The effects of crop planting pattern and alternative cropping systems and wild oat population ecology and interference in barley
by Stephen Ronald Canner

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Agronomy
Montana State University

Abstract:
Wild oat (Avena fatua L.) is a costly weed problem in wheat and barley production in Montana. Wild oat reduces yield and quality of barley, and is particularly troublesome because of a persistent seed bank. Due to increasing economic and environmental costs of herbicides and instances of wild oat resistance to herbicides, non-chemical management strategies are needed which maximize wild oat seed bank decline and crop competitiveness with wild oat.

Models which predict individual plant size based on the location of neighboring plants may be useful in predicting the economic value of different crop planting patterns in various situations. A simple model was developed which predicts individual plant size based on the distance and dispersion of neighboring plants. This model compared favorably with published models in its ability to predict plant size and in its ease of computation in a variety of applications.

Experiments were conducted in Bozeman in 1993 and 1994 to determine whether different patterns of crop planting at a constant plant density influenced wild oat seed production or barley yield response to wild oat. Barley planted in wide rows (30-36 cm) suffered a significant yield loss due to competition, while there was no significant yield loss when barley was planted in narrow rows (15-18 cm), or in diagonally offset double rows created by driving a grain drill over the plots twice with a 20° angle between the passes. Barley planting pattern did not have a significant impact on wild oat seed production.

Eight different three-year dryland crop rotation treatments were established at two on-farm sites near Big Sandy, MT from 1993-1995 to evaluate the impact of alternative cropping systems on wild oat population ecology and barley yield. The treatment where a grain crop was followed by alfalfa which was cut for hay in the second year and plowed down for green manure in the third year showed the strongest reduction in wild oat seed bank numbers. Pea green manures did not significantly differ from fallow in any effect on wild oat populations. Analysis of wild oat demography revealed that recruitment rates and timing of tillage were strong determinants of wild oat population dynamics. When green manures were properly managed, they did not result in significant yield loss in barley crops in subsequent years, and in one case resulted in yield increase.

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A thesis submitted in partial fulfillment
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APPROVAL

of a thesis submitted by

Stephen Ronald Canner

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

Bruce D. Maxwell — (Signature) — April 16, 1996 — Date

Approved for the Department of Plant, Soil, and Environmental Sciences

Jeffrey S. Jacobsen — (Signature) — 4/15/96 — Date

Approved for the College of Graduate Studies

Robert L. Brown — (Signature) — 4/29/96 — Date

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Date 21 April 1996

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ABSTRACT

Wild oat (*Avena fatua* L.) is a costly weed problem in wheat and barley production in Montana. Wild oat reduces yield and quality of barley, and is particularly troublesome because of a persistent seed bank. Due to increasing economic and environmental costs of herbicides and instances of wild oat resistance to herbicides, non-chemical management strategies are needed which maximize wild oat seed bank decline and crop competitiveness with wild oat.

Models which predict individual plant size based on the location of neighboring plants may be useful in predicting the economic value of different crop planting patterns in various situations. A simple model was developed which predicts individual plant size based on the distance and dispersion of neighboring plants. This model compared favorably with published models in its ability to predict plant size and in its ease of computation in a variety of applications.

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CHAPTER 1

LITERATURE REVIEW

Wild Oat

Wild oat (*Avena fatua* L.) is an annual grass (family Poaceae, tribe Avenae) which is a troublesome weed wherever spring-planted cool season small grains are grown. Wild oat is native to Eurasia but has spread throughout the world as an impurity in crop seeds and feed. It is widespread in North America, Europe, North Africa, Asia, Australia, and New Zealand. (Sharma and Vanden Born 1978). Wild oat is primarily a weed of cultivated fields of cool season crops, but is also found in disturbed sites in pastures, roadsides, and waste areas.

Wild oat has been documented to reduce yield and quality of several crops. Wild oat can cause yield and/or quality reduction in wheat (Wilson et al. 1990, Carlson et al. 1981, O'Donovan et al. 1985, Bell and Nalewaja 1968), barley (Bell and Nalewaja 1968, Wilson and Peters 1982, Barton et al. 1992, O'Donovan et al. 1985, Evans et al. 1991, Wilson et al. 1990, Morishita and Thill 1988), flax (Bell and Nalewaja 1968, Dew 1972), and rapeseed (Dew and Keys 1976). Worldwide, wild oat is estimated to cause annual yield losses of wheat and barley of 12,940,100 metric tons, of which approximately half are yield losses in North America alone (Nalewaja 1977). Wild oat is the most costly weed problem in Montana (Fay and Stewart 1981). Yield reductions due to wild oat in Montana are estimated to cost $50 million. An estimated 60% of wild oat infested acres in Montana are treated annually with herbicides valued at about $10 million. Wild oat is a controlled 'noxious

weed' under Montana law, which provides for restrictions on the sale of crop seed contaminated with seeds of wild oat.

Description and Biology of Wild Oat

Wild oat resembles cultivated oat (*Avena sativa* L.), to which it is closely related. Crosses between the two species are commonly observed (Coffman and Wiebe 1930). Wild oat may be distinguished visually from cultivated oat by its typically greater height and its loose, large panicle. Wild oat florets disarticulate from their pedicels, leaving a prominent circular basal scar, or "sucker mouth". This feature is absent in cultivated oat. Wild oat florets bear a long awn which is bent at about its midpoint, and which is twisted basal to the point of bending. Awns on cultivated oat florets are absent or confined to the lowest floret, and are usually shorter and straight. The twisted awn of wild oat, which reversibly untwists under humid conditions, facilitates dispersal and burial of the seed (Somody et al. 1985).

Wild oat is genetically variable and phenotypically plastic. Wild oat is generally considered a spring annual in the northern Great Plains of the United States and Canada, although in regions with mild winters it may persist as a winter annual. A variable but significant percentage of wild oat seeds have a degree of dormancy which prevents germination in the first season after seed shed (Wilson 1978). However, Wilson (1978) emphasizes that wild oat seeds are relatively short lived compared to many other annual weeds with dormant seed banks. He found that wild oat seed banks declined at a rate of about 80% per year when seed return was not permitted. This rate varied with tillage regime. Wilson (1978) also found that wild oat seeds experienced significantly higher mortality when they were allowed to remain on the soil surface without tillage over a winter than when they were tilled into the soil in the fall.

Sexsmith (1969) noted that wild oat is less problematic in warmer, drier portions of Alberta than in the cool and moist sections of the province. He proposed that differences in dormancy of wild oat seeds produced under different environmental conditions could be partially responsible. In a greenhouse study where wild oat plants were grown under varying temperature and moisture conditions, Sexsmith (1969) found that cool and moist conditions were conducive to the production of large numbers of dormant seeds, while warmer and dryer conditions resulted in the production of fewer, less dormant seeds. Similarly, Peters (1982, 1984) found that wild oat plants grown under moisture stress produced fewer seeds than those grown without moisture stress, and that those seeds were less dormant than the seeds produced on non-stressed plants.

Wild oat seed germination and emergence reach maxima in spring and fall, in response to cool temperatures, although germination may occur throughout the growing season. In northern regions of North America, fall germinating wild oats typically do not survive. The dormancy characteristics of wild oat lead to emergence of wild oat over an extended period of time in the spring. The timing of emergence of wild oat is an important factor in both its fecundity and in its capacity to reduce barley yields (Wilson and Peters 1982, Peters 1984, O'Donovan et al. 1985), with earlier emerging wild oat plants producing more seed and causing a greater reduction in barley yield than later emerging plants.

Wild Oat Interference with Barley

Barley is an important crop in Montana, occupying 1.1 million harvested acres with a total crop value of $137.2 million in 1993 (Montana Agricultural Statistics Service 1993). The state of Montana ranks second in the United States in total barley production (Montana Agricultural Statistics Service 1993).

Wild oat has been shown to reduce both yield and quality of harvested barley. The exact magnitude of the reduction has been observed to be widely variable between sites and years (Wilson and Peters 1982). This variability in barley response to wild oat infestation has been attributed to weather conditions, relative time of emergence of crop and weed (Peters and Wilson 1983, Peters 1984, O'Donovan et al. 1985), nitrogen fertility (Bell and Nalewaja 1968), soil type (Firbank et al. 1990), barley density (Wilson et al. 1990, Evans et al. 1991), and barley variety (Dhaliwal et al. 1993, Siddiqi et al. 1985, Ray and Hastings 1992, Konesky et al. 1989). Wilson et al. (1990) also attributed some of the variation between yield loss estimates in reported studies to differences in harvest methods in different experiments.

Wilson et al. (1990) fitted Cousens' (1985) hyperbolic model of crop yield loss as a function of weed density to data from infestations of wild oat in wheat and barley. This model describes crop yield loss due to weed density as a curvilinear function where yield loss increases rapidly with increasing density at low densities, but levels off to an asymptotic maximum total percentage yield loss at higher densities. The two model parameters estimate the maximum yield loss due to high densities of weeds and the yield loss per plant as the density approaches zero. The values of the model parameters led them to conclude that in a range of situations at usual crop densities, the yield reduction due to low infestations of wild oat can be approximated by 1% yield loss for each wild oat plant$\cdot m^{-2}$. They also concluded that at or near economic threshold densities of wild oats, yield loss would cause a considerably greater economic impact than would contamination of grain by wild oat seeds, unless the grain were being grown for seed, where tolerance for weed seed contamination is much lower.

The timing of the onset of interference between barley and wild oat has been investigated by several researchers, and seems to be highly variable, depending to some extent on crop and weed density as well as on environmental conditions. Chancellor and Peters (1974) investigated the time

of onset of the competitive effect of wild oat on barley by weeding different plots as soon as barley emerged or at successively later dates. They concluded that significant yield-reducing competition did not begin until after the four leaf stage of the crop, although they suggested that in higher densities of wild oats, the onset of competition would be earlier. These results were supported by Peters (1984), although Morishita and Thill (1988) did not detect significant wild oat competition until the two node stage of barley growth, while other researchers cited in Sharma and Vanden Born (1978) found significant competition to occur earlier.

Morishita and Thill (1988) investigated the effect of wild oat infestation on the levels of water and nitrogen both in the soil and in barley plants. They concluded that wild oat may reduce barley yield in part by reducing the total water and turgor potential in barley at the time of head formation on tillers. Barley yield loss due to wild oat may also be related to allelopathic chemical exudates of wild oat plants (Ray and Hastings 1992, Schumacher et al. 1983, Fay and Duke 1977).

Dew (1972), Dew and Keys (1976), and Cousens et al.(1987) concluded that barley was more competitive with wild oat than was wheat. Morishita and Thill (1988) grew wild oat and barley plants alone and in mixture. They determined that although the two species had very similar growth patterns throughout the growing season when grown in monoculture, barley was significantly more competitive than wild oat when grown in mixture.

Herbicides and tillage have been key tools for wild oat management in Montana barley production. Concerns about erosion and loss of soil organic matter have led producers to investigate minimum or no-till options for small grain production, while concerns about groundwater quality and economic efficiency have led to substantial interest in the potential for reduction of herbicide use. Widespread resistance of wild oat to many common herbicides has further accentuated the need for profitable alternative management strategies.

Bioeconomic models have the potential to significantly increase the net profit of producers by recommending the least expensive control tactic which will successfully bring a weed population below its economic threshold level (Cousens et al. 1987, Cousens et al. 1986, Lybecker et al. 1991). A simple schematic diagram for a bioeconomic model is shown in Figure 1.1. This model predicts net return from the interactions between the weed population cycle, producer-controlled management variables, crop biology, and economic parameters. By accounting for weed reproduction under a proposed management plan, a bioeconomic model can account for the long term economic impact of that management plan. A bioeconomic model may also be useful as a conceptual framework for identifying research priorities and organizing research results.

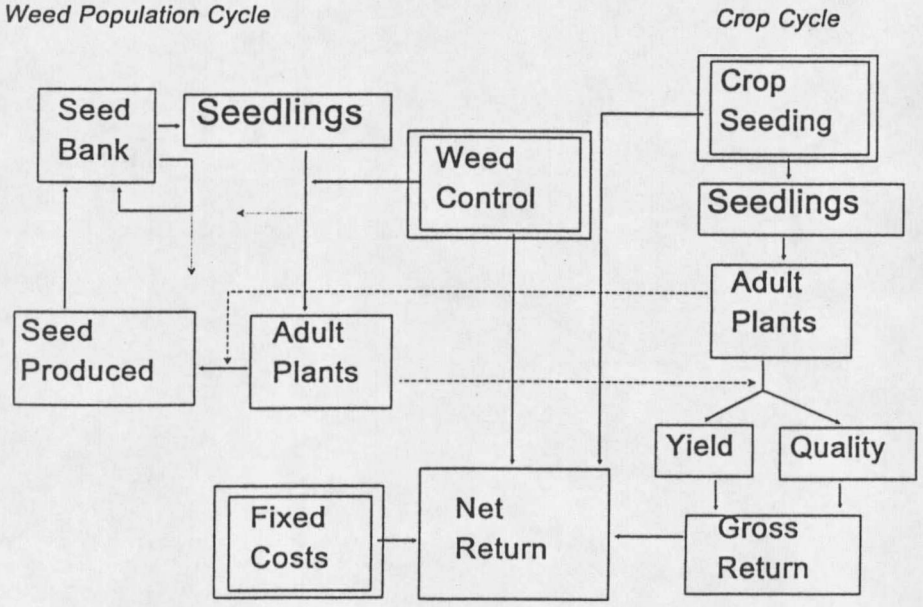

Figure 1.1. A schematic diagram of a bioeconomic model, showing the interactions between the weed population cycle, management variables, crop biology, and economic parameters. The double boxes represent producer-controlled management variables.

In the above diagram, crop seeding and weed control are marked with double boxes, indicating components of the model which are producer-controlled management variables. Traditional weed science research has focused on the efficacy of weed control measures in reducing

weed density or biomass, with much less attention to the effects of crop seeding on interactions between crops and weeds. Crop seeding management could include variations in crop density, planting time, planting pattern, or crop species. Maxwell et al. (1994) are developing a bioeconomic model for prediction of long-term economic optimum thresholds for wild oat control in barley. They note that environmental conditions and cultural practices have the potential to cause variation in parameters of the model. If parameters of the weed population cycle or the competitive relationship between a crop and a weed are affected by crop seeding practices such as crop rotations or the planting pattern of the crop, the model's prediction of an optimal management plan could be significantly affected. Crop seeding practices which improve the competitive ability of the crop relative to the weed or which contribute to reductions in weed population densities may even allow producers to use chemical or mechanical weed controls less often or at lower rates than would otherwise be economical. Increased understanding of how crop seeding practices impact the parameters of a bioeconomic model may facilitate the development of optimal weed managment strategies. This thesis focuses on the effects of crop planting pattern and alternative cropping systems on parameters of the bioeconomic model diagrammed in Figure 1.1. A component study of models of interference between individual plants was included in order to increase understanding of how planting pattern might influence competition between crops and weeds.

Models of Individual Plant Performance

Interference between plants is generally accepted to be important in controlling the structure, composition, and function of plant populations and plant communities (Harper 1977). The influence of mean density of plants in a population on the mean productivity (biomass or reproductive output) of those plants has been widely studied and is characterized by a few simple equations (reviewed in Willey and Heath 1969, Harper 1977). As density increases, mean yield per plant decreases

monotonically, and productivity per unit area tends to plateau, suggesting the sharing of a finite resource pool. However, plants do not respond, typically, to overall mean density but to the resource limitations of their local environment (Antonovics and Levin 1980), which may be mediated by other plants in the immediate neighborhood. It may be convenient to refer to the availablility of "biological space" in the neighborhood of emerging seedlings (Ross and Harper 1972). "Biological space" can be considered to be some integration of the light, water, nutrients, and space which are needed by all plants, and is closely related to the physical space where these resources are found and collected by plant organs. A number of studies, several of which will be reviewed in this paper, have demonstrated that the growth rate and final size of an individual plant is related to the number, size, location, species, or relative emergence time of neighboring plants, all factors which may be considered to influence the biological space available to an emerging seedling. Since biological space cannot be completely defined, many analyses of biological space have focused on competition for physical space, which in even aged, monospecific populations may be an adequate surrogate for biological space.

Since plant populations are often composed of a hierarchy of individuals with a skewed distribution of different sizes, the mean plant performance may not represent the most common plant in a population (Weiner 1985). Similarly, when plants are distributed non-uniformly in space, mean density may not represent the local competitive effect experienced by most of the plants in the population. Since plant performance and local competitive effect are generally related non-linearly, it is not reasonable to expect that mean density can predict plant performance well over a range of situations. Spatially explicit models which account for variation in local competitive effect may provide superior predictions of individual plant performance.

Practical Uses of Spatially Explicit Individual Plant Models

There are several practical situations where the consequences of competition for biological space by individual plants may not always be adequately described by models which describe only effects of mean density on populations of plants. For decades agronomists have pursued the question of how the planting pattern of crops might be manipulated to maximize yields, using available equipment. Researchers have investigated the effects of changing the uniformity of crop seed placement by changing the distance between crop rows, broadcast seeding of crops instead of row planting, pairing of crop rows, or precision planting of seeds at a uniform distance within the row. Several studies have found that at constant mean densities, different planting patterns have resulted in statistically significant differences in yield in monocultures, intercrops, and in weedy crops (for examples, see subsequent literature review). These effects can not be predicted by models which describe the effects of mean density on mean plant yield. Theoretical analyses have related these effects to the shape of the physical space available to individual plants in monospecific stands (Pant 1979) and to the ability of crop plants to capture physical space in the presence of weeds (Fischer and Miles 1973). Spatially explicit models of local competitive effect on individual plant performance may be scaled up to simulate the effects of different planting patterns on monoculture crops, designed intercrops, or weedy crops. These simulations will be particularly useful when considering that the optimal planting pattern in a given situation will be restricted by the availability of appropriate equipment for planting the crops, and by the costs of modifying that equipment or making multiple passes over the field in order to alter the crop planting pattern

Models of local competition for biological space are relevant in silvicultural situations, where thinning of trees and management of competition between differently valued species are common management practices. Models which predict the effects of different vegetation

management schemes must account for the resulting plant spatial arrangements (Opie 1968, Bella 1971, Wagner and Radosevich 1991).

Individual plant fecundity and age at reproduction are often closely related to the characteristics of the local neighborhood (Powell 1990, Rice 1990, Heywood 1986, Bonan 1991). Models of evolution may be improved by accounting for variation in spatial pattern and the concomitant variation in individual plant performance and life history characteristics. Similarly, directed selection by crop breeders may be improved by better understanding of the effects of competition on individual plant performance (Hamblin and Rosielle 1978).

Types of Individual Plant Models

Researchers have used a wide variety of methods for predicting individual plant performance from the characteristics of its environment. In a review of the literature, Benjamin and Hardwick (1986) delineated five general categories of models based on the assumptions of each model about the extent of the area of resource use (the "domain") of a given plant. The categories they suggested are:

a) "non-overlapping domain" models, where individual plants are the sole occupants and resource users within a certain region of two-dimensional space,

b)"overlapping domain" models, where individual plants are assigned a circular domain proportional to their size, which may overlap with the domain of other plants, and plant growth is related to the area of the domain and the extent of overlap with the domains of neighboring plants,

c)"unbounded areas of influence" models, where the competitive effect of a neighbor is a declining function of its distance, but may never decline to zero,

d)"diffuse population effect" models, which relate individual plant growth to mean density of the plot and to other factors, but not to localized neighborhood effects, and

e)"tiers of vegetation" models, which describe competition for light based on the canopy structures of neighboring plants.

Although it is limited, the categorization system of Benjamin and Hardwick (1986) is convenient for summarizing the literature pertaining to models of individual plant growth. A group of models which I refer to as "nearest neighbor" models will be discussed as an additional category, although they might technically be a sub-category of "unbounded area of influence" models. A few recent models (e.g. Silander and Pacala 1985, Lindquist et al. 1994) bear strong resemblance to the models assigned by Benjamin and Hardwick (1986) to the "unbounded areas of influence" category, although they might not strictly meet the definitions of that category. These will be discussed along with the "unbounded areas of influence" models which they resemble. "Diffuse population effect" models, represented by the model of Aikman and Watkinson (1980) will not be discussed further, since they do not relate individual plant growth to the characteristics of the plant neighborhood.

Different models predict different measures of plant performance, including final plant size (used primarily in annual populations), reproductive output, growth rate, survival, or some combination of these. The proposed application of the model, if there is one, usually determines which of these is predicted by the model.

Another characteristic of a given model which is of some importance is whether it includes neighbor plant size in the analysis, and if it does, how it does. Several models (e.g. Bella 1971, Hegyi 1974) predict plant growth rates as a function of neighbor plant size, and may be useful in forestry situations or in simulation experiments such as described by Spitters and Aerts (1983) Kropff (1988) and Kropff et al. (1992). Models which predict target plant final size and which use neighbor plant final size as a predictor variable (e.g. Soetono and Puckridge 1982, Mack and Harper 1977) may yield insights into the nature of competition, but can not actually be predictive, since the values of the causal variable are not known a priori.

"Non-overlapping Domain" Models

If one assumes that occupation of biological space by plants in a neighborhood can be represented by non-overlapping two-dimensional zones, then a map of the plant population may be inscribed with the boundaries of these zones to form a series of polygons, each representing the space capture zone of each plant. This process of dividing a planar area into non-overlapping polygons and the resulting map are both referred to as tesselations (Watkinson 1986, Upton and Fingleton 1985). If one further assumes that the zones of space capture begin as circles with the plant at the center, that the zones of all plants begin at the same size at the same time, and the zones expand radially at a rate which is the same for all plants until they abut a neighboring zone, then the appropriate tesselation is called the Dirichlet tesselation. The resulting polygons may also be referred to as Thiessen or Voronoi polygons. The Dirichlet tesselation may also be simply defined as the subdivision of the plane where every point in the plane is associated with the plant to which it is closest. The Thiessen polygon may also be constructed as the smallest polygon which can be constructed around a plant bounded by the perpendicular bisectors of the line segments connecting that plant with neighboring plants. The performance of a plant is often correlated to the area of its Thiessen polygon, but has also been hypothesized to be related to the shape of the polygon. Statistics can be calculated which describe the shape of a polygon such as "eccicurcularity", which describes the deviation of the polygon from circularity, and "abcentricity", which describes the displacement of the plant from the centroid of the polygon (Mead, 1966). Holmes and Reed (1991) attribute the pioneering of polygon methods to Brown (1965).

Mead (1966) related the size of individual carrot plants to the area, eccicurcularity, and abcentricity of their Thiessen polygons. He found that all three measurements had significant effects on carrot diameter in a regression model, with area being the most important and eccicurcularity least important. Matlack and Harper (1986) performed a similar analysis on maps of a natural population

of *Silene dioica*, recorded over a period of several seasons. They found that in general Thiessen area and abcentricity were both positively correlated with plant size, despite confounding factors such as variation in plant age or genotype, non-random spatial patterns of recruitment, and a heterogenous background environment. Their discussion of the results, as well as examination of the maps, suggests that polygon area and abcentricity were probably closely correlated with each other due to the aggregated spatial pattern, confounding the interpretation of the effect of abcentricity. Mithen et al. (1984) performed a similar experiment with a greenhouse-sown population of *Lapsana communis*, finding significant correlation of plant size to Thiessen area. By regressing log plant size against log Thiessen area, they found that prior to self-thinning of the population, plant size was related to area to the power of about 1/2, while after thinning, plant size was related to area to the power of 3/2, in accordance with the -3/2 power self thinning law (Yoda et al. 1963). Liddle et al. (1982) found that plant size of *Festuca rubra* in establishing swards in the field was significantly correlated with Thiessen polygon area. Watkinson et al. (1983) investigated the effects of Thiessen area and emergence time on the probability of survival of greenhouse-sown seedlings of *Helianthus annuus*. They found that the probability of survival was positively correlated with polygon area, and negatively correlated with emergence date and with the number of neighbors within a 2.5 cm radius.

Other non-overlapping domain models have modified polygon dimensions according to the size of the neighbors (Adlard 1973, cited in Benjamin and Hardwick (1986), several methods described in Upton and Fingleton 1985, several workers cited in Holmes and Reed 1991).

"Overlapping Domain" Models

Overlapping domain models have in the past primarily been used by researchers in forestry. These models assume that each plant has a domain (also called zone of influence, ZOI, or area of influence), which is a circular area with the plant at its center over which the plant obtains or competes for resources. The domain is usually assumed to be proportional in area to the size of the

plant. The most common approach to this type of model seems to have been pioneered by Opie (1968), although Bella (1971) cites two earlier papers which used similar basic assumptions. In Opie's (1968) model, competition effect is evaluated as the proportion of the target plant's area which is overlapped by the circles of its neighbors. Bella (1971) reasoned that Opie's model did not take into account assymetric competition, and thus proposed a model which modifies the influence zone overlap ratio according to the ratio of the sizes of the plants involved. The definition of the influence radius, and further refinements of the weighting became a subject of concern for subsequent researchers using this approach (Ek and Monserud 1974, Arney 1973). Several spatially explicit growth models (e.g. Bonan 1991, Benjamin 1988, Miller and Weiner 1989) fall into this category based on their assumptions about the domain from which a plant takes resources.

"Unbounded Areas of Influence" Models

The "unbounded areas of influence" approach to analyzing plant neighborhoods is often attributed to Mack and Harper (1977), but Benjamin and Hardwick cite three earlier papers utilizing this type of model (Spurr 1962, Currah 1975, Steneker and Jarvis 1963). Daniels (1976) and Holmes and Reed (1991) also cite Hegyi (1974), whose index of local competitive intensity falls into this category.

In the "unbounded areas of influence" models, a "search radius" is usually defined, and the effects of any neighbors within this area are cumulated to yield an index of the competitive effect of neighbors. This "search radius" is often referred to by the authors as a "neighborhood". In these models, the effect of a neighbor is often, but not always, weighted as a decreasing function of distance from target to neighbor, and/or as an increasing function of the size of the neighbor relative to the target. In addition, information about the dispersion of the neighbors angularly around the target may also be taken into account. These characteristics of these models will be discussed.

Search Radius There is some potential for confusion arising from the terms "domain", "area of influence", "neighborhood" and "search radius". Benjamin and Hardwick (1986) use the terms "domain" and "area of influence" synonymously, and intend them to refer to the two-dimensional zone from which a plant might extract resources. These terms should not be confused with the term "neighborhood", which was not used by Benjamin and Hardwick (1986), and has been used loosely and variously by the authors who have used it. In several papers, authors have used the term "neighborhood" to be synonymous with Benjamin and Hardwick's "search radius", which is the radius within which neighbors are identified for analysis.

Benjamin and Hardwick (1986) and Benjamin (1993) asserted that "unbounded areas of influence" models do not put a limit on the domain, the area over which a plant draws upon resources. The specification of a search radius is thus assumed to be arbitrary, and simply a matter of computational convenience. However, of the papers reviewed by Benjamin and Hardwick (1986) that were reviewed for this thesis (five out of nine papers), none explicitly asserted that the domain of a plant was believed to be infinite. Benjamin and Hardwick's (1986) assertion that these models assume an infinite domain appears to be drawn from the fact that in several of these models, the impact of neighbor plants is defined as a declining function of the inverse of their distance from the target, and thus in theory will never equal zero, no matter how far the neighbor might be from the target. However, Waller (1981) and Silander and Pacala (1985) asserted that there was a correct non-arbitrary choice of search radius. This they called the neighborhood radius, and they implicitly defined the neighborhood as the zone outside of which neighbors could not impact the target. Waller (1981) proposed that the neighborhood radius should be estimated statistically by creating several independent variables based on the number and arrangement of plants within each of several concentric annuli, and using stepwise multiple linear regression to determine which annuli have a significant influence on target plant size. Silander and Pacala (1985) argued that this method was

inappropriate, since the relationships are non-linear. They proposed that the best method was to perform a non-linear regression of individual plant size against the neighbor density at each of several radii, using the hyperbolic model of Kira et al. (1953),

$$S = \frac{M}{1 + C \cdot NN} \tag{1.1}$$

where S = the size (biomass or seed production) of the plant, M = the maximum biomass production, C is a slope parameter which has been interpreted to represent the area required to achieve that maximum production, and NN is the number of neighbors (local density, excluding the target individual). The radius at which the coefficient of determination (R^2) was a maximum was determined to be the neighborhood radius. While this may result in good model fits in a given experiment, it does not necessarily correspond to the true neighborhood radius as defined above, unless the experiment includes very low densities. In particular, the largest neighborhood examined must still have some data points where the number of neighbors is zero, and considerable attention should be paid to the fit of the regression at the lowest densities. If the neighborhood size were to be determined by the method of Silander and Pacala (1985) in an experiment without adequate data at low densities, then the probability is high that few or none of the target plants in the experiment are actually free from competition, making it difficult to estimate the numerator term of the hyperbolic model (Eq. 1.1) with any accuaracy. Similarly, when larger radii are evaluated, there will be few target plants with small numbers of neighbors. Then the effects of closer neighbors will greatly outweigh the effects of more distant neighbors, even if more distant neighbors could potentially impact the target in the absence of the nearer neighbors. The more distant neighbors then only serve to add noise to the regression when large neighborhood radii are tested, leading to an underestimate of the neighborhood radius. If the neighborhood radius is to be applicable to a range of situations, it must be estimated using data at low densities. Then improvement of the fit of a predictor at higher

densities becomes the role of neighborhood spatial arrangement models which give more importance to nearer neighbors than to more distant neighbors.

An alternative method of estimating the neighborhood radius utilizes the parameters in the hyperbolic yield equation (Eq. 1.1), and also requires adequate data at low densities. For purposes of this method, it is assumed that there is some maximum size potential for a plant in a given environment, and that this size can be achieved given some adequately large but finite amount of space. Any plant with more than this amount of space available to it will not utilize the additional space. If the space over which resources are drawn upon by a plant is its "domain", this space resulting in the maximum growth can be called the "maximum domain". If the maximum domain is represented by a circle surrounding each plant in a population, then any place where the maximum domain circles of two plants overlap represents a zone of potential interference between plants as they approach the maximum size. If the plant neighborhood is defined as the zone surrounding a target plant outside of which a neighbor cannot reduce the performance of the target, then the radius of the neighborhood is, in theory, twice the radius of the circle which represents the maximum domain (Figure 1.2).

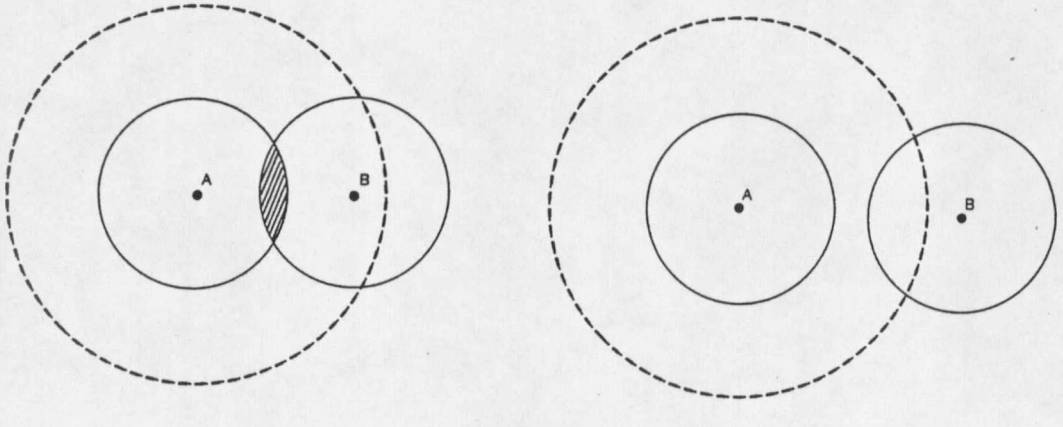

Figure 1.2 On the left, plant B has the potential to interfere with A through competitive use of resources in the zone (hatched) where their maximum domains (solid circles) overlap. On the right, B does not interfere with A when its distance away is greater than twice the radius of the maximum domain. That critical distance is the neighborhood radius (dashed circle).

The slope parameter (C) in Eq. 1.1 can be interpreted to be an estimate of the area per plant required to achieve the maximum yield per plant (Watkinson 1986), that is, the maximum domain. The parameter C is in units that are the reciprocal of the units of the density measurement, thus if the density measurement is simply plants per neighborhood, then C is in units of neighborhoods. If the parameters of the hyperbolic yield model (Eq. 1.1) are estimated for a series of progressively larger search radii, the number of plants per search area will on average increase, and the value of C will decrease. Conversely, as the search radius decreases, C increases. When C reaches a value of 0.25, it represents an area whose radius is one-half the search radius. Then the search radius can be assumed to approximate the true neighborhood radius since, as discussed above, the true neighborhood radius is twice the radius of the maximum domain. None of the experiments whose data are examined in this thesis have adequate data at low densities to effectively determine the neighborhood radius using either this method or the method of Silander and Pacala (1985). Data found in Ellison et al. (1994), from experiments on *Arabidopsis thaliana*, were used to compare this method with the method of Silander and Pacala (1985). The two methods yielded very similar estimates of the true neighborhood radius, although it is not clear that this data set adequately represented low densities.

In situations where it is not possible to investigate a range of search radii, the true neighborhood radius can be approximated from the value of C estimated from data collected at any arbitrary search radius by the expression

$$R \approx 2 \cdot r \cdot \sqrt{C} \qquad (1.2)$$

where r is the arbitrary search radius and R is the true neighborhood radius.

In any case, this definition of "neighborhood" as the area outside of which no neighbor can impact the target implicitly acknowledges the assumptions of the "overlapping domains" models. Thus it is conceivable that models which assume that there is a discrete neighborhood outside of

which a neighbor can have no effect (e.g. Silander and Pacala 1985, Lindquist et al. 1994) could more appropriately be categorized with the "overlapping domains" models, even though their authors claim their heritage is with the Mack and Harper (1977) "unbounded areas of influence" model. As noted above, these models will be discussed here, along with the "unbounded areas of influence" models they resemble.

Neighbor Distance If neighbor plants usurp space, and thus resources, their proximity will reduce the biological space available to the target individual, and can be presumed to reduce the performance of the target. The intensity of interference between neighboring plants has been shown to decline with increasing distance apart (Pielou 1960). The exact functional form of this declining influence has not been clearly demonstrated, and probably depends to a considerable extent on how many different neighbors are interfering with a given target.

Angular Dispersion of Neighbors Most plants respond plastically to variation in their local environment, and have been observed to concentrate growth in the direction of least interference (Ross and Harper 1972, Ballare et al. 1990, Ballare et al. 1992, Regnier and Bakelana 1995). When neighbor plants are clustered in one sector of the neighborhood area, the target plant may be able to grow in the other direction, avoiding interference. Thus in theory, when plants are completely dispersed around the target, there will be no direction in which the target can grow to avoid interference. Angular dispersion measures attempt to modify the index of competition intensity to account for this possibility. Mack and Harper (1977) introduced the use of the formula from Zar (1974) for the calculation of angular dispersion, AD:

$$AD = 1 - \sqrt{\left(\frac{\sum_{i=1}^{n}\cos(\theta_i)}{n}\right)^2 + \left(\frac{\sum_{i=1}^{n}\sin(\theta_i)}{n}\right)^2} \qquad (1.3)$$

where θ_i is the azimuth of neighbor plant i, and n is the number of neighbors. Angular dispersion varies from 0 to 1.0 as the neighbors in any annulus vary from tightly clumped to regularly dispersed.

There is some disagreement about the correct form of Zar's (1974) angular dispersion index, since apparently several authors, including this one, have actually never seen the original description of it. Puettman et al. (1993) suggested that Silander and Pacala (1985), and Wagner and Radosevich (1991) used erroneous forms. They reprinted a form of the equation different from that used by any other paper reviewed here. Waller (1981) claimed that the form used by Mack and Harper (1977) was in error and proposed a correction, while Weiner (1984) claimed that Waller's (1981) correction was in error as well, proposing yet another version which due to misplaced parentheses is probably itself incorrect.

Puettmann et al. (1993) offered a critique of the angular dispersion index used by Mack and Harper (1977). They noted that this equation for angular dispersion is only appropriate for unimodal distributions of neighbors around a target, and proposed a revised formulation of angular dispersion which is related to the variance of the angular differences between adjacent neighbors. For calculation purposes, the plants are numbered sequentially clockwise, starting with the plant whose angle has the smallest numerical value. The angular difference between adjacent plants is calculated as

$$\alpha_i = \begin{cases} \theta_{i+1} - \theta_i & \text{for } i = 1,2,\ldots n-1 \\ 2\pi - \theta_i + \theta_1 & \text{for } i = n \end{cases} \qquad (1.4)$$

where the variables are as in Eq. 1.3 and α is the angular difference between adjacent plants. The mean angular difference, μ is thus $2\pi/n$, and the variance of the angular distribution, δ is

$$\delta = \frac{\sum_{i=1}^{n} \left(\alpha_i - \frac{2\pi}{n}\right)^2}{n-1} \qquad (1.5)$$

where the variables are as in Eqns. 1.3 and 1.4. The angular dispersion index is then

$$AD=1-\delta_t/\delta_c \qquad (1.6)$$

where δ_c is the variance for the most concentrated distribution in which all plants have the same azimuth, and δ_t is the variance for the observed arrangement.

Studies of "Unbounded Areas of Influence" Models. Mack and Harper (1977) performed a study of dune annuals where the size of individual plants was related to an index of the intensity of interference from neighboring plants. They calculated a measure of the intensity of interference which was the sum of the biomass of neighbors within a neighborhood radius, with the biomass of a given neighbor weighted according to its location within the neighborhood. In order to simplify the calculations, they divided the neighborhood into concentric annuli and calculated their indices based on the characteristics of the neighbors within an annulus. Neighbors were weighted less heavily if they were in an annulus more distant from the target individual, and they were weighted according to the angular dispersion (Zar 1974) of neighbors in the annulus. A correction factor was added to account for interactions between neighbors in different annuli. High correlations between individual plant biomass and the index of interference were obtained when these weighting factors were fit by hand to obtain best fitting combinations of parameters.

Waller (1981) utilized similar calculations, but suggested that the method of Mack and Harper (1977) was limited because they made arbitrary assumptions about the size of the neighborhood and about exactly which characteristics of the neighborhood are important. Waller suggested that it would be statistically more appropriate to calculate several simple indices on a series of concentric annuli, and to utilize stepwise multiple regression to determine which indices and which annuli were significant determinants of target plant size. Waller did not find any set of variables which could consistently explain the variation in plant size in those violet populations

studied, but suggested that lack of knowledge about the functional forms of the relationships may limit this methodology.

Weiner (1982) suggested the utilization of a form of the hyperbolic yield equation of Kira et al. (1953), which can be expressed as

$$S = \frac{M}{1+W} \tag{1.7}$$

where S is the productivity of a plant, M is the maximum possible productivity, and W is the weighted cumulative effect of the neighbors. In the simplest case W is a constant times the number of neighbors, making this equation equivalent to Eq. 1.1 . Weiner also divided the neighborhood into concentric annuli, suggesting that W could be expressed as the sum over all annuli of some constant multiplied by the weight for each annulus, where the weight for each annulus was determined by the number of individuals in that annulus divided by the square of the distance to that annulus. A slight variation of this calculation allowed for individuals of different species to be weighted differently. Weiner found that this formula yielded significant regressions, accounting for 83% and 86% of the variation in individual reproductive output in *Polygonum minimum* Wats. and *P. cascadense* Baker, respectively.

Soetono and Puckridge (1982) developed an index of competition based on the sizes and locations of plants within an arbitrary neighborhood radius:

$$z = \sum_{i=1}^{n} \frac{M_i}{D_i^{\phi}} \tag{1.8}$$

where M_i is the mass of neighbor i, D_i is its distance of neighbor i from the target, ϕ is a fitted shape parameter, and summation is over all neighbors in the neighborhood. They utilized z (Eq. 1.8) as the explanatory variable in a form of the hyperbolic yield equation:

$$\frac{1}{S} = a + bz \tag{1.9}$$

where a and b are fitted parameters and S is individual plant final grain yield. They tested their model using data from harvest of individual barley plants whose locations were known. They found that correlations were low, and that spatial arrangement was less important at high densities than at low densities. They concluded that under field conditions, many factors such as differential emergence time or varying planting depths may cause enough variation to mask effects of spatial arrangement. However, it should be noted that they restricted their analyses to plants within single quadrats with relatively uniform densities. These quadrats by themselves may not have had a wide enough range of densities or spatial arrangements for this model to detect strong effects.

Weiner (1984) expanded upon his earlier model (Weiner 1982) by including neighbor size in the index of neighborhood competition, which was used as an explanatory variable for the growth rates of *Pinus rigida* individuals. The resulting index is very similar to that of Soetono and Puckridge (1982):

$$W = C\sum_{i=1}^{n} \frac{M_i}{D_i^{\,2}} \qquad (1.10)$$

where W is substituted into Eq. 1.7, C is a constant, and the definitions of other variables are as in Eqns. 1.7 and 1.8. Weiner found that the size of neighbors was the most important explanatory variable, while the number and distance of those neighbors was less important. He also found that angular dispersion was not negatively correlated with growth rate.

Silander and Pacala (1985) suggested that Mack and Harper (1977) and Weiner (1982, 1984) had not adequately justified the neighborhood radii they had used in their research, and proposed that an appropriate determination of the neighborhood radius could be made by finding the neighborhood radius which resulted in the best fit of the hyperbolic yield model (Eq. 1.1) to density data. They further suggested that once this radius had been found, an appropriate index for the declining influence of neighbors with increasing distance was:

$$W = C\sum_{i=1}^{n}(1-\frac{D}{R})^{\gamma} \qquad (1.11)$$

where W is substituted into equation 1.7, C is a constant, D_i is the distance to the ith neighbor, R is the neighborhood radius, and γ is a parameter which adjusts the shape of the function. Silander and Pacala (1985) also calculated the angular dispersion of plants in the neighborhoods, using a variant of the angular dispersion equation from Zar (1974). Silander and Pacala utilized the hyperbolic yield equation in the same way as did Weiner (1982), replacing W in Eq. 1.7 with the angular dispersion (Eq. 1.3) or the distance weighted number of neighbors (Eq. 1.11). In a greenhouse experiment utilizing *Arabidopsis thaliana*, they found that within the small radius that they determined to be the effective neighborhood radius, there was little effect of distance, but that inclusion of angular dispersion in the model resulted in a significant reduction in the residual sum of squares for their regression. Silander and Pacala (1985) did not propose a method for combining angular dispersion and the distance weight into a single measure.

Firbank and Watkinson (1987) utilized a model which combined elements of those of Soetono and Puckridge (1982) and Weiner (1982) to examine neighborhood effects in mixtures of wheat and *Agrostemma githago*. They found that their model could explain only a small amount of the variation (17%) in plant size. They attributed the rest to variation in emergence time and to the possibility of assymetric competition arising from that variation in emergence time. Examination of their figures suggests that they may have had inadequate numbers of plants at low density to fully elucidate the effects of neighborhood spatial arrangement, which tend to be relatively stronger at low densities than at higher densities.

Wagner and Radosevich (1991) tested a model similar to that of Silander and Pacala (1985) with plantations of young Douglas-fir (*Pseudotsuga menziesii*). The model included several additional measures involving target and neighbor height, canopy area, percent cover, and stem

diameter. They utilized a multiple linear regression approach to relate target height and stem diameter to indices of neighborhood competition which included various combinations of these variables. They determined that if the search radius was selected that optimized model fit, there was no effect of increasing distance of neighbors within that radius. There was also no effect of angular dispersion. The optimal index for predicting target height was the sum of percent cover of woody neighbors, with neighbors shorter than the target height excluded, and explained 11% of the variation in target height. The optimal index for predicting target stem diameter was the sum of percent cover of woody neighbors with neighbors shorter than ½ the target height excluded, and explained 19% of the variation in stem diameter. They found that the intensity of competition was age-dependent, with the slope of the decline in target size being greater with target age.

Ellison et al. (1994) offered a critique of the model of Silander and Pacala (1985) based on their observation that large plants take up space, and thus will, on average, have fewer neighbors within a small radius than will smaller plants. The result of this is that the correlation between number of neighbors and target plant size may be interpreted incorrectly. They suggested a null model which does not assume that plants compete, but instead assumes that large plants can result from variable growth rates, and that these large plants will have fewer neighbors because there is less space for neighbors to exist. However, they did not explain how a large plant can exclude potential neighbors from its neighborhood without competition. Their repetition of the experiment of Silander and Pacala (1985) lead them to reject their null model and admit that neighborhood competition may play a role in reducing plant size and fecundity.

Lindquist et al. (1994) utilized a variant of the method of Weiner (1982) for combining angular dispersion and distance weighting into a single measure of the competitive influence of the neighbors in a neighborhood. They divided the neighborhood into concentric annuli, calculated the angular dispersion (Eq. 1.6, from Puettman et al. 1993) for each, and multiplied this by the distance

weighting index for each annulus. These values were weighted by the proportion of neighbors which were found in each annulus, and summed over all annuli. This index was used for W in Eq. 1.7. They found a significant relationship between this index and target plant size in greenhouse experiments with oat (*Avena sativa*) when all parameters were fit with iterative non-linear regression methods.

Bussler et al. (1995) presented a three-dimensional space capture model where the space occupied by a plant is represented by a cylinder whose height is the height of the plant and whose diameter is the average of the width of the plant canopy at its widest and the width of the plant canopy at right angles to the first measurement. They found that plant size of corn (*Zea mays*), velvetleaf (*Abutilon theophrasti*), and cocklebur (*Xanthium stramonium*) was closely correlated to cylindrical volume, and that interference between plants could be summarized by the ratio of the volume of the target plant to the total volume of plants in the search radius. The volume ratio calculated in June could account for a significant proportion of the variation in plant size at harvest in September.

Grace and Platt (1995) examined the effect of neighboring trees on survival and size of juveniles of *Pinus palustris* using a multiple regression approach similar to that of Waller (1981). They found that the effects of neighbors decreased quickly with distance and increased with the size of the neighbor.

"Tiers of vegetation" models

Numerous researchers have proposed spatially explicit growth models which in some fashion account for spatially variable resource capture. Many of these would simply be put in one of the other categories, based on their assumptions about resource capture over a two-dimensional area. In contrast, models in the "tiers of vegetation" category deal with light capture as well, requiring that plant height and/or canopy structure be taken into account.

The models of Ford and Diggle (1981), Sorrensen-Cothern et al. (1993), and Aikman and Benjamin (1994) predict the growth rates of individual plants based on competition for light, which is a functions of plant height (Ford and Diggle 1981) or canopy structure (Aikman and Benjamin, 1994), or both (Sorrensen-Cothern et al. 1993).

"Nearest neighbor" models

Strictly speaking, nearest neighbor models belong in the "unbounded areas of influence" category of Benjamin and Hardwick (1986). However, they are dealt with separately in order to avoid confusion with the "search radius" types of models which characterize that category.

Pielou (1960) demonstrated that the sum of the sizes of two trees was significantly correlated with their distance apart. She observed a correlation of .416 (n=148) between the logs of the two variables in a population of *Pinus ponderosa*. Similar analysis was applied to populations of desert shrubs by Yeaton and Cody (1976), Yeaton et al. (1977), and Nobel (1981). They found highly significant correlations demonstrating competition both within and between species. Powell (1990) found that the distance to the nearest neighbor was an important predictor of mortality, growth rate, and age at flowering for the semelparous perennial ("biennial") weed *Centaurea diffusa*. Tyler and D'Antonio (1995) found that the mean distance to the first two nearest neighbors in a post-burn population of *Ceanothus impressus* explained 37% of the variation in dry weight of four-year old individuals, up to 41% of the variation in relative growth rates, and up to 84% of the variation in survivorship. These relationships were strongest in drier years, suggesting competition for moisure, a conclusion corroborated by significant correlations between the nearest neighbor distance measure and pre-dawn xylem pressure potentials.

Comparisons of Different Model Types.

Daniels (1976) examined a set of data describing positions, sizes, and growth rates of *Pinus taeda*. He calculated several competition indices and compared their correlations with annual tree growth, including the simple Hegyi (1974) size ratio index, which is:

$$H = \sum_{j=1}^{n} \frac{\frac{DBH_j}{DBH_i}}{D_{ij}} \qquad (1.12)$$

where DBH is tree stem diameter at breast height, D_{ij} is the distance between target i and competitor j, and N is the number of competitors. Daniels (1976) noted that a modification of the Hegyi (1974) index was better correlated with the data than were most other indices, including the more computationally complicated overlapping domain indices.

Holmes and Reed (1991) performed a similar analysis with a wider array of indices and a multi-species data set. Their indices included several non-overlapping domain (polygon) models, some variations on the Hegyi (1974) size ratio index, overlapping domain models, and a new set of indices which they developed. They concluded that the simple size-ratio indices performed as well as or better than more complex indices for their study of the effects of neighbors on the growth rates of individuals of *Quercus rubra*, *Betula papyrifera*, *Acer rubrum*, and *Populus tremuloides*.

Benjamin (1993) set out to experimentally discriminate between contrasting models of competition for space. His simple set of experiments with carrots led him to propose that the "overlapping domains" type of model was correct and that the other models were false. However, the experiments only falsified the "non-overlapping domains" and the "diffuse population effect" types of models. Discrimination between the remaining types of model was apparently accomplished by other means not described in the article.

Effects of Planting Pattern on Crop Yield and Weed Interference

Effects of Planting Pattern on Crop Yield

Spatial distribution of crop seed can be influenced by altering planter row spacing, by use of band, broadcast, or precision seeding, or by means of multiple passes of a crop planter. Since changes in seeding rate interact with the method of planting to influence the spatial distribution of crop seed, effects of seeding density are often investigated in combination with effects of row spacing. Nelder (1962) proposed that the effects of plant density and planting pattern could be studied with systematic designs, where plants are placed in specific locations at non-uniform intervals such that local plant spacing could be varied systematically over the experimental area. These designs have been adapted to design optimal planting patterns for row crops (Bleasdale 1967), but so far have been little used to investigate interspecific competition (Radosevich et al. 1984). Probably due in part to statistical complications with these designs, the majority of published research on the effects of planting pattern on crop performance and weed interference have instead used randomized plot designs where experimental plots of differing planting patterns are compared using standard analysis of variance.

Based on a review of early research relevant to the effects of crop seeding rate and row spacing on cereal grain yield, Holliday (1963) concluded that narrowing row width in general resulted in increased yields, and that wider than normal row widths usually resulted in decreased yields. These effects were typically larger with either very low or very high seeding rates. Results varied substantially between experiments, suggesting that year, site, cultivar, and/or cultural effects might influence results.

A large number of more recent studies have found that narrow row spacings or decreased rectangularity can increase yield relative to wider spacings in winter wheat (Johnson et al. 1988, Brinkman et al. 1979, Lawrence et al. 1974, Joseph et al. 1985, Bishnoi 1980, Stoskopf 1967), rye

and triticale (Bishnoi 1980), safflower (Mundel et al. 1994), soybean (Beatty et al. 1982, Cooper 1977, Taylor 1980, Costa et al. 1980, Ethredge et al. 1989, Boquet 1990, Boerma et al. 1982), rape (Morrison et al. 1990, Kondra 1975, Christensen et al. 1984), poppy (Yadav et al. 1983, Chung 1990), quinoa (Risi et al. 1991), and apples (Cripps et al. 1975).

Brinkman et al. (1979) reported that barley yielded significantly higher in narrower rows when row spacings of 7.5, 15, and 30 cm were compared and results pooled over a range of environments. The largest improvement in yield resulted from going from 30 to 15 cm, with a smaller improvement between 15 and 7.5 cm. They also found that lodging was reduced with the narrower row spacings.

Effects of Planting Pattern on Yield Components and Mechanisms

Marshall and Ohm (1987) examined the effects of row spacing and seeding rate on 16 winter wheat cultivars, and concluded that in most cases, reducing the row spacing from 19.2 cm to 6.4 cm resulted in an increased yield, with the magnitude of the effect depending on the cultivar, the seeding rate, and the year. A significant interaction between seeding rate and row width suggested that the impact of row width was greater at a higher than normal seeding rate. They were unable to draw general conclusions about how variation in plant morphology influenced the response to row spacing, but concluded that narrower row spacings increased yield primarily through increased tillering and spike number.

Stoskopf (1967) found that several varieties of wheat produced higher yields in narrow (8.9-11.4 cm) rows than in wide (17.8-22.8 cm) rows. The yield increase was slightly, but not significantly, greater for short-strawed, upright leaved varieties than for the tall, droopy-leaved check, suggesting the possibility that the taller and droopier plants might be better able to utilize space in wider row spacings.

Dhillon and Kler (1981) investigated the effects of a variety of planting patterns on yield and radiation interception by wheat. They found that patterns which more completely intercepted solar radiation, such as planting of two sets of rows perpendicular to each other, also attained higher yields. They concluded that higher yields in more dispersed planting patterns were probably due to more complete utilization of available light and soil resources.

Planting pattern may have effects on disease development in some crops, perhaps due to differences in ventilation and humidity or associated arthropod disease vectors in the crop canopy. Bowman et al. (1986) reported that seedborne *Alternaria* hyphae recovery was higher in soybean seeds from narrow row spacings than in those from wider rows. Some results from other studies are contradictory. For example, Mmbaga (1995) reported increasing severity of brown spot in soybean with decreasing row spacing, while Pataky and Lim (1981) reported the opposite trend.

In Montana, where grain production is usually moisture limited, barley is typically planted in rows 30-36 cm apart. Farmers avoid narrower row spacings, based on the perception that crop plants which are more evenly spaced draw extensively on stored soil water early in the season, and subsequently will not have adequate moisture for grain filling later in the growing season. The closer within-row spacing of plants in wider rows is believed to limit early root growth, due to inter-plant competition, so that moisture between the rows remains available later in the season. This perception is supported by results such as those of Winter and Welch (1987), who found that increasing row width in dryland winter wheat from 20 or 25 cm to 51 or 76 cm increased soil water availability and decreased crop water deficits late in the season. Nonetheless, they found reduced yields at the wider row spacings.

Similarly, Tompkins et al. (1991) studied water use by winter wheat over two row spacings (9 cm or 36 cm) and two seeding rates (35 kg ha^{-1} or 140 kg ha^{-1}). They found that earlier canopy closure in the higher seeding rate and narrow row treatments resulted in lower evaporation and higher

transpiration early in the season. Although early season water use was higher in the high seeding rate and narrow row treatments than in lower seeding rate or wider row spacing treatments, total water use and water use efficiency were higher in the high seeding rate and narrow row treatments, resulting in higher grain yield, even in the uncharacteristically hot and dry conditions of these experiments.

Jones and Johnson (1991) studied these effects in sorghum on the Texas high plains, where sorghum is grown in very wide rows (152 cm) in order to minimize early season water use. They concluded that in years of normal precipitation, this practice reduced yield over standard (76 cm) row spacing to an extent that the practice was not justified even though in occasional dry years it could result in a small yield advantage.

Auld et al. (1983) reported finding a significant improvement in yield with a square planting pattern in one experiment where weed-free wheat yield was compared for several precision planted patterns of varying rectangularity. These researchers also found general trends toward lower yield with higher rectangularity, with trends becoming stronger at lower planting densities. However, they reported that standard non-precision planting patterns did not yield significantly less well than the best precision patterns they examined, suggesting that the variability in microscale sowing rates within the row might provide a hedge against environmental variability. These findings are in accordance with early studies by Sprague and Farris (1931), who also found that uneven spacing of plants in rows did not negatively impact yield of small grains compared to evenly spaced plantings.

Grain varieties planted in Montana are bred and evaluated in wide-row (30-36 cm) nurseries, and are thus well adapted to wide-row conditions in weed-free environments.

Rectangularity

Holliday (1963), Willey and Heath (1969) and Auld et al. (1983) described the uniformity of a crop plant distribution in terms of rectangularity, the ratio of the distance between crop rows and

the distance between plants within a row. Lower values of rectangularity describe more uniform spacings, with a rectangularity of 1 denoting the case where plants are located at the vertices of a square grid, while higher values of rectangularity at a given overall crop density denote less uniform distributions of crop plants, specifically in the case of wider row spacings, with plants more closely spaced within the row.

At a crop planting density of 130 plants m^{-2}, which is a typical commercial planting rate for barley in Montana, and a 30 cm row spacing, the mean rectangularity of crop plants is 11.7. With rows half that wide, the mean rectangularity would fall to 2.9. At a density of 130 plants m^{-2}, a rectangularity of 1 would be achieved at a row width of 8.8 cm, again assuming plants are evenly spaced within rows. Since few seeders in use or available to producers are equipped to plant in rows less than 15 cm apart, other methods of lowering rectangularity, such as broadcast or air seeding, are in use. However, with planting patterns other than parallel rows, rectangularity can no longer be used as a simple basis of comparison of different planting patterns.

The definition of rectangularity becomes confusing when plants are not evenly spaced within rows, and a mean distance between plants is used to calculate it, since the amount and shape of the space available to a given plant may vary widely. However, based on the findings of Auld et al. (1983) and Sprague and Farris (1931), irregularity in intra-row spacing may not substantially affect grain yield.

Rectangularity also fails to differentiate between different patterns where plants in adjacent rows have different relationships to each other, for example a square grid pattern and a equilateral triangle (also called hexagonal or rhomboid) grid pattern, which actually has a more uniform distribution of plants (Pant 1979).

A more general measure of plant arrangement might involve constructing Thiessen polygons for each plant based on the criterion that each point in a planar space is assigned to the plant to

which it is closest. A measure such as the ratio of the longest axis to the shortest axis of such a polygon would provide a measure comparable to rectangularity. A slightly simpler measure with equal generality, but greater sensitivity to uneven plant spacing might involve computing a mean nearest neighbor distance E for a sample of plants. This measure can be calculated as the mean of the distance from a plant (the target) to its nearest neighbor and the distance to the nearest neighbor which is not on the same side of the target as the first neighbor (i.e. it is on the other side of a line drawn through the target and normal to the direction of the first neighbor, Figure 1.3) It can then be shown algebraically that rectangularity (R) can be approximated by the calculation

$$R \approx \left(\bar{E}^2 \cdot D\right)^{-1} \tag{1.13}$$

where $\bar{E}$ is the mean value of E for the sampled plants in meters and D is the mean density of the area in m^{-2}. Other units of length may be used, as long as they are consistent within the calculation.

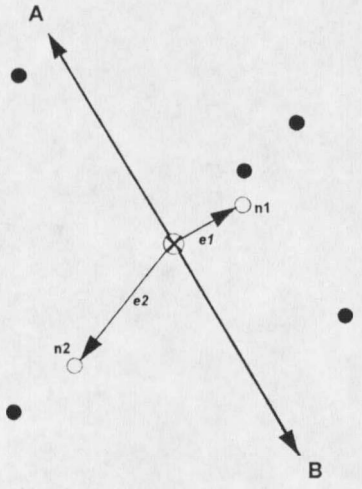

Figure 1.3. The mean nearest neighbor distance, E, is the mean of distances e_1 and e_2 from the target (x) to the two nearest neighbors (n_1 and n_2, open circles) on either side of line AB. Line AB is defined as the line perpendicular to the line through the target and its nearest neighbor, n_1. Note that distances to other near neighbors on the same side as n1 (closed circles) are not considered relevant.

Either of these calculations of rectangularity will be equivalent to the standard definition of rectangularity when the plants are arranged in a rectangular lattice pattern, but will increase the computed value of rectangularity (suggesting less regular pattern) when plants are not evenly distributed in rows. In order to obtain mean rectangularity for a plot, it is important to take means of the component distances prior to computing rectangularity, due to biases involved in averaging ratios.

Effects of Planting Pattern in Intercrops

Planting pattern has been examined in studies where two or more desirable species are grown together in an intercrop. In the design of an intercrop, optimal planting patterns must be developed which maximize the yields of each crop, particularly the most valuable one(s), while minimizing interference between the crops (Vandermeer 1989). Duncan and Schapaugh (1993) and Rao and Mittra (1994) reported that planting pattern of two-species intercrops influenced the relative yields and land equivalence ratios (LER) of the respective intercrop systems.

Effects of Planting Pattern on Interference between Crops and Weeds.

Fisher and Miles (1973) developed a simulation model where they assumed that the performance of an individual plant was proportional to the area of its Thiessen polygon. They concluded that in the presence of randomly distributed weeds, a uniform arrangement of crop plants at any given density would maximize total crop yield by allowing for more complete occupation of available space by the crop.

The effects of planting pattern on weed development and on weed-crop interactions have been extensively studied in several crops, most notably soybeans, edible dry beans, and cotton, all of which have traditionally been sown in wide rows approaching or exceeding 100 cm in width. Due to

dramatic effects of narrow rows on soybean yield, narrow row seeding of soybeans is becoming increasingly common in the United States. The effects have been less thoroughly examined in small grains, which are more generally seeded in relatively narrow rows, allowing for less potential improvement in performance.

In general, direct impacts of row spacing or planting arrangement on crop yield can be separated from impacts of row spacing on crop-weed interference by comparing weed-free to weedy crop yields with various planting patterns. Main effects of planting pattern will suggest direct impacts of planting pattern on crop yield, while a significant interaction between presence (or density) of weeds and planting pattern will usually be evidence of an impact of planting pattern on the interference between crop and weed. In the absence of a weed-free check, these types of effects cannot be differentiated (e.g. Kirkland 1993).

Soybeans and Other Large-Seeded Legumes Due to dramatically improved yields when soybeans are sown in narrow row spacings, narrow row seeding of soybeans has become common. Since mechanical cultivation for weed control becomes difficult or impossible with narrow rows, substantial research has gone into the effects of narrow rows on interactions between soybeans and weeds. Similar effects have been seen on other large seeded legumes which are less extensively grown, such as edible dry beans and lupine.

Smith and Jordan (1993) examined the effect of distance from soybean row on the canopy structure of sicklepod plants. They found that weed plants closer to the crop row were shorter in stature and less branched than plants further from the crop row. They concluded that this had implications for weed competitiveness, suggesting that narrow row spacings might decrease the competitiveness of the weed relative to the crop.

Yelverton and Coble (1991) found that density and biomass of weeds emerging after early control with non-persistent herbicides increased with increasing row width. Weaver (1986) reported

that a soybean row spacing of 18 cm resulted in greater seedling mortality of jimsonweed (*Datura stramonium*) than 60 cm rows. Soybean yield loss, however, was not affected significantly by row width. Numerous other studies have demonstrated similar effects of soybean row width on weed growth (Burnside et al. 1964, Wax et al. 1977, Wax et al. 1968, Kust et al. 1969, Burnside 1979, Walker et al. 1984, Howe et al. 1987, McWhorter et al. 1988)

Legere and Schreiber (1989) studied the effects of row width and density of soybean on competition and canopy architecture of pigweed (*Amaranthus retroflexus*). They found that narrow row spacings resulted in higher soybean grain yield and a lower proportion of pigweed in the total biomass. Narrow row width was associated with upward shifts of pigweed dry matter and leaf area distribution in the canopy, suggesting that competition for light is an important mechanism of interaction.

Putnam et al. (1992) found that row spacing of 15 cm resulted in higher yields of white lupine (*Lupinus albus*) than row spacing of 76 cm in both weed free and weedy conditions. In some cases, weed biomass was also reduced in narrow row spacings.

Buchanan and Hauser (1980) reported that weed biomass was significantly reduced and peanut yield was significantly increased in most cases by reducing row spacing from 81.2 cm to 40.6 cm or from 40.6 cm to 20.3 cm. In several experiments, there was a significant interaction effect of weed-free period and row spacing on these response variables due to row spacing being more important in weedier treatments than in weed free treatments, suggesting that narrower row spacing increased the competitiveness of peanut with weeds.

Malik et al. (1993) examined the effects of row spacing and seeding density of white bean (*Phaseolus vulgaris*) on annual weed density and biomass. They concluded that weed biomass in narrow rows (23 or 46 cm) was less at crop flowering than weed biomass in traditional wide rows (69 cm), although weed density was unaffected. Correlation of crop Leaf Area Index (LAI) with

weed biomass suggested that crop density by row spacing combinations which maximize LAI are most effective at reducing weed biomass.

Teasdale and Frank (1982) investigated the effects of weed control systems for snap beans planted in wide (91 cm) or narrow (25 cm) rows. They concluded that if herbicidal control was good, narrow rows could suppress subsequent weed growth sufficiently to yield better than wider row beans which were cultivated to control late emerging weeds. However, if herbicidal control of weeds was poor, the cultivation of wide rows allowed wide row plots to achieve yields as high as or higher than narrow row plots. These results are supported by those of Mullins et al. (1988), who reported that decreasing the row spacing of snap beans from 92 cm to 46 cm in a weedy situation not only increased the yield of snap beans but also improved grass weed control with metolachlor.

Cotton Bryson (1990) reported that increasing cotton (*Gossypium hirsutum*) row spacing from 1 meter to 2 m resulted in greater growth of bermudagrass (*Cynodon dactylon*), due to later canopy closure in the wider rows. Growth of some bermudagrass biotypes was influenced by row width more than others. These results are consistent with the findings of Rogers et al. (1976) that weed competition is less intense in 53 cm rows than in 79 or 106 cm rows, and those of Brown et al (1985), who reported that bermudagrass ground cover was reduced in cotton row spacings of 50 cm compared to cotton row spacing of 150 cm. Cotton yield was significantly higher for the narrower row spacing. Cotton yield and bermudagrass ground cover were intermediate in a cotton row width of 100 cm. Miller et al. (1983) found that cotton in narrow (51 cm) rows yielded more lint than cotton in wider rows, but found no differences in weed control. Weed densities were significantly higher in narrow rows early in the season, due to escapes from cultivation being found in the cotton rows, but by the end of the season, weed densities were similar between the two row widths. Andries et al. (1974) found that narrow rows did not significantly improve herbicidal weed control in cotton.

Other Crops Blackshaw (1993) found that decreasing row spacing from 22 to 11 cm slightly improved competition of safflower (*Carthamus tinctorum*) with green foxtail (*Setaria viridis*), but that increasing seeding rate had a much greater effect. Similarly, Choudhary (1981) reported that increasing plant population had a much greater effect on maize yield and weed growth than did row spacing. They found that decreasing the row spacing of maize from 90 cm to 60 cm or 45 cm did not significantly increase maize (*Zea mays*) yield in weedy plots, but did result in lower weed biomass production. Harvey and McNevin (1990) studied the effects of row spacing and herbicide treatments on sweet corn and field corn yield and wild proso millet (*Panicum miliaceum*) control. They found that wild proso millet control was better in narrow rows (76 cm) than in wide (102 cm) rows. Although there was no main effect of row spacing on yield, significant interaction effects point to the greater yield loss due to weeds in wide rows compared to narrow rows. Alessi and Power (1970) investigated the effects of row spacings of 7.5, 15, and 30 cm and weed (primarily *Setaria viridis*) removal on dryland flax (*Linum usitatissinum*) yield, quality, and water use. They reported that flax yield responded to narrower row spacings only in unweeded plots, and that yield loss to weeds increased with increasing row spacing. Total water use was not influenced by row spacing, but water use efficiency increased with reduced row spacing (averaged over weed treatments), since the crop yield was higher.

Small Grains Koscelny et al. (1991) conducted research in Oklahoma examining the effects of wheat (*Triticum aestivum*) row spacing, wheat seeding rate, cultivar, and injection of water in the crop row on wheat yield and cheat (*Bromus secalinus*) seed production. They found that in some cases, weed free wheat yield was increased by narrower row spacings, but that row spacing did not consistently affect the competitive ability of wheat with cheat. Justice et al. (1993) found that decreasing row spacing and or increasing seeding rate of winter wheat in Oklahoma decreased cheat seed in harvested grain in plots with no herbicides or low herbicide rates, but that the row spacing

and seeding rate did not interact. Decreasing row width increased wheat yields, regardless of the level of cheatgrass control, at one site but not at two others. Analysis of net returns of various management practices, where narrow row planting was assumed to be more costly than wider row planting, did not suggest a consistent economic benefit from narrow row planting.

Teich et al. (1993) studied the effects of seeding rate and row spacing on winter wheat production in Ontario. They found that decreasing row spacing from 20 cm to 10 cm did not have a significant effect on yield in the presence of low densities of weeds. The density of lambsquarter (*Chenopodium album*) plants, counted in May, was significantly lower in narrower row plots, but no other weed species was affected by row width.

Medd et al. (1985) investigated the effects of rectangularity and seeding density on yield of wheat at various densities of annual ryegrass (*Lolium rigidum*). They found no effect of row spacing on ryegrass growth or wheat yields for a given planting density. The highest rectangularity examined in these experiments was 6.4, corresponding to a row width of 18 cm.

Vander Vorst et al. (1983) reported that decreasing row spacing did not influence the yield of winter wheat or the subsequent corn crop in a winter wheat-corn rotation in Nebraska, but that in one year it significantly reduced weed plant numbers and weed biomass at wheat harvest time. This difference carried over in the seed bank two years, resulting in lower weed densities in the fallow year following corn.

<u>Barley and Wild Oat</u> Kirkland (1993) in Saskatchewan investigated barley row spacings of 11, 22, 33, or 46 cm in combination with seeding rates of 50, 90 150, and 220 kg/ha, in a field with a mixed infestation of wild oat, wild mustard (*Brassica kaber*), and volunteer canola (*Brassica campestris*). Decreasing row spacing and increasing seeding rate were both found to decrease weed biomass for each species and to increase barley yield. No interaction was detected between row spacing and seeding rate.

Barton et al. (1992) researched the effects of barley row spacing, barley seeding density, wild oat herbicide, and herbicide application rate on barley yield and wild oat biomass in Idaho. They concluded that there were no difference of practical importance between row spacings of 9 cm and 18 cm.

Alternatives to Fallow in Montana Agriculture

Summer fallow has been used for nearly a century in dryland farming in Montana as a means of accumulating moisture, allowing consistent yields of small grains in areas with as little as 20 cm of annual precipitation. Approximately 18 to 28 % of the precipitation falling during the summer fallow period actually becomes available for the crop, the remainder being lost to evaporation, leaching, and runoff (Badaruddin and Meyer 1989, Smika 1990). Excess moisture flowing through the soil profile leaches out salts and may raise the groundwater table. Land becomes unproductive due to salinity where elevated water tables seep to the surface. Excess water also carries free nitrates and pesticides from the soil into the groundwater or to seep sites. Erosion potential is also substantially increased on fallowed land due to lack of soil surface cover and increased runoff. In addition, organic matter decline in fallowed soils has resulted in increasing need for nitrogen fertilizer inputs to sustain economic yields of grain crops.

In response to these concerns, Montana researchers are recommending that farmers replace summer fallow with a green manure cover crop which can be terminated when it uses an allotted amount of soil moisture (Sims et al. 1985). If sufficient moisture is available, the cover crop may be utilized as a forage or seed crop. These crops offer protection against erosion, reduce the risk of saline seep, and can maintain organic matter levels in the soil by utilizing excess moisture for biomass production. Many of the recommended crops are leguminous, and can accumulate excess nitrates which become available in the soil, as well as fixing atmospheric nitrogen. Increased yields

of the subsequent grain crop have been seen in response to higher nitrogen levels, soil aeration, and water holding capacity following green manuring of a legume crop (Badaruddin and Meyer 1990, Abernethy and Bohl 1987, Badaruddin and Meyer 1989). Some of these green manure crops are interseeded with a grain crop, then become established during the subsequent fallow year either by reseeding from seeds produced during the previous season or, more commonly, by overwintering as biennials or short-lived perennials. In some cases, the interseeded legume produces enough seed that it never has to be reseeded, while in other cases it may be reseeded every time it is desired to have a green manure in the following year.

In addition to green manure crops, many farmers are being encouraged to investigate a variety of alternative cash crops in response to the impending possibility of changes in farm programs and international markets, as well as the need for increased flexibility in weed control and soil management.

Crop rotation and interseeding of a green manure crop have frequently been reported to have impacts on weed populations. This literature was thoroughly reviewed by Liebman and Dyck (1993), Altieri and Liebman (1986), Liebman (1988), and Froud-Williams (1988).

Effects of Crop Rotation on Weed Populations

Froud-Williams (1988) asserted that of several cultural practices affecting weeds, "the most obvious and fundamental changes in weed populations result from the use of crop rotation" (p 220). The most thorough and recent review of examples of crop rotation influencing weeds is found in Liebman and Dyck (1993). They found that among published articles, crop rotation and intercropping appeared to be favorable strategies for managing weeds. Among 27 cases where emerged weed densities in crop rotations were compared to those in monocultures, densities were lower in the rotation than in the monoculture in 21 cases, higher in one case, and equivalent in five

cases. Among 12 cases where seed densities were compared, rotations had lower seed densities in 9 cases, and equivalent densities in three.

Liebman and Dyck (1993) and Froud-Williams (1988) discuss possible reasons for changes in weed populations with crop rotation. In general, it is believed that crop rotation works in opposition to the extreme oversimplification of many modern agroecosystems. Where a single crop is grown continuously, a population of one or a few weed species which are very well adapted to growth with that crop and its corresponding management regime will become established. Crop rotation, it is proposed, by providing a different environment for weeds each season, disrupts the development of a population of a dominant weed species, resulting in a more diverse weed community. Ideally, lack of a consistent environment and competition between weed species will prevent the population of any single weed species from becoming a serious problem during those years when its favored crop is grown. Froud-Williams (1988) gives differences in planting time and differences in available herbicides as possible reasons for the ability of crop rotations to reduce weed populations. Liebman and Dyck (1993) focus on the ability of different categories of crops to put pressure on different types of weeds, such that a rotation between crop categories will result in all types of weeds receiving some type of cultural pressure. The crop categories and their benefits include: row crops, where weeds are reduced via cultivation between the rows, sod crops, where weed seeds are discouraged from germinating and may die before the soil is tilled for the next crop in the rotation, and grain and smother crops, which may inhibit weed growth by means of competition from fast-growing, densely planted crop plants, or by means of allelopathy. They also cite that differences in planting date and manipulation of nitrogen fertility may play a role in the effects of crop rotation on weed populations.

Martin and Felton (1993) studied the long term effects of different fallow methods and rotation with sorghum on populations of wild oats in a dominantly wheat cropping system. They

found that chemical fallow resulted in fewer wild oats than cultivated fallow, which they attributed to reduced mortality of seeds in the cultivated fallow due to seed burial. They also found that rotation with sorghum resulted in fewer wild oats than systems with only wheat. The effects on wild oat populations of replacing fallow with green manures have not been reported in existing literature.

Effects of Intersown Green Manure Crop on Weed Populations

In a review of 54 studies where a 'smother crop' was intersown to grow below a cash crop, weed biomass was lower than in the monoculture in 47 cases, higher in 4 cases, and variable in three (Liebman and Dyck 1993). Altieri and Liebman (1986) emphasize that a variety of factors may influence the balance of intercrop plants and weeds. These include crop density, spatial arrangement of crop plants, relative proportions of component crops, crop species and cultivar, and resource levels, as well as several other factors which have not yet been reported on in the literature.

Altieri and Liebman (1986), Liebman (1988) , Liebman and Dyck (1993), and Vandermeer (1989) all suggest possible reasons for the effects of "smother" intercrops on weed populations. Altieri and Liebman (1986), Liebman (1988), and Liebman and Dyck (1993) note that adequate ecophysiological data is not available for a precise accounting for these effects. However, they suggest that increased preemption of light and/or soil resources by the crop mixture compared to sole crops is the most likely explanation, although when these have been measured they have not always been tightly linked to weed suppression. They also suggest that allelopathy may be a possible mechanism of weed suppression.

Vandermeer (1989) graphically presents a clear framework for summarizing and analyzing the often confusing effects of multiple species mixtures. In essence, given a mixture of three species, two crops (C1 and C2) and a weed species, each species will have some direct effect on each of the other two species. Supposing that all direct effects are negative, it is still possible that if one crop species (C1) has a strong negative effect on the weed and a weak negative direct effect on the other

crop species (C2) that the net effect of C1 on C2 will include both its direct effects and the indirect effects which result from its negative effect on the weed. Ultimately, this could result in a net facilitation effect of C1 on C2. If all of the direct effects can be summarized mathematically, which they often can given adequate data (using, for example, hyperbolic yield loss equations), it should be possible to optimize the crop combination in the presence of a given weed density.

As an example with some relevance to this study, Hartle (1989) studied the influence of undersown clovers on weeds and on the yield of winter wheat in organic systems. He found that undersowing wheat with Persian clover (*Trifolium resupinatum*) or black medic (*Medicago lupulina*) significantly reduced aboveground biomass of annual weeds, as well as significantly reducing wheat yield. In a separate experiment, wheat undersown with white clover (*Trifolium repens*) yielded slightly, but non-significantly, higher than wheat without undersown clover, as well as reducing biomass of weeds.

Studies of Weed Population Dynamics

"Population dynamics" refers to the ways that the characteristics of a biological population changes in time (Silvertown 1993). Population dynamic models give structure to analyses of data on weed population changes, but many of the articles in weed science literature which describe weed population dynamics do not make use of any identifiable model (e.g. Buhler 1992, Schreiber 1992). Some do not even display or discuss data showing whether or not weed populations changed over the course of the study (e.g. Buhler 1992). While it is important to document changes in weed populations due to various management practices, investigation of the demographic processes which underlie those changes, such as by estimation of the parameters of a population dynamic model, can be very useful in developing efficient weed management strategies which target the most sensitive life stage of the weed (Jordan et al. 1995).

A number of books and articles detail the various equations that would be appropriate to use in a demographic description of the population dynamics of plants (Silvertown and Doust 1993, Doyle 1991, Sagar and Mortimer 1976, Maxwell and Ghersa 1992). However, it is difficult to find a literature source which adequately describes appropriate sampling or experimental designs and statistical techniques for estimating the parameters of these equations. Some population dynamic models in the ecological literature are accompanied by a mathematically rigorous treatment of some of these issues (e.g. Horvitz and Schemske 1995, Caswell 1989), but straightforward guidelines are not as readily discernible. There is a distinct need for clear guidelines for weed population dynamics studies.

On-Farm Research

History and Perceptions of On-Farm Research

Kittrell (1974) surveyed the history of on-farm demonstration and research from its inception in the late 1800's. He emphasized the importance of demonstrating new technologies under the conditions experienced by average farmers as a key part of the powerful capacity of these techniques to inspire farmers to try new technologies.

Rzewnicki (1991) surveyed Nebraska and Iowa farmers to gauge their opinions about small-plot experiment station research, on farm demonstrations, and randomized, replicated on-farm trials. Farmers viewed on-farm trials quite favorably relative to experiment station research. Very strong support was shown for programs which incorporate farmer input during the planning process. Rzewnicki (1991) also found that many farmers already do some form of experimentation on their farms prior to adopting a new technology. Many farmers who have university educations have been exposed to concepts of experimental design. Farmers who had more exposure to randomized and

replicated experiments indicated more willingness to cooperate with university researchers in establishing trials on their own farms.

The literature surrounding on-farm research reveals that the majority of the impetus for on-farm research is focused in two areas: 1) very specific and conventional agronomic questions, usually variety yield trials and occasionally fertilizer or herbicide trials, or 2)"farming systems research", where the farm and its enterprises are holistically viewed as a unit, and the emphasis of research is on understanding the interactions and characteristics of these complex systems, rather than on specific agronomic questions. Although the philosophical justifications for these two foci are in some ways quite different, the basic reasons, the methodologies, and the end results are often essentially the same. On-farm variety yield trials and fertilizer trials are justified primarily on statistical grounds, since farms allow for a more complete coverage of the desired "inference space" then do the usually widely scattered and often abnormally productive public experiment stations (Bradley et al. 1988). Researchers with this focus seem to view it as a somewhat peripheral bonus that farmers view on-farm research trials more favorably than on-station small-plot research (Rzewnicki 1991), and are more likely to adopt technology based on experience with on-farm trials than based on experiment station recommendations (Kittrell 1974). Researchers with the farming systems research orientation tend to be most interested in either third world agriculture or the development of "sustainable" or "alternative" agriculture in North America. The view of these researchers can be simplistically summarized by the words of Taylor (1990), who suggests that there are two primary "unique roles of on-farm research in assisting the development of sustainable agriculture". These are 1) "distilling credible knowledge from the practices and experiences of existing commercial sustainable farmers." and 2)"test possible improved sustainable practices/enterprises under a wider variety of production circumstances and in a more realistic whole-farm environment than is feasible on-station." This view is iterated repeatedly and in many forms in extensive articles and entire books on the subject of

farming systems research and extension (Zandstra et al. 1981, Lockeretz and Anderson 1993, Shaner et al. 1981, Tripp 1991, Hildebrand 1986, National Research Council 1991), most of which do not even mention statistics or experimental design. Oddly, Taylor's second "unique role" above is essentially identical, conceptually, to the reason that more and more crop variety trials, including those done by major crop breeding corporations, are being done on farms, and it is precisely the reason that farmers consider on-farm research of whatever kind to be more valuable than on-station research. Further unifying these two philosophical approaches to on-farm research is the fact that to date, lacking clear methodology for studying the complexity of whole-farm systems (with the exception of strictly economic analyses), most of the research advances cited as exemplary by those interested in "farming systems research" are actually trials of single agronomic technologies or narrowly defined technological packages (e.g. Doll and Francis 1992). Multiple farm trials where treatments are more complex, such as a weed control system, or where conditions or treatments vary from farm to farm often yield results which are very difficult to interpret in any general way (e.g Smith and Carter 1993, Hartzler et al. 1993).

Doll and Francis (1992) review the importance of participatory research and extension strategies for sustainable agricultural systems. They quote Lockeretz (1984) for the following reasons that commercial farms should be used as research sites:

-to obtain soil types or conditions not found on a research station
-to study phenomena that require larger areas for interactions to occur
-to analyze systems that involve interactions among past and current enterprises
-to compare experimental performance with real farm conditions
-to evaluate technologies that are sensitive to farmer management
-to study long-term effects of systems already established
-to analyze a system used by farmers but not yet formally researched.

Doll and Francis (1992) add that in addition to these factors, perhaps the most important resource on the farm or ranch is "the decision maker who works with these systems each day and has at least a practical knowledge of the physical and biological interactions that make them work."

Methodologies for On-Farm Research

On-farm trials have been used most extensively for yield tests and variety selection. Since the late 1970's, variety trials have been shifting emphasis from an approach aimed at maximizing precision at a few high-quality sites to research approaches which maximize predictive value of data across a range of sites and years representative of conditions and practices on working farms (Bradley et al. 1988). Bradley et al. (1988) suggest that in addition to providing more useful information, this type of research will result in greater farmer confidence in the results of the trials. Dofing and Francis (1990) compared the efficiency of single-replicate, multiple location trials to that of multiple-replication trials at a few sites. They concluded that in many cases, single replicate trials could be expected to provide equivalent or better information at a lower cost than replicated trials. This would be particularly true where the cost of additional locations is low relative to the cost of additional replications at one location.

Johnson et al. (1994) investigated various experimental designs for on-farm evaluation of cultivar performance. They found that unreplicated tests performed on a number of farms throughout a region successfully reduced the probability of erroneously releasing an inferior cultivar. However, they suggested that single-replicate on-farm tests probably should not totally replace small-plot research on experiment stations, because many more cultivars could be evaluated in the small plot experiments.

Wuest et al. (1994) studied the effect of increasing plot length on experimental error of on-farm tests with crop yield as the dependent variable. They discovered that increasing length of combine-width experimental plots reduced error variance in all of 14 site years. Variance was related to plot length with an exponential decay curve whose parameters varied considerably between site-years. The experiment was also done at a smaller scale using 1.2 meter wide plots and a range of shorter lengths, and they found, interestingly, that the results were similar, with error variances being

of the same magnitude in the shortest small plots as in the much longer combine-width plots of approximately the same proportional shape. They suggested that this was probably due to the presence of different scales of spatial heterogeneity.

Hildebrand (1982) reported a simple methodology for relating variability of responses across sites to the variation in the productivity of the sites. He demonstrated this technique using a comparison of yield between two cultivars, showing that one cultivar responded more strongly in better quality sites, while the other was better on poorer quality sites. This methodology could be used to adjust cultivar recommendations depending on the quality of the site in question.

Virtually all on-farm research experiments documented in the literature are laid out in a way that makes it convenient to perform most, if not all, relevant operations with farmer equipment. It appears to be widely accepted, without being stated, that much of the advantage of on-farm research is lost if farmer equipment is not used in the laying out of on-farm research.

There are very few reported instances of weed population studies being carried out on farms, so it is difficult to glean appropriate methodologies from the literature. Hartzler et al. (1993) studied impacts of mechanical and chemical weed management practices in corn on farms in 64 site-years in Iowa. Differences in management practices and histories among farms led them to analyze each site-year separately. No effects on weed populations were reported, nor were data linked across years. Data from each site year was not reported separately, undoubtedly due to the massive amount of data involved. Plots were relatively small (270-540 m^2), depending on farmer equipment, but standard farmer equipment was used to plant and cultivate the plots.

Young et al. (1994) examined the effect on crop rotation and weed and pest management systems on winter wheat yield in on-farm experiments in the Palouse region of Washington and Idaho. However, the effects of the treatments on weed population levels were not reported. In this study, standard farmer equipment was used in large (field-length) plots.

Objectives

The objectives of this work were to 1)compare and evaluate new and existing models which describe effects of neighbor plant spatial arrangment on individual plant size; 2)quantify the effects of different barley planting patterns on crop yield and wild oat interference; and 3)quantify the effects of alternative cropping systems on wild oat populations on two dryland organic farms in Montana.

CHAPTER 2

EFFECTS OF PLANT NEIGHBORHOOD SPATIAL ARRANGEMENT ON INDIVIDUAL PLANT YIELD

Introduction

Interference between plants is important in controlling the structure, composition, and function of plant populations and plant communities (Harper, 1977). Plant interference is of considerable importance in agronomy, relating to questions of crop-weed interference, optimum crop density and planting pattern, and intercrop design. Nonetheless, methodology for measuring the intensity of interference is not universally defined or accepted. The influence of mean density of plants in a population on the productivity (biomass or reproductive output) of those plants has been widely studied and is characterized by equations related to the hyperbolic yield law (Watkinson, 1986, Willey and Heath, 1969). However, plants do not respond, typically, to overall mean density but to the resource limitations of their local environment, which are mediated by other plants in the immediate neighborhood. A number of studies have demonstrated that the growth rate and final size of individual plants is related to the number, size, location, species, and relative emergence time of neighboring plants (Ross and Harper 1972, Pielou 1960, Silander and Pacala 1985, Opie 1968). An understanding of the effects of local plant density and spatial arrangement on the performance of individual plants can have consequences for the management of crop, forage, and forest production systems, crop variety selection, rare plant conservation, management of exotic invaders, and for research in all aspects of plant science, including population genetics and population dynamics.

A number of measures of the pattern of plant location have been developed. Rectangularity, the ratio of the distance between crop rows to the distance between plants within a row, has been used to quantify the uniformity of plant spacing in crop systems (Auld et al. 1983). However, this method is not useful for quantifying effects at the scale of individual plants, particularly in situations where plant locations are not regularly spaced. A variety of measures of pattern are based on statistical considerations, such as the variance to mean ratio of quadrat counts, or point-plant distances (Upton and Fingleton 1985). These measures can evaluate the degree of aggregation or uniformity in the spatial pattern of plants in a population, but again are not particularly useful for the description of effects of local density and spatial arrangement on individual plants. Researchers have shown that the performance of individual plants is significantly related to the distance to one or more nearest neighbors (Pielou 1960, Hickman 1979). Other researchers have adopted analyses which depend on the assumption that plant performance is proportional to some simpler measure of physical space (Mead 1966, Fischer and Miles 1973, Bussler et al. 1995). Thiessen polygons and their variants are commonly used measures of this type, where the planar area occupied by a plant population is divided into a matrix of adjacent polygons, each plant occupying a polygon whose boundaries are determined by the locations of its neighbors. The biological space available to a plant presumed to be proportional to the area of the polygon. Measures based on Thiessen polygons are limited by the assumption that there is no sharing of space between plants, and that there is no effect of non-adjacent plants.

Mack and Harper (1977) developed an index of competition which summarized various characteristics of the plant neighborhood. They defined the neighborhood as a circle with a fixed radius around each individual plant, the target, and related the final productivity of each target to the size, species, distance, and angular dispersion of its neighbors. This analysis was developed and extended by several researchers (Weiner 1982, Silander and Pacala 1985, Wagner and Radosevich

1991, Puettmann et al. 1993, Lindquist et al. 1994). Lindquist et al. (1994) demonstrated that their formulation of what they termed the dispersion index could explain up to 55% of the variation in individual oat (*Avena sativa*) plant size. However, this dispersion index is limited by the difficulty of accounting for interactions between neighbors at different distances from the target, and by computational difficulties.

Development of Existing Models

Polygon Models Fisher and Miles (1973) proposed that individual plant performance could be related to the two-dimensional area which the plant captures during its early growth. Assuming that all plants in an area emerge at the same time and capture space at an equal rate of radial expansion, then the amount of space a plant captures is equal to the area of the smallest polygon whose edges can be described by the perpendicular bisectors of the line segments connecting the plant to each of its neighbors (Figure 2.1). These polygons have been referred to by a variety of names, including Thiessen or Voronoi polygons or the Dirichlet tesselation, and have been constructed using a variety of different algorithms (Green and Sibson 1978).

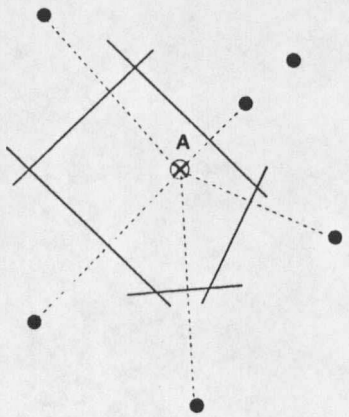

Figure 2.1 Thiessen polygon boundaries are defined by the perpendicular bisectors of the line segments connecting each plant to its neighbors.

The Thiessen radius (TR) is the radius of a circle with the same area as the Thiessen polygon,

$$TR = \sqrt{\frac{Area}{\pi}} \qquad (2.1)$$

where Area is the Thiessen polygon area. A polygon shape index (PSI) of the deviation of the spatial arrangement from a uniform pattern can then be calculated

$$PSI = \frac{2 \cdot TR}{D_{nn}} \qquad (2.2)$$

where TR is the Thiessen radius (Eq. 2.1)and D_{nn} is the distance to the nearest neighbor (Comerford et al. 1994). When the Thiessen polygon is a circle with the target plant at its center, the shape index will take on a value of 1.0. In a perfectly uniform arrangement of plants, where plants are located at the vertices of adjacent equilateral triangles, each polygon will take the shape of an equilateral hexagon and this shape index will equal 1.05. Where the plants are less uniformly arranged, plants may not be at the center of their polygons, and the polygons may take on a variety of shapes, often much narrower than they are long. As the arrangement becomes less like a circle with a central target plant, the polygon shape index increases. Target plant size was regressed against Theissen area and the polygon shape index (PSI).

Neighborhood models A plant neighborhood is defined as the region of space around a target plant outside of which no neighbor can have an impact on the target. In practice, most researchers exploring neighborhood models have defined an arbitrary search radius around each target plant based on convenience, statistical assumptions, or other criteria. Plants within this search radius are defined as neighbors for use in calculations.

A simple hyperbolic model has been used to model the effect of neighborhood density on individual yield (Weiner 1982, from Kira et al. 1953):

$$S = \frac{M}{1 + C \cdot NN} \tag{2.3}$$

where S = the size (biomass or seed production) of the plant, M = the maximum biomass production, C is a slope parameter which has been interpreted to represent the area required to achieve that maximum production (Watkinson 1986), and NN is the number of neighbors (local density, excluding the target individual).

In order to improve the description of the plant neighborhood, NN can be replaced with an index of plant interference where the effect of each neighbor is weighted, based on a more detailed description of the size or location of neighbor plants:

$$S = \frac{M}{1 + C \cdot \sum_i W_i} \tag{2.4}$$

where W_i represents the weighted effect of neighbor i, and summation is over all neighbors. In these neighborhood models, as in Weiner's (1982) model, weighting will be accomplished by taking into account information about the distance of neighbors or their location relative to other neighbors. Thus ΣW_i represents the index of neighborhood interference, which may also be termed the Dispersion Index (DI), (Lindquist et al. 1994). Different neighborhood models will be delineated in this paper according to what quantity is substituted for W_i in Eq. 2.4. In the special case where W_i=1, and therefore ΣW_i=NN, the model is equivalent to Eq. 2.3, which will be referred to as the neighbor number, or NN model. The sizes of neighbors are not included in any of the models in this paper, therefore these models will be most effective in predicting the size of individual plants in even-aged stands.

The size of a target individual has been shown to be related to the distance to its neighbors (Pielou 1960), although use of a search radius which may be too small reduces the impact of this effect (e.g. Pacala and Silander 1985). In order to account for the declining impact of a neighbor

with distance from the target, each neighbor is assigned a weight which is substituted for W_i in Eq. 2.4. This weight, termed the distance weight or DW_i, is assigned to neighbor i according to its distance from the target, using the formula developed by Pacala and Silander (1985):

$$\mathbf{DW_i} = (1 - \tfrac{d_i}{R})^{\gamma} \qquad (2.5)$$

where d_i is the distance to the neighbor, R is the neighborhood radius, and γ is a fitted weighting parameter which influences the shape of the function. The weight decreases from one at the center of the neighborhood to zero at the perimeter, with a concave function for values of γ greater than one, and a convex function for values less than one. It should be noted that the fitted value of γ is strongly correlated with the value chosen for R, such that an incorrect choice of neighborhood radius can lead to faulty conclusions about the functional form of the decline in weight with distance. The model of individual plant size resulting when W_i in Eq. 2.4 is replaced with the distance weight DW_i (Eq. 2.5) will be termed the "DW model". In this case, since most or all neighbors will be assigned weights less than one, the value of C in the hyperbolic yield equation will tend to be higher than it is when using neighbor number alone.

The weighting factor (W_i) can be further modified by including information about the spatial relationship of neighbor plants to each other. Mack and Harper (1977), noting that plants tend to grow most in the direction of least interference, proposed that individual plant performance would be related to the angular arrangement of neighboring plants around the target plants, such that plants evenly spaced around the target would have a greater effect than plants which are clumped to one direction from the target. They proposed a measure of angular dispersion taken from Zar (1974), which ranged from 1 where neighbors were totally angularly dispersed to 0 where neighbors were completely clustered in one direction. This calculation was used by several other researchers (Waller 1981, Silander and Pacala 1985, Wagner and Radosevich 1991). Puettman et al. (1993) proposed a revised method of calculating angular dispersion which is more appropriate for a variety of

situations, particularly where there is a multimodal distribution of neighbor plants. This method is based on the variance of the angular difference between adjacent plants, and also varies from 1 for the most dispersed distribution to 0 for the least dispersed. Lindquist et al. (1994) assembled this angular dispersion (AD) index (Puettman et al. 1993) and the distance weight (DW, Eq. 2.5) into a single dispersion index (DI) by dividing the neighborhood into several concentric annuli and calculating DW and AD for each annulus:

$$DI = \sum_{j=1}^{annuli} DW_j \cdot n_j \cdot AD_j \qquad (2.6)$$

where DW_j is the distance weight for annulus j, AD_j is the angular dispersion for annulus j, n_j is the number of neighbors in annulus j. When DI (Eq. 2.6) replaces Σw_i in Eq. 2.4, this model will be referred to simply as the "Lindquist model".

The Lindquist model is limited in a few major respects. The division of the neighborhood into discrete annuli presents a number of difficulties. First, there is no means to account for the possibility that plants in adjacent annuli may interact with each other. Plants in four different annuli could be dispersed around the target, yet be clumped within their own respective annuli (Fig. 2.2, diagram on left). While this could be solved by the use of a wider annulus (Fig. 2.2, diagram on right), it becomes obvious that the choice of the size and number of annuli is arbitrary, with no clear rules. If annuli are too large, neighbors near the inside radius of an annulus would be under-weighted, while those near the outside radius would be over-weighted, assuming the distance to that annulus is measured as some intermediate radius.

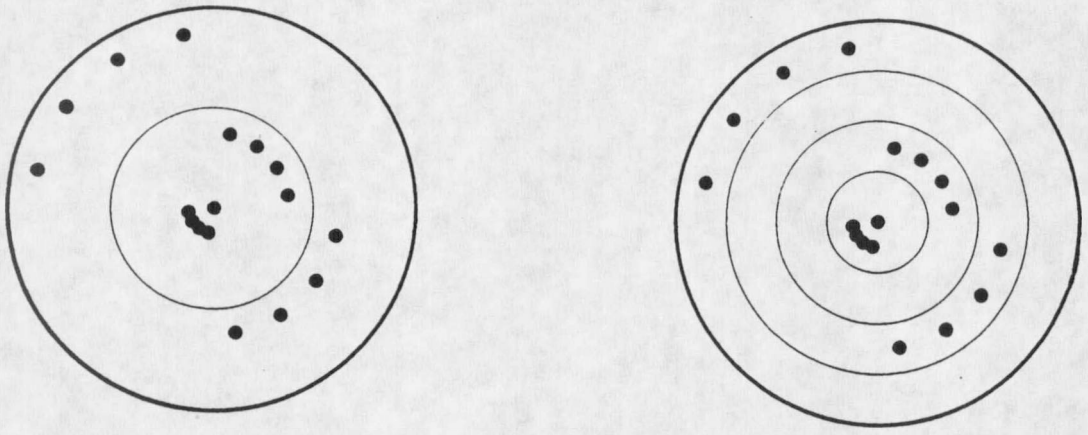

Figure 2.2. The dispersion index (Lindquist model, Eq. 2.6) calculated for this neighborhood depends on the choice of annular boundaries.

A related limitation of the Lindquist model is the failure to include radial dispersion, which is related to the variation in the distance of neighbor plants from the target. For example, their model will not distinguish between two neighborhoods where in one neighborhood, all of the neighbors are at the same distance from the target (Fig 2.3, diagram on left), while in the other, the neighbors are dispersed at different distances (Figure 2.3, diagram on right), but with the same weighted mean distance as in the first neighborhood. Based on the work of researchers who found that the size of individual plants was related to the distance to a few of the closest plants (e.g., Pielou 1960, Powell 1990, and Tyler and D'Antonio 1995), it may be appropriate to distinguish between these scenarios by allowing for the impact of a neighbor on the target to be reduced if there are other neighbors between it and the target.

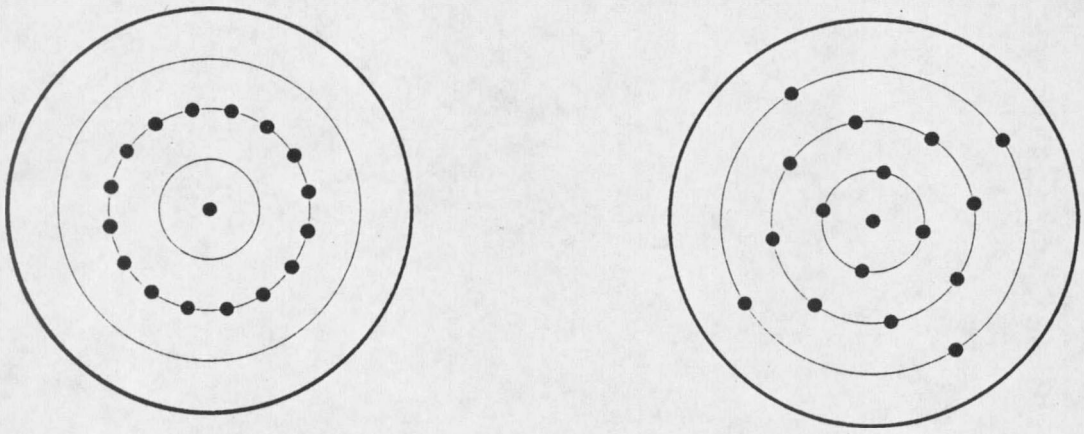

Figure 2.3. These two neighborhoods would be given the same dispersion index with the Lindquist model (Eq. 2.6).

Objectives

The objectives of this study were to (1)develop an index of neighborhood competition which is flexible, theoretically sound, and computationally tractable, and (2)compare this new index of spatial arrangement with existing methods of quantifying the spatial arrangement of plant populations as predictors of individual plant yield.

Materials and Methods

Development of New Models

New models were developed after the pattern of the model of Lindquist et al. (1994, the "Lindquist model"), but in hopes of minimizing some of the limitations of that model. Due to limitations related to the division of the neighborhood into discrete compartments, the proposed models were developed with relationships between plants being calculated in a continuous space. The proposed models were also developed with the intention of allowing for the inclusion of radial dispersion information.

The proposed models utilize the hyperbolic yield equation (Eq. 2.4), with different models being distinguished by the substitution into Eq. 2.4 of different values of W_i. The hyperbolic yield equation can be conceptualized as representing the amount of space available to the target, assuming that the space available is divided evenly among all of the plants. An intrinsic characteristic of this equation is that as the number of neighbors increases, the marginal impact of each additional neighbor decreases, resulting in the target size assymptotically approaching, but never reaching, zero. As long as the neighbors are evenly distributed throughout the neighborhood, the hyperbolic model should provide a reasonable prediction of the target size. When the neighbors are not evenly distributed, the hyperbolic yield equation may under- or over-predict target size. If the neighbors are clustered around the target, thr hyperbolic yield equation will over-predict target size, while if neighbors are clustered anywhere else, under-prediction will result. Under-prediction of target size can also be thought of as overestimation of the competitive impact of the neighbors. In order to adjust for these effects, the new model will describe the competitive impact of plants in a neighborhood (ΣW_i in Eq. 2.4) in terms of equivalent numbers of evenly distributed plants.

Expansion of the hyperbolic yield model to include spatial arrangement begins with the theoretical consideration that a neighbor at a certain distance from the target has a maximum potential impact on the target, and that this maximum effect will occur when that neighbor is the only neighbor in the neighborhood. When there is only one neighbor in a plant neighborhood, this maximum impact will be defined by substituting the distance weight (DW, Eq. 2.5) for W_i in Eq. 2.4. If there is more than one plant in the neighborhood, the hyperbolic yield equation reduces the calculated impact of each additional neighbor, due to interactions between neighbors, but this reduction is limited by the assumption that plants are evenly distributed. The new models provide for a further reduction in the impact of each neighbor when neighbors are not evenly distributed. The reduction in impact is based on the number of neighbors within a secondary neighborhood. The

secondary neighborhood for neighbor A may be defined as the region around neighbor A within which other neighbors may reduce the impact of neighbor A on the target beyond the reduction inherent in the hyperbolic yield law.

In order to derive a mathematical formulation for the concept of a secondary neighborhood, consider the case where two neighbors are growing in exactly the same location (Figure 2.4). It may be reasonable to assume that the effect of these two neighbors on the target is not much different from the effect of one neighbor. A third neighbor in exactly the same location will again have almost no additional effect on the target. Three neighbors will have approximately the same effect as one had, that effect being DW, or the maximum effect possible for one plant at that distance. Thus the effect of each neighbor can be calculated as

$$W_i = \frac{DW_i}{NN} \tag{2.7}$$

where NN is the total number of neighbors in the same location.

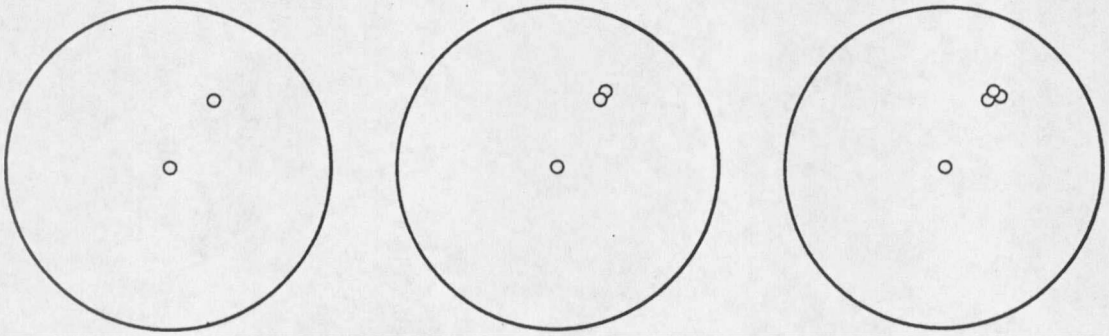

Figure 2.4 Two or three neighbors occupying the same location may not have significantly greater effect on the target than a single neighbor.

To generalize Eq. 2.7, a weight W_i is computed for each neighbor separately, with the secondary neighborhood extended to include neighbors that are not in the same immediate location as the neighbor in question (the "primary"), and the number of additional neighbors ("secondaries") modified with a slope parameter to adjust for the fact that on average they are not immediately on top of each other:

$$W_i = \frac{DW_i}{1 + b * SNN_i} \tag{2.8}$$

where SNN_i is now the number of secondaries within the as-yet undefined secondary neighborhood, not including the primary. The 1 in the denominator adjusts the value for the presence of the primary in its own secondary neighborhood. The model of individual plant size resulting from substituting this expression (Eq. 2.8) into Eq. 2.4 will be termed the secondary neighbor number model, or "SNN model". When the fitted value of the parameter b is set to zero, this model is equivalent to the DW model. The SNN model indirectly assesses angular dispersion, since neighbors which are angularly dispersed will fall into the secondary neighborhood of other neighbors less often than will neighbors which are angularly clustered (Fig. 2.5). It may be noticed that Eq. 2.8 bears a resemblance to the hyperbolic yield model (Eq. 2.3), whose conceptual derivation is similar.

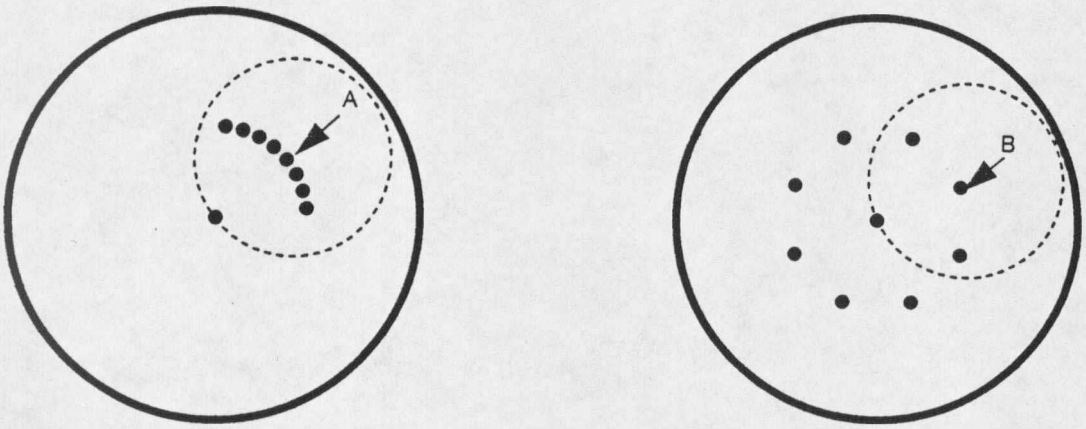

Fig. 2.5. Both neighborhoods (bold outer circles) contain the same number of neighbors, but the angularly clustered neighbors in the diagram on the left will be weighted less strongly than the angularly dispersed neighbors in the diagram on the right. For example, the calculated competitive impact of neighbor A (diagram on the left) will be lower than the competitive impact of neighbor B (diagram on the right), which has fewer secondary neighbors within its secondary neighborhood (smaller circles).

Delineation of the boundaries of the secondary neighborhood can proceed by any of several methods. An empirical delineation would require a large and carefully designed study which allowed for the impact of each neighbor to be estimated with small error. Delineations based in theory may not be clearly distinct from arbitrary delineations. The secondary neighborhood might reasonably include the entirety of the target neighborhood, but at some distance from each neighbor, the effect of secondary neighbors is described adequately by reductions of impact described by the hyperbolic yield law. Since the hyperbolic yield law describes impacts of secondaries resulting from an even distribution of neighbors, the secondary neighborhood should include any secondaries closer to the primary than expected in an even distribution. The secondary neighborhood can be delineated as a circle whose radius is the distance of the neighbor from the target. This circle delineates a reasonable secondary neighborhood at any density, because in an even distribution, it does not include any secondary neighbors when the primary is among the closest plants to the target (Figure 2.6).

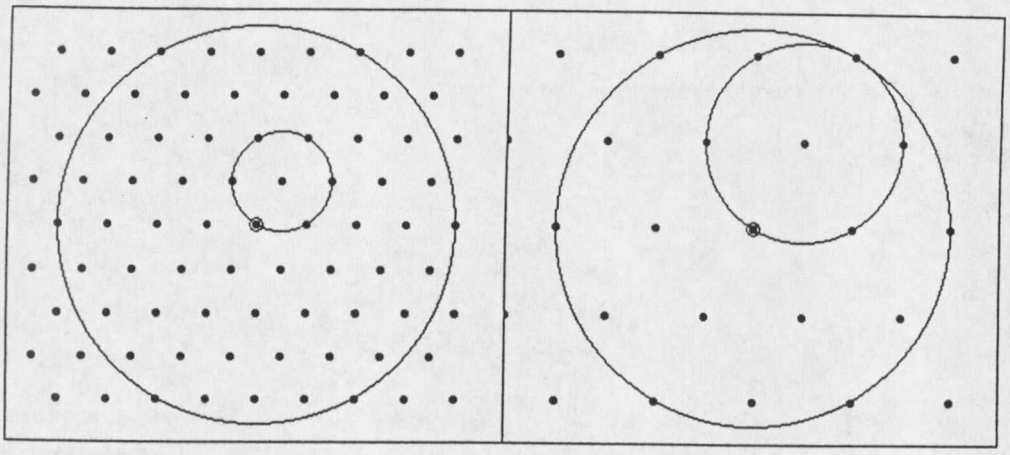

Figure 2.6 The inner circle denotes the secondary neighborhood for the neighbor at its center. This circle does not contain any secondary neighbors when the plants are evenly distributed, but will include any secondary neighbors too clustered to be adequately described by the hyperbolic yield equation.

When a neighbor is more distant from the target than other neighbors in the same direction, its larger secondary neighborhood will contain the nearer neighbors as secondaries, while the reverse may not be true (Fig. 2.7). Since the calculated effect of a primary will be reduced more, on average, when other neighbors intervene between the primary and the target than when other neighbors are more distant from the target than the primary, radial dispersion becomes an inherent component of any model utilizing this delineation of the secondary neighborhood (Fig. 2.7). Although other delineations of the secondary neighborhood are possible, this one was used in this study.

It should be noted that the designations "primary" and "secondary" are not mutually exclusive: primaries will also be secondaries if they are within the secondary neighborhood of another primary, while secondaries will also be primaries if they are within the primary neighborhood of the target (they could be outside of the primary neighborhood, too).

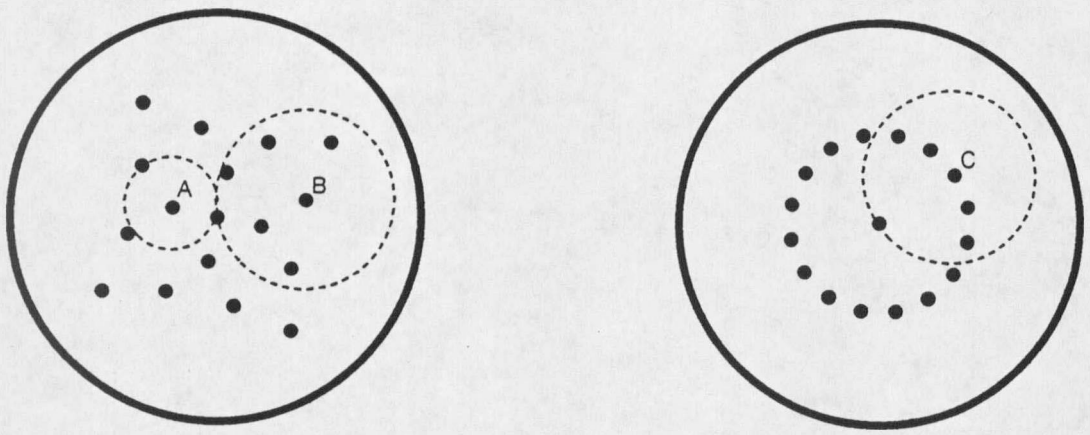

Figure 2.7. When neighbors are radially dispersed (diagram on left), closer neighbors have fewer secondary neighbors and a greater competitive impact than more distant neighbors. This will result in calculation of a greater neighborhood competitive effect in the radially dispersed neighborhood on the left than in the neighborhood on the right, which has the same mean neighbor distance.

The SNN model may be further refined by adjusting the weight of each primary even more, according to how far it is from its secondaries. If it is assumed that secondaries more distant from the primary reduce its impact less than do secondaries closer to the primary, then the impact of each secondary on the primary could be described by an equation similar to that used for defining DW (Eq. 2.5), such that secondaries immediately adjacent to the primary would have a weight of near one, while secondaries at the border of the secondary neighborhood would have a value of zero. Each secondary around the ith primary would be given a value of SDW_{si}, the secondary distance weight for secondary s:

$$SDW_{si} = (1 - \frac{d_{si}}{sr})^{\phi} \qquad (2.9)$$

where d_{si} is the distance between primary i and secondary s and sr is the radius of the secondary neighborhood. This distance weighting of secondaries is assembled into a weight for the primary using:

$$W_i = \frac{DW_i}{1 + b \cdot \sum_s SDW_{si}} \qquad (2.10)$$

where all variables are as defined in previous equations, and summation is over all secondaries s around the ith primary. The resulting primary weights W_i can be summed in Eq. 2.4, resulting in a model which will be termed the secondary distance weight model, or "SDW model". When the fitted value of ϕ in Eq. 2.9 is zero, $SDW_s = 1$ and this model is the same as the SNN model (from Eq. 2.8 and Eq. 2.4). The SDW model is consistent with the assumption that the competitive effect of a primary at a certain distance from the target is mainly a function of the size of that primary. The size of the primary will be determined by the number, distance, and size of its secondaries, whose size will be related to the characteristics of their own neighborhoods, etc. *ad infinitum*. The model described by Eqns. 2.9 and 2.10 is the perhaps the simplest reasonable expression of this concept. The SDW model refines the calculation of spatial dispersion, since neighbors which are more dispersed will always be weighted more heavily than neighbors which are more tightly clustered.

A second method of refining the secondary weights derives from the terminology of angular dispersion used by previous researchers, and allows for distinction between effects of angular distance and radial distance between neighbors, if desired. Here the angular weight of a secondary neighbor can be described with an expression such as

$$AD_s = \left(1 - \frac{2 \cdot \theta_{si}}{\pi}\right)^{\omega} \tag{2.11}$$

where θ_{si} is the angle in radians between the primary and the secondary, relative to the target, and ω is a shape parameter. As before, this can be assembled into a weight for the hyperbolic yield model:

$$W_i = \frac{DW_i}{1 + b \cdot \sum_s AD_s} \tag{2.12}$$

When this value of W_i is used in Eq. 2.4, the resulting model will be referred to as the secondary angular dispersion model, or "SAD model". As with the SDW model, when ω (Eq. 2.11) is fit to zero, this model is the same as the SNN model.

While the delineation of the secondary neighborhood used here implicitly takes radial dispersion into account by giving more distant neighbors larger secondary neighborhoods than nearer ones, there may be some circumstances where additional compensation for radial dispersion is desired in the model.

Radial dispersion could be described by some function which fits the researcher's particular data or assumptions about how secondaries nearer the target than the primary might be different from secondaries further from the target. For example, secondaries nearer the target might screen the effect of the primary, thus giving them considerably more influence on the primary than other secondaries further from the target than the primary. While it would be desirable to empirically determine the functional form of this effect, an arbitrary starting point for the radial dispersion (RD) of secondary s might be:

$$RD_s = 2 \cdot \left(1 + \delta \cdot \exp(d_s - d_i)\right)^{-1} \qquad (2.13)$$

where d_s is the distance from the target to the secondary, d_i is the distance from the target to the primary, and δ is a parameter which influences the shape of the curve. For non-zero values of δ, this function takes on a value above 1 when the secondary is closer to the target than the primary, and a value below 1 when the secondary is more distant from the target than the primary. When δ is zero, RD equals 1, and does not change the influence of a secondary on the primary. The two dispersion factors AD and RD may be multiplied together to yield a single index of the importance of a secondary. This combined index gives values near 1 when the secondary strongly reduces the effect of the primary and values near 0 where the secondary does not reduce the effect of the primary. The sum over all secondaries would then be be substituted for SNN in Eq. 2.8, and the resulting primary weight W_i substituted into Eq. 2.4. Due to difficulties with convergence of the iterative fitting procedures, results of the testing of this angular-radial dispersion index are not presented here. Empirical studies should test the extent and functional form of the effects of radial dispersion.

Greenhouse Studies

Greenhouse experiments were conducted during February through April 1994, and during August 1994 to evaluate the effect of different spatial arrangements of neighboring barley plants on individual target barley plants. Barley (*Hordeum vulgare* L., cultivar Gallatin) plants were grown from seed in round pots (30 cm deep, 27 cm mean diameter) in 17 liters of steam-pasteurized greenhouse soil mixture (1:1:1 Bozeman Silt Loam:sand:peat moss v:v:v) amended with Aqua-Gro wetting agent. A single plant at the center of each pot was considered the target individual, while treatments were imposed by planting additional seeds with varying densities and spatial arrangements. Single seeds were planted 3 cm deep through cardboard templates. Where seedlings did not emerge by 14 days after planting, seedlings were transplanted into those locations. Greenhouse temperatures ranged from 19°C to 26°C. Plants were grown under a 14:10 day:night light regime, were watered twice weekly, and were fertilized once every two weeks with 100 ppm 10-30-20 fertilizer in the irrigation water. Pots were arranged in a completely random design within the greenhouse and were rearranged weekly. In the first experiment, plants were harvested when the most mature plants were at hard dough stage. In the second experiment, a serious infestation of thrips and aphids led to the experiment being terminated after five weeks, when plants were in vegetative growth stages. At harvest, target plants were cut off at the soil surface, bagged, dried at 35°C for 5 days, then weighed to determine aboveground biomass.

Distance dispersion treatments were created by assigning neighbors to be planted at specific distances away from the target. Three distances were selected (4, 8, and 12 cm from the target) and for a given dispersion treatment specific numbers of neighbors would be assigned to one, two, or all three of the distances. Angular dispersion treatments were similarly assigned, with plants placed at specific angles relative to each other, so they would uniformly occupy one, two adjacent, two opposite, or four quadrants of the pot.

In the first experiment, three neighbor densities, four distance treatments, and four angular dispersion treatments were combined in a factorial yielding 48 treatment combinations, each having three replicates. Plant placement diagrams for all 48 treatments are shown in Appendix A. In the second experiment, 24 additional treatments, including combinations involving 2 additional neighbor densities and one additional distance treatment, were added to the first 48 treatments, for a total of 72 treatments. The additional 24 treatments are also diagrammed in Appendix A. The treatments were not replicated in the second experiment. In addition to pots with the neighborhood treatments, six pots in each experiment contained only a target individual with no neighbors.

Analysis also used additional data from greenhouse experiments performed in Minnesota using oat plants (*Avena sativa* L.). These experiments were previously described in Lindquist et al. (1994), to whom I am grateful for the use of the data.

Field Studies

Field experiments were conducted in May through August 1994 at the Arthur J. Post Agronomy research farm 5 miles west of Bozeman, MT on Amsterdam silt loam soil (fine-silty, mixed Typic Haploboroll, pH 7.0, OM 3%). Barley (*Hordeum vulgare* L., cultivar Gallatin) was sown in early May, using an International Harvester double-disk grain drill . Two circular plots of 1.0 m^2 in size where selected for harvest of individual plants from areas with differing densities and spatial arrangement. The circular plots were in areas where a grain drill turned around while planting an experiment examining the effects of different row spacings of barley. One of the areas had been planted twice, with seeds planted in rows 15 cm apart on one pass and in rows 30 cm apart in another approximately perpendicular pass, resulting in a plant density of 205 plants m^{-2}. The other area had been planted only once, with seeds in rows 30 cm apart, resulting in 118 plants m^{-2}.

In early August 1994, individual plants were harvested at maturity from both of the two circular plots. In order to determine the coordinates of each plant on x and y axes, two steel stakes

were driven into the ground near the boundaries of the circle. Both stakes were outside of the circular area harvested, such that a line segment connecting the two stakes did not intersect the circle. The distance from both of the two fixed stakes to each plant was measured with a tape measure. The x and y coordinates of each plant were calculated using the equations

$$x = \frac{d_2^{\,2} - d_{12}^{\,2} - d_1^{\,2}}{2 \cdot d_{12}} \qquad (2.14)$$

and

$$y = \sqrt{d_1^{\,2} - x^2} \qquad (2.15)$$

where d_{12} is the distance between the two fixed stakes, and d_1 and d_2 are the distances from each plant to the first and second stakes, respectively. The first stake defines the origin of the x-y coordinate system, and the line through both stakes defines the x-axis.

The individual plants were cut off at the soil surface, bagged, and dried at 35° for five days. Aboveground biomass was recorded for each plant. Data from the two circles were pooled for all analyses in order to provide a wider range of different spatial arrangements.

Analyses

Polygon areas and the shape index were determined for each target plant in all experiments from data files containing x and y coordinates of all relavent plants, using Microsoft QuickBasic programs (Appendix B) patterned after the methods of Comerford et al. (1994). In the Montana greenhouse experiments, the edge of the pot defined the boundary of any target polygons which were not completely bounded by the presence of neighbors. In the Minnesota experiments, where flats (36x52x6 cm) were used, it was not recorded how the neighborhood patterns were oriented relative to the edges of the flats. Thus polygon areas were determined on the basis of a neighborhood with a radius of 16 cm with the target at the center, and the boundary of this neighborhood was treated as a

pot edge. In the field experiments, any plant whose polygon contained points closer to the edge of the harvested circle than to that plant was considered an edge plant, and was not included as a target in the polygon analysis. A map of one of the harvested field plots and the polygon boundaries is shown in Figure 2.8. Aboveground target plant biomass was regressed against polygon area and the shape index using SAS PROC REG (SAS Version 6.1. Statistical Analysis System Institute, Inc. Cary, NC 27512).

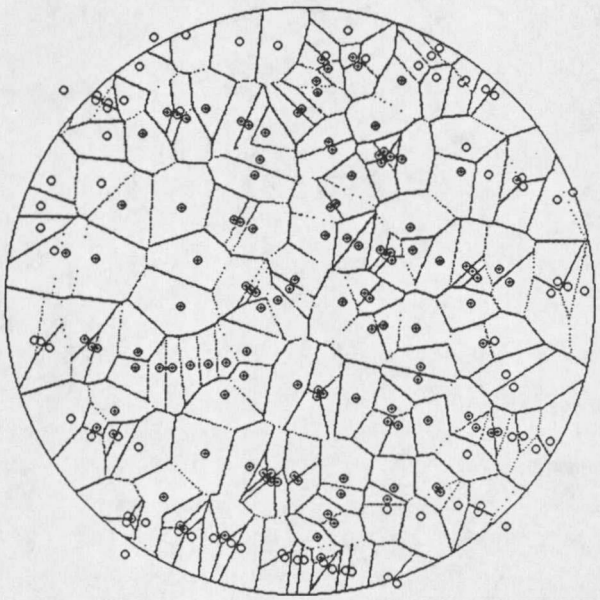

Figure 2.8. Map of plant locations and Thiessen polygon boundaries for one of the field harvest sites. The open circles designate plants which were excluded from analysis because a plant outside of the circle could have changed their polygon boundaries.

For all neighborhood analyses, an arbitrary neighborhood radius ("search radius", Benjamin and Hardwick 1986) of 20 cm was used initially for all of the experiments. For the greenhouse experiments, as long as all neighbors within the pot or flat are included, the size of the neighborhood will make no difference except in the estimate of the weighting exponent (γ) on the distance weighting factor (DW, Eq. 2.5), and in the fit of the model.

For the field data, the 20 cm radius included very large numbers of neighbors in some cases, making the calculations very intensive and causing non-convergence of the iterative fitting procedures. A radius of 16 cm was more manageable, and was used for the analysis of the field data. In analysis of the field data, any plant closer to the edge of the circle than the neighborhoood radius was excluded as a target, since information about its full neighborhood was not collected. These plants could still provide information about the neighborhoods of other plants closer to the interior of the circle.

In all of the neighborhood analyses, secondaries were only considered for calculations if they were also primaries within the boundaries of the neighborhood radius.

Data from the four greenhouse experiments was analyzed using the Lindquist et al. (1994) model. Distinction of annuli in these experiments was a simple matter, since plants were placed on predetermined radii. The angular dispersion (Puettman et al. 1993) was calculated for each radius, and target individual sizes were regressed against the calculated dispersion index using an iterative non-linear fitting procedure (SAS PROC NLIN) which fit the best values for all parameters in a hyperbolic model. Due to difficulties associated with dividing neighborhoods into distinct annuli, the field data were not analyzed using this method.

All five data sets were analyzed using the proposed new secondary neighborhood models (Eqns. 2.8 through 2.12 with Eq. 2.4). Target individual sizes were regressed with a hyperbolic model against the sum of the neighbor weights using an iterative non-linear fitting procedure (SAS PROC NLIN) which fit the best values for all parameters for each data set. The models were tested as a nested series including the simple hyperbolic model (NN model, Eq. 2.3), the distance weighting model (DW, Eq. 2.5), the secondary neighbor number model (SNN, Eq. 2.8) and the two weighted secondary neighbor models (SDW and SAD, Eqns 2.9-2.12). The nesting structure of the models tested was branched, with NN being a special case of DW, DW being a special case of SNN, and

SNN being a special case of both SAD and SDW. For these nested models, an F-statistic was computed comparing each model with the simpler model which it generalizes, to test the probability that any reduction in the error (residual) sum of squares was due to chance alone. However, in order to compare these models with the Lindquist model or other models, the approximate adjusted R^2 was calculated as

$$\mathrm{Adj}R^2 \approx 1 - \frac{\mathrm{MSE}_{\mathrm{residual}}}{\mathrm{MSE}_{\mathrm{total}}} \qquad (2.16)$$

where $\mathrm{MSE}_{\mathrm{residual}}$ is the mean squared error for the residuals, while $\mathrm{MSE}_{\mathrm{total}}$ is the total mean squared error. This measure indicates the value of the model relative to other models with different numbers of parameters. While residual mean squared error ($\mathrm{MSE}_{\mathrm{residual}}$) by itself could be used equally well to compare models for one data set, the adjusted R^2, which approximates the proportion of total variance which is explained by the model, has the advantage of being scaled for easy reference across data sets.

In these analyses, the model with the highest value of the adjusted R^2 was determined to be the best model for a given data set. This criterion was closely linked to the results of the F-test, such that the model with the highest adjusted R^2 in a group was always the best-fitting model that was still significantly better than all simpler models with a probability level of 90%.

Results and Discussion

All of the models explored in this research explained a significant proportion of the variation in plant size for all five data sets, suggesting at a minimum that plant size is modified by the density of neighbors. This study further examined whether our ability to predict plant size can be significantly improved by the incorporation of information about the exact location of neighboring plants.

Polygon Analysis

Regression of target plant size against polygon area and the polygon shape index (PSI, Eq. 2.2) resulted in significant regressions for all data sets (Table 2.1). With all data sets, the parameter estimates for the intercept and for area were significantly different from zero ($p \leq .05$), but in only two cases was the parameter for the shape index significantly different from zero at this level. In those cases where the slope parameter for the shape index was significant, it was negative, suggesting that plant utilization of space may be optimized when the area available approaches a circle with the target at the center. However, the relative unimportance of the shape index suggests that to some extent plants respond plastically to limitations of space, filling the space available regardless of its shape. These results are in accordance with those of Mead (1966), who found that carrot diameter was related to the area of the Thiessen polygon, but was not as strongly related to statistics which described the shape of the polygon.

Examination of residual plots from regression analyses demonstrated that when there was a wide range of values, the response was concave upward, suggesting that individual plant size may not be directly proportional to space available, but may rather be proportional to space to some power. White and Harper (1996) suggested that plant biomass may be proportional to the volume occupied by the plant. Bussler et al. (1995) calculated volume as the plant height multiplied by the canopy area, and showed that the ratio of target volume to neighbor volume was a good predictor of target performance. Studies of mortality in perennial plant populations have determined that mean individual plant biomass is often proportional to plant density raised to the power of -3/2, suggesting in dimensionality that plants occupy and respond to available physical volume (Yoda et al. 1963, Mithen et al. 1984). When regression was performed using area to the power of 3/2 as the explanatory variable, the adjusted R^2 improved in all cases (Table 2.1), and the non-linearities in the residuals appeared to be reduced.

Data Set	Index	Adjusted R^2 Untransformed	Adjusted R^2 Area raised to power of 3/2
Montana GH#1	**	.4566	.5425
Montana GH#2		.1050	.1062
Minnesota GH#1		.6902	.6916
Minnesota GH#2	**	.8112	.9088
Montana Field		.1027	.1030

Table 2.1. Adjusted R^2 for polygon analyses. ** in Index column indicates that the parameter estimate for the shape index (Eq. 2.2) was significantly different from 0 at the 95% confidence level.

Neighborhood Analysis

In all cases, the adjusted R^2 of the best neighborhood analysis (Table 2.2) was better than the adjusted R^2 of the polygon analysis (Table 2.1), suggesting that the polygon model may not fully account for the effects of neighbors.

The nested structure of the new secondary neighborhood models allowed the determination of the 'best' model given alternatives of increasing levels of complexity. For the Minnesota greenhouse studies and the field study, the adjusted R^2 was maximized for the secondary neighbor number model (SNN, Eq. 2.8). For the first Montana greenhouse study, the model with maximum adjusted R^2 was the next most complex model, the SDW model (Eqns. 2.9-2.10), although the .0743 probability level for the F-test suggests that the improvement over the SNN model is only marginally significant. For the second Montana greenhouse study, the adjusted R^2 was maximized with the next simpler model, the DW model (Eq. 2.5). Realizing that this data set resulted from an experiment which was infested with insects and harvested prematurely, limiting the extent to which the spatial arrangement of neighbors could have become influential in determining plant size, the difference between the adjusted R^2 of these two models cannot be considered large. These results suggest that the SNN model may be quite effective in a range of situations.

	MT Greenhouse #1			MT Greenhouse #2			MN Greenhouse #1			MN Greenhouse #2			MT Field Harvest		
Model	df	P(F>f)	Adj R^2	df	P(F>f)	Adj R^2	df	P(F>f)	Adj R^2	df	P(F>f)	Adj R^2	df	P(F>f)	Adj R^2
NN	147	1.42×10^{-40}	0.7009	69	6.38×10^{-8}	0.3379	65		0.5520	64		0.9212	188	7.63×10^{-5}	0.0752
DW	146	0.2550	0.7015	68	0.0770	0.3586	63	0.0028	0.6467	62	0.018	0.9317	187	0.0209	0.0964
SNN	145	0.0016	0.7095	67	0.7888	0.3498	62	0.0061	0.6823	61	6.18×10^{-6}	0.9505	186	3.11×10^{-4}	0.1531
SDW	144	0.0743	0.7237	66	0.9600	0.3399	61	0.9848	0.6771	60	N/A	0.9344	185	0.9167	0.1486
SAD	144	0.1534	0.7215	66	0.9638	0.3399	61	0.4177	0.6805	60	0.4963	0.9500	185	N/A	0.1261
Lindquist	145		0.7022	67		0.3488	62		0.7067	61		0.9490			

Table 2.2 Summary statistics for neighborhood analyses. N/A indicates that the model was worse than the next simpler model. NN models for Minnesota Greenhouse experiments do not have an F-statistic because they are equivalent to the mean model.

The Lindquist model, with the same number of parameters as the SNN model, performed nearly as well in explaining variation in the data. In one case, the first Minnesota greenhouse experiment, the adjusted R^2 for the Lindquist model was marginally better than the SNN model, while in the remaining four data sets, the SNN model was better (Table 2.2).

Based on the similar performance of these models, selection of a model should be based on biological or computational considerations, or both. Computational considerations suggest a preference for the SNN model for most situations in the natural world. The computation of the SNN model is more readily automated than that of the Lindquist model, and may be more biologically realistic, because the SNN model operates in continuous space, while the Lindquist model requires the arbitrary positioning of discrete, non-interacting annuli. The SNN model has somewhat more potential for improvement and adaptation in future research, such as by altering the definition of the secondary neighborhood, or by adding other weighting factors for secondary neighbors to account for differences between secondaries of different species, biotype, or age.

The SNN model is an appropriate answer to the study objectives of developing an index of neighborhood competition which is flexible, theoretically sound, computationally tractable, and which compares faborably with existing models in its ability to predict individual plant yield. This model of individual plant performance in response to neighborhood spatial arrangement can also be scaled up to yield predictions of the effects of varying plant spatial patterns on total plant yield both in mixtures and in monocultures.

In agricultural systems, where dispersion of most species is moderated at least to some extent by humans, a practical model of the effects of spatial pattern on plant yield may result in practical management prescriptions, such as varying the pattern of crop seed placement or modifying equipment which may spread or stimulate germination of weed seeds. It may also alter calculation of economic threshold weed densities for weed management.

Pacala and Silander (1990) proposed that population dynamic models which account for individual plant performance in response to variable spatial distributions may in some systems represent a significant improvement over models which predict mean response. Integration of spatial arrangement into existing and new models of plant population dynamics and multiple species interactions may help clarify the causes of variation in the systems being modeled.

In the experiments which contained low or zero neighbor densities, density explained a substantially larger proportion of the variation in target plant size than did spatial arrangement, possibly calling into question the utility of the more complicated spatial model relative to simpler density models. However, the data do not suggest that spatial arrangement is an unimportant factor in predicting individual plant size. Rather, the results of this study suggest that differences in spatial arrangement may contribute to significant variation in plant performance between situations with higher mean plant densities, where the curve of the hyperbolic yield equation (Eq. 2.3) is relatively flat. For example, in the field data, where there were no particularly low density neighborhoods, neighborhood spatial arrangement actually explained a greater proportion of the variation than did neighborhood density. In a practical situation, such as when designing a crop planting system for optimal competitiveness with weeds, substantial advantage will be gained by simply increasing the crop density, but at higher densities, a greater advantage may be gained by optimizing the crop planting pattern.

While this model would in most cases uphold the conclusion of Fisher and Miles (1973) that the most competitive crop planting pattern will simply be the most uniform pattern, this model would still be useful in evaluating the relative economic value of practical planting pattern options given the limitations of available equipment. This model will also be useful in predicting the optimal planting pattern in situations where two or more crop species with different economic values are to be planted together, particularly in the presence of a weed. This model could also be applied in the

determination of an optimal planting pattern in no-till cropping, where there is a tradeoff involved in the selection of a row spacing in a weedy situation. Since the disturbance caused by planting equipment will often stimulate the germination of weed seeds, wider rows (which leave more space undisturbed) may be preferred, but in wide row plantings, crop yield potential and competitiveness with weeds emerging between the rows will be compromised. A practical model of the effects of different row spacings on crop yield in the presence of non-randomly distributed weed seedlings would be a useful tool in evaluating available planting strategies for these situations.

All of the models explored in this study explained a smaller proportion of the variation in the field data than in the greenhouse data. While this is probably due in large part to the lack of very low densities in the field data, it also suggests that other sources of variation were prominent in the field. The proportion of variation explained in the second Montana greenhouse experiment, which was infested by insects and harvested prematurely, was also low. These results confirm the predictions of Lindquist et al. (1994) that these models will explain less variation in field conditions or anywhere that environmental conditions are heterogenous. However, as noted by Lindquist et al. (1994), this does not suggest that variation in spatial arrangement is not important in heterogenous conditions. In fact, inclusion of spatial arrangement in the models improved the fit of models to the field data set as much as or more than in the greenhouse data sets. Rather, these results suggest that attention should also be paid to other sources of variation, including resource distributions, variations in the height or leaf area of neighboring plants, variations in individual genetic potential, and variation in age or emergence time of plants.

CHAPTER 3

INFLUENCE OF BARLEY PLANTING PATTERN ON GRAIN YIELD OF BARLEY AND INTERFERENCE WITH WILD OAT

Introduction

Wild oat (*Avena fatua* L.) is a troublesome weed wherever spring-planted cool season small grains are grown. Worldwide, it is estimated to cause annual yield losses of wheat and barley of 12,940,100 metric tons, of which approximately half are yield losses in North America alone (Nalewaja, 1977). Wild oat is the most costly weed problem in Montana (Fay and Stewart, 1981). Yield reductions due to wild oat in Montana are estimated to cost $50 million. An estimated 60% of wild oat infested acres in Montana are treated annually with herbicides valued at about $10 million. In recent years, concerns about environmental quality and economic efficiency have led to substantial interest in the potential for reduction of herbicide use. Widespread resistance of wild oat to many common herbicides has further accentuated the need for profitable alternative management strategies.

Bioeconomic weed management models have the potential to significantly increase the net profit of producers by recommending the least expensive control tactic which will successfully bring a weed population below its economic threshold level (Lybecker et al. 1991). Maxwell et al. (1994) are developing a bioeconomic model for prediction of long-term economic optimum thresholds for wild oat control in barley. They note that environmental conditions and cultural practices have the potential to cause variation in parameters of the model. If the competitive relationship between a crop and a weed is affected by the planting pattern of the crop, this could be an important consideration in prediction of crop yield loss or weed reproductive ability in a given situation.

Based on a review of early research relevant to the effects of crop seeding rate and row spacing on cereal grain yield, Holliday (1963) concluded that decreasing the distance between rows usually resulted in increased yields, and that increasing inter-row distances resulted in decreased yields. Holliday also noted that effects due to varying inter-row distance were typically amplified at either very low or very high seeding rates. Results varied substantially between experiments, suggesting that year, site, cultivar, and/or cultural effects might influence results.

Several more recent studies have found that narrow row spacings or decreased rectangularity can increase yield potential in barley (Brinkman et al. 1979, Sharratt 1993, Photiades and Hadjichristodoulou 1984, Finlay et al. 1971). However, barley yield response to narrow rows is not consistent over years, sites, and cultivars, as noted by Finlay et al. (1971) and Photiades and Hadjichristodoulou (1984).

In Montana, where grain production is usually moisture limited, barley is typically planted in rows 30-36 cm apart. Farmers avoid narrower row spacings, based on the perception that crop plants which are more evenly spaced draw extensively on stored soil water early in the season, and subsequently will not have adequate moisture for grain filling later in the growing season. The closer spacing of plants within rows in wider row planting arrangements is believed to limit early root growth due to inter-plant competition, so that moisture between the rows remains available later in the season. Research so far suggests that although early water use is indeed reduced in wider row spacings, evaporation from the soil surface is increased. As a result, final yields are rarely increased, and are more often decreased, by wider row spacing (Winter and Welch 1987, Tompkins et al. 1991, Jones and Johnson 1991).

Growth rate and final size of plants has been related to the number, size, location, species, and relative emergence time of neighboring plants, all of which contribute to limiting the "biological space" available to an emerging seedling (Ross and Harper 1972). Biological space can be

considered to be some integration of the light, water, nutrients, and space which are needed by all plants, and is closely related to the physical space where these are found. Fisher and Miles (1973) constructed a mathematical model of plant occupation of space based on the assumption that plants have non-overlapping zones of influence which represent their occupation of biological space. They further assumed that plants expand their zones of influence radially at predictable rates, and that final plant performance is proportional to the space which a plant has occupied. They concluded that in the presence of randomly distributed weeds, a uniform arrangement of crop plants at any given density would maximize crop yield by allowing for faster occupation of available biological space by the crop.

In general, direct impacts of row spacing or planting arrangement on crop yield can be separated from impacts of row spacing on crop-weed interference by comparing weed-free to weedy crop yields with various planting patterns. In analysis of variance, significant main effects of planting pattern will suggest direct impacts of planting pattern on crop yield, while a significant interaction between presence (or density) of weeds and planting pattern will be evidence of an impact of planting pattern on the intensity of interference between crop and weed. Differences in weed biomass or weed reproductive success between planting patterns may provide additional evidence that the planting pattern influences the competitive relationship of the two species. In the absence of a weed-free check, direct effects of planting pattern on crop yield cannot be differentiated from effects of planting pattern on yield loss due to weeds.

Favorable shifts in the competitive balance between crop and weeds when the crop is planted in narrow rows, as measured by increased crop yield or decreased weed growth, have been shown in soybeans and other large seeded legumes (Weaver 1986, Yelverton and Coble 1991, Burnside and Colville 1964, Wax et al. 1977, Wax and Pendleton 1968, Kust and Smith 1969, Burnside 1979, Walker et al. 1984, Howe and Oliver 1987, McWhorter and Sciumbato 1988, Legere and Schreiber

1989, Putnam et al. 1992, Buchanan and Hauser 1980, Malik et al. 1993, Teasdale and Frank 1982, Mullins et al. 1988), cotton (Bryson 1990, Rogers et al. 1976, Brown et al. 1985), maize (Choudhary 1981, Harvey and McNevin 1990), and wheat (Vander-Vorst et al. 1983, Teich et al. 1993). In other cases, no effect of row spacing on crop-weed interference have been found (Miller et al. 1983, Andries et al. 1974, Koscelny et al. 1991, Justice et al. 1993, Medd et al. 1985).

Kirkland (1993) in Saskatchewan investigated barley row spacings of 11, 22, 33, or 46 cm in combination with seeding rates of 50, 90, 150, and 220 kg/ha, in a field with a mixed infestation of wild oat, wild mustard (*Brassica kaber*), and volunteer canola (*Brassica campestris*). Decreasing row spacing and increasing seeding rate were both found to decrease weed biomass for each species and to increase barley yield. No interaction was detected between row spacing and seeding rate. Weed free responses to row spacing were not investigated, so impacts of row spacing on increased crop competitiveness with weeds cannot be clearly separated from direct effects of row spacing on crop yield.

Barton et al. (1992) conducted research in Idaho examining the effects of barley row spacing, barley seeding density, wild oat herbicide, and herbicide application rate on barley yield and wild oat biomass. They concluded that there were no differences of practical importance between row spacings of 9 cm and 18 cm.

The objectives of this research were to quantify the effect of planting pattern on grain yield of barley, on barley yield response to wild oat, and on wild oat seed production.

Materials and Methods

Field experiments were conducted in 1993 and 1994 at research farms in the Gallatin Valley of Montana. In 1993 the experiment was conducted at the Livestock Teaching and Research Center, located immediately southwest of Bozeman, on a Meadowcreek loam soil (fine-loamy over sandy-

skeletal, mixed Fluvaquentic Haploboroll, pH 8.2, OM 4%). In 1994 the experiment was conducted at the Arthur J. Post Agronomy Research Farm, located five miles west of Bozeman on Amsterdam silt loam (fine-silty, mixed Typic Haploboroll, pH 7.0, OM 3%).

In both experiments, plots were arranged in a randomized complete block design with three replications. Treatments were a factorial combination of four planting patterns and two wild oat treatments. For all planting pattern treatments, barley density was adjusted to a standard commercial planting density of 67 kg ha^{-1}.

In 1993, field preparation consisted of moldboard plowing of an established pasture of mixed perennial grasses and legumes followed by one pass of a disc harrow and two passes of a sweep cultivator. Established plots were 3 meters wide by 9 meters long, and blocking was along a gradient of depth to water table. Barley was planted with a double disk press wheel drill with an 18 cm row spacing. Four row spacing treatments were established: 18 cm row spacing, alternate drill rows plugged to produce a 36 cm row spacing, a double pass of the seed drill (18 cm row width) with the second pass at a 20° angle to the first, and a double pass of the drill (18 cm row width) with the second pass parallel to the first. Wild oat treatments were either no wild oats, or wild oat seeds scattered over the plot at a rate of 8.6 g m^{-2} or approximately 480 seeds m^{-2} , immediately prior to the final two cultivation passes on the day of barley planting. Precipitation during the period April to August was 47.1 cm, and the daily average temperature was 13.0 °C. Normal precipitation for the same period is 27.4 cm, and normal daily average temperature is 18.8 °C.

In 1994, field preparation consisted of three passes of a sweep cultivator in the spring prior to planting. Established plots were 3 meters wide by 4 meters long, and blocking was along a slight elevation gradient. Planting pattern treatments were 15 cm row spacing, diagonal double planting, 30 cm row spacing, or barley seed scattered over the plot immediately prior to the final two cultivation passes. For the row and diagonal treatments, barley was planted with an International

Harvester double disk drill with a 15 cm row spacing, with alternate drill rows plugged to produce a 30 cm row spacing, or two passes of the drill with a 15 cm row spacing, with the second pass at a 20° angle to the first. Wild oat treatments were either no wild oats, or wild oat seeds scattered over the plot at a rate of 17.3 g m^{-2} or approximately 800 seeds m^{-2} , immediately prior to the final two cultivation passes, which preceded barley planting by four days. Precipitation during the period April to August was 21 cm, 2 cm less than normal precipitation for that period, and the daily average temperature was 14.6 , 3.3 degrees cooler than normal daily average temperatures for the same period.

Wild oat and barley seedling densities were estimated each spring based on counts of seedlings in either two (1993) or three (1994) 0.25 m^2 quadrats in each plot. Wild oat seed production was estimated for each plot based on quadrat subsamples harvested immediately prior to barley harvest. In 1993, subsamples were harvested when wild oat plants were in the soft dough stage, and in 1994 when wild oat plants were mature. All wild oat and barley plants were collected from each quadrat and separated by species at barley hard dough stage. Roots and crowns were removed and above ground biomass was dried for three days at 55 °C. Seed was threshed from the plants of both species and weighed. Seeds were counted in random samples of wild oat seed, and mean mass per seed was computed from the slope of the regression of seed number against seed mass. The slope of the regression was never significantly affected by treatment. An estimate of harvested seed number was obtained for each sample by dividing the mass of harvested seed by the estimated mass per seed. An estimate of the number of seeds which had already dehisced from the plants in the quadrat prior to sampling was derived from visual estimates of the number of seeds missing from each empty or partially empty glume pair, based on the size of the glume pair and the number of seeds in undehisced spikelets on the same panicle. The estimated harvested seed number and the estimated dehisced seed number were added together to obtain a composite estimate of wild

oat seed production for each quadrat. In 1993, wild oats were harvested in three 0.10 m^2 quadrats per plot, while in 1994, wild oats were harvested in two 0.25 m^2 quadrats per plot. Barley grain was harvested from the center 1.4 meters of each plot using a HEGE plot combine. Harvested barley grain was subdivided and wild oat seed removed by hand from subsamples constituting approximately 10% of each plot sample. Wild oat free barley grain yield (kg ha^{-1}) was calculated based on the measured harvest area, corrected for the sample area removed in quadrat sampling.

In spring of 1995, wild oat populations resulting from each planting pattern treatment were estimated on plots relocated from the 1994 experiment based on counts of seedlings in three 0.25 m^2 quadrats in each plot.

In the 1993 experiment, the two parallel drill pass treatment, which was intended to approximate a 9 cm drill spacing, did not achieve this pattern consistently. In the 1994 experiment, barley establishment was low and uneven on the scattered treatment, probably due to poor soil-seed contact. These treatments were eliminated from the analyses, since they did not represent what they were intended to represent.

Pooling of data over years was considered, given the basic similarity between the remaining treatments, with the three pooled treatments being wide row spacing (30-36 cm), narrow row spacing (15-18 cm), and diagonal planting. Data for a dependent variable were pooled only if there were no significant year by treatment interactions and if error variances were similar for the two years.

Data were subjected to analysis of variance and treatment means were separated using the Tukey Studentized range procedure using SAS PROC GLM (SAS Version 6.1. Statistical Analysis System Institute, Inc. Cary, NC 27512). All tests were made at the α=0.05 level.

Wild oat seed production was analyzed using ANOVA with subsampling, with wild oat seed production as the dependent and planting pattern as the independent variables. This methodology, where the pooled sample variance among subsamples within plots is used as MSE (the estimate of

σ^2), takes into account random variation inherent in subsampling, as well as allowing the evaluation of block by treatment interaction effects, which must be used as MSE in a traditional randomized complete block analysis.

Wild oat density and seed production were analyzed using one-factor ANOVA for a randomized complete block design, and barley grain yield was analyzed using two factor ANOVA for a factorial treatment randomized complete block design.

Results and Discussion

Rectangularity

Barley establishment varied between years, probably due to seedbed differences, differences in seed lots, and possibly differences in planter calibration. Mean estimated barley density was 105 m^{-2} in 1993 and 132 m^{-2} in 1994. Barley density did not vary significantly by plot or planting pattern treatment. In 1993, mean rectangularities for the 36 cm and 18 cm row spacings were 13.3 and 3.3, respectively. In 1994, mean rectangularities for the 30 cm and 15 cm row spacings were 11.7 and 2.9, respectively. The rectangularity of the diagonal treatment could not be calculated directly, but since plants were distributed between as well as within 15-18 cm rows, the rectangularity of these treatments can be assumed to be comparable to that of a row spacing narrower than 15-18 cm. Therefore, the rectangularity would be less than 3.0. By assuming that the rectangularity was comparable to that of a crop at these densities planted in 8-9 cm rows, the rectangularity of these treatments can be calculated to be approximately 1.5.

Wild Oat Establishment and Reproduction

Wild oat establishment varied between years due to differences in seed lots, seeding rates, and weather patterns. Mean estimated wild oat density in infested plots in 1993 and 1994 was 77 m^{-2} and 42 m^{-2}, respectively. Wild oat density did not vary significantly by plot or planting pattern

treatment in either year, although there was a trend toward higher wild oat plant density in the diagonal treatment in both years (Table 3.1). Wild oat seed germination may have been stimulated in the diagonal treatment by seed bed disturbance and packing caused by the double pass of the tractor and drill.

Barley Planting Pattern	≈R	Wild oat plants m^{-2}			
		1993		1994	
		Mean	Std. Dev.	Mean	Std. Dev.
30-36 cm rows	12	74.4	48.5	30.0	11.0
15-18 cm rows	3	73.3	48.0	38.7	41.1
Diagonal	1.5	83.3	38.4	58.0	35.8

Table 3.1. Estimate of mean number of wild oat plants m^{-2} in each treatment. No significant differences were found at p=0.05 level. ≈R signifies approximate rectangularity.

Since there were significant year by treatment interactions, wild oat seed production was analyzed separately by year. There were no significant differences in wild oat seed production between planting patterns. Wild oat seed production means are shown in Table 3.2. Although it is possible that barley planting pattern may in the long term influence wild oat populations, no differences were detectable based on single year measures of seed production. The trend toward higher seed production in the diagonal treatment in both years seems to be related to the trend toward higher wild oat plant numbers in the diagonal treatment.

Barley Planting Pattern	≈R	Wild oat seed produced m^{-2}			
		1993		1994	
		Mean	Std. Dev.	Mean	Std. Dev.
30-36 cm rows	12	1927.2	2853.4	582.0	227.87
15-18 cm rows	3	2337.8	3255.2	523.3	528.25
Diagonal	1.5	2768.3	3839.6	1184.7	586.07

Table 3.2. Estimate of mean number of wild oat seeds produced per m^2. No significant differences were found at p=0.05 level. ≈R signifies approximate rectangularity.

Barley grain yield

Barley grain yield data were pooled across years, since there were no significant year by treatment interactions, and since the error variances were homogenous across years. Neither planting pattern nor wild oat infestation exerted significant main effects on barley yield, but the interaction effect between planting pattern and wild oat infestation was significant (p=.037). Means separation with Fisher's LSD test (Table 3.3) showed that only in the 30-36 cm wide rows did the weedy treatment yield significantly less than the weed-free treatment. As illustrated in Figure 3.1 and Table 3.3, although weed free barley yield was not affected by planting pattern, there was a significant decline in barley yield due to wild oats in the wide row (30-36 cm row width) spacing treatment, but no such decline in the narrower row spacing treatments. Higher wild oat densities might have resulted in significant declines in yield of the other treatments. Decreasing rectangularity of barley planting pattern from 12 to 3 decreases the susceptibility of the barley crop to yield loss from wild oats, however, in agreement with the work of Barton et al. (1992), further reductions in rectangularity did not influence barley competitiveness with wild oat. At higher wild oat and/or barley densities, differences between the 15-18 cm pattern and the diagonal pattern might have been more apparent. These results suggest that Montana barley producers should consider using a relatively narrow (15-18 cm) row spacing in situations where wild oat infestations are problematic.

Furthermore, research into bioeconomic wild oat management thresholds should further investigate the variable effects of row spacing on the interference between wild oat and barley.

Barley Planting Pattern	≈R	Barley grain yield (kg/ha)			
		No Wild Oat		Wild Oat Infested	
		Mean	Std. Dev	Mean	Std. Dev
30-36 cm rows	12	3102.3 A	1335.8	2487.5 C	1379.4
15-18 cm rows	3	2836.0 ABC	1468.3	2956.8 AB	1620.5
Diagonal	1.5	2602.7 BC	1274.9	2606.7 BC	1418.2

Table 3.3. Barley grain yield (kg/ha). Means followed by the same letter are not significantly different at p=0.05 level, compared across all treatments. ≈R signifies approximate rectangularity.

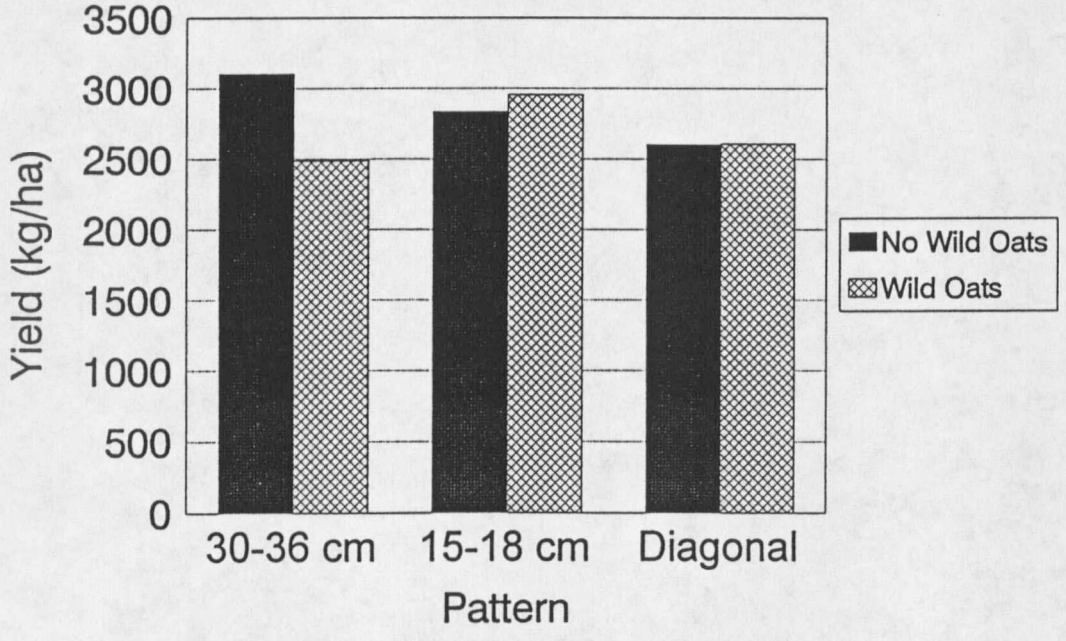

Figure 3.1 Barley grain yield (kg/ha).

CHAPTER 4

POPULATION DYNAMICS OF WILD OAT IN ALTERNATIVE CROPPING SYSTEMS

Introduction

Summer fallow has been used for nearly a century in dryland farming in Montana as a means of accumulating moisture, allowing consistent yields of small grains in areas with as little as 20 cm of annual precipitation. Approximately 18 to 28 % of the precipitation falling during the summer fallow period actually becomes available for the crop, the remainder being lost to evaporation, leaching, and runoff (Badaruddin and Meyer 1989, Smika 1990). Excess moisture flowing through the soil profile leaches out salts and may raise the groundwater table. Land becomes unproductive due to salinity where elevated water tables seep to the surface. Excess water also carries free nitrates and pesticides from the soil into the groundwater. Erosion potential is also substantially increased on fallowed land due to lack of soil surface cover and increased runoff. In addition, organic matter decline in fallowed soils has resulted in an increasing need for nitrogen fertilizer inputs to sustain economic yields of grain crops.

In response to these concerns, Montana researchers are recommending that farmers replace summer fallow with a green manure cover crop which can be terminated when it uses an allotted amount of soil moisture (Sims et al. 1985). If sufficient moisture is available, the cover crop may be utilized as a forage or seed crop. These crops offer protection against erosion, reduce the risk of saline seep, accumulate excess nitrates which might otherwise leach into the groundwater, and can maintain organic matter levels in the soil by utilizing excess moisture for biomass production. In

addition, most of the recommended crops are leguminous, and can fix atmospheric nitrogen. Increased yields of the subsequent grain crop have been seen in response to higher nitrogen levels, water infiltration rates, and water holding capacity following green manuring of a legume crop (Badaruddin and Meyer 1990, Abernethy and Bohl 1987, Badaruddin and Meyer 1989). Some of these green manure crops are interseeded with a grain crop, then become established during the subsequent fallow year either by reseeding from seeds produced during the grain crop season or, more commonly, by overwintering as biennials or perennials. In some cases, the interseeded legume produces enough seed that it never has to be reseeded, while in other cases it may be reseeded every time it is desired to have a green manure in the following year.

In addition to green manure crops, many farmers are being encouraged to investigate a variety of alternative cash crops in response to the impending possibility of changes in farm programs and international markets, as well as the need for increased flexibility in weed control and soil management.

Crop rotation and interseeding of a green manure crop have frequently been reported to have impacts on weed populations. This literature was thoroughly reviewed by Liebman and Dyck (1993), Altieri and Liebman (1986), Liebman (1988), and Froud-Williams (1988). They found that examples of weed suppression by crop rotation and green manure interseeding were far more numerous in the literature than examples of weed facilitation by crop rotation and green manure.

In response to the changes occurring in Montana dryland agriculture, it was our goal to quantify the effects of green manures and alternative cash crops on wild oat population dynamics in a spring cropping system on two organic farms in north central Montana. The experiment reported here was designed as a pilot study with multiple objectives. These include:

a)development of working relationships with Montana dryland organic farmers,

b)development of a better understanding of the alternative cropping systems being used by Montana dryland organic farmers,

c)Investigation of the magnitude and variability of effects of alternative cropping systems on weed population dynamics, for purposes of future experimental design,

d)development of hypotheses for testing in future experiments, and

e)evaluation of experimental methodology for research on the effect of cropping systems on weed populations.

Materials and Methods

Two experiment sites were established, one at the farm of Robert Quinn, 20 km south-southeast of Big Sandy, MT, and one at the farm of Jon Tester 19 km west of Big Sandy, MT, hereafter referred to as the Quinn site and the Tester site, respectively. Both of the farms on which the plots were established are certified organic, preventing the use of herbicide treatments. The experimental areas on both farms were selected for their very high populations of wild oats. Except where noted, the experiment was carried out in the same manner at the two sites.

Eight treatments were randomized into three blocks. Each treatment consisted of a three-year crop sequence beginning in spring of 1993 and continuing through the growing season of 1995. These treatments are outlined in Table 4.1. Details of the cropping systems and data collection varied from year to year.

1993	1994	1995
1. No crop (weedy control)	No crop (weedy control)	No crop (weedy control)
2. Barley	Cultivated Fallow	Barley
3. Cultivated Fallow	Barley	Cultivated Fallow
4. Barley + black medic intercrop	Black medic green manure	Barley+Black medic intercrop
5. Barley + alfalfa intercrop	Alfalfa green manure	Barley
6. Buckwheat +alfalfa intercrop	Alfalfa hay	Alfalfa green manure
7. Field pea green manure	Barley	Field Pea green manure
8. Buckwheat	Field pea green manure	Barley

Table 4.1. Outline of cropping sequence for treatments 1 through 8.

1993 Cropping Details

At both sites, the soil was worked twice with field cultivators in April-May. The second cultivation was timed to be within three days prior to planting. All crops at both sites were planted on May 13 1993. Barley and field pea were planted with farmer equipment. At the Quinn site this was an 8 foot John Deere hoe drill. At the Tester site, this was an 8 foot Minneapolis Moline double disk drill. Barley (cultivar "Hector") was planted at a rate of 79 kg/ha (70.5 lb/A), field pea (cultivar "Sirius") was planted at 121 kg/ha (108 lb/A), buckwheat was planted at 53.8 kg/ha (48 lb/A), and alfalfa (cultivar "Ladak") and black medic (cultivar "George") were both planted at 11.2 kg/ha (10 lb/A). At the Quinn site, one half of each of the field pea plots (treatment 7) was planted with tame oats (cultivar "Monida", planted at 79 kg/ha) in addition to the peas. At both sites, the field peas or pea/oat mixtures (treatment 7) were harvested on August 11 as a hay crop, with biomass above 10 cm removed from the plots. The barley, buckwheat, and no-crop treatments (treatments 1, 2, 4, 5, 6, and 8) were harvested on September 10 with a HEGE plot combine. At the Quinn site, the fallow plots (treatment 3) were fallowed once in early July and once on August 18, both times with a rototiller. At the Tester site, wet weather precluded an early fallow cultivation. The site was not visited again until early August, when wild oat plants heading and seeds were in the milk stage. Thus, to limit the production of viable seed, the fallow treatment was mowed by hand on August 11

and biomass above 10 cm removed from the plots. On August 18, this treatment was then fallowed with a rototiller. At the Quinn site, the plots were not disturbed following harvest until spring of 1994. At the Tester site, the plots were accidentally cultivated with a field cultivator in late September, which severely reduced black medic and alfalfa densities in 1994.

1994 Cropping Details

At the Quinn site, primary tillage was accomplished in treatments 1, 2, 3 and 7 with a disc cultivator on April 2 and April 18. Treatment 8 was hand-hoed on April 2. At the Tester site, primary tillage was accomplished in treatments 1, 2, 3, 7, and 8 with a field cultivator on April 1. Secondary tillage in treatments 3 and 7 was accomplished with a hand hoe on April 17. Treatment 8 (field pea) was planted on April 2 at the Quinn site with a Planet Jr. single row push-type seeder, and April 4 at the Tester site with a John Deere double disk drill (6 inch row spacing). Treatments 3 and 7 (barley) were planted on April 19 at both sites using the Planet Jr. seeder. Barley (cultivar "Coors Moravian 3) was planted at a rate of 79 kg/ha (70.5 lb/A), and field pea (cultivar "Trapper") was planted at a rate of 123 kg/ha (108 lb/A). Due to fall cultivation at the Tester site, the plant populations were damaged in all alfalfa and black medic plots. Alfalfa seed was scattered over all alfalfa plots at the Tester site at a rate of approximately 11 kg/ha, in hopes that some would re-establish in soil cracks. Treatments 2, 5, and 8 (fallow and green manure treatments except for black medic) were cultivated on June 14 with a field cultivator at Tester site. The black medic treatment was allowed to continue because the black medic plants had not yet produced viable seed. Treatments 2, 4, 5, and 8 (fallow and all green manure treatments) were cultivated on June 15 with a disc cultivator at the Quinn site. Treatment 6 (alfalfa hay) was clipped on June 15 at Tester site with a hand scythe. Clipping height varied from 1-14 cm. Treatment 6 was clipped on July 6 at The Quinn site with Robert Quinn's swather at a height of 10 cm. Clipped biomass was removed from plots at both sites. A hailstorm on July 10 severely damaged the barley in treatments 3 and 7 at the Quinn

site. Treatments 2, 4, 5, and 8 (fallow and green manure treatments) were cultivated a second time on July 15 at both sites with a field cultivator. Barley and no crop treatments (treatments 1, 3, and 7) were harvested with a HEGE plot combine at both sites on August 16.

1995 Cropping Details

All treatments were tilled with a field cultivator on April 29 at the Tester site and on May 2 at the Quinn site. At the Tester site, a rolling tine harrow was used in addition to the field cultivator. Field pea and barley treatments (treatments 2, 4, 5, 7, and 8) were planted at both sites on May 2. Peas (treatment 8) were planted with a Planet Jr. while barley was planted with farmer planting equipment. The same drill was used at the Quinn site as in 1993, while at the Tester site, a Case IH hoe drill was used. Barley (cultivar "Hector") was planted at a rate of 79 kg/ha (70.5 lb/A), and field pea (cultivar "Trapper" was planted at rate of 122 kg/ha (109 lb/A). At the Tester site, fallow and green manure plots (treatments 3, 6, and 7) were cultivated with a rototiller on June 16. At the Quinn site, fallow and pea plots (treatments 3 and 7) were mowed with a hand scythe on July 13. Fallow and green manure plots (treatments 3, 6, and 7) were mowed with a gas-powered trimmer at the Tester site on July 13. At the Quinn site, alfalfa hay plots (treatment 6) were swathed for hay on August 6. Biomass above 10 cm was removed from the plot. On August 8, treatments 3, 6, and 7 were fallowed again by hand hoeing at the Tester site. At the Quinn site, treatments 3 and 7 were fallowed with a field cultivator on 8 August. Treatment 6 (alfalfa green manure) did not appear to have the capacity to re-grow, so the stubble was allowed to remain.

Measurements

During each season, wild oat numbers were counted at least once using quadrat samples within the plots. Sampling methods and timing varied among years, but in general, a count was made prior to any destruction of wild oat plants due to tillage, fallow, green manure termination, or grain

harvest. In some cases, additional counts were made at other times. Quadrat samples typically included 2 to 5% of the area of the plot.

Wild oat seed bank size was estimated from soil samples taken in spring (April 1, prior to any emergence) and fall (October 23) of 1994. Twenty-seven cores with a diameter of 5.6 cm and a depth of 11 cm were removed from each plot. The cores were taken in a systematic sample, where the first core was taken from a random point within a one-meter square area in one corner of the plot. The remaining cores were removed in a one-meter square grid pattern (3 samples across the width of the plot, 9 samples down the length of the plot) starting from the first random point. The twenty seven cores were thoroughly mixed together and then two (spring) or three (fall) equal volume subsamples were taken from the mixed soil. These samples were dried, weighed, and washed through a sieve with 2mm by 2mm openings. Wild oat seeds were picked out of the remaining debris by hand. Seeds were considered viable and counted if they appeared intact and did not yield to firm pressure applied to their surface. Soil seed bank in the top 11 cm was calculated based on the number of seeds per gram of soil in the samples and the bulk density of the soil at each site, as calculated from samples of known bulk volume taken at each site. In fall of 1995 (11 October) 12 soil cores were taken from each plot, using a 1.5 meter square grid with a random starting point. These samples were pooled and all of the seeds in the pooled bulk of soil were washed out and counted in the same manner as in 1994.

Each year, grain heads and wild oat panicles were harvested just prior to combine harvest from three 0.1 m^2 quadrats (Tester site 1993) or two 0.25m^2 (remaining site-years) quadrats in each plot. Grain was threshed from the heads as an estimate of grain yield, and wild oat spikelets were counted as the best available estimate of wild oat seed production.

Grain from combine harvests was weighed separately for each plot and the proportion of that mass which was wild oat seeds was determined by weighing three small subsamples from each plot

sample, separating wild oat seeds out of the grain for these subsamples from each plot sample, and weighing the wild oat seeds. The proportion of the weight which was wild oat or barley was multiplied by the total sample mass to obtain an estimate of the amount of wild oat or barley harvested. In 1993, quadrat data were incomplete, so the estimated mass of combine harvested wild oat seed was used as a relative measure of wild oat seed production. This number was correlated ($r=0.82$, $p \leq 0.0001$) with the quadrat estimate of spikelet number for those plots at both sites with complete quadrat data ($n=29$) for 1993.

Analyses

The effect of treatment was evaluated for four different variables which describe wild oat populations: wild oat seed production in 1993 (as estimated by combine harvested wild oat mass), final soil weed seed density (estimated in fall of 1995), the change in soil weed seed density between spring 1994 and fall 1995, and the numbers of adult wild oat plants infesting the crop in each of three years were summarized using analysis of variance to evaluate the effects of treatment. Analyses were performed separately for the two sites using analysis of variance for randomized complete block designs for data within each site. The Tukey Studentized Range test was used for means separation.

Grain yields for each year and were analyzed using analysis of variance for randomized complete block designs. Barley and buckwheat grain yields were estimated from combine harvest in four out of six site-years and from quadrat harvest in five out of six site years. Yields were analyzed for differences between treatments using SAS (Version 6.1. Statistical Analysis System Institute, Inc. Cary, NC 27512) PROC GLM. When yields were estimated from quadrat harvest, the pooled within-plot variance is used as the mean square error, allowing estimation of treatment by block effects. When yields were estimated from combine harvest, within-treatment variance is used as the mean square error. The Tukey Studentized Range test was used to separate means.

Life Stage Population Model Parameter Estimation

In order to further elucidate the processes driving the variation in population dynamics of wild oats in different cropping systems, the data were also examined in the context of a life stage population model (Figure 4.1). In these analyses, data were pooled over sites and years, when similar data from more than one year were available. All standard errors and probability values given in the analysis are approximate and only relevant in relation to other standard errors in the experiment, due to the inflation of errors resulting from using population estimates rather than censused population totals for prediction.

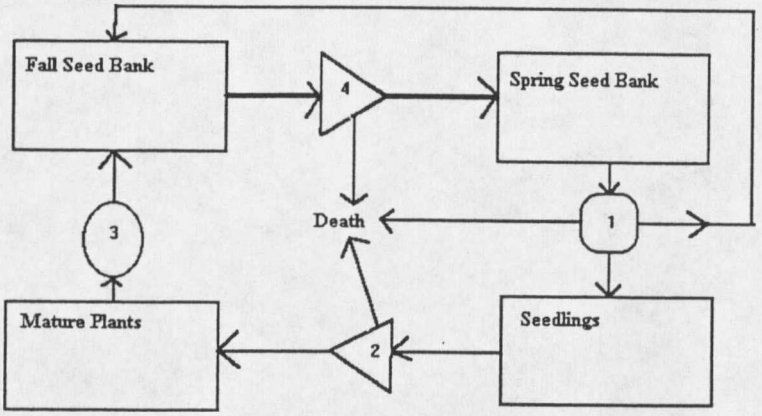

Figure 4.1. A life stage model of population dynamic processes, where large rectangles represent state variables, triangles represent binomial proportions, the square with rounded corners represents a multinomial proportion, and the ellipsoid represents a non-constant rate with some other undefined functional form.

The conceptual model shown in Figure 4.1 contains four rate functions. Two of these were binomial, one was multinomial, and the fourth had an undefined non-constant rate. A binomial quantifies a process with two possible outcomes, each with a distinct probability of occurrence, where the probabilities sum to one. For example, each seed which exists in the fall seed bank has some probability of dying or otherwise disappearing (due to emigration or predation) over the winter, and some probability of remaining viable until the spring. These probabilities sum to one. Binomial

probabilities were estimated using SAS PROC GLM to perform a weighted linear regression of the number of occurrences of one outcome against the total number of possible occurrences of either outcome (i.e. the total number of trials, or seeds in the seed bank in the above example) for a given plot with the intercept term suppressed. Continuing the winter seed survival example above, the number of surviving seeds was regressed against the total number of seeds at the beginning of the period. Since the variance of a binomial population is proportional to the number of possible occurrences of either outcome, the regression weights were 1/n, where n was the total number of trials. This method gives the maximum likelihood estimate of the binomial probability, and was used for estimation of all binomial probabilities in this experiment.

The multinomial function generalizes the binomial to processes which can have three or more possible outcomes. The fate of seeds in the spring seed bank is an example of a multinomial process, where seeds may either germinate and emerge as seedlings, they may die, or they may remain alive and dormant in the soil, to appear in the fall seed bank. This was the only multinomial process in the conceptual model (Figure 4.1), and it was estimated as a combination of two binomial processes.

<u>Spring Seed Bank Transition to Seedlings, Death or Fall Seed Bank</u> The rate function (#1 in Figure 4.1) describing the transition from the spring seed bank to either seedlings, death, or the fall seed bank was assumed to be a multinomial function. A seed which exists as part of the spring seed bank was assumed to have some probability of disappearing from the system (through death, emigration, or other losses), some probability of emerging as a seedling (recruitment), and some probability of remaining dormant until fall. These three probabilities should sum to one. While it was straightforward to estimate the probability of emergence as a seedling, there was no direct way of distinguishing between seed death and dormancy as causes for non-emergence in this study. Seed death and dormant survival were lumped into "non-emergence", allowing seed

emergence and non-emergence to be regarded as a binomial process, with the probability of non-emergence and the probability of emergence summing to one. Then, among non-emerged seeds, seed death and dormant survival were regarded as two possible outcomes of another binomial process.

Spring seed bank estimates were only made in 1994. The emergence probability was estimated for 1994 using weighted linear regression. This analysis was performed with the 1994 crop as a covariate, enabling a test of the hypothesis that the emergence probabilities were different for different crops.

The 1995 emergence probability was calculated on the basis of the fall 1994 seed bank. Weighted linear regression was used to estimate the probability that a seed in the fall seed bank would emerge in the spring. The probability of emergence was actually then the product of the probability that a seed would survive over the winter and the probability that a surviving seed would emerge. The probability of non-emergence was the sum of the probability that a seed died over the winter, and the probability that a surviving seed would not emerge.

The probability of survival for non-emerged seeds was estimated for the green manure, hay, and fallow treatments, where seed rain was not allowed. By assuming that negligible seed rain occurred in these plots, the transition of non-emerged seeds to the fall seed bank could be considered a binomial process, since the probability of non-emerged seed survival and the probability of non-emerged seed disappearance sum to one. The number of non-emerged seeds in 1994 was estimated for each plot from the difference between the estimated size of the spring seed bank in 1994 and the estimated number of seedlings in 1994. The number of non-emerged seeds in 1995 was estimated for each plot from the difference between the estimated size of the fall seed bank in 1994 and the estimated number of seedlings in 1995. The probability of seed survival was estimated using weighted linear regression in SAS PROC GLM, with the green manure species, hay, or fallow as a covariate. In 1994, the estimated probability was of survival of non-emerged seeds over the summer,

while for 1995, the probability was the probability of survival over the winter as well as survival of non-emerged seeds over the summer. These probabilities were used later to estimate seed rain.

Seedling Transition to Mature Plants or Death The transition from seedlings to mature plants (#2 in Figure 4.1) was assumed to be a binomial process, with the two possible outcomes being that a seedling survived to maturity or that a seedling died before maturity. Mature plants were defined as plants which produce viable seed. Several possible causes of mortality might be of interest. For example, the mortality rate may be density dependent, or dependent on the crop with which wild oats were growing. A cursory examination of the data revealed that tillage was apparently the major cause of mortality prior to maturation of plants, and the number of seedlings killed by tillage depended primarily on the date of the tillage operation. Since more seedlings emerged as the season progresses, the later a tillage operation occurred, the more seedlings were killed. The mortality rate was then be expressed as a function of the last tillage date prior to maturation of plants:

$$M = 1 - \frac{\text{Mature Plants}}{\text{Seedlings}} = f(DLT) \tag{4.1}$$

where M is the mortality proportion and DLT is the date of last tillage. Logistic regression was performed using SAS PROC CATMOD. The logistic regression was expressed as

$$\log \frac{\text{MaturePlants}_i}{\text{Seedlings}_i - \text{MaturePlants}_i} = b_0 + b_1 * DLT_i + \varepsilon_i \tag{4.2}$$

where b_0, b_1 are parameters of a linear regression, DLT_i is the date of last tillage for observation i and ϵ_i is a random deviate. Seedling density and treatment were included as covariates, in order to detect other variables which might have influenced mortality rates.

Mature Plant Transition to Fall Seed Bank Mature plants were assumed to produce seeds at a non-constant rate (#3 in Figure. 4.1) which declined with mature wild oat plant density, and which was related to the species composition of the plot (Harper 1977). In this study, the number of wild oat spikelets and the number of mature wild oat plants were counted in each quadrat where mature plants existed, and the number of spikelets was related to the number of mature plants with a non-linear fitted function. In order to complete the population dynamic model, the number of seeds that fell to the ground ("seed rain") was estimated. This number was used to estimate the ratio seed rain to spikelets for 1994 and 1995 data.

Spikelet Production per Plant. A common model of seed production per plant relates the inverse of the seed yield of a single plant to a linear function of the density of neighboring plants:

$$\frac{1}{W} = \beta_0 + \beta_1 * (N - 1) \qquad (4.3)$$

where W denotes single plant yield, β_0 and β_1 are regression parameters, and N denotes the density of neighboring plants (Willey and Heath 1969). The reciprocal of the parameter β_0 provides an estimate of the seed yield of a plant grown without competition, and the reciprocal of β_1 is an estimate of the maximum seed yield per unit area. This formula is consistent with what has been termed the "Law of Constant Final Yield", where total yield per unit area asymptotically approaches a maximum value. Eq. 4.3 may be rearranged to directly predict total seed yield per unit area:

$$Y = \frac{N}{\beta_0 + \beta_1 * (N - 1)} \qquad (4.4)$$

where Y denotes total seed yield, N denotes total crop density, and β_0 and β_1 are the same as in Eq. 4.3. It was assumed that these equations could also be used to quantify spikelet production in wild oats in this study. The parameters of Eq. 4.3 were fit using a generalized linear models procedure with the inverse link and gamma distributed errors, using the statistical package GLIM (version 3.77,

update 0, Royal Statistical Society, London 1985). This procedure, which is recommended for data of this type by McCullagh and Nelder (1989) and Crawley (1993), estimates the maximum likelihood values of the parameters when the data are non-normally distributed.

In order to test whether cropping system treatments had an effect on the functional relationship between weed density and weed seed production , the crop species and the intercrop or previous green manure crop species were included as covariates in the analysis. The significance of each covariate was judged by an F-test on the change in scaled deviance when a factor was eliminated from analysis. Scaled deviance is a generalized calculation of the deviation of the data from a model, and includes the sum of squares as a special case when errors are normally distributed.

Spikelet Transition to Seed Rain Since seed rain was never directly measured, the best estimate for seed rain was the size of the fall seed bank less the estimated number of seeds which survived from the most recent previous seed bank measurement. Seed rain was estimated for fall of 1994 using the estimated probability of seed survival from spring of 1994, while seed rain for fall of 1995 was estimated using the estimated probability of seed survival from fall of 1994. The use of these survival probabilities assumed that the probabilities of wild oat seed survival were not significantly affected by the crop species. The ratio of estimated seed rain to spikelets was estimated using weighted linear regression with current and previous crop species as covariates for both 1994 and 1995.

Fall Seed Bank Transition to Spring Seed Bank. The rate of transition from the fall seed bank to the spring seed bank (#4 in Figure 4.1) was assumed to be of a binomial form because a seed in the fall seed bank had two possible fates, either disappearance (which could include death, emigration, predation, or late fall germination) or survival until spring. In this study the spring seed

bank was never estimated following an estimate of the seed bank the previous fall, therefore it was not possible to estimate the probability of winter survival with the data from this experiment.

Results and Discussion

The summer of 1993 was cooler and wetter than normal, creating ideal conditions for wild oat emergence and growth (Table 4.2). Buckwheat, a warm season crop, did not grow well in 1993, and was inundated by wild oats. Wild oat seed production in 1993, shown in Figure 4.2 and Table 4.3, was higher in the buckwheat treatments than in barley treatments, significantly higher at the Quinn site. The poor performance of buckwheat under these conditions led to the decision not to repeat the use of buckwheat in this study. Also notable in the 1993 wild oat seed production data (Figure 4.2, Table 4.3) were the consistently higher wild oat seed production in alfalfa intercrops with barley and buckwheat than in the barley and buckwheat sole crops, suggesting that alfalfa may somehow encourage wild oat growth. Black medic intercrops with barley also had slightly lower wild oat seed production than barley monocultures at both sites (Figure 4.2, Table 4.3). The no crop control showed significantly higher wild oat seed production than all crop rotation treatments at the Quinn site, while at the Tester site, the no crop control showed significantly higher wild oat seed production than all of the barley treatments, but was not significantly different from the buckwheat treatments (Figure 4.2, Table 4.3).

	Precipitation, cm	Mean Temperature, °C
Normal	22.9	16.2
1993	33.7	13.7
1994	14.9	16.1
1995	41.8	13.4

Table 4.2. Total precipitation and mean temperature for the period April-August for 1993-1995, from the weather station at Big Sandy, MT.

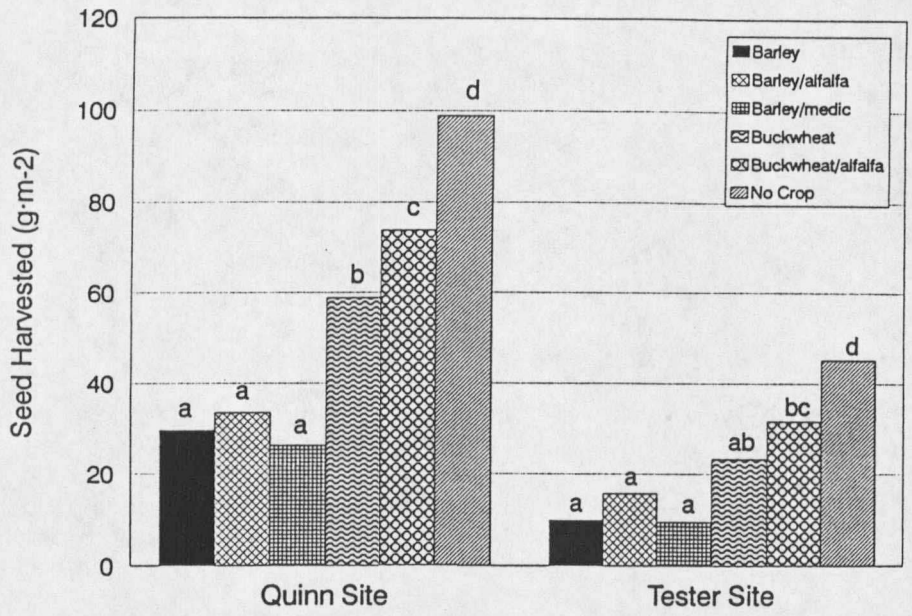

Figure 4.2. Relative wild oat seed production in 1993, by treatment and site, estimated from proportion of combine harvested seed which was wild oat seed, by weight. Bars with the same letter are not significantly different at the 0.05 level.

Treatment	Quinn			Tester		
		Mean (grams seed/m²)	Std.Dev.		Mean (grams seed/m²)	Std.Dev.
1)No Crop	A	98.916	14.514	A	45.138	9.206
6)Buckwheat-Alfalfa hay-Alfalfa	B	73.782	2.782	AB	31.626	8.756
8)Buckwheat-Pea-Barley	B	58.822	5.049	AB	23.312	13.225
5)Barley-Alfalfa-Barley	C	33.490	4.689	B	15.727	2.697
2)Barley-Fallow-Barley	C	29.673	6.321	B	9.924	6.146
4)Barley-Black medic-Barley	C	26.240	0.908	B	9.562	1.229

Table 4.3. Relative wild oat seed production in 1993, by treatment and site, estimated from proportion of combine harvested seed which was wild oat seed, by weight. Means with the same letter are not significantly different at the 0.05 level.

Adult wild oat densities at each site and year are summarized in Table 4.4. Wild oat densities reflect a number of different population processes, including the number of seeds in the seed bank and the probability that seeds will emerge after the last tillage date. In 1993, at the

beginning of the experiment, plants seemed to be randomly distributed among treatments. The significant difference between the barley-alfalfa and the buckwheat treatment is difficult to explain, and may be an anomaly. If the buckwheat inhibited wild oat emergence, the effect was not as strong when the buckwheat was intercropped with alfalfa. The higher density of wild oats in the barley-alfalfa intercrop and the buckwheat-alfalfa intercrop compared to the barley and buckwheat sole crops, respectively, lend further support to the suggestion that alfalfa intercrops may positively influence wild oat emergence and growth.

Year	Treatment	Quinn			Tester		
		Mean (plants·m^{-2})		Std.Dev.	Mean (plants·m^{-2})		Std.Dev.
1993	5)Barley-Alfalfa-Barley	A	1070.2	220.54	A	77.78	1.92
	4)Barley-Black medic-Barley	AB	829.8	438.43	A	37.78	21.43
	2)Barley-Fallow-Barley	AB	838.0	159.33	A	72.22	6.98
	1)No Crop	AB	490.4	153.38	A	74.44	19.25
	6)Buckwheat-Alfalfa hay-Alfalfa	AB	416.2	112.89	A	134.45	124.02
	8)Buckwheat-Pea-Barley	B	220.0	14.14	A	33.33	26.46
1994	1)No Crop	A	1470.2	572.02	A	646.2	128.28
	3)Fallow-Barley-Fallow	A	532.2	363.31	A	416.4	524.33
	7)Pea-Barley-Pea	B	405.3	49.55	A	318.2	231.87
1995	1)No Crop	A	406.00	35.16	A	481.81	89.48
	4)Barley-Black medic-Barley	A	250.67	41.68	A	454.26	173.40
	5)Barley-Alfalfa-Barley	A	314.02	65.21	AB	233.88	22.65
	8)Buckwheat-Pea-Barley	A	334.02	134.01	B	116.38	98.16
	2)Barley-Fallow-Barley	A	417.33	196.22	B	105.13	53.08

Table 4.4. Adult wild oat densities (plants·m^{-2}) for each year at both sites. Means preceded by the same letter are not significantly different at the 0.05 probability level, as estimated by the Tukey studentized range test.

In 1994, average wild oat densities had increased in the no crop treatment at both sites, by 30% at the Quinn site and by 730% at the Tester site. The lower rate of increase at the Quinn site

probably reflects density dependent population regulation of the higher initial population. The fallow-barley-fallow and pea-barley-pea treatments at the Tester site also showed higher wild oat plant densities than any treatment had in 1993, suggesting either population increase or differences in recruitment between the two years. Since these two treatments were fallowed late in 1993, the increases may have been due to seed rain that occurred in 1993 prior to the fallowing operations. In 1994 the pea-barley-pea treatment had the lowest number of wild oat adults at both sites (Table 4.4).

In 1995, significant differences in adult populations had evolved at the Tester site, but not at the Quinn site. The no crop treatment again had the highest densities, but there were no consistent trends across sites among the other treatments. The barley-black medic treatment had the highest densities, after the no crop treatment, at the Tester site, but the lowest densities at the Quinn site. The high densities at the Tester site were readily attributable to the fact that this was the only treatment where wild oats were allowed to produce viable seed in all three years, because of the late fallowing of the green manure in 1994, while at the Quinn site, no wild oat seeds were produced in this treatment when it was fallowed in 1994. The relatively low density of wild oat plants in the buckwheat-pea-barley treatment at the Tester site in 1995 was notable, given that a relatively large amount of wild oat seed was produced in the buckwheat treatments in 1993 (Figure 4.2, Table 4.3).

The ultimate effects of each treatment can be summarized most completely by characterizing the soil seed bank at the end of the experiment in fall of 1995 (Table 4.5). The initial wild oat seed bank at the beginning of the experiment was assumed to be randomly variable within blocks at each site. At the Tester site, there were no significant differences in final seed bank between treatments, except for the no crop treatment, whose soil seed density was at least twice as high as that in any other treatment. Similarly, the no crop treatment had the highest soil seed density at the Quinn site. At both sites, the two treatments that had barley in 1994 and fallow in the other years had the lowest final seed banks. This is probably because 1994, the only year that wild oat plants in these

treatments were allowed to produce seed was not a particularly favorable year for wild oat emergence and growth (Table 4.2), while 1993 and 1995, both of which years most other treatments were allowed to produce seed, were favorable years for wild oat emergence and growth. At the Quinn site, no other significant differences appear, although the appearance of the buckwheat-alfalfa hay-alfalfa green manure treatment near the bottom of the list is again of interest, considering the very high numbers of seeds produced by wild oats in the buckwheat treatments in 1993.

Treatment	Quinn			Tester		
	Mean (seeds·m^{-2})		Std.Dev.	Mean (seeds·m^{-2})		Std.Dev.
1)No Crop	A	12357.0	2173.9	A	8829.2	1349.5
8)Buckwheat-Pea-Barley	AB	11011.1	575.35	B	2090.6	1329.4
5)Barley-Alfalfa-Barley	AB	9789.2	490.18	B	4048.2	3099.7
4)Barley-Black medic-Barley	AB	9556.5	1011.5	B	3128.7	1679.9
2)Barley-Fallow-Barley	B	8637.1	602.91	B	2887.6	2548.6
6)Buckwheat-Alfalfa hay-Alfalfa	B	7626.7	1680.3	B	1207.6	193.15
3)Fallow-Barley-Fallow	C	2135.0	667.47	B	1064.3	810.62
7)Pea-Barley-Pea	C	1760.2	1119.5	B	1171.6	94.682

Table 4.5. Estimated final densities of soil seed pool, fall 1995. Means preceded by the same letter are not significantly different at the $p<0.05$ level.

Because the buckwheat treatments did produce such high numbers of wild oat seeds in 1993, those treatments were not on an equal footing with those treatments that were planted to barley in 1993, when comparing the effects of different green manure regimes. To adjust for this, the change in wild oat soil seed density (ΔS) between spring of 1994 and fall of 1995 was computed. Analysis of variance on this quantity revealed that there were no significant site by treatment interactions, so the sites were pooled for the analysis. The change in estimated seed bank density (ΔS) ranged from an increase of 4535 seeds m^{-2} in the no crop treatment to a decrease of 3247 seeds m^{-2} in the buckwheat-alfalfa hay-alfalfa treatment, with significant treatment effects (Figure 4.3, Table 4.6).

Again, the two treatments which had barley in 1994 and green manure or fallow in 1993 and 1995 compared favorably to other treatments, having decreasing seed densities (negative ΔS).

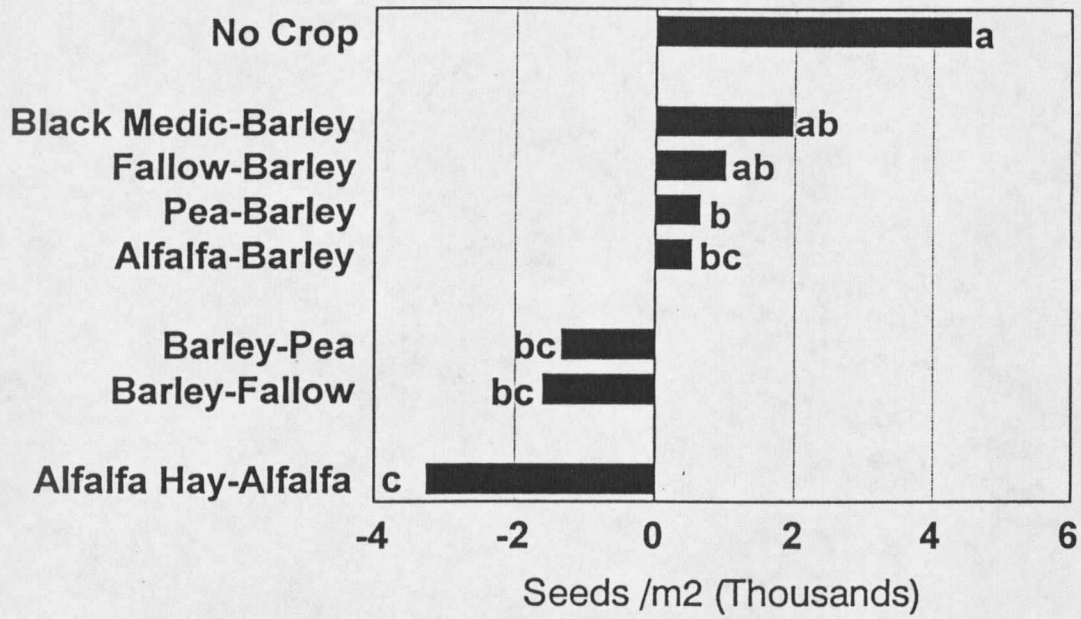

Figure 4.3. Change in estimated density of soil seed pool from spring 1994 to fall 1995 (ΔS). Bars with the same letter are not significantly different at the $p<0.05$ level.

Treatment	ΔS (seeds m^{-2})		Std.Dev.
1)No Crop	A	+4535.5	2046.6
4)Barley-Black medic-Barley	AB	+1956.9	1352.5
2)Barley-Fallow-Barley	AB	+996.7	1683.4
8)Buckwheat-Pea-Barley	B	+632.4	2272.8
5)Barley-Alfalfa-Barley	BC	+514.0	1945.6
7)Pea-Barley-Pea	BC	-1333.8	1142.7
3)Fallow-Barley-Fallow	BC	-1597.9	1907.1
6)Buckwheat-Alfalfa hay-Alfalfa	C	-3246.7	2436.0

Table 4.6. Change in estimated density of soil seed pool from spring 1994 to fall 1995 (ΔS). Means preceded by the same letter are not significantly different at the $p<0.05$ level.

Barley yield means and standard deviations are summarized by year, site and treatment in Tables 4.7 and 4.8 and in Figures 4.4, 4.5, and 4.6. At the Quinn site in 1994, barley following fallow yielded significantly more than barley following peas. This difference may be a result of moisture stress, because the field pea crop in 1993 was not terminated until late in the season, by which time the vegetation could have used a considerable amount of soil moisture. The lack of differences in the Tester site in 1994 was attributed to the fact that the vegetation in the pea and the fallow treatments was not terminated until late in the season in 1993. A hailstorm practically destroyed the crop at the Quinn site in 1994, which may explain why the yield in the properly fallowed treatments was no higher than the yields at the Tester site, where fallowing was late in 1993.

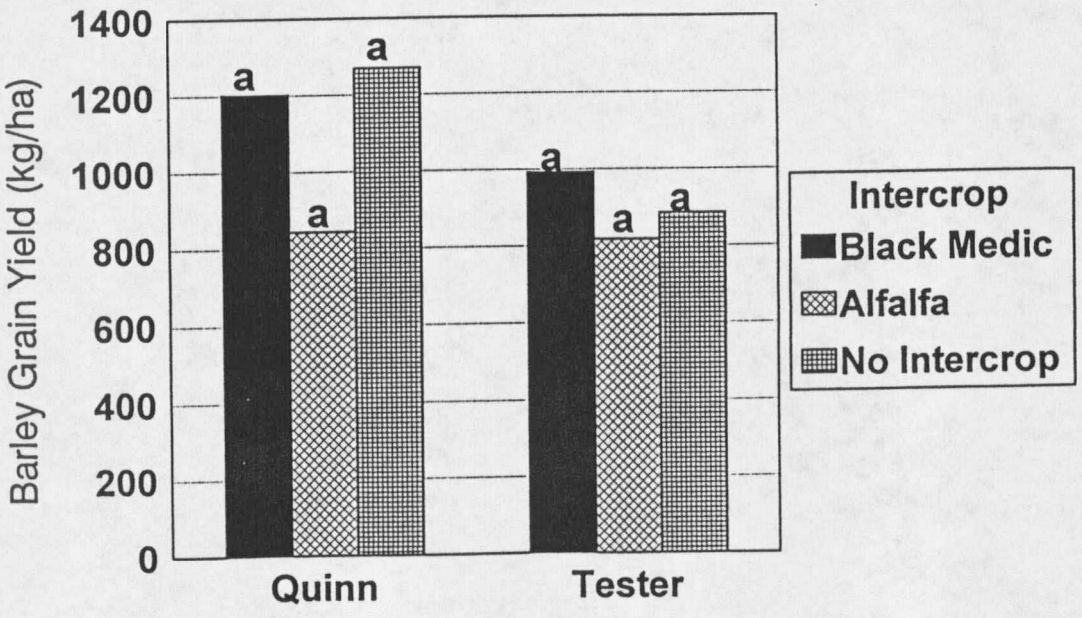

Figure 4.4. Barley yields in 1993, from combine harvest. Bars with the same letter within a site are not significantly different at the $p<0.05$ level.

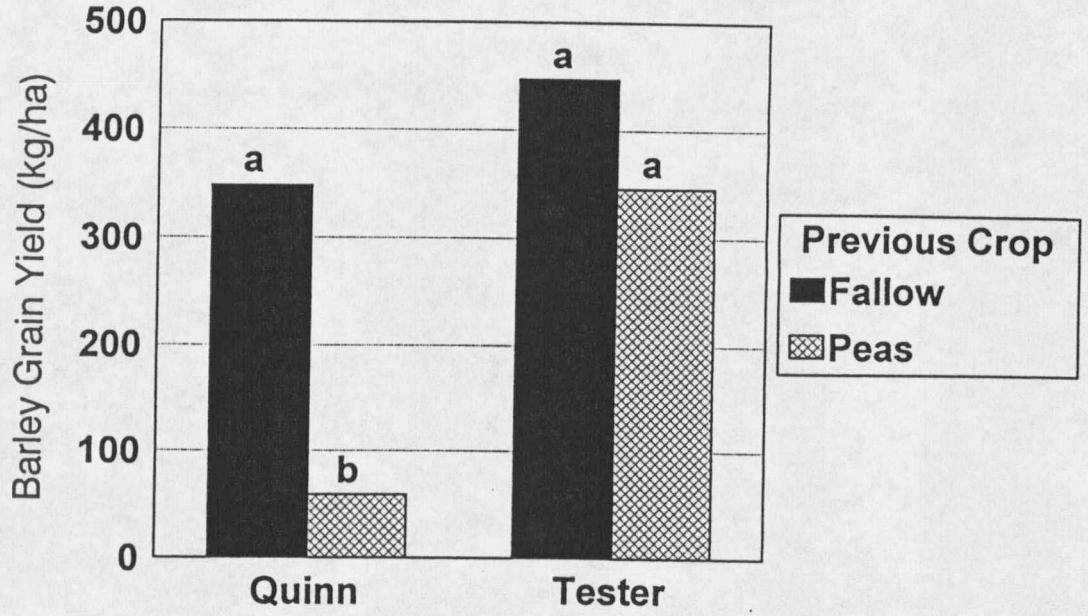

Figure 4.5. Barley yields in 1994, from combine harvest. Bars with the same letter within a site are not significantly different at the $p<0.05$ level.

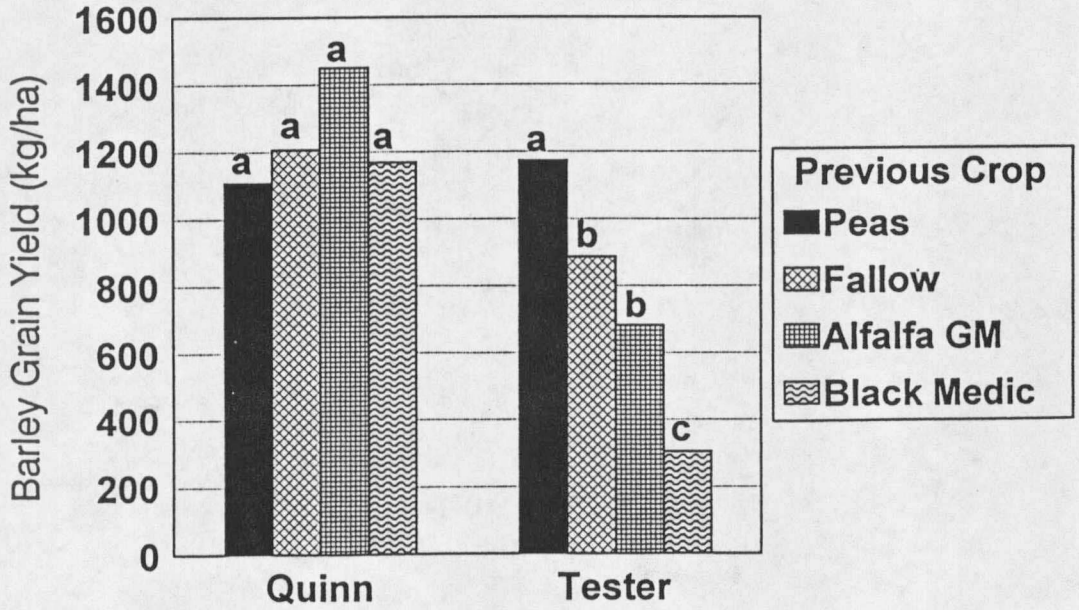

Figure 4.6. Barley yields in 1995, from quadrat harvest. Bars with the same letter within a site are not significantly different at the $p<0.05$ level.

Year	Intercrop (1993) or Previous Crop	Quinn			Tester		
		Mean (g/m2)		Std.Dev.	Mean (g/m2)		Std.Dev.
1993	Black Medic				A	103.06	21.22
	Alfalfa				A	78.74	33.74
	No Intercrop				A	76.47	26.24
1994	Fallow	A	47.53	28.04	A	43.58	10.79
	Peas	B	9.96	5.62	A	35.38	27.68
1995	Peas	A	110.69	37.87	A	117.27	20.39
	Fallow	A	120.57	45.79	B	88.573	24.67
	Alfalfa GM	A	144.97	37.12	B	68.08	6.81
	Black Medic	A	116.69	33.06	C	30.367	9.50

Table 4.7. Barley yields from quadrat estimates. Means with the same letter within a site-year are not significantly different at the $p<0.05$ level.

Year	Intercrop (1993) or Previous Crop	Quinn			Tester		
		Mean (g/m2)		Std.Dev.	Mean (g/m2)		Std.Dev.
1993	Black Medic	A	120.98	37.03	A	99.08	3.75
	Alfalfa	A	84.30	49.92	A	81.64	19.94
	No Intercrop	A	126.86	31.95	A	88.43	29.96
1994	Fallow	A	34.77	4.08	A	44.72	13.12
	Peas	B	5.87	2.68	A	34.58	9.31

Table 4.8. Barley yields from combine estimates. Means with the same letter within a site-year are not significantly different at the $p<0.05$ level.

At the Tester site in 1995, barley following peas yielded significantly more than all other treatments, while barley following black medic yielded significantly less than all other treatments. These differences were probably due mostly to the differing balances between moisture use and nitrogen contribution by different green manure species. The 1994 alfalfa green manure treatment may have contributed less nitrogen than the pea treatment, since the alfalfa stand was damaged by fall cultivation. The black medic green manure treatment was not fallowed until a month later than

the other treatments in 1994, possibly allowing it to use more moisture. The relatively low yields in the black medic and alfalfa treatments at the Tester site may also be due in part to higher wild oat plant numbers growing with the crop in 1995 in these treatments than in the pea and fallow treatments (Table 4.4). This experiment demonstrated the importance of timely fallowing of green manures, even in wet years.

Life Stage Population Model Parameter Estimation

In order to further elucidate the processes driving the variation in populations of wild oats in different cropping systems, the data were examined in the context of a life stage population model (Figure 4.1).

Spring Seed Bank Transition to Seedlings, Death, or Fall Seed Bank Estimated emergence probabilities for 1994 and 1995 are shown in Figure 4.7 and in Table 4.9. The probability of emergence from the most recently measured seed bank was significantly different between treatments in 1994 ($p=.0007$) and in 1995 ($p=.0231$). In 1994, differences were due to the alfalfa hay and alfalfa green manure treatments having very low emergence rates, while in 1995, differences seem to be due primarily to the high wild oat emergence rate in barley following alfalfa green manure.

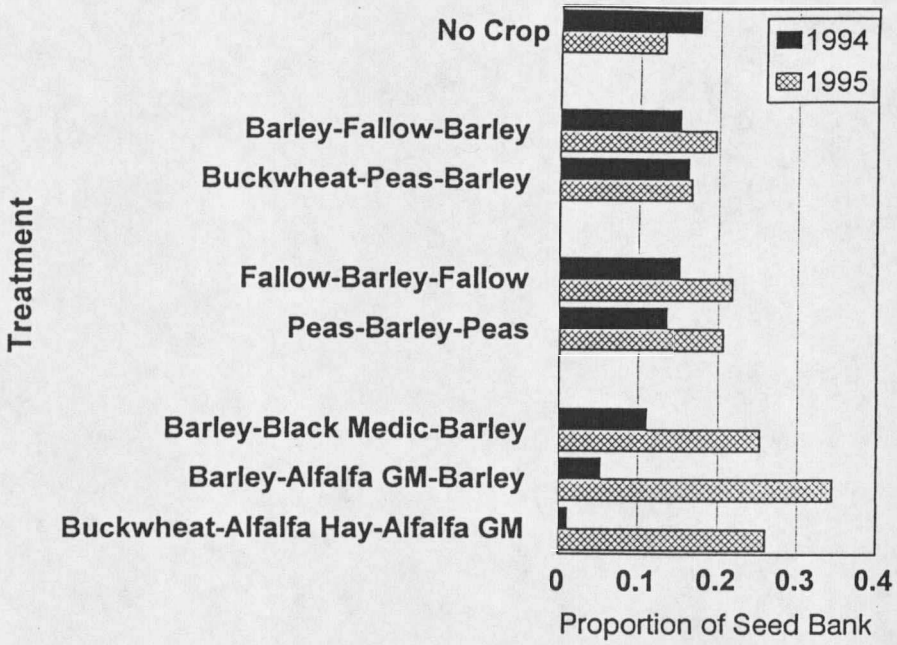

Figure 4.7. Estimated probabilities of emergence (pE) in different crops in 1994 and 1995. For 1994, the probabilities are based on emergence from the spring seed pool, while for 1995, the probabilities are based on emergence from the seed pool the previous fall.

	1994		1995	
Treatment	pE	Std. Error	pE	Std. Error
1)No Crop	0.1747	0.0267	0.1312	0.0283
2)Barley-Fallow-Barley	0.1511	0.0302	0.1957	0.0416
3)Fallow-Barley-Fallow	0.1512	0.0368	0.2174	0.0465
4)Barley-Black Medic-Barley	0.1103	0.0334	0.2527	0.0373
5)Barley-Alfalfa GM-Barley	0.0525	0.0299	0.3436	0.0403
6)Buckwheat-Alfalfa Hay-Alfalfa GM	0.0108	0.0267	0.2596	0.0321
7)Pea-Barley-Pea	0.1354	0.0390	0.2061	0.0452
8)Buckwheat-Pea-Barley	0.1615	0.0271	0.1659	0.0429

Table 4.9. Estimated probabilities of emergence (pE) in different treatments in 1994 and 1995. For 1994, the probabilities are based on emergence from the spring seed pool, while for 1995, the probabilities are based on emergence from the seed pool the previous fall.

To compare emergence probabilities directly across years, the rate of winter survival of wild oat seeds would need to be known. The rates for 1995 were actually the probabilities of emergence

from the spring seed bank multiplied by the probability of surviving the winter. Thus the rates of emergence from the spring seed bank in 1995 would actually be higher than the rates shown, which were already higher than the rates in 1994. The higher emergence probabilities in 1995 can probably be largely explained by the fact that 1994 was an unusually dry year, while 1995 was cooler and wetter (Table 4.2). Emergence probabilities for 1993, which was also cooler and wetter, would be expected to be similar to those in 1995.

In all treatments, at least 66% of the seeds did not emerge and could either have died or survived, remaining dormant until the fall. The summer seed survival probability for 1994 and the winter-summer seed survival probability for 1995 were estimated for the fallow and green manure treatments using a method which requires the assumption that no viable wild oat seeds were produced in these treatments. The estimated probability of summer survival in 1994, given non-germination, was 0.7896, with a standard error of 0.1059. Treatment had no significant effect on this probability (p=0.9479). The estimated probability of survival from fall 1994 to fall 1995, given non-germination, was 0.7519, with a standard error of 0.1161. Treatment had no significant effect on this probability (p=0.4705). Although there was no way of estimating rates for the barley or no crop treatments in either year, the absence of significant differences between different green manures, hay, and fallow suggests that survival of dormant seeds was not an important determinant of variation in wild oat populations between cropping systems in this experiment.

Since the alfalfa hay treatment was not tilled in 1994, and there were no significant differences in summer seed survival between treatments, it was assumed that tillage and crop species do not substantially influence summer survival. Then the probability of survival, given non-emergence, was combined with the probability of emergence(pE, Table 4.9), to yield estimates of the probabilities of the three outcomes of the multinomial process. For 1994, the probability of dormant

survival over the summer (pSS) was 0.7896*(1-pE), while the probability of death or disappearance was (1-pSS-pE).

An independent estimate of seed rain would allow summer survival to be estimated from the size of the fall seed bank less the amount of seed rain. We did not directly estimate seed rain in this experiment for logistical reasons. It has been suggested (R. Davidson, pers. comm.) that an effective way to estimate these proportions is to sample the seed bank at three times during the season: in the spring immediately prior to germination, during the growing season after all emergence is finished but before new seed rain, and then after seed rain.

Seedling Transition to Mature Plants or Death The logistic regression procedure indicated that the date of last tillage was a significant predictor of the probability of seedling mortality. The observed mortality rates for all plots, shown as scattered points, and the fitted line are shown in Figure 4.8. The statistical fit was good, suggesting that the date of last tillage was an important variable determining the populations dynamics of wild oats in these cropping system. In the interest of investigating the effect of other factors on seedling mortality, current crop, previous crop or intercrop, and seedling density were included as covariates in the logistic regression. All of these and their accumulated interaction effects significantly improved the regression, resulting in a very complex model. The effects of factors other than tillage date are very difficult to interpret in this context, because they could have a variety of causes. The observed mortality rate will be influenced in large part by the relative speed of emergence before and after the last tillage date, which may be influenced by weather variables, the amount of tillage prior to the last tillage date, and by effects of the crop on seedling emergence after the last tillage. Mortality actually caused by interference between weed seedlings and other weed or crop seedlings would be indistinguishable from other causes of mortality.

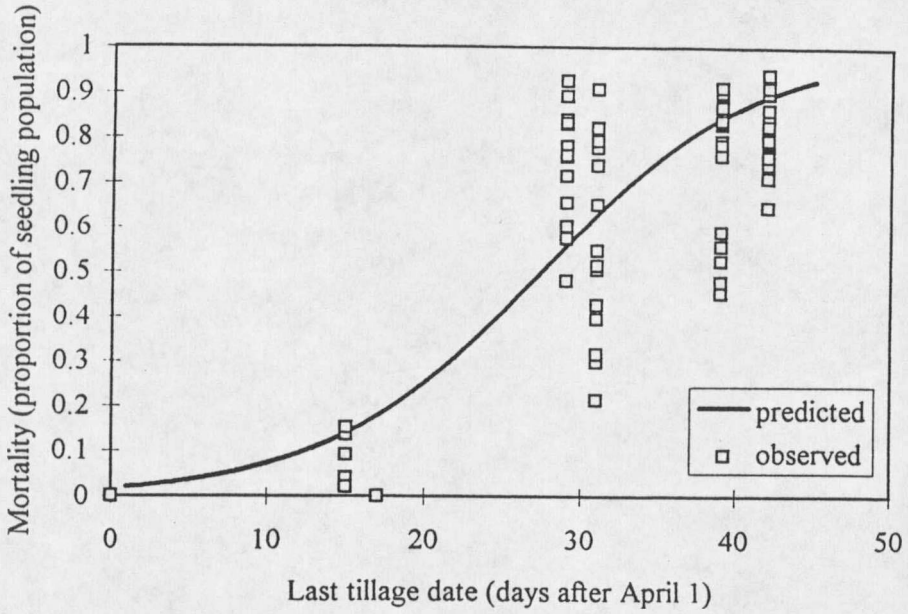

Figure 4.8. Prediction of seedling mortality as a function of date of last tillage.

Spikelet Production per Plant The rate of spikelet production per plant was described well by a function of the density of adult plants (Eq. 4.3) when the parameters were fit by generalized linear models. When this equation is arranged to represent the relationship between wild oat spikelets·m^{-2} and wild oat plants·m^{-2} (Eq. 4.4), it describes a saturating curve which increases toward an upper asymptote, representing the mean maximum number of spikelets produced per unit area. The slope parameter β_1 of Eqns. 4.3 and 4.4 is interpreted as the reciprocal of the upper asymptote of this hyperbolic yield-density curve, while the intercept parameter β_0 is interpretable as the reciprocal of the initial slope of the hyperbolic yield-density curve. The crop in which the wild oat plants were growing was determined to be a significant covariate, with both the slope parameter β_1 ($p<0.0001$) and the intercept parameter β_0 ($p=.0133$) of Eq. 4.3 varying significantly between crops (Table 4.10). The curve for spikelet production of wild oats growing in no crop had a significantly steeper initial slope and a significantly lower asymptote than the curve for wild oats growing in

barley (Figure 4.9). The higher initial slope was not surprising, since at low wild oat densities with no crop plants, there would be minimal competition for resources between plants. The low asymptote was more difficult to interpret. It was apparently due to the strong leverage imposed by two points at very high densities (Figure 4.9). Such an effect could be due to some intraspecific inhibitory impact of wild oats on their spikelet production at high densities. A scatter plot of the residuals of the spikelet prediction in the no crop treatment against the wild oat plant density (Figure 4.10) more clearly demonstrates how such an effect might be imposed. It appears that wild oat spikelet production peaks within a density range of 100-600 plants·m^{-2}, then declines to a minimum in a range of 800-1200 plants·m^{-2}. This was consistent with the qualitative observation that in the first year of the study, the no crop plots flourished, but by the end of the second season and continuing through the third season, the wild oat plants in these plots looked less healthy than any other wild oat plants in the experiment, and adult plant densities were actually lower in 1995 than they had been the previous year. There may be a monoculture effect such as the yield depression observed when the same crop is grown continuously in the same location. This phenomenon has been attributed to possible soil microbial inhibition (Johnson et al. 1991, 1992).

Crop	β_0	SE(β_0)	β_1	SE(β_1)
Barley	0.0643	0.006112	0.0001724	0.0000267
No Crop	0.0034	0.003558	0.0002881	0.0000304
Buckwheat	0.0143	0.003149	0.0001907	0.0000489

Table 4.10. Estimates and standard deviations for parameters of Eqns. 4.3 and 4.4, for the prediction of wild oat spikelet production from wild oat plant density.

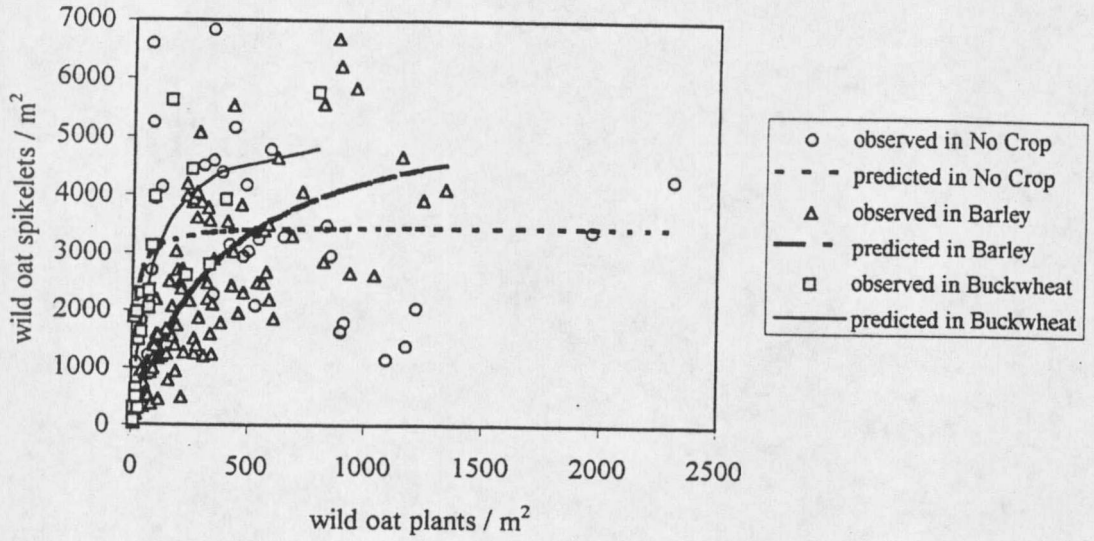

Figure 4.9. Observed values and predicted curves for wild oat spikelet production per m^2 as a function of wild oat plant density per m^2.

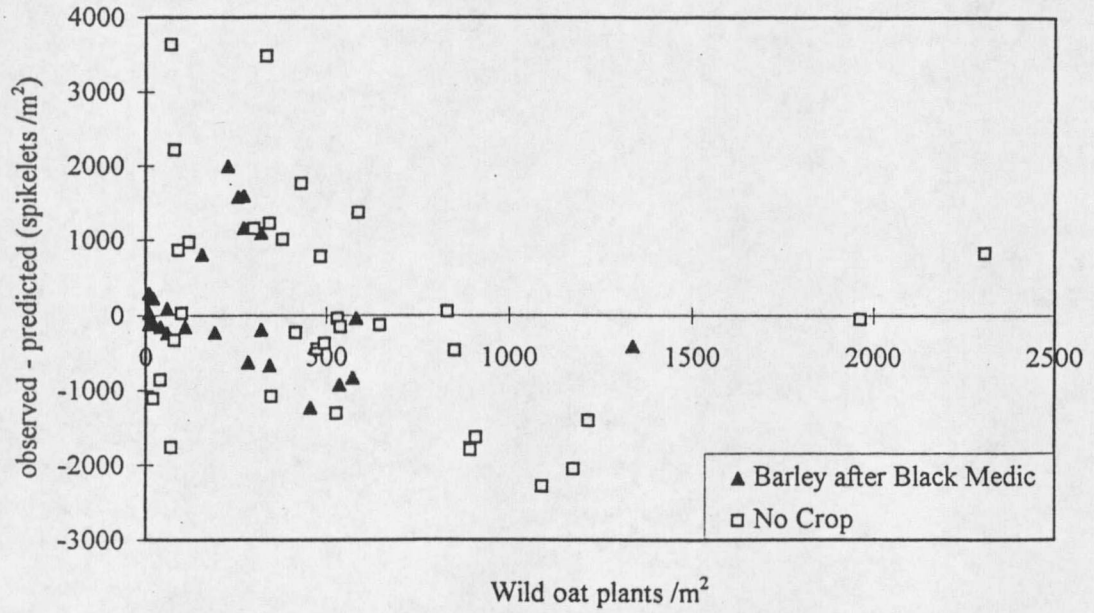

Figure 4.10. Residuals of wild oat spikelet prediction model, demonstrating systematic lack of fit for no crop and barley/black medic treatments.

Wild oat plants in barley following black medic green manure exhibited very similar residuals (Figure 4.10) to those of the wild oat monocultures. If this was also an effect of some soil inhibitory effect, it may corroborate the observations of some farmers and researchers (D. Oien and J. Clapperton, pers. comm.) that over the long term, black medic green manures seem to have an inhibitory effect on wild oat growth and seed production. The declining curve of these data points could be represented by fitting a negative value of the intercept term β_1 in equations 3 and 4. However, such parameter values result in negative predicted values of spikelet production for low plant densities, which was not allowed by GLIM. Given this constraint, the previous crop and 1993 intercrop did not significantly influence either parameter of this model. Fitting with non-linear regression or appropriately transforming the data and fitting with linear regression both resulted in a negative fitted intercept for the prediction of wild oat spikelet production in barley following black medic. While the resulting fitted curve fits the declining data well over some portion of the range, it inevitably results in some biologically impossible predictions, such as negative seed production and infinitely high seed production.

The fitted parameters for wild oat spikelet production in buckwheat give an asymptote which was similar to that for wild oat spikelet production in barley, but a significantly higher initial slope than for wild oat spikelet production in barley, causing the wild oat spikelet production curve in buckwheat to be significantly higher than that in barley over the entirety of their common range of wild oat plant densities (Figure 4.9). This is consistent with the higher wild oat seed production in buckwheat plots than that in barley plots in 1993 (Table 4.3).

Spikelet Transition to Seed Rain The estimated transition rate of spikelets to seed rain is the ratio of estimated seed rain per unit area to the number of spikelets per unit area. This ratio (Table 4.11) was significantly lower in barley than in the no crop treatment ($p=0.0001$) in 1994, but

was not significantly different between barley and no crop in 1995 (p=0.2999). In neither year was the previous crop a significant determinant of this transition rate for wild oats growing in barley.

1995	1994Crop	Ratio	Standard Error
	Barley	0.5432	0.1206
	No Crop	1.920	0.1641
1995	1995Crop	Ratio	Standard Error
	Barley or No Crop	1.5448	0.1468

Table 4.11. Estimated transition rate between spikelets and seed rain for 1994 and 1995.

The lower seed rain-to-spikelet ratio for wild oats growing with barley and those growing without barley in 1994 may be due to interference from barley or to higher levels of wild oat seed retention in the combine when barley is present. Shirtliffe (1996, unpubl. data) found that wild oat seed distribution from a combine was substantially higher after the combine exited the field than it was during grain harvest, suggesting that the processing of grain in the combine impedes the release of wild oat seeds from the combine until most of the grain is processed and the machine is leaving the field.

The ratio of wild oat seed rain to the number of wild oat spikelets is the product of a) the mean number of viable seeds per spikelet and b) the proportion of those seeds which survive intact until the time of measurement of the fall seed bank. Direct estimation of these two numbers would yield further insight into the processes influencing changes in wild oat population.

Conclusions from Life Stage Model Analysis The estimation of population transition parameters allows for the formulation of specific hypotheses about how different cropping systems may impact wild oat populations (Jordan et al. 1995). The most obvious impacts of the different cropping systems that we studied on wild oat populations were differences in emergence probabilities

of wild oat seeds. Some general trends were evident. First, wild oat seeds in those treatments that had perennial green manures in 1994 (black medic, alfalfa, or alfalfa hay) had relatively low emergence probabilities in 1994, and relatively high emergence probabilities in 1995. It is likely that the reduced emergence in 1994 was due primarily to the lack of soil disturbance in the spring of 1994, but could also have been related to edaphic influence of the cover crop on the soil environment, such as through reduced moisture or reduced temperature variation (Liebman and Dyck 1994). Seeds which survived through 1994 without germinating may have lost some dormancy by spring of 1995, and were more likely to germinate at that time. In those treatments that returned to barley in 1995, many of the germinating seeds came up in the crop and went on to produce more seeds, while in the treatment that was hayed in 1994 and fallowed in 1995, the germinating seeds were destroyed, explaining the substantial reduction in wild oat soil seed density in that treatment (Table 4.6). The timing of emergence and of tillage operations in the year following the green manure may be an important determinant of whether these perennial green manures result in lower or higher seed populations than other green manures or fallow, as suggested by the overriding importance of tillage date in determining seedling mortality rates. More research is needed to determine whether different green manure crops differentially influence the timing of emergence of wild oat seeds in subsequent crops.

If there was an inhibitory effect of black medic intercrops or green manures on wild oat seed production (Figure 4.10), it was not an important impact on final wild oat populations in this study (Tables 4.5, 4.6). Such an effect may take some years to manifest itself as a decline in the actual population density of wild oat seeds or plants, which seems to be controlled much more strongly by factors relating to emergence probabilities and seedling mortality. Perhaps a three-year cycle such as that used in the buckwheat-alfalfa hay-alfalfa green manure treatment would allow black medic to more rapidly impact wild oat population densities.

In both 1994 and 1995, emergence probabilities were lower in barley following peas than in barley following fallow or any other green manure (Table 4.9). Such an effect should be investigated further, since it could, in the long term, reduce economic wild oat population impacts on crops. Although some residual influence on soil moisture may be the cause, other possible causes, such as changes in soil chemistry, may warrant further investigation.

Magnitude of Variances and Future Experimental Design

One objective of a pilot study is the estimation of the magnitude of errors in the treatment effects. The simplest error variance that can be reported for this study is the error in estimating wild oat population densities. The number of individual wild oat plants that emerged in a plot was usually estimated with some error, by sampling within the plot. It became clear that errors were non-homogenous, and that the estimated variance of samples taken from a plot was closely proportional to the square of the mean of samples taken from the plot, suggesting a constant coefficient of variation. The coefficient of variation for sampling plot populations seemed to hover between 0.3 to 0.4, and was 0.5 for the soil seed bank sampling scheme used in 1994. The coefficient of variation may depend to some extent on the size and number of quadrats in the sampling scheme. This level of variation was within acceptable limits for this study, but future researchers may wish to evaluate the precision of their sampling schemes if they are concerned with reducing the coefficient of variation to a lower level.

Although a standard error was reported for each of the population dynamic model parameter values reported in this paper, these errors were not estimated very accurately. As noted earlier, most parameter estimates in the population dynamic analysis were based on the relationship between two estimated quantities, neither of which was known with certainty, and which may have been estimated with differing degrees of certainty. This can lead to serious underestimation of the error of an analysis, and it may bias the parameter estimates (Neter, Wasserman, and Kutner 1990).

The estimation of population dynamic model parameter values and their variability could be improved by the use of a data set obtained from a study designed for that purpose. Such a study would purposely include a range of initial weed populations. In order to reduce errors associated with using estimated population densities for estimation of parameters, the experiment could be designed with small permanent subplots whose populations could be estimated with more accuracy, within larger plots representing different cropping system treatments, in order to reduce edge effects, and blocks of plots representing a range of environments of interest for the inference space of the final model.

Alternatively, if the primary interest of the study is to evaluate long term population changes with different cropping systems, it may be most convenient to evaluate soil seed bank densities on an annual basis, and perform analysis of variance on the changes in seed density in different cropping systems. In this case, attention should be paid to characterizing the initial soil seed population, selecting an area of uniform populations, and establishing enough replications to characterize the effects desired. The data from this experiment could be used in calculations of statistical power to estimate the amount of replication that would be required.

The results of this experiment emphasize a few other points which should be considered when establishing experiments of this type. This experiment demonstrated the substantial differences in wild oat populations that can result from starting rotations in different years. Ideally, all starting points should be represented in crop rotation experiments, and although comparisons may still be possible between treatments which started in the same year, generality of results will be compromised if these are all that is available. This study demonstrated the importance of timely fallowing of fallow and green manure treatments. Treatments should be established with the intention and resources to maintain them properly. This study was characterized by logistical problems associated with the distance from Bozeman to the sites (approximately 400 km).

Summary

Different crops had significant effects on wild oat population dynamics, as evidenced by the high wild oat seed production in crops of buckwheat compared to barley (Table 4.3). Green manure crops may successfully replace fallow if they are managed to prevent excessive moisture use by the green manure. When the pea green manure was properly managed (1994), barley following the pea green manure (1995) yielded significantly more than barley following bare fallow (Table 4.7, Figure 4.6). If managed properly, green manure crops in general will not necessarily compromise wild oat control, although sod crops such as black medic or alfalfa which are interseeded with the grain crop and survive the winter may reduce wild oat recruitment in the subsequent fallow year, reducing the amount of seed bank reduction which can be achieved in the fallow year. However, if the sod crop can be utilized for an economic return, such as for hay or for grazed forage, wild oat seed bank reduction can be greatly enhanced by waiting to fallow until the second year. The economic analysis of this strategy could be complicated.

The importance of last tillage date in impacting seedling mortality suggests that rotation of main crops with different planting dates may be an important practice in wild oat management. Several organic farmers in Montana rotate cool-season small grains with late-planted warm-season crops such as buckwheat and millet in order to decrease wild oat populations.

Many interesting questions remain to be answered. Long term studies are needed to examine the effects of green manures on wild oat seedling emergence or spikelet production rates. The possibility that intercrops may influence wild oat emergence or growth deserves further study. Studies are needed to more effectively elucidate seed survival and other aspects of seed bank dynamics. More research is needed to determine the stability of results over a range of sites and years, and with other crop and weed species. Finally, economic analyses would assist researchers and

producers in effectively judging the costs and benefits of various cropping systems with regard to profitability and long term soil and pest management.

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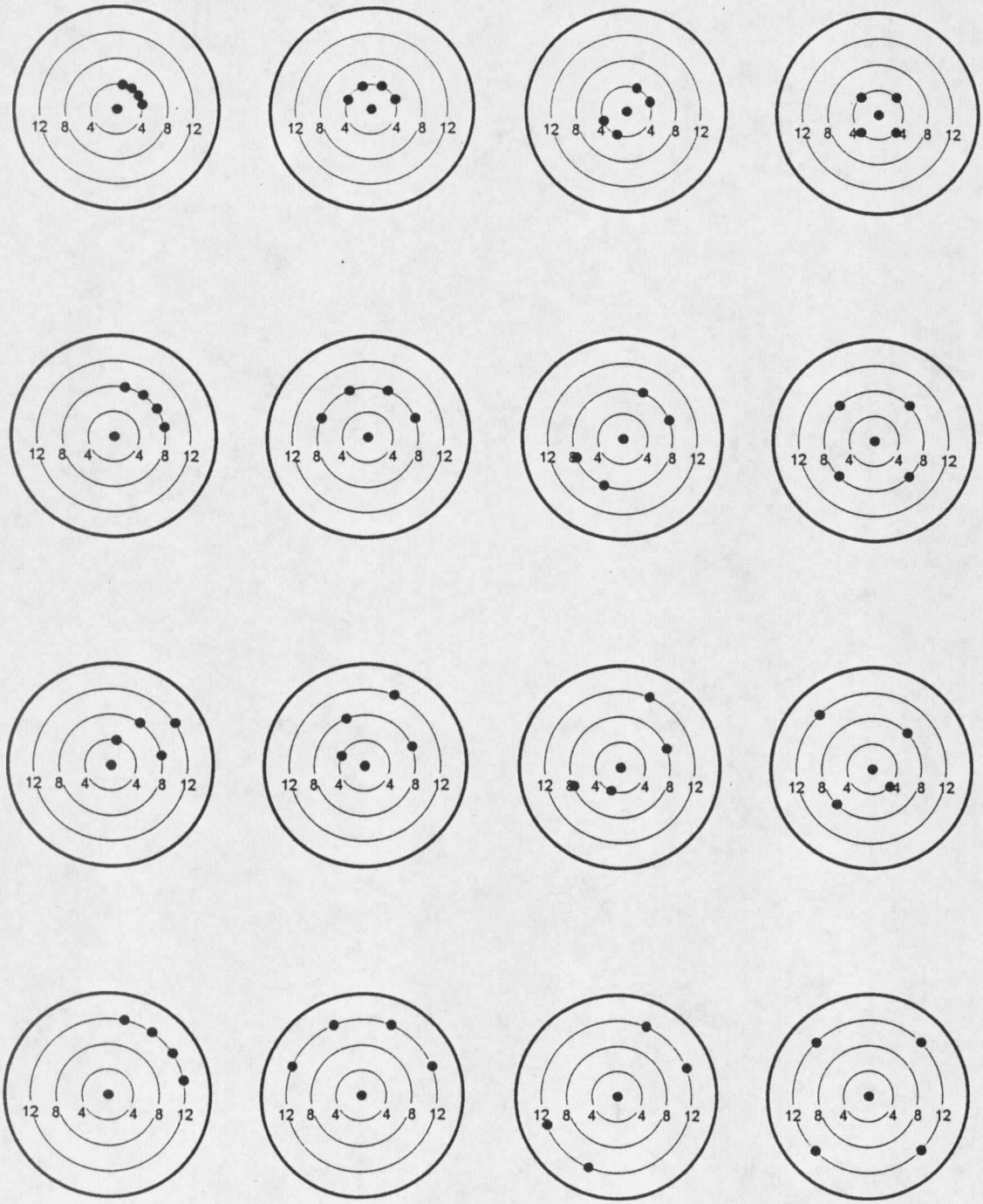
APPENDICES

APPENDIX A

PLANT LOCATION DIAGRAMS FOR GREENHOUSE EXPERIMENTS

PLANT LOCATIONS FOR MONTANA GREENHOUSE EXPERIMENTS 1 AND 2

Neighbor Number NN=4



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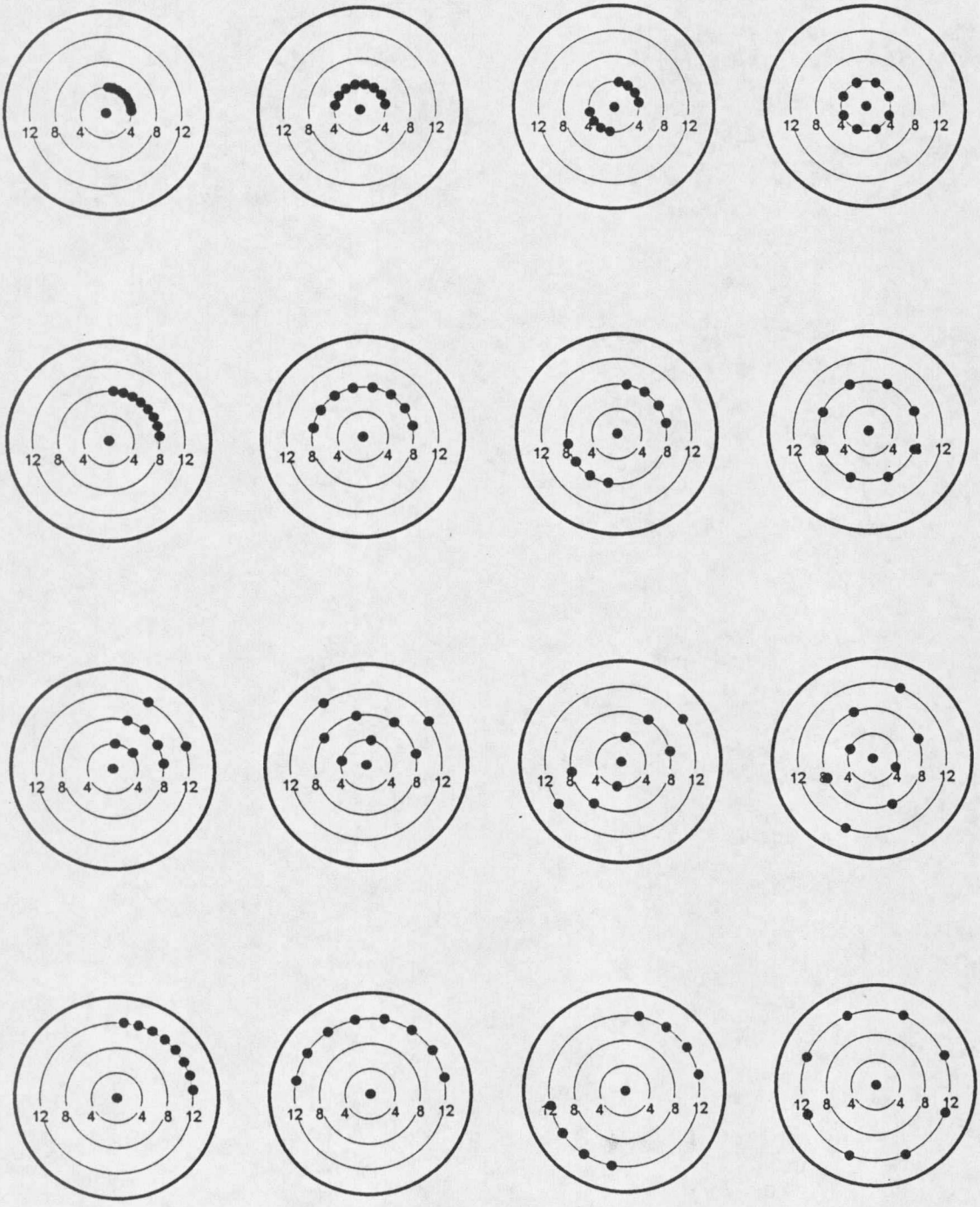
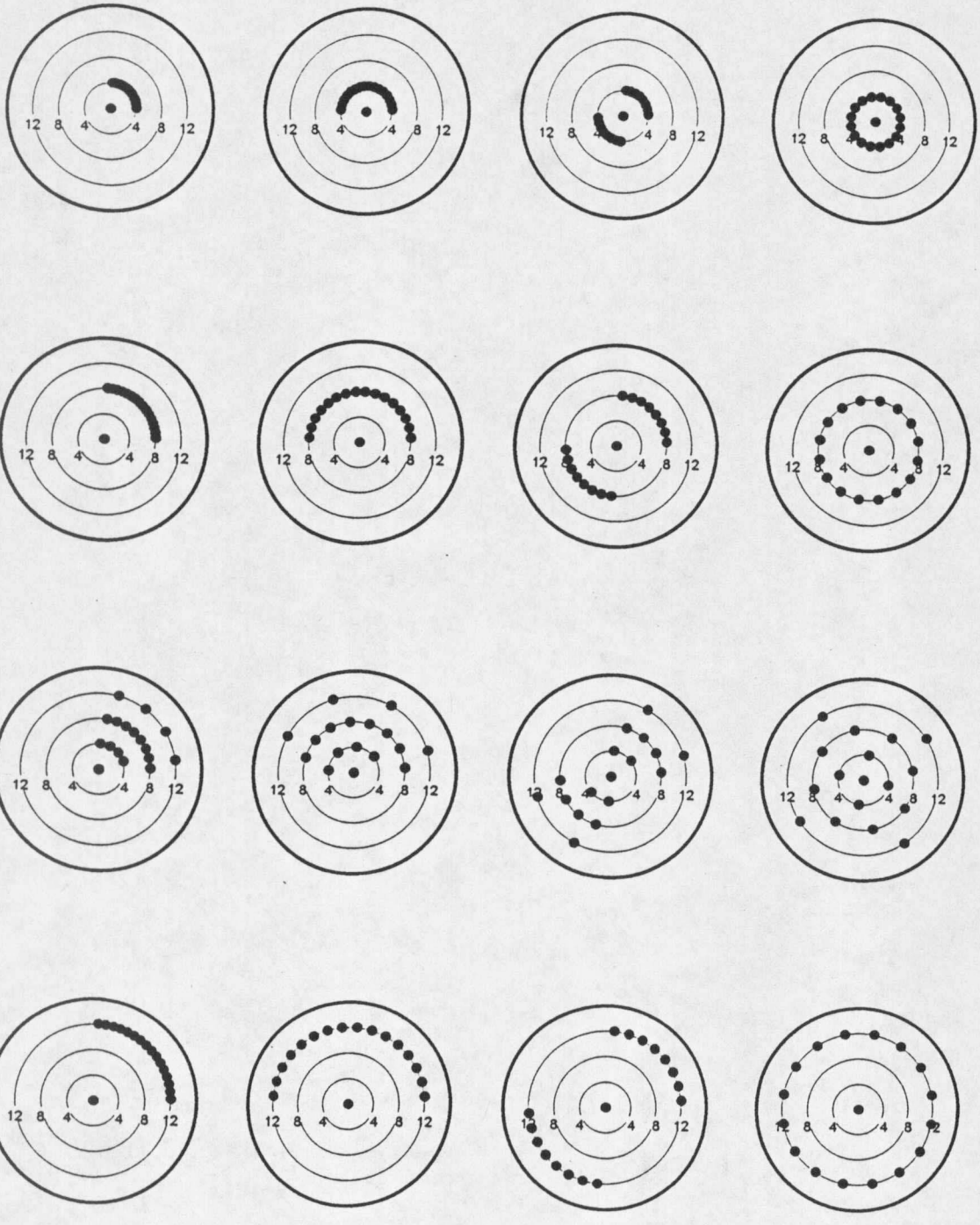
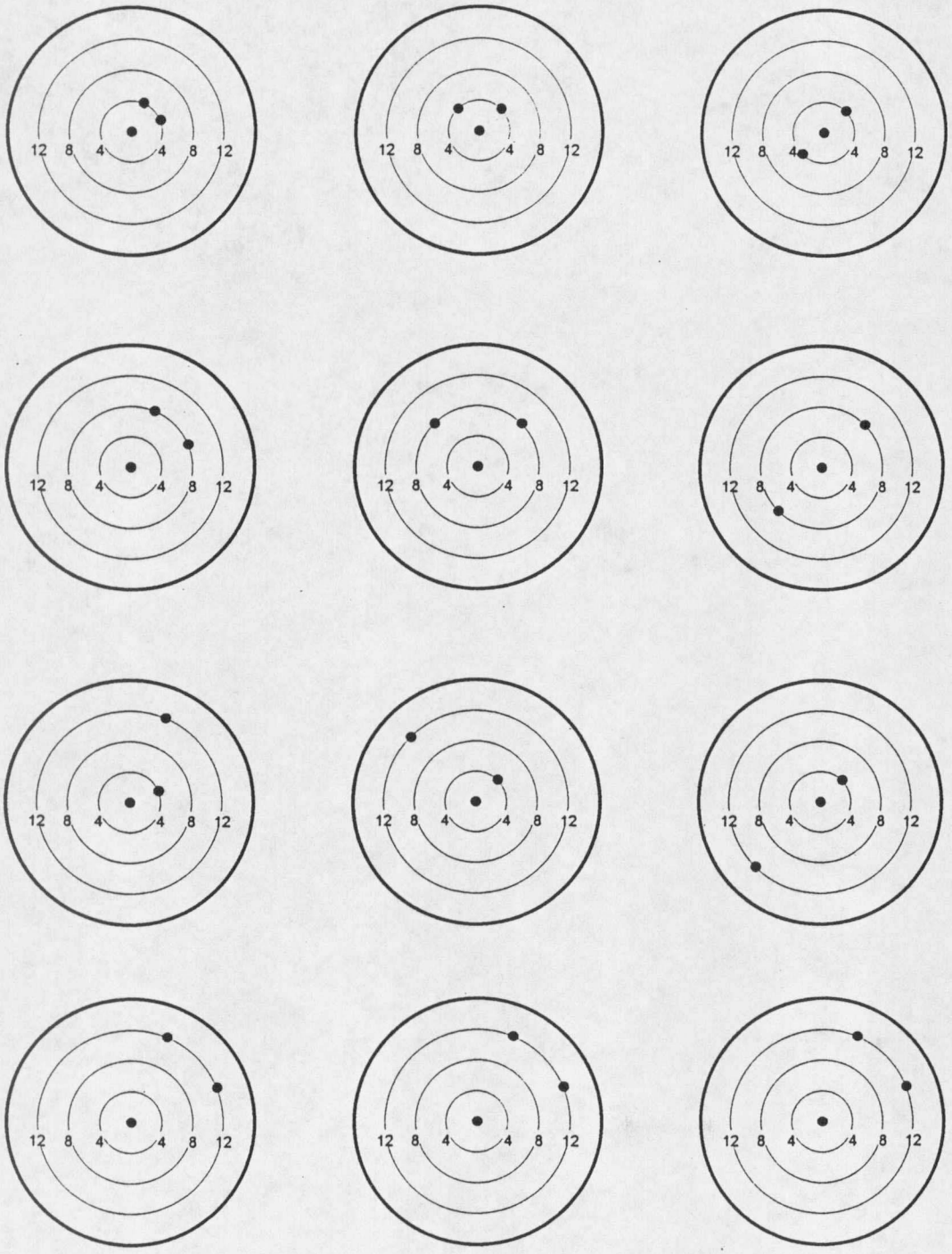
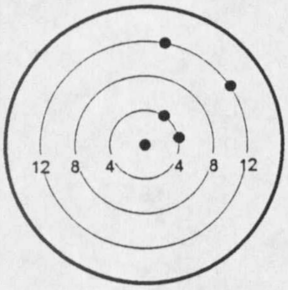


Neighbor Number NN=16



PLANT LOCATIONS FOR ADDITIONAL TREATMENTS IN MONTANA GREENHOUSE EXPERIMENT 2

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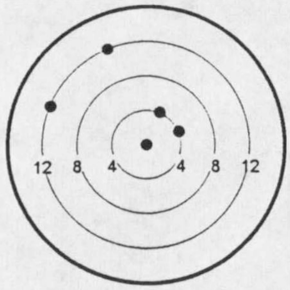
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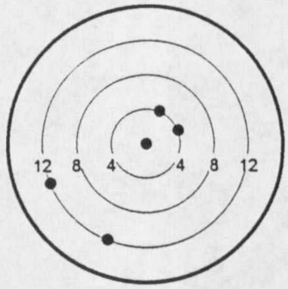
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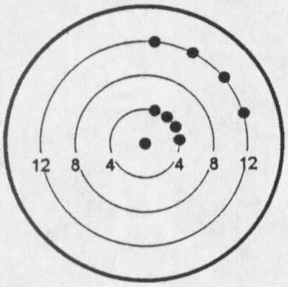
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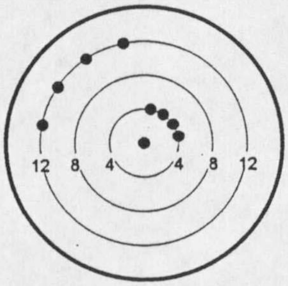
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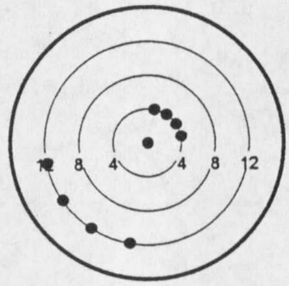
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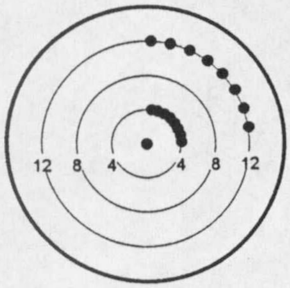
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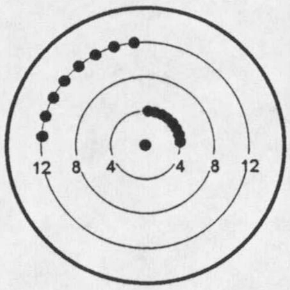
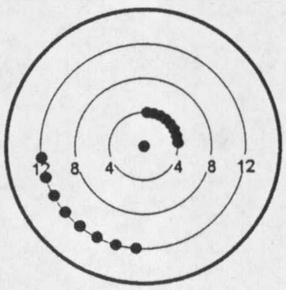
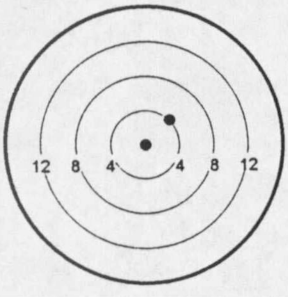
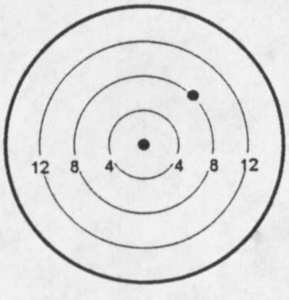

12 8 4 4 8 12


12 8 4 4 8 12


12 8 4 4 8 12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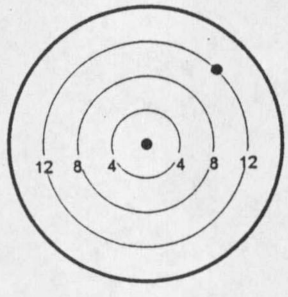
12 8 4 4 8 12

APPENDIX B

COMPUTER CODE FOR THIESSEN POLYGON ANALYSES

MICROSOFT QUICKBASIC CODE FOR THIESSEN POLYGON ANALYSIS OF GREENHOUSE EXPERIMENTS

```
'Subroutines

DECLARE SUB INDATA ()
DECLARE SUB thiessen ()
DECLARE SUB startup ()
DECLARE SUB pause ()

'variables and arrays

DIM SHARED pots
DIM SHARED xpix
pots = 60

DIM SHARED size(pots)
DIM SHARED thet(pots, 16)
DIM SHARED dist(pots, 16)
DIM SHARED x(pots, 16)
DIM SHARED y(pots, 16)
DIM SHARED num(pots)
DIM SHARED ang(pots)
DIM SHARED dis(pots)
DIM SHARED area(pots)
DIM SHARED xplant(17)
DIM SHARED yplant(17)

1000    CLS
RESTORE
Bestmode = 12
CLS
SCREEN Bestmode

 '************************  MAIN PROGRAM ************************


CALL startup
CALL INDATA

CLOSE


'*****************************END OF MAIN
PROGRAM*****************************



SUB INDATA
CONST pi = 3.14159

CLOSE
OPEN "c:\user\phen\gh1dist.prn" FOR INPUT AS #1
```

```
pot = 1
DO
  'input the treatment labels for each pot
INPUT #1, num(pot), ang(pot), dis(pot)

 'input the distance from the target of each plant;
FOR plantnum = 1 TO 16
INPUT #1, dist(pot, plantnum)
NEXT plantnum
pot = pot + 1
LOOP UNTIL (EOF(1))
CLOSE #1

OPEN "c:\user\phen\gh1thet.prn" FOR INPUT AS #1
pot = 1
DO
  'input the treatment labels for each pot again
INPUT #1, num(pot), ang(pot), dis(pot)
  'input the angle of each plant relative to the target
FOR plantnum = 1 TO 16
INPUT #1, thet(pot, plantnum)
NEXT plantnum
pot = pot + 1
LOOP UNTIL (EOF(1))
CLOSE #1

CALL thiessen

OPEN "c:\user\phen\gh1test.prn" FOR OUTPUT AS #2
FOR pot = 1 TO pots
WRITE #2, num(pot), ang(pot), dis(pot), area(pot)
NEXT

END SUB


SUB pause

LOCATE 30, 30: PRINT "hit any key to continue"
DO UNTIL INKEY$ <> ""
LOOP

END SUB



SUB startup

INPUT "resolution? (number of pixels per side)"; xpix

END SUB
```

```
SUB thiessen

ypix = xpix
radius = 16
pi = 3.14159
radpix = INT(xpix / 2)

xplant(17) = 0
yplant(17) = 0

FOR pot = 1 TO pots
SCREEN 12
CLS
VIEW (0, 0)-(460, 460)
WINDOW SCREEN (-16, -16)-(16, 16)

CIRCLE (0, 0), 16
CIRCLE (0, 0), .25

FOR plantnum = 1 TO 16
xplant(plantnum) = dist(pot, plantnum) * COS(pi * thet(pot, plantnum) /
180)
yplant(plantnum) = dist(pot, plantnum) * SIN(pi * thet(pot, plantnum) /
180)
CIRCLE (xplant(plantnum), yplant(plantnum)), .25
NEXT plantnum

xmarker0 = 17
xmarker1 = 17

'the following algorithm scans the pot surface area pixel by pixel,
'scanning in concentric circles starting at the center of the pot.
'each pixel is assigned to the plant to which it is closest.

FOR rad = 1 TO radpix
r = rad * 16 / radpix    'the radius of the circle being scanned
theta = 0             'the angle of the point on the circle being scanned
DO
p = (r * COS(theta) + xcenter)
                          'p=the x coordinate of the point being scanned
q = (r * SIN(theta) + ycenter)  'q=the y coordinate of the point
d = 35       'd=starting value for the distance from the point to a plant
pl = 0              'pl=starting value for the closest plant to the point

FOR plantnum = 1 TO 17
'distance from point to each plant
dist = ((xplant(plantnum) - p) ^ 2 + (yplant(plantnum) - q) ^ 2) ^ .5
IF dist <= d THEN
d = dist
pl = plantnum             'finding the closest plant to the point
END IF
NEXT plantnum

'assigning area to the target plant.
IF pl = 17 THEN area(pot) = area(pot) + 1

'the following algorithm is for drawing the polygon boundaries.
xmarker1 = pl
IF xmarker1 <> xmarker0 THEN PSET (p, q)
```

```
xmarker0 = xmarker1
'PSET (p, q), pl

theta = theta + 2 * pi / (CINT(2 * pi * rad))   'next point
LOOP WHILE theta < (2 * pi)
NEXT rad                                        'next concentric circle

PRINT num(pot); ang(pot); dis(pot)
'CALL pause
NEXT pot

'adjusting area from pixels to square centimeters.
FOR pot = 1 TO pots
area(pot) = (area(pot) * (pi * 16 ^ 2) / (pi * (radpix) ^ 2))
NEXT pot

END SUB
```

MICROSOFT QUICKBASIC CODE FOR THIESSEN POLYGON ANALYSIS OF FIELD EXPERIMENTS

```
'Subroutines

DECLARE SUB indata ()
DECLARE SUB thiessen ()
DECLARE SUB STARTUP ()
DECLARE SUB pause ()

'variables and arrays

DIM SHARED plants
DIM SHARED xpix
DIM SHARED ypix
DIM SHARED xmax, xmin, ymin, ymax, xscale, yscale, xcenter, ycenter
plants = 205

DIM SHARED xloc(plants)
DIM SHARED yloc(plants)
DIM SHARED size(plants)
DIM SHARED xplant(plants)
DIM SHARED yplant(plants)
DIM SHARED area(plants)
DIM SHARED bound(plants)

CLS
Bestmode = 12
SCREEN Bestmode

 '************************  MAIN PROGRAM ***********************
CALL STARTUP
CALL indata
CLOSE


'*****************************END OF MAIN
PROGRAM*****************************

SUB indata

CLOSE

OPEN "c:\user\phen\spatial\red1data.prn" FOR INPUT AS #1

count = 1
DO
'the input file contains x coordinate, y coordinate, and size of each
plant in 'the plot
INPUT #1, xloc(count), yloc(count), size(count)
count = count + 1
LOOP UNTIL (EOF(1))

n = plants
```

```
ypix = xpix

SCREEN 12
CLS
VIEW (0, 0)-(460, 460)
WINDOW SCREEN (0, 0)-(xpix, ypix)

CIRCLE (xcenter, ycenter), pixradius

'the following converts x and y coordinates from centimeters to pixels
'and defines scaling variables
xcenter = -4
ycenter = 59
radius = 55
xscale = 2 * radius
yscale = xscale
xmin = xcenter - radius
ymin = ycenter - radius
xcenter = xpix / 2
ycenter = ypix / 2
pixradius = xpix / 2

 FOR plantnum = 1 TO plants
 xplant(plantnum) = xpix * (xloc(plantnum) - xmin) / (xscale)
 yplant(plantnum) = ypix * (yloc(plantnum) - ymin) / (yscale)
 CIRCLE (xplant(plantnum), yplant(plantnum)), xpix / 150, 2
 NEXT plantnum

CALL thiessen

OPEN "c:\user\phen\spatial\red1test.prn" FOR OUTPUT AS #2
FOR c = 1 TO n
WRITE #2, c, xloc(c), yloc(c), size(c), area(c), bound(c)
NEXT

END SUB



SUB STARTUP

INPUT "resolution? (number of pixels per side)"; xpix

END SUB



SUB thiessen

pi = 3.14159
xmarker0 = 0
xmarker1 = 0

'The following alogrithm scans the entire plot area point by point,
'at the
'resolution defined in the STARTUP subroutine, using concentric circles.
'Each point is assigned to the plant to which it is closest.

theta = 0
```

```
FOR r = 1 TO INT(xpix / 2) + 1     'radius of the circle being scanned
theta = theta MOD (2 * pi)         'angle of the point on the circle
being scanned

DO
p = (r * COS(theta) + xcenter)
            'x coordinate of the point being scanned
q = (r * SIN(theta) + ycenter)
            'y coordinate of the point being scanned
d = xpix + 1          'starting value for distance from point to plant
pl = 0
FOR plantnum = 1 TO plants
dist = ((xplant(plantnum) - p) ^ 2 + (yplant(plantnum) - q) ^ 2) ^ .5
IF dist < d THEN
d = dist                           'assigns point to the nearest plant
pl = plantnum
END IF
NEXT plantnum


'the following draws the boundaries between polygons on screen and
'determines whether the plant is far enough from the edge of the plot to
'be counted. If any point in a plant's polygon is closer to the edge of
'the plot than to the plant, then the plant is disqualified (bound is
'set to 1), because a plant outside of the plot could change the plant's
'polygon boundary.

xmarker1 = pl
area(pl) = area(pl) + 1
IF (xpix / 2) - r <= d THEN bound(pl) = 1
IF xmarker1 <> xmarker0 THEN PSET (p, q)
xmarker0 = xmarker1


theta = (theta + 1 / r)          'next point
LOOP WHILE theta < (2 * pi)
NEXT r                           'next concentric circle



FOR plantnum = 1 TO plants
'area is converted to square centimeters
area(plantnum) = (area(plantnum) / (pixradius ^ 2)) * (radius ^ 2)

'bound is set to zero if the plant is disqualified, one if it is to be
'included.
bound(plantnum) = 1 - bound(plantnum)

'plants within bounds are marked with additional circle on screen map
CIRCLE (xplant(plantnum), yplant(plantnum)), (xpix / 100),
bound(plantnum)*11
NEXT plantnum

END SUB
```