R-Square	Coeff Var	Root MSE	jl3 Mean
0.450968	46.58196	21.03434	45.15556

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	9187.755556	9187.755556	20.77	<.0001
site	1	96.266667	96.266667	0.22	0.6423
density	2	1062.288889	531.144444	1.20	0.3069
trt	4	8393.488889	2098.372222	4.74	0.0019
year*trt	4	3455.077778	863.769444	1.95	0.1109
site*trt	4	4334.566667	1083.641667	2.45	0.0537

The GLM Procedure  
 Repeated Measures Analysis of Variance  
 Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
time	5	46326.89167	9265.37833	95.84	<.0001	<.0001	<.0001
time*year	5	3053.21389	610.64278	6.32	<.0001	0.0095	0.0057
time*site	5	605.73333	121.14667	1.25	0.2838	0.2751	0.2822
time*density	10	2132.52963	213.25296	2.21	0.0170	0.1052	0.0913
time*trt	20	3393.92778	169.69639	1.76	0.0239	0.1318	0.1147
time*year*trt	20	312.71667	15.63583	0.16	1.0000	0.9743	0.9864
time*site*trt	20	3878.07222	193.90361	2.01	0.0067	0.0869	0.0707
Error(time)	365	35286.72037	96.67595				

**Volunteer Canola**

Dependent Variable: m29

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	27770.43333	1735.65208	13.68	<.0001
Error	103	13071.43333	126.90712		
Corrected Total	119	40841.86667			

R-Square	Coeff Var	Root MSE	m29 Mean
0.679950	30.41937	11.26531	37.03333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	18900.30000	18900.30000	148.93	<.0001
site	1	5576.03333	5576.03333	43.94	<.0001

density	2	1392.31667	696.15833	5.49	0.0054
trt	4	788.28333	197.07083	1.55	0.1926
year*trt	4	578.11667	144.52917	1.14	0.3425
site*trt	4	535.38333	133.84583	1.05	0.3829

Dependent Variable: j3

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	25072.35000	1567.02187	10.17	<.0001
Error	103	15874.64167	154.12273		
Corrected Total	119	40946.99167			

R-Square	Coeff Var	Root MSE	j3 Mean
0.612312	29.80104	12.41462	41.65833

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	15847.00833	15847.00833	102.82	<.0001
site	1	4928.00833	4928.00833	31.97	<.0001
density	2	2409.81667	1204.90833	7.82	0.0007
trt	4	532.11667	133.02917	0.86	0.4888
year*trt	4	598.61667	149.65417	0.97	0.4268
site*trt	4	756.78333	189.19583	1.23	0.3038

Dependent Variable: j8

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	26403.86667	1650.24167	11.77	<.0001
Error	103	14447.33333	140.26537		
Corrected Total	119	40851.20000			

R-Square	Coeff Var	Root MSE	j8 Mean
0.646342	27.67142	11.84337	42.80000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	18007.50000	18007.50000	128.38	<.0001
site	1	3853.33333	3853.33333	27.47	<.0001
density	2	2948.75000	1474.37500	10.51	<.0001
trt	4	442.95000	110.73750	0.79	0.5346
year*trt	4	483.08333	120.77083	0.86	0.4901
site*trt	4	668.25000	167.06250	1.19	0.3192

Dependent Variable: j21

	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	28061.38333	1753.83646	12.30	<.0001
Error	103	14681.60833	142.53989		
Corrected Total	119	42742.99167			

R-Square	Coeff Var	Root MSE	j21 Mean
0.656514	27.29436	11.93901	43.74167

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	18228.67500	18228.67500	127.88	<.0001
site	1	4851.40833	4851.40833	34.04	<.0001
density	2	3295.01667	1647.50833	11.56	<.0001
trt	4	525.61667	131.40417	0.92	0.4543
year*trt	4	519.28333	129.82083	0.91	0.4607
site*trt	4	641.38333	160.34583	1.12	0.3489

Dependent Variable: j26

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	27797.08333	1737.31771	12.04	<.0001
Error	103	14858.24167	144.25477		
Corrected Total	119	42655.32500			

R-Square 0.651667    Coeff Var 27.40584    Root MSE 12.01061    j26 Mean 43.82500

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	17983.00833	17983.00833	124.66	<.0001
site	1	4826.00833	4826.00833	33.45	<.0001
density	2	3303.05000	1651.52500	11.45	<.0001
trt	4	568.78333	142.19583	0.99	0.4188
year*trt	4	516.11667	129.02917	0.89	0.4702
site*trt	4	600.11667	150.02917	1.04	0.3903

Dependent Variable: j13

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	27747.85000	1734.24063	11.99	<.0001
Error	103	14892.81667	144.59045		
Corrected Total	119	42640.66667			

R-Square 0.650737    Coeff Var 27.43250    Root MSE 12.02458    j13 Mean 43.83333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	17958.53333	17958.53333	124.20	<.0001
site	1	4813.33333	4813.33333	33.29	<.0001
density	2	3288.51667	1644.25833	11.37	<.0001
trt	4	568.16667	142.04167	0.98	0.4206
year*trt	4	512.46667	128.11667	0.89	0.4751
site*trt	4	606.83333	151.70833	1.05	0.3857

The GLM Procedure

Repeated Measures Analysis of Variance  
Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F	Adj Pr > F	G - G	H - F
time	5	4202.056944	840.411389	169.36	<.0001	<.0001	<.0001	<.0001
time*year	5	77.190278	15.438056	3.11	0.0089	0.0470	0.0386	0.0386
time*site	5	82.012500	16.402500	3.31	0.0060	0.0390	0.0312	0.0312

time*density	10	330.597222	33.059722	6.66	<.0001	<.0001	<.0001
time*trt	20	471.519444	23.575972	4.75	<.0001	<.0001	<.0001
time*year*trt	20	25.913889	1.295694	0.26	0.9996	0.9770	0.9859
time*site*trt	20	53.341667	2.667083	0.54	0.9507	0.8262	0.8524
Error(time)	515	2555.534722	4.962203				

**Wild Mustard**

Dependent Variable: m29

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	12824.91667	801.55729	5.26	<.0001
Error	103	15701.05000	152.43738		
Corrected Total	119	28525.96667			

R-Square	Coeff Var	Root MSE	m29 Mean
0.449587	77.08566	12.34655	16.01667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	8534.533333	8534.533333	55.99	<.0001
site	1	2412.033333	2412.033333	15.82	0.0001
density	2	470.866667	235.433333	1.54	0.2183
trt	4	339.883333	84.970833	0.56	0.6941
year*trt	4	746.716667	186.679167	1.22	0.3050
site*trt	4	320.883333	80.220833	0.53	0.7167

Dependent Variable: j3

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	18707.63333	1169.22708	6.74	<.0001
Error	103	17858.23333	173.38091		
Corrected Total	119	36565.86667			

R-Square	Coeff Var	Root MSE	j3 Mean
0.511615	61.14900	13.16742	21.53333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	11290.80000	11290.80000	65.12	<.0001
site	1	4915.20000	4915.20000	28.35	<.0001
density	2	470.51667	235.25833	1.36	0.2620
trt	4	332.28333	83.07083	0.48	0.7510
year*trt	4	1308.95000	327.23750	1.89	0.1182
site*trt	4	389.88333	97.47083	0.56	0.6906

Dependent Variable: j8

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	16538.73333	1033.67083	5.45	<.0001
Error	103	19547.23333	189.77896		
Corrected Total	119	36085.96667			

R-Square	Coeff Var	Root MSE	j8 Mean
0.458315	54.70296	13.77603	25.18333



Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	9434.133333	9434.133333	49.71	<.0001
site	1	3286.533333	3286.533333	17.32	<.0001
density	2	1152.516667	576.258333	3.04	0.0523
trt	4	773.883333	193.470833	1.02	0.4009
year*trt	4	1293.283333	323.320833	1.70	0.1549
site*trt	4	598.383333	149.595833	0.79	0.5354

Dependent Variable: j21

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	24861.23333	1553.82708	7.31	<.0001
Error	103	21903.96667	212.65987		
Corrected Total	119	46765.20000			

R-Square	Coeff Var	Root MSE	j21 Mean
0.531618	49.10055	14.58286	29.70000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	13356.30000	13356.30000	62.81	<.0001
site	1	6690.13333	6690.13333	31.46	<.0001
density	2	1390.20000	695.10000	3.27	0.0420
trt	4	665.36667	166.34167	0.78	0.5393
year*trt	4	2017.03333	504.25833	2.37	0.0572
site*trt	4	742.20000	185.55000	0.87	0.4832

Dependent Variable: j26

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	25947.61667	1621.72604	7.63	<.0001
Error	103	21906.35000	212.68301		
Corrected Total	119	47853.96667			

R-Square	Coeff Var	Root MSE	j26 Mean
0.542225	48.10442	14.58366	30.31667

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	14040.03333	14040.03333	66.01	<.0001
site	1	6571.20000	6571.20000	30.90	<.0001
density	2	1502.31667	751.15833	3.53	0.0328
trt	4	672.63333	168.15833	0.79	0.5339
year*trt	4	2302.63333	575.65833	2.71	0.0343
site*trt	4	858.80000	214.70000	1.01	0.4061

Dependent Variable: j13

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	25655.30000	1603.45625	7.50	<.0001
Error	103	22032.82500	213.91092		
Corrected Total	119	47688.12500			

R-Square	Coeff Var	Root MSE	j13 Mean
0.537981	48.15043	14.62569	30.37500

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	13889.00833	13889.00833	64.93	<.0001
site	1	6468.00833	6468.00833	30.24	<.0001
density	2	1466.55000	733.27500	3.43	0.0362
trt	4	674.00000	168.50000	0.79	0.5357
year*trt	4	2292.86667	573.21667	2.68	0.0357
site*trt	4	864.86667	216.21667	1.01	0.4055

Source	DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
time	5	20444.59583	4088.91917	319.74	<.0001	<.0001	<.0001
time*year	5	629.49583	125.89917	9.85	<.0001	0.0003	0.0001
time*site	5	966.99583	193.39917	15.12	<.0001	<.0001	<.0001
time*density	10	335.60833	33.56083	2.62	0.0040	0.0497	0.0405
time*trt	20	591.28611	29.56431	2.31	0.0011	0.0337	0.0254
time*year*trt	20	416.96944	20.84847	1.63	0.0416	0.1384	0.1252
time*site*trt	20	395.69167	19.78458	1.55	0.0611	0.1628	0.1499
Error(time)	515	6585.85694	12.78807				

**Wild Oat**

Dependent Variable: m29

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	6743.06667	421.44167	6.79	<.0001
Error	103	6389.60000	62.03495		
Corrected Total	119	13132.66667			

R-Square	Coeff Var	Root MSE	m29 Mean
0.513458	42.96124	7.876227	18.33333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	2167.500000	2167.500000	34.94	<.0001
site	1	0.533333	0.533333	0.01	0.9263
density	2	161.816667	80.908333	1.30	0.2758
trt	4	3587.750000	896.937500	14.46	<.0001
year*trt	4	526.916667	131.729167	2.12	0.0832
site*trt	4	298.550000	74.637500	1.20	0.3141

Dependent Variable: j3

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	5937.60000	371.10000	4.52	<.0001
Error	103	8458.26667	82.11909		
Corrected Total	119	14395.86667			

R-Square	Coeff Var	Root MSE	j3 Mean
0.412452	38.50691	9.061959	23.53333

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	740.033333	740.033333	9.01	0.0034
site	1	116.033333	116.033333	1.41	0.2373
density	2	540.066667	270.033333	3.29	0.0413
trt	4	3344.366667	836.091667	10.18	<.0001
year*trt	4	873.633333	218.408333	2.66	0.0369
site*trt	4	323.466667	80.866667	0.98	0.4193

Dependent Variable: j8

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	16558.50000	1034.90625	4.23	<.0001
Error	103	25186.49167	244.52905		
Corrected Total	119	41744.99167			

R-Square    Coeff Var    Root MSE    j8 Mean  
0.396658    42.95012    15.63742    36.40833

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	52.008333	52.008333	0.21	0.6456
site	1	4236.408333	4236.408333	17.32	<.0001
density	2	2010.216667	1005.108333	4.11	0.0192
trt	4	8099.200000	2024.800000	8.28	<.0001
year*trt	4	578.200000	144.550000	0.59	0.6698
site*trt	4	1582.466667	395.616667	1.62	0.1754

Dependent Variable: j21

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	16498.00000	1031.12500	4.05	<.0001
Error	103	26199.20000	254.36117		
Corrected Total	119	42697.20000			

R-Square    Coeff Var    Root MSE    j21 Mean  
0.386395    42.75792    15.94870    37.30000

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	116.033333	116.033333	0.46	0.5009
site	1	3967.500000	3967.500000	15.60	0.0001
density	2	2067.800000	1033.900000	4.06	0.0200
trt	4	8163.200000	2040.800000	8.02	<.0001
year*trt	4	537.133333	134.283333	0.53	0.7154
site*trt	4	1646.333333	411.583333	1.62	0.1753

Dependent Variable: j26

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	16856.46667	1053.52917	4.06	<.0001
Error	103	26734.52500	259.55850		
Corrected Total	119	43590.99167			

R-Square    Coeff Var    Root MSE    j26 Mean

0.386696 42.85742 16.11082 37.59167

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	170.408333	170.408333	0.66	0.4197
site	1	4141.875000	4141.875000	15.96	0.0001
density	2	2125.516667	1062.758333	4.09	0.0195
trt	4	8108.200000	2027.050000	7.81	<.0001
year*trt	4	526.466667	131.616667	0.51	0.7306
site*trt	4	1784.000000	446.000000	1.72	0.1516

Dependent Variable: jl3

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	16	16856.46667	1053.52917	4.06	<.0001
Error	103	26734.52500	259.55850		
Corrected Total	119	43590.99167			

R-Square 0.386696  
 Coeff Var 42.85742  
 Root MSE 16.11082  
 jl3 Mean 37.59167

Source	DF	Type I SS	Mean Square	F Value	Pr > F
year	1	170.408333	170.408333	0.66	0.4197
site	1	4141.875000	4141.875000	15.96	0.0001
density	2	2125.516667	1062.758333	4.09	0.0195
trt	4	8108.200000	2027.050000	7.81	<.0001
year*trt	4	526.466667	131.616667	0.51	0.7306
site*trt	4	1784.000000	446.000000	1.72	0.1516

Source	DF	Type III SS	Mean Square	F Value	Pr > F	G - G	H - F
time	5	44191.45694	8838.29139	191.38	<.0001	<.0001	<.0001
time*year	5	1101.55694	220.31139	4.77	0.0003	0.0274	0.0222
time*site	5	6456.71250	1291.34250	27.96	<.0001	<.0001	<.0001
time*density	10	1146.69722	114.66972	2.48	0.0065	0.0822	0.0728
time*trt	20	3298.95278	164.94764	3.57	<.0001	0.0068	0.0042
time*year*trt	20	396.04722	19.80236	0.43	0.9866	0.8066	0.8330
time*site*trt	20	1702.86389	85.14319	1.84	0.0145	0.1182	0.1065
Error(time)	515	23784.21250	46.18294				