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plant propagated from a single 3-cm rhizome segment has grown to produce 318 m of rhizome with 6,587 buds (Wilcox, unpublished data).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 kernel 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 then 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 m² quadrat was laid in the centre of its randomly allocated 1 m² quadrat and above and below ground plant samples were harvested. This is substantially smaller then the 4 m² sample recommended by Lemieux et al. (1990) but when resources and cost are were taken into account the \( \frac{1}{4} \) m² 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 m² 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
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 \((Yw\%)\) was determined to be related to spring
quackgrass shoot counts m$^{-2}$ ($Q_s$) thirty days after planting by the following model:

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

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:

$$QR_B = 4.297 \times Q_s^{1.075}.$$ 

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
(\textit{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 (\textit{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.