

**MODELS OF INTERFERENCE IN MONOCULTURES AND MIXTURES OF  
WHEAT (Triticum aestivum L.) AND  
QUACKGRASS (Elytrigia repens (L.) Nevski.)**

**BY**

**DOUGLAS HOWARD WILCOX**

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**Department of Plant Science  
University of Manitoba  
Winnipeg Manitoba**

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**QUOTE**

*"When it has been necessary to enter upon a study of our most notorious weeds (e.g. Quackgrass and Canada Thistle) the investigator has found himself faced with a vast amount of literature on control, a surprisingly small part of which consists of fundamental research or even a critical study of the plant in question."*

William F. Tildesley, 1933

- opening paragraph from his University of  
Manitoba M.Sc. Thesis.

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**ABSTRACT**

**Wilcox, Douglas Howard. Ph.D., The University of Manitoba, October, 1994. Models of Interference in Monocultures and Mixtures of Wheat (*Triticum aestivum* L.) and Quackgrass (*Elytrigia repens* (L.) Nevski.). Major Professor: Dr. I.N. Morrison.**

Quackgrass is the most serious perennial grassy weed of wheat in Manitoba. Field experiments and surveys investigating the nature and extent of interference in monocultures and mixtures of quackgrass and wheat were conducted over the years 1987 to 1989 at Portage La Prairie, Manitoba, Canada.

Intraspecific and interspecific interference between spring wheat and quackgrass was investigated in the field using an additive series design consisting of five replacement series proportions at total stand densities of 75, 150, and 300 plants m<sup>-2</sup>. A revised synthetic no-interaction analysis determined that wheat was superior to quackgrass in both intraspecific and interspecific interference and that niche differentiation was large. Quackgrass reproductive variables were less sensitive to interspecific interference than were vegetative variables.

Surveys of commercial fields of spring wheat infested with quackgrass were conducted using a dynamic stratified random sampling design in which systematic samples were taken at approximately 30, 60 and 93 days after planting. Wheat yield loss, as a percentage of

weed-free yield, ( $Y_{w\%}$ ) was related to spring quackgrass shoot counts/ $m^{-2}$  ( $Q_s$ ) by a rectangular hyperbolic model of the form

$$Y_{w\%} = 98.7(1 - 0.433(Q_s)/100(1 + (0.433(Q_s)/193.7))).$$

Wheat kernel weight was the wheat yield component most influenced by quackgrass infestation. In quackgrass populations the majority of new rhizome production occurred during wheat senescence and biomass partitioning to heads increased as quackgrass infestation increased. Allometric models of the relationship between quackgrass parts were site specific and generally became more accurate the later the sampling date.

A set of models relating spring quackgrass infestation to yield losses in hard red spring wheat, flax, and polish canola were combined with allometric models in a multi-year spreadsheet (Lotus 1-2-3, v 3.1) model. Simulations run using the multi-year model demonstrated the potential of a spreadsheet model for assisting in weed control decisions.

## **FOREWORD**

This thesis was written in manuscript style following the format of Weed Science. It is expected that manuscripts 1 to 3, and appendix 1, will be submitted for publication in Weed Science and that manuscript 4 will be submitted for publication in another refereed journal.

The bulk of the thesis text was printed using a 12 pt Adobe Garamond typeface with headers and captions printed using a 12 pt Franklin Gothic Condensed typeface.

## INTRODUCTION

Wheat has been produced in Manitoba since the arrival of the Selkirk settlers at Fort Garry in 1812. However, it was not until 1906 that quackgrass (*Elytrigia repens* (L.) Nevski.), a weed introduced to eastern North America from Europe around 1663, was reported as occurring in Manitoba fields (Alex, 1987). Quackgrass is now recognized to be the most serious perennial grassy weed of spring wheat in Manitoba (Thomas and Wise, 1984). Of the 4.4 million acres of wheat now grown in Manitoba, quackgrass occurs in 11% of the fields with a mean mid-season density of 10.4 shoots  $\text{m}^{-2}$  (Thomas and Donaghy, 1991).

Quackgrass is a long-lived perennial weed that spreads both by seed and an extensive underground rhizome system. In temperate climates around the world it is considered to be one of the three most serious weeds in 37 different crops (Holm *et al*, 1977). Quackgrass is difficult to control culturally and although herbicides can provide effective short-term suppression, long-term control is inconsistent. It has been estimated that the lack of quackgrass control in Manitoba causes an annual total revenue loss of \$21 million (Fox and Furtan, 1990). Not only does quackgrass result in direct yield loss it also is a major impediment to producers adopting soil conservation practices (Todd, 1987).

In response to the severity and importance of the quackgrass problem in Canada the

Canadian Expert Committee on Weeds established the National Quackgrass Action Committee in 1986. The objective of this committee was to focus research and extension activities towards developing a clearer understanding of the quackgrass problem so that a coordinated approach could be developed which would minimize the impact of this weed in Canada. The research outlined in this thesis was conducted as one step in the coordinated effort to achieve this objective.

Except for some investigations in Quebec (Leroux, 1990) and preliminary reports from this thesis (Wilcox and Morrison, 1988a, 1988b, 1989; Morrison *et al*, 1990; Wilcox, 1990) there is no published information on quackgrass interference in spring wheat in North America. To address this deficiency research was conducted to investigate the short-term and long-term implications of wheat-quackgrass interference.

Short-term implications were studied using both an experimental and survey approach. The experimental approach was used to investigate and model the relative importance of interspecific and intraspecific forces in wheat-quackgrass interference (Manuscript 1). As far as I am aware this is first report of a perennial species being studied in this kind of additive series design. The experimental approach was also used to elucidate and model some of the mechanisms responsible for wheat-quackgrass interference (Appendices 1, 3 and 4). The experimental approach was also used to study the growth of quackgrass plants from rhizome segments and seed in the absence of interference. The results of this research has been partially reported elsewhere (Wilcox and Morrison, 1987) and has not been included in this thesis.

A survey approach was used to model the relationship between quackgrass infestation

and wheat yield loss in commercial fields in Manitoba (Manuscript 2). To determine the most accurate measure of quackgrass interference in wheat a survey approach was also used to model the allometry between the various quackgrass parts (Manuscript 3). For both models the main survey approach used was an innovative dynamic stratified sampling design which has been adopted by other quackgrass researchers (Chikoye, 1990).

Long-term implications of quackgrass-wheat interference were studied by developing an integrated empirical spreadsheet model for instructional purposes (Manuscript 4). This spreadsheet model is useful for demonstrating the utility of a model for assisting in weed control decisions, even when based on limited data and using simple hardware and software.

A major theme in all this work has been to demonstrate the utility of new, or relatively recently developed, analytic techniques and models to explore the interference relationship between crops and weeds.



## **LITERATURE REVIEW**

### **WEED CENTRED MANAGEMENT**

Historically there has been a gap between weed management and weed biology/demographics. Weed management traditionally has concerned itself only with immediate crop yield with short-term economics being the primary consideration. Zimdahl (1980) has cited more than 550 papers that describe the outcome of various weed-crop interactions, the majority of which have focused only on the immediate yield losses. By focusing on the outcome of weed-crop interference many weed scientists have failed to adequately describe the mechanisms of this interference (Weldon and Slausen, 1986).

This crop-centred approach was acceptable when mechanical and chemical inputs were relatively inexpensive and considered to have only limited environmental and health effects. However, increasing necessity to reduce input costs, increasing environmental safety concerns, and increasing weed resistance to herbicides, are all putting greater pressure on producers to reduce herbicide use and to consider the long-term impact of their weed management decisions. Evaluation of weed management systems under this weed-centred approach requires more sophisticated techniques and analysis than does the traditional crop-centred approach. Adoption of these more sophisticated techniques and analysis will provide weed scientists with a more thorough quantitative insight into weed biology/demographics and their

effects on crop yield. Such insights will lead to more effective and integrated weed management systems and encourage the use of alternate non-chemical methods of weed suppression.

## **PLANT CHARACTERIZATION**

### **Characteristics of the Ideal Weed**

Many researchers have tried to describe the typical characteristics of plants that assure their survival and competitiveness. These descriptions range from the evolutionary strategies described by Pianka (1970), the life history theories of Grime (1977) to the competitive trait lists of Baker (1974) and Patterson (1982).

The relationship of a plant to its environment can be described on the basis of its evolutionary specialization. One approach of this type is the widely used concept of r- and K-selection (Holt, 1988). In relation to another organism an r-selected organism is one which is better adapted to survival in unpredictable environments whereas a K-selected organism is relatively better adapted to survival in a stable environment. Weeds and crops generally tend to be r-selected organisms (Radosevich and Holt, 1984).

Grime (1977) proposed that plants can be characterized by the degrees of stress and disturbance to which they were adapted. In his triangular system plants adapted to low levels of stress and disturbance are termed competitive, those adapted to high stress and low disturbance are termed stress-tolerant, and those adapted to low stress and high disturbance are termed ruderals. The ruderal and stress tolerant strategies correspond to r- and K-selection, respectively. Competition is an alternative strategy devised by Grime. Grime has

stated that competition is largely a reflection of a plants ability to capture resources and that relative growth rate is one of the best indicators of a plants competitive ability.

Weeds have characteristically similar traits which have been compiled in various lists by different researchers (Baker, 1974; Bazzaz, 1979; Patterson, 1982 ). These lists often include several of the following characteristics which can generally, but not exclusively, be classified as either "longevity (survival) aids or interference aids:

#### Longevity (Survival) Aids

1. Physiological and/or morphological crop mimicry
2. Vigorous, easily fragmentable vegetative reproduction
3. Copious and continuous seed production
4. Seed production in a wide range of environments
5. Short and long distance dispersal of reproductive components
6. Self-compatible with some outcrossing by general vectors
7. Internally controlled dormancy and longevity of seed
8. Non-specific germination requirements

#### Interference Aids

1. Effective physical or chemical interspecific interference mechanisms  
(e.g. smothering growth, climbing habit, allelopathy)
2. Phenotypic plasticity
3. Photosynthetic efficiency (C<sub>4</sub> vs. C<sub>3</sub>)
4. High water use efficiency
5. High initial relative growth rate and rapid growth

The weed traits listed above are considered, by the researchers who compiled these lists, to be the major characteristics important for weed success. Many of these traits can be quantified and are characteristic of specific weeds in populations and in isolation.

Knowledge of how weeds grow is a fundamental requirement of understanding the many characteristics of weeds that are responsible for their survival and interference. Applying the techniques of growth analysis is one way to obtain this fundamental knowledge.

### **Growth Analysis**

Over the years researchers have developed indices to summarize or facilitate interpretation of primary measurements of plants or plant components. The calculation of such indices is referred to as growth analysis. Because growth analysis simply restates primary measurements in some new form it is considered a deductive rather than a predictive process.

The term growth analysis encompasses all approaches used to measure and interpret physiological, developmental, environmental and genetic sources of yield variation. The particular approach used is dependent on the goal of the analysis and falls into three main categories: conventional plant growth analysis, yield component analysis, and sub-organismal demographic analysis (Jolliffe - personal communication).

### **Conventional Growth Analysis.**

Conventional growth analysis began in 1919 with the discussions of Blackman on what

is now termed relative growth rate (Hunt, 1978a). This method assumes that growth and yield are a function of contributing primary elements. This approach is time based and therefore requires primary observations to be made more than once over the growing season.

Conventional growth analysis has evolved into two main sub-approaches, the classical and the functional. The classical approach is characterized by a large number of plants being sampled at relatively infrequent harvests whereas the functional approach is characterized by frequent harvests where relatively few plants are sampled. The functional approach, first introduced by Vernon and Allison (1963), is now generally considered to be the superior approach (Radford, 1967; Hunt, 1979). The main debate associated with the functional approach is the appropriateness of various functions for fitting the data (Hurd, 1977; Venus and Causton, 1979; Meek *et al.*, 1991).

• **Conventional Analysis Growth Indices.** Conventional plant growth analysis embraces a large number of indices for interpreting plant growth. It can be classified into five major categories: indices of plant persistence (Leaf Area Duration, LAD; Biomass Duration, BMD); indices of plant presence (Species Population Density,  $D$ ; Species Biomass Density,  $B_D$ ) ; indices of rates and efficiencies of growth (Absolute Growth Rate, AGR; Relative Growth Rate,  $R$ ; Crop Growth Rate, CGR); indices of the extent of the assimilatory system (Leaf Area Ratio, LAR; Specific Leaf Area, SLA; Leaf Weight Ratio, LWR; Leaf Area Index, LAI); and an index of dry matter partitioning (Harvest Index,  $H$ ) (Jolliffe - personal communication). Further details on the various classical growth analysis indices and their

functions can be found in the references and reviews of Causton and Venus (1981), Evans (1972), Hunt (1978a, 1982), and Wall (1989).

### **Yield Component Analysis**

Yield component analysis began in 1923 with Engeldow and Wadhams research on wheat and barley grain yield (Fraser and Eaton, 1983). This approach assumes that variation in yield is the result of variation among yield components. Many analytic approaches have been used for yield component analysis (Fraser and Eaton, 1983) and continue to be developed (Eaton *et al.*, 1986). Yield component analysis is beneficial in that it not only determines that there is yield variation but also determines the relative role of each yield component or stage in this yield variation as well as allowing each yield component to be tested against another.

Testing yield components against one another can establish correlations which are useful in establishing the mechanism of yield variability. Negative correlations reveal compensation whereas positive correlations suggest reinforcement. Compensation is not inevitable as increases in yield can occur without compensation (Eaton - personal communication).

### **Sub-organismal Demographic Analysis**

This approach to growth analysis was introduced by Bazzaz and Harper (1977) who applied it to flax (*Linum usitatissimum* L.). Although their paper has been criticised (Hunt, 1978b) the technique itself is considered an important advancement to growth analysis. This

technique assumes that every organism consists of a population of structures that can be analyzed demographically. The general procedure is that plant components are tagged as they occur so that their chronology and relative contribution to final yield can be determined. One of the main advantages of this technique over conventional plant growth analysis is that by tagging there is less need for destructive harvesting. A good example of the utility of this technique for answering practical questions is the work of Lovett Doust and Eaton (1982) with beans.

Although growth analysis has been available and applied to crops since before 1920 the use of growth analysis for the study of weeds is a relatively recent innovation. Growth analysis is a tool that can, and should, be used by weed researchers to assist in understanding and explaining differences between treatments from a weed-centred perspective. Such understanding will lead to a more rapid understanding of weed biology and in turn, more effective weed management decisions.

### **Allometry**

Allometry has been defined many ways (Gould, 1966) and generally refers to the growth relationship that exists among the different parts of an organism. A good overview of plant allometry is presented in Niklas (1994). Pearsall (1927) proposed a generalized model for an allometric relationship between plant parts of the form

$$\theta_i = \beta \theta_p^\alpha$$

where  $\theta_i$  is plant part "*i*",  $\theta_p$  is plant part "*p*",  $\beta$  is a scalar that equals  $\theta_i$  when  $\theta_p = 1.0$ . The allometric exponent  $\alpha$ , represents the relative growth rate of  $\theta_i$  and  $\theta_p$  (Whitehead and Myerscough, 1962).

$$\alpha = R_i/R_p$$

Although many other functions could be used to describe allometric relationships the power function developed by Pearsall is the most accepted. Huxley (1932), even suggested that this function was a universal biological law for relating parts of an organism. Gould (1966) has demonstrated that this equation does work well in many instances.

Pearsall's power function and the methods used to derive the function and interpret the results have become accepted routine conventions (Smith, 1980). The dangers associated with the routine nature of the usage and interpretation of this function have been outlined. Smith (1980) demonstrated how some procedures are unnecessary or misleading and has proposed methodologies to avoid pitfalls. Seim and Sather (1983) demonstrated the importance of selecting an appropriate regression analysis for the objective of the allometric study particularly for data-sets with low correlation coefficients.

Allometry is of agronomic importance. Indices such as harvest index are simple allometric ratios and yield component analysis (Fraser and Eaton, 1983) often involves allometric relationships. Allometric relationships can be used in general modelling of plant productivity and in investigating the nature of interference (Whitehead and Myerscough, 1962; Jolliffe *et al.*, 1988).



## **Vegetation Sampling**

Properly conducted vegetation sampling enables a researcher to make inferences about a population by intensive examination of only a small portion of the population. Choice of a sampling method depends on the goal of the survey, the morphology of the species, the spatial pattern of the species and the research resources available (Chapman, 1976). Additionally, sampling methods must be precise (able to detect population differences), accurate (truly reflect the population) and efficient (minimum cost).

Vegetation sampling usually is conducted for one of two goals; either to estimate a characteristic or attribute of a population (descriptive survey) or to explore relationships or test hypotheses (analytic survey) (Satin and Shastry, 1983; Ives and Moon, 1987). Analytic surveys are often conducted only after a descriptive survey of the population has been completed.

### **Quadrat Size, Shape and Numbers**

Efficient vegetation sampling and analysis is in part dependent on proper quadrat selection. In vegetation surveys a quadrat is simply the sampling unit or portion of the population sampled. This sampling unit can be square, rectangular or circular (Knight, 1978).

A review by Van Dyne *et al.* (1963) determined that, in general, low perimeter-to-area ratios decreased accuracy because of edge effects and that perimeter-to-area ratios are lowest in circular quadrats. Bormann (1953) discovered that the best precision was obtained from rectangular quadrats because they encompass more heterogeneity per quadrat than square or

circular quadrats.

The best quadrat size is dependent on the morphology and homogeneity of the population being measured as well as the type of analysis that will be conducted on the collected data. If a population consists of regularly or randomly distributed clumps, and the size of the quadrat is much different from the mean size of the clumps of individuals, then the population will appear to be random, when in fact it is not (Elliot, 1977). Greig-Smith (1964) has suggested as a rule-of-thumb to use a quadrat that is twice as large as the mean canopy spread of the largest species. If the species being measured are at several scales, nested quadrats can be used with different sized quadrats fixed at the same sample site to sample each of the different scales of the hierarchy. Generally the choice of quadrat size is made subjectively by combining intuition and convenience.

From a statistical point of view, a general rule for sampling is 'the more the better' (Chapman, 1976). From a practical standpoint determining the number of samples is a matter of establishing a balance between statistical requirements and research resources available. As a rule of thumb, Knight (1978) indicates that to characterize a site at least 20 quadrats are required. A simple approach is to manipulate quadrat size and number so that a certain percentage, usually between 1 and 20%, of a stand is sampled (Chapman, 1976). Analytically the number of quadrats to use can be determined by intensively sampling a test site, plotting the running means (or some other statistic of interest), and assessing the point on the resulting graph at which additional quadrats yield diminishing returns (Knight, 1978; Nyrop *et al.*, 1986). Alternatively one could sample until the standard error of the quadrat data is within some acceptable bound (Eckblad, 1991). The bound could be the standard

error of sampling, as it is usually desired that standard errors should be no more than 15-20 % of the mean (Menzies - personal communication). The bound could also be that the variability within sample areas should be less than variability between sample areas (Chapman 1976).

### **Survey Methods**

There are several survey methods that are commonly utilized to sample vegetation. These survey methods are: representative; random; systematic (includes transects); stratified (includes restricted random); and cluster (Chapman, 1978; Benoit *et al.*, 1989).

In representative sampling, sampling units are arranged subjectively, usually to selectively include special features. The subjectivity of this method induces bias that limits statistical analysis except for some multivariate techniques such as ordination (Chapman, 1976).

In random sampling, a predetermined number of sampling units is selected in a way that every unit in the population has an equal chance of being sampled. Because every sample must have an equal chance of being sampled, by simply throwing a quadrat over ones shoulder does not assure randomness (Chapman, 1976). A concern with random sampling is that the population may not be uniformly sampled over the full range of the population and the samples will not be representative.

In systematic sampling, a selection interval is used to determine where a sample unit falls following a random start. This ensures increased population representation and in turn results in relatively greater accuracy than achieved with random sampling. Transects are

simply a form of systematic sampling in which sample units are arranged linearly (Chapman, 1976). Accuracy of systematic sampled units can be a problem if the periodicity of the selection interval coincides with some natural periodicity (Satin and Shastry, 1983).

In stratified sampling, the population is subdivided into relatively homogeneous subdivisions called strata and every stratum is sampled with randomly selected sample units. This method usually involves laying out a grid defining strata boundaries although using a baseline with perpendicular transects and multiple starts can achieve the same effect. The goal of stratification is to increase precision by increasing population representation. Cochran (1977) indicates that no more than six strata are required as further subdivision leads to diminishing returns. Strata can be homogeneous on a proportional basis or on some optimization basis. Optimum allocation is usually used when allocation on a proportional basis will be unsatisfactory in increasing precision (Satin and Shastry, 1983). A simple form of stratified sampling is referred to as restricted random sampling (Chapman, 1976). In this simpler form, the population is simply subdivided on some subjective basis and each subdivision sampled at random.

In cluster sampling, a number of primary sample areas (clusters) containing several secondary sample units are selected randomly from a population. All secondary sample units within a cluster are then sampled. The main advantage of cluster sampling is that samples units are concentrated which can simplify sampling and, in turn, increase sampling resource efficiency (Satin and Shastry, 1983). Green (1979) has suggested that cluster sampling could be used for sampling strongly aggregated populations. A problem with cluster sampling is that neighbouring sample units within a cluster may have more characteristics in common

than the general population (strong autocorrelation). Optimum precision in cluster sampling is obtained when clusters are as heterogeneous as possible; this effect is the opposite of what occurs in stratified sampling (Stuart, 1976).

Information on sampling vegetation or general survey techniques has been compiled into a large number of comprehensive reviews or texts. The author recommends the following: Stuart (1976), Southwood (1976), Cochran (1977), Elliot (1977), Green (1979) Satin and Shastry (1983), and Ives and Moon (1987).

## **PLANT INTERFERENCE**

### **Terminology**

#### **Interaction Types**

Regardless of the means of interaction, species in mixture invariably affect the probabilities of one another exploiting some resource or being exploited or manipulated by some external agent.

Burkholder (1952) catalogued a list of ten biologically possible interactions between organisms, only seven of which were examined enough to be named. Each interaction is symbolically represented for its influence on each of two species in a mixture using +, 0, and -, for stimulation, no effect, and depression, respectively. This symbolism allows for rapid definition of the various terms used for interactions between pairs of species. The six main interactions when two plants are in contact are: neutralism (0,0); competition (-,-); mutualism

(+,+); commensalism (+,0); amensalism (0,-); and parasitism, predation, herbivory (+,-).

Connell (1990) has suggested that the term amensalism be changed to asymmetrical competition to reflect the way this interaction is discussed in the literature.

### **Interference vs. Competition**

Often used in a loose fashion with little scientific basis, the term competition is frequently applied to agronomic phenomena (Hall, 1974a). Donald (1963) was among the first to come up with a relatively clear definition of competition:

"Competition occurs when each of two or more organisms seeks the measure it wants of any particular factor or thing and when the immediate supply of the factor or thing is below the combined demand of the organisms".

Using this definition the term competition does not refer to all mutual relationships among neighbouring individuals, as the expression is commonly misapplied, but is applicable only to those specific relationships where individuals compete for a resource. The most recent weed science (Anonymous, 1985) definition of competition is:

"The reduction in supply of resources to one organism as a result of active acquisition by another".

Plants require the resources of light, water, nutrients, carbon dioxide and oxygen for growth and these are the resources over which plant competition may occur. Other plant-plant interactions which occur, such as changes in environment and allelopathy are non-competitive interactions (Harper, 1977).

Other researchers have classified competition into "real" and "apparent" competition (Holt, 1977). A plant may appear to be affected by another but in reality it is some other indirect interaction that has facilitated the response. Real competition occurs as a result of direct interaction or indirect interaction on a shared resource (exploitation). Apparent competition occurs as the result of indirect interaction by some shared enemy (Connell, 1990). For example one plant species may encourage increased predation on an adjacent species and as a result will increase. This increase might incorrectly be interpreted as the increasing species being more competitive than the other (Holt, 1984).

The term interference has been proposed to describe all mutual relationships between plants and encompasses competitive and non-competitive and apparent competition interactions. Harper (1961) was the first to propose a definition of interference with this meaning. He defined plant interference as:

"... the response of an individual plant or plant species to its total environment as this is modified by the presence and/or growth of other individuals or species".

Thus the term interference can be used to describe a broader range of interactions between individuals than can the term competition. For example, if a plant is affected by another through the production of toxins, changing the behaviour of predators, or affecting conditions such as temperature or wind, then the term interference is applicable and not the term competition.

It should also be noted that this definition of interference allows for beneficial interactions and not just the obstruction effect that is typically understood by interference. The management practice of intercropping is based on the concept that potential competitors

may also benefit each other. A good review of beneficence in plants has been composed by Hunter and Aarssen (1988).

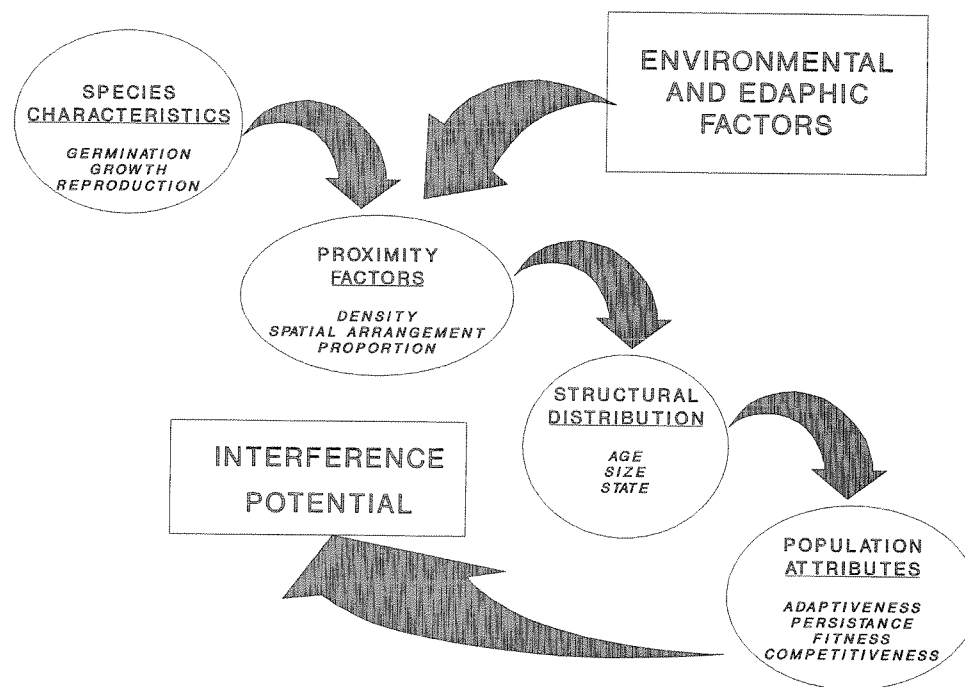
### **Considerations**

Weed management programs developed using the weed-centred approach will axiomatically focus on the weed population. The characteristics of the weed population are determined by the interaction of genotype and environment. The genotype determines the species potential for germination, growth, and reproduction as well as the species response to environment. The environment determines what proportion of the population survives and the variation among individuals in the population. In turn, population survival may be characterized in terms of proximity factors (Radosevich, 1987) and the population variability may be characterized in terms of structural distribution factors (Watkinson, 1986).

Proximity factors in combination with species characteristics and environment determine the structural distribution of a population. Many population attributes described by broad terms such as fitness or competitiveness are simply functions of the characteristic structural distribution, proximity factors, species composition and environmental qualities determined in a particular population. All these population characteristics ultimately determine the interference potential of a population. This authors interpretation of the interrelationships of these various population characteristics are illustrated in Figure 1.

Most of the techniques and analyses developed for the weed-centred approach have emphasized the role of proximity factors. The main reasons for the proximity emphasis are:





**Figure 1.** A generalized illustration of the interconnectiveness of various population characteristics towards determining a subpopulation's ultimate potential for interference.

(1) the historical recognition of the importance of density in interference (Aldrich, 1987), (2) the central role of proximity factors in determining the interference potential of a population (Figure 1), and (3) the relative ease of manipulation of proximity factors for experimentation (Radosevich, 1987). The techniques and analytical approaches for quantifying the role of proximity factors in interference are the focus of this review.

### **Proximity Factors**

The interference relationship between plants is dependent not only on the characteristics of the neighbours but also depends on the proximity factors of spatial position (arrangement) and concentration (density and proportion). Many models have been developed to deal with density effects, usually based on the reciprocal yield law of Shinozaki and Kira (1956), but few satisfactory models exist to deal with the effects of arrangement or proportions. Dealing with the influence of spatial arrangement in some quantitative manner is one of the major challenges to researchers modelling crop/weed interference (Radosevich, 1988). New quantitative approaches that might ultimately assist in overcoming this challenge are multivariate techniques such as those reviewed by Cormack (1979) or the use of fractal models (Sugihara and May, 1990).

- **Importance of Space.** Interference by capturing resources and depriving neighbours brings about a competitive advantage. Successful capture depends on distance from neighbours and size and activity of the neighbours. Ross and Harper (1972) determined that growth of individual seedling grasses was a function of the biological space available to each

plant where biological space was defined not only by position but also by stage of growth.

Density is not the exclusive cause of yield variation. After reviewing the literature Benjamin and Hardwick (1986) concluded that space per plant typically only accounts for roughly 20% of the variation in plant size. The remainder was dependent on the size and activity of neighbouring plants. Research by Mack and Harper (1977) indicated that an individual reacts to the effects of its neighbours and not to the density of the population. Spitters (1983a and b) demonstrated the importance of species proportion by including it in his yield density model. Their model results suggest that the density of each species relative to the other influences the yield of both. Weiner (1982) states that plant plasticity and the importance of spatial pattern limits the use of density in describing a plant population. In addition to numbers, size, distance, age, species and angular dispersion are relevant factors.

Simulations by Firbank and Watkinson (1987) indicate that the role of local competition may almost be completely obscured as the result of differences in emergence times of neighbours. O'Donovan *et al.* (1985) have shown that the per cent yield loss in barley and wheat was dependent, at any constant wild oat density, on the wild oat emergence time. For every day wild oats emerged before the crop the yield loss increased three per cent whereas for every day wild oats emerged after the crop yield loss decreased by three percent.

Ford (1975), studying *Tagetes patula* in a lattice arrangement, was able to show that plants that emerged as dominant were regularly distributed whereas the population as a whole was non-uniform. He suggested that the dominant plants were only seriously affected by competition from other dominant plants. Benjamin and Hardwick (1986) have suggested

that the limiting factor for yield is not deployment of plant size but is resource utilization. Pitelka and Ashmun (1984) have stated that clonal plants have mechanisms for minimizing intraplant competition while allowing effective interclonal competition.

- **Domain Models.** Researchers have generally picked one of four assumptions when modelling density relations. The zone of influence of individual plants at various densities is assumed to be either non-overlapping, overlapping, unbounded or diffuse (Benjamin and Hardwick, 1986).

Non-overlapping domain models generally assume that plants grow from emergence until they meet another plant whereupon expansion ceases and the domain occupied by each plant is proportional to its biomass. These non-overlapping zones of influence are usually drawn as tessellation polygons and are referred to as Dirichlet domains, Meijering cells, and Theissen or Voronoi polygons (Benjamin and Hardwick, 1986). Examples of this approach are the experiments and models of Mead (1966), Fischer and Miles (1973), Armstrong (1974), Slatkin and Anderson (1984) and Sutherland and Benjamin (1987). By studying the influence of eccentricity and abcentricity on growth of carrots, Mead (1966) was able to show that the shape of a polygon and the position of a plant within a polygon were less important than the area of a polygon. Subsequent research using cocksfoot, *Dactylis glomerata*, by Ross and Harper (1972) supported this observation.

Results from experiments with cocksfoot by Ross and Harper (1972) indicate that the zones of influence of individual plants is diffuse with considerable overlap. Overlapping domain models generally assume that the zone of influence of a plant extends for some radius

out from each plant. The influence of neighbouring plants within the plants zone of influence is then described through some function. An example of this approach can be found in the studies of Mack and Harper (1977) on a population of dune annuals. Goldberg and Werner (1983) proposed a mathematical function that takes into account the diminishing effects of one or more distant neighbours. Benjamin (1993) has recently completed experiments which indicate that overlapping domain models are more appropriate than non-overlapping domain models in simulating competition.

Unbounded domain models assume that all plants affect all other plants within the population. This working hypothesis was used by Aikman and Watkinson (1980) when they developed a model which assumed that the growth of each plant is proportional to a crowding index determined from the growth rate of the entire population.

Diffuse population models assume that the immediate neighbours have no greater influence than distant neighbours. This hypothesis rarely, if ever, holds true for plants and is therefore considered to be purely theoretical.

- **Agricultural Studies.** In agriculture, interest in modifying plant arrangement or spacing practices has been limited because of the practical limits of the tools available for planting and management as well as good success with traditional practices. With changes in technology, such as new planter<sup>s</sup> designs, changes in crop management approaches, such as targeting economic weed thresholds instead of clean fields, and changes in consumer/industry preferences for more uniform and higher quality products, the importance of spatial pattern is no longer simply a subject of curiosity.

Traditionally crop-weed interference studies have documented weed density while neglecting crop density. Neglecting crop density can be a problem as Hume (1985) has shown that in spring wheat crop density is an important component of weed competition. He determined that wheat density in adjacent quadrats varied as much as 25 plants per square meter and that under competition yield per plant as well as dry weight and tillering all decreased with increasing crop density.

Holiday (1963) investigated the influence of row width on the yield of wheat, barley, oats and rye. He determined that at a constant seed rate decreasing the row width below 7 to 8" generally resulted in an increased yield, whereas, increasing the row width above the 7 to 8" standard has generally resulted in a decreased yield. Donald (1963) states that there are benefits to be gained by maximizing the distance to the nearest neighbour casting shade and in minimizing the distance from the centre of the plant to any point in the soil. However he also states that cultural factors such as seeding precision, fertilizer placement, and weed control may mean that in many circumstances the advantages of precision planting may be obscured.

Rectangularity is the ratio of the distance between rows to the distance between plants in the row. Willey and Heath (1969) reviewed research on plant rectangularity and determined that in general as rectangularity increases by increasing seed rate, or row width, yield per area declined. Willey (1982) has stated that the ideal spatial arrangement is one in which there is equidistance between any given plant and its neighbours. He also states that the extent to which rectangularity affects yield depends on plant plasticity. He cites the example of sugarbeets which begin to suffer a loss if rectangularity exceeds 2:1 whereas

rectangularities of 6:1 are acceptable for most tillering cereals. Mead (1966) observed for carrots that as rectangularity was reduced product uniformity was increased.

Jagannath (1978) studied sorghum and finger millet planting arrangements and observed triangular planting arrangements to result in less competition than rectangular or square plantings. This observation was particularly noticeable at higher planting densities. He also observed that the rectangular pattern was slightly better than square planting only when the rectangularity ratio was in the 1:2 to 1:2.5 range. Using a purely mathematical approach Pant (1979) assumed that plants had zones of influence that were either plate-like, cylindrical or hemispherical. Irrespective of the zone of influence his calculations of packing fractions suggest that the most effective planting patterns in decreasing effectiveness were as follows: hexagonal arrangement, a square arrangement and finally a rectangular arrangement.

Walker and Buchanan (1982) noted that, at equal seeding rates, crops are generally more competitive with weeds when sown in narrower as compared to wider rows. This finding is consistent with the statement by Harper (1977) that competition between plants increases as the distance between plants decreases. Fischer and Miles (1973) used models to investigate the importance of spatial arrangement on weed-crop competition. Results from their study suggest that the most effective planting patterns for weed competition in order of decreasing effectiveness were as follows: triangular lattice, square lattice, hexagonal lattice, rectangular lattice.

Sakai (1957) sowed rice cultivars in a hexagonal arrangement around a central test plant. He determined that both the number and the arrangement of the various cultivars influenced the yield of the central plant. Harper (1961) studied interference in two annual

grasses. The arrangement of species was varied between treatments while density and proportions were kept constant. At the end of the experiment the yields of the two species differed significantly by arrangement. Lindquist *et al* (1994) grew oat plants at various angular arrangements in concentric circles around a target oat plant and observed that yield of the target plant differed significantly by arrangement. All these researcher observed that with increasing aggregation competition was reduced.

- **Impact of Aggregation.** Most studies of pattern in plant populations has revealed that purely random patterns are rare; some degree of aggregation is the norm (Taylor *et al.*, 1978; Hutchings, 1986). Such aggregations may act on species to enable them to avoid competitive exclusion (Weiner, 1982). A clumped superior competitor is subject to heavy interspecific interference and leaves gaps for an inferior competitor.

Weed scientists often assume a uniform pattern of weeds (Hughes, 1990; Thornton *et al.*, 1990). If the weed pattern is actually patchy this can lead to an overestimation of yield loss and over-encourage herbicide use. It has been determined that weed populations are usually aggregated and spatially variable (Thornton *et al.*, 1990; Wiles *et al.*, 1992; Mortenson *et al.*, 1994). Hughes (1990) demonstrated that Cousens (1985) basic yield loss model predicts decreasing yield loss with increase variability (aggregation) of weed density, his explanation being that crop-weed competition becomes less and less as aggregation increases.

Brain and Cousens (1990) have suggested that assuming a regular distribution is not costly in terms of herbicide spraying decision making. The decision to spray or not to spray is usually made at low weed infestation levels and at low weed infestation levels weed



patchiness has less impact on yield loss than at heavy weed infestation levels. This assumption has generally been supported by the results of simulations by Wiles *et al.* (1992) on broadleaved weeds in soybeans.

### **Plant Size**

- **Importance.** In agriculture, understanding the mechanisms of variation in plant size is important; important to consumers who want uniformity in produce and important to producers who want to maximize yields (Benjamin and Hardwick, 1986). In a crop-centred approach, size variation has not been a major concern because through agricultural practices of seed grading and uniformity in planting depths, timing and densities, size variation within crops has been reduced. However, in weed populations size variation is a major concern due to natural variability in characteristics such as seed vigour, size, depth of emergence and dormancy. In a weed-centred approach, weed population size variability makes understanding the mechanisms of variation in plant size particularly important.

- **Mathematical Expression.** Plant size hierarchies are typically summarized mathematically by their skewness or their Gini coefficient. Skewness indicates whether the frequency distribution is asymmetric and can be J-shaped ( $\text{skew} < 0$ ), L-shaped ( $\text{skew} > 0$ ) or bell-shaped ( $\text{skew} = 0$ ). The Gini coefficient ( $G$ ) is a measure of size inequality;  $G = 0$  when all individuals are the same size and  $G = 1$  in a population of infinite size where all but one

of the plants is infinitely small. A good review of the value of these two mathematical methods for expressing the magnitude of size hierarchy can be found in Weiner and Solbrig (1984). The Gini coefficient and the more commonly used coefficient of variation (CV) give almost identical results (Kenkel, 1995, personal communication).

Given that the Gini coefficient and skewness values would be expected to increase with stronger competition it has been suggested that they could be used as measures of intraspecific competition (Rejmanek *et al.*, 1989). Analysis of the results of competition between Japanese millet and tomato determined that the Gini coefficient and skewness were inferior to other methods of assessing intraspecific interference (Rejmanek *et al.*, 1989).

- **Distributions and Influencing Factors.** Koyama and Kira (1956) were among the first to publish results showing that although the frequency distribution of mass per plant was approximately normally distributed at emergence, as time progressed, the distribution becomes increasingly positively skewed (L-shaped). This skewed distribution consists of few large individuals and many smaller ones and is referred to as a size hierarchy (Weiner and Solbrig, 1984). Koyama and Kira (1956) suggested that the L-shaped distribution is the natural outcome of the exponential nature of plant growth and that it is simply enhanced by competition. When increased plant growth and increased competition occur in a complementary fashion this is referred to as "snowball" cumulation (Wilson, 1988). Bimodality can also occur where there is a uniform two-tiered canopy of large plants and small plants (Westoby, 1984).

Size hierarchy tends to develop more quickly in high density populations. Weiner and

Thomas (1986) determined that increases in density resulted in increased size inequality in fourteen out of sixteen relevant studies they reviewed. The two studies where there was no size inequality reported were unique in that the plants were grown from seed and studied for only a short period after emergence. Weiner (1988) later suggested that the difference occurred because early plant interference is two-sided (for nutrients), whereas late plant interference is one-sided (for light). One-sided asymmetric competition, where larger plants have a disproportionate effect on smaller plants, is the most common situation (Thomas and Wiener, 1989).

A plant population size hierarchy can develop as a result of several influences (Benjamin and Hardwick, 1986). Biotic influences on size inequality include herbivory, pathogens, parasites, age/stage, genetics and interference. Abiotic influences on size inequality include spatial differences in microclimate and resources.

Age is a primary determinant of size variation in populations (Ross and Harper, 1972; Firbank and Watkinson, 1987). A small difference in age can result in a minor size difference that over time is exaggerated through interference. For example it has been shown by some researchers that time of emergence was the major influence on final plant size in their experiments (Ross and Harper, 1972; Firbank and Watkinson, 1987). These observations are consistent with work by Gan (1994) in Manitoba who did field studies on the emergence and growth of red spring wheat plants grown from seed lots of large and small seed at various planting depths. He observed that Haun stage and yields of individual plants were strongly correlated with date of emergence. He also observed that the first plants to emerge averaged over 3 times the yield of those plants that emerged 7 to 9 days later.

Wilson (1988), based on results from partitioned pot studies with *Festuca* species, argued that the importance of initial advantage in size or establishment is not as great as many has stated. Initial competition advantage by size is simply an artifact of light competition and is less important for nutrient competition.

Weiner (1988) indicates that size variation due to age may be distinct from size variation due to other causes. A plant that is small because of its age will have a greater prospect of continued growth than a plant of the same size because of suppression by herbivory or disease.

In most herbaceous plants age and size are not synonymous (Ogden, 1970). Stage of growth may be more important in determining the fate of an individual plant, especially with perennials, than is absolute age (Hutchings, 1986). Gan (1994) studied red spring wheat and observed that Haun stage was a good indicator of the yield of individual plants in a population. Use of stages recognizes both the major changes in morphology and the differences in duration of time spent in each stage better than absolute age does.

Size variation can be due to genetic differences in plants. Genetic differences that result in small plants and in turn reduced fecundity or death of those plants may be offset by subsequent improved adaptation of the population as a whole (Antonovics and Levin, 1980). However, since genetic variability is only one of many potential causes of small size it is likely that significant selection pressure on the population as a whole would be rare.

When interference occurs between plants, dominance and suppression are major influences on the size hierarchy. This influence may not be to increase the size hierarchy. Interference may actually slow the development of the hierarchy by slowing growth (Turner

and Rabinowitz, 1983 (cited in Hutchings, 1986)). The 'interference slows growth' hypothesis has yet to be proven and has been labelled an inappropriate interpretation of skewness by Weiner and Solbrig (1984). Ross and Harper (1972) suggest that in a grass population they studied the low weights exhibited by late emerging plants were lower than would be expected from the reduction in growing period alone. They attributed the relatively lower weights to the earlier plants capturing "space" that was subsequently unavailable to later emerging plants. These findings are consistent with that of Gan (1994) who investigated the growth of red spring wheat plants in Manitoba populations and determined that a greater proportion of plants that emerged late were infertile.

Whereas population weight distributions become positively skewed over time, the height distribution either remains symmetrical or becomes negatively skewed (J-shaped) (Hara, 1984). With interference for light small plants etiolate to maintain the same height as larger plants. Continued insufficient light following etiolation can result in mortality. Hara (1986) has modelled plant size hierarchy as a functional process of interference using light interception and extinction.

In plant populations the development of size hierarchy is an important determinant of performance and survival of individual plants in the population. Small etiolated plants are subject to mortality resulting in self thinning.

### **Self Thinning**

Despite its universal occurrence mortality is often assumed to be negligible or is ignored when yield density relationships are described. Density-dependent mortality or self

thinning is a common phenomena. For example, Gan (1994) observed an inverse relationship between uniformity of emergence and self thinning in red spring wheat populations. As a plant population grows and density increases the height distribution of plants within the population gradually changes from a relatively normal distribution to a skewed one consisting of many small plants and a few large plants (Obeid *et al.*, 1967). Under the competitive conditions imposed by high population densities those plants under the most competitive stress, usually the smallest plants, will eventually die decreasing the population skewness (White and Harper, 1970). As the plants continue to grow the skewness of the height distribution eventually exceeds the plasticity capacity of the remaining plants under the competitive stress and more of the plants die.

- **Mathematical Expression.** Yoda *et al.* (1963), in experiments with buckwheat, determined that the relationship between per plant biomass ( $\beta$ ) and stand density ( $\delta$ ) could be expressed by an equation of the form

$$\beta = \kappa \delta^{-3/2}$$

where  $\kappa$  is a constant. This equation can be represented in its log transformed form

$$\ln \beta = \ln \kappa - 1.5 \ln \delta$$

The basis for the exponent term being "-3/2" has not been scientifically proven although it is likely related to packing a three dimensional organism into a two dimensional area (Weller, 1987). As a population grows it eventually reaches the carrying capacity of the habitat. At the carrying capacity any increase in an individual plants biomass must be at the expense of

an equal amount of biomass in some other member of the population. At this stage as individuals grow the population undergoes self-thinning and there is a gradient of -1. Eventually self-thinning results only in an increase in surface area and no more shared volume. At this stage a  $-3/2$  gradient develops. The  $-3/2$  gradient has been determined to be widely applicable to many species (White, 1981) and the equation is often referred to as the  $-3/2$  thinning law or power law.

- **Influencing Factors.** Site fertility and light intensity are two variables which have been shown to modify the  $-3/2$  power law. Ford (1975) and White and Harper (1970) have demonstrated that as light intensity declines the gradient moves down towards -1. If the nutrient supply is increased the gradient is reached more rapidly but the gradient is not changed (Hutchings and Budd, 1981).

Researchers (Hutchings and Barkham, 1976; Hutchings, 1979) have demonstrated that clone forming perennial plants do not follow the  $-3/2$  power law. In such plants each shoot is connected to other shoots and the translocation of carbohydrates and other materials is possible. In clonal plants shoot mortality does not occur until after maturation. Biomass accumulation in clonal plants stops just short of the point where density dependent mortality would occur (Pitelka and Ashmum, 1984). Inter-ramet interactions, such as competition for light, results in reduced spacial overlap (Kenkel, 1993). This indicates that in clonal plants the  $-3/2$  power law limits clonal growth but does not result in mortality.

- **Criticisms.** Weller (1987) reanalysed much of the data from previous studies

supporting the self-thinning rule and indicates that the data do not support the power law. His major criticism against the power law is that density dependent mortality begins before a stand reaches the  $-3/2$  gradient. An additional criticism is that the current definition of self thinning is too broad (Osawa and Sugita, 1989; Weller, 1990). Studies on self thinning must specify whether they are dealing with interspecific size-density relationships, the species boundary line or the dynamic thinning line. Ziede (1987) concluded that thinning lines could not be generalized as straight lines and was critical of many authors for their uncritical acceptance of the "rule". Lonsdale (1990) expanded on the critical reviews of Weller (1987) and Ziede (1987) and reached similar conclusions.

There have been yield-density models developed that incorporate density dependence (Watkinson, 1980; Firbank and Watkinson, 1985). Such models are more complex than required for most weed crop situations. With good field management, density dependent mortality should only be of minor importance.

## **Approaches and Quantification**

### **Experimental Designs**

Given that investigators have a wide range of interests when investigating plant interference it should be no surprise that several approaches have been developed to assess interference between species. Generally the only element in common between the various approaches is that each approach is a type of bioassay in which the response of one species is used to assess the influence of the other. The four main classes of experiments used to



assess competition in mixed stands are : additive, substitutive, systematic, and neighbourhood. Reviews of these experimental designs to assess interference are found in Oliver and Buchannon (1986), Radosevich (1987 and 1988), Snaydon (1991) and Sackville Hamilton (1994).

- **Additive Experiments.** Additive experiments are probably the most common approach used to study weed crop competition. In this approach an indicator species at a some fixed density is grown with a competitor species at a range of densities. Because it is only the density of one species that is varied this specific approach might more appropriately be called a partial additive design (Rejmanek *et al.*, 1989). This approach has historically been the most widely used approach for assessing crop losses due to weeds (Zimdahl, 1980; Radosevich and Holt, 1984). It has the advantage of simulating what happens in weed-crop situations and therefore can be used to develop weed threshold levels at which crop loss justifies control measures. Implicit in this approach is the assumption that the single crop density used is optimum for both weedy and weed free conditions.

The weakness of the additive approach is that interpretation of the competitive relationships that occur in an additive approach are confounded with concurrent changes in total population density and proportions (Harper, 1977; Firbank and Watkinson, 1985; Radosevich, 1987). Other associated criticisms include the assumptions that intraspecific competition remains constant, spatial arrangement has no influence, and that the technique is unable to distinguish between intra- and interspecific competition (Radosevich, 1987 and 1988). Snaydon (1991) has suggested that because overall density has no meaning the

criticisms of the additive approach are invalid.

• **Substitutive Experiments: Replacement Series Design.** Next to additive designs the use of a substitutive approach introduced by DeWit (1960) is probably the most widely used experimental approach for studying weed crop competition. In this approach, also referred to as a replacement series, the overall population density of a plot is kept constant while the proportion of the density allocated to each component species is varied from 0 to 100%. One key aspect of this approach is that monocultures of each species are included in the design. In this approach it is assumed that the plant population density chosen is beyond the point of constant yield (DeWit, 1960). The replacement series design was developed to overcome the confounding of density and proportions criticism of additive designs (Harper, 1977).

Harper (1977) and Inouye and Shaffer (1981) have criticised the replacement series design on its artificiality in that in natural infestations, populations will shift over time to densities not included in the original design. Radosevich (1988) has pointed out that the design can be cumbersome when the species have different life histories or growth forms. Mead (1979) criticised the technique for the confounding of density with spatial arrangement. Firbank and Watkinson (1985) criticised the design on the basis that it did not allow the prediction of the yield of both species to be estimated at any mixture proportion or density. Jolliffe *et al.* (1984) criticised the design on the basis that it did not allow the separation of competition into intraspecific and interspecific effects. Connolly (1986) has criticised the derived indices from replacement series designs because of their density dependence. He has

also determined that many of the commonly derived indices of competition from a replacement series experiment showed variability in results, indicating that replacement series experiments could lead to erroneous conclusions when researching competition.

- **Substitutive Experiments: Additive Series Design.** In order to maximize interpretation of replacement series designs it has been stated that monoculture data at a range of densities is required (Jolliffe *et al.*, 1984). The importance of varying both total population density and frequency in mixtures has also been emphasized by Firbank and Watkinson (1985).

One approach to address these suggestions is the additive series design. In this design several replacement series are combined over a range of densities in an additive fashion (Rejmanek *et al.*, 1989). Snaydon (1991) considers an additive series design to be only those designs in which the densities of each component in mixture is identical to that which also occurs in pure stand. Additive series designs provide a balanced data set which is highly recommended for weed-crop competition studies (Rejmanek *et al.*, 1989).

- **Substitutive Experiments: Diallel Design.** Mixture diallels are simplified versions of replacement series experiments that have been used by population geneticists for interference studies (Trenbath, 1974). In this approach a set of genotypes is grown in a 1:1 mixture of all possible pairs, including monocultures. The analysis of mixture diallel data provides information on both the productivity and aggressiveness of genotypes in mixtures compared

to monocultures. Trenbath (1978) has reviewed the interpretation of mixture diallel experiments.

The advantage of this design is its simplicity (Harper, 1977). The disadvantages of this design include its artificiality, since resources will be relatively nonlimiting with only one pair of plants per pot.

- **Systematic Experiments: Nelder Design.** As a way to determine optimum intercropping densities, Nelder (1962) devised fan-shaped 'systematic experiments' that have been modified to a parallel row approach by Bleasdale (1967). With this approach plants are grown at a wide range of densities without changing the pattern of arrangement. These designs usually consist of plants arranged in a grid arrangement such that the amount of space available to each plant varies systematically over the different parts of the grid (Radosevich, 1987). This design maximizes the efficient use of experimental material by minimizing the amount of non-experimental area (Mead, 1979). The problem with systematic designs is they lack randomization which limits the statistical analysis that can be performed on the data collected. Additionally, only individual plants are measured, which means that the influence on a population is unavailable.

Radosevich (1987) has also criticised the Nelder design as it is normally conducted for allowing confounding of density and proportion effects. He has also criticised the design for not allowing partitioning of intraspecific and interspecific interference.

- **Systematic Experiments: Addition Series Design.** In his investigations on

intercropping Spitters (1983 a and b) developed a systematic approach called an addition series. The addition series is not a design, but instead it is a method of analysing data from mixtures grown in an ascending progression of total densities (Radosevich, 1987). This method has also been called a completely additive design (Rejmanek, 1989). The approach is based on using Spitters (1983 a and b) multispecies reciprocal yield model to determine the yield of a species based on the densities available in the mixtures. Firbank and Watkinson (1985) used this approach for two species and were able to separate the effects of intra- and interspecific interference.

A criticism of this approach is that it does not account for spatial arrangement and that a lack of sufficient randomization can be a concern (Radosevich, 1987).

• **Neighbourhood Experiments: Partitioning Design.** Several experimental approaches have been developed to provide physiological insight into the mechanisms and sites of interference between plants. Several designs are available that separate root and shoot interference for light and nutrients using separating panels in pot cultures (Schreiber, 1967; Evetts and Burnside, 1975; Snaydon, 1979; Wilson, 1988). Hall (1974 a and b) was the first attempt to integrate this approach with the DeWit (1960) approach. Snaydon (1979) developed a comprehensive approach that combines the complementary additive and replacement series experiments as well as allowing adjusting the relative density of species in soil and in aerial space. The main criticism of this approach is that interference is restricted in two dimensions and that the procedure creates artificial microclimate effects.

• **Neighbourhood Experiments: Proximity Design.** When an investigator is interested in how the yield of an individual plant is affected by the presence of its neighbours a proximity neighbourhood approach may be appropriate. In this design the performance of an individual plant is recorded in relation to some characteristic of its neighbours. Most of these experiments have focused on the amount of neighbours (Mack and Harper, 1977; Weiner, 1982, Goldberg and Werner, 1983), whereas others have focussed on zones of influence (Bridges and Chandler, 1984; Gunsolus and Coble, 1986) or spatial arrangements (Silander and Pacala, 1985; Lindquist *et al*, 1994).

A criticism of neighbourhood models is that these approaches are usually based on the performance of individual plants and that variation in microsite quality can limit their usefulness, particularly at low densities (Waller, 1981).

A summary of the practical merits and limitations of the four major designs used to investigate weed interference are listed in Table 1.

### **Indices of Interference and Combined Yield**

Indices are used to combine or summarize data. Many indices have been proposed to aid in the interpretation of the results of mixture experiments and no standard indices have been adopted for quantifying interactions in mixture experiments. The applicability and appropriateness of each index is dependent on the users objective. These objectives can range from elucidating the effects of density and proportion on plant interaction to the differentiation between intra- and interspecific interference.

**Table 1.** Some of the practical relative merits and limitations of various general experimental approaches used to investigate weed interference.

Merits	Limitations
<b>Additive Experiments</b>	
<ul style="list-style-type: none"> <li>• Directly applicable to the field</li> <li>• Easily conducted in the field</li> </ul>	<ul style="list-style-type: none"> <li>• Specific competitive relationships difficult to determine</li> <li>• Assumes intraspecific interference constant and spatial arrangement not important</li> </ul>
<b>Substitutive Experiments</b>	
<ul style="list-style-type: none"> <li>• Ideal for interference models</li> <li>• Good for use in green-house studies</li> <li>• Excellent for evaluating the role of proximity factors on competition</li> </ul>	<ul style="list-style-type: none"> <li>• Not directly applicable to practical weed problems</li> <li>• Can be difficult to conduct in the field</li> <li>• Confounds density and spatial arrangement</li> <li>• Interpretation limited by density dependence</li> </ul>
<b>Systematic Experiments</b>	
<ul style="list-style-type: none"> <li>• Good for intraspecific interference studies</li> <li>• Guard plants only needed around outer edge of plants</li> <li>• Allows study of a wide range of densities without changing pattern</li> </ul>	<ul style="list-style-type: none"> <li>• Difficult to plant and establish</li> <li>• Not readily adapted to interspecific interference studies</li> </ul>
<b>Neighbourhood Experiments</b>	
<ul style="list-style-type: none"> <li>• Effective for studying the influence of spatial arrangement on individual plants</li> <li>• Good for computer models</li> <li>• Utilizes little land area</li> </ul>	<ul style="list-style-type: none"> <li>• Variability between weeds can mask significance</li> <li>• Critical germination timing and seed placement</li> <li>• Focused on arrangement</li> <li>• Not directly applicable to practical weed problems</li> </ul>

Connolly (1986) has demonstrated that many of the indices used for interpreting the results of replacement series experiments developed prior to 1984 are limited in usefulness because of their density dependence. Changing pure stand density, and in turn pure stand performance, often will result in a change in index value.

Snaydon and Satorree (1989) have suggested that indices of interference and combined yield can be grouped into three categories: (i) indices of resource complementarity, (ii) indices of competitive ability, and (iii) indices of competition severity. To date these categorizations have not been widely adopted.

To facilitate cross-referencing of the indices described in this review a list of symbols used is provided in Table 2.

- **Dew's Index of Competition.** Dew (1972) developed an equation to predict potential crop losses by wild oats. It has subsequently been used by various researchers to assess yield losses in various crops by other weeds. It is of the form:

$$YL = Y_{ii} (IC) \sqrt{N_j}$$

Where YL is yield loss,  $Y_{ii}$  is the weed free yield,  $N_j$  is wild oat density, and IC is Dew's index of competition. With Dew's index of competition the larger the value the greater is the competition.

The IC is derived from an additive series by a simple regression of crop yield ( $Y_i$ ) on the square root of the population density of an associated weed ( $N_j$ ). The regression is of the form



**Table 2.** List of symbols used in formulae to derive indices of interference and combined yield.

Symbol	Name or description
A	Coefficient of aggressivity
a	Equation parameter
b	Equation parameter
CI	Competition index
CR	Competition ratio
d	Population density (plants per land area)
EF	Species equivalence factor
i	Subscript indicating plant species
ii	Subscript indicating plant species i in monoculture
Ij	Subscript indicating plant species i and j in mixture
IC	Index of competition
j	Subscript indicating plant species
jj	Subscript indicating plant species j in monoculture
ji	Subscript indicating plant species j and i in mixture
k	Subscript indicating variable at point where Y is 50% of $Y_{\max}$
K	Relative crowding coefficient
Kc	Index of competitive ability
L	Subscript indicating loss
LER	Land equivalent ratio
m	Subscript indicating monoculture
max	Subscript indicating maximum
N	Number of plants
NDI	Niche differentiation index
P	Subscript indicating projected in absence of interference
RC	Relative competitive ability
RM	Relative monoculture response
RX	Relative mixture response
RY	Relative yield
RRT	Relative resource total
RYT	Relative yield total
Ty	Reciprocal of maximum theoretical y
x	Subscript indicating mixture
y	Yield per plant
Y	Total yield per land area or variable
Z	Sown proportion of a species (in mixture)
u	Theoretical maximum $Y_{ii}$

$$Y_i = a_i - (b_{ij}) \sqrt{N_j}$$

where  $b_{ij}$  is the regression coefficient and the IC is simply the ratio of  $b_{ij}$  over  $a_i$ . This index has been determined useful for studying the competitive abilities of crops against weeds (Dew and Keys, 1976).

There are two assumptions in the IC that limit its utility. The IC assumes that the weeds and crops emerge at the same time and it also assumes that crops and weeds have equal access to resources.

- **Relative Crowding Coefficient.** One index of mixture productivity is the relative crowding coefficient (K) of DeWit (1960). It is calculated for two species mixtures as follows:

$$K_i = ((1 - Z_i) / ((y_{ii})/(y_{ij}))) - Z_i$$

$$K_j = ((1 - Z_j) / ((y_{jj})/(y_{ji}))) - Z_j$$

$$K_{ij} = K_i \times K_j$$

The species are said to crowd for the same space if the product ( $K_{ij}$ ) is 1.0. If the product is larger than 1.0 then the species are said to crowd only partially for the same space. If the product is smaller than 1.0, then one species interferes with the other through some means other than crowding (Willey, 1979a).

- **Competition Index.** McIntyre (*in* Donald, 1963) formulated a competition index

(CI) for a species grown in mixture. The CI is based on the calculation of equivalence factors for each species in mixture. For any species "i" the equivalence factor (EF) is the number of plants of "i" required to be as equally competitive as one plant of species "j". This is established by determining what monoculture plant number ( $N_i$ ) is required to give a comparable yield per area ( $Y_{ij}$ ) in the mixture. The CI is then calculated as follows:

$$CI = (EF_i * EF_j) / (Z_i * Z_j).$$

When the CI is less than 1.0 there is minimal competitive interference and the mixture over yields. The major problem with this approach is that a large number of monoculture population densities are required to estimate equivalent plant numbers (Willey, 1979a).

- **Coefficient of Aggressivity.** An index of aggressiveness of one species towards another is that of McGilchrist and Trenbath (1971) called the coefficient of aggressivity (A). It is calculated for two species as follows:

$$A = (((y_{ij} / y_{ii}) - (y_{ji} / y_{jj}))) / 2$$

A high positive value indicates that "i" is aggressive and a high negative value indicate that "j" is aggressive. The greater the numerical value, the greater the difference in competitive species ability (Willey, 1979a). Because this index incorrectly assumes that yield changes are exclusively related to competitive ability the index has been shown to give inconclusive results in practice (Hall, 1974b; Willey and Rao, 1980).

• **Competitive Ratio.** Another index of the aggressiveness of one species towards another is the competitive ratio (CR) of Willey and Rao (1980). The CR simply the ratio of the individual relative yields of the two component crops. It is similar to the coefficient of aggressivity but corrects for the proportion in which the crops were initially sown. This allows for a direct comparison of values. It is calculated for two species as follows:

$$CR = (y_{ij} / y_{ii}) / (y_{ji} / y_{jj})$$

Intensity of competition is easily quantified using the CR. For example a CR of 2 indicates that  $i$  could be regarded to be twice as competitive as  $j$ . Willey and Rao (1980) have suggested that this index could be useful for identifying plant characteristics that are associated with competitive ability.

• **Relative Yield Total / Land Equivalence Ratio.** As an index the relative yield total (RYT) of DeWit and Van den Bergh (1965) is one of the most stable. It is an index that is used to describe the productivity of pairs of species that have access to the same resources. It is simply the sum of the relative yields (RY) for each species. It is also sometimes referred to as the land equivalent ratio (LER) (Willey and Osiru, 1972). It is calculated for two species mixtures as follows:

$$RY_i = Y_{ij} / Y_{ii}$$

$$RY_j = Y_{ji} / Y_{jj}$$

$$RYT_{ij} = RY_i + RY_j$$

Values of RYT near 1.0 indicates that the two species are interfering with one another.

A RYT greater than 1.0 implies that the species are showing some kind of amensalism either by making different demands on resources or having a symbiosis. A RYT less than 1.0 indicates that there is some kind of antagonism between the two species (Willey, 1979a).

For a replacement series, the LER is identical to the RYT. The RYT by definition is limited to replacement series designs whereas the LER can be applied to both additive and replacement series designs. Mead (1986) has recommended that the term RYT be restricted to use in replacement series designs whereas the term LER should be restrictively used for agronomic studies. Mead and Riley (1981) have reviewed the various methods used to calculate the LER and have presented some statistical concerns with this method.

- **Relative Resource Total.** All the indices discussed previously are based on the performance in mixture relative to the performance in pure stand. A difficulty arises in that pure stand performance is likely different than that in mixtures. Connolly (1987) has proposed a new index that overcomes this density dependent weakness. It is called the relative resource total (RRT) and is based on the assumption that whether in mixture or in pure stand the amount of resources required to produce an individual of given size is the same. The relative resource total is an index of whether species are capturing the same amount of resources in mixture as in pure stand. The relative resource total for two species in mixture is calculated as follows:

$$RRT = d_{ij}/d_i + d_{ji}/d_j$$

Where  $d_{ij}$  is the density of 'i' in mixture (where per plant yield = 'a'),  $d_{ji}$  is the

density of 'J' in mixture (where per plant yield = 'b'),  $d_i$  is the monoculture density when 'i' per plant yield = 'a', and  $d_j$  is the monoculture density when 'J' per plant yield = 'b'.

A RRT of 1.0 implies that the mixture does not yield more than an equivalent proportioned combined pure stand configuration. A RRT greater than 1.0 implies that the mixture utilizes more resources or is utilizing existing resources more efficiently. A RRT less than 1.0 implies reduced resource use in the mixture or some antagonism. A RRT of 2.0 or greater indicates that there is no competition between the individuals for resources and higher values suggest some synergistic effect in the mixture.

• **Index of Competitive Ability.** The index of competitive ability ( $K_c$ ) was proposed by Jolliffe *et al.* (1984) as a measure of competitiveness of species in a specific mixture. The values obtained are inversely related to the effectiveness of one species interfering with another. (i.e. the larger the value the less the interference). It is calculated as follows:

$$K_c = (d_k \times d_j \times Y_{ij}) / ((u \times d_i) - (d_i \times Y_{ij}) - (d_k \times Y_{ij}))$$

Where  $d_k$  is the planting density at which  $Y_{ij} = u/2$ ,  $d_i$  is the planting density of species i,  $u$  is the theoretical maximum yield at infinite planting density,  $d_j$  is the planting density of competing species j,  $Y_{ij}$  is the yield per land area of species i in mixture, where  $Y_{ii} =$  monoculture yield of species i.

$K_c$  is an index that is not based on the density dependent replacement series monoculture yield but is based on a standardized expected monoculture yield density ( $K_z$ ).

The weakness of this index is that it is based on the theoretical , and thus arbitrary, maximum monoculture yield ( $u$ ).

• **Relative Competitive Ability and Niche Differentiation Index.** When species are partly limited by the same resources they partially avoid each other; this is referred to as niche differentiation. A measure of the degree of niche differentiation between two species is the niche differentiation index (NDI). The NDI is simply the product of the reciprocal yield ratios for each species. The reciprocal yield ratios comes from the reciprocal yield analysis approach of Spitters (1983a) where regression equations are used to describe the relationship of the mean individual plant yield to the density of each species. The regression equation for each species used is of the form:

$$1/y_i = Ty_i + (b_{i1} \times N_i) + (b_{i2} \times N_j)$$

Where  $1/y_i$  is the reciprocal of the mean yield/plant of species  $i$  (i.e. Reciprocal Yield),  $Ty_i$  is the reciprocal of the maximum theoretical yield/plant,  $N_i$  is the density of species  $i$ ,  $N_j$  is the density of species  $j$ ,  $b_{i1}$  is the parameter reflecting intraspecific competition,  $b_{i2}$  is the parameter reflecting interspecific competition.

The parameters  $b_{i1}$  and  $b_{i2}$  can then be used to calculate the relative competitive abilities (RC) and NDI for each species as follows:

$$RC_i = b_{i1} / b_{i2}$$

$$NDI = RC_1 \times RC_2.$$

In a wheat and ryegrass interference experiment, Roush *et al.* (1989) compared the relative utility of the relative yield total, reciprocal yield, and relative monoculture and relative mixture response to assess interference. They determined that the reciprocal yield approach was the simplest method for assessing the relative importance of intra- and interspecific competition in addition to it being the most sensitive to density and proportion in mixtures.

• **Relative Monoculture and Relative Mixture Response.** Jolliffe *et al.* (1984) has proposed a density independent method that determines indices of interspecific and intraspecific competition. This approach has also been referred to as the synthetic no-interaction approach by Roush *et al.* (1989). A detailed description of the model used to calculate these indices is found in Jolliffe (1988). They have proposed that the yield response to density is of the form

$$1/Y = 1/Y_{\max} + (d_k/Y_{\max})(1/d)$$

Where  $Y$  is the yield per unit area,  $Y_{\max}$  is the maximum yield or final yield constant,  $d$  = plant density, and  $d_k$  is the density at which 50% of  $Y_{\max}$  is achieved.

A line of projected yield ( $Y_{p_i}$ ) expected if there was no intraspecific or interspecific interference can then be determined as follows:

$$Y_{p_i} = (Y_{\max}/d_k)(d).$$

They proposed that interpretation of data from replacement series data should involve comparisons among actual mixture yields ( $Y_{x_i}$ ), actual monoculture yields ( $Y_{m_i}$ ) and



projected monoculture yields ( $Y_{p_i}$ ). The difference between  $Y_{p_i}$  and  $Y_{m_i}$  would represent the effect of interspecific interference. That difference over the  $Y_{p_i}$  denominator is called the relative monoculture response index ( $RM_i$ ).

$$RM_i = (y_{io} - y_{ii}) / y_{io}$$

The difference between  $Y_{m_i}$  and  $Y_{x_i}$  represents the effect of interspecific interference. This difference over the  $Y_{m_i}$  denominator is called the relative mixture response index ( $RX_i$ ).

$$RX_{ij} = (y_{ii} - y_{ij}) / y_{ii}$$

In a wheat and ryegrass interference experiment Roush *et al.* (1989) comparing the relative utility of the relative yield total, reciprocal yield, and relative monoculture and relative mixture response to assess interference. They determined that the relative monoculture and mixture response approach provided the most detailed analysis of the influence of proportion on interference.

## MODELLING

### Terminology

A model is an abstract expression of the features of an object or system. A mathematical model is an equation or set of equations which attempts to represent the behaviour of a system (France and Thornley, 1984). Simulation is the art of taking a model and using it to perform experiments to study the properties of a system under study (DeWit, 1982). Good reviews of the philosophical basis of modelling can be found in Baker and

Curry (1976) and Walker (1977).

Models are described using various terms depending on whether a model is being classified by its purpose or by the attributes of the system being modelled or by the attributes of the model itself.

When a model is classified by its purpose it is described as either descriptive (empirical) or explanatory (mechanistic) (Penning de Vries, 1983; France and Thornley, 1984; Cousens *et al.*, 1987). Empirical models are simple descriptions of data or response whereas mechanistic models incorporate perceived knowledge of underlying processes.

When a model is classified by the attributes of the system being modelled it is described as either discrete, continuous or spatial (Cousens *et al.*, 1987; Edelstein-Keshet, 1988). A discrete model is one that reflects a system that occurs in stages. A continuous model refers to a system that is viewed as continuous in time. A spatial model indicates a system that has surface coverage as an important component.

A model can be classified by the attributes of the model itself and classified in terms of model output as either deterministic or stochastic and in terms of model parameters as static or dynamic or in terms of mathematical approach as either analytic or simulation (Anderson, 1972; Hall and Day, 1977; France and Thornley, 1984). A deterministic model makes a definite prediction of some value whereas a stochastic (probabilistic) model is one that predicts a value and gives some indication of its variance. Static models do not have time as a parameter whereas dynamic models do contain a time parameter. As a generalization analytic models represent systems in the language of mathematical formulae whereas simulation models estimate solutions using computer language (Knepell and Arangno,

1993).

In a comprehensive review, Cousens *et al.* (1987), categorized models into one of three classes: short-term (discrete), long-term (continuous), other (spatial).

Modellers develop models with differing degrees of refinement depending on the availability of data and the modellers goal. As the mathematical foundation for their models, modellers use what ever is convenient for their goal, whether simple or linear algebra or differential calculus or mathematical programming. As long as the model closely mimics and foretells the relevant features of the system under study it does not matter what mathematical approach is taken. The only rule of thumb is that simplicity and consistency of approach is preferred over complexity and inconsistency.

## **Evaluation**

Having defined the problem, collected the data and developed the model the next step is to evaluate the model. Models are generally evaluated on two major criteria; practicality and mathematical soundness.

Models are usually developed with one of three purposes in mind: advancing science; predicting correct results; or instructing people (Penning de Vries, 1977). An ideal model will achieve all three purposes by being realistic, workable and communicatable. A realistic model will provide realistic results over the range of real world situations to which it might be applied. A workable model will use readily accessible input data and hardware. Models should be communicatable by being of a form easily understood and utilized by the end user.

Establishing the mathematical soundness of a model is predominantly a process of

verification, validation and sensitivity analysis (Anderson, 1972; France & Thornley, 1984).

Verification (model truthfulness) is the process of determining whether a hypothesis used in a model is correct. Verification is used in model evaluation when the model contains an untested hypothesis. Verification of a model is actually verification of a hypothesis and is often achieved by experimentation. Applying a predictive model to independent data and evaluating how close the model output reflects the actual output is one method of verification. Verification of a model is not possible if a system has information that is scanty or absent.

Validation (model usefulness) is the process of determining whether the model represents the system for which it is intended. For some models the correlation coefficient is a measure of how effective a model is in representing the system. Applying a model to some independent data and evaluating how well the model reflects this system is another method of validating a model.

When model optimization is a goal, sensitivity analysis is often used to evaluate a model (Anderson, 1972; Penning de Vries, 1983). Sensitivity analysis is the testing for the robustness of parameters and structures. It is a form of behaviour analysis where the value of a single parameter or group of parameters is changed within a reasonable range and the output is compared with what is expected. When the model's output is relatively insensitive to changes in model structure or parameters then the model is considered robust. Testing for this robustness and ranking sensitivities enables the modeller to determine where any further model refinements are best concentrated.

However described or calculated, mathematical models are important tools

complementing experimentation. Modelling complements experimentation by forcing succinct mathematical expression of response, revealing knowledge gaps and allowing interpolation and cautious extrapolation in the absence of data (Cousens *et al.*, 1987).

### **Models of Intraspecific Interference**

Interference among plants involves the response of plants to the presence or growth of neighbouring plants. When the neighbouring plants are of the same species this monoculture interference is termed intraspecific. As the proximity between neighbouring individuals is reduced the interaction between individuals intensifies. In monocultures, except when plants are small or widely spaced, total plant yield is independent of density.

When the yield of individual plants in monocultures is considered there is a dependence on density. Holiday (1960) was the first to recognize that there are two basic monoculture yield density relationships. He recognized monoculture yield density relationships can be either asymptotic or parabolic. An asymptotic yield-density relationship usually occurs when yield is a measure of a vegetative trait and a parabolic yield-density relationship when yield is a measure of some reproductive characteristic.

A large number of models have been used to describe yield-density relationships and many of them have been compared in a review by Willey and Heath (1969). They singled out reciprocal yield models such as those proposed by Bleasdale and Nelder (1960) as showing the best promise for describing yield density relationships.

Much of the early work on intraspecific interference was done by Japanese researchers on several crop species and published in a series of papers from 1953 to 1957 (Kira *et al.*,

1953; 1954; 1956; Ikusima *et al.*, 1955; Hozumi *et al.*, 1955; 1956; Shinozaki and Kira, 1956; Koyama and Kira, 1956; and Yoda *et al.*, 1957). Kira *et al.* (1953) were the first to demonstrate an asymptotic relationship between shoot dry weight and population density. This relationship was expressed mathematically by Shinozaki and Kira (1956) in a reciprocal model of the following form:

$$y_i^{-1} = a_i + b_{ii}X_i$$

Where  $a_i$  and  $b_{ii}$  are constants,  $y_{ii}$  is the per plant yield and  $X_i$  is plant density. To account for parabolic yield density relationships this equation was extended to its quadratic form by Holiday (1960).

$$y_i^{-1} = a_i + b_{ii}X_i + b_{ii}X_i^2$$

Willey (1982) has determined this quadratic equation to describe experimental data well despite its empirical nature.

Bleasdale and Nelder (1960) proposed a more flexible version of the Shinozaki and Kira (1953) reciprocal model that could describe both asymptotic and parabolic yield density relationships. Based on the Richards' function (Richards, 1959) it was of the form:

$$y_i^{-\theta} = a_i + b_{ii}X_i^{\theta'}$$

where  $\theta$  and  $\theta'$  are constants. Bleasdale (1967) later demonstrated that it was possible to take  $\theta'$  as unity and thus the reciprocal yield-density equation took the final form:

$$y_i^{-\theta} = a_i + b_{ii}X_i$$

This model has been used to describe both parabolic and asymptotic yield-density

relationships (Jolliffe, 1988; Bleasdale, 1967). Although originally developed as an empirical model biological meaning has been ascribed to the parameters in the model (Shinozaki and Kira, 1956; Jolliffe, 1988). Parameter  $a_i$  may be considered an index of plant yield in the absence of interference. Parameter  $b_{ii}$  is a factor expressing the responsiveness of a species to changes in its own density. Parameter  $\theta$  has been related to the efficiency of resource acquisition and utilization (Watkinson, 1980, 1984; Jolliffe, 1988) and its value determines the form of the yield density relationship. When  $\theta=1$  the model describes an asymptotic curve and when  $\theta<1$  the model describes a parabolic curve.

A criticism of the Bleasdale (1967) model is that except when  $\theta=1$  there is no clear biological meaning to the equations parameters (Willey and Heath, 1969; Gillis and Ratkowsky, 1978; Watkinson, 1980). To address this deficiency Watkinson (1980, 1984) choose to reparameterize the Bleasdale Model to the following form:

$$y_i = y_i' (1 + a_{ii}' X_i)^{-b_i'}$$

This model was derived by setting  $a' = a^{-1}b$ ,  $b' = \theta^{-1}$ , and  $y' = a^{-1/\theta}$ . In this model Watkinson interprets  $y_i'$  as the yield of an isolated plant,  $a_{ii}'$  is the minimum density at which interference becomes important and  $b_i'$  is the efficiency of resource utilization.

The monoculture yield-density models are of agronomic importance. Quantitative yield-density relationships are useful for determining optimum crop population density, in general purpose modelling of crop productivity, and for determining many of the indices used to analyze plant performance in mixtures.

### **Models of Quackgrass Intraspecific Interference**

Intraspecific interference modelling in quackgrass has been limited to the work of Mortimer and coworkers (Mortimer *et al*, 1980; Mortimer and Putwain, 1981; McMahon and Mortimer, 1980). They indirectly modelled quackgrass interspecific interference using a sophisticated modelling approach. Using a transition matrix (Leslie matrix), which included quackgrass survivorship and fecundities, they were able to analyze net reproductive rates and project quackgrass infestation levels in subsequent years. In their model system they determined that an annual mortality level of 73.7% was required to keep their model quackgrass population static and that an annual mortality of 99.2% was required to enable eradication (Mortimer *et al*, 1980). Mortimer was able to incorporate density dependent elements by making selected elements of the matrix functionally dependent on population density.

### **Models of Interspecific Interference**

DeWit (1960) was the first to introduce a descriptive model of interference between two species. Subsequently Baeumer and DeWit (1968) developed a simulation model to predict interference between two species. Spitters and Van den Bergh (1982) then extended the Baeumer-DeWit model to crop weed relations. Since DeWit's (1960) descriptive model was proposed many descriptive indices have been proposed and these are discussed in the indices of interference and combined yield section of this literature review.

Spitters (1983) took the reciprocal yield-density model for monocultures of Bleasdale (1966, 1967) and extended to a multispecies hyperbolic equation of the form :



$$y_{xi}^{-1} = a_i + b_{ii}X_i + b_{ij}X_j$$

In this model  $Y_{xi}$  is the derived mixture per plant yield variable mean,  $a_i$  is the parameter that is related to the scale of the yield variable in the absence of competition,  $b_{ii}$  is a model parameter related to the extent of intraspecific interference,  $X_i$  is the population density of species "i",  $b_{ij}$  is a model parameter related to the extent of interspecific interference and  $X_j$  is the population density of species "j".

Firbank and Watkinson (1985) modified the Spitters (1983) equation to a form that accounts for mortality. Their approach presents a pair of equations for each of a pair of species in mixture. The equations for a species "A" are as follows:

$$W_A = W_{mA} (1 + a_A (N_A + \beta N_B))^{-ba}$$

and

$$W_A = W_{iA} (1 + m_A (N_{iA} + \delta N_{iB}))^{-1}$$

By substituting B for A, and A for B, in the equations the formulas could be applied to species B. In the equations shown  $\delta$  and  $\beta$  are competition parameters describing the effect of species B on the yield and survival of species A. N is the number of plants at harvest.  $W_m$  is the mean yield of isolated plants. Parameter a is the area required by a plant to achieve a yield equal to  $W_m$ . The parameter b is a measure of the efficiency of resource utilization by the population.

Jolliffe (1988) modified the Spitters (1983) equation to a form:

$$y_{xi}^{-\phi_i} = a_i + b_{ii}X_i + b_{ij}X_j$$

which is more flexible. The model parameter  $-\phi_i$  is related to the efficiency of resource utilization and determines whether the response function will be hyperbolic or parabolic. Many of the commonly used weed-crop loss models including the Firbank and Watkinson (1985) model presented earlier and Cousens (1985) hyperbolic model

$$y_{xi} = aX_i / (1 + bX_i + fX_j)$$

and the exponential model of Gill *et al.* (1987)

$$y_{xi} = (a + be^{-kX_j}) / X_i$$

can be demonstrated to be reparameterized versions of Jolliffe's (1988) model.

There are two potential criticisms of all these models. They assume population size is normally distributed and they assume that intraspecific competition is the same in monoculture as in mixture. As discussed previously these assumptions are only rarely valid.

### **Models of Quackgrass Interspecific Interference**

Interspecific interference by quackgrass has often been monitored, but only rarely modelled. The literature contains many reports of the estimated yield losses associated with particular quackgrass infestations. Cussans (1970) investigated quackgrass competition between quackgrass and barley, wheat and field beans and reported that their yields were unaffected by low infestations of quackgrass but a population of 180 shoots  $m^{-2}$  reduced yields as much as 20 %. Quackgrass has been found to reduce the stem diameter of sweet corn by 42% and ear yield from 26.5 kg to 6.1 kg per 100 plants (Bouchard and Doyon,

1983). In field corn, quackgrass at densities of up to 390 shoots  $\text{m}^{-2}$  caused yield reductions up to 16 % and densities up to 900 shoots  $\text{m}^{-2}$  were observed to cause yield losses of 37% (Young *et al*, 1984). In soybeans yield reductions due to quackgrass averaged up to 1% for infestations up to 160 shoots  $\text{m}^{-2}$  and 19% to 55% for heavy infestations of 520 and 910 shoots  $\text{m}^{-2}$  respectively (Young *et al*, 1982). In potatoes, Baziramakenga and Leroux (1994) determined that quackgrass infestation influenced marketable yields more than total tuber yields and that yields losses were positively correlated with infestation level and interference period. For example, at one site, when left weed free for 10, 20 and 30 days after emergence, marketable potato yields were reduced by 35%, 14%, and 11%, respectively.

Quackgrass interspecific interference in barley and wheat in Quebec has been modelled using linear regression. The relationship between quackgrass shoot density  $\text{m}^{-2}$  ( $Q_s$ ), approximately 30 days after planting, and predicted crop yield as a percentage of the expected quackgrass free crop yield ( $Y_i\%$ ) was determined in barley, by Rioux (1982), to be of the following form:

$$Y_b\% = 100 - 0.16 (Q_s), R^2=0.80 .$$

In wheat, Leroux (1990) determined the regression to be of the following form:

$$Y_w\% = 100 - 0.48 (Q_s), R^2=0.60 .$$

These models estimate that at a quackgrass infestation of 100 shoots  $\text{m}^{-2}$  that the predicted crop yields would be 84 and 52% of their quackgrass free yields for barley and wheat, respectively.

Interspecific interference between annual crops and quackgrass has also been modelled

using a rectangular hyperbola. O'Donovan (1991) reported that yield loss in polish canola (*Brassica rapa*) in Alberta was related to quackgrass shoots  $\text{m}^{-2}$  as follows:

$$Y_c\% = 100 \{1 - 0.41 (Q_s)/100 (1 + (0.41 (Q_s)/141))\}, R^2=0.66 .$$

Chikoye (1990) reported that flax (*Linum usitatissimum* (L)) grown in Manitoba could be related to quackgrass shoots  $\text{m}^{-2}$  as follows:

$$Y_f\% = 100 \{1 - 2.07 (Q_s)/100 (1 + (2.07 (Q_s)/130))\}, R^2=0.42 .$$

In preliminary reports from this thesis (Wilcox and Morrison, 1988a; Morrison *et al*, 1990) it has been determined that the relationship between percentage wheat yield and quackgrass shoots  $\text{m}^{-2}$  in Manitoba was of the following form:

$$Y_w\% = 98.7 \{1 - 0.433 (Q_s)/100 (1 + (0.433 (Q_s)/193.7))\}, R^2=0.41 .$$

These models estimate that at a quackgrass infestation of 100 shoots  $\text{m}^{-2}$  that the predicted crop yields would be 47, 0 and 46% of their quackgrass free yields for canola, flax and wheat, respectively.

Rauber (1984) conducted a replacement series experiment with mixtures of winter wheat and quackgrass. Using the DeWitt competition model and crowding coefficients he was able to demonstrate that wheat was less impaired by quackgrass than was the growth of quackgrass by wheat.

Fawcett (1985) used a complex quackgrass management model (AGROMOD) to model the impact of various management practices on quackgrass infestations. This matrix model included a density dependence component. After using this model to simulate effects of crop rotations, soil tillage and herbicide application, it was observed that the relative

competitiveness of the crop was a major factor in controlling quackgrass infestations.

## QUACKGRASS

Quackgrass is a long-lived herbaceous perennial weed that spreads both by seed and an extensive underground rhizome system. Rhizomes are white or light buff, long, branching, slender, smooth surfaced and very sharp-pointed, with many nodes each containing a scale leaf and bud or branch and a fine root system (Palmer and Sagar, 1963). Culms can be up to 120 cm tall and typically have three to five nodes. Leaves are flat 5 to 13 mm wide and 6 to 30 cm long. Auricles are short and clasping with sheaths rounded on the back and a membranous, narrow, flat-topped ligule. Spikes are erect, with numerous wedge-shaped overlapping spikelets. Spikelets are 3 to 8 flowered, alternating in two rows on opposite sides of the axis flat-wise to the rachis. The caryopsis is tightly enclosed by a hard lemma and palea. The lemmas and glumes may have awns. (Palmer and Sagar, 1963; Werner and Rioux, 1977). As a self-sterile, polyploid species (Stebbins, 1950) quackgrass infestation is often the result of vegetative reproduction from rhizome segments. However, the ability of quackgrass to express genetic variation through seed production contributes to its environmental adaptability.

Until relatively recently, quackgrass was most often referred to by the species name *Agropyron repens* (L.) Beauv. (Scoggan, 1978). Authorities now generally refer to quackgrass by the species name *Elytriga repens* (L.) Nevski. (Love, 1984; Dewey, 1984) although some

taxonomists argue that *Elymus repens* (L.) Gould (Melderis, 1978) would be more appropriate.

Quackgrass is notorious for being one of the most difficult weeds to manage in many agricultural areas of the northern temperate zone (Holm *et al.*, 1977). Quackgrass commonly grows in open disturbed areas (Werner and Rioux, 1977) and although able to grow on a wide range of soils it seems to prefer well-drained to medium textured soils (Dale *et al.*, 1965). Native to southern temperate Europe, it has followed European settlers and travellers to almost every part of the temperate world. Quackgrass was probably first introduced to North America around 1672 in the Boston region of New England and to Canada near Prescott, Ontario in 1861 (Alex, 1987). Quackgrass was first reported as occurring in Manitoba in 1906 (Alex, 1987). Of the 4.4 million acres of wheat now grown in Manitoba it is estimated that quackgrass occurs in 11% of the fields with a mean mid-season density of 10.4 shoots m<sup>-2</sup> (Thomas and Donaghy, 1991).

Effective quackgrass control requires a combination of control methods. Crop rotations, tillage, and use of graminicides are the major management approaches to consider for quackgrass control. Crop rotations work by taking advantage of the differing ability of crops and specific crop management practices to influence quackgrass infestation. Recent research by Pessala (1981) and Harker and O'Sullivan (1993) has demonstrated that crop selection does influence long-term infestation densities of quackgrass. By 'shredding' or 'dragging-out' quackgrass rhizomes, appropriately timed tillage operations can reduce quackgrass infestation levels. However, care must be taken with tillage operations not to spread quackgrass rhizome segments to new regions of the field. A large body of literature confirms that as cultivation is reduced quackgrass infestation increases (Bachthaler, 1974;

Cussans, 1975; Donaghy and Stobbe, 1972; Harker *et al.*, 1986; Mueller-Warrant and Koch, 1980; Nielson and Pinnerup, 1982; Pollard and Cussans, 1976; Stobbe, 1978). However, other researchers (Derksen *et al.*, 1993) have determined that reduced cultivation does not mean increased quackgrass infestation. Control of quackgrass by graminicides can range from poor to good, depending on the graminicide and application conditions. Herbicides recommended in Manitoba for quackgrass control include glyphosate, quizalofop-ethyl, sethoxydim, clethodim, and fluazifop. Glyphosate is listed as providing 'good' control as a pre-harvest treatment, whereas the previously listed post-emergent products are listed as providing only 'fair' control (Anonymous, 1995). A review of quackgrass control with graminicides and factors affecting their activity is presented in Harker (1987) and Harker and Dekker (1988a and b).

More thorough descriptions of quackgrass biology and control can be found in the following reviews: Palmer and Sagar (1963), Frankton and Mulligan (1971), Werner and Rioux (1977), Holm *et al.* (1977), Glick (1987) and Chikoye (1990).

## **SYNTHESIS**

Assessing interference in mixtures of plants can be done either through surveys or through experimental investigation. In interference research the characteristics of plants and populations can be measured and summarized through indices or models to indicate the influence of interference on plant growth.

Radosevich (1987) has suggested that the important factors involved in plant interference should be considered and controlled in interference studies or else varying results, sensitivities, and interpretations will occur. He specified that proximity factors should be controlled. Harper (1977) has stated that in addition to the easy to manipulate proximity factors, other factors such as the environment, emergence characteristics, growth rates and other components of plant size and function are also important influences on the interference process. Plant interference researchers need to recognize and account for the relative importance of all relevant factors (Figure 1) to the outcomes of their experiments and or analysis. With such recognition the interference researcher can optimize experiments or surveys to be as comprehensive as possible, so that as far as practical all relevant factors are measured and documented.

From a weed science perspective, once the factors that influence the process of interference are understood, weed suppression methods can be developed with greater certainty as to their impact both in terms of weed control and crop yield.



**MANUSCRIPT 1**

**Interference Modelling of Wheat (*Triticum aestivum*) and Quackgrass  
(*Elytrigia repens*) Grown in an Additive Series**

**Abstract.** Intraspecific and interspecific interference between spring wheat and quackgrass was investigated in the field using an additive series design consisting of five replacement series proportions at total stand densities of 75, 150, and 300 plants m<sup>-2</sup>. Several variables were measured and modelled using a revised synthetic no-interaction analysis. The revised synthetic no-interaction model was flexible enough to fit both the hyperbolic yield-density response of wheat and the parabolic yield-density response of quackgrass. Whether the models were subjected to reciprocal yield or synthetic no-interaction analysis similar interpretations were obtained. For all mixture proportions and yield variables niche differentiation in the wheat-quackgrass mixtures was large. Interpretation of interference varied with yield variable(s) selected. Quackgrass reproduction was less sensitive to interspecific interference than was vegetative growth. Wheat was superior to quackgrass in both intraspecific and in interspecific interference.

Nomenclature: Quackgrass, Elytrigia repens L. Nevski #<sup>1</sup> AGGRE; wheat, Triticum aestivum L. 'Katepwa'; bromoxynil, 3,5-dibromo-4-hydroxybenzonitrile; MCPA, (4-chloro-2-methylphenoxy) acetic acid; chloropyrifos, 0,0-diethyl 0-(3,5,6-trichloro-2-pyridyl) phosphorothioate; Mancozeb, manganese ethylenebis (dithiocarbamate) (polymeric) complex with zinc salt.

Additional index words. Replacement series, interspecific interference, intraspecific interference, Agropyron repens L. Beauv., competition.

## INTRODUCTION

Intra- and interspecific interference can be accurately investigated using either a synthetic no-interaction or a reciprocal yield analysis of the results from an additive series experiment (Roush *et al*, 1989). An additive series experiment consists of a replacement series experiment conducted over a range of total stand densities (Rejmanek *et al*, 1989). Snaydon (1991) has indicated that in his opinion an additive series design is one in which the density of each component in mixture has a corresponding density in pure stand. However he does not propose an alternate terminology, to that of Rejmanek *et al* (1989), for a design consisting of a replacement series design conducted over a range of total stand densities. For

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<sup>1</sup>Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Weed Sci. 32, Suppl. 2. Available from WSSA, 309 West Clark Street, Champaign, IL 61820.

the purposes of this manuscript the terminology of Rejmanek *et al* (1989) is used. The additive series design is useful for investigating interference because the replacement series technique prevents confounding of stand density and mixture proportion effects and the use of several stand densities enables differentiation of intra- and interspecific interference. Jolliffe (1988) has proposed a revised synthetic no-interaction model of interference that is a hybrid of the synthetic no-interaction and reciprocal yield models, as described by Roush *et al* (1989). With this new hybrid model one can derive the interpretive indices of both older models thereby improving the interpretation of results.

Indices are valuable for summarizing and interpreting results from interference experiments. However Connolly (1986) has shown that many of the indices used to interpret the results of interference experiments are limited in usefulness because they are density dependent. Two density independent indices of intraspecific and interspecific interference are the Relative monoculture ( $R_{mi}$ )<sup>2</sup> and Relative mixture ( $R_{xi}$ ) response of Jolliffe *et al* (1984), and the reciprocal yield ratio of Spitters (1983a). Jolliffe (1988) has shown how both these indices can be calculated from a modified version of reciprocal yield equation of Spitters (1983a).

Many published replacement series experiments present results for models fit to only

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<sup>2</sup>Abbreviations:  $R_{mi}$ , relative monoculture response;  $R_{xi}$ , relative mixture response;  $y_{xi}$ , actual mixture yields;  $y_{mi}$ , actual monoculture yield;  $y_{pi}$ , projected monoculture yields; WBIO, wheat biomass size; WSHT, wheat vegetative biomass; WREP, wheat reproductive effort; WFEC, wheat fecundity; QBIO, quackgrass biomass size; QSHT, quackgrass vegetative biomass; QREP, quackgrass reproductive effort; QFEC, quackgrass fecundity; NDI, niche differentiation index.

one yield variable, usually above-ground whole plant biomass (Jolliffe *et al*, 1984; Jolliffe, 1988; Rejmanek, 1989; Roush *et al*, 1989). Generally yield variable response to increasing densities, on a per area basis, is asymptotic for vegetative characteristics and parabolic for reproductive characteristics (Holiday, 1960). Accordingly any universal model of interference describing many different yield variables must have the flexibility to be either asymptotic or parabolic. A flexible model of this type has been proposed by Jolliffe (1988). Such flexibility is extremely important in characterizing the response of a perennial species such as quackgrass where rhizomes can be considered to be both vegetative and/or reproductive in importance.

The primary objective of this study was to investigate the influence of density and mixture proportion on wheat-quackgrass interference in the field using the revised synthetic no-interaction models of Jolliffe. A secondary objective was to investigate the role of yield variable selection in interpretation of wheat-quackgrass interference.

## **MATERIALS AND METHODS**

### **Experimental Design**

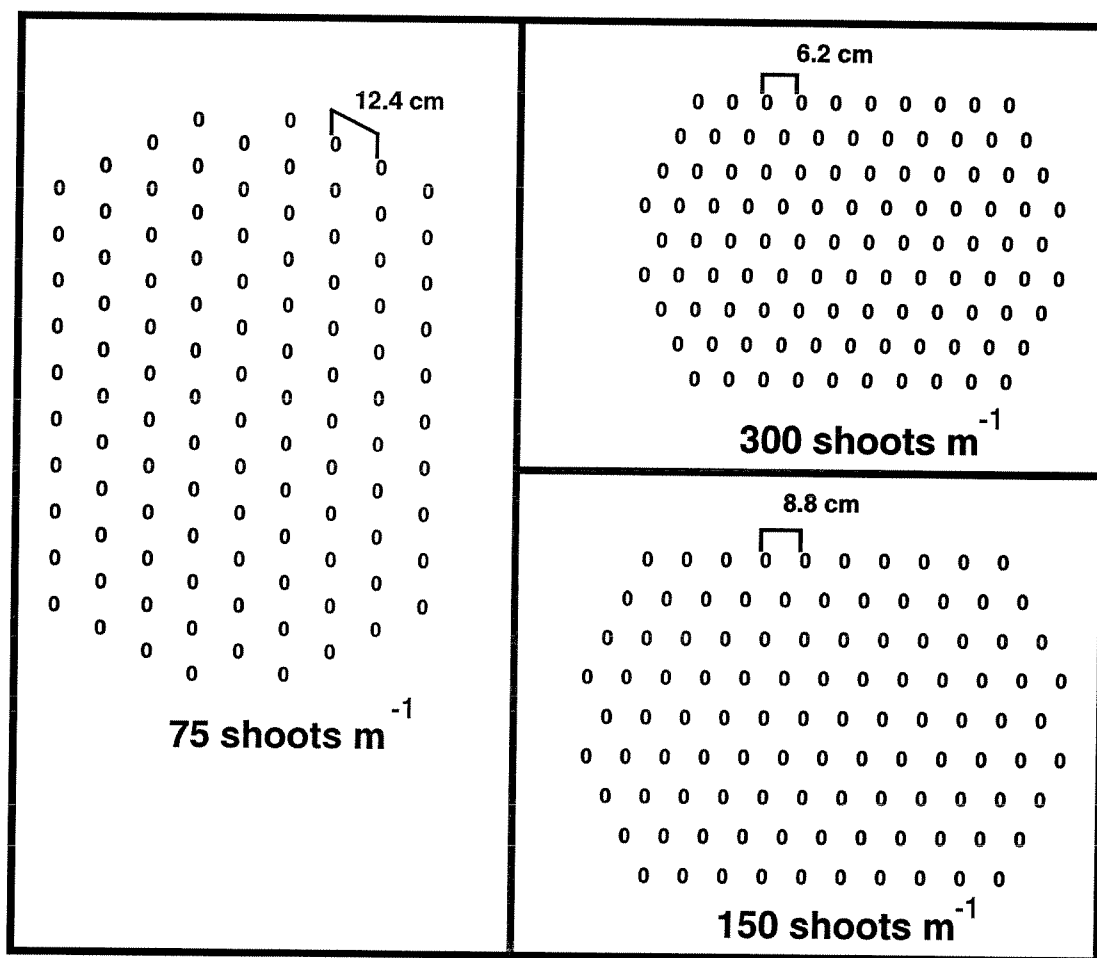
The wheat-quackgrass additive series experiment was conducted in 1987 and repeated in 1988 at the University of Manitoba Portage la Prairie research station on a Neuhorst series silty clay composed of 19% sand, 39% silt, 42% clay, with 8.6% organic matter and a pH of 7.8. At planting the soil fertility at the site was high. The levels of nitrate nitrogen (0 to 60 cm), available phosphorous (0 to 15 cm), and available potassium (0 to 15 cm) were

72, 17, and 198 ppm in 1987, and 44, 25 and 284 ppm in 1988, respectively. The growing season precipitation in both years was lower than average. In May and June of both years precipitation was only 60% of the long-term mean. However the soil water table at this site was high, with soil at depths of 60 cm or more being at field capacity, or greater, throughout the growing season in both years.

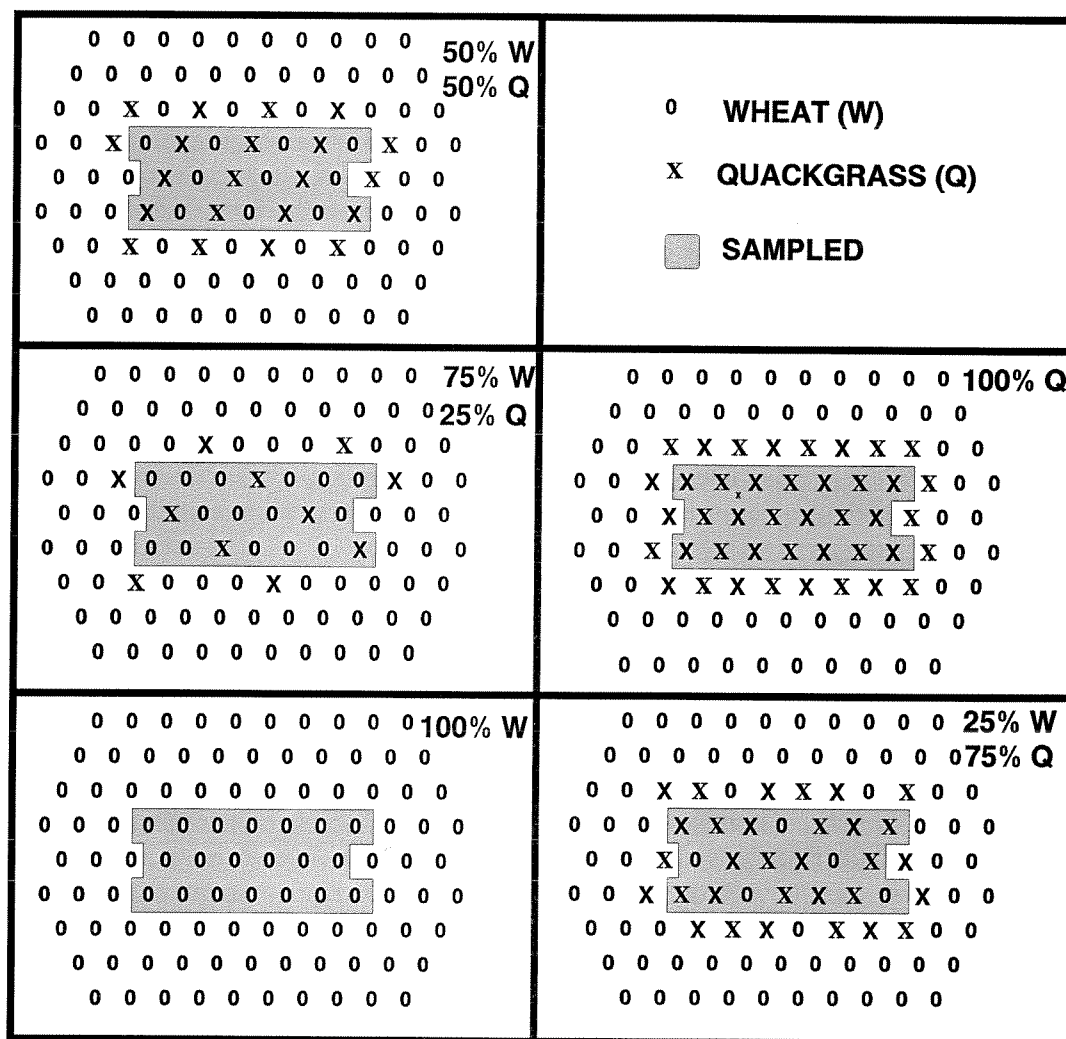
The experiment consisted of 15 treatments, with four replicates, arranged in a randomized complete block design. The 15 treatments were derived from a five by three factorial design in which five replacement series proportions (100:0, 75:25, 50:50, 25:75, and 0:100 (wheat:quackgrass respectively)) were grown at the three total stand densities of 75, 150 and 300 plants  $\text{m}^{-2}$ . In Manitoba, commercial wheat stands are often grown with stand densities of 150 plants  $\text{m}^{-2}$ .

Each plot contained 104 plants and the plot area depended on stand density (Figure 2). Each plant position was precisely marked out in a honeycomb design using a template. Yield measurements were made on the centre 20 plants of each plot (Figure 3).

In early May 3cm long rhizome fragments from quackgrass plants (Clone # UM08) were planted into 4 cm x 4 cm peat pots containing field soil and placed out-of-doors. In late May uniform quackgrass plants at the one-leaf stage were transplanted and two wheat seeds were planted (2cm deep) into their designated positions. Following emergence wheat plants were thinned to one plant per position. To ensure plant survival, plots were watered for three days following transplanting to a total equivalent of 3cm of water. Bromoxynil (280 g  $\text{L}^{-1}$ ) and MCPA ester (280 g  $\text{L}^{-1}$ ) at 560 g a.i.  $\text{ha}^{-1}$  was applied at the two-leaf stage of wheat to control broadleaved weeds. All other weeds were removed by hand-weeding at weekly



**Figure 2.** Diagram illustrating the relative areas of each of the total stand densities used in the wheat quackgrass additive series.



**Figure 3.** Diagram illustrating the plant arrangement at each of the mixture proportions in the wheat-quackgrass additive series.



intervals. In 1987 chloropyrifos (480 g/l) was applied at 480 g a.i. ha<sup>-1</sup> to control cutworms in June and in 1988 mancozeb (80%) was applied at 1.5 kg a.i. ha<sup>-1</sup> in August to control leaf rust (*Puccinia recondita* Rob. ex Desm.) and tan spot (*Pyrenophora tritici-repentis* (Died.) Drechs.) in the wheat.

In late August when the wheat was mature all shoots emerging within the area occupied by the centre 20 plants in each plot were clipped at ground level. Quackgrass rhizome samples were excavated from a soil sample (20 cm<sup>3</sup>) from the centre of each plot. Roots and any crown region material below the soil surface were discarded. The collected samples were separated by species and divided into vegetative and reproductive (heads, rhizome fragments) components. These components were counted, dried at 100 C for 48 hours, and weighed. The biomass was converted to a mean per plant basis by dividing the harvest yield by the original parental plant number. Biomass per unit area was then obtained by multiplying the derived per plant value by the number of parental plants within the area under consideration.

To assess the effect of the additive series treatments on wheat and quackgrass the experimental data was grouped into indicators of biomass size and dispersion and indicators of reproductive effort and fecundity. In wheat, total dry matter was considered to be an indicator of biomass size (WBIO) and was defined as the sum of the dry matter of all above-ground portions of the plant. Total dry matter was similarly selected as an indicator of quackgrass biomass size (QBIO) except that, in addition to above-ground portions, rhizome dry matter was also included. Wheat biomass dispersion (WSHT) and quackgrass biomass dispersion (QSHT) were defined as the number of shoots per species including those of

daughter quackgrass plants. Wheat grain yield was considered to be a measure of wheat reproductive effort (WREP) while for quackgrass the sum of spike and rhizome dry matter was considered as a measure of quackgrass reproductive effort (QREP). A measure of wheat fecundity (WFEC) was the number of wheat kernels produced whereas quackgrass fecundity (QFEC) was the number of rhizome buds. Data from the 1987 and 1988 experiments were pooled following confirmation of appropriateness by conducting an F-test on the homogeneity of variances (Gomez and Gomez, 1984).

### **Bivariate Analysis**

When investigating interference between two species in which it is unlikely that the yield variables of both species are independent, bivariate analysis, which simultaneously examines the joint pattern of yield variation, is considered the most appropriate form of analysis (Mead, 1986). Bivariate analysis is similar to covariance analysis except instead of major and minor covariance variables, bivariate variables are treated symmetrically.

Each of the yield variables was analyzed using bivariate analysis and interpretations are based on the bivariate analysis of variance tables and bivariate graphs. Details and examples of bivariate analysis calculations and graphs can be found in Dear and Mead (1983) and Mead (1986).

### **Revised Synthetic No-Interaction Analysis**

The revised synthetic no-interaction approach utilized in this paper is similar to the two-stage approach described by Jolliffe (1988) except that the technique of curve fitting

differed. In the first stage of this approach the model of Bleasdale (1966,1967) was fit to the per plant monoculture yield data using a derivative-free nonlinear regression procedure<sup>3</sup> (Freund and Littell, 1986), whereas Jolliffe (1988) used a stepwise regression approach. The basic monoculture yield-density model fit to the data was:

$$(y_{mi})^{-\phi_i} = a_i + b_{ii}X_i.$$

Where  $y_{mi}$  is the predicted per plant yield variable mean,  $\phi_i$  is a model parameter related to efficiency of resource utilization (Watkinson, 1980),  $a_i$  is a model parameter that is related to the magnitude of the yield variable in the absence of competition,  $b_{ii}$  is a model parameter that is related to the extent of intraspecific interference, and  $X_i$  is the population density of species "i". In the second stage of this approach the model was extended to the Firbank and Watkinson (1985) yield density model for mixtures except that the density-dependent mortality factor was removed. No plant mortality was observed in these experiments.

The basic mixture yield-density model fit to the data was:

$$(y_{xi})^{-\phi_i} = a_i + b_{ii}X_i + b_{ij}X_j.$$

In this model  $y_{xi}$  is the derived mixture per plant yield variable mean,  $b_{ij}$  is a model parameter related to the extent of interspecific interference and  $X_j$  is the population density of the species "j". The mixture yield-density model was also fit using the derivative-free nonlinear regression procedure. However, in applying this model the parameters  $\phi_i$ ,  $a_i$ , and  $b_{ii}$  were fixed at the same parameter values derived for the monoculture yield-density model.

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<sup>3</sup>PROC NLIN, METHOD=DUD, SAS V5. SAS Institute, Cary, NC.

The two-staged approach avoided the correlation association between  $X_i$  and  $X_j$  that would make the direct multiple regression approach invalid (Jolliffe, 1988). Inclusion of an additional interaction term (  $+(bX_iX_j)$  ) did not significantly improve the regressions and thus was not included in the mixture model.

The coefficient of determination,  $R^2$ , was calculated as recommended by Kvalseth (1985). Corresponding parameter estimates were compared to determine significant differences using the nonlinear comparison method of Ratkowsky (1983). Unless otherwise noted significant differences were considered to be those at  $\alpha=0.05$ .

## Indices

### Reciprocal Yield Ratio

According to Spitters (1983a) in the reciprocal yield model the relative interference ability of species "i" compared to "j" is given as a ratio of the model parameters  $b_{ii}$  and  $b_{ij}$  which expresses the relative importance of intra- and interspecific interference to two species in mixture. These ratios were used to calculate the degree of niche differentiation (NDI) which is simply the product of the reciprocal yield ratios for each species. Reciprocal yield ratios and NDI were calculated for each yield variable and mixture proportion as described elsewhere (Spitters, 1983a; Roush *et al*, 1989).

### Relative Monoculture and Relative Mixture Response

Jolliffe *et al* (1984) have proposed an alternate density-independent analysis of

replacement series design that allows the determination of indices of interspecific and intraspecific interference. They proposed that interpretation of data from replacement series experiments should involve comparisons among actual mixture yields ( $y_{xi}$ ), actual monoculture yields ( $y_{mi}$ ), and projected monoculture yields ( $y_{pi}$ ). The  $y_{pi}$  is the expected yields if there was no intraspecific or interspecific interference. The  $y_{mi}$  is the yield expected from a monoculture and thus the difference between  $y_{pi}$  and  $y_{mi}$  would represent the effect of intraspecific interference. That difference over the  $y_{pi}$  denominator is called the relative monoculture response ( $R_{mi}$ ). The  $y_{xi}$  is the yield of the species in mixture and thus the difference between  $y_{mi}$  and  $y_{xi}$  is assumed to represent the effect of interspecific interference. This difference over the  $y_{mi}$  denominator is called the relative mixture response ( $R_{xi}$ ). These indices were derived for each yield variable in the wheat quackgrass additive series. A description of the model used for calculation of these indices in this paper is found in Jolliffe (1988) and the theory behind the indices has been described in detail by Jolliffe *et al* (1984).

## RESULTS AND DISCUSSION

### Bivariate Analysis

As a species proportion in the mixture increased, the greater was its per area yield variable value (Table 3). This observation is consistent with that of a replacement series in which quackgrass and winter-wheat were grown in mixture (Rauber, 1984).

Yield variables varied in their response to stand density. As stand density increased the

**Table 3. Mean yields and standard errors of means for the pooled 1987 and 1988 wheat-quackgrass additive series variables on a per area basis.**

Mixture Proportion			Wheat Variable*			
Wheat	Quackgrass	Total Stand Density	WBIO	WREP	WSHT	WFEC
----- (%) -----	----- (plants m <sup>-2</sup> ) -----	----- (plants m <sup>-2</sup> ) -----	----- (g m <sup>-2</sup> ) -----	----- (g m <sup>-2</sup> ) -----	----- (number m <sup>-2</sup> ) -----	----- (number m <sup>-2</sup> ) -----
0	100	75				
25	75	75	288.72 ± 33.783	109.92 ± 17.645	222 ± 17.4	4006 ± 567.0
50	50	75	473.31 ± 36.510	177.00 ± 19.958	366 ± 18.6	6606 ± 612.8
75	25	75	638.38 ± 38.549	216.00 ± 20.470	488 ± 24.6	8284 ± 618.3
100	0	75	728.23 ± 52.065	257.23 ± 32.215	590 ± 23.2	9659 ± 906.4
0	100	150				
25	75	150	314.23 ± 19.912	116.41 ± 11.743	245 ± 18.0	4419 ± 371.8
50	50	150	531.32 ± 61.561	194.41 ± 28.788	437 ± 42.0	7233 ± 938.4
75	25	150	724.03 ± 59.269	262.82 ± 32.801	627 ± 26.4	9970 ± 1044.0
100	0	150	838.71 ± 69.849	313.28 ± 35.419	713 ± 24.4	11625 ± 1224.5
0	100	300				
25	75	300	327.38 ± 43.618	112.05 ± 26.188	336 ± 19.8	5217 ± 738.0
50	50	300	573.98 ± 39.049	212.47 ± 13.807	561 ± 38.4	8286 ± 337.6
75	25	300	839.18 ± 48.575	316.65 ± 27.974	758 ± 24.7	12000 ± 978.8
100	0	300	863.12 ± 35.318	311.19 ± 28.562	765 ± 29.0	11988 ± 943.1
			Quackgrass Variable*			
			QBIO	QREP	QSHT	QFEC
			----- (g m <sup>-2</sup> ) -----	----- (g m <sup>-2</sup> ) -----	----- (number m <sup>-2</sup> ) -----	----- (number m <sup>-2</sup> ) -----
0	100	75	690.23 ± 44.295	200.50 ± 37.661	545 ± 21.6	3556 ± 832.2
25	75	75	460.49 ± 24.425	137.47 ± 18.399	352 ± 27.8	2573 ± 358.5
50	50	75	302.03 ± 29.122	99.43 ± 13.861	246 ± 11.6	1703 ± 267.4
75	25	75	134.30 ± 27.753	43.90 ± 14.721	121 ± 24.8	1022 ± 284.0
100	0	75				
0	100	150	880.77 ± 75.133	194.62 ± 23.258	840 ± 56.8	2872 ± 385.3
25	75	150	623.67 ± 61.617	148.06 ± 20.542	559 ± 84.0	2381 ± 325.7
50	50	150	375.57 ± 23.513	82.58 ± 8.852	399 ± 26.3	1475 ± 193.5
75	25	150	129.76 ± 30.877	38.76 ± 9.096	128 ± 26.6	709 ± 128.3
100	0	150				
0	100	300	905.36 ± 108.875	156.96 ± 27.780	984 ± 119.2	2822 ± 324.3
25	75	300	590.74 ± 78.068	117.32 ± 24.639	651 ± 66.7	2150 ± 453.4
50	50	300	432.69 ± 31.585	86.72 ± 16.307	519 ± 46.9	1503 ± 262.5
75	25	300	195.12 ± 43.953	34.32 ± 10.329	233 ± 56.4	734 ± 190.6
100	0	300				

\* Abbreviations: W=Wheat; Q=quackgrass; BIO=Total dry matter; REP=Spike and rhizome dry matter; SHT=Number of shoots; FEC=Kernel number (W), Rhizome bud number (Q).

yields per unit area also increased, except for the quackgrass reproductive yield variables (Table 3). The results of bivariate analysis indicated that quackgrass reproductive yield variables were insensitive to changes in stand density, although there was a trend that, as stand density increased, the value of the quackgrass reproductive yield variable declined.

Yield variable values, on a per plant basis, decreased as stand density increased (Table 4). The results of bivariate analysis indicate that on a single plant basis quackgrass yield variables were insensitive to changes in mixture proportion. However there was a trend that as quackgrass proportion in mixture decreased, quackgrass per plant yield variables decreased. This quackgrass response contrasted with the wheat response. As wheat proportion in mixture decreased there was an increase in wheat yield variable values on a single plant basis. The wheat response to mixture proportion change was particularly evident at the lowest stand density. Contrasting response for wheat and quackgrass indicates that the wheat yield variables are being influenced primarily by intraspecific competition whereas with quackgrass interspecific interference from wheat was at least equal to intraspecific interference.

### **Revised Synthetic No-Interaction Analysis**

Significant  $R^2$  values indicate that the flexible model fit the yield variables well (Table 5). Model fit depended on yield variable. The vegetative yield variables had higher  $R^2$  values than the corresponding reproductive yield variables. Generally the fit of the monoculture models was superior to the mixture models and fit declined as percentage proportion in mixture declined. The decline in fit with the decrease in mixture proportion is related to the increase in standard error of the means for the yield variables (Table 3).

**Table 4. Mean yields and standard errors for the pooled 1987 and 1988 wheat-quackgrass additive series variables on a per plant basis.**

Mixture Proportion		Total	Wheat Variable*			
Wheat	Quackgrass	Stand Density	WBIO	WREP	WSHT	WFEC
----- (%) -----	----- (plants m <sup>-2</sup> ) -----		----- (g plant <sup>-1</sup> ) -----		-- (number plant <sup>-1</sup> ) --	
0	100	75				
25	75	75	15.40 ±1.802	5.86 ±0.941	11.8 ±0.93	214 ±30.2
50	50	75	12.62 ±0.974	4.72 ±0.532	9.7 ±0.49	176 ±16.3
75	25	75	11.35 ±0.685	3.84 ±0.364	8.7 ±0.44	147 ±11.0
100	0	75	9.71 ±0.694	3.43 ±0.430	7.9 ±0.31	129 ±12.1
0	100	150				
25	75	150	8.38 ±0.531	3.10 ±0.313	6.5 ±0.48	118 ± 9.9
50	50	150	7.08 ±0.821	2.59 ±0.384	5.8 ±0.56	96 ±12.5
75	25	150	6.44 ±0.527	2.34 ±0.292	5.6 ±0.23	89 ± 9.3
100	0	150	5.59 ±0.466	2.09 ±0.236	4.8 ±0.16	77 ± 8.2
0	100	300				
25	75	300	4.37 ±0.582	1.49 ±0.349	4.5 ±0.26	70 ± 9.8
50	50	300	3.83 ±0.260	1.42 ±0.092	3.7 ±0.26	55 ± 2.3
75	25	300	3.73 ±0.216	1.41 ±0.124	3.4 ±0.11	53 ± 4.4
100	0	300	2.88 ±0.118	1.04 ±0.095	2.6 ±0.10	40 ± 3.1
Quackgrass Variable*						
			QBIO	QREP	QSHT	QFEC
			----- (g plant <sup>-1</sup> ) -----		-- (number plant <sup>-1</sup> ) --	
0	100	75	9.20 ±0.591	2.67 ±0.502	7.3 ±0.29	47 ±11.1
25	75	75	8.11 ±0.430	2.42 ±0.324	6.2 ±0.49	45 ± 6.3
50	50	75	8.05 ±0.777	2.65 ±0.370	6.6 ±0.31	45 ± 7.1
75	25	75	7.16 ±1.480	2.34 ±0.785	6.5 ±1.32	40 ±11.0
100	0	75				
0	100	150	5.87 ±0.501	1.30 ±0.155	5.6 ±0.38	19 ± 2.6
25	75	150	5.54 ±0.548	1.32 ±0.183	5.0 ±0.75	21 ± 2.9
50	50	150	5.01 ±0.314	1.10 ±0.118	5.3 ±0.35	20 ± 2.6
75	25	150	3.46 ±0.823	1.03 ±0.243	3.4 ±0.71	19 ± 3.4
100	0	150				
0	100	300	3.02 ±0.363	0.52 ±0.093	3.3 ±0.40	9 ± 1.1
25	75	300	2.63 ±0.347	0.52 ±0.110	2.9 ±0.30	10 ± 2.0
50	50	300	2.88 ±0.211	0.58 ±0.109	3.5 ±0.31	10 ± 1.8
75	25	300	2.60 ±0.586	0.46 ±0.138	3.1 ±0.75	10 ± 2.5
100	0	300				

\* Abbreviations: W=Wheat; Q=Quackgrass; BIO=Total dry matter; REP=Spike and rhizome dry matter; SHT=Number of shoots; FEC=Kernel number (W), Rhizome bud number (Q).



Large variations in  $\phi$  occurred. The generalization has been made that on a per area basis vegetative characteristics express an asymptotic yield density relationship ( $\phi=1$ ) whereas for reproductive characteristics a parabolic yield-density relationship ( $\phi<1$ ) is expressed (Holliday, 1960). With wheat  $\phi$  was closer to one for the vegetative variable fits than for reproductive variable fits (Table 5). For quackgrass the Holliday generalization was not valid. The QFEC model had a  $\phi$  of 0.92 and the largest quackgrass vegetative yield  $\phi$  was 0.52. Whether this difference is attributable to quackgrass being a perennial and wheat being an annual is not clear and warrants further investigation. Wide difference in  $\phi$  have also been observed when this model was applied to orchardgrass (*Dactylis glomerata* L.) and timothy (*Phleum pratense* L.) at different growth stages (Jolliffe *et al*, 1988). This variation was attributed to shifts in plant performance and changes in the relative importance of interference over the growing season.

Using a nonlinear curve testing procedure (Ratkowski, 1983), for comparing parameter estimates from each yield variable monoculture and mixture model, determined that the wheat monoculture model was not significantly different from at least one or more of the mixture models. This differed from quackgrass in which the monoculture model was always significantly different from the respective mixture models. The ability to distinguish between all mixture and monoculture models in quackgrass but not in wheat indicated that in quackgrass interspecific interference by wheat is more significant than interspecific interference by quackgrass on wheat.

## Indices

### Reciprocal Yield Ratio

With wheat intraspecific interference was more important than interspecific interference from quackgrass. The  $b_{ii}/b_{ij}$  ratios for the wheat yield variables ranged from 1.18 to 4.51 (Table 5). The  $b_{ii}/b_{ij}$  ratios were greater than two for WSHT, WFEC, and WBIO, whereas for WREP the ratios were less than 2.0 but more than 1.0. This difference likely occurred because WBIO, WSHT, and, to a lesser degree, WFEC have all been determined largely in the early critical growth stages of wheat whereas WREP develops primarily during the later, less competitive, stages of wheat growth (Fischer, 1985; Bauer *et al.*, 1987).

With quackgrass intraspecific interference was comparable or inferior to the interspecific interference from wheat. The  $b_{ii}/b_{ij}$  ratios ranged from 0.51 to 1.58 (Table 5). Ratio values for QBIO and QSHT were approximately one-half that of QFEC and QREP. This difference in ratios indicates that quackgrass vegetative yield variables were influenced more by interspecific interference than were the reproductive yield variables.

Calculated NDI varied with yield variables and mixture proportion and ranged in value from 1.08 to 5.25 (Table 6). According to Spitters (1983a) NDI values greater than one indicate niche differentiation. Roush *et al.* (1989) observed no niche differentiation in their comparable studies of wheat and Italian ryegrass (*Lolium multiflorum* Lam. #<sup>3</sup> LOLMU) interference. In contrast the NDI values from these experiments suggest that wheat and quackgrass grown in mixture were not competing for limited resources. When based on fecundity, niche differentiation was larger than when based on other yield variables. The NDI values of vegetative yield variables increased as the percentage of wheat in mixture

**Table 5. Derived parameters and statistics from models\* fit to pooled 1987 and 1988 per plant variable data from the wheat-quackgrass additive series**

Variable	Mixture Proportion		Model Parameter					R <sup>2</sup>	b <sub>ii</sub> /b <sub>ij</sub>
	Wheat	Quackgrass	$\phi$	a <sub>i</sub>	b <sub>ii</sub>	b <sub>ij</sub>			
	----- (%) -----								
WBIO	25	75	0.934	0.0376	0.001093	0.000435	0.68	2.51	
	50	50	0.934	0.0376	0.001093	0.000463	0.77	2.36	
	75	25	0.934	0.0376	0.001093	0.000267	0.84	4.09	
	100	0	0.934	0.0376	0.001093	0.000000	0.95		
WREP	25	75	0.702	0.2383	0.002080	0.000898	0.48	2.32	
	50	50	0.702	0.2383	0.002080	0.001117	0.62	1.86	
	75	25	0.702	0.2383	0.002080	0.001767	0.65	1.18	
	100	0	0.702	0.2383	0.002080	0.000000	0.69		
WCULM	25	75	0.825	0.0905	0.001225	0.000476	0.73	2.57	
	50	50	0.825	0.0905	0.001225	0.000520	0.80	2.36	
	75	25	0.825	0.0905	0.001225	0.000362	0.88	3.38	
	100	0	0.825	0.0905	0.001225	0.000000	0.95		
WFEC	25	75	0.723	0.0165	0.000176	0.000053	0.52	3.32	
	50	50	0.723	0.0165	0.000176	0.000056	0.68	3.14	
	75	25	0.723	0.0165	0.000176	0.000039	0.74	4.51	
	100	0	0.723	0.0165	0.000176	0.000000	0.72		
QBIO	0	100	0.522	0.2311	0.001103	0.000000	0.78		
	25	75	0.522	0.2311	0.001103	0.001809	0.77	0.61	
	50	50	0.522	0.2311	0.001103	0.001556	0.71	0.71	
	75	25	0.522	0.2311	0.001103	0.001898	0.32	0.58	
QREP	0	100	0.255	0.6944	0.001604	0.000000	0.70		
	25	75	0.255	0.6944	0.001604	0.001229	0.63	1.31	
	50	50	0.255	0.6944	0.001604	0.001378	0.62	1.16	
	75	25	0.255	0.6944	0.001604	0.001742	0.27	0.92	
QCULM	0	100	-0.064	1.1538	-0.000250	0.000000	0.75		
	25	75	-0.064	1.1538	-0.000250	-0.000487	0.43	0.51	
	50	50	-0.064	1.1538	-0.000250	-0.000281	0.62	0.89	
	75	25	-0.064	1.1538	-0.000250	-0.000395	0.17	0.63	
QFEC	0	100	0.927	0.0000	0.000430	0.000000	0.61		
	25	75	0.927	0.0000	0.000430	0.000272	0.64	1.58	
	50	50	0.927	0.0000	0.000430	0.000358	0.61	1.20	
	75	25	0.927	0.0000	0.000430	0.000441	0.32	0.98	

\* Fit to the model  $(Y_{xi})^{-oi} = (a_i + b_{ii} X_i) + b_{ij} X_j$ . See text for parameter descriptions.  
 \*\* Abbreviations: W=Wheat; Q=Quackgrass; Bio=Total Dry Matter, REP=Spike and Rhizome Dry Matter; SHT=Number of Shoots; FEC=Kernel number (W), Rhizome Bud Number (Q).

**Table 6. Calculated niche differentiation indices (NDI) for the different mixture proportions and variables from the wheat-quackgrass additive series.**

Variable	Mixture Proportion		
Reciprocal Yield	-----		
Ratios Used*	Wheat	Quackgrass	NDI
-----			
	------(%)-----		
WBIO,QBIO	25	75	1.53
	50	50	1.67
	75	25	2.37
WREP,QREP	25	75	3.04
	50	50	2.16
	75	25	1.08
WSHT,QSHT	25	75	1.31
	50	50	2.10
	75	25	2.13
WFEC,QFEC	25	75	5.25
	50	50	3.77
	75	25	4.42

\* Abbreviations: W = Wheat; Q = Quackgrass; BIO = Total dry matter; REP = Spike and rhizome dry matter;

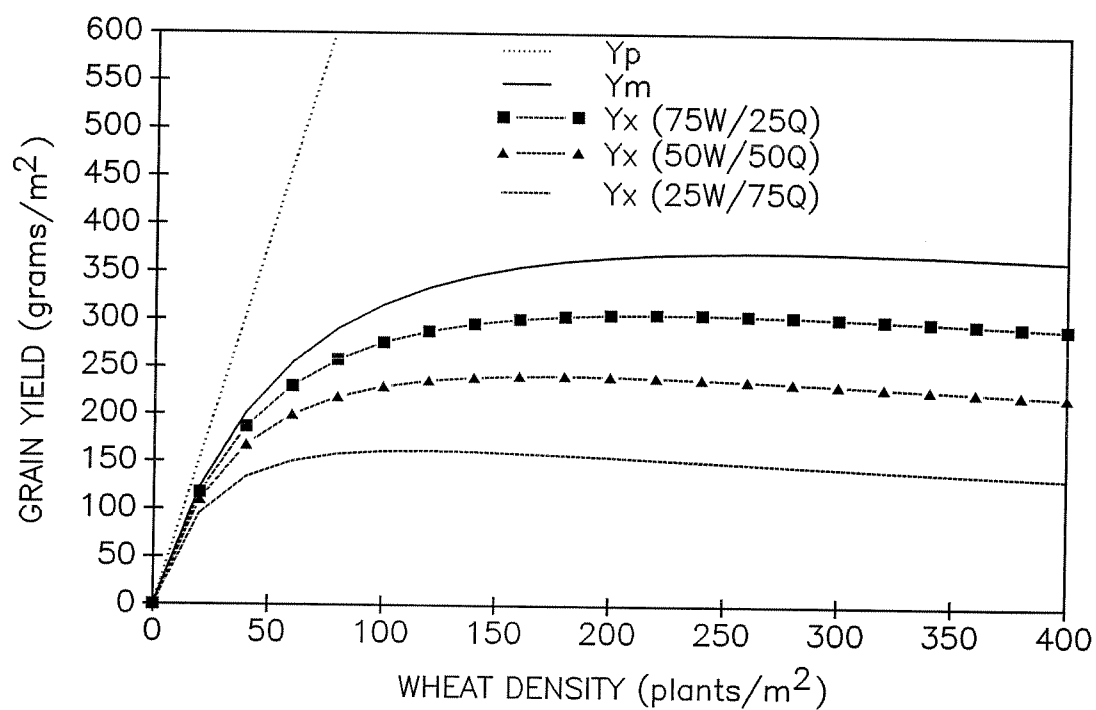
SHT = Number of shoots; FEC = Kernel number (W), Rhizome bud number (Q).

proportion increased. However, when based on reproductive characteristics, the largest NDI values occurred when the wheat percentage proportion in mixture was least.

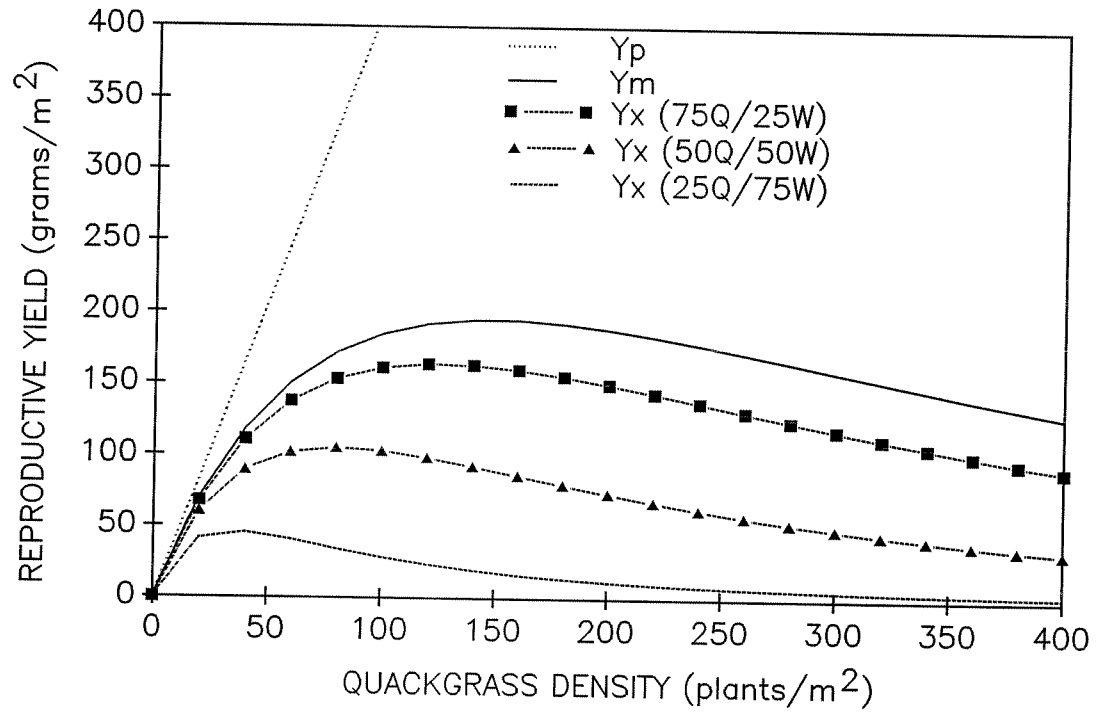
### **Relative Monoculture and Relative Mixture Response**

The interpolated additive, monoculture and mixture response curves for WREP and QREP, on a per area basis, are presented in Figures 4 and 5, respectively. Interpolated values for these figures were derived using the model parameters in Table 5. Similarly, interpolated curves were generated for all the yield variables and the results used to calculate  $R_m$  and  $R_x$ . Except for QFEC, Figures 4 and 5 are characteristic of the interpolated response curves obtained from all the yield variables in each respective species. Actual wheat yield-density responses were relatively asymptotic; whereas with quackgrass the yield-density responses were relatively parabolic. Quackgrass had an optimum yield density whereas wheat had a yield plateau. The  $Y_x$  curves also consistently illustrated that as a species proportion in mixture declined, yield variable values also declined. These findings indicated that mixture proportion was generally more important than actual wheat density in determining wheat yield; whereas with quackgrass both mixture proportion and stand density were important. The importance of mixture proportion in both species substantiates Rauber's hypothesis that in wheat-quackgrass mixtures, yield of each species is determined more by relative plant frequency than the absolute plant density (Rauber, 1984).

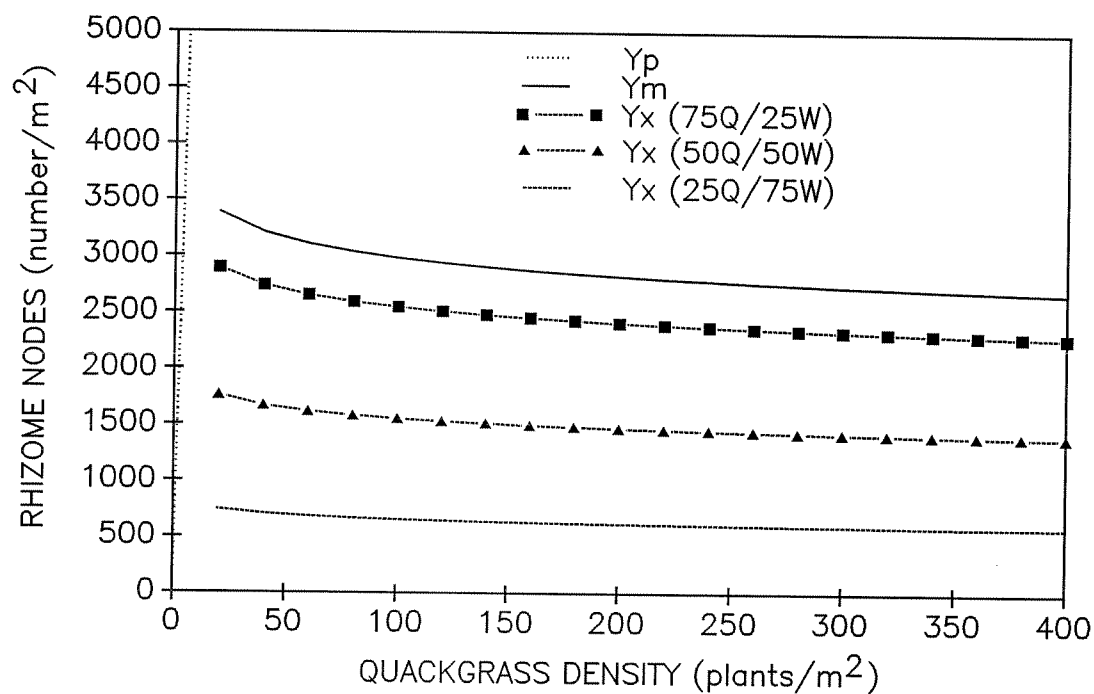
The QFEC response differed from the other quackgrass yield variables (Figure 6). QFEC was relatively insensitive to interspecific interference, particularly at the higher quackgrass densities. Instead of a parabolic response QFEC exhibited a weakly negative



**Figure 4.** The interpolated wheat reproductive effort as additive ( $Y_p$ ), monoculture ( $Y_m$ ), and mixture ( $Y_x$ ) functions derived from wheat-quackgrass additive series experiments.



**Figure 5.** The interpolated quackgrass reproductive effort as additive ( $Y_p$ ), monoculture ( $Y_m$ ) and mixture functions derived from wheat-quackgrass additive series experiments.



**Figure 6.** The interpolated quackgrass fecundity as additive ( $Y_p$ ), monoculture ( $Y_m$ ), and mixture ( $Y_x$ ) functions derived from wheat-quackgrass additive series experiments.



asymptotic response to increases in interspecific interference. As quackgrass density increased QFEC declined slightly to some minimum QFEC plateau. Although QFEC was relatively interspecific interference dependent, quackgrass rhizome biomass was sensitive to interspecific interference. Thus at higher densities, vitality of the rhizome nodes measured as rhizome dry weight declined. A similar relative insensitivity of rhizome node numbers compared to rhizome dry weight, in response to increased interference has previously been observed (Permin, 1985).

All yield variables except for QFEC, had the value of  $R_m$  increase with increases in stand density (Table 7). It would be expected that interspecific interference would increase as density of that species increased.

Interpretation of intraspecific interference was yield variable dependent. The  $R_m$  values for vegetative yield variables were larger for wheat than quackgrass at comparable densities indicating that intraspecific interference was more important in wheat than in quackgrass (Table 7). With reproductive yield variables, except for QFEC, the  $R_m$  values were similar at comparable densities indicating similar levels of wheat and quackgrass intraspecific interference. With QFEC, a constant  $R_m$  value of 1.0 at all densities implies a density independence of intraspecific interference over the density range of this experiment.

Irrespective of the yield variable, the  $R_x$  value of a species increased as the proportion of the other species increased in mixture (Table 7). For each yield variable pair, at each particular density, the level of wheat interspecific interference on quackgrass was larger than that of quackgrass on wheat. Except for QFEC, the sensitivity of  $R_x$  to changes in mixture

**Table 7. Calculated relative monoculture (Rm) and relative mixture (Rx) values of the pooled 1987 and 1988 variables from the wheat-quackgrass additive series.**

Total Stand Density	Mixture Proportion		Variable*							
	Wheat	Quackgrass	WBIO	WREP	WSHT	WFEC	QBIO	QREP	QSHT	QFEC
(plants m <sup>-2</sup> )	----- (%) -----		----- (Rm) -----							
75	0	100					0.44	0.47	0.23	1.00
75	25	75	0.37	0.19	0.24	0.22	0.37	0.38	0.17	1.00
75	50	50	0.55	0.33	0.39	0.37	0.27	0.28	0.12	1.00
75	75	25	0.65	0.43	0.50	0.48	0.15	0.15	0.06	1.00
75	100	0	0.71	0.51	0.57	0.56				
150	0	100					0.64	0.69	0.40	1.00
150	25	75	0.55	0.33	0.39	0.37	0.56	0.60	0.31	1.00
150	50	50	0.71	0.51	0.57	0.56	0.44	0.47	0.23	1.00
150	75	25	0.79	0.62	0.67	0.66	0.27	0.28	0.12	1.00
150	100	0	0.83	0.70	0.74	0.73				
300	0	100					0.82	0.87	0.65	1.00
300	25	75	0.71	0.51	0.57	0.56	0.75	0.81	0.54	1.00
300	50	50	0.83	0.70	0.74	0.73	0.64	0.69	0.40	1.00
300	75	25	0.88	0.79	0.82	0.82	0.44	0.47	0.23	1.00
300	100	0	0.91	0.84	0.86	0.86	0.00	0.00	0.00	0.00
----- (Rx) -----										
75	0	100								
75	25	75	0.31	0.21	0.23	0.18	0.19	0.11	0.12	0.19
75	50	50	0.19	0.16	0.15	0.11	0.31	0.23	0.13	0.48
75	75	25	0.05	0.12	0.05	0.04	0.49	0.39	0.26	0.78
75	100	0								
150	0	100								
150	25	75	0.40	0.33	0.33	0.27	0.28	0.18	0.23	0.19
150	50	50	0.24	0.24	0.21	0.17	0.45	0.37	0.25	0.48
150	75	25	0.06	0.17	0.07	0.05	0.67	0.60	0.46	0.78
150	100	0								
300	0	100								
300	25	75	0.47	0.45	0.43	0.37	0.38	0.28	0.41	0.19
300	50	50	0.27	0.32	0.26	0.22	0.59	0.54	0.45	0.48
300	75	25	0.07	0.22	0.08	0.07	0.81	0.79	0.72	0.78
300	100	0								

\* Abbreviations: W=Wheat; Q=Quackgrass; BIO=Total dry matter; REP=Spike and rhizome dry matter; SHT=Number of shoots; FEC=Kernel number (W), Rhizome bud number (Q).

proportion decreased as stand density decreased. Rx values for QFEC were dependent only on mixture proportion and not on stand density.

## Conclusions

The revised synthetic no-interaction model of Jolliffe (1988) allowed both the interpretation and quantitative determination of the relative intraspecific and interspecific interference abilities of wheat and quackgrass. This model addresses the density and proportion interaction limitations (Roush *et al.* 1989) of the original synthetic no-interaction analysis of Jolliffe *et al.* (1984). The model had the flexibility to accurately represent a wide range of yield-density responses. By not pre-imposing an asymptotic yield-density relation on the species it was determined that the per area yield-density response of wheat was relatively asymptotic whereas that for quackgrass it was relatively parabolic. The practical implication of this finding is that maximum suppression of quackgrass by wheat will be achieved by maximizing wheat density. High wheat densities had relatively greater effect on quackgrass yield than on wheat yields.

Generally the interpretation of the relative importance of intraspecific and interspecific interference was consistent for all analysis. In the wheat-quackgrass mixtures, intraspecific interference was the dominant force on wheat whereas in quackgrass both intraspecific and interspecific interference were of relatively similar importance. Additionally, interspecific interference of wheat on quackgrass was larger than interspecific interference of quackgrass on wheat. Niche differentiation was large for all yield variables and mixture proportions. Clearly quackgrass did not strongly interfere with wheat. Similar results were reported from

a replacement series experiment where interspecific interference by winter wheat on quackgrass was determined to be greater than *vice versa* (Rauber, 1984).

Interpretation of the relative extent of interspecific and intraspecific interference was dependent on the yield variable selected. For example, interspecific interference on quackgrass by wheat was demonstrated to be less important for reproductive yield variables, particularly QFEC, than for vegetative yield variables. In a practical sense although wheat may appear to suppress growth of quackgrass vegetatively, in terms of a yield variable such as quackgrass fecundity, there may actually be very little suppression. This result varies with the findings of Rauber (1984) who observed a greater reduction in rhizomes than above-ground portions with high winter wheat crowding. The discrepancy in results may be attributed to many factors ranging from differences in wheat type and quackgrass clone to differences in experimental design. The most appropriate yield variable to use in interpreting interference would depend on the specific experimental objectives. In most situations the use of several yield variables, representing several biological strategies, will enable the most complete interpretation of the relative importance of interspecific and intraspecific interference in the mixture.

**MANUSCRIPT 2**

**Models of Quackgrass (*Elytrigia repens*) Interference  
in Spring Wheat (*Triticum aestivum*)**

**Abstract.** Yield losses in spring wheat due to quackgrass were assessed using a dynamic stratified random sampling design in a total of six commercial fields of spring wheat in Manitoba in 1988 and 1989. Each field site was systematically sampled at approximately 30, 60 and 93 days after planting. Quackgrass infestation levels increased over the growing season and the majority of new rhizome production occurred during wheat senescence. Of the 16 variables evaluated, only six were satisfactory for modelling the relationship between quackgrass infestation to wheat grain yields. These models were validated using a dataset collected at independent sites. Relative quackgrass ( $QS_{\%}^4$ ), or the ratio of quackgrass shoots to total wheat and quackgrass shoots, was the best variable and was related to percentage wheat yield ( $WY_{\%}$ ) by the equation;  $WY_{\%} = 98.0 - 101.0 (QS_{\%})$ . The wheat

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<sup>4</sup>Abbreviations: Variate abbreviations are listed in Table 8; DAP, days after planting;  $Q_L$ , light quackgrass infested population;  $Q_H$ , heavy quackgrass infested population; ANOVA, analysis of variance; MANOVA, multivariate analysis of variance; SW%, Shoot dry matter as a percentage of total dry matter; RW%, rhizome dry matter as a percentage of total dry matter; HW%, head dry matter as a percentage of total dry matter.

yield component most affected by quackgrass infestation was wheat kernel weight. As the level of quackgrass infestation increased, biomass accumulation to the heads also increased with no significant effect on partitioning to shoots or rhizomes.

Nomenclature: Quackgrass, Elytrigia repens L. Nevski #<sup>5</sup> AGGRE; wheat, Triticum aestivum L. 'Katepwa'; bromoxynil, 3,5-dibromo-4-hydroxybenzonitrile; MCPA, (4-chloro-2-methylphenoxy) acetic acid.

Additional index words. Agropyron repens L. Beauv., competition, modeling, rectangular hyperbola, AGGRE, survey.

## INTRODUCTION

Quackgrass is the most troublesome perennial grass weed of cereals on the Canadian prairies. The weed is of European origin and was first observed in the Red River region of Manitoba about 1900. Field surveys have determined that quackgrass occurs on 15% of the fields in Manitoba, 4% of the fields in Saskatchewan, and 5% of the fields in Alberta (Thomas and Wise, 1983; 1984; 1985). With more and more farm operators using reduced tillage and shifting to continuous cropping it is expected that the incidence of quackgrass in farm fields on the prairies will increase (Stobbe, 1978).

Although in the ninety years since quackgrass was introduced to the Canadian prairies

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<sup>5</sup>Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Weed Sci. 32, Suppl. 2. Available from WSSA, 309 West Clark Street, Champaign, IL 61820.

a large body of world literature has been published on the weed, only a few papers have reported on yield losses caused by quackgrass in small grain cereals. Rioux (1982) determined that in Quebec the relation between barley yield in  $\text{g m}^{-2}$  ( $BY$ ) and quackgrass shoot density as shoots  $\text{m}^{-2}$  ( $QS$ ) at crop heading was described by the linear model:

$$BY = 345.3 - 0.5682 ( QS ), R^2=0.80.$$

He also reported that the relation between quackgrass shoot biomass ( $QS_w$ ) at crop heading and barley yield was described by the linear model:

$$BY = 327.2 - 0.7509 ( QS_w ), R^2=0.63.$$

In Michigan oat plots it was determined that where quackgrass made up 23% of the surface dry matter of sampled areas, yields were 30% less than uninfested checks (Wolcott and Carlson, 1949). In England an infestation of 45 quackgrass shoots  $\text{yard}^{-2}$  ( $54 \text{ m}^{-2}$ ) 10 weeks after planting had no effect on the yields of wheat and barley, whereas an infestation of 180 shoots  $\text{yard}^{-2}$  ( $215 \text{ m}^{-2}$ ) reduced the yields of wheat and barley by about 20% (Cussans, 1970). In Germany, in the second year of a replacement series experiment, quackgrass infestations of 180, 340, 560 and 680 shoots  $\text{m}^{-2}$  caused yield losses in winter wheat of 6, 17, 38 and 63%, respectively (Rauber and Bottger, 1984). From field trials in Denmark it was determined that yield losses due to quackgrass densities of 100 shoots  $\text{m}^{-2}$  in winter rye, winter wheat, barley, canola and pea were roughly 8%, 12%, 18%, 28% and 35%, respectively (Melander, 1993).

A serious criticism of many of these field interference studies is that they relate only one or two aboveground variables of quackgrass infestation to yield loss in cereals. It may



be that variables such as spike number, shoot number or shoot biomass are not the best variables for estimating the interference potential of quackgrass. Differences in the crop yield loss predictability of quackgrass variables were demonstrated by Rioux (1982). He determined that quackgrass shoot counts were better correlated with barley yield loss than quackgrass biomass. Given that established quackgrass patches are known to have extensive underground rhizome systems one might hypothesize that some rhizome variable might be closely correlated with the interference potential of quackgrass. It has been shown that quackgrass leaf counts, visual density scoring and quantity of active rhizome are not closely correlated (Proctor and North, 1971).

There is a need for information on the yield losses associated with quackgrass in wheat so that farmers can make valid economic management decisions. The objective of this study was to determine the yield losses in spring wheat associated with various quackgrass infestations and to determine which variables are most useful in estimating yield losses caused by quackgrass in spring wheat.

## **MATERIALS AND METHODS**

### **Survey Data**

In south central Manitoba spring wheat (cv. Katepwa) fields infested with quackgrass were surveyed using a dynamic stratified random sampling design. Six commercial fields were surveyed, four in 1988 and two in 1989. A range of soil fertilities was represented by the sites (Table 8).

high as 0.94 between variable pairs in individual plants. He also contrasted the relationship between rhizome weight and shoot weight of plants from arable fields with those from grasslands (1980). Cussans and Wilson (1975) graphed the relationship between total dry matter and new rhizome dry matter production in quackgrass. Their results indicated that the relationship between total dry matter and new rhizome dry matter did not vary with quackgrass density when grown in competition with barley. Rioux (1982) determined the relationship between quackgrass shoot number  $m^{-2}$  ( $S$ ) and quackgrass biomass in  $g\ m^{-2}$  ( $S_W$ ) in barley to be  $S_W = -0.20 + 0.537 (S)$ ,  $R^2 = 0.711$ . Reekie and Bazzaz in a series of papers (1987a,b,c) presented graphically the allometric relationship between leaf dry matter and other plant parts and between nutrient content and respiration. As well they listed correlations between measures of reproductive effort. Unfortunately they failed to partition out rhizomes as a component of reproductive effort. With two exceptions (Cussans and Wilson, 1975; Rioux, 1982) none of the papers present allometric equations or determines allometric relationships in quackgrass growing competitively with a crop.

The primary objective of this manuscript is to present some allometric models for reproductive variables of quackgrass grown in association with wheat. By linking these allometric models to simple wheat yield-loss models (Manuscript 4) one can then assess the long-term impact of quackgrass following various treatments. Additionally, given that allometric relationships have been demonstrated to vary with time of sampling (Jolliffe *et al*, 1988), a secondary objective is to present some auto-regression models from which a quackgrass variable at 93 DAP (i.e. wheat maturity) can be predicted from the variables

**Table 8. Site characteristics of the dynamic stratified random sampled sites.**

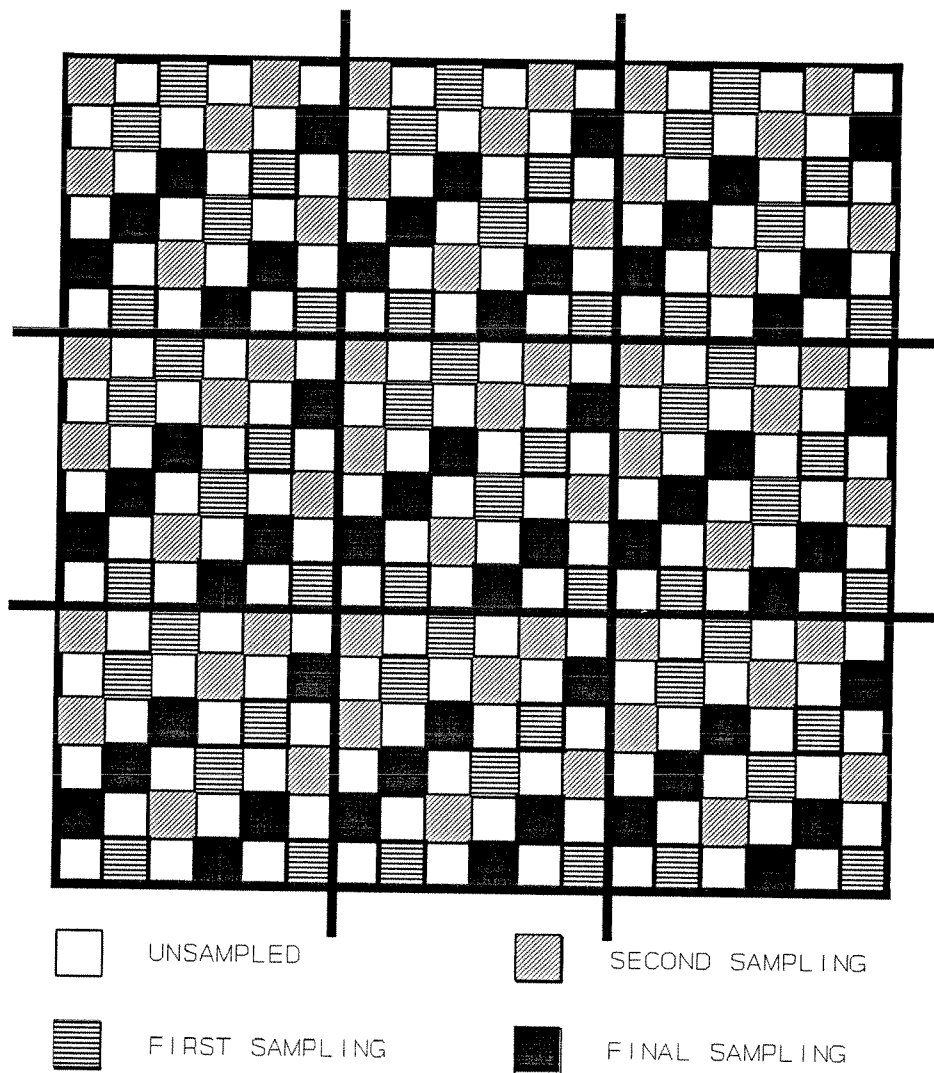
Soil <sup>a</sup>										
Site	Year	Previous Crop	Texture	Sample Depth	Carbonate Content	pH	Salinity	Nitrate Nitrogen	Available Phosphorus	Available Potassium
				-(cm)-			(ms/cm)	----- (PPM) -----		
Portage(UM)	1988	no crop	SiC	0-15	low	7.3	1.0	142	60	358
				15-60	med		0.9	73		
Delta	1988	canola	SiC	0-15	low	7.9	1.0	20	37	255
				15-60	med		0.6	7		
Rosendale	1988	flax	VFS	0-15	low	7.5	2.5	47	17	70
				15-60	med		2.1	20		
Poplar Point	1988	canola	SiC	0-15	absent	7.4	0.8	29	13	440
				15-60	absent		1.0	8		
Portage(UM)	1989	flax	SiC	0-15	low	7.5	0.9	82	25	384
				15-60	med		0.7	34		
Portage(BW)	1989	wheat	SiC	0-15	low	7.6	0.9	46	20	270
				15-60	med		0.7	18		

<sup>a</sup> Sampled shortly after wheat emergence.

Stratified random sampling is a technique for obtaining an unbiased, representative sample of an area. In stratified random sampling a site is divided into two or more strata of known size and each stratum is then sampled independently using random sampling. The data from each stratum is then assembled to obtain estimators for each individual stratum or for the site as a whole. When each stratum is sampled over time the sampling is referred to as 'dynamic'.

Experimental fields were maintained throughout the growing season using the same conventional commercial practices as the farm operator used on the remainder of the field. In addition to herbicides for annual weed control, hand weeding was done weekly to eliminate undesired species.

At each site, immediately after planting, an area enclosing a range of quackgrass infestation densities was selected and a 1 m<sup>2</sup> permanent grid system was superimposed over an 18 x 18 m area using twine. The demarcated area was divided into 9 strata, each stratum being 6 x 6 m. To facilitate sampling over time within each stratum a "checkerboard" grid was mapped out in which only adjacent diagonal 1 m<sup>2</sup> subplots could be sampled. The checkerboard sampling method allowed the distance between destructively sampled quadrats to be maximized, while still allowing representative sampling. Each stratum had 18 possible sampling sites, of which six were selected randomly to be sampled at approximately 30, 60 and 90 days after planting (DAP), with the last date corresponding with crop harvest. Each stratum was uniquely randomized. A generalized illustration of the sampling design is shown in Figure 7. Average wheat stand density within each stratum was determined approximately 14 DAP.



**Figure 7.** A generalized illustration of the "checkerboard" sampling pattern used in the dynamic stratified random sampling grid.

At each sampling date a 0.25 m<sup>2</sup> quadrat was placed in the centre of its subplot and all wheat and quackgrass shoots were clipped off at ground level and separated by species. The soil was then excavated to a depth of 15 cm (or deeper when required) and all the rhizomes removed. Dark coloured and desiccated rhizomes were considered non-viable and were discarded. Roots attached to viable rhizomes were removed and discarded. The vegetative material was then placed in plastic bags and frozen at -10 C until measurement of variables could be undertaken.

The vegetative material was removed from the freezer, warmed to room temperature, then separated into various components and counts and length determinations were done. For dry matter determinations the plant material was dried in a convection oven for a minimum of 24 hours at 101 C, then removed and allowed to equilibrate to room conditions before weighing. Complete descriptions of the measured and derived variables and their abbreviations are listed in Table 9.

### **Validation Survey Data**

Commercial fields distinct from those used for the stratified survey were selected in south central Manitoba for a validation survey. An area of approximately 20 m<sup>2</sup> was selected in each of six commercial fields of spring wheat (cv. Katepwa) soon after the wheat emerged. Two fields were sampled in 1987, three in 1988, and one in 1989. Sites were selected on the basis of wheat stand uniformity and the presence of a wide range of quackgrass densities. Field sites were maintained through the growing season as described previously for the stratified random sampled survey sites.

**Table 9. Variable abbreviations used in the manuscript.**

Abbreviation <sup>a</sup>	Description	Units
<b>Wheat</b>		
$WS_i$	shoot number	# m <sup>-2</sup>
$WS_{wi}$	shoot dry matter (including heads)	g m <sup>-2</sup>
$WY$	grain yield	g m <sup>-2</sup>
$WY_{\%}$	relative grain yield	%
$WP$	plant number	# m <sup>-2</sup>
$WH$	head number	# plant <sup>-1</sup>
$WK$	kernel number	# head <sup>-1</sup>
$WK_w$	kernel dry matter	mg kernel <sup>-1</sup>
<b>Quackgrass</b>		
$QS_i$	shoot number	# m <sup>-2</sup>
$Ql_i$	plant height (extended)	m
$QH_i$	head number	# m <sup>-2</sup>
$QH_{wi}$	head dry matter	g m <sup>-2</sup>
$QS_{wi}$	shoot dry matter	g m <sup>-2</sup>
$QR_{wi}$	rhizome dry matter	g m <sup>-2</sup>
$QW_i$	total dry matter	g m <sup>-2</sup>
$QR_{Bi}$	rhizome bud number	# m <sup>-2</sup>
$QR_{li}$	cummulative rhizome length	m m <sup>-2</sup>
$QBW_i$	rhizome bud dry matter ( $QR_{wi} / QR_{Bi}$ ) x 1000	mg bud <sup>-1</sup>
$QBl_i$	rhizome bud length ( $QR_{li} / QR_{Bi}$ ) x 100	cm bud <sup>-1</sup>
$QRS_i$	rhizome to shoot ratio( $QR_{wi} / ( QS_{wi} + QH_{wi} )$ )	unitless
$QHR_i$	reproductive partitioning ( $QH_{wi} / QR_{wi}$ ) x 100	%
$QS_{Di}$	shoot density ( ( $QS_{wi} + QH_{wi}$ ) / $Ql_i$ )	g m <sup>-3</sup>
$QW_{Di}$	total density ( $QW_i / Ql_i$ )	g m <sup>-3</sup>
$QS_{\%i}$	relative quackgrass ratio ( $QS_i / ( QS_i + WS_i )$ )	unitless
<b>Others</b>		
$\Theta$	any variable	varies
$\beta_k$	model parameter	varies

<sup>a</sup> The subscript "i" denotes harvest number. 1 ≈ 30 DAP, 2 ≈ 60 DAP, 3 at wheat harvest (≈ 93 DAP) and  $\Sigma$  is the pooled data from all 3 harvest dates.

When the wheat matured, the wheat and quackgrass at the sites were sampled using approximately thirty 1 m<sup>2</sup> quadrats established using a baseline stratified random sampling method (Knight, 1978). Random numbers that resulted in overlapping quadrats were disregarded. All samples were harvested and treated in a similar fashion to those from the dynamic stratified random sampled surveys.

### Model Development and Selection

The results from all the dynamic stratified random sampling surveys were converted to a 1 m<sup>2</sup> basis and the results from each stratum were pooled and averaged to facilitate comparison to the average wheat yield from each stratum. To help compensate for the natural variation in wheat yields from the various locations and years, the relative wheat yield (  $WY_{\%}$  ) was determined for each stratum.  $WY_{\%}$  was determined by fitting<sup>6</sup> each individual site to a rectangular hyperbolic yield density model (Cousens, 1985) and setting the y-intercept to 100% and transforming the strata wheat yields at that site accordingly. The same transformation procedure was used on the independent validation survey data. The  $WY_{\%}$  were then used in a linear regression model of the form

$$WY_{\%} = \beta_F - \beta_I ( \Theta )$$

or in a rectangular hyperbolic model of the form

$$WY_{\%} = \beta_F x (1 - ((\beta_I x \Theta) / (100x(1 + ((\beta_I x \Theta) / \beta_A))))))$$

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<sup>6</sup>PROC NLIN, METHOD=DUD, SAS V5. SAS Institute, Cary, NC.



where  $\beta_F$  is an estimate of the weed free yield,  $\beta_I$  can be interpreted as a measure of the competitiveness of the individual quackgrass unit and  $\beta_A$  is the maximum percentage yield loss.

The ranking of a models ability to predict  $WY_{\%}$  was based on the models fit to the data, data robustness, data distribution and the simplicity of variable collection.

The quality of fit of the models to the data was assessed by comparing the coefficients of determinations ( $R^2$ ) calculated as described by Kvalseth (1985). For a model to be considered useful its  $R^2$  value had to be significant and, if significant, the larger the  $R^2$  value the better the model was considered to be.

Model robustness was evaluated by fitting individual models to each of the three harvest dates and then comparing this fit to a combined model using a parameter invariance testing procedure (Ratkowsky, 1983). Models were considered robust if they were applicable over the full growing season.

The data distribution was evaluated for contagiousness by looking at the variance to mean ratio. A random distribution would have a variance equal to the mean, a regular distribution would have a variance less than the mean and a contagious distribution will have a variance greater than the mean (Elliot, 1977). The more uniformly distributed the data over its range the more desirable the variable and its associated model was considered to be.

Simplicity was emphasized in model selection. First only one or two variables were included in the models and one variable models were considered superior to two variable models. Secondly the amount of effort involved in obtaining a measure was also a criterion.

For example, if counting shoots was as accurate in all other respects as rhizome dry weights, shoot counts would be considered the superior yield variable because of the comparative ease of counting shoots relative to digging up rhizomes.

The models that survived the screening procedure to this stage were tested for their ability to fit the independent datasets described earlier. This was accomplished by first fitting the independent datasets on their own and then comparing whether the interpolated line for a particular variable differed significantly from the interpolated stratified random sampling derived model using a parameter invariance technique (Ratkowsky, 1983). If the models were not significantly different, then the model for that particular variable would be considered 'valid'.

### **Component Analysis**

The models discussed previously will indicate the relation between wheat yield losses and quackgrass infestation but will not indicate the nature of these yield losses. To determine the nature of these yield losses the model that was identified as the best indicator of yield loss due to quackgrass was used to separate the data from the stratified random sampling surveys into two data groups, lightly infested and heavily infested. This was accomplished by ranking the data in descending fashion according to the variable values for the variable model that was determined to best describe the quackgrass infestation. The ranked data was then divided into the upper and lower 50 percentiles. Datasets included in the upper percentile group were considered to be representative of that from fields with heavy infestations, whereas the datasets in the lower percentile group were considered to be representative of that from fields

with light infestations. Wheat yield component data from both groups was subjected to two-dimensional partitioning of yield variation (Eaton *et al*, 1986) with each data group considered a treatment. The yield component model used was:

$$WY = WP \times WH \times WK \times WK_W.$$

Two-dimensional partitioning is used to identify the significant yield component variation in wheat associated with each treatment.

Yield component analysis of quackgrass could not be performed as the number of quackgrass plants initially present was not determined. However, biomass partitioning in quackgrass in the two groups was analyzed using a stepwise multivariate analysis of variance (MANOVA) technique (Jolliffe and Hoddinott, 1986). The assumption in this analysis was that

$$QW_3 = QS_{W3} + QR_{W3} + QH_{W3}.$$

This procedure identifies the significant contributions by the different quackgrass components to changes in net dry matter partitioning induced in this case by the relatively high and low quackgrass population densities.

## RESULTS AND DISCUSSION

### Survey Data

The standard error of mean (SEM) values for the wheat variables at the third sampling

date averaged 3.4 % whereas quackgrass averaged 18.1 % (Table 10). Given that these sites were selected for uniformity in wheat stand and for diversity in quackgrass stand, as well as the relative genetic uniformity of the wheat cultivar compared to the natural adaptive plasticity of a weedy species such as quackgrass, the greater variability in quackgrass compared to wheat was expected. On average the grain yield loss in these trials was 17% and the average  $WY$  was  $182 \text{ g m}^{-2}$  ( $27 \text{ bu acre}^{-1}$ ). All aboveground quackgrass variables measured were of a single seasons in-crop growth. Farm operators thoroughly tilled the survey fields prior to sowing and no viable shoots remained at the soil surface during sowing. However, there were old rhizomes in the soil and if at least a portion of a rhizome fragment appeared viable it was included. No attempt was made to distinguish between old and new rhizome growth.

All variables, except for  $QBI$  and  $QRS$ , increased in value as the growing season progressed (Table 10).  $QBI$  and  $QRS$  were constant throughout the growing season at each site. In wheat 94 % of  $WS$  that were present at harvest were already present by 30 DAP, whereas in quackgrass  $QS$  production was relatively additive with an increase of about 50  $QS$  occurring every 30 days.  $WS_w$  increased more than 10-fold in the 30 to 60 DAP interval and then only increased 20% in the remaining 60 DAP-wheat maturity interval. In contrast quackgrass showed relatively slow and steady growth in that for  $QW$  a three-fold increase in growth occurred in the 30 to 60 DAP interval followed by a two-fold increase in the 60 DAP-wheat maturity interval.

**Table 10.** Mean and standard error of mean (SEM) for the wheat and quackgrass variables from the pooled stratified random sampled surveys.

		Harvest <sup>a</sup>					
Variable <sup>b</sup>	Units	1		2		3	
		MEAN	±SEM	MEAN	±SEM	MEAN	±SEM
Wheat							
WS	# m <sup>-2</sup>	466	±20.9	487	±15.6	497	±15.8
WS <sub>W</sub>	g m <sup>-2</sup>	47.22	±2.760	480.09	±16.750	574.00	±23.200
WY	g m <sup>-2</sup>					182	±7.4
WY <sub>%</sub>	%					83	±3.3
WP	# m <sup>-2</sup>					125	±4.2
WH	# plant <sup>-1</sup>					4.2	±0.15
WK	# head <sup>-1</sup>					15.7	±0.49
WK <sub>W</sub>	mg seed <sup>-1</sup>					24	±0.5
Quackgrass							
QS	# m <sup>-2</sup>	55	±9.5	94	±16.1	144	±26.8
Ql	m	0.15	±0.009	0.42	±0.031	0.51	±0.035
QH	# m <sup>-2</sup>	0.5	±0.15	15	±4.0	17	±4.8
QH <sub>W</sub>	g m <sup>-2</sup>	0.04	±0.011	1.56	±0.452	2.26	±0.637
QS <sub>W</sub>	g m <sup>-2</sup>	7.49	±1.315	41.17	±7.590	83.11	±17.839
QR <sub>W</sub>	g m <sup>-2</sup>	9.74	±2.119	17.68	±2.818	34.17	±5.310
QW	g m <sup>-2</sup>	17.27	±3.353	60.41	±10.436	119.54	±21.995
QR <sub>B</sub>	# m <sup>-2</sup>	350	±73.6	574	±97.2	890	±146.2
QR <sub>I</sub>	m m <sup>-2</sup>	11.33	±2.286	18.22	±2.949	25.57	±4.131
QBW	mg bud <sup>-1</sup>	28	±6.1	31	±4.9	38	±6.1
QBl	cm bud <sup>-1</sup>	3.2	±0.64	3.2	±0.52	2.9	±0.47
QRS		1.30	±0.234	0.43	±0.080	0.41	±0.074
QHR	%	0.4	±0.11	8.8	±2.55	6.6	±1.90
QS <sub>D</sub>	g m <sup>-3</sup>	44.8	±6.66	75.8	±10.47	115.2	±17.89
QW <sub>D</sub>	g m <sup>-3</sup>	104.1	±17.79	115.1	±14.78	173.3	±23.47
QS <sub>%</sub>		0.11	±0.018	0.15	±0.020	0.18	±0.025

<sup>a</sup> Harvest 1 ≈ 30 days after planting (DAP), 2 ≈ 60 DAP, 3 = wheat maturity (≈ 93 DAP).

<sup>b</sup> See Table 9 for detailed description of variable abbreviations.

Growth of the various components of quackgrass biomass was component dependent.  $QS_w$  increased four-fold during the 30 to 60 DAP interval and then doubled during the 60 DAP-wheat maturity interval. Rhizomes harvested at 30 DAP had little if any additional biomass and were assumed to be similar to the rhizome infestations that were present at wheat sowing. Although  $QR_w$  increased relatively uniformly throughout the growing season, doubling in mass during both the 30 to 60 DAP and the 60 DAP-wheat maturity intervals, the majority of new rhizome growth only occurred during the 60 DAP-wheat maturity interval. This finding agrees with studies from Europe that have demonstrated that under competition most of the quackgrass rhizome growth occurs during the crop senescence phase (Cussans, 1968; Rauber and Bottger, 1984). Even though wheat in this experiment was interfering with quackgrass; there was, on average, a three-fold increase in  $QS_w$  from wheat sowing to wheat harvest. Wheat interference did not satisfactorily suppress the growth of quackgrass in these commercial fields.

### **Model Development and Selection**

It was assumed that the nonlinear rectangular hyperbolic model of Cousens (1985) was the most appropriate one for all variables except  $QS_{\%}$ . For  $QS_{\%}$ , fitting a rectangular hyperbola always resulted in a visually linear response. This consistently linear response combined with the knowledge that the largest  $QS_{\%}$  value biologically possible was 1.0 lead us to conclude that a linear regression model was appropriate for representing the  $QS_{\%}$  response.

The  $R^2$  values from models fit to each quackgrass variable listed in Table 10 was calculated for each harvest date and any variable that did not have a significant ( $P=0.05$ )  $R^2$  value at all three harvest dates was eliminated from further analysis. The seven eliminated variables were  $QI$ ,  $QH$ ,  $QH_w$ ,  $QBW$ ,  $QBI$ ,  $QRS$ , and  $QHR$ . The remaining variables with significant  $R^2$  values are listed in Table 11 .

Although significant, the  $R^2$  values were not as large as would have been desired. The low  $R^2$  values are possibly a result of the  $1/4$  m<sup>2</sup> sampling area being sub-optimal and/or inefficient site stratification that failed to satisfactorily account for the patchy nature of the quackgrass infestations.

The parameter  $\beta_F$  is an estimate of the weed-free yield and when expressed as  $WY_{\%}$  the weed-free yield should be 100. Estimated  $\beta_F$  values ranged from 92.9 for  $QS_{W\Sigma}$  to 103.2 for  $QW_{D\Sigma}$  (Table 11). Except for  $QS_{W\Sigma}$ , all estimated  $\beta_F$  values were not significantly ( $P=0.05$ ) different from 100.

The parameter  $\beta_I$  can be interpreted as a index of the competitiveness of the individual quackgrass variable unit. For every variable the estimated  $\beta_I$  value declined in size with time (Table 11). This declining  $\beta_I$  indicates a decline in quackgrass competitiveness as the growth within the crop progressed. This temporal variation in  $\beta_I$  emphasizes the importance of knowing assessment time when interpreting the competitiveness of quackgrass in wheat. The parameter  $\beta_A$  indicates the maximum percentage yield loss. The estimated  $\beta_A$  values were often poorly estimated for the third harvest as indicated by the values greater than 100 (Table

**Table 11. Parameter estimates, associated  $R^2$  values and model invariance F-values for selected variables from the pooled random sampled surveys.**

Variable <sup>b</sup>	Harvest <sup>c</sup>	Parameter <sup>a</sup>			Coefficient of Determ. ( $R^2$ ) <sup>d</sup>	Variance Ratio (F) <sup>d,e</sup>
		$\beta_F$	$\beta_I$	$\beta_A$		
$QR_B$	1	97.9 (5.5)	0.076 (0.047)	81.7 (27.1)	0.37**	
	2	99.4 (6.4)	0.058 (0.044)	60.3 (27.0)	0.30*	
	3	96.0 (3.0)	0.015 (0.000)	9.5E+11 (1.2E+11)	0.41**	
	$\Sigma$	96.7 (3.1)	0.041 (0.017)	70.6 (23.8)	0.31*	2.009 <sub>ns</sub>
$QR_i$	1	97.3 (5.3)	2.206 (1.369)	81.3 (41.1)	0.35**	
	2	97.6 (5.8)	1.366 (1.099)	72.6 (54.1)	0.30*	
	3	97.0 (3.3)	1.000 (0.080)	3.6E+9 (11.4)	0.43**	
	$\Sigma$	94.8 (2.6)	0.822 (0.284)	154.4 (226.9)	0.32**	1.512 <sub>ns</sub>
$QR_W$	1	97.9 (5.3)	3.114 (1.903)	71.3 (26.6)	0.37**	
	2	100.0 (7.3)	2.458 (2.306)	47.1 (17.9)	0.27*	
	3	97.4 (4.8)	0.560 (0.356)	124.3 (170.7)	0.34*	
	$\Sigma$	97.8 (3.5)	1.893 (0.924)	48.7 (10.5)	0.26**	2.064 <sub>ns</sub>
$QS$	1	98.7 (5.2)	0.433 (0.240)	193.7 (331.8)	0.41**	
	2	99.2 (5.9)	0.278 (0.178)	72.6 (35.8)	0.32*	
	3	96.4 (4.2)	0.113 (0.057)	203.4 (293.5)	0.43**	
	$\Sigma$	97.3 (2.8)	0.233 (0.072)	92.8 (29.1)	0.36**	1.404 <sub>ns</sub>
$QS_D$	1	98.3 (5.2)	0.426 (0.253)	95.7 (65.4)	0.37**	
	2	100.8 (6.4)	0.317 (0.199)	111.9 (106.4)	0.35**	
	3	97.4 (4.7)	0.139 (0.070)	541.1 (2432.6)	0.45**	
	$\Sigma$	101.3 (4.0)	0.469 (0.179)	59.6 (11.5)	0.30**	3.349 <sub>ns</sub>
$QS_W$	1	96.1 (4.2)	2.124 (1.137)	202.4 (368.5)	0.40**	
	2	96.8 (5.3)	0.567 (0.379)	77.5 (47.7)	0.31*	
	3	94.7 (3.9)	0.180 (0.100)	184.6 (258.7)	0.42**	
	$\Sigma$	92.9 (2.7)	0.487 (0.212)	61.5 (17.9)	0.23*	5.510*
$QS_{\%}$	1	96.0 (18.1)	117.3 (19.6)		0.42**	
	2	99.7 (13.4)	111.8 (15.4)		0.48**	
	3	100.6 (16.2)	94.9 (12.5)		0.54**	
	$\Sigma$	98.0 (1.9)	101.0 (9.0)		0.45**	1.526 <sub>ns</sub>
$QW$	1	97.5 (4.8)	1.380 (0.785)	90.3 (53.3)	0.39**	
	2	97.4 (5.5)	0.414 (0.292)	72.8 (45.6)	0.30*	
	3	95.5 (3.7)	0.115 (0.054)	539.7 (2334.6)	0.45**	
	$\Sigma$	94.8 (2.8)	0.393 (0.165)	59.4 (15.9)	0.26**	4.729*
$QW_D$	1	101.4 (6.4)	0.299 (0.174)	86.9 (40.2)	0.41**	
	2	101.9 (7.3)	0.229 (0.175)	98.4 (106.9)	0.33*	
	3	99.4 (3.5)	0.100 (0.012)	6.9E+8 (20.9)	0.48**	
	$\Sigma$	103.2 (4.5)	0.300 (0.121)	62.5 (12.2)	0.32**	3.330 <sub>ns</sub>

<sup>a</sup> Fit to the nonlinear equation:  $WY_{\%} = \beta_F x (1 - ((\beta_I x \Theta) / (100x(1 + ((\beta_I x \Theta) / \beta_A))))$  or in the case of  $QS_{\%i}$  the linear equation  $WY_{\%} = \beta_F - \beta_I (\Theta)$ , where  $\Theta$  is the quackgrass variate. Standard errors for the parameter estimates are enclosed in brackets beside value.

<sup>b</sup> See Table 9 for a detailed description of variable abbreviations.

<sup>c</sup> Harvest number: 1 = 30 DAP, 2 = 60 DAP, 3 at wheat harvest (= 93 DAP), and  $\Sigma$  is the result for fitting to pooled data from all 3 harvests.

<sup>d</sup> \*, \*\*, and *ns* denote significant at  $P=0.05$ ,  $P=0.01$ , and not significant, respectively.

<sup>e</sup> Variance ratio calculated as the ratio of the MS of the change in RSS between the sum of the independent fits and the combined fit divided by RMS of the sum of individual fits.



11). Cousens (1985) has indicated that the parameter  $\beta_A$  is extremely sensitive to data distribution along the X-axis. The survey results became relatively more skewed towards lower X-axis values as harvest date increased and this could have contributed to  $\beta_A$  being more poorly estimated at later harvests.

The assessment-time specificity of yield loss models can create difficulties in comparing competitiveness of plants. For example QS, at 21 DAP, has been related to yield loss in canola (*Brassica rapa*) in Alberta (O'Donovan, 1991). The estimated  $\beta_I$  determined for the relation between QS and canola yield was 0.41, whereas in this paper the estimated  $\beta_I$  in the relation between QS and WY at 30 DAP was 0.43. If we assume no location effect, these results suggest that quackgrass was more competitive against wheat than against canola. However, it could be argued that even if there is no location effect comparing the results from an assessment conducted 30 DAP with one assessed 21 DAP is questionable, particularly considering that canola (*B. rapa*) takes 81 days on average to mature whereas wheat takes 97 days<sup>7</sup>. To minimize such difficulties in comparing yield losses it is recommended that either assessment time be included as a variable in yield loss equations or that time independent robust "general" models be used.

If the derived model for the pooled harvest data was significantly different ( $P=0.05$ ) from one or more of the derived models for the individual harvests the variable was not

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<sup>7</sup> 1990 Field crop recommendations for Manitoba, Manitoba Agriculture, Publications Distribution, 411 York Avenue, Winnipeg, Manitoba, Canada, R3C 3M1.

considered robust enough to use without including an assessment time parameter. The variables,  $QW$  and  $QS_W$ , had significant variance ratio values indicating that the models for the individual harvests were significantly distinct and that a single pooled model cannot adequately describe the response (Table 11). For the remaining seven variables,  $QS$ ,  $QR_W$ ,  $QR_B$ ,  $QR_I$ ,  $QS_D$ ,  $QW_D$ , and  $QS_%$ , the pooled harvest models were not significantly different from any individual harvest date model and were therefore considered robust.

For any particular variable, a continuous random distribution of the data over its range would be better for estimating yield loss than data that tended to be clustered, even if the clustered model had a superior fit. The variables selected for robustness were then ranked according to data distribution. Data distribution was determined using the variance to average ratio with smaller ratios considered superior to larger ratios. The resulting ranking was  $QS_% > QR_B > QW_D > QS_D > QS > QR_I > QR_W$  with variance to mean ratio values of 0.49, 0.65, 0.77, 0.91, 0.96, 1.17, and 1.19, respectively.

To validate the utility of these selected variables in wheat yield loss models the variables were tested for their ability to fit independently collected data. The estimated parameter values for models fit to the independently collected pooled data from the baseline stratified random sampled surveys are presented in Table 12. Model fits as indicated by the  $R^2$  values were superior for the validation data (Table 12) than for the stratified random sampled data (Table 11). The  $R^2$  values for the models fit to the validation data ranged from 0.59 for  $QS$  to 0.72 for  $QS_%$ . The superior fit is attributed to using a larger (1 m<sup>2</sup>) quadrat and/or using quackgrass and wheat variable values from specific quadrats instead of stratum

**Table 12. Parameter estimates, associated  $R^2$  values and model invariance F-values for selected variables from the pooled baseline stratified random sampled surveys.**

Variable <sup>b</sup>	Parameter <sup>a</sup>			Coefficient of determination ( $R^2$ ) <sup>c</sup>	Variance Ratio (F) <sup>cd</sup>
	$\beta_F$	$\beta_I$	$\beta_A$		
QS	99.5 (2.0)	0.225 (0.032)	179.3 (47.1)	0.5927**	2.629 <sub>ns</sub>
QR <sub>W</sub>	95.6 (1.7)	0.354 (0.056)	258.4 (114.5)	0.6508**	7.294**
QR <sub>B</sub>	97.8 (1.9)	0.023 (0.004)	199.6 (62.5)	0.6212**	1.603 <sub>ns</sub>
QR <sub>I</sub>	97.2 (1.8)	0.727 (0.116)	194.4 (62.3)	0.6302**	0.820 <sub>ns</sub>
QS <sub>D</sub>	98.1 (1.9)	0.227 (0.031)	250.0 (93.4)	0.6272**	1.257 <sub>ns</sub>
QW <sub>D</sub>	97.5 (1.6)	0.124 (0.015)	148.6 (56.7)	0.6809**	0.265 <sub>ns</sub>
QS <sub>%</sub>	99.8 (1.3)	96.936 (4.450)		0.7195**	0.879 <sub>ns</sub>

<sup>a</sup> Fit to the nonlinear equation:  $WY_{\%} = \beta_F x (1 - ((\beta_I x \Theta) / (100x(1 + ((\beta_I x \Theta) / \beta_A))))))$  or in the case of QS<sub>%</sub>, the linear equation  $WY_{\%} = \beta_F - \beta_I (\Theta)$ , where  $\Theta$  is the quackgrass variate. Standard errors for the parameter estimates are enclosed in brackets beside value.

<sup>b</sup> See Table 9 for detailed descriptions of abbreviations.

<sup>c</sup> \*, \*\*, and <sub>ns</sub> denote significant at  $P=0.05$ ,  $P=0.01$ , and not significant, respectively.

<sup>d</sup> Variance ratio calculated as the ratio of the MS of the change in RSS between the sum of the independent fits and the combined fit divided by RMS of the sum of individual fits.

averages.

Similar to pooled harvest models of Table 11, the estimated  $\beta_F$  values did not significantly ( $P=0.05$ ) differ from 100, except for the estimate for  $QR_W$  (Table 12). The estimates values of  $\beta_I$  from the validation data (Table 12) were lower than those from fits to the pooled stratified random sampled surveys (Table 11). The lower  $\beta_I$  values are the result of the validation data having been collected at wheat maturity, whereas the pooled harvest models were derived from data collected at three harvest throughout the growing season. Similar to the pooled harvest data the estimated  $\beta_A$  values were generally poorly estimated as indicated by the large ( $>100$ ) estimates. Poor estimation of  $\beta_A$  can be attributed to the survey results having data distribution that is less than optimum for fitting this type of model.

The model invariance F-values in Table 12 are the result of comparing the pooled harvest models in Table 11 with the validation models of Table 12. Only the  $QR_W$  validation model was significantly different from the corresponding pooled harvest model. Given that the  $QR_W$  model was not validated and that the pooled harvest  $QR_W$  model ranked lowest in the earlier data distribution ranking the use of  $QR_W$  as a variable to relate quackgrass infestation to  $WY$  was dropped. However, the validation models describing the remaining six quackgrass variables were not significantly different from the corresponding pooled harvest models. Thus  $QS_0$ ,  $QR_B$ ,  $QW_D$ ,  $QS_D$ ,  $QS$ , and  $QR_I$  were all validated for their appropriateness in relating quackgrass infestations to  $WY$ .

Simplicity of quackgrass variable estimation is an important practical consideration in

utilization of these models. Three of the variables  $QR_B$ ,  $QR_l$ , and  $QW_D$  require digging up rhizomes and counting bud numbers, measuring cumulative length, or determining dry matter, respectively.  $QW_D$  and  $QS_D$  require that culm dry matter and heights also be determined. All that is required for  $QS$  and  $QS_{\%}$  are culm counts, either of quackgrass alone or of quackgrass and wheat. Clearly  $QS$  and  $QS_{\%}$  are the easiest quackgrass variables to measure. Of the two,  $QS_{\%}$  had the better data distribution and the best fit and thus would be the "best" variable.

In western Canada, until recently, the most commonly used model to relate yield loss to density is that of Dew (1972). For wild oats in wheat grown at Winnipeg, Dew derived the following equation  $WY_{\%} = 100 - 3.36 \sqrt{OS}$  where  $OS$  is the number of wild oat plants  $m^{-2}$ . To facilitate comparison of the relative competitiveness of quackgrass with wild oats a similar model was derived for quackgrass in wheat using the pooled harvest data. The resulting derived equation for yield loss in wheat due to quackgrass was  $WY_{\%} = 100 - 2.19 \sqrt{QS}$ . The parameter value of 2.19 for quackgrass compared to the parameter value of 3.36 for wild oats suggests that in wheat, a wild oat plant is about 1.5 times as competitive as a quackgrass shoot. The problem with Dew's simple model is that it systematically predicts yields less than zero. The use of asymptotic nonlinear equations, at least in theory, can avoid such biologically unrealistic possibilities.

### Component Analysis

Having decided on  $QS_{\%}$  as the best quackgrass variable it was then used to separate the pooled harvest data into two equal-sized low ( $Q_L$ ) and high ( $Q_H$ ) quackgrass infested populations. The average values and standard errors of mean (SEM) of the resulting populations are listed in Table 13. Data from each survey site were relatively uniformly distributed between both populations. On average the  $QS_{\%}$  value in the  $Q_H$  population was six times greater than the value in the  $Q_L$  population. The greater quackgrass infestation in  $Q_H$  was primarily responsible for the average  $WY$  in the  $Q_H$  population being 21% less than in the  $Q_L$  population.

To understand the nature of the difference in wheat yield between the two populations two-dimensional partitioning of yield variation was used (Eaton *et al*, 1986). This technique first partitions yield using sequential yield component analysis (Eaton and Kyte, 1978) and then ordinary ANOVA to partition the variation in the orthogonal variables. A summary table of the results of this analysis conducted on the wheat yield components of the  $Q_L$  and  $Q_H$  populations are presented in Table 14. The most important contributor to wheat yield in the pooled harvest surveys was  $WK$  and  $WK_W$ , each contributing 49 and 20 % to yield, respectively. The only yield component significantly affected by treatment was  $WK_W$ . Variations in  $WK$ ,  $WP$ , and  $WH$  contributed to yield but were not attributed to treatments (population differences). Possible sources of this variation are compensatory growth by other components and other factors not considered in the ANOVA.

**Table 13.** Mean and standard error of mean (SEM) for the wheat and quackgrass variables from samples grouped into high ( $Q_H$ ) and low ( $Q_L$ ) quackgrass infestations.

		Population <sup>a</sup>			
Variable <sup>b</sup>	Units	Q <sub>L</sub>		Q <sub>H</sub>	
		MEAN	±SEM	MEAN	±SEM
Wheat					
WS	# m <sup>-2</sup>	535	±19.9	471.7	±24.1
WS <sub>W</sub>	g m <sup>-2</sup>	633.02	±6.121	528.99	±35.426
WY	g m <sup>-2</sup>	207.15	±8.488	164.35	±11.171
WY <sub>%</sub>	%	94.6	±3.88	75.1	±5.10
WP	# m <sup>-2</sup>	129	±6.6	121	±5.2
WH	# plant <sup>-1</sup>	4.4	±0.26	4.0	±0.22
WK	# head <sup>-1</sup>	15.7	±0.74	15.7	±0.63
WK <sub>W</sub>	mg seed <sup>-1</sup>	25.5	±0.82	22.3	±0.61
Quackgrass					
QS	# m <sup>-2</sup>	29	±4.4	253	±41.9
QI	m	0.32	±0.033	0.69	±0.039
QH	# m <sup>-2</sup>	1.0	±0.28	32.2	±8.22
QH <sub>W</sub>	g m <sup>-2</sup>	0.12	±0.039	4.25	±1.102
QS <sub>W</sub>	g m <sup>-2</sup>	14.55	±2.891	148.62	±28.247
QR <sub>W</sub>	g m <sup>-2</sup>	7.49	±1.524	60.71	±7.260
QW	g m <sup>-2</sup>	22.16	±4.207	213.58	±33.567
QR <sub>B</sub>	# m <sup>-2</sup>	171	±32.9	1580	±203.0
QR <sub>I</sub>	m m <sup>-2</sup>	4.85	±0.939	46.00	±5.691
QBW	mg bud <sup>-1</sup>	44	±8.9	38	±4.9
QBI	cm bud <sup>-1</sup>	2.8	±0.53	2.9	±0.37
QRS		0.51	±0.102	0.41	±0.078
QHR	%	1.6	±0.52	7.0	±1.79
QS <sub>D</sub>	g m <sup>-3</sup>	35.97	±5.454	185.55	±27.645
QW <sub>D</sub>	g m <sup>-3</sup>	55.18	±7.827	279.16	±33.173
QS <sub>%</sub>		0.05	±0.007	0.31	±0.033

<sup>a</sup> Divided into two equal-sized "low" ( $Q_L$ ) and "high" ( $Q_H$ ) quackgrass infestation populations as determined using QS<sub>%</sub>.

<sup>b</sup> See Table 9 for detailed description of variable abbreviations.

**Table 14. Partitioning of yield variation as a percentage of the total SS for relative wheat yield.**

Source	Transformed Yield Components <sup>a</sup>					Products	WY
	WP	WH	WK	WK <sub>w</sub>			
Treatment <sup>b</sup>	0	0	0	2.91** <sup>c</sup>	-0.05	2.91**	-(ln)-
Error	18.67	12.83	48.69**	16.90	0.05	97.09	
Total	18.67	12.83	48.69**	19.81**		100	

<sup>a</sup> The values presented are the  $\ln$ -transformed, orthogonalized, and scaled values of the wheat yield components listed. Descriptions of the yield component abbreviations can be found in Table 9.

<sup>b</sup> Treatments are the QS<sub>%</sub> based "light" and "heavy" quackgrass infested populations from the pooled stratified random sampled surveys.

<sup>c</sup> Significance in treatment row refers to the analysis of variance and in the Total row refers to regression analysis. \*\* denotes significance at P=0.01.



The determination of treatment effect on  $WK_W$  and not on the other components indirectly indicates that the majority of quackgrass competition occurs during the later stages of wheat growth. It has been established that changes in  $WK_W$  occur primarily as a result of post-anthesis stress rather than pre-anthesis stress (Ford and Thorne, 1975; Jenner, 1979).

Quackgrass response to the different population treatments was also of interest. The  $Q_L$  population not only had a low quackgrass infestation but also had a relatively higher wheat population. On average the  $Q_L$  population had 14 % more wheat shoots than the  $Q_H$  population (Table 13).

A stepwise multivariate analysis of variance technique (Jolliffe and Hodinott, 1986) was used to determine the effects of population treatment on net dry matter partitioning in quackgrass. The technique involves the joint application of ANOVA to identify the dominant component and then utilizes MANOVA to remove the intrinsic correlations between components. The stepwise MANOVA is then utilized to determine how the addition of each component to the dominant component improves the expression of treatment effects.

The ANOVA detected a significant treatment effect only for HW% (Table 15A). Therefore HW% was the plant component that dominated the treatment response. MANOVA performed on the combined set of all components confirmed this treatment effect (Table 15B). Even when correlations between components were removed all test statistics were still significant.

The stepwise MANOVA "subset " results shows the results of combining each or all

**Table 15. Combined analysis of net dry matter partitioning among quackgrass vegetative and reproductive components at wheat harvest<sup>a</sup>.**

(A) ANOVA, each component taken alone

Source	df	F-values <sup>b</sup>		
		SW <sub>%</sub> <sup>c</sup>	RW <sub>%</sub>	HW <sub>%</sub>
Treatment	1	0.31	0.67	12.91**

(B) MANOVA, all components taken together

Source	df	Test Statistics		
		Roy's Maximum Root	Wilk's u	F-Approximation
Treatment	3,50	0.437**	0.696**	7.28**

(C) Stepwise MANOVA, additional information on treatment effects

Subset		Conditional Set			
Set <sup>d</sup>	Wilk's u	Set <sup>d</sup>	df	Wilk's u	F-Approximation
HW <sub>%</sub>	0.801	QH <sub>w</sub> /Q <sub>w</sub>	1,52	0.801	12.91**
HW <sub>%</sub> +RW <sub>%</sub>	0.698	QH <sub>w</sub> /QR <sub>w</sub>	1,51	0.871	7.55**
HW <sub>%</sub> +SW <sub>%</sub>	0.782	QH <sub>w</sub> /QS <sub>w</sub>	1,50	0.976	1.25 <sub>ns</sub>
HW <sub>%</sub> +SW <sub>%</sub> +RW <sub>%</sub>	0.696	QH <sub>w</sub> /QS <sub>w</sub> /QR <sub>w</sub>	1,50	0.997	0.15 <sub>ns</sub>

<sup>a</sup> Treatments are the QS% based "light" and "heavy" quackgrass infested populations from the pooled stratified random sampled surveys.

<sup>b</sup> Significant at P=0.05(\*), P=0.01(\*\*), P=0.001(\*\*\*) or not significant (<sub>ns</sub>).

<sup>c</sup> SW<sub>%</sub> is shoot dry matter as a percentage of the total dry matter, RW<sub>%</sub> is rhizome dry matter as a percentage of total dry matter, and HW<sub>%</sub> is head dry matter as a percentage of total dry matter.

<sup>d</sup> Variable abbreviations are described in Table 9.

of the components with the dominant component. There was a decline in Wilk's  $\lambda$  with the addition of non-dominant components (Table 15C). This decline is attributed to the additional components adding additional variation.

The "conditional set" in the stepwise MANOVA evaluates the contribution of each additional quotient after responses to earlier quotients in the set have been taken into account. HW% alone was able to show a significant treatment effect (Table 15C). Addition of RW% did lower the expression of treatment effects but there was still a significant treatment effect. Addition of any other components removed the significance of any treatments. The results indicate that if variability of the data was less, RW% may have also showed a significant treatment response. This indicates that increases in HW% are more likely to have occurred at the expense of RW% rather than at the expense of SW%. This has yet to be proved.

In general, the stepwise MANOVA results indicate that quackgrass dry matter partitioning was altered by population treatment. The component that was affected by treatment was HW%. SW% and RW% were not significantly affected by the  $Q_L$  and  $Q_H$  populations.  $QH_W$  was 35 times greater in the  $Q_H$  population compared to the  $Q_L$  population (Table 13); whereas  $QS_W$  and  $QR_W$  were ten and eight times greater in the  $Q_H$  compared to the  $Q_L$  population, respectively. This indicates quackgrass head formation is relatively more dependent on the levels of interference than are rhizome or culm formation.

Quackgrass is extremely plastic and subject to great environmental influence. The resulting variability means that the absolute quantitative predictive ability of these models in

a particular instance will be poor. However, in terms of qualitative predictions the models developed in this paper are valuable for use in assaying the economics of controlling quackgrass and comparing the relative competitiveness of other weed and crop species to quackgrass. For more accurate quantitative predictions, complex models including allometric, environmental and temporal information would have to be developed.

**MANUSCRIPT 3**

**Allometry in Quackgrass (Elytrigia repens)****Infesting Spring Wheat (Triticum aestivum)**

**Abstract.** Growth of natural infestations of quackgrass in spring wheat fields was monitored during the 1988 and 1989 growing seasons at six locations in southern Manitoba. At each site quackgrass was systematically sampled at 30, 60 and 93 days after planting (DAP<sup>8</sup>) to wheat. Rhizome bud weight, rhizome bud length and rhizome to shoot ratio 93 DAP were not significantly correlated with the corresponding variable values at 30 and 60 DAP. Allometric relationships between selected vegetative variables and reproductive variables were determined for each sampling date. Correlation coefficients for the strength of the allometric relationships generally increased with sampling time and varied significantly from harvest to harvest. For any specific vegetative variable, allometric relationships with rhizome variables were usually stronger than those with head variables. Linking the allometric models with a wheat yield-loss model was determined to give accurate estimates when compared to data from the pooled dynamic stratified random sampling design used to develop the models. The allometric relationships from this design differed significantly from those from an independently collected dataset, thereby indicating that such models are not "universally" applicable.

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<sup>8</sup>Abbreviations: DAP, days after planting; Variate abbreviations are listed in Table 15.

Nomenclature: Quackgrass, Elytrigia repens L. Nevski #<sup>9</sup> AGGRE; wheat, Triticum aestivum L. 'Katepwa';

Additional index words. Agropyron repens L. Beauv., growth, competition, modelling, AGGRE, survey.

## INTRODUCTION

Weed scientists want to determine the relation between crop yield and weed infestation easily, accurately, and with a minimum of observations. Although both crop yield loss and weed population dynamics are important components in any assessment of the long-term impact of a weed, most crop yield-loss models do not include corresponding weed growth/population models. If practical application of yield loss models to assessment of long-term weed impact is desired then more sophisticated approaches will be required.

One approach is to link simple yield-loss models with weed population dynamics through regression and allometry. Allometry refers to the growth relationship that exists among the different parts of an organism. Although many mathematical expressions could be used the most common model for describing an allometric relationship is the simple empirical power function provided by Pearsall (1927):

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<sup>9</sup>Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Weed Sci. 32, Suppl. 2. Available from WSSA, 309 West Clark Street, Champaign, IL 61820.

$$\Theta_i = \beta \Theta_p^\alpha.$$

The allometric coefficient,  $\beta$ , is the value of  $\Theta_i$  when  $\Theta_p = 1.0$  and is a scalar parameter.

The allometric exponent,  $\alpha$ , is a measure of the relative growth rates of  $\Theta_i$  and  $\Theta_p$  (Whitehead and Myerscough, 1962). Although originally developed to relate growth of a part to the whole, the equation is commonly applied to relate the growth between various parts of an organism. Huxley (1932) has even suggested that this allometric equation is a true biological law for relating growth of parts of an organism.

The allometric relationship is usually utilized in its  $\ln$ -transformed form:

$$\ln (\Theta_i) = \ln (\beta) + \alpha \ln (\Theta_p) (+ \ln (\epsilon)).$$

The term  $\ln (\epsilon)$  is added to account for residual variation not accounted for through allometry itself. The error parameter is usually ignored but should not be forgotten as its presence can limit the utilization of this allometric equation. Even though the methodology involved in determining allometric relations is relatively standardized, the interpretation of results requires certain precautions (Niklas, 1994; Seim and Saether, 1983; Smith, 1980) and can be aided using techniques which attribute part of the residual variation to treatment effects (Jolliffe *et al*, 1983). An excellent overview of plant allometry is presented in the text of Niklas (1994).

The growth of quackgrass, both in crop and in isolation, has been extensively analyzed. However, only a few studies have provided any information on the allometric relationship between quackgrass variables (Cussans and Wilson, 1975; Neuteboom, 1975; 1980; Reekie and Bazzaz, 1987a; 1987b; 1987c; Rioux, 1982). Neuteboom (1975) listed correlations as



determined from earlier sampling.

## MATERIALS AND METHODS

### Survey Data

In south central Manitoba, six commercial fields of spring wheat (cv. Katepwa) infested with quackgrass were surveyed using a dynamic stratified random sampling design. Of the six fields, four were surveyed in 1988 and two in 1989. Sites were sampled three times throughout the growing season using 0.25 m<sup>2</sup> quadrats. The three sampling times were approximately 30, 60 and 93 days after planting (DAP). Details of the sites and sampling techniques are presented elsewhere (Manuscript 2).

For the purposes of this paper the variables selected for discussion can be categorized as measures of vegetative size and dispersion and measures of reproductive effort and fecundity. The relative quackgrass ratio and culm number were categorized as indicators of vegetative plant dispersion. Height, shoot density, total density, and shoot dry matter were categorized as indicators of plant size. Rhizome length and head dry matter were categorized as measures of reproductive effort. Head number and rhizome bud number were considered measures of reproductive fecundity. Complete descriptions of the measured and derived variables and their abbreviations are listed in Table 16.

To assist in assessing the cross-site utility of the stratified random sampled results independent data was collected over 1987 to 1989. Areas of approximately 20 m<sup>2</sup> were

**Table 16. Description of quackgrass variable abbreviations.**

Abbreviation <sup>a</sup>	Description	Units
$Bl_i$	rhizome bud length ( $R_{li} / R_{Bi}$ ) x 100	cm bud <sup>-1</sup>
$BW_i$	rhizome bud dry matter ( $R_{wi} / R_{Bi}$ ) x 1000	mg bud <sup>-1</sup>
$H_i$	head number	# m <sup>-2</sup>
$H_{wi}$	head dry matter	g m <sup>-2</sup>
$HR_i$	reproductive partitioning ( $H_{wi} / R_{wi}$ ) x 100	%
$l_i$	plant height (extended)	m
$R_{Bi}$	rhizome bud number	# m <sup>-2</sup>
$R_{li}$	cumulative rhizome length	m m <sup>-2</sup>
$R_{wi}$	rhizome dry matter	g m <sup>-2</sup>
$RS_i$	rhizome to shoot ratio( $R_{wi} / ( S_{wi} + H_{wi} )$ )	unitless
$S_{Di}$	shoot density ( ( $S_{wi} + H_{wi}$ ) / $l_i$ )	g m <sup>-3</sup>
$S_i$	shoot number	# m <sup>-2</sup>
$S_{wi}$	shoot dry matter	g m <sup>-2</sup>
$S_{\%i}$	relative quackgrass ratio ( $S_i / ( S_i + WS_i^b )$ )	unitless
$W_i$	total dry matter	g m <sup>-2</sup>
$W_{Di}$	total density ( $W_i / l_i$ )	g m <sup>-3</sup>
Others		
$\Theta$	any variable	varies
$\beta_k$	model parameter	varies

<sup>a</sup> The subscript "i" denotes harvest number. 1 ≈ 30 DAP, 2 ≈ 60 DAP, 3 at wheat harvest (≈ 93 DAP).

<sup>b</sup>  $WS_i$  is the wheat shoot number m<sup>-2</sup>

selected in each of six commercial fields of spring wheat (cv. Katepwa) soon after each emerged. Two fields were sampled in 1987, three fields in 1988, and one field in 1989. All fields were located in south central Manitoba. At wheat maturity these sites were sampled using approximately thirty 1 m<sup>2</sup> quadrats whose sampling positions were determined using baseline stratified random sampling (Knight, 1978). Further details of the sampling techniques have been reported elsewhere (Manuscript 2).

## **Model Development and Selection**

### **Auto-Regressions**

The results from each dynamic stratified random sampled survey were converted to a 1.0 m<sup>2</sup> basis and the results from each stratum pooled and averaged to simulate the type of data one would expect farm operators to collect. The surveys were pooled and linear regression<sup>10</sup> used to relate quackgrass variable values at the 30 or 60 DAP to the values at 93 DAP. In this manuscript these regressions are referred to as auto-regressions.

To facilitate comparisons between harvests and treatments, linear regression was used. Linear regressions were usually significant ( $P=0.05$ ), and any improvement of fit by quadratic or higher order relationships was frequently not significant.

The auto-regression models were of the form

$$\Theta_3 = \beta_0 + \beta_1 ( \Theta_i ).$$

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<sup>10</sup> PROC REG, SAS V5., SAS Institute, Cary, NC.

Where  $\Theta_3$  is the predicted value of the variable at the third harvest and  $\Theta_i$  the variable values at harvests  $i = 1$  or  $2$ .  $\beta_0$  and  $\beta_1$  are the regression line intercept and slope, respectively. The comparative strengths of the regressions were determined using coefficients of determinations ( $R^2$ ) calculated as described by Kvalseth (1985). Individual models for each variable were compared to a pooled model to determine if the individual models were significantly different from one another according to a parameter invariance testing procedure (Ratkowsky, 1983).

### **Allometric Relationships**

The allometric models discussed in this manuscript are limited to allometry between vegetative components and reproductive components as these relationships were considered most important in terms of relating field measurements to long-term quackgrass population dynamics. Additionally, the relationship between a derived variable and any of its components was not determined because of the expected autocorrelation.

The allometric relations were developed using simple regression. It was felt that for the comparative and predictive purposes, for which this data would be used within this manuscript, that simple regression analysis would be satisfactory. However, for cross species or other confounded comparisons, particularly when there are weak allometric correlations, major axis analysis or reduced major axis analysis (Seim and Saether, 1983) would be a more appropriate form of analysis.

At each harvest an allometric model for each variable pair was determined using linear

regression on *ln*-transformed variable values. The relative strength of the derived allometric relationships was assessed by comparing the coefficients of determinations ( $R^2$ ) calculated as described by Kvalseth (1983). For an allometric model to be considered useful its  $R^2$  value had to be significant ( $P=0.05$ ). Individual models derived for each variable were compared to a pooled model to determine if the models were significantly different according to a parameter invariance testing procedure (Ratkowsky, 1983).

Cross utility of the models was evaluated by comparing the allometric relationships derived for variables at 93 DAP to similarly derived relationships from the baseline stratified random sampling surveys (validation survey). The independent models were compared to a pooled model using a parameter invariance testing procedure (Ratkowsky, 1983). If the models were significantly ( $P=0.05$ ) different then the allometric relationships were considered to not have cross-utility.

## RESULTS AND DISCUSSION

### Auto-Regressions

Linear regression relationships between quackgrass variable values at 30 and 60 days after planting (DAP) and variable values at wheat harvest (93 DAP) were determined for all variables listed in Table 16. Six of the variables had non-significant coefficients of determination ( $R^2$ ) values for one or more of the harvests. Using the 30 DAP data these

variables were  $l$ ,  $H_W$ ,  $B_W$ ,  $B_l$ ,  $RS$ , and  $HR$ , whereas using 60 DAP values these variables were  $B_W$ ,  $B_l$ , and  $RS$ . Values for  $B_W$ ,  $B_l$  and  $RS$  at 30 and 60 DAP were consistently independent of final harvest values, and were of no predictive value.

Except for  $B_W$ ,  $B_l$  and  $RS$ , the estimated parameter values and associated  $R^2$  values for the auto-regression relationships are listed in Table 17.

Except for  $HW_1$  and  $l_1$ , all models had significant  $R^2$  values. Significant  $R^2$  values ranged from 0.24 for  $H_1$  to 0.84 for  $W_2$ . Often, but not in every instance,  $R^2$  values for auto-regressions from 60 DAP were superior to auto-regressions from 30 DAP. Sixty DAP variable values are closer temporally to 93 DAP harvest values relative to 30 DAP values and would be expected to have stronger relationship to final values.

Sampling time was important in determining both the strength of fit and the model structure. The 30 DAP and 60 DAP auto-regressions differed significantly for every variable. There was always a significant difference in slope (parameter  $\beta_1$ ) and the slope for 60 DAP auto-regressions was usually less than 30 DAP auto-regressions. Intercepts (parameter  $\beta_0$ ) in the auto-regression models were often poorly estimated and as a result often did not differ significantly between sample dates.

### **Allometric Relationships**

The allometric relationships for determining reproductive variables at the 30, 60, and 93 DAP sample dates are presented in Tables 18,19, and 20, respectively. Head production

**Table 17. Parameter estimates and associated  $R^2$  values for selected temporal autoregressions for quackgrass variables in the pooled stratified random surveys.**

Variable <sup>b</sup>	Harvest <sup>c</sup>	Parameter <sup>a</sup>		$R^2$ <sup>d</sup>
		$\beta_0$	$\beta_1$	
<i>H</i>	1	7.052 (4.5289)	13.401 (2.5294)	0.36**
	2	2.109 (2.2624)	0.939 (0.0612)	0.83**
<i>H<sub>w</sub></i>	1	1.421 (0.7042)	22.695 (7.5648)	0.14 <sub>ns</sub>
	2	0.265 (0.2876)	1.294 (0.0794)	0.84**
<i>I</i>	1	0.150 (0.1020)	2.458 (0.6118)	0.24**
	2	0.122 (0.0489)	0.922 (0.0998)	0.63**
<i>R<sub>B</sub></i>	1	336.520 (97.2979)	1.656 (0.1490)	0.72**
	2	197.965 (112.7521)	1.209 (0.1226)	0.66**
<i>R<sub>I</sub></i>	1	10.384 (3.2375)	1.431 (0.1575)	0.63**
	2	3.667 (2.8440)	1.201 (0.0989)	0.75**
<i>R<sub>w</sub></i>	1	7.194 (4.2312)	1.565 (0.1509)	0.69**
	2	19.669 (4.9467)	1.624 (0.2715)	0.41**
<i>S</i>	1	6.227 (17.7374)	2.479 (0.1946)	0.77**
	2	3.129 (15.7047)	1.4952 (0.1040)	0.80**
<i>S<sub>D</sub></i>	1	9.000 (12.2819)	2.482 (0.1849)	0.79**
	2	5.198 (14.7751)	1.409 (0.1308)	0.70**
<i>S<sub>w</sub></i>	1	-7.207 (11.3599)	11.705 (0.9018)	0.77**
	2	-0.667 (10.5517)	2.032 (0.1529)	0.78**
<i>S<sub>%</sub></i>	1	0.051 (0.0168)	1.212 (0.0953)	0.77**
	2	0.021 (0.0187)	1.096 (0.0900)	0.75**
<i>W</i>	1	3.447 (19.2444)	4.556 (0.4889)	0.64**
	2	13.545 (11.0751)	2.040 (0.1239)	0.84**
<i>W<sub>D</sub></i>	1	28.508 (20.1612)	0.981 (0.0952)	0.69**
	2	23.975 (18.9844)	1.464 (0.1342)	0.70**

<sup>a</sup> From the regression model  $\Theta_3 = \beta_0 + \beta_1 ( \Theta_i )$ . Standard errors for the parameter estimates are enclosed in brackets beside the estimate.

<sup>b</sup> Descriptions of variable abbreviations are found in Table 16.

<sup>c</sup> Harvest number: 1 = 30 DAP, 2 = 60 DAP, 3 at wheat harvest (= 93 DAP).

<sup>d</sup> \*, \*\* and <sub>ns</sub> indicate significant at  $P=0.05$ ,  $P=0.01$ , and not-significant, respectively.

was minimal at 30 DAP and consequently the strength, as indicated by the  $R^2$  value, of the allometric relationships for the dependent variables  $H_{W1}$  and  $H_1$  are relatively poor or not significant (Table 18). At later sample dates, the strength of the allometric relationships involving the dependent variables  $H_W$  and  $H$  increased as head production increased. However, even at 93 DAP, the strength of the allometric relationships involving the dependent head variables was comparatively weak relative to those involving rhizome variables. In contrast Neuteboom (1980) determined that the correlations from reproductive variables  $R_W$  and  $H$  regressed against  $S$  and  $S_W$  were of similar strengths. The contrasting results may be attributed to Neuteboom's relationships having been determined on plants grown in the absence of interference whereas quackgrass in this study was competing with wheat.

In general, the strength of the allometric relationships between vegetative and reproductive variables increased over time. The mean  $R^2$  values were 0.50, 0.58, and 0.73, at the 30, 60 and 93 DAP sample dates, respectively (Tables 18, 19 and 20). The lower  $R^2$  value for the 30 and 60 DAP allometric relationships compared to 93 DAP relationships can be attributed to the smaller range in variable size of the two variables at earlier sample dates.

An increase in size will result in a change of form. For the quackgrass variables this was reflected in significantly different allometric relationships for every variable from one sample date to the next (Tables 18, 19 and 20). Differences in the allometric relationships were as much to do with parameter  $\alpha$  as parameter  $\beta$ .

In the allometric equation, parameter  $\beta$  is of little interest. As a scalar  $\beta$  lacks



**Table 18. Parameter estimates and associated  $R^2$  values for selected quackgrass allometric relationships at approximately 30 days after planting wheat.**

Variable <sup>a</sup>		Parameter <sup>b</sup>		
Indep.	Depend.	$\beta$	$\alpha$	$R^2$ <sup>c</sup>
-----( <i>ln</i> )-----				
I	$R_W$	6.481 (0.8738)	2.233 (0.4517)	0.34**
	$R_I$	5.867 (0.6886)	2.152 (0.3559)	0.43**
	$H_W$	1.216 (4.5051)	6.628 (2.3291)	0.13 $ns$
	$H$	4.827 (5.4874)	7.986 (2.8370)	0.13 $ns$
	$R_B$	9.134 (0.6677)	2.058 (0.3452)	0.42**
S	$R_W$	-0.447 (0.4537)	0.782 (0.1237)	0.45**
	$R_I$	-1.441 (0.1605)	0.936 (0.0438)	0.90**
	$H_W$	-22.135 (2.2376)	3.128 (0.6101)	0.35**
	$H$	-23.528 (2.7094)	3.833 (0.7387)	0.35**
	$R_B$	2.145 (0.1662)	0.895 (0.0453)	0.89**
$S_D$	$R_W$	-0.248 (0.4759)	0.770 (0.1379)	0.39**
	$R_I$	-1.151 (0.2563)	0.906 (0.0743)	0.76**
	$H$	2.442 (0.2581)	0.861 (0.0748)	0.73**
	$R_B$	-22.657 (2.7838)	3.809 (0.8068)	0.31**
$S_W$	$R_W$	1.281 (0.2104)	0.721 (0.1088)	0.47**
	$R_I$	0.696 (0.0891)	0.813 (0.0507)	0.84**
	$H_W$	-14.999 (1.0817)	2.720 (0.5589)	0.32**
	$H$	-23.528 (2.7093)	3.833 (0.7387)	0.35**
	$R_B$	4.194 (0.1010)	0.774 (0.0522)	0.82**
$S_{\%}$	$R_W$	4.375 (0.3595)	0.760 (0.1163)	0.47**
	$R_I$	4.260 (0.1422)	0.884 (0.0460)	0.89**
	$H_W$	-3.287 (1.8357)	2.884 (0.5938)	0.32**
	$H$	-0.416 (2.2220)	3.539 (0.7188)	0.33**
	$R_B$	7.568 (0.1570)	0.835 (0.0508)	0.85**
W	$R_I$	-0.507 (0.2417)	0.847 (0.0814)	0.69**
	$H$	-20.262 (2.3494)	3.673 (0.7916)	0.30**
	$R_B$	3.079 (0.2466)	0.794 (0.0831)	0.65**
$W_D$	$R_I$	-2.491 (0.5482)	0.929 (0.1163)	0.57**
	$H$	-29.744 (4.5996)	4.218 (0.9757)	0.27**
	$R_B$	1.243 (0.5510)	0.866 (0.1169)	0.59**

<sup>a</sup> Descriptions of the variable abbreviations can be found in Table 16.

<sup>b</sup> From the allometric model  $\Theta_i = \beta \Theta_p^\alpha$ . Standard errors for the parameter estimates are enclosed in brackets beside the estimate.

<sup>c</sup> \*, \*\* and  $ns$  indicate significant at  $P=0.05$ ,  $P=0.01$ , and not-significant, respectively.

**Table 19. Parameter estimates and associated  $R^2$  values for selected quackgrass allometric relationships at approximately 60 days after planting wheat.**

Variable <sup>a</sup>		Parameter <sup>b</sup>		
Indep.	Depend.	$\beta$	$\alpha$	$R^2$ <sup>c</sup>
-----( <i>ln</i> )-----				
I	$R_W$	2.266 (0.3058)	0.773 (0.2682)	0.13 <sub>ns</sub>
	$R_l$	3.866 (0.2457)	1.716 (0.2155)	0.57**
	$H_W$	3.289 (1.0706)	7.123 (0.9389)	0.54**
	$H$	6.232 (1.2367)	8.110 (1.0847)	0.53**
	$R_B$	7.206 (0.2318)	1.556 (0.2034)	0.55**
S	$R_W$	-0.896 (0.5041)	0.608 (0.1199)	0.34**
	$R_l$	-2.016 (0.2821)	1.066 (0.0672)	0.84**
	$H_W$	-18.380 (1.9633)	3.737 (0.4673)	0.57**
	$H$	-18.157 (2.3189)	4.184 (0.5519)	0.54**
	$R_B$	1.799 (0.2589)	0.985 (0.0616)	0.84**
$S_D$	$R_W$	-1.783 (0.5361)	0.842 (0.1313)	0.46**
	$R_l$	-2.666 (0.3776)	1.247 (0.0825)	0.79**
	$H$	1.131 (0.3260)	1.170 (0.0799)	0.82**
	$R_B$	-18.537 (3.1132)	4.347 (0.7628)	0.40**
	$R_W$	-0.056 (0.3227)	0.535 (0.0964)	0.38**
$S_W$	$R_l$	-0.428 (0.1708)	0.899 (0.0510)	0.87**
	$H_W$	-12.761 (1.2824)	3.137 (0.3833)	0.58**
	$H$	-11.827 (1.5238)	3.499 (0.4554)	0.55**
	$R_B$	3.258 (0.1529)	0.834 (0.0457)	0.87**
	$R_W$	2.898 (0.3362)	0.579 (0.1269)	0.29**
$S_{\%}$	$R_l$	4.840 (0.1691)	1.102 (0.0638)	0.86**
	$H_W$	5.288 (1.3145)	3.705 (0.4959)	0.53**
	$H$	8.384 (1.5395)	4.166 (0.5801)	0.51**
	$R_B$	8.112 (0.1637)	1.009 (0.0618)	0.85**
	$R_l$	-1.388 (0.2663)	1.089 (0.0749)	0.81**
W	$H$	-14.712 (2.2240)	3.985 (0.6251)	0.45**
	$R_B$	2.327 (0.2265)	1.022 (0.0637)	0.84**
	$R_l$	-2.714 (0.7655)	1.160 (0.1750)	0.47**
$W_D$	$H$	-15.322 (4.7398)	3.253 (1.0842)	0.14 <sub>ns</sub>
	$R_B$	0.957 (0.6762)	1.118 (0.1545)	0.52**

<sup>a</sup> Descriptions of the variable abbreviations can be found in Table 16.

<sup>b</sup> From the allometric model  $\Theta_i = \beta \Theta_p^\alpha$ . Standard errors for the parameter estimates are enclosed in brackets beside the estimate.

<sup>c</sup> \*, \*\* and *ns* indicate significant at  $P=0.05$ ,  $P=0.01$ , and not-significant, respectively.

**Table 20. Parameter estimates and associated  $R^2$  values for selected quackgrass allometric relationships at approximately 93 days after planting wheat (wheat harvest).**

Variable <sup>a</sup>		Parameter <sup>b</sup>		
Indep.	Depend.	$\beta$	$\alpha$	$R^2$ <sup>c</sup>
-----( <i>ln</i> )-----				
I	$R_W$	4.567 (0.1882)	2.258 (0.2064)	0.71**
	$R_l$	4.330 (0.1717)	2.399 (0.1884)	0.77**
	$H_W$	2.481 (1.1832)	8.299 (1.2981)	0.45**
	$H$	4.465 (1.4397)	9.131 (1.5795)	0.40**
	$R_B$	7.859 (0.1623)	2.369 (0.1780)	0.79**
S	$R_W$	-1.454 (0.3184)	1.006 (0.0704)	0.81**
	$R_l$	-2.084 (0.2569)	1.073 (0.0568)	0.88**
	$H_W$	-20.031 (2.2484)	3.789 (0.4977)	0.55**
	$H$	-20.583 (2.7408)	4.230 (0.6067)	0.50**
	$R_B$	1.458 (0.1985)	1.075 (0.0439)	0.93**
$S_D$	$R_W$	-2.149 (0.4658)	1.169 (0.1048)	0.72**
	$R_l$	-2.774 (0.4320)	1.235 (0.0972)	0.77**
	$H$	0.746 (0.3781)	1.242 (0.0851)	0.82**
	$R_B$	-25.651 (3.1700)	5.413 (0.7132)	0.54**
	$R_W$	-0.202 (0.2356)	0.869 (0.0609)	0.81**
$S_W$	$R_l$	-0.723 (0.2008)	0.920 (0.0519)	0.87**
	$H_W$	-15.915 (1.5531)	3.439 (0.4017)	0.60**
	$H$	-15.985 (1.9152)	3.843 (0.4953)	0.55**
	$R_B$	2.830 (0.1649)	0.920 (0.0426)	0.91**
	$R_W$	5.414 (0.1666)	1.191 (0.0699)	0.86**
$S_{\%}$	$R_l$	5.211 (0.1322)	1.256 (0.0555)	0.91**
	$H_W$	5.489 (1.3752)	4.329 (0.5770)	0.54**
	$H$	7.731 (1.7069)	4.742 (0.7166)	0.47**
	$R_B$	8.733 (0.1123)	1.243 (0.0471)	0.94**
	$R_l$	-1.405 (0.1474)	0.982 (0.0343)	0.94**
W	$H$	-17.698 (2.2547)	3.821 (0.5250)	0.52**
	$R_B$	2.197 (0.1186)	0.969 (0.0276)	0.96**
	$R_l$	-3.988 (0.3668)	1.137 (0.0751)	0.87**
$W_D$	$H$	-28.062 (3.8205)	5.401 (0.7822)	0.50**
	$R_B$	-0.352 (0.3342)	1.354 (0.0684)	0.89**

<sup>a</sup> Descriptions of the variable abbreviations can be found in Table 16.

<sup>b</sup> From the allometric model  $\Theta_i = \beta \Theta_p^\alpha$ . Standard errors for the parameter estimates are enclosed in brackets beside the estimate.

<sup>c</sup> \*, \*\* and ns indicate significant at  $P=0.05$ ,  $P=0.01$ , and not-significant, respectively.

biological significance and its accuracy is weak because it incorporates the measurement error ignored in the model determination.

Parameter  $\alpha$  is related to relative growth rates of  $\Theta_i$  in respect to  $\Theta_p$  ( $R\Theta_i/R\Theta_p$ ) (Whitehead and Myerscough, 1962). For all variables parameter  $\alpha$  differed significantly from sample date to sample date indicating change in relative growth rates during plant development (Tables 18,19 and 20). There was no *a priori* reason to suppose that the relative growth rates should remain proportional to one another. Similar variations in relative growth rate proportions in other species have been reported by others (Jolliffe *et al*, 1988; Stanhill, 1977a).

When  $\alpha=1$  the relative growth rates of the two variables are equal. Positive allometry is where  $\alpha>1$  and negative allometry is where  $\alpha<1$  (Richards, 1969). All three types of allometry were present and not all variables were consistent from sample date to sample date in any particular type. The lowest negative allometry  $\alpha$  value was 0.579 and occurred at 60 DAP with the independent variable  $S_{\%}$  and dependent variable  $R_w$  (Table 19). The highest positive allometry  $\alpha$  value was 9.131 and occurred at 93 DAP with the independent variable  $l$  and dependent variable  $H$  (Table 20). The greatest change in  $\alpha$  was a 2.9 fold difference for the independent variable  $l$  and the dependent variable  $R_w$  from 0.773, at 60 DAP to 2.258 at 93 DAP (Tables 19 and 20).

The allometric relationships for quackgrass in the pooled baseline stratified random sampling survey (validation data) are presented in Table 21. The  $R^2$  values for the allometric relationships ranged from 0.00 for the independent variable  $S_{\%}$  and dependent variables  $H_w$

**Table 21. Parameter estimates and associated  $R^2$  values for selected quackgrass allometric relationships at wheat harvest from the pooled baseline stratified random surveys.**

Variable <sup>a</sup>		Parameter <sup>b</sup>		
Indep.	Depend.	$\beta$	$\alpha$	$R^2$ <sup>c</sup>
----- <i>(ln)</i> -----				
I	$R_W$	3.586 (0.1739)	2.071 (0.4363)	0.11*
	$R_I$	3.155 (0.1549)	1.911 (0.3887)	0.11*
	$H_W$	-1.674 (0.7400)	15.022 (1.8571)	0.26**
	$H$	0.243 (0.8493)	16.609 (2.1313)	0.25**
	$R_B$	6.717 (0.1478)	2.003 (0.3708)	0.13**
S	$R_W$	-1.178 (0.1701)	1.035 (0.0402)	0.78**
	$R_I$	-1.157 (0.1472)	0.935 (0.0347)	0.80**
	$H_W$	-11.169 (1.6718)	1.242 (0.3952)	0.05**
	$H$	-9.954 (1.9084)	1.297 (0.4511)	0.04**
	$R_B$	2.407 (0.1253)	0.927 (0.0296)	0.84**
$S_D$	$R_W$	2.761 (0.1661)	0.076 (0.0440)	0.01 <sub>ns</sub>
	$R_I$	2.368 (0.1481)	0.080 (0.0392)	0.02 <sub>ns</sub>
	$H$	-7.883 (0.8269)	1.188 (0.2193)	0.13**
	$R_B$	5.829 (0.1414)	0.108 (0.0375)	0.04**
	$R_W$	-0.307 (0.1239)	0.935 (0.0323)	0.82**
$S_W$	$R_I$	-0.339 (0.1118)	0.835 (0.0291)	0.05**
	$H_W$	-10.271 (1.3321)	1.163 (0.3476)	0.05**
	$H$	-8.981 (1.5221)	1.205 (0.3972)	0.04**
	$R_B$	3.257 (0.1011)	0.817 (0.0263)	0.84**
	$R_W$	3.760 (0.1395)	0.273 (0.0325)	0.28**
$S_{\%}$	$R_I$	3.293 (0.1248)	0.245 (0.0291)	0.28**
	$H_W$	-5.972 (0.7693)	0.080 (0.1794)	0.00 <sub>ns</sub>
	$H$	-4.622 (0.8749)	0.050 (0.2039)	0.00 <sub>ns</sub>
	$R_B$	6.788 (0.1215)	0.231 (0.0283)	0.26**
	$R_I$	-1.106 (0.0817)	0.916 (0.0190)	0.93**
W	$H$	-8.347 (1.7821)	0.890 (0.4144)	0.02 <sub>ns</sub>
	$R_B$	2.551 (0.0775)	0.886 (0.0186)	0.93**
	$R_I$	2.272 (0.1664)	0.097 (0.0407)	0.03 <sub>ns</sub>
$W_D$	$H$	-8.404 (0.9426)	1.155 (0.2308)	0.12*
	$R_B$	5.724 (0.1588)	0.123 (0.0389)	0.05*

<sup>a</sup> Descriptions of the variable abbreviations can be found in Table 16.

<sup>b</sup> From the allometric model  $\Theta_i = \beta \Theta_p^\alpha$ . Standard errors for the parameter estimates are enclosed in brackets beside the estimate.

<sup>c</sup> \*, \*\* and <sub>ns</sub> indicate significant at P=0.05, P=0.01, and not-significant, respectively.

and  $H$ , to 0.93 for independent variable  $W$  and dependent variable  $R_B$ . The mean  $R^2$  for the allometric relationships from the validation data was 0.28 and is much less than the mean  $R^2$  of 0.73 from Table 20. The difference either reflects true differences in the quackgrass populations sampled or may be an artifact of the validation data using actual quadrat values, whereas the data in Table 20 was fit to the stratum averages.

The allometric relationships presented have practical value. If a farm operator determines a quackgrass infestation of 55 shoots  $m^{-2}$  then this paper presents the equations required to determine the infestation that might be present at harvest. Substitution into the equation  $S_3 = 6.227 + 2.479 (S_1)$  from Table 17 predicts that at harvest 143 shoots could be present. Further substituting this estimated harvest culm density of 143 shoots  $m^{-2}$  into the allometric equation  $R_B = 4.297 (S_3)^{1.075}$  indicates that there could be 892 rhizome buds associated with this infestation.

The example value of 55 shoots  $m^{-2}$  is the actual mean value for the 30 DAP in the dataset used to develop these allometric relationships. In addition the actual mean 93 DAP variable values for  $S$  and  $R_B$  were 144 and 890  $m^{-2}$ , respectively. Clearly, the models work well in estimating variable values from which the models were derived.

The allometric relationships can be linked to yield loss models presented elsewhere (Manuscript 2). For example substituting the harvest 3 quackgrass infestation of 143 shoots  $m^{-2}$  into the equation :

$$WY_{\%} = 96.4 \times (1 - ((0.113 \times S_3) / (100 \times (1 + ((0.113 \times S_3) / 203.4))))$$

results in an estimated wheat yield ( $WY_{\%}$ ) of 82 per cent of what would occur in a weed

free situation. The actual mean  $WY_{\%}$  in these surveys was 83 per cent.

It is important that allometric relationships be linked in stepwise fashion rather than merged with the yield-loss model into some unified equation. The mathematically unsound nature of such a merged allometric yield-loss model in most situations has been discussed by Jolliffe *et al* (1988).

The cross-utility of the allometric relationships was tested using the models based on the 93 DAP data (Table 20) and comparing to the independent validation survey allometric relationships (Table 21). For all variables, the models and model parameter  $\alpha$  differed significantly between the two datasets. The allometric relationships were specific to the specific environment from which they were derived. Other researchers have demonstrated the dependence of allometry on environmental conditions including population density, temperature and soil nutrients (Jolliffe *et al*, 1988; Stanhill, 1977b). The implication of this finding is that there is no "universal" allometric equation at any particular time for quackgrass growing with wheat. Until allometric models can account for environmental variation they will be unable to provide information on the underlying biology.

The following example will illustrate the scale of the errors that might result in using an allometric model developed for one dataset on a different dataset. The mean  $S$  at 93 DAP in the pooled dynamic stratified random sampled was 144  $m^2$ . Substituting into the equation

$$R_B = 11.101 ( S )^{0.927}$$

gives an estimated  $R_B$  of 1,011  $m^2$ . The actual mean  $R_B$  value was 890  $m^2$ . The allometric

model from the different dataset overestimated the rhizome buds present by 14 per cent. However, given that the standard error of means for the mean quackgrass variable values were often around 18 per cent (Manuscript 2), then an allometric model that is "off" by 14 per cent might be considered satisfactory for many practical applications.

The damage caused in wheat due to quackgrass may be assessed in relation to existing and future crops. Estimation of impact on the current crop is dependent on wheat yield response to quackgrass and has been addressed elsewhere (Manuscript 2). The damage to future cropping cycles is related to quackgrass carryover into future cycles and simple models for estimating this potential have been expressed in this manuscript. However, the conventional allometric model utilized in this manuscript is inherently limited in applicability due to time dependence and restricted applicability to the specific environmental and biological conditions for which it was derived. To avoid such limitations and be universal in applicability allometric models for quackgrass will have to be more sophisticated accounting for environmental and temporal variation.



**MANUSCRIPT 4**

## **A Deterministic Empirical Model of Quackgrass (*Elytrigia repens*)**

### **Interference in Spring Annual Crops**

**Abstract.** The amalgamation of two recent developments in quackgrass research has enabled the development of a discrete empirical deterministic model of quackgrass interference and infestation for instructional purposes. One development has been the determination of a set of models relating spring quackgrass infestation to yield losses in hard red spring wheat, flax, and polish canola. A second development is the determination of an allometric model relating spring quackgrass culm number to quackgrass rhizome bud numbers in the fall. These yield loss and allometric models have been linked in a multi-year spreadsheet model. Spreadsheet simulations were run to determine the influence of various quackgrass infestations and crop management practices on long term infestation, crop yield loss and simple economic impact. Simulations indicate that crop rotations, particularly when influencing herbicide selection, were a primary determinant of the level of quackgrass infestation. Sensitivity analysis determined that model output was most dependent on the input parameters herbicide kill, bud survival and buds emerging. Using the quackgrass spreadsheet model for simulation has demonstrated the utility of a model, based on simple hardware and software,

for weed control decisions.

Nomenclature: Quackgrass, Elytrigia repens L. Nevski #<sup>11</sup> AGGRE; wheat, Triticum aestivum L. 'Katepwa'; flax, Linum usitatissimum L.; 'polish' canola, Brassica rapa L..

Additional index words. Agropyron repens L. Beauv., Wheat, Triticum aestivum, Flax, Linum usitatissimum, canola, Brassica campestris, competition, modelling, rectangular hyperbola, AGGRE, allometry.

## INTRODUCTION

Considering that quackgrass has been one of the major troublesome and economically important weeds in temperate agriculture, there has been surprisingly little information collected on the effects of quackgrass on yield loss in small grain cereals and oilseeds (Wolcott and Carlson, 1949; Cussans, 1970; Rioux, 1982; Rauber and Bottger, 1984; Wilcox and Morrison, 1988; Chikoye, 1990; Morrison *et al*, 1990; O'Donovan, 1991; Melander, 1993). Although many herbicides have been evaluated for quackgrass control only rarely have the associated quackgrass densities been recorded numerically. Even where the data is available the results suggest the yield losses caused by a particular quackgrass infestation can be highly variable (Anonymous, 1989). This variability can be attributed to differences in environment, crop management, genotypes, and assessment methods.

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<sup>11</sup>Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Weed Sci. 32, Suppl. 2. Available from WSSA, 309 West Clark Street, Champaign, IL 61820.

After reviewing the distribution and economic importance of quackgrass in Canada, Ivany (1985) concluded that there was inadequate existing data for calculating economic yield losses due to quackgrass in Canada. Since Ivany's review several hyperbolic models relating yield loss in canola, flax and wheat to quackgrass spring shoot infestation levels have been developed (Chikoye, 1990; O'Donovan, 1991; Manuscript 2). Moreover, the temporal relationship between quackgrass shoot number and the allometry between quackgrass shoot number and rhizome bud number at harvest, while exposed to wheat interference, has also been determined (Manuscript 3).

In eastern Canada yield loss in barley in relation to quackgrass infestation has been determined using a linear model (Rioux, 1982). This model determined that 10 quackgrass shoots  $\text{m}^{-2}$  would reduce the yield of barley by 1.6% and that 100 shoots  $\text{m}^{-2}$  would reduce the yield of barley by 16%. Wheat yield losses due to quackgrass in eastern Canada have also been modelled using a linear model (Leroux, 1990). This model determined that a spring infestation of 10 quackgrass shoots per  $\text{m}^{-2}$  would reduce the yield of wheat by 4.8% and that 100 shoots  $\text{m}^{-2}$  would reduce the yield of wheat by 48%. The applicability of these models in western Canada is questionable.

Despite the availability of effective herbicides quackgrass has proven to be very tenacious and difficult to eradicate. Eradication of quackgrass through use of herbicides is difficult to achieve and may not be economically justifiable or practical on many farms. An integrated management program which maintains quackgrass population levels at an economic threshold density and involving all available methods of quackgrass management may be a more cost effective approach. Establishing an economic threshold density implies that weeds

are left in the field and that the future impact of the weeds also needs to be assessed when establishing economic thresholds (Maxwell, 1992).

Most weed researchers have limited research resources available to them. Limited resource availability constrains the determination of integrated management strategies for quackgrass management because of the limited number of treatments that can be evaluated in the field in any particular year. However, by the application of models which integrate currently available information, it is possible to evaluate an "unlimited" number of integrated management scenarios as well as to identify priority research topics for any future in-field research.

Some quackgrass population models have been developed in the United Kingdom (Mortimer *et al*, 1978; McMahon and Mortimer, 1980; Mortimer *et al*, 1980; Mortimer, 1983). These models have been reported as incomplete by their developers, fail to link the quackgrass population to crop yield losses, and have limited applicability under western Canadian conditions. A quackgrass model is also being developed in Quebec, Canada, (Cloutier *et al*, 1990) but, being based on eastern Canadian conditions, it is expected that this model will also have limited applicability in western Canada.

In order to estimate the impact of quackgrass interference on yield losses in annual crops grown in western Canada the amalgamation of yield loss models for canola, flax and wheat with the allometric models of quackgrass shoots and buds has been undertaken in an integrated spreadsheet simulation model. The spreadsheet simulation model is limited in utility because it uses site specific equations and subjective model user assumptions to provide deterministic results. This limitation means that the objective of the modelling activity

described in this manuscript is not to develop recommendations for specific fields using economic risk analysis. Instead, the simulation model objectives are as follows: (1) to present a simple approach for demonstrating the long term economic impact of quackgrass control, (2) to illustrate the relative impact of various management decisions on the model system, and (3) to determine areas of knowledge weakness for which there should be a priority placed in future quackgrass research.

## **MATERIALS AND METHODS**

### **Spreadsheet Model Design**

#### **Modelling Approach**

Many models of weed population dynamics and control use transition or Leslie matrixes to summarize the mathematical relationships involved (Cousens *et al*, 1987; Maxwell *et al*, 1988). This transition matrix approach has been successfully used in quackgrass modelling (McMahon and Mortimer, 1980; Mortimer *et al*, 1980; Mortimer and Putwain, 1981). Whilst these matrix models have been useful, they are limited in that the fluxes (rate of change) between the various plant stages and their components are not constant over time as is assumed in the matrix approach. Ideally, flux values need to be dynamic and vary according to different conditions in the biotic and abiotic environment. To address this concern, wherever possible the spreadsheet model presented in this paper has been developed using a dynamic flux approach instead of a transition matrix fixed flux approach. The matrix approach may be satisfactory for species with non-overlapping generations and one-form of reproduction but for species such as quackgrass, with overlapping generations and iteroparous

reproduction, more elaborate techniques are required.

Models are developed with either scientific advancement, prediction, or instruction as the primary objective (Penning de Vries, 1977). The primary objective of this modelling activity was to develop a model for instructional purposes. For instructional purposes the model has to be both easily usable as well as easily communicatable. To achieve this goal the model was kept simple and was developed on a common PC-based Spreadsheet Software package<sup>12</sup> for ease of use and transferability. The quackgrass spreadsheet model is available to interested individuals from the Department of Plant Science at the University of Manitoba.

### **Annual Model System**

Model development requires a thorough comprehension of the interactions that occur in the model system. One way of expressing the model system interactions is the use of flux diagrams (Sagar and Mortimer, 1976). A diagrammatic model of the annual life history variables and fluxes considered in the quackgrass-annual crop model system used in the spreadsheet model is presented in Figure 8. The model system flux parameters are as follows:

Fb = The number of rhizome buds produced by the vegetative shoots

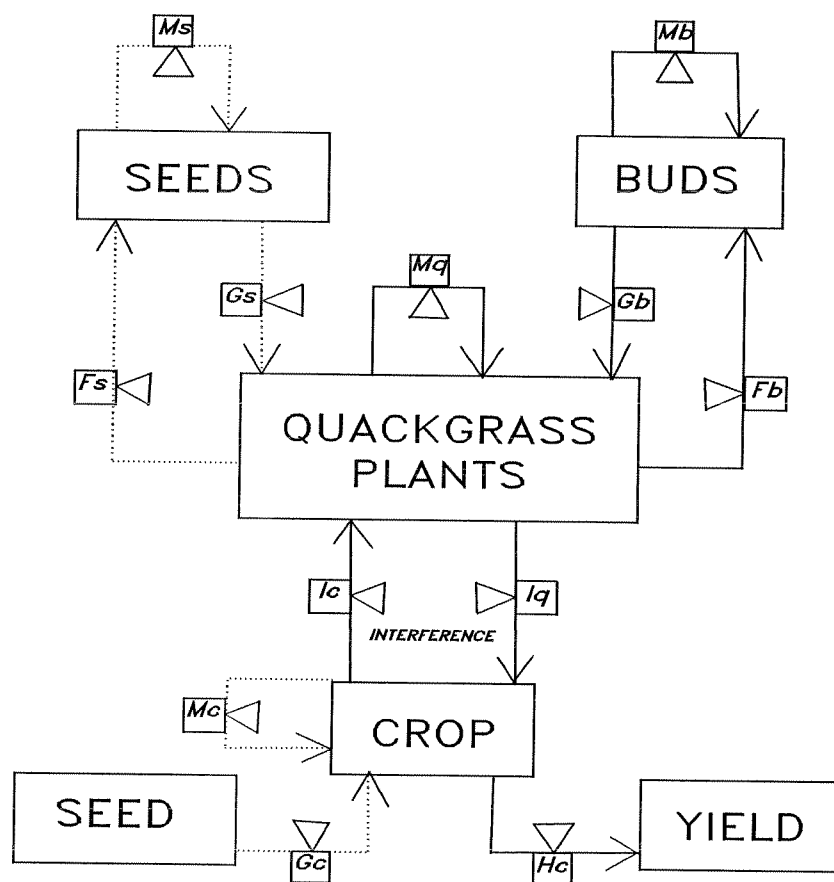
Fs = The number of seeds that enter the seed bank

Gb = The number of rhizome buds sprouting to produce vegetative shoots

Gc = The number of crop seed germinating into seedlings

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<sup>12</sup> Lotus 123, v 3.1



**Figure 8.** Diagrammatic representation of the annual model system considered in the development of the spreadsheet model, including life history variables and fluxes.



$G_s$  = The number of seeds in the seed bank that germinate to produce seedlings

$H_c$  = The commercial harvest yield

$I_c$  = Interspecific interference of the crop on the quackgrass

$I_q$  = Interspecific interference of quackgrass on the crop

$M_b$  = The number of rhizome buds that remain viable in the soil

$M_c$  = The number of plants surviving to maturity

$M_s$  = The number of seeds that remain viable in the seed bank

$M_q$  = The number of vegetative shoots surviving

### **Spreadsheet Model Assumptions**

The spreadsheet model uses the assumption that  $G_s$  in the model system is equal to zero. It is known that seed produced on quackgrass populations in mixed genotype populations is likely to be viable and produce at least some seedlings (Williams and Attwood, 1970). However it is also known that seedling quackgrass shoots are less vigorous than shoots produced from rhizomes (Wilcox, 1987). The spreadsheet model assumes that seedling quackgrass would generally be unable to survive under a well established crop. Additionally, any that might survive are expected to be an insignificant component of the population. Mortimer *et al* (1980) in field measurements of plots of pure quackgrass in Britain determined that less than 1 in 10,000 of the seeds in the seed bank emerged to form mature quackgrass plants.  $F_s$  and  $M_s$  from the model system have also been ignored in the

spreadsheet model because of the assumption that  $G_s$  is zero. The importance of quackgrass seed production and emergence under crop interference towards long term infestation has not been investigated in Canada.

The spreadsheet model assumes complete survival of vegetative quackgrass shoots ( $M_q$ ) in the model system. Density dependent mortality is known to occur in plants and has been included in yield-density models (Firbank and Watkinson, 1985). Density dependent mortality generally does not occur in weeds at the infestation densities typically observed in managed fields (Firbank and Watkinson, 1985). Moreover, clonal species such as quackgrass are known to avoid density dependent mortality (Hutchings, 1979; Pitelka and Ashmun, 1984). Mortimer (1984) reported that in pure stands of quackgrass natural mortality was only 5% per annum. In the spreadsheet model the maximum number of quackgrass shoots that can be present at harvest has been limited by the software program coding to 500 shoots  $m^{-2}$ . This is roughly the maximum number that was observed in any of the cropped fields investigated by Wilcox (Manuscript 2).

In the model system  $M_q$  is assumed to have a dynamic aspect. The temporal relationship between number of quackgrass shoots at assessment time and at crop harvest has been described in the spreadsheet model using a linear regression equation developed from the results of quackgrass shoot number changes over time while in competition in wheat (Manuscript 3). A linear model of the form;

$$\%D = 2.50 + 1.061 (DAP)$$

where  $\%D$  is the final stand density percentage and  $DAP$  is the number of days after

sowing the crop that the assessment is made, was developed for the purposes of this spreadsheet using data from previous research (Manuscript 2). Although the linear model was derived for quackgrass competing with wheat in the spreadsheet model, it is applied to all three crops. The generalization that increases in quackgrass shoot number over time is the same for all crops may result in the spreadsheet model tending to underestimate the extent of quackgrass shoot development under the less competitive flax and overestimating the extent of quackgrass shoot development under the more competitive canola crop. The generalized equation was determined to accurately predict harvest infestation levels of quackgrass in one of three of Chikoye's (1990) flax sites (data not presented). However, given that the temporal progression of quackgrass shoot development is as dependent on other factors such as quackgrass genotype and micro-environment, and that this spreadsheet model is intended for instructional purposes only, it was decided that any crop specificity of quackgrass shoot progression could be ignored. There is little information on comparative quackgrass shoot development dynamics under various crops.

The spreadsheet model also allows the model user to select an in-crop "herbicide kill factor". In Manitoba flax and canola producers have several post-emergent herbicide options for quackgrass suppression (fluazifop-p-butyl, sethoxydim, and quizalofop ethyl). In the spreadsheet model the estimated quackgrass shoot numbers at harvest are simply reduced by the percentage determined by the model user for each crop/herbicide combination.

Rhizome bud numbers produced are derived in the spreadsheet model using the allometric relationship between the predicted quackgrass final shoot number and rhizome bud numbers. This allometric relationship was determined in infested wheat fields in previous

research (Manuscript 3). The allometric equation used in the spreadsheet model is of the form;

$$R_b = 1.458 (S_3)^{1.075}$$

where  $R_b$  is the rhizome bud number per square meter under the soil surface and  $S_3$  is the number of above ground shoots per square meter. In the spreadsheet model the same allometric relationship is applied to quackgrass infesting canola and flax as that described for wheat. The justification and the potential errors associated with the generalization of quackgrass growth pattern under wheat to that in flax and canola has been outlined previously. Allometry between quackgrass plant parts is very site specific (Manuscript 3) and the nature of that specificity has not been adequately studied.

In the spreadsheet model the combined impact of rhizome bud viability in the soil ( $M_b$ ) and the number of rhizome buds sprouting to form new rhizome shoots ( $G_b$ ) from the model system are assumed to be accounted for in the temporal component of the equation described previously for  $M_q$ .

Interference between the crop and quackgrass is described by the fluxes  $I_c$  and  $I_q$ . The impact of interspecific interference by the crop on quackgrass ( $I_c$ ) is assumed in the spreadsheet model to be accounted for in the quackgrass growth equations described previously. The generalization of quackgrass growth under wheat competition to quackgrass growth under canola and flax competition limits the applicability of the spreadsheet model.

In the spreadsheet model, crop specific yield loss equations are used to describe the

impact of interference by quackgrass on the crop (Iq). For estimating wheat yield losses the equation determined by Wilcox (Manuscript 2) is used, and is of the form

$$Y_w\% = 98.7 \{1 - 0.433 (Q_s)/(100(1 + 0.433 (Q_s)/193.7))\}.$$

To estimate yield losses in flax the equation determined by Chikoye (1990) has been used, and is of the form

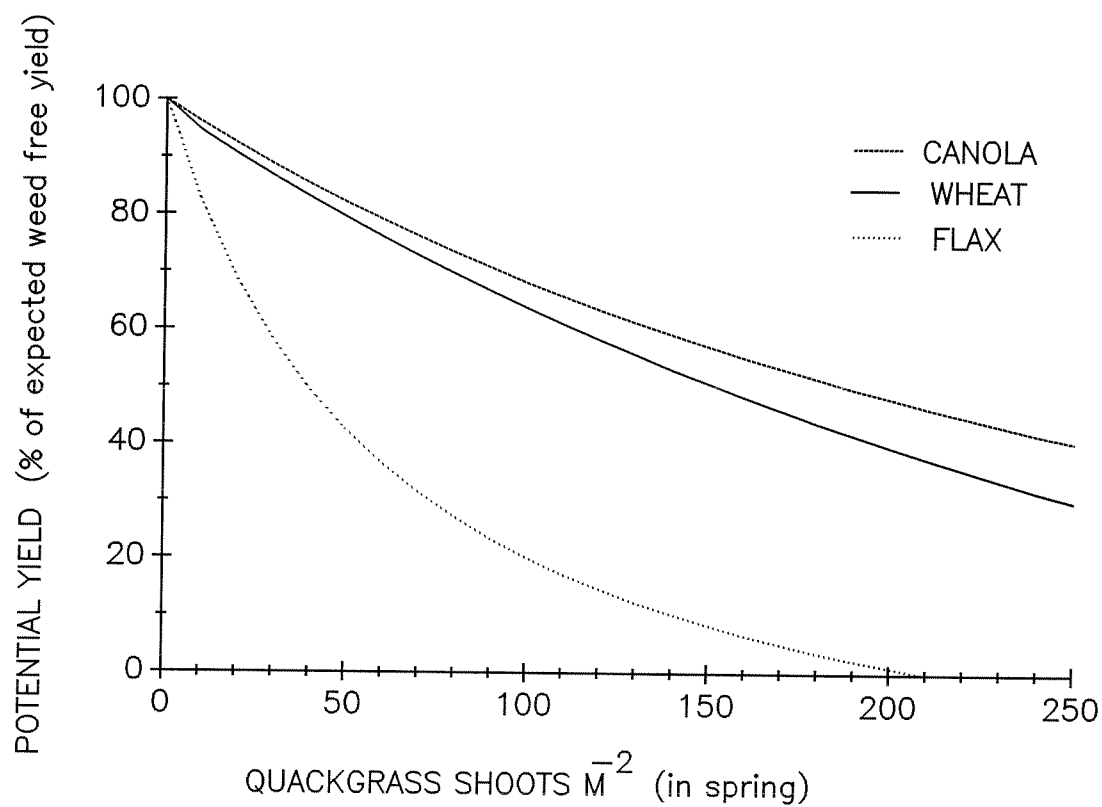
$$Y_f\% = 100 \{1 - 2.07 (Q_s)/(100(1 + 2.07 (Q_s)/130))\}.$$

Yield loss in polish canola has been described by O'Donovan (1991) and is of the form

$$Y_c\% = 100 \{1 - 0.41 (Q_s) / (100(1 + 0.41 (Q_s)/141))\}.$$

In these equations  $Q_s$  is the mean density of quackgrass shoots infesting the crop approximately 30 days after planting and  $Y_i\%$  is the predicted crop yield as a percentage of expected quackgrass-free yield.  $Y_i\%$  is also equivalent to  $H_c$  in the diagrammatic representation of the model system. A graphical illustration of the yield loss response curves for the three crops is presented in Figure 9.

In the crop component of the model system the number of crop seeds germinating into seedlings ( $G_c$ ) and the number of plants surviving to maturity ( $M_c$ ) are assumed to be irrelevant in determining crop yield in the spreadsheet model. It is known that crop density can be important in determining final crop yield (Firbank and Watkinson, 1985; Hume, 1985). However in most cropping situations optimum stand establishment can be assumed and the spreadsheet model assumption of negligible crop density impact is justifiable.



**Figure 9.** An illustration of the relationship between crop yield and density of quackgrass shoots 30 days after planting for wheat, flax and polish canola.

### **Multi-Year Model System**

The multi year model used in the spreadsheet model is simply a series of linked annual models. The temporal link between each year used is the quackgrass "bud cycle" applied over winter. A diagrammatic representation of the over winter linkage submodel and influencing factors is presented in Figure 10. The temporal linkage flux parameters were described as follows:

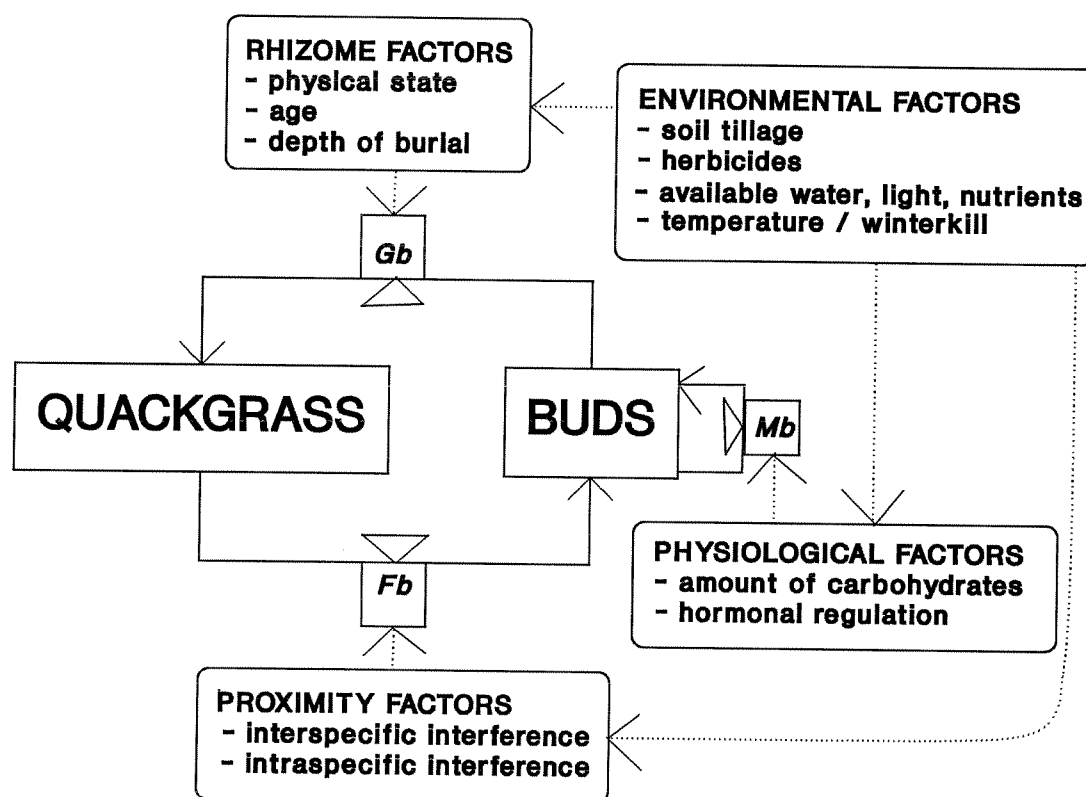
$Fb$  = The number of rhizome buds produced by the vegetative shoots after crop harvest.

$Gb$  = The number of rhizome buds germinating to produce vegetative shoots in the spring.

$Mb$  = The number of rhizome buds that remain viable in the soil over winter.

### **Spreadsheet Model Temporal Linkage Assumptions**

In the spreadsheet model it is assumed that the number of rhizome buds produced in the fall after harvest ( $Fb$ ) is negligible or else off-set by winterkill ( $Mb$ ). The spreadsheet model also allows the model user to select rhizome bud mortality ( $Mb$ ) over winter. The impact of preharvest application of glyphosate on subsequent spring quackgrass bud viability can be simulated by modifying  $Mb$  to reflect the expected mortality from the preharvest treatment. Although the temporal pattern of bud formation and mortality through fall, over the winter, and into the spring prior to seeding has not been the focus of much investigation to date, researchers who have compared spring rhizome bud numbers to that in the previous



**Figure 10.** Diagrammatic representation of the overwinter linkage model system considered in development of the spreadsheet model (adapted from Fawcett, 1985)



fall usually observe little if any net mortality of rhizome buds (Chikoye, 1990). Further investigation of the temporal dynamics of quackgrass rhizome bud demographics in non-crop growing periods is required.

The extent of spring bud germination (Gb) in the spreadsheet model is left to the discretion of the model user. In non-herbicide treated fields subjected to standard fall and spring tillage operations in Manitoba, rhizome bud emergence was on the order of 20 to 30% (Wilcox- unpublished data). From studies with quackgrass treated with recommended rates of sethoxydim Chikoye (1990) determined that this treatment increased viable bud germination to 60 %. Chikoye (1990) indicates that this increased bud germination following herbicide treatment may be an artifact of reduced bud crowding and not a primary response to herbicide treatment. Other researchers have similarly observed increases in viable bud germination percentage following systemic herbicide treatments (Harper and Decker, 1988).

Yield loss percentage in the spreadsheet model is determined as

$$100 - Y_i\%$$

where  $Y_i\%$  the predicted crop yield as a percentage of the expected weed free yield. The economic value of the derived crop yield loss is then determined based on expected crop yield and price predefined by the model user on the input section of the spreadsheet. An illustration of the spreadsheet input and output screens is presented in Figures 11 and 12, respectively.

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ANNUAL CROP – QUACKGRASS INTERFERENCE CALCULATOR

MODEL INPUT			
<b>CROP</b>			
<b>CROP CHARACTERISTICS</b>			
	<b>WHEAT</b>	<b>FLAX</b>	<b>P. CANOLA</b>
<b>CROP YIELD</b>	32.8 (bu/A)	17.8 (bu/A)	18.1 (bu/A)
<b>CROP PRICE</b>	\$3.00 (\$/bu)	\$6.00 (\$/bu)	\$6.50 (\$/bu)
<b>CROP ROTATION</b>			
	<b>YEAR 1</b>	<b>YEAR 2</b>	<b>YEAR 3</b>
<b>CROP GROWN</b>	C	W	F
(USE: C = POL. CANOLA, F = FLAX, W = RS WHEAT)			
<b>QUACKGRASS</b>			
<b>INITIAL INFESTATION</b>			
YEAR 1 QUACKGRASS SHOOTS/sqM <input type="text" value="10"/> AT			
<input type="text" value="30"/> DAYS AFTER PLANTING			
(Model based on 30 DAP)			
<b>WINTER SURVIVAL OF BUDS</b>			
	<b>BETWEEN YEARS 1 and 2</b>	<b>BETWEEN YEARS 2 and 3</b>	
<b>PER CENT SURVIVAL</b>	<input type="text" value="95"/> (95 %)	<input type="text" value="95"/> (95 %)	
<b>SPRING BUD EMERGENCE</b>			
	<b>SPRING 2</b>	<b>SPRING 3</b>	
<b>PER CENT OF BUDS EMERGING</b>	<input type="text" value="60"/>	<input type="text" value="25"/>	
(25% if no herbicide, 60% if herbicide applied)			
<b>IN-CROP HERBICIDE KILL FACTOR</b>			
	<b>WHEAT</b>	<b>FLAX</b>	<b>CANOLA</b>
<b>% MORTALITY</b>	<input type="text" value="0"/>	<input type="text" value="90"/>	<input type="text" value="95"/>

**Figure 11.** Example of the quackgrass spreadsheet model input screen.

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ANNUAL CROP – QUACKGRASS INTERFERENCE CALCULATOR

MODEL OUTPUT				
<b>QUACKGRASS</b>				
	YEAR 1	YEAR 2	YEAR 3	
SPRING SHOOT NUMBERS	10	5	33	
SHOOT NUMBERS AT HARVEST	2	26	10	
BUD NUMBERS AT HARVEST	9	140	49	
<b>CROP</b>				
	YEAR 1 C	YEAR 2 W	YEAR 3 F	TOTAL
YIELD LOSS PER CENT	4%	3%	45%	
YIELD LOSS \$ VALUES	\$4.68	\$3.31	\$48.09	\$56.08

**Figure 12.** Example of the quackgrass spreadsheet model output screen.

## Model Simulations

The spreadsheet model allows its users to examine the impact of initial quackgrass infestations, crop rotation and of herbicide application on later quackgrass infestations and crop yield. Rotations are limited to various three year combinations of polish canola, flax and wheat. Herbicides that can be simulated are both post-emergent products and pre-harvest systemic products. The model user does not specify a herbicide treatment by product name, instead the model user indicates the expected in-crop herbicide kill-factor (post-emergent products) or by the herbicide's real winter survival impact (pre-harvest products). The impact of various spring and fall tillage practices can also be simulated by the model user adjusting the winter bud survival parameter to reflect the impact of these treatments. The impact of herbicides and tillage practices on subsequent spring bud emergence is also established by the model user.

A wide range of scenarios that can be simulated using this model. For the purposes of this manuscript only a limited number of scenarios are presented to illustrate some of the capabilities of the model. Crop yields and prices used in the simulations are typical of those currently determined for each crop in Manitoba. These were tonnes/hectare (bu/acre) yields of 2.17 (32.8), 1.12 (17.8) and 1.02 (18.1) and \$CDN/tonne (\$CDN/bu) prices of \$110.23 (\$3.00), \$236.21 (\$6.00) and \$286.60 (\$6.50) for wheat, flax and polish canola, respectively. Initial quackgrass infestation levels of 10, 60 and 160 shoots/m<sup>2</sup> were selected in the simulations to represent the "typical" low, medium and high quackgrass shoot infestation levels in these crops in Manitoba. In Manitoba, weed surveys have determined that the average quackgrass density in occurrence fields is 10 shoots m<sup>-2</sup> with a maximum density of

infestation in these surveys of 176 shoots m<sup>-2</sup> (Thomas and Donaghy, 1991).

### **Sensitivity Analysis**

Sensitivity analysis can be used to indicate model changes that would optimize a model. Sensitivity analysis is conducted by changing the value of one parameter within a reasonable range and comparing the output with what was expected. Maxwell *et al* (1988) determined sensitivity values in their sensitivity analysis of a leafy spurge development model. Large sensitivity values indicated which parameters had disproportionably large effects on the model output. Sensitivity analysis was conducted on the quackgrass model parameters using the approach of Maxwell *et al* (1988). In this approach the sensitivity value is calculated as follows:

$$\text{Sensitivity Value} = (\nabla \text{output/output})/(\nabla \text{parameter/parameter}).$$

## **RESULTS AND DISCUSSION**

The quackgrass spreadsheet model is able to simulate the long term impact of a wide range of initial quackgrass infestations under various crop management regimes. Although the spreadsheet model is limited to a three year period, longer rotation periods could be investigated by allowing the third year spring output data to be entered as the first year in the spreadsheet model. Running the spreadsheet model twice in this fashion would allow

investigation of a five year rotation. Similarly, running the spreadsheet model three times would allow investigation of a seven year rotation. For the purposes of this paper analysis and discussion has been limited to three year rotations simulations.

One practical objective of many weed modelling activities is to determine the economic weed threshold. An economic weed threshold level is the infestation level at which a particular weed management practice "cost" can be recovered by the corresponding production increase. Realistically an economic weed threshold can not be calculated with this spreadsheet model. A weed threshold economic calculation is dependent not only on fixed costs (e.g. herbicide cost and crop value) but also variable costs (scale of operation) and producer psychology (*viz*: risk averseness, environmental/social attitudes) (Mortimer, 1983). These parameters have not been factored into this spreadsheet model.

### **Quackgrass Infestation**

The long-term infestation and crop yield loss impact of various initial quackgrass infestations simulated by the quackgrass spreadsheet model is presented in Table 22. In all the simulations run, except those where quackgrass infestation was limited by the spreadsheet model, there was a positive relationship between spring shoot number increase in first year and the amount of quackgrass infestation level present in the third year.

One of the limitations of the spreadsheet model is that it assumes a uniform level of quackgrass infestation across a field. Quackgrass populations are usually aggregated. Assuming a uniform estimation can lead to an overestimation of loss when the reality is otherwise although the error at weed densities where practical weed control decisions would

**Table 22. Spreadsheet model derived crop yield loss value and final quackgrass infestations at selected initial quackgrass infestations after 3 years of selected management practices.**

Rotation <sup>b</sup>	Herbicide <sup>c</sup>	Initial Infestation 30 DAP	Quackgrass <sup>a</sup>			Crop Yield Loss Value (3 Year Total)
			Spring Shoot Numbers	Shoot Numbers At Harvest	Bud Numbers At Harvest	
			(year3)			
C-W-F	y	10	33	10	49	\$56.08
	y	60	100	26	143	\$120.30
	y	160	254	64	378	\$183.78
	n	10	208	500	3424	\$131.75
F-W-C	y	10	52	7	36	\$46.51
	y	60	198	25	138	\$148.22
	y	160	500	63	367	\$242.04
	n	10	208	500	3424	\$101.97
C-W-W	y	10	33	96	580	\$22.21
	y	60	100	261	1699	\$70.50
	y	160	254	500	3424	\$146.15
	n	10	208	500	3424	\$85.81
W-W-C	y	10	208	26	145	\$88.71
	y	60	500	63	367	\$188.75
	y	160	500	63	367	\$247.26
	n	10	208	500	3424	\$88.27
F-W-W	y	10	52	143	894	\$45.46
	y	60	198	500	3424	\$146.36
	y	160	500	500	3424	\$242.15
	n	10	208	500	3424	\$100.18
W-W-F	y	10	208	53	305	\$132.43
	y	60	500	125	774	\$197.27
	y	160	500	125	774	\$255.77
	n	10	208	500	3424	\$132.43
W-W-W	y	10	32	94	566	\$28.31
	y	60	141	362	2419	\$102.55
	y	160	308	500	3424	\$196.57
	n	10	208	500	3424	\$86.48

<sup>a</sup> Quackgrass shoot numbers are limited in the spreadsheet model to 500/m<sup>2</sup> and in turn rhizome bud numbers are also limited to 3424/m<sup>2</sup>.

<sup>b</sup> C = Polish Canola, W = Red Spring Wheat, F = Flax.

<sup>c</sup> n = no herbicides applied, y = herbicides applied (In rotations with broadleaved crops included, herbicides only applied postemergent in broadleaved crop years. In continuous wheat preharvest herbicide applied in all years).

be made is likely to be minimal (Brain and Cousens, 1990). Assuming uniformity also means that quackgrass dispersal is ignored in the spreadsheet model even though it is known to be an important process in weed competition (Maxwell and Ghera, 1992).

Third year spreadsheet model output values were not proportional to the initial quackgrass infestations. Increasing the initial quackgrass infestation from 10 to 60 shoots  $\text{m}^{-2}$  caused only a 2.4 to 3.9 increase in third year harvest quackgrass shoot numbers and a 1.5 to 3.6 increase in yield loss dollar values. Increasing the initial quackgrass infestation from 60 to 160 shoots  $\text{m}^{-2}$  resulted in up to a 2.5 fold increase in third year harvest quackgrass numbers and a 1.3 to 2.1 increase in yield loss dollar values.

From a practical standpoint the spreadsheet model simulations demonstrate that a producer with twice the quackgrass infestation of another does not necessarily have twice the problem.

### **Crop Rotations**

The long-term infestation and crop yield loss impact of various selected wheat, canola and flax rotations as simulated by the quackgrass spreadsheet model is presented in Table 22. In these rotations, except where noted, it is assumed that post-emergent quackgrass herbicides were applied in flax and canola but not in wheat. Of the rotations simulated, when there was a low initial quackgrass infestation (10 shoots  $\text{m}^{-2}$ ) the least quackgrass infestation and economic yield loss after three years occurred with a canola-wheat-flax rotation. At a high initial quackgrass infestation (160 shoots  $\text{m}^{-2}$ ) the simulations indicate that the least quackgrass infestation and economic yield loss after three years will also occur with a canola-



wheat-wheat rotation. The simulation that resulted in the highest infestation of quackgrass and highest economic yield loss after three years was the wheat-wheat-flax rotation.

From a practical standpoint the spreadsheet model demonstrates how long-term quackgrass infestation build up can be influenced by crop rotation, particularly when the rotation influences herbicide application.

### **Herbicide Impact**

The long-term infestation and crop yield loss impact of various selected postemergent and preharvest herbicide treatments as simulated by the quackgrass spreadsheet model is presented in Table 22. The spreadsheet model simulations assumed that postemergent products result in 90% control in flax and 95% control in canola as well as increase bud emergence of the remaining viable buds in the following spring from 25% to 60%. For preharvest application of glyphosate in wheat the simulations assumed that the resulting overwinter survival of quackgrass buds drops from 95% to 15% and that there was an increase in bud emergence of the remaining viable buds from 25% to 60%. This assumption is based on results from field testing of these herbicides in western Canada. Implicit in these assumptions is that eradication of quackgrass using herbicides cannot occur in this spreadsheet model system.

The simulation assumed herbicides were only applied postemergent on broadleaved crops in the simulated rotations involving broadleaved crops and preharvest in the continuous wheat scenario. The spreadsheet model simulations indicated that with low initial year spring quackgrass infestations (10 shoots  $\text{m}^{-2}$ ) herbicide application either as a postemergent

treatment in the broadleaved crop or as a preharvest treatment in wheat would not always be economically justified within the three year rotation. For the purposes of this manuscript an economically justified management practice will be defined as one which causes the monetary value of the crop over the long term to exceed the monetary investment in the management practice. For example in the flax-wheat-wheat simulation the net return for applying herbicide in the flax year was \$135.16/ha {\$54.72/a (\$100.18-\$45.46)}. Assuming that the cost of chemical would not exceed \$95.27/ha (\$38.57/a) and that the typical application cost would be \$3.70/ha (\$1.50/a) then the simulation indicates that the producer in this simulation would have profited by \$36.19/ha {\$14.65/a (\$54.72 - \$40.07)} by applying herbicide in the flax year. In contrast in the wheat-wheat-flax simulation there was no net return from herbicide application in the flax year. It should be noted that by extending the rotation period analyzed, using spot applications, and/or using different herbicide cost/crop price combinations the simulation outputs and conclusions could change substantially. Additionally it should also be noted that where the table indicates it was economical to apply herbicides when the initial infestation was 10 shoots m<sup>-2</sup>, logic dictates that it would be even more economically justified at higher initial quackgrass infestation densities.

From a practical standpoint, the spreadsheet model simulations indicate that even when quackgrass eradication does not occur, considering fixed costs at current crop/herbicide prices, it is usually profitable over the long-term, to apply currently recommended herbicides at most infestation levels.

## **Sensitivity Analysis**

The results of a sensitivity analysis of the impact of changing various spreadsheet model input parameters is presented in Table 23.

Sensitivity analysis of the simulations indicates that the spreadsheet model output is most sensitive to the parameters herbicide kill, percent survival and percent buds emerging and least sensitive to the initial infestation and days after planting. These parameters with the highest sensitivity are also those subjectively estimated by the model user. Given the sensitivity of the model to these parameters, and the fact that there is little information on these parameters future quackgrass model research should focus on developing more sophisticated representation of these parameters in the model system.

The only model output to be sensitive to the parameters crop yield and crop price was the yield loss dollar value. Given that these are independent parameters within the spreadsheet model this observation was not unexpected.

Fawcett (1985) determined that his AGROMOD quackgrass management model was most sensitive to crop rotation. The mathematical approach used in this sensitivity analysis does not allow an assessment of the relative sensitivity of the spreadsheet model to changing crop rotation. However, the simulation results listed in Table 22 indicate a sensitivity of the spreadsheet model to crop rotations particularly when comparisons are made between rotations including and excluding flax.

## **Validation**

Validation of the spreadsheet model as a whole using independent data was not

conducted. However, validation of several of the spreadsheet model subcomponents have been done previously (Manuscript 2), and these subcomponents were generally determined to be site specific. On that basis it is expected that the spreadsheet model would also be site specific. Further refinement of the subcomponents of the spreadsheet model itself would be required before the model is used for purposes other than instruction.

### **Suggested Future Enhancements**

In reviewing the quackgrass model system and developing the spreadsheet model, several gaps in quackgrass knowledge were identified. The importance of quackgrass seed production, dissemination and emergence, under crop competition, is not well understood. The nature of the site specificity and influence of various crops, herbicides and crop densities on quackgrass shoot development, growth characteristics and allometry has not been adequately investigated. Further research is also required to investigate the temporal dynamics of quackgrass bud viability and emergence in the non-crop portion of the quackgrass life cycle. Collection of definitive data in these areas could be used to enhance the spreadsheet model and/or be used in other quackgrass models.

To be of practical benefit to producers future quackgrass models need to be more "real world" than the current spreadsheet model. Quackgrass model systems need to reflect the fact that fields are environmentally variable and that quackgrass infestation is dynamic and usually only one component of a multiple species weed community. The influence of crop density and crop management practices also needs to be incorporated into these model systems. Additionally, models need to be stochastic and coupled to economic risk analysis

**Table 23. Sensitivity values for various spreadsheet model year two output predictions in response to reducing input parameters by 10% (top value) or 20 % (bottom value).**

Input Parameter	Spreadsheet Model Sensitivity Value <sup>a</sup>				
	Quackgrass Output			Crop Output	
	Spring Shoot Numbers	Harvest Shoot Numbers	Harvest Percent Bud Numbers	Yield Yield Loss	Loss \$ Value
Percent	0.98	0.84	0.97	0.95	0.84
Survival	0.98	0.87	0.96	0.94	0.83
Initial	0.56	0.55	0.65	0.45	0.57
Infestation	0.64	0.55	0.62	0.67	0.54
Days After	-0.65	-0.54	-0.59	-0.41	-0.51
Planting	-0.54	-0.52	-0.54	-0.50	-0.47
Percent Buds	0.98	0.84	0.97	0.95	0.84
Emerging	0.98	0.87	0.96	0.94	0.83
Crop	0.00	0.00	0.00	0.00	1.00
Yield	0.00	0.00	0.00	0.00	1.00
Crop	0.00	0.00	0.00	0.00	1.00
Price	0.00	0.00	0.00	0.00	1.00
Herbicide	6.00	3.41	3.50	4.50	4.11
Kill	3.27	2.24	2.29	2.67	2.53

<sup>a</sup> With the exception of herbicide kill, the base for the sensitivity analysis was a W-W-W rotation where: potential wheat yield was set at 32.8 bu/a, the wheat price was set at \$CDN 3.00/bu, initial quackgrass infestation was 10 shoots/m<sup>2</sup> at 30 D.A.P., winter bud survival was set at 95%, spring bud emergence was set at 25% and in crop mortality was set at 0%. The base for the herbicide kill sensitivity analysis involved modifying the rotation to C-W-W and assuming an in Canola weed mortality of 95%.

to be of greatest utility to producers.

Conducting the long-term detailed studies required to fill in the quackgrass knowledge gaps and then applying this knowledge to "real world" systems is the next challenge to quackgrass modelling.

### **Summary**

The quackgrass spreadsheet model is an instructional tool which can be used to demonstrate the value of weed modelling. The spreadsheet model has demonstrated how models can be used to assist in making weed control decisions; specifically, by tracking how fast quackgrass infestations change under various management strategies, by allowing determination of how much of a specific quackgrass management strategy is required to maintain or reduce infestation, and by assessing the yield loss cost associated with various management strategies. The quackgrass modelling approach outlined in this paper has also demonstrated how the process of organizing weed knowledge into a model system and applying this knowledge to a spreadsheet model allows identification of areas of weed knowledge weakness and modelling limitations. The quackgrass spreadsheet model has also shown that weed models can be developed for instructional purposes using simple hardware and software even when knowledge of all elements of the model system is incomplete.

The quackgrass management scenarios simulated with the quackgrass spreadsheet model have illustrated the tremendous above and below ground growth of quackgrass. No combination of control measures simulated were able to eradicate quackgrass. The simulations suggest that the spread of quackgrass can only be halted by constant crop

competition and chemical and mechanical attack. In simple terms the quackgrass spreadsheet model simulations illustrate that for quackgrass control "persistence" is the most effective control strategy.

## GENERAL DISCUSSION

It is interesting that despite all the advances made in weed science since the first half of the century that the quote from Tildesley (1933) at the beginning of this thesis is still appropriate today. The majority of quackgrass literature continues to take the crop-centred approach, focusing on crop response and quackgrass control, instead of the weed-centred approach, focusing on fundamental quackgrass population biology. For example, after a review of the 620 quackgrass papers on file with the author it was determined that, at best, only 26% have taken a weed-centred approach. By focusing on the crop response and providing only limited concurrent information on quackgrass in the short-term, the bulk of quackgrass literature has only limited utility for developing effective long-term quackgrass management strategies. Driven by a necessity for producers to reduce input costs, a fear of herbicide resistance, and the failure of the crop-centred approach to provide a long-term solution to the quackgrass problem, the weed-centred approach is gaining ground.

The studies reported in this thesis have taken a weed-centred approach which, although focusing on quackgrass, does not neglect the practical benefit of concurrently monitoring crop response. By taking the weed-centred approach it was hoped that insights into quackgrass population biology would be obtained that could ultimately assist in developing an effective



long-term management strategy. The development of a deterministic empirical model of quackgrass interference (Manuscript 4), a first step in developing a long-term management strategy, would not have been possible without taking this weed-centred approach.

A native of Europe, quackgrass currently thrives in most of the agricultural regions of Canada. A ruderal, with many characteristics that insure its survival and competitiveness in agricultural systems, quackgrass is in many ways an ideal weed. Quackgrass is a successful weed primarily because of its vigorous rhizome system. For example, it has been observed in the field that in a single season a quackgrass plant propagated from a single 3-cm rhizome segment has grown to produce 318 m of rhizome with 6,587 buds (Wilcox, unpublished data).

To understand why quackgrass is a successful weed requires a fundamental understanding of its growth and development. Many of the results presented in Manuscripts 1 to 3 provide unique insight into quackgrass vegetative and reproductive growth and development, both in the presence and absence of crop competition in the field. These fundamental results are potentially of practical value as a benchmark reference for researchers to interpret the relative importance of various plant components in weed longevity and interference and, in turn, weed success.

One approach towards understanding quackgrass biology is through yield component analysis (YCA). The focus of YCA is to relate a yield to its contributing components. When yield component analysis was studied in quackgrass grown in high and low density populations it was determined that quackgrass dry matter partitioning was altered by population treatment (Manuscript 2). The production of heads was much greater in the

higher infestations than in the lower infestations. Additionally, although not statistically verifiable, there appeared to be an increase in head production at the expense of other rhizomes and not shoots.

Yield component analysis was also conducted on the wheat growing within the high and low quackgrass infestation populations (Manuscript 2). Wheat kernel weight was determined to be the yield component most effected by quackgrass infestation level. Changes in wheat kernal weight indicates that the majority of quackgrass competition on wheat occurs during the later stages of crop growth, as it has been established that changes in wheat kernel weight usually occur only as result of post-anthesis stress (Ford and Thorne, 1975; Jenner, 1979).

Allometry can simply be described as the growth relationship between plant parts. The empirical power function of Pearsall (Pearsall, 1927) is the relationship usually used to describe allometric relationships. Determining the allometric relationships in quackgrass infesting spring wheat was a major component of this thesis (Manuscript 3). By knowing the relationship between the growth of an easily observable above ground plant part and the below-ground rhizomes, much labour can be saved when trying to assess the viability of a particular population. Knowing the relationship between fall quackgrass shoot numbers and rhizome bud number determined in Manuscript 3 was a critical component in the long-term spreadsheet model (Manuscript 4).

Many of the allometric relationships between quackgrass vegetative and reproductive variables have been determined at three stages in the growing season (Manuscript 3). However, it was determined that these allometric relationships were not consistent across sites

and sampling periods. The dependence of allometric relationships on sampling time has been observed elsewhere (Jolliffe *et al*, 1988). The inconsistency between sites indicates that allometric relationships in quackgrass are environment and/or biologically specific. Allometric models must be more sophisticated than Pearsall's power function to be universally applicable.

Interference in mixtures of plants can be investigated through either the survey or the experimental approach. The experimental approach was used to obtain data for analysis in Manuscripts 1 and Appendix 1. The survey approach was used to obtain data for analysis in Manuscripts 2 and 3.

Dynamic stratified random sampling was the survey method used to obtain an unbiased representative sample of quackgrass infestation in spring wheat fields (Manuscripts 2 and 3). The main purpose of these surveys was more analytic than descriptive. These surveys used nine strata, although Cochran (1977) has suggested that no more than six strata are required. Since the purpose of the surveys was to get a wide range of quackgrass densities and not just to obtain the required precision it was felt that extra effort involved in having nine strata would be justified.

In the dynamic stratified random surveys at each sampling date a 0.25 m<sup>2</sup> quadrat was laid in the centre of its randomly allocated 1 m<sup>2</sup> quadrat and above and below ground plant samples were harvested. This is substantially smaller than the 4 m<sup>2</sup> sample recommended by Lemieux *et al* (1990) but when resources and cost are taken into account the 1/4 m<sup>2</sup> sampling area was assessed to be satisfactory.

An independent dataset for model validation was obtained by surveying and sampling mature commercial wheat fields infested with quackgrass (Manuscripts 2 and 3). Baseline

stratified random sampling, in which thirty 1 m<sup>2</sup> quadrats were harvested at each site, was the survey method used. This sampling method was useful for obtaining the data required for the analytic and validation objective of this survey.

Stratified random sampling was the preferred approach for all surveys in this thesis because this method increases population representation without potential systematic bias. This unbiased representation was important for the analytic objective of the surveys.

It is the opinion of the author that plant interference researchers have focused too often only on one set of population interference characteristics while making minimal, or no, attempt to account for other aspects of a populations biology relevant to interference. This myopic approach unnecessarily limits the potential utility of their research for other researchers. To enhance the utility of interference research researchers need to take a more holistic approach towards understanding the interconnectiveness of various population characteristics in determining interference. Figure 1 is an empirical illustration of some of the interrelationships that should be considered.

The additive series design reported in Manuscript 1 and Appendix 1 was selected and conducted with this holistic approach in mind. Environmental and edaphic factors at the site were monitored and reported in Appendices 1 to 4 (light, air and soil temperature, precipitation, soil water, and soil nutrients). By using one quackgrass clone and one wheat variety and planting to stand, species characteristics were uniform at the experiment sites (Manuscript 1 and Appendix 1). The additive series design used at the experimental sites had template defined proximity factors (density, spatial arrangement, proportion) and a monitored generally uniform structural distribution (age, size, state). The additive series experiment also

provided population attribute information by measuring a wide range of various plant attributes which in turn were used to calculating various indices of interference (Manuscript 1 and Appendix 1). Ideally this additive series design would have been dynamic, with multiple sampling dates providing population attributes information at various stages, but the scale of such an experiment was considered impractical. Some dynamic information over the experimental period can be inferred from the light interception data of Appendix 1.

In contrast by not controlling many of these interference potential factors in the stratified random sampling surveys (Manuscripts 2 and 3) the fundamental nature of interference in these surveys is neither interpretable nor are the findings directly transferable to other sites.

There are many indices of interference and combined yield that could be used to help summarize and interpret the results from the addition series experiment. However, many of these indices, particularly those published prior to 1983, have either unrealistic assumptions or an undesirable density dependence (Connolly, 1986). Many of these indices have been calculated from the 1987 wheat-quackgrass addition series experiment reported in Manuscript 1 and the results were consistent with Connolly's criticisms (Wilcox, 1988b). Two newer experimental designs and indices are not subject to the density dependent criticism. They are the reciprocal yield approach developed by Spitters (1983a) and the revised synthetic no-interaction approach of Jolliffe *et al* (1988); both approaches have been used in this thesis (Manuscript 1). Although Roush *et al* (1989) advocates use of the reciprocal yield approach because of its simplicity and sensitivity, if this author had to recommend any one technique it would be the revised synthetic no-interaction approach. The revised synthetic no-

interaction approach provides greater detail in the analysis and has greater response flexibility. However, it is likely that there is no single appropriate form of analysis. In fact, it is likely that to optimize interpretation of results it may be preferable to use several forms of analysis.

The development of a long-term economically and ecologically acceptable approach to quackgrass management is a complex problem. A solution requires data from many fundamental investigations on quackgrass and infested crops, determination of the efficacies of various control methods, and knowledge of the economic and social systems in which the management practice is to take place. Complex problems of this type require decision support systems, often a computer model. Using a computer model, management decisions that are risky, difficult or expensive can be simulated to provide quantitative estimates for system parameters which can be used in the decision process. Such a decision support model has not existed for quackgrass infestations in western Canada until the development of the deterministic empirical model of quackgrass interference in spring annual crops presented in Manuscript 4.

The spreadsheet model provides a coherent framework which can be used to explore the long-term implications of management practices and interference on a theoretical basis. However, in view of the gaps in knowledge and climatic and site limitations in the data used to develop the model, a caveat needs to be applied that the model is instructional only and not to be used for applied decision support. Only with further enhancement can the model framework described in Manuscript 4 be used for applied decision support. Additionally, given that there is great potential variability both in quackgrass genotypes and site environmental conditions it is advisable that any decision support model provide a stochastic

output.

A potential criticism of the approach used in this model is that it is confined to a single species, whereas weeds occur in communities. Cousens *et al* (1987) have suggested that this is not too great a concern as practical management decisions are often made on a single species basis. Alternatively, this approach can be modified to account for multi-species communities (Swinton *et al*, 1994).

The modelling approach used in Manuscript 4 is basically descriptive in nature and provides only limited insight into the process of quackgrass-crop competition. Given the complexity of relating biological variables to yield loss, it may be more appropriate to use mechanistic models (Spitters and Aerts, 1983; Ball and Shaffer, 1993). Usually the mechanistic approach used for plant interference involves determining the effects of interference through the underlying growth limiting resources of light, water, and nutrients. The advantage of the mechanistic approach is that it would have potential applicability over a wide range of environments. Fundamental information that could assist in developing such mechanistic models for quackgrass in wheat has been provided in Appendices 1, 3 and 4.

Interspecific interference was modelled using two different equations in this thesis. In Manuscript 1 the flexible multi-species equation of Jolliffe (1988) is used, whereas in Manuscript 2 the non-linear rectangular hyperbolic model of Cousens (1985) was used. Because of its flexibility to be either parabolic or hyperbolic, as required, the equation of Jolliffe (1988) would have been preferred throughout the thesis. However, given that the equation of Cousens (1985) has become generally accepted as the standard model for expressing yield loss in relation to weed density it was adopted for expressing the in field

survey results of Manuscript 2. There is a risk in using the strictly hyperbolic model of Cousens in that it is known that reproductive parameters often have parabolic yield density responses (Holliday, 1960) which will be lost in a forced hyperbolic model. It should be noted that Cousens rectangular hyperbolic model is a reparamatized version of the Jolliffe model (Jolliffe, 1988) and the potential discrepancy between the two models may not be great.

A potential criticism of both these models (or any least squares fit model) when they are applied to plant population characteristics is that they assume errors are normally distributed about the mean. It is known that in most plant populations that plant size characteristics are skewed in a size hierarchy (Weiner and Thomas, 1986). This potential error source appears to have been overlooked or ignored in the literature. Consistent with the literature this potential error source has been ignored in this thesis because plant material was harvested on an area basis and not on an individual plant basis which would allow corrections.



## SUMMARY AND CONCLUSIONS

Using high wheat planting densities may contribute to quackgrass suppression. Wheat is superior to quackgrass in interspecific interference and increasing wheat densities has a greater influence on quackgrass yield than on wheat yield. In a wheat-quackgrass additive series experiment it was determined that the yield of each species is determined more by their proportion in mixture than their absolute density.

Use of pre-harvest quackgrass suppression methods in wheat are likely to be beneficial by contributing to long-term quackgrass suppression and providing immediate wheat yield gains. In field surveys it appears that the majority of quackgrass interference on wheat yield occurs post-anthesis influencing kernel test weight. Additionally the majority of quackgrass rhizome production occurs during wheat senescence.

Reliance on interference from wheat alone as a means for long-term quackgrass suppression is unlikely to be effective. In surveys of commercial wheat fields infested with quackgrass it was determined that there was on average a three fold increase in quackgrass shoot biomass from wheat sowing to wheat harvest. Niche differentiation between wheat and quackgrass in mixtures is substantial. For example, competition for light in mixtures of wheat and quackgrass involves temporal partitioning of light interception for wheat to the first half of the growing season and for quackgrass to the last half of the growing season. Interspecific

interference by wheat on quackgrass has a significant influence on wheat-quackgrass mixtures but predominantly on quackgrass vegetative components and not reproductive components. In the wheat-quackgrass mixtures interspecific interference of quackgrass on wheat is relatively insignificant compared to wheat on wheat intraspecific interference.

The revised synthetic no-interaction model approach for analysis of interference is superior to the reciprocal yield model approach for analysing interspecific and intraspecific interference from a wheat-quackgrass additive series design. Although similar interpretations can be expected when additive series data is subjected to either the reciprocal yield or synthetic no-interaction approaches, the revised synthetic no-interaction model is more biologically realistic in that it can fit both the hyperbolic yield density response of wheat and the parabolic yield density response of quackgrass.

The quackgrass variables of greatest utility for estimating potential yield loss due to quackgrass interference are rhizome length and bud number; shoot counts, density, and proportion; and total plant density. Of these six, when consideration is given to model fit, situational robustness and ease of determination the shoot proportion variable of relative quackgrass ratio is the estimator of choice. Quackgrass shoot counts are as useful as rhizome variables for estimating yield loss due to quackgrass in wheat when practical considerations are taken into account. Some quackgrass variables such as head number or mean rhizome bud weight are not considered useful estimators.

Yield loss in wheat due to quackgrass could be effectively modelled using a rectangular hyperbolic model. Yield loss in wheat ( $Y_w\%$ ) was determined to be related to spring

quackgrass shoot counts  $m^{-2}$  ( $Q_s$ ) thirty days after planting by the following model:

$$Y_w\% = 98.7 (1 - 0.433 (Q_s)/100(1 + (0.433(Q_s)/193.7))).$$

Allometric models of the relationship between various quackgrass parts are site and time specific. The allometric model for relating quackgrass shoot number ( $Q_s$ ) and rhizome bud ( $QR_B$ ) numbers at wheat harvest is of the form:

$$QR_B = 4.297 (Q_s)^{1.075}.$$

This model differs significantly from the equivalent model derived from data 30 and 60 days after planting at the same site. This model also differs significantly from an equivalent model fit to an equivalent independent dataset.

Development of a simple spreadsheet model of quackgrass competition in annual crops is an effective approach to identify research needs and assay the implications of various quackgrass management strategies. However, because quackgrass is extremely plastic and very susceptible to environmental influence the quantitative predictive ability of descriptive models in any particular instance can be poor. For more accurate quantitative estimates more complex models including allometric, environmental and temporal information will have to be developed.

### **Suggestions For Further Work**

Improvement of the quackgrass spreadsheet model will require a greater understanding of the growth of quackgrass under various crops, cropping densities and management practices. Of immediate utility would be investigations to quantify the impact of herbicide

application and tillage practices on the production, overwinter survival and viability of rhizomes. Quantitative assessment of the extent and importance of mechanical support of quackgrass shoots by crops towards intraspecific interference and quackgrass survival is required. Detailed temporal monitoring of quackgrass growth and development in the non-crop phase of the field cropping cycle could provide original and useful information.

An evaluation of the importance of quackgrass seed production, dissemination and emergence throughout the field cropping cycle is required. Although quackgrass seedlings are generally believed to be of negligible importance in competition there is a need to confirm this assumption by field investigation.

Further work developing the quackgrass spreadsheet model is required. To be of utility to producers this quackgrass spreadsheet model needs to be developed from its current deterministic instructional form to an applied stochastic model. This will require more sophisticated representation of parameters such as herbicide kill, percent survival and percent buds emerging. Fundamental research on these parameters is required to develop more sophisticated sub-models to be used in future models.

It is important that the fundamental mechanisms involved in quackgrass interference continue to be investigated. The dominating influence of environment and the complexity of quackgrass interference is so great at the descriptive level that it may be determined that only a mechanistic model can provide the required accuracy for applied decision analysis in the field.

In a spreading perennial such as quackgrass it would be useful to study the spatial dynamics of quackgrass rhizome growth in order to fully model the spreading nature of its

interference and growth. Sub-organismal demographic analysis, which analyses individuals and their demographic growth as a population of structures, is a technique which might be adapted towards this goal. Additionally, a technique for overcoming the practical difficulty of tagging underground rhizomes would need to be developed.

An evaluation of the utility of tissue analysis for assessing competition for nutrients in plant mixtures involving quackgrass in the field is required. Experience in this thesis has shown that nutrient competition can not easily be assessed based on soil nutrient changes.

Further work is required to develop a "standard" allometric model that is less sampling time and site dependent than the current standard Pearsall equation. Ideally this allometric model would be able to compensate for environmental and temporal sampling variation.

Further investigation of the yield density response in quackgrass is required. It was observed in the additive series experiments that the yield density response of some quackgrass vegetative characteristics were parabolic whereas they were asymptotic for some reproductive characteristics. These responses are the opposite of what would generally be assumed. Whether this non-general observation is an artifact of the experimental design, or some special response characteristic of quackgrass, or perennials in general, needs to be ascertained.

An investigation of the significance of "misuse" of Cousen's hyperbolic yield-density model should be conducted. Plant reproductive yield-density response is commonly a parabolic function whereas Cousen's asymptotic model, the recent weed science standard, has often been fit to reproductive yield-density responses. Additionally, the model is often fit using a least squares approach which assumes that errors are normally distributed about the mean; this is likely rarely the case in a typically size skewed mature plant population. Finally,

depending on the yield variable modelled, Cousen's model can be very sampling time dependent, suggesting the need for investigators to document or incorporate assessment time in predictions derived from this model.

An evaluation of the yield losses associated with quackgrass in argentine canola (*Brassica napus*) is required. Argentine canola is currently not only the major type of canola in Manitoba but it is also the major crop. Losses due to quackgrass in polish canola (*Brassica rapa*) has been modelled but may not be transferable to argentine canola. Ideally such investigations would enable a comparison of the relative competitiveness of quackgrass in both canola types as well as provide some insight into the mechanisms responsible for any differences.

In a similar vein, it would be of interest to investigate the relative interference due to quackgrass in the various distinct types and varieties of wheat grown in Manitoba. Differing wheat plant heights and maturation periods could result in significant differences in quackgrass suppression.

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## **APPENDIX 1**

## Modelling Light Transmittance and Light Use Efficiency in Wheat

### (*Triticum aestivum*) and Quackgrass (*Elytrigia repens*)

#### Grown in an Additive Series

**Abstract.** A line quantum sensor was used to monitor the transmission of photosynthetically active radiation (PAR<sup>13</sup>) in a wheat-quackgrass additive series experiment at Portage la Prairie, Manitoba, in 1987 and 1988. PAR transmittance over time was described using a fourth order polynomial which partitioned the PAR transmittance pattern into five phases. In the first half of growing season the canopies of wheat-dominated mixtures transmitted less PAR than did quackgrass-dominated mixtures but the opposite was true during the last half of the season. PAR transmittance through mixture canopies was generally intermediate to PAR transmittance through the two monocultures. At all sampling dates PAR transmittance was negatively correlated with stand density. Minimum PAR transmittance values ranged from 4 to 16 % and averaged 9.6 % through the canopies of all treatments. Light use efficiency (LUE) was observed to vary with treatment and yield variable used. When based

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<sup>13</sup>Abbreviations: LUE, Light use efficiency; PAR, Photosynthetically active radiation; DAP, Days After Planting; TBIO, Community vegetative size; TSHT, Community vegetative dispersion; TREP, Community reproductive effort, TFEC, Community fecundity.



on biomass calculated LUE values did not significantly differ between treatments and averaged  $1.9 \text{ g MJ}^{-1}$ . However, when based on reproductive effort, there was a positive correlation between the proportion of wheat in mixture and LUE. The opposite was true when LUE values were calculated based on vegetative dispersion. LUE values based on reproductive fecundity were an order of magnitude larger than values calculated using the other yield variables. When based on reproductive effort or vegetative dispersion, LUE values would decrease as stand density increased, whereas the LUE values would increase as stand density increased, when based on reproductive fecundity or biomass. At comparable stand densities the LUE of mixtures was generally superior to either species in monoculture. Superior LUE of mixtures was attributed to leaf positioning of quackgrass in mixture canopies during wheat senescence. It was hypothesized that the improved leaf positioning of quackgrass in mixtures during the last half of the season may largely offset any negative impacts on quackgrass productivity due to wheat competition for light during the first half of the season.

Nomenclature: Quackgrass, Elytrigia repens L. Nevski #<sup>14</sup> AGGRE; wheat, Triticum aestivum L. 'Katepwa'. Additional index words. Replacement series, interspecific interference, intraspecific interference, Agropyron repens L. Beauv., light use efficiency, competition.

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<sup>14</sup>Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Weed Sci. 32, Suppl. 2. Available from WSSA, 309 West Clark Street, Champaign, IL 61820.

## INTRODUCTION

Quackgrass is recognized to be the most serious perennial grass weed of spring wheat in Manitoba (Thomas and Wise, 1984). Quackgrass infestations can cause severe yield losses in wheat. For example, in Manitoba, a quackgrass infestation of 100 shoots  $\text{m}^{-2}$  in the spring caused a 30 percent yield loss in spring wheat (Wilcox and Morrison, 1988). It is well established that quackgrass interferes with wheat but the mechanism(s) involved has yet to be determined.

Yield of a plant community is dependent on the amount of solar radiation intercepted. Light competition is often an important mechanism of interference except in situations with acutely limiting nutrient or water availability (Donald, 1963). In many studies of wheat-quackgrass interference competition for light has been reported to be the major interference mechanism (Cussans, 1968; Maillette, 1986; Skuterud, 1977; Thurston and Williams, 1968). Cussans (1968) attributed quackgrass etiolation and growth suppression by wheat to competition for light. Skuterud (1977) attributed the greater productivity of quackgrass under wheat than under oats to greater light penetration into the wheat canopy; 27 versus 21 % light penetration into wheat and oats, respectively. Maillette (1986) observed in glasshouse conditions that quackgrass was consistently shaded by wheat leaves and produced significantly less biomass than quackgrass in pure stands. It has also been stated that quackgrass is unlikely to affect cereals by shading them because quackgrass stems usually elongate slower than those of cereals (Thurston and Williams, 1968).

Intra- and interspecific interference response interpretation is dependent on the yield

variable selected (Manuscript 1). Research with quackgrass grown under screens and in growth chambers at reduced light intensities has shown that rhizome production is more dependent on light than production of aerial parts (Hakansson, 1969; Palmer, 1958; Skuterud, 1984; Williams, 1970). In wheat it has been demonstrated that, depending on the timing and duration of shading, reductions in tillering, grains ear<sup>-1</sup> or 1000 kernel weight will occur (Fischer, 1985; Fischer and Stockman, 1980; Ford and Thorne, 1975; Puckridge, 1968; Willey and Holliday, 1971). This dependence of growth response on timing of light interference indicates that light use efficiency values will be dependent on yield variable measured.

The primary objective of this study was to determine the extent and duration of PAR transmittance in monocultures and mixtures of quackgrass and wheat. A secondary objective was to determine the comparative light use efficiencies of wheat and quackgrass in monocultures and mixtures and to determine the extent to which light use efficiency is dependent on the particular yield variable utilized.

## **MATERIALS AND METHODS**

### **Experimental Design**

A wheat-quackgrass additive series experiment was conducted in 1987 and repeated in 1988 at the University of Manitoba, Portage la Prairie research station. The site description and experimental design are the same as those described in Manuscript 1.

To assess the effect of the additive series treatments on PAR transmittance and LUE in the wheat-quackgrass additive series treatments the experimental data was grouped into indicators of biomass size and dispersion and indicators of reproductive effort and fecundity. Community biomass (TBIO) was defined as the sum of the dry matter of all above-ground plant portions and rhizomes. Community biomass dispersion (TSHT) was defined as the number of shoots per unit area including those of daughter quackgrass plants. Community reproductive effort (TREP) was defined as the combination of wheat grain mass and quackgrass spike and rhizome dry matter. Community fecundity (TFEC) was defined as the sum of the number of wheat kernels produced and the number of rhizome buds.

### **Light Transmittance**

Except on overcast days, at weekly intervals at a time between 1200 to 1400 hours, the transmittance of photosynthetically active radiation (PAR) to the soil surface of each plot was determined using a 1 m long line quantum sensor<sup>15</sup>. The percentage light transmittance was calculated as

$$T_{\%} = 100(I_t/I_o)$$

Where  $T_{\%}$  is the percentage transmittance,  $I_t$  is the PAR recorded at ground-level, and  $I_o$  is the PAR recorded above the canopy. Values of  $T_{\%}$  calculated in this fashion will often be overestimated as the quantum sensor measures both the direct and diffuse radiation and the diffuse radiation is generally greater within the canopy than above the canopy (Monteith,

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<sup>15</sup>LI-191SA LI-COR Inc., Lincoln, Nebraska.

1973). However, for the comparative purposes of this manuscript, this quantitative error was not considered important.

The dynamics of canopy light transmittance was determined by fitting polynomials to the raw data for each of the 15 treatments from the 4 replicates using a linear regression procedure<sup>16</sup>. The order of polynomial that consistently provided the best fit for all individual treatments in both years was then used for all plots. The coefficient of determination was calculated as recommended by Kvalseth (1985). Polynomial curves were compared to determine if there were significant differences using the nonlinear comparison procedure of Ratkowsky (1983). Significant differences were considered to be those at  $\alpha = 0.05$ .

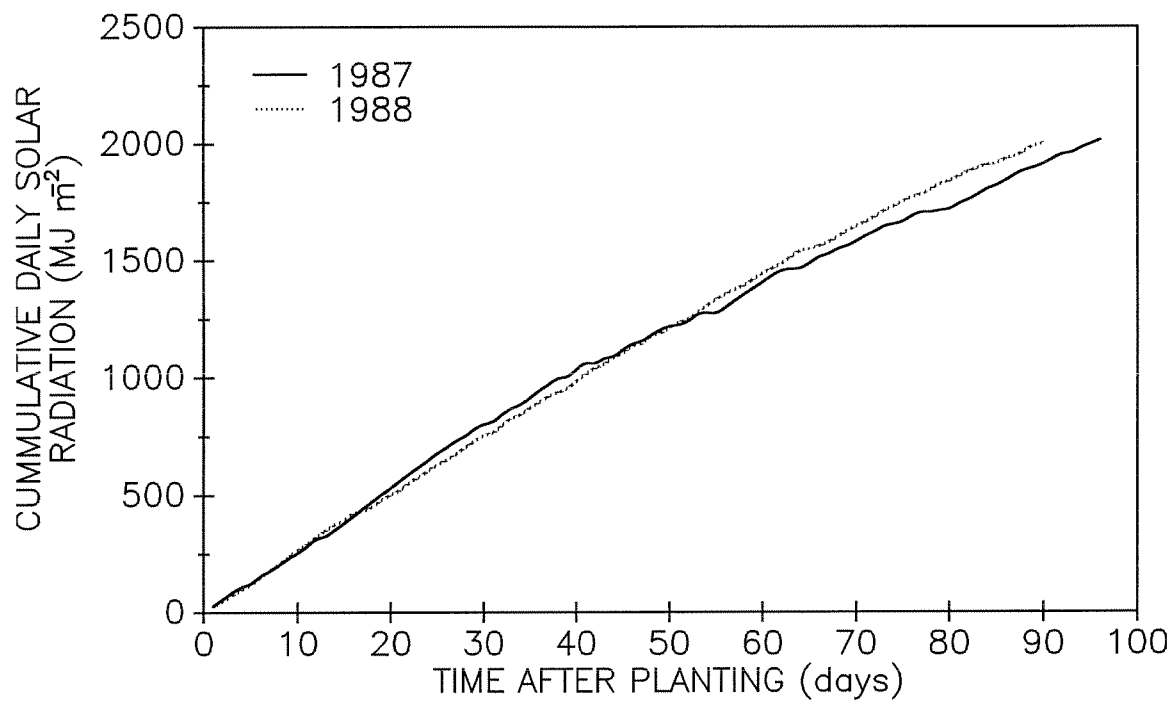
### **Light Use Efficiency**

Total daily solar radiation at the site was measured using a pyranometer sensor<sup>17</sup> attached to a minimum dataset recorder. The total cumulative solar radiation over the growing seasons in 1987 and 1988 is presented in Figure 13. The pyranometer sensor has an operational wavelength response of 400 - 1100 nm. Although this sensor is not spectrally ideal (280 -2800 nm), pyranometer calibration adjusts for the difference in spectral response and the pyranometer sensor gives a response that differs from the spectrally ideal irradiance

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<sup>16</sup>PROC REG, SAS V5. SAS Institute, Cary, NC.

<sup>17</sup>LI-200SA LI-COR Inc., Lincoln, Nebraska.



**Figure 13.** Cumulative incident light (pyranometer sensor) received by the wheat-quackgrass additive series experiments at Portage la Prairie, Manitoba, in 1987 and 1988.

by less than 5%<sup>18</sup>. Light use efficiency was determined as

$$LUE = y_k/Q_c = y_k / \sum_{K=1}^n \{(100 - T_{\%k}) [0.5(I_{opk})]\}$$

where  $y_k$  is the yield variable yield,  $Q_c$  is the cumulative sum of intercepted solar irradiance over each intervals quanta use,  $T_{\%k}$  is the mean percent transmittance of the interval, and  $I_{opk}$  is the cumulative incident radiation recorded for the interval on the pyranometer sensor. Monteith (1973) indicates that for practical purposes the PAR fraction can be assumed to average 50% of solar irradiance.  $I_{opk}$  is multiplied by the scaler 0.5 to convert the pyranometer values to PAR. Treatment results from both years were pooled following validation by an F-Test for homogeneity of variance. Results were analyzed by ANOVA as a randomized complete block and when treatments were significant at  $\alpha=0.05$ , treatment means were separated by the least significant difference test at  $\alpha=0.05$ .

## RESULTS AND DISCUSSION

### PAR Transmittance

Incident solar radiation reaching the top of the canopy was similar in 1987 and 1988 (Figure 13). Additionally, the general form of the canopy PAR transmittance curves were

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<sup>18</sup> LI-COR LI-200SB Users Manual. Anonymous. LI-COR Inc. Lincoln. Nebraska.

similar in 1987 (Figure 14) and 1988 (Figure 15). A fourth order polynomial most consistently provided the best fit to the canopy PAR transmittance versus time plots. Over both years the  $R^2$  values ranged from 0.84 to 0.98. Canopy PAR transmittance patterns for each year were significantly different and therefore corresponding polynomial curves for each treatment could not be pooled.

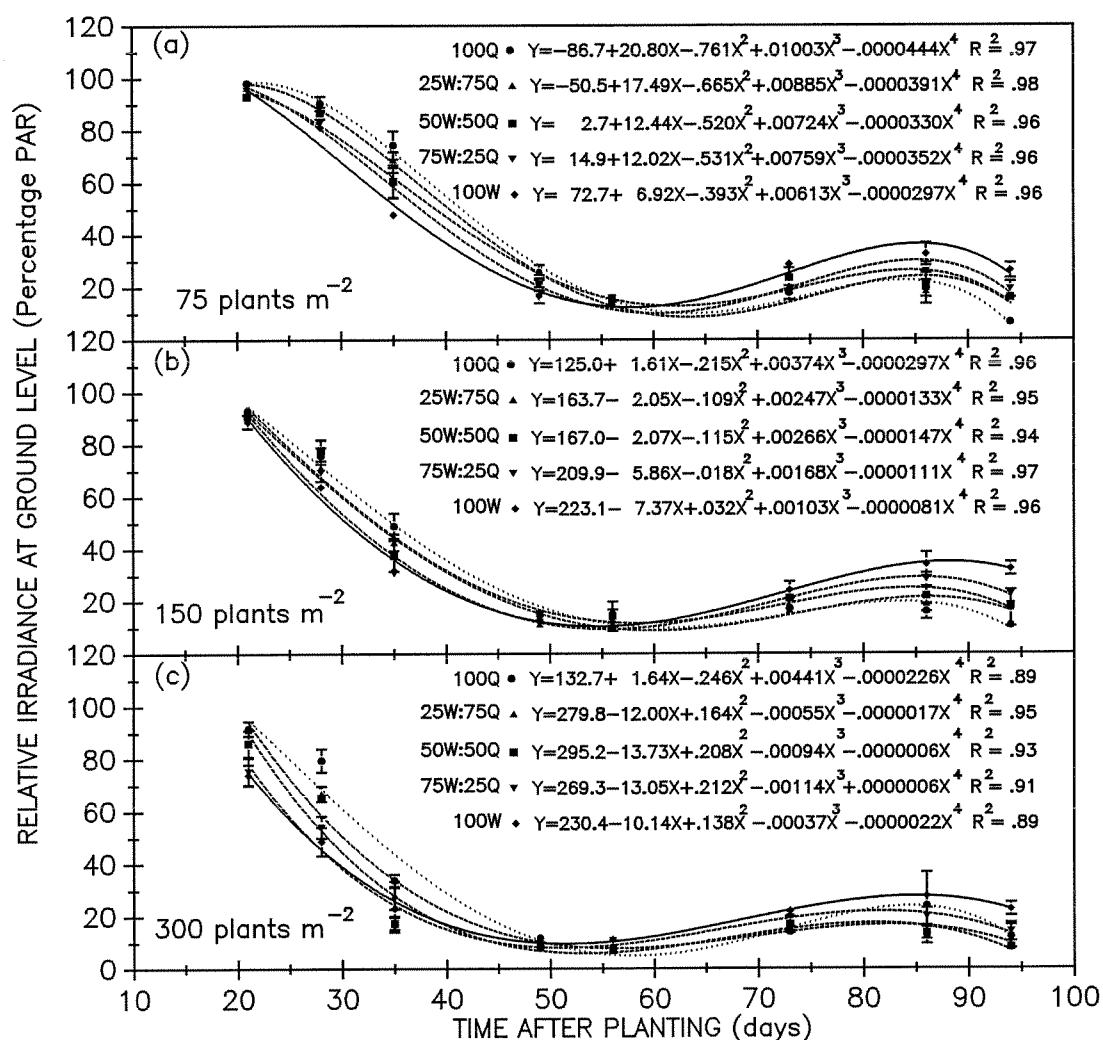
Canopy PAR transmittance gradually changed with mixture proportion (Figures 14 and 15). A nonlinear curve testing procedure (Ratkowsky, 1983) determined that for adjacent pairs of treatments, at any stand density in either year, the canopy PAR transmittance curves were often not significantly different. In contrast, only rarely were any three adjacent curves at any particular stand density and year not significantly different. Canopy PAR transmittance curves for wheat and quackgrass monocultures were always significantly different.

In 1988 the cumulative daily solar radiation was greater than in 1987 for the last half of the growing season (Figure 13). This extra light availability may have been reflected in wheat having matured six days earlier in 1988 than in 1987. Similarly the dynamics of PAR transmittance through the canopies was such that, on average, curve inflections occurred six days earlier in 1988 (Figure 15) than in 1987 (Figure 14).

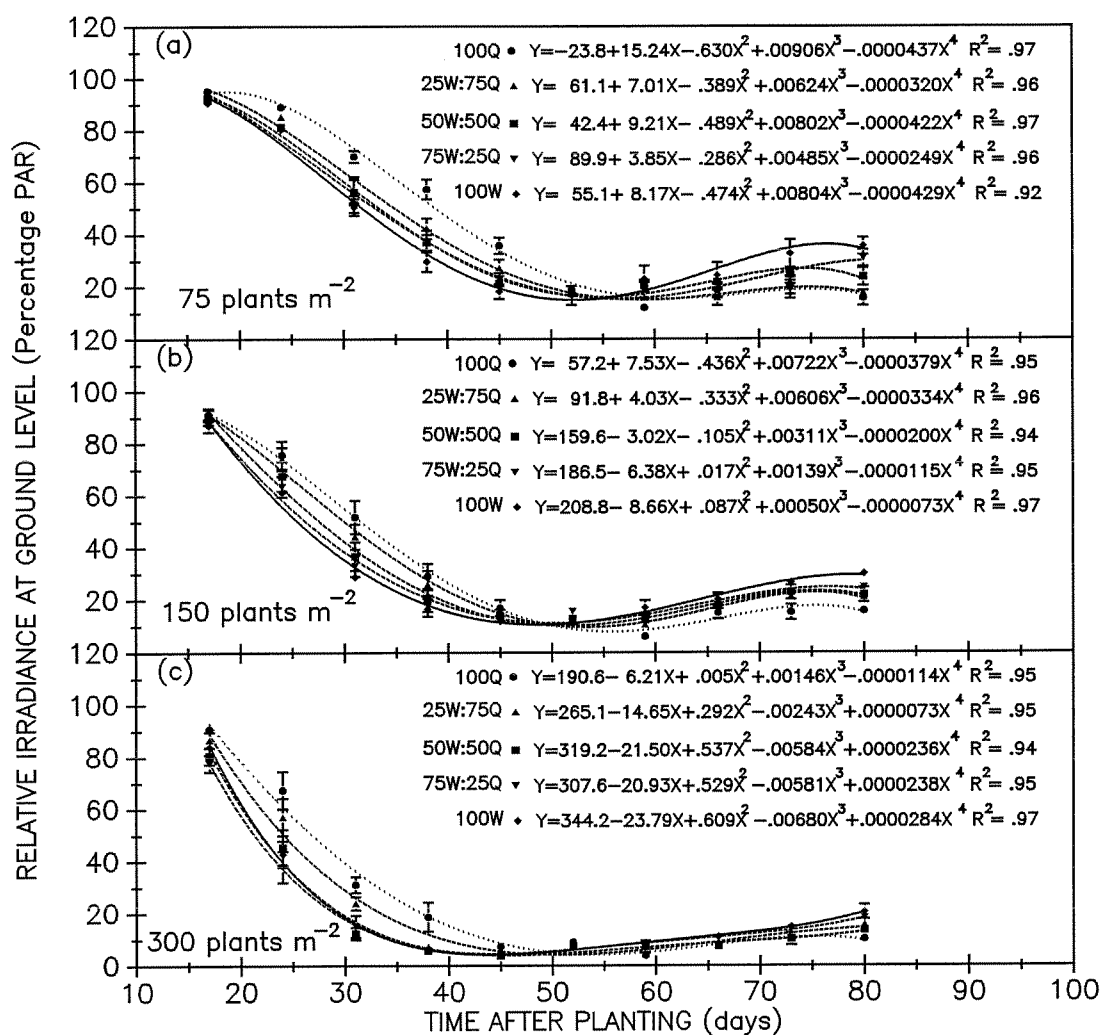
Canopy PAR transmittance dynamics in the wheat-quackgrass mixtures was characterized into five phases:

Phase 1. Vegetative growth phase - A steady decline in PAR transmittance associated with increased vegetative growth of wheat and/or quackgrass.





**Figure 14.** Photosynthetically active radiation (PAR) transmittance dynamics of the various mixture proportions and total stand densities in the 1987 wheat-quackgrass additive series experiment.



**Figure 15.** Photosynthetically active radiation (PAR) transmittance dynamics of the various mixture proportions and total stand densities in the 1988 wheat-quackgrass additive series experiment.

Phase 2. Maximum leaf area index phase - The transition point between phase 1 and 2 associated with the least PAR transmittance and late anthesis in both wheat and quackgrass.

Phase 3. Early maturation phase - A steady increase in PAR transmittance associated with increasing leaf senescence in wheat and rapid stem elongation and more erect habit in quackgrass.

Phase 4. Late maturation phase - The transition point between phase 3 and 5 associated with complete senescence and grain ripening in wheat and the most erect habit of quackgrass.

Phase 5. Displacement phase - A slight decline in canopy PAR transmittance to the ground associated with displacement of wheat culms by heavy heads and increased lodging in quackgrass.

Similar multiphase canopy irradiance transmittance patterns have been shown under both pasture ryegrass (*Lolium rigidum*) (Stearn and Donald, 1962) and wheat (Fischer, 1983; Skutterud, 1977).

During growth phase 2 the interpolated minimum canopy PAR transmittance to the soil surface ranged from 4 to 16 % and averaged 9.6 % over the two years (Figures 14 and 15). The PAR transmittance indicated in these experiments is less than those obtained by Skuterud (1977). He observed that spring wheat intercepted all but 15 % of the sunlight to

5 cm above the soil.

In both years there was a trend that the more quackgrass present in the mixture the later the interpolated minimum PAR transmittance value occurred. For example in 1988 the date of minimum light transmittance for the 75 plants  $\text{m}^{-2}$  stand density occurred 52 days after planting (DAP) for monoculture wheat versus 62 DAP for monoculture quackgrass (Figure 15). This indicates that quackgrass was slower to achieve its maximum leaf area index than was wheat.

The maximum canopy PAR transmittance during growth phase 4 ranged from 11 to 37 % and averaged 24 % over both years (Figures 14 and 15). On average the interpolated phase 4 values for 1987 were 3 % more than the 1988 values. This is likely the result of the more rapid maturation, due to hotter dryer conditions, in 1988 compared to 1987.

For all growth phases, in all mixture proportions, there was a trend towards higher densities transmitting less PAR than the lower densities. For example, in 1988 monoculture wheat at 30 DAP had intercepted 40, 65, and 82 % at 75, 150, and 300 plants  $\text{m}^{-2}$ , respectively (Figure 15). Maillette (1986) similarly observed that low density stands of wheat and quackgrass grew slower and produced fewer leaves than at higher densities.

During the vegetative growth phase (phase 1) the larger the quackgrass proportion in mixture the more PAR was transmitted through the canopies. However, the opposite was true during phase 4 growth. For example at 75 plants  $\text{m}^{-2}$  at 40 DAP in 1987 PAR transmittance was 37 and 56 % whereas at 80 DAP PAR transmittance was 33 and 23 %, for wheat and quackgrass monocultures, respectively. The temporal difference in PAR transmittance indicates that wheat is more effective at PAR interception during the first half

of the growing season whereas quackgrass is more efficient at PAR interception during the later half. In wheat-quackgrass mixtures the superior PAR interception by quackgrass late in the growing season may explain the marked dry weight increases that have been observed to occur in quackgrass during the crop ripening phase (Cussans, 1968; Rauber and Bottger, 1984; Skutterud, 1984).

PAR transmittance in the wheat-quackgrass mixtures was comparable to that for the species in monoculture. A similar result for species in monocultures and mixtures has been noted by Willey (1979) for intercrops.

### **Light Use Efficiency**

Light use efficiency (LUE) values varied with yield variable used in its calculation. When based on TBIO, TREP, TSHT and TFEC the LUE values ranged from 1.68 to 2.00 g MJ<sup>-1</sup>, 0.31 to 0.67 g MJ<sup>-1</sup>, 1.08 to 1.99 # MJ<sup>-1</sup>, and 5.70 to 24.95 # MJ<sup>-1</sup>, respectively (Table 24). TREP is a major component of TBIO and this explains the smaller and similar range of LUE values for TREP relative to TBIO. LUE values based on TFEC were an order of magnitude larger than LUE values based on the other yield variables. This difference in magnitude is simply a reflection of the scale of the fecundity values being in the thousands, whereas the other yield variables were in the hundreds.

When calculated using TBIO there was no significant difference between LUE values between treatments (Table 24). This lack of difference can be explained by the complementary light use patterns of wheat and quackgrass over the growing season. Wheat intercepts more light for the first half of the growing season, whereas quackgrass intercepts

**Table 24. Wheat-quackgrass additive series light use efficiency (LUE) values calculated using selected variables.**

Total Stand Density	Mixture Proportion		LUE <sup>a</sup>			
	Wheat	Quackgrass	TBIO <sup>b</sup>	TREP	TSHT	TFEC
(plants m <sup>-2</sup> )	-----(%)-----		----(g MJ <sup>-1</sup> )----		----(# MJ <sup>-1</sup> )----	
75	0	100	1.76	0.51	1.39	9.14
75	25	75	1.82	0.60	1.27	15.92
75	50	50	1.86	0.66	1.27	19.92
75	75	25	1.86	0.62	1.23	21.70
75	100	0	1.77	0.62	1.08	23.40
150	0	100	1.90	0.42	1.82	6.17
150	25	75	2.00	0.56	1.61	14.51
150	50	50	1.96	0.60	1.61	18.82
150	75	25	1.80	0.64	1.34	22.63
150	100	0	1.80	0.67	1.15	24.95
300	0	100	1.83	0.31	1.99	5.70
300	25	75	1.84	0.46	1.78	14.79
300	50	50	1.94	0.57	1.72	18.80
300	75	25	1.93	0.63	1.59	22.85
300	100	0	1.68	0.60	1.12	23.31
	S.E.M. <sup>c</sup>		(0.114)	(0.052)	(0.105)	(1.483)
Pooled	0	100	1.83	0.41	1.73	7.00
Pooled	25	75	1.89	0.54	1.56	15.07
Pooled	50	50	1.92	0.61	1.53	19.18
Pooled	75	25	1.86	0.63	1.39	22.39
Pooled	100	0	1.75	0.63	1.11	23.89
	S.E.M.		(0.066)	(0.030)	(0.061)	(0.886)
75	Pooled		1.81	0.60	1.25	18.02
150	Pooled		1.89	0.58	1.51	17.42
300	Pooled		1.84	0.52	1.64	17.09
	S.E.M.		(0.051)	(0.023)	(0.047)	(0.686)

<sup>a</sup> Average of the 1987 and 1988 experiments LUE values.

<sup>b</sup> TBIO = community biomass, TREP = community reproductive effort, TSHT = community vegetative dispersion, and TFEC = community reproductive fecundity

<sup>c</sup> Standard error of mean (S.E.M.) for column values.

more light over the last half (Figures 14 and 15). The net effect of this complementary PAR interception pattern is similar LUE values for the treatments when based on vegetative biomass. LUE values on the scale of  $1.9 \text{ g MJ}^{-1}$  for TBIO are comparable to LUE values reported by other researchers in other crops.

When calculated using TREP there were significant differences in LUE values between treatments (Table 24). The dominant effect was that the monoculture quackgrass treatments resulted in lower LUE values compared to any of the mixtures or monoculture wheat. There was also a trend that the greater the proportion of wheat the greater was the LUE value. Thus in terms of reproductive effort wheat was more efficient in using PAR over the growing season than was quackgrass. There were no significant mixture or mixture by density interactions for LUE based on TREP. The LUE of the mixtures, particularly the mixtures with higher proportions of quackgrass, was often greater than could be accounted for by the greater LUE of wheat present alone. It was observed that quackgrass stood more erect in mixtures because of the mechanical support of the wheat. That quackgrass is supported by wheat in mixtures was also reported by Maillette (1986). This more erect habit of quackgrass in mixtures late in the season would allow for more efficient PAR interception by the quackgrass in mixture with wheat and, in turn, greater reproductive effort. Rhizome development in quackgrass primarily occurs during the crop ripening phase (Cussans, 1968; Rauber and Bottger, 1984; Skutterud, 1984).

LUE values based on TSHT showed a significant trend that as quackgrass proportion in mixture increased LUE value increased (Table 24). This increasing LUE can be explained by comparing the spreading habits of the two species. Wheat is a determinate, erect plant

that produces tillers close to its primary shoot. In contrast quackgrass is an invasive, indeterminate plant that produces tillers adjacent to the primary shoot as well as in daughter plants far from the main shoot. Thus the naturally greater tillering potential of quackgrass, due to greater dispersion ability, provided larger LUE values based on TSHT. LUE values based on TSHT also increased as total stand density increased. At higher plant densities plants filled the smaller interplant spaces more rapidly and with less shoots than at lower stand densities. There were no density by mixture interactions for LUE values based on TSHT.

LUE values based on TFEC were positively correlated with increases in wheat proportion. The quackgrass monoculture was much less efficient in irradiance utilization in terms of TFEC than any of the mixtures or the wheat monocultures. This lowered LUE is more a reflection of the fecundity values for wheat being much larger than those from quackgrass, rather than a true reflection of a trend due to treatment effects. For example, over the two years the average quackgrass monoculture produced 3083 rhizome nodes  $\text{m}^{-2}$  and the average wheat monoculture produced 11,090 kernels  $\text{m}^{-2}$  (Wilcox - unpublished).

LUE of mixtures, particularly mixtures with high proportions of quackgrass, were usually greater than LUE values calculated for monocultures (Table 24) and PAR transmittance values for mixtures were usually intermediate to monocultures (Figures 14 and 15). This treatment response difference between LUE and PAR transmittance for wheat-quackgrass mixtures suggests that the greater LUE of mixtures was not due to increased PAR interception. Instead, improved PAR utilization efficiency, perhaps through improved quackgrass leaf positioning last half of the growing season, was responsible for greater LUE



of mixtures. In the wheat-quackgrass mixtures it was observed that wheat shoots often supported the quackgrass in an upright habit which would allow more of the quackgrass plant to receive irradiance than when in a more prostrate habit. Quantitative assessment of quackgrass leaf positioning in the additive series was not conducted. Alternatively, late season shifts in radiation spectral quality and radiation quantity could also contribute or be responsible for the greater LUE of mixtures (Allen *et al.*, 1975; Norman and Arkebano, 1991). Greater LUE for mixtures relative to monocultures has also been reported by Willey (1979) in intercrops.

Competition for light in the wheat-quackgrass mixtures was variable and temporally dependent. Wheat was superior to quackgrass in irradiance interception in the first half of the growing season and underwent progressive senescence in the latter half of the growing season. Losses induced in quackgrass by wheat PAR interception in the first half of the growing season were possibly offset by more efficient quackgrass leaf positioning in the latter half. Unlike annual species, early shading is not likely to be effective against quackgrass as the majority of its light requirements for rhizome production occurs after crop growth ceases (Cussans, 1968; Rauber and Bottger, 1984; Skutterud, 1984). From a practical standpoint these results indicate that depending only on competition for light from wheat to suppress quackgrass can be unsuccessful over the long run. Successful quackgrass management in wheat will require the integration of wheat competition for light with other control measures.

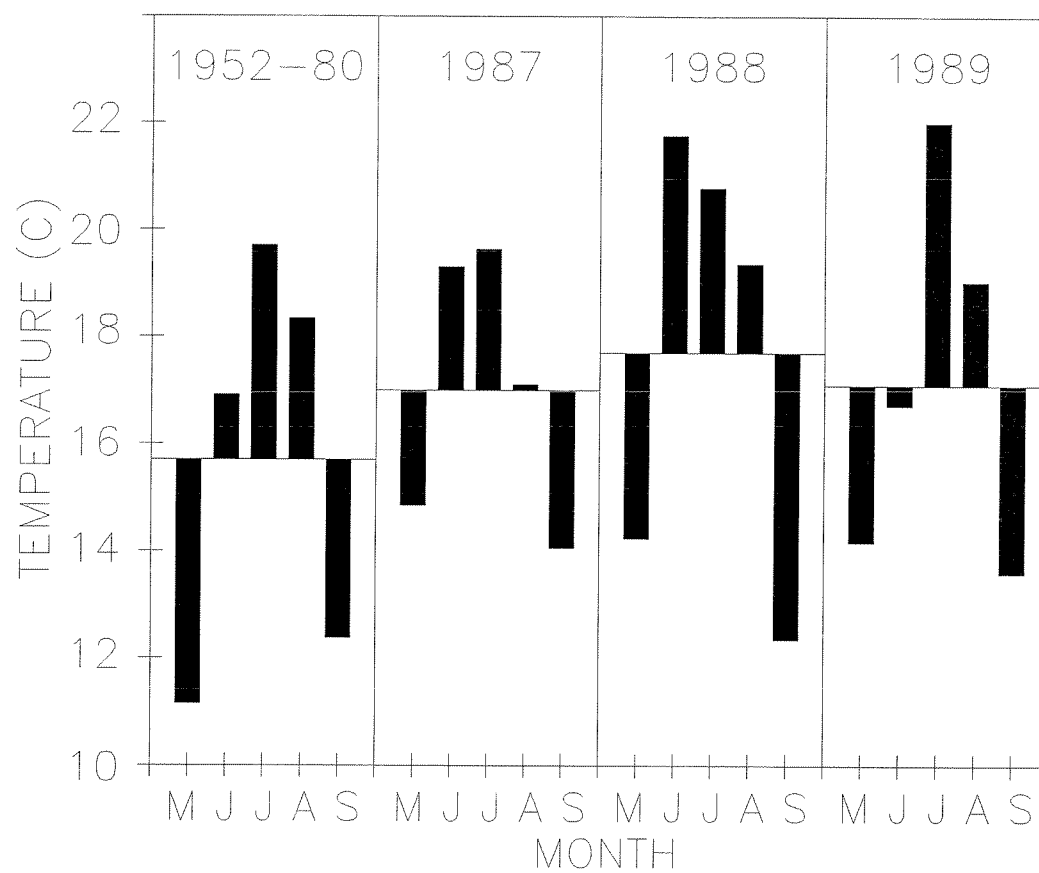
**APPENDIX 2.**

**Climatic data for the University of Manitoba, Portage la Prairie, Research Station**  
**(latitude 49° 56' N, longitude 97° 14' W)**  
**during the growing seasons of 1987, 1988 and 1989.**

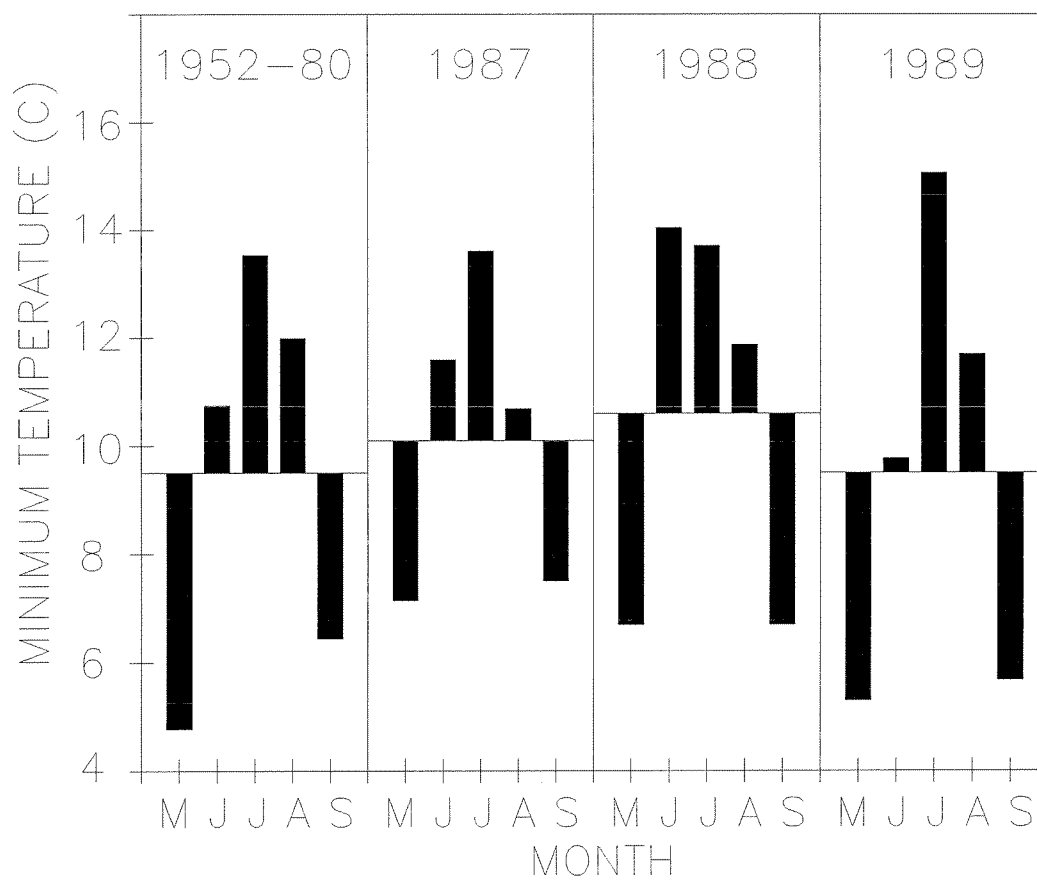
All meteorological data were collected using a minimum dataset recorder<sup>19</sup> except for the 30 year average (*sic*) data which was collected by Environment Canada at CFB Portage la Prairie. All 24 hour readings were from midnight to midnight and all integrated readings were determined at one-minute intervals. Solar irradiance was based on 24 hour integration of readings from a pyronometer sensor. A linearized thermistor at a height of four feet recorded the 24 hour integrated mean temperature and minimum and maximum temperatures. A linearized thermistor placed at a 10 cm depth in the soil recorded the 24 hour mean integrated temperatures beneath the grass covered lawn area surrounding the recorder. The 24 hour total precipitation was determined using a 20.3 cm orifice diameter (American style) tipping bucket (1mm content) rain guage.

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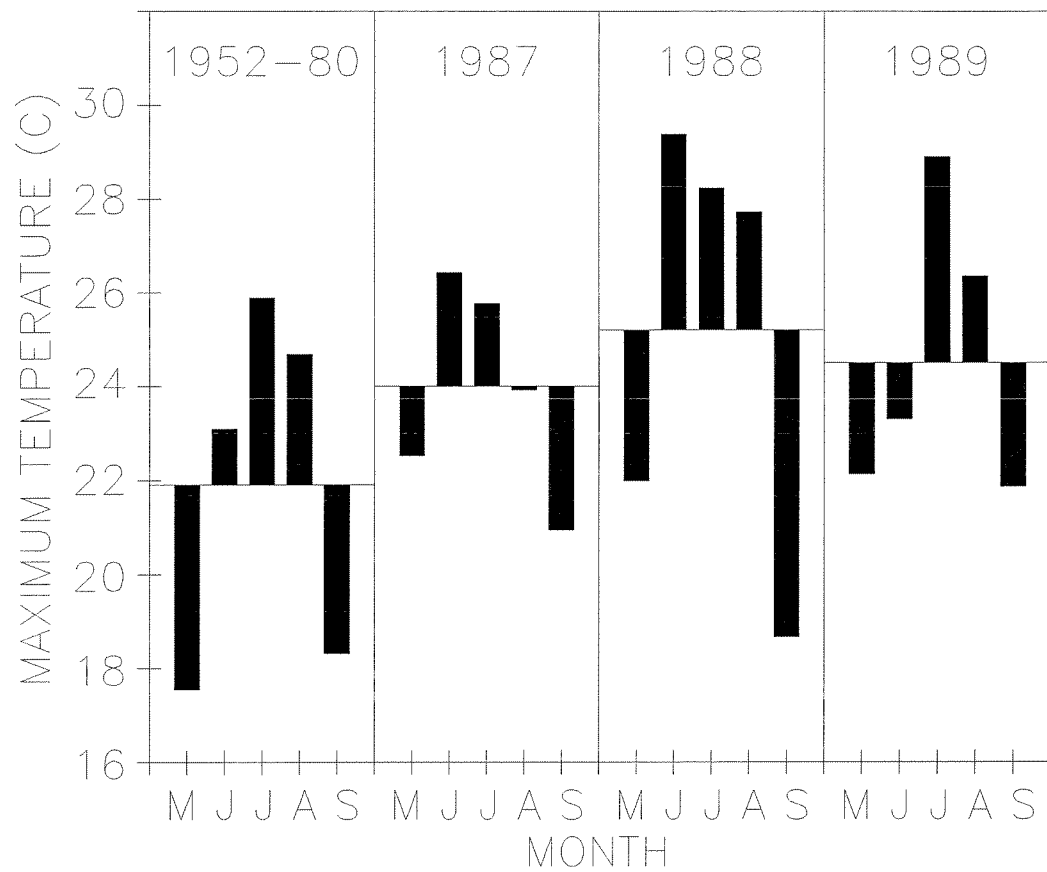
<sup>19</sup> Licor LI-1200S, LI-COR, LTD. Lincoln, Nebraska.



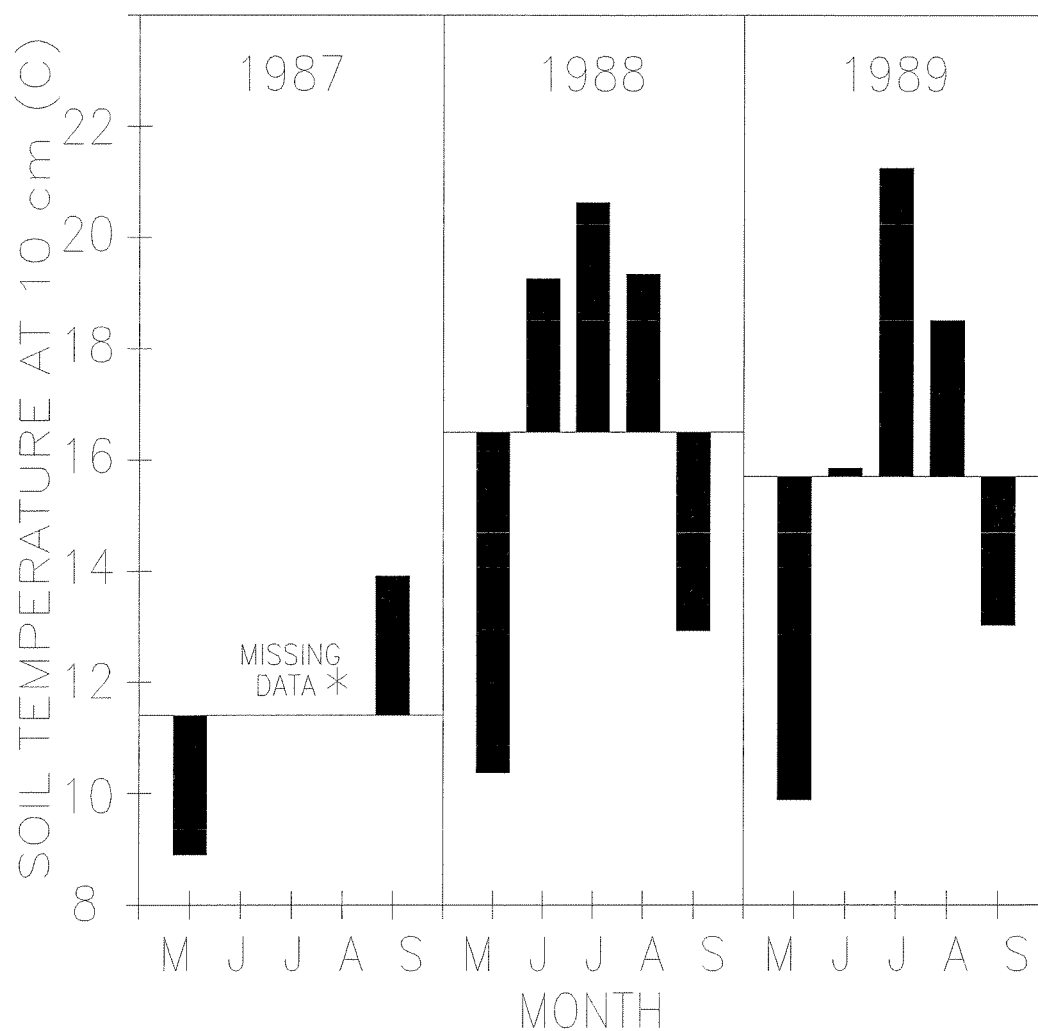
**Figure 16.** Seasonal subseries graph illustrating mean air temperatures recorded during the growing seasons of 1987, 1988, and 1989, relative to a 30 year (sic) average.



**Figure 17.** Seasonal subseries graph illustrating minimum air temperatures recorded during the growing seasons of 1987, 1988, and 1989, relative to a 30 year (sic) average.



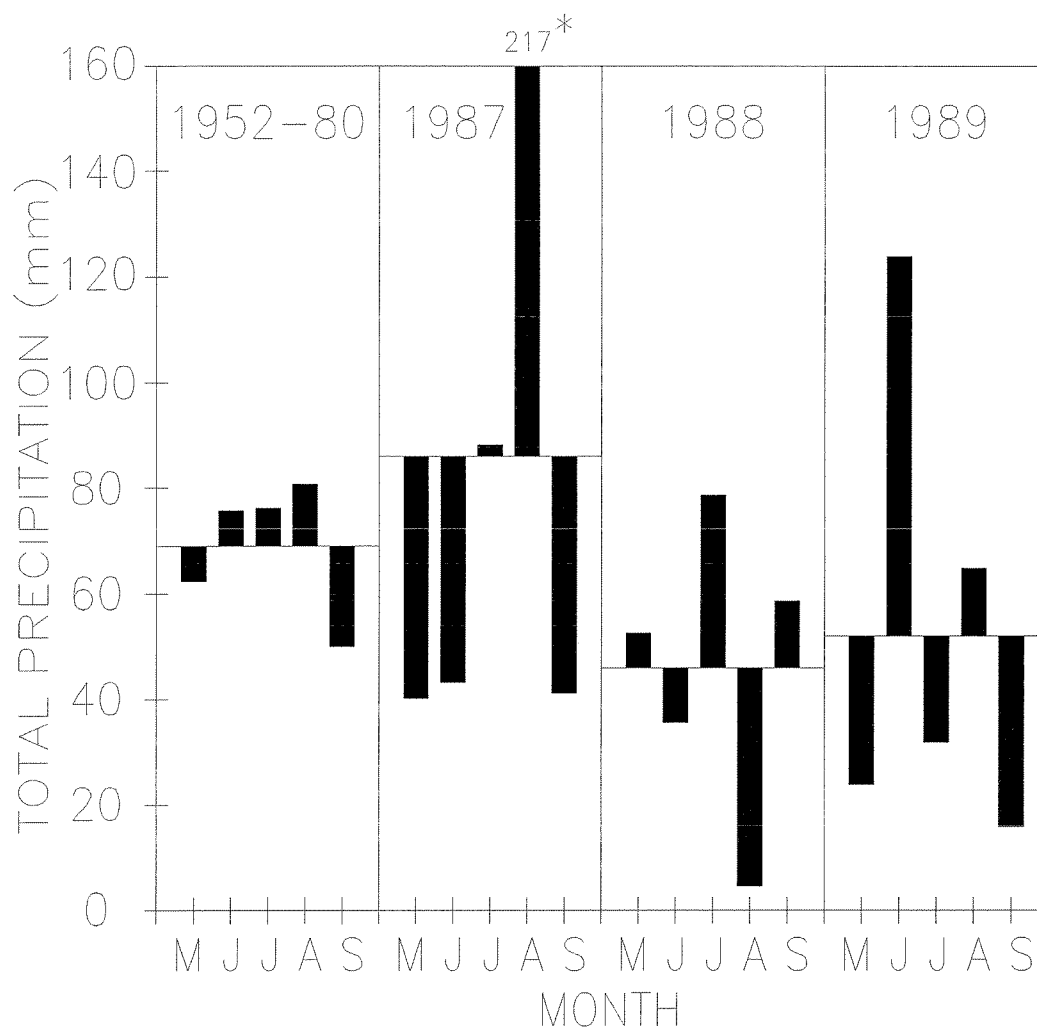
**Figure 18.** Seasonal subseries graph illustrating maximum air temperatures recorded during the growing seasons of 1987, 1988, and 1989, relative to a 30 year (sic) average.



**Figure 19. Seasonal subseries graph illustrating the mean daily soil temperature (at 10cm depth, below lawn) during the growing seasons of 1987, 1988, and 1989, at the Portage Research Station.**

20

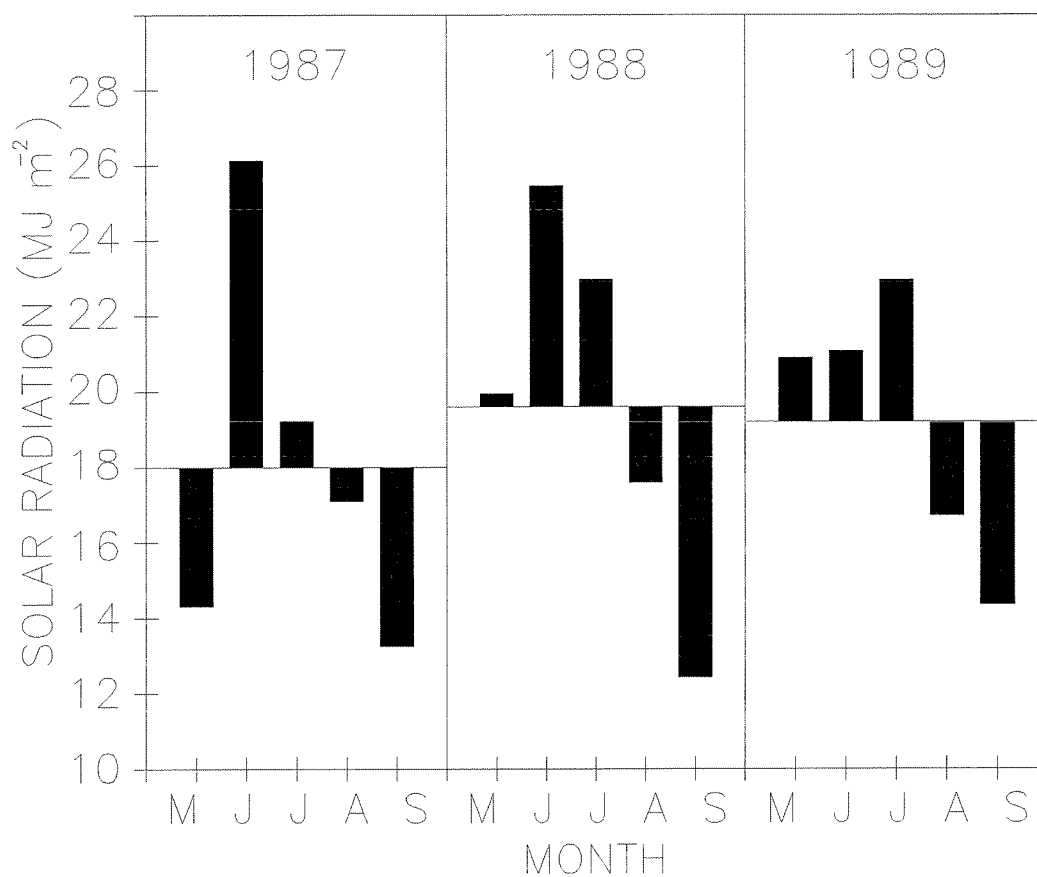
<sup>20\*</sup> Technical difficulties with soil thermocouple resulted in lost data in 1987 for last part of May until the end of August.



**Figure 20. Seasonal subseries graph illustrating mean monthly precipitation recorded during the growing seasons of 1987, 1988, and 1989 relative to a 30 year (sic) average.**

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<sup>21\*</sup> The majority of the 217mm of rain that fell in August, 1987, was 182mm that fell on August 14. CFB Portage recorded 86.4mm while a farm adjacent to the station recorded 120mm. Clearly rainfall on this date was both torrential and highly localized.



**Figure 21.** Seasonal subseries graph illustrating the mean daily solar radiation (400-1100nm) recorded during the growing seasons of 1987, 1988, and 1989, at the Portage Research Station.



### **APPENDIX 3.**

#### **Water Use and Water Use Efficiency (WUE) in the Additive Series Experiment.**

Competition is the most common interference mechanism in plants. It has been stated that in quackgrass-cereal mixtures, under British conditions, competition for water is less important than is competition for light and nutrients (Thurston and Williams, 1968). This suggestion conflicts with field research in North America that has shown that much of the interference by quackgrass in corn and soybeans can be alleviated by the addition of supplemental water (Young *et al*, 1983, 1984). Further research is needed to determine the relative importance of competition for water in quackgrass interference.

#### **Experimental Design**

Soil moisture use below the additive replacement series was monitored using a neutron attenuation technique to determine if the technique has potential to detect competition for water between quackgrass and wheat. The general experimental layout and procedures have been described in detail elsewhere (Manuscript 1).

## Water Use

In both 1987 and 1988 one block of the additive replacement series experiment was monitored for soil water. Volumetric water content was determined at depths of 15, 30, 45, 60, and 100 cm using a neutron moisture meter<sup>22</sup>. Access tubes were installed at the centre of each plot just prior to planting and readings were taken at approximately weekly intervals until plot harvest at wheat maturity. The neutron probe readings were converted to volumetric moisture using the relationship described in Figure 22. Soil field capacity and permanent wilting point of the soil at each monitored depth was determined and the maximum potential available water was defined as the difference between field capacity and the permanent wilting point. Soil physical characteristics at the site are listed in Table 25. Daily precipitation was determined by a tipping bucket rain gauge attached to a minimum dataset recorder<sup>23</sup>. The mean monthly precipitation at the site has been presented elsewhere (Appendix 1).

Water use efficiency at the site was determined as

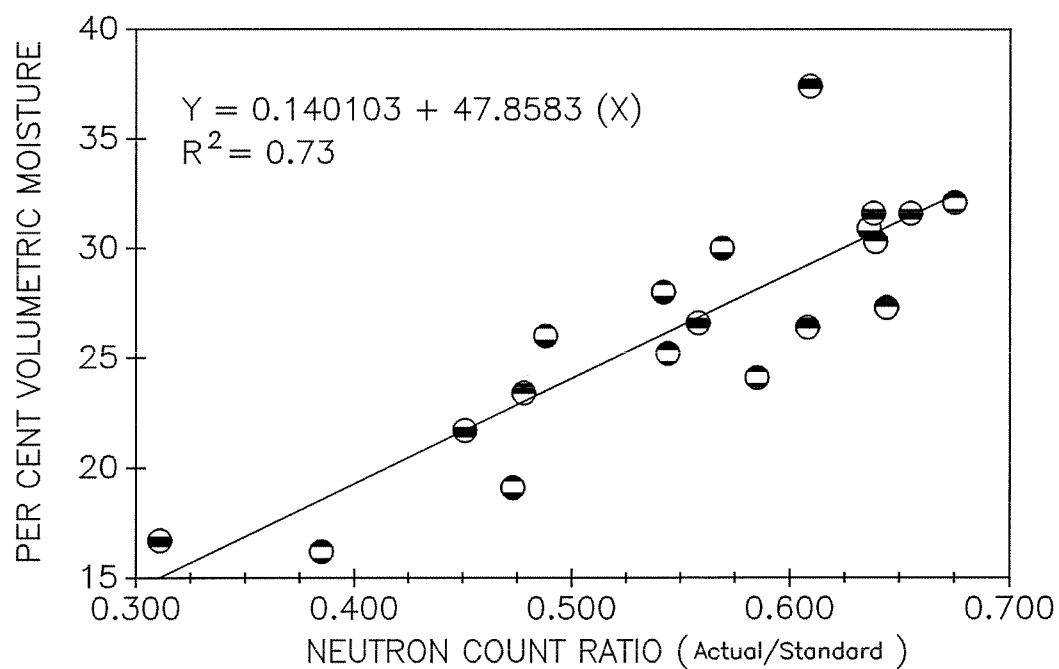
$$WUE = Y_k/W_c = Y_k/\sum_k(W_{o_k} + PPT_k - W_{f_k}).$$

Where  $Y_k$  is the per area variable yield in the monitored block,  $W_c$  is the total water consumed over the growing season,  $W_{o_k}$  is the intervals initial volume of available soil water to the 1.0 m depth,  $PPT_k$  is the total precipitation over the interval, and  $W_{f_k}$  is the intervals final volume of available soil water to the 1.0 m depth. The calculated water use efficiencies

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<sup>22</sup>Troxler, Model 3000

<sup>23</sup>LI-1200S. LI-COR Inc., Lincoln, Nebraska.



**Figure 22.** Calibration line for the neutron probe developed for range 10 of the Portage Research Station. Each point is the mean of at least three soil samples.

**Table 25. Soil physical properties at the site of the wheat-quackgrass additive series experiment.**

Depth	Bulk Density	Wilting Point <sup>a</sup>	Field Capacity	Potential Available Water
--(cm)--	-(g cm <sup>-3</sup> )-	------(%)-----		
15	1.01	17.7	34.1	16.4
30	0.99	15.1	30.5	15.4
45	1.17	13.1	32.7	19.6
60	1.16	11.4	29.0	17.6
100	1.23	10.9	26.6	15.7

<sup>a</sup> Wilting point determined using tomato plants.

for each treatment were analyzed by ANOVA as a randomized complete block design with each years data being considered a replicate. When significant by ANOVA at  $\alpha=0.05$  means were separated by the LSD test at  $\alpha=0.05$ .

## Results and Discussion

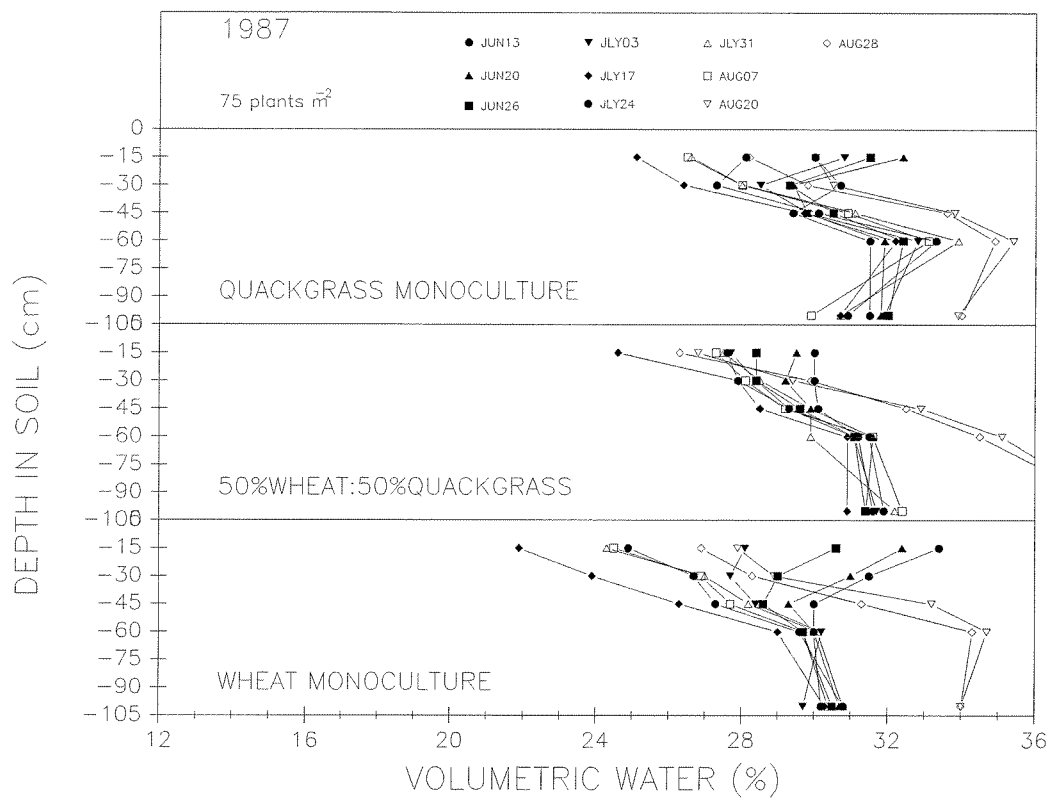
The months of May and June in 1987 were dryer than average and the entire growing season in 1988 was considerably dryer than average (Appendix 1). However the experimental site had a high water table and the soil water content from as shallow as 60 cm exceeded or was equal to soil field capacity throughout both growing seasons. The dry conditions in the surface soil layers would have been expected to encourage competition for soil water between plants.

The plot area covered by plants at the 150 and 300 plants  $\text{m}^{-2}$  was determined to be inadequate for comparing soil moisture use in the treatments. It was initially assumed that because there was greater than a 15 cm radius of plants around the axis tubes, that moisture use could be adequately assessed. This assumption failed to account for horizontal water flow in the soil. The guard-rows did not adequately buffer the higher density treatments from horizontal water movement. This was demonstrated by the counter-intuitive result of 300 plants  $\text{m}^{-2}$  having more soil water available than the lower density treatments (Data not presented). However the 150 plants  $\text{m}^{-2}$  treatment did have less soil water available than did the 75 plants  $\text{m}^{-2}$  treatments and thus it was assumed that the size of the 75 plant  $\text{m}^{-2}$  plots adequately buffered the monitored area from horizontal water movement. As a result the water use results for the 150 and 300 plant  $\text{m}^{-2}$  treatments are not considered accurate.

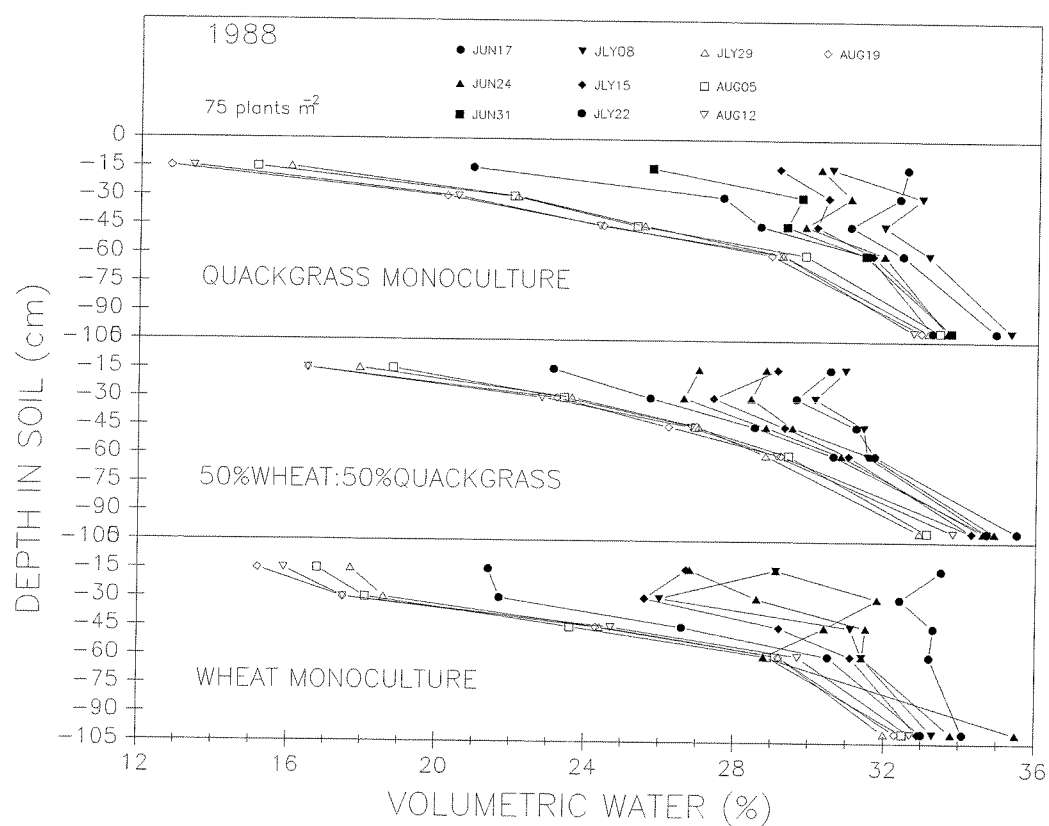
The seasonal water use patterns for three of the 75 plant  $\text{m}^{-2}$  treatments are illustrated in Figures 23 and 24 . The graphs illustrate the high volumetric water contents at the 60 and 100 cm depths. They also show the extreme variability in soil water contents from one year and one week to the next.

The calculated values of WUE in 1988 were approximately twice that of 1987 (Data not presented). For ease of presentation and discussion the pooled mean WUE for both years is presented (Table 26).

The magnitude of the WUE values depended on yield variables selected. WUE based on TFEC yield variables showed the widest relative range in values and WUE based on TBIO yield variables the narrowest range in values (Table 26). For every yield variable there was a trend that high wheat mixture proportions at high densities had larger WUE values than low density high quackgrass mixture proportions. However a significant mixture by density interaction was not detected. The non-significance is attributable to a lack of sensitivity for mixture by density interactions because of only two years data and the horizontal water movement obscuring density effects. For the reproductive yield variables there were significant mixture effects with the 75 and 100 percent quackgrass mixture proportions having significantly lower WUE values than the 50, 75, and 100 percent wheat mixture proportions. A similar trend was observed for the vegetative yield variables. There was a significant density effect where the 75 plants  $\text{m}^{-2}$  treatment had significantly lower WUE than the 300 plants  $\text{m}^{-2}$  treatments. A similar trend also occurred with the reproductive yield variables. In the case of TBIO this WUE difference due to stand density was only detected when  $\alpha$  was raised from 5 to 6 percent. For vegetative yield variables there



**Figure 23.** Growing season volumetric water content in relation to soil depth beneath 3 treatments of the wheat-quackgrass additive series at the Portage Research Station in 1987.



**Figure 24.** Growing season volumetric water content in relation to soil depth beneath 3 treatments of the wheat-quackgrass additive series at the Portage Research Station in 1988.



**Table 26. Wheat-quackgrass additive series water use efficiency (WUE) values calculated for selected variables.**

Total Stand	Mixture Proportion		Variable <sup>a</sup>		WUE <sup>b</sup>	
Density	Wheat	Quackgrass	TBIO	TREP	TSHT	TFEC
(# m <sup>-2</sup> )	------(%)-----		------(g Kg <sup>-1</sup> )-----		------(# Kg <sup>-1</sup> )-----	
75	0	100	2.39	2.20	0.60	8.48
75	25	75	2.71	2.32	0.76	20.06
75	50	50	2.75	2.31	0.94	30.00
75	75	25	2.36	1.97	0.80	29.16
75	100	0	2.85	2.37	0.98	38.39
150	0	100	2.85	2.56	0.62	11.65
150	25	75	3.19	3.11	0.78	21.43
150	50	50	3.88	3.17	1.22	39.43
150	75	25	3.56	3.06	1.20	45.94
150	100	0	2.86	2.64	0.99	38.60
300	0	100	2.29	2.54	0.32	8.52
300	25	75	2.86	3.41	0.64	26.70
300	50	50	4.53	4.58	1.33	42.41
300	75	25	4.08	3.68	1.43	56.28
300	100	0	3.45	3.48	1.04	40.36
		S.E.M. <sup>c</sup>	(0.507)	(0.502)	(0.168)	(7.121)
Pooled	0	100	2.51	2.43	0.51	9.55
Pooled	25	75	2.92	2.94	0.73	22.73
Pooled	50	50	3.72	3.35	1.16	37.28
Pooled	75	25	3.33	2.90	1.14	43.79
Pooled	100	0	3.05	2.83	1.00	39.12
		S.E.M.	(0.293)	(0.290)	(0.097)	(4.111)
75	Pooled		2.61	2.23	0.81	25.22
150	Pooled		3.26	2.9	0.96	31.41
300	Pooled		3.44	3.53	0.95	34.85
		S.E.M.	(0.226)	(0.224)	(0.075)	(3.180)

<sup>a</sup> Abbreviations: TBIO=vegetative size, TREP=reproductive effort, TSHT=vegetative dispersion, and TFEC=reproductive fecundity.

<sup>b</sup> Average of the 1987 and 1988 WUE.

<sup>c</sup> Standard error of means for combined 1987 and 1988 results.

was no significant mixture response and for the reproductive yield variables there was no significant density response. Stand density effects for all variables can not be unambiguously interpreted as there was horizontal water movement into the smaller plots of the higher density treatments which would skew the results of these treatments to higher WUE values. However, mixture effects that were detected are likely realistic and strong despite the horizontal water movement into the smaller plots.

The results of this investigation demonstrate the promising potential of the neutron attenuation technique for investigating competition for water beneath an additive replacement series design. However, the minimum plot size should be at least as large as the 75 plant  $\text{m}^{-2}$  plot (40 cm radius) used in this trial. A site with a lower water table than this location would also be desirable to better promote and measure competition for water between these species.

## **APPENDIX 4.**

### **Soil Nutrient Change in the Soil Beneath Treatments of the Additive Series Experiment.**

Quackgrass is considered to be a luxuriant consumer of nutrients. Researchers have observed that quackgrass is one of the most effective plants for reclaiming nutrients from sprayed-on municipal sewage effluent (Mitich, 1987; Adriano *et al*, 1975). Analysis of soil from pots in which quackgrass was grown has shown reductions in the levels of available nitrate nitrogen and potassium (Plhak, 1987). In pot studies, established quackgrass plants were more effective than adjacent alfalfa or oat plants in withdrawing nutrients from a nutrient solution; particularly nitrogen, and to a lesser degree phosphorus and potassium (Ohman and Kommedahl, 1964). In pot studies where adequate light and water were provided, wheat and quackgrass competed for nutrients, most likely nitrogen (Williams, 1969). In pot studies with quackgrass and sugar beet it was determined that competition for nitrogen was more important than competition for potassium (Welbank, 1964). The relative importance of various nutrients to quackgrass competition in the field has not been determined.

## Experimental Design

Soil nutrient status below the additive replacement series was monitored to determine if the changes in nutrient status could be related to competition for available nitrogen, phosphorous or potassium by quackgrass in wheat. The general experimental layout and procedures for the additive replacement series experiment have been described elsewhere (Manuscript 1).

## Nutrient Use

Prior to planting and immediately after harvest 2.5 cm diameter soil cores were removed from each plot to a depth of 60 cm. The soil cores from each block were then air-dried and bulked by treatment and submitted for analysis to the Manitoba Provincial Soil Testing Laboratory<sup>24</sup>. Additionally a set of cores was removed 1.5 m from each block that served as unplanted checks. Samples were analyzed for sodium-bicarbonate extractable nitrate-nitrogen, sodium-bicarbonate extractable phosphorous and ammonium-acetate exchangeable potassium. The change in soil nutrient status as a result of treatment was determined as the difference between at-planting soil nutrient content and at-harvest nutrient content minus the same difference in unplanted check plots. The calculated change in nutrient status values for each treatment were analyzed by ANOVA as a randomized complete block design with each years data considered a replicate. When determined significant by ANOVA at  $\alpha = 0.05$  the means were separated by the LSD test at  $\alpha=0.05$ .

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<sup>24</sup> Ellis Building, University of Manitoba, Winnipeg, MB.

## Results and Discussion

The levels of available nitrate nitrogen, phosphorous and potassium under all treatments at all sampling times was high (Tables 27,28 and 29). This high nutrient status would minimize the competition for nutrients by quackgrass in wheat.

Reduction in soil nutrient levels from planting to harvest occurred but were not related to treatments (analysis not presented). There was natural variability in soil nutrient levels from treatment to treatment. This is demonstrated by variability in the at-planting nutrient levels which in theory should be relatively uniform (Tables 27,28 and 29). The natural variability within plots may have obscured detection of any treatment differences.

Soil is a dynamic substrate and nutrient levels present are more than just a function of plant uptake. In situations with abundant nutrients, exchangeable ions removed by roots will be rapidly replaced from the soil colloids. For example it has been observed that available nitrate levels in soils that were depressed by quackgrass growth recovered after 14 days rest to the levels that were present in a control soil (Plhak, 1967). Through nitrification  $\text{NO}_3$  can be released from mineral and organic matter in the soil. Potassium can be released from clay minerals and phosphorous can be re-solubilized.

Another source of soil nutrient variability in this experiment is the highly mobile nature of nitrate nitrogen. There could have been horizontal movement of nitrate from unplanted areas outside these relatively small plots to the sampled areas inside the plots. There was evidence of horizontal water movement into plots (Appendix 2). Vertical movement of  $\text{NO}_3$  could also occur as it moves upward with the soil water as evaporation dries the soil surface.

**Table 27. Average available nitrate nitrogen in the soil beneath each treatment of the wheat-quackgrass additive series in 1987 and 1988.**

		Available Nitrate Nitrogen (0 - 60 cm)			
		1987		1988	
Total Stand Density	Mixture Proportion Wheat      Quackgrass	At Planting	At Harvest	At Planting	At Harvest
(# m <sup>-2</sup> )	(%)	(kg ha <sup>-1</sup> )			
75	0      100	465	208	239	299
75	25      75	465	170	328	353
75	50      50	640	123	353	307
75	75      25	410	93	353	307
75	100      0	515	160	353	290
150	0      100	750	192	299	312
150	25      75	330	176	292	299
150	50      50	580	154	304	233
150	75      25	350	185	363	421
150	100      0	510	129	312	301
300	0      100	700	138	296	330
300	25      75	745	192	368	389
300	50      50	655	115	388	339
300	75      25	610	106	372	403
300	100      0	480	146	380	315
	Unplanted	547	369	340	328

**Table 28. Average available phosphorus in the soil beneath each treatment of the wheat-quackgrass additive series in 1987 and 1988.**

		Available Phosphorous (0 - 15 cm)			
		1987		1988	
Total	Mixture Proportion				
Stand		At	At	At	At
Density	Wheat      Quackgrass	Planting	Harvest	Planting	Harvest
(# m <sup>-2</sup> )	(%)	(kg ha <sup>-1</sup> )			
75	0      100	106	87	138	176
75	25      75	106	41	187	152
75	50      50	134	108	214	109
75	75      25	96	59	198	97
75	100      0	140	62	141	65
150	0      100	132	62	147	99
150	25      75	114	78	187	102
150	50      50	141	120	129	109
150	75      25	103	49	198	126
150	100      0	188	56	143	93
300	0      100	96	50	216	96
300	25      75	147	105	169	108
300	50      50	184	138	257	85
300	75      25	161	67	214	100
300	100      0	112	55	284	103
	Unplanted	132	155	188	112

**Table 29. Average available potassium in the soil beneath each treatment of the wheat-quackgrass additive series in 1987 and 1988.**

		Available Potassium (0 - 15 cm)			
		1987		1988	
Total Stand Density	Mixture Proportion Wheat      Quackgrass	At Planting	At Harvest	At Planting	At Harvest
(# m <sup>-2</sup> )	(%)	(kg ha <sup>-1</sup> )			
75	0      100	1665	1445	2204	1862
75	25      75	1510	1445	2417	1854
75	50      50	1535	1535	2257	1573
75	75      25	1370	1370	2120	1588
75	100      0	1670	950	1930	1588
150	0      100	1600	1240	1915	1558
150	25      75	1445	1445	2204	1619
150	50      50	1650	1475	2219	1581
150	75      25	1460	1270	2219	1839
150	100      0	1520	1480	2090	1710
300	0      100	1445	1270	2409	1710
300	25      75	1445	1545	2143	1748
300	50      50	1590	1560	2090	1725
300	75      25	1550	1370	2090	1824
300	100      0	1510	1400	2022	1816
	Unplanted	1528	1670	2155	1766



The results of this investigation illustrate the problems and ineffectiveness of monitoring soil nutrient changes over the whole growing season for determining the extent of nutrient competition by quackgrass on wheat. Future investigations should utilize plant nutrient analysis, as others have done (Welbank, 1964), to provide discrimination between treatments. Plot sizes should also be larger than those of this experiment to minimize the potential for nitrate movement outside the plots to the sampling areas. The multi-faceted dynamics of the soil system will always make determination of soil nutrient competition between species in the field particularly difficult.

## APPENDIX 5

### Quackgrass Spreadsheet (Lotus 123 v.3.1) Model Cell Format Codes

A:C2: {SWISS14 Bold} PR 'UNIVERSITY OF MANITOBA  
 A:O2: {SWISS14 Bold} PR 'UNIVERSITY OF MANITOBA  
 A:C3: {SWISS14 Bold} PR 'ANNUAL CROP - QUACKGRASS INTERFERENCE  
 CALCULATOR  
 A:O3: {SWISS14 Bold} PR 'ANNUAL CROP - QUACKGRASS INTERFERENCE  
 CALCULATOR  
 A:C6: {Bold} PR 'MODEL INPUT  
 A:O6: {Bold L} PR 'MODEL OUTPUT  
 A:C9: {Bold} PR ' CROP  
 A:O9: {Bold L} PR ' QUACKGRASS  
 A:D11: {Bold} PR 'CROP CHARACTERISTICS  
 A:S11: {S1} PR ^YEAR 1  
 A:U11: {S1} PR ^YEAR 2  
 A:W11: {S1} PR ^YEAR 3  
 A:F12: {S1} PR ^WHEAT  
 A:H12: {S1} PR ^FLAX  
 A:J12: {S1} PR ^P. CANOLA  
 A:P13: {Italics} PR ' SPRING SHOOT NUMBERS  
 A:S13: {Shadow LRTB} (F0) PR +F78  
 A:U13: {Shadow LRTB} (F0) PR +H78  
 A:W13: {Shadow LRTB} (F0) PR +J78  
 A:D14: {Italics} PR ' CROP YIELD  
 A:F14: {Shadow LRTB} (F1) U 32.8  
 A:G14: {DUTCH8} (F1) PR [W5] ^ (33bu/A)  
 A:H14: {Shadow LRTB} (F1) U 17.8  
 A:I14: {DUTCH8} (F1) PR [W5] ^ (18bu/A)  
 A:J14: {Shadow LRTB} (F1) U 18.1  
 A:K14: {DUTCH8 R} PR [W5] ^ (18bu/A)  
 A:P15: {Italics} PR ' SHOOT NUMBERS AT HARVEST  
 A:S15: {Shadow LRTB} (F0) PR +F79  
 A:U15: {Shadow LRTB} (F0) PR +H79  
 A:W15: {Shadow LRTB} (F0) PR +J79

A:D16: {Italics} PR ' CROP PRICE  
 A:F16: {Shadow LRTB} (C2) U 3  
 A:G16: {DUTCH8} (C2) PR [W5] '(\$5.31/bu)  
 A:H16: {Shadow LRTB} (C2) U 6  
 A:I16: {DUTCH8} (C2) PR [W5] '(\$8.80/bu)  
 A:J16: {Shadow LRTB} (C2) U 6.5  
 A:K16: {DUTCH8 R} PR [W5] '(\$8.34/bu)  
 A:P17: {Italics} PR ' BUD NUMBERS AT HARVEST  
 A:S17: {Shadow LRTB} (F0) PR +F80  
 A:U17: {Shadow LRTB} (F0) PR +H80  
 A:W17: {Shadow LRTB} (F0) PR +J80  
 A:D19: {Bold} PR 'CROP ROTATION  
 A:F20: {S1} PR ^YEAR 1  
 A:H20: {S1} PR ^YEAR 2  
 A:J20: {S1} PR ^YEAR 3  
 A:O20: {Bold L} PR ' CROP  
 A:D22: {Italics} PR ' CROP GROWN  
 A:F22: {Shadow LRTB} U 'W  
 A:H22: {Shadow LRTB} U 'W  
 A:J22: {Shadow LRTB} U 'F  
 A:S22: {S1} PR ^YEAR 1  
 A:U22: {S1} PR ^YEAR 2  
 A:W22: {S1} PR ^YEAR 3  
 A:Y22: {S1} PR ^TOTAL  
 A:F23: {DUTCH8} PR ^ (USE : C = POL. CANOLA, F = FLAX, W = RS WHEAT)  
 A:S23: {S1} PR +F22  
 A:U23: {S1} PR +H22  
 A:W23: {S1} PR +J22  
 A:P24: {Italics} PR ' YIELD LOSS PER CENT  
 A:S24: {Shadow LRTB} (P0) PR +F81/100  
 A:U24: {Shadow LRTB} (P0) PR +H81/100  
 A:W24: {Shadow LRTB} (P0) PR +J81/100  
 A:C26: {Bold} PR ' QUACKGRASS  
 A:P26: {Italics} PR ' YIELD LOSS \$ VALUES  
 A:S26: {Shadow LRTB} (C2) PR +F82  
 A:U26: {Shadow LRTB} (C2) PR +H82  
 A:W26: {Shadow LRTB} (C2) PR +J82  
 A:Y26: {Shadow LRTB} (C2) PR +L82  
 A:D28: {Bold} PR 'INITIAL INFESTATION  
 A:D30: {Italics} PR ' YEAR 1 QUACKGRASS SHOOTS/sqM  
 A:H30: {Shadow LRTB} U 60  
 A:I30: {Italics} PR [W5] "AT  
 A:F32: {Shadow LRTB} U 30  
 A:G32: {Italics} PR [W5] ' DAYS AFTER PLANTING  
 A:F33: {DUTCH8} PR ^ (Model based on 30 DAP)  
 A:D35: {Bold} PR 'WINTER SURVIVAL OF BUDS  
 A:F37: {S1} PR ^BETWEEN

A:H37: {S1} PR ^BETWEEN  
 A:F38: {S1} PR ^YEARS  
 A:H38: {S1} PR ^YEARS  
 A:F39: {S1} PR ^1 and 2  
 A:H39: {S1} PR ^2 and 3  
 A:D40: {Italics} PR ' PER CENT SURVIVAL  
 A:F40: {Shadow LRTB} U 95  
 A:G40: {DUTCH8} PR [W5] "(95 %)  
 A:H40: {Shadow LRTB} U 95  
 A:I40: {DUTCH8} PR [W5] "(95 %)  
 A:D43: {Bold} PR 'SPRING BUD EMERGENCE  
 A:H45: {S1} PR ^SPRING 2  
 A:J45: {S1} PR 'SPRING 3  
 A:D47: {Italics} PR ' PER CENT OF BUDS EMERGING  
 A:H47: {Shadow LRTB} U 25  
 A:J47: {Shadow LRTB} U 25  
 A:H48: {DUTCH8} PR "(25% if no herbicide, 60% if herbicide applied)  
 A:D50: {Bold} PR 'IN-CROP HERBICIDE KILL FACTOR  
 A:F52: {S1} PR ^WHEAT  
 A:H52: {S1} PR ^FLAX  
 A:J52: {S1} PR ^CANOLA  
 A:D54: {Italics} PR ' % MORTALITY  
 A:F54: {Shadow LRTB} (F0) U 0  
 A:H54: {Shadow LRTB} (F0) U 90  
 A:J54: {Shadow LRTB} (F0) U 95  
 A:B60: {Bold} PR [W3] 'WORKSHEET  
 A:C62: PR 'WHEAT VALUE / ACRE  
 A:F62: {B} (C2) PR +F14\*F16  
 A:C63: PR 'FLAX VALUE / ACRE  
 A:F63: {B} (C2) PR +H14\*H16  
 A:C64: PR 'CANOLA VALUE / ACRE  
 A:F64: {B} (C2) PR +J14\*J16  
 A:C66: PR 'SAMPLE DATE FORMULA  
 A:F66: PR '2.5+1.061\*(DAP)=DTM%  
 A:I66: PR [W5] 2.5+1.061\*(30)  
 A:J66: PR '% is 30 DAP  
 A:C67: PR 'SHOOT AUTOREGRESSION  
 A:F67: (F0) PR '13.407+(2.479\*SS)=FS  
 A:C68: PR 'SHOOT/BUD ALLOMETRY  
 A:F68: (F0) PR '(@EXP(1.458))\*(FS^1.075)=FB  
 A:C69: PR 'WHEAT YIELD FORMULA  
 A:F69: (F1) PR '98.7\*(1-((0.43\*FS)/(100\*(1+(0.43\*(FS/194))))))=WY%  
 A:C70: PR 'FLAX YIELD FORMULA  
 A:F70: (F1) PR '100\*(1-((2.07\*FS)/(100\*(1+(2.07\*(FS/130))))))=FS%  
 A:C71: PR 'CANOLA YIELD FORMULA  
 A:F71: (F1) PR '100\*(1-((0.41\*FS)/(100\*(1+(0.41\*(FS/141))))))=CY%  
 A:C74: PR 'OVERWINTER BUD SURVIVAL

A:H87: (F1) PR  $100 * (1 - ((0.41 * H78) / (100 * (1 + (0.41 * (H78 / 141))))))$

A:J87: (F1) PR  $100 * (1 - ((0.41 * J78) / (100 * (1 + (0.41 * (J78 / 141))))))$

A:E89: (F1) PR ^YL%

A:F89: {S1} (F1) PR @IF(F22="F",100-F86,@IF(F22="W",100-F85,@IF(F22="C",100-F87,'ERR')))

A:H89: {S1} (F1) PR

@IF(H22="F",100-H86,@IF(H22="W",100-H85,@IF(H22="C",100-H87,'ERR')))

A:J89: {S1} (F1) PR @IF(J22="F",100-J86,@IF(J22="W",100-J85,@IF(J22="C",100-J87,'ERR')))

A:C91: (F1) PR '% HERBICIDE MORTALITY

A:F91: {S1} (F1) PR @IF(F22="F",\$H54,@IF(F22="W",\$F54,@IF(F22="C",\$J54,'ERR')))

A:H91: {S1} (F1) PR @IF(H22="F",\$H54,@IF(H22="W",\$F54,@IF(H22="C",\$J54,'ERR')))

A:J91: {S1} (F1) PR @IF(J22="F",\$H54,@IF(J22="W",\$F54,@IF(J22="C",\$J54,'ERR')))