DEVELOPMENT OF A TOTAL SYSTEMS APPROACH TO MULTI-PEST MANAGEMENT DECISION ANALYSIS

by

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ABSTRACT

The concentration of wheat production in the Northern Great Plains has resulted in the development of specialized multitrophic agricultural pest complexes whose members interact in both positive and negative ways. In this context, management recommendations based on the traditional single-species pest control paradigm may lead to undesirable outcomes. Our goal was to develop a modeling framework to make multi-pest management decisions that take into account the existence of direct and indirect interactions among pests. We a Bayesian decision theory approach in combination with a analysis where observed intermediate nodes were replaced with error terms. This model holds several advantages current decision models, in particular it allows intuitive of coefficient estimates as the total, direct and through pest interactions, impact of management on the. We evaluated interactions between *Bromus tectorum*), *Fusarium* crown rot, and *Cephus cinctus* (wheat stem sawfly) as well as assessed the joint response of these pests to wheat seeding rates, cultivar competitiveness, and cultivar stem sawfly tolerance. Results indicate that yield differences be more readily explained as a result of the effects of on pests and multi-pest interactions, rather than just by direct effect of any particular management scheme on yield. Our provides a framework for finding the balance between simplicity and the complexity of the process being modeled, also bridges the gap between making inferences from experimental observational studies and ecological management decisions.

CHAPTER 1

INTRODUCTION

In the Northern Great Plains (NGP), the concentration of wheat production has resulted in the selection of specialized pest complexes threatening the economic and environmental sustainability of the small grain production system (Cochran *et al.*, 2006; Gan *et al.*, 2010). In this region, agricultural production systems rely on heavy subsidies of off-farm chemical and energetic inputs to manage and control pests. For example, every year wheat producers in Montana chemically treat 2,349,000 ha for weed control, 180,225 ha for insect control, and 101,250 ha for disease control (USDA-NASS, 2010).

Across the NGP, the wheat stem sawfly [*Cephus cinctus* Norton (Hymenoptera: Cephidae)], downy brome (*Bromus tectorum* L.), and *Fusarium spp.* causing crown rot of wheat (FCR, hereafter) form a multitrophic pest complex whose synergistic impacts on yield and grain quality pressures wheat cropping systems with their joint impact reaching $120 million per year in input costs alone (USDA-NASS, 2010). Traditional approaches to evaluate management practices consider these pests isolated from each other, limiting the scope of inference and potential of ecological research, environmental education, and natural resource management programs (Grant, 1998). To fill this knowledge gap, we systematically investigated the interconnected relationships between these pests and their management to develop a framework for assessing joint pest management approaches that integrate economically viable and environmentally sensible pest management tactics (NRC, 2010).

Wheat stem sawfly, downy brome and *Fusarium spp.*, represent three major pest categories: herbivorous insects, grassy weeds and pathogens. As such they have

distinctive biology and respond differently to crop management practices. The wheat stem sawfly is a widely distributed, destructive, and one of the most economically important insect pests of wheat (Beres *et al.*, 2011a). Except for a short flight period in the spring, all immature stages of the sawfly are spent inside protective plant stems where larvae feed on host tissues and overwinter in crop residue. Larvae activity throughout the growing season weakens the plant which is subsequently lodged causing reduced harvest efficiency and yield (Holmes, 1977; Morrill *et al.*, 1992).

Downy brome is an increasingly problematic weed in range, wildlands, and cropping systems across the NGP (Duncan *et al.*, 2004; Mack, 2011). Downy brome is typically a winter annual but could exhibit summer annual life history traits. The life form similarities between downy brome and wheat allow it to effectively compete for resources such as light, water and nutrients (Zimdahl, 2007). It has been estimated that crop yield reductions due to downy brome range between 28% and 92% (Rydrych and Muzik, 1968).

FCR has become a wide-spread disease of cereals in Montana and the NGP as the popularity of no-till methods grows (Moya-Elizondo *et al.*, 2011; Paulitz *et al.*, 2002). Infective propagules of *Fusarium spp.* overwinter in the crop residue or in the soil surface and infect newly sown plants, colonizing their crowns and lower internodes as they develop. Symptoms of FCR include stand and grain yield reduction, and rotting of root, crown and stem tissues (Chełkowski, 1989; Smiley *et al.*, 2005). Under drought conditions plant defenses weaken and *Fusarium spp.* can also invade and obstruct vascular tissue (Beddis and Burgess, 1992; Cook and Christen, 1976).

Despite the intensity of pest control practices utilized across the NGP, crop losses due to arthropods, pathogens, and weeds still represent a major economic burden to the farming enterprise. Furthermore, the chemically-centered pest management paradigm is challenged by the reality of wheat stem sawflies, *Fusarium spp.*,

and weeds. For example, there are no registered products that provide effective control of wheat stem sawfly larvae and FCR. In the absence of effective conventional insecticides, reduction of wheat stem sawfly populations and damage is best achieved through solid-stem wheat cultivars that restrict tunneling of boring larvae (Holmes and Peterson, 1962). At present, the availability of crop varieties resistant to FCR is limited and disease management has focused on cultural practices related to moisture management such as reduced seeding densities which limit foliage and plant biomass (Paulitz *et al.*, 2002; Smiley *et al.*, 2005). Furthermore, while fall herbicide application is commonly used to manage downy brome in reduced tillage wheat-fallow systems (Blackshaw, 1991), the heavy reliance on herbicides may result in the selection of herbicide resistant biotypes, limiting weed management options with serious economic consequences (Beckie, 2006; Beckie *et al.*, 2008; Rainbolt *et al.*, 2004).

Utilizing ecologically sound pest management strategies that encourage positive biotic interactions and take advantage of the crop's inherent preventive strengths for tolerating a pest species can reduce reliance on external inputs and their negative unintended consequences while maintaining an economically viable level of production (Norris *et al.*, 2003; Shennan, 2008). For example, considering agronomic traits such as crop drought hardiness or stem solidness and manipulating its density may influence pest population dynamics and decrease pest impacts (Beddis and Burgess, 1992; Beres *et al.*, 2010, 2011b; Dyer *et al.*, 2009; Holmes and Peterson, 1962; Lemerle *et al.*, 2001, 2004). Still, in a 2009 survey farmers across the NGP indicated that non-chemical pest management practices such as choosing resistant wheat varieties and modifying planting densities were applied only to 33% and 12% respectively of the area planted with spring wheat (USDA-NASS, 2010).

Wheat stem sawfly, downy brome, and *Fusarium spp.* do not occur in isolation and application of pest management schemes may affect all three species, often in contradictory ways. For example, the use of solid-stemmed wheat varieties that resist wheat stem sawfly lodging is the dominant cultural practice of Montana wheat producers. However, this practice could result in yield reductions due to agronomic limitations associated with these cultivars which may not be as competitive as other commonly used varieties. Furthermore, sawfly - lodging tolerant varieties have been shown to exhibit mixed results as a pest management practice as stem solidness can be reduced due to environmental factors as well as intra- and inter-specific competition (Beres *et al.*, 2009; Weaver *et al.*, 2004). In contrast, hollowed-stem drought tolerant varieties which are susceptible to wheat stem sawfly are more competitive with downy brome (Beres *et al.*, 2010; Lemerle *et al.*, 2001). Increasing crop seeding rates can suppress weed emergence (Blackshaw, 1994; Weiner *et al.*, 2001), reducing inter-specific competition. However, the increased intra-specific competition could also have a negative impact on stem solidness, increasing wheat stem sawfly lodging. Moreover, the management practice of increasing seeding rates to reduce weed pressure not only results in potentially higher crop lodging due to sawfly infestations, it contradicts the recommendation of reducing pressure and infection rates of FCR by lowering crop residue and conserving water which can be achieved by lowering seeding rates (Paulitz *et al.*, 2002).

The conflicts between the management recommendations highlighted above challenge the single-pest control paradigm and emphasize the need to develop whole-system pest management programs. Yet, the difficulties in joint management of wheat stem sawfly, downy brome and FCR are further amplified by the interdependencies between them. Not only do grassy weeds reduce crop yield and quality, they may exert both positive and negative impacts on the population dynamics of *Fusarium*

spp. and wheat stem sawfly. For example, crop-weed competition decreases soil moisture further exacerbating drought conditions which leads to increased population densities of *Fusarium spp.* and FCR damage. In contrast, downy brome may play an important role in the survival and dynamics of wheat stem sawfly populations where infestation in downy brome could be up to 2-fold higher than for wheat with significantly greater larval mortality as the host plants mature (Perez-Mendoza *et al.*, 2006). *Fusarium spp.* can also impact the population dynamics of wheat stem sawfly. Evidence suggests considerable field mortality in wheat stem sawfly larvae due to the presence of *Fusarium spp.* species (Sun, 2008; Wenda-Piesik *et al.*, 2009).

While in its conception, the concept of integrated pest management (IPM) emphasized the need of considering the ecological context where multiple organisms coexists, IPM programs are often designed around a single category of pests (Kogan, 1998). These single-pest programs may not provide satisfactory solutions when confronted with the dynamic and complex interactions occurring within the agroecosystem between multiple target pests occurring at different trophic levels (Capinera, 2005; Lewis *et al.*, 1997; Norris and Kogan, 2005). The trophic interactions and contradictions between single-pest management recommendations make the wheat stem sawfly-downy brome-*Fusarium spp.*-wheat complex a suitable case study to develop new approaches in the design of holistic management recommendations. In this study, we integrated research on wheat stem sawfly, downy brome, and *Fusarium spp.* from a joint replicated field experiment assessing how three easy to manage cropping-system variables (stand density, herbicide management approach, and crop variety) may be manipulated to minimize the combined impact of different groups of pests and enhance crop yield.

Understanding the outcome of the biological interactions described above and providing management recommendations is further complicated by inherent statis-

tical challenges. To make natural resources managerial decisions based on scientific knowledge, experimental results or observations should be evaluated, interpreted, and related back to the set of choices. However, in agroecological crop management, as in our field experiment, no clear (experimental) control is usually imposed on the multiple interrelated variables. Pest pressures and their joint impact on crop yield are all linked to the applied treatments in a complex causal network which confounds parameter estimation and challenges statistical inference (de la Fuente *et al.*, 2003; Powell and Swanton, 2008; Price *et al.*, 1980).

The aim of many ecological studies is to develop and falsify hypotheses regarding observed natural phenomena with a wide array of available statistical tools. Statistical analysis with emphasis on quantitative decision-making, constrained by a finite set of choices and suffering from high uncertainty due to complex correlated outcomes, seems to have received less attention. As a result, many inferential procedures and statistical models of natural resource management do not fully address the goals of decision theory and may be less suitable for use as decision aiding tools. Moreover, frequentist statistical inference is a statement about the long-term expected outcomes and assumes that the observed state of the system reflects the true state of nature. Relating such estimates and their standard errors to unknown parameter values for the construction of realistic predictive models is often not intuitive or straightforward (Ellison, 1996; Stauffer, 2008). The future uncertainty in the implementation of a selected action is not accounted for in the analysis which could mislead management recommendations, a problem amplified in an ecological system where complex interactions between organisms often result in observed outcomes that can only be understood within the context of a certain model rationality (Colbach, 2010; Prato, 2005; Real, 1996).

Our objective was therefore three-fold: first, increase our understanding of interactions occurring among pest groups in ecological systems. Second, quantify the synergistic impacts of management practices on wheat stem sawfly, downy brome, and *Fusarium spp.*. Third, develop analytical approaches that incorporate estimates of direct and indirect biological interactions into the management decision process, allowing quantitative results that are applicable to the construction of holistic, ecological knowledge-based pest management programs.

This work, which summarizes our efforts, is presented in the following three chapters. Chapter 2 establishes the foundation of our approach to statistical inference where the underlying goal is to inform a finite set of natural resources management recommendations. We developed and present a methodology we termed "annihilation" to estimate total effects, a composite of direct and indirect pathways in ecological causal networks. Annihilation is conceptually rooted in path analysis which provides the framework for evaluating complex multivariate hypotheses about ecological systems. Path analysis by annihilation efficiently derives the estimates for total effects which can then be intuitively interpreted as quantifying the risks and agronomic consequences of pest management decisions. We applied this approach to data analysis to aspects of our experiment related to management of downy brome. Our results demonstrate the advantages that annihilation may hold over current path analysis procedures in the interpretation of treatment effects, and in overcoming confounding effects of multiple variables. In chapter 3 we investigated the interactions between wheat stem sawfly and *Fusarium spp.* and evaluate the impact biological interactions and agronomic traits of the crop may have on observations and assessments of the later. We demonstrated that the presence of interactions holds important implications for monitoring, research, and analysis of joint pathogen and insect damage to different crop varieties. In chapter 4 we integrated the concepts of the

previous two chapters, estimation of total treatment effects through annihilation and modeling biological interactions between pests, under a Bayesian decision theoretic approach. This approach allowed us to develop a complete crop management (choice of variety, seeding density, and herbicide application) decision model which accounts for the joint effects of management scenarios on wheat stem sawfly and downy brome complex interactions, abundance, and impact on wheat yield. Finally, in chapter 5 we summarize our major outcomes and suggest potential avenues for future research.

The modeling framework developed produces probabilistic answers to natural resource management questions that reflect the variability of ecosystem dynamics. Furthermore, the annihilated Bayesian model provides the ability to combine sources of prior knowledge on the interactions between pests and their respective responses to management actions. By quantifying these different biological processes, our joint model informs management and provides insights which may not be available from a standard analysis of empirical data on any single pest- or crop-management tactic.

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CHAPTER 2

ANNIHILATION: A METHODOLOGY TO COMBINE DIRECT AND INDIRECT EFFECT COEFFICIENTS IN CAUSAL NETWORKS

1. Abstract

In path analysis, some intermediate nodes in a graphical model of causal relationships are both responses and predictors and total effects are the composite of estimates along all direct and indirect paths between any two nodes in the graph. Path analysis by "annihilation" refers to replacing observed intermediate nodes with their corresponding error terms. Estimates for directed edges can then be viewed as total effects in the sense that they estimate all direct and indirect effects between any two nodes. In this paper we review and discuss unresolved issues in estimation of path coefficients, introduce the methodology of annihilation, and illustrate its application to a natural resources management problem in agricultural settings. The annihilated model presents several advantages when implemented via Gibbs sampling such as eliminating collinearity and providing intuitive interpretation of the parameters in the context of ecological research. Our approach provides a framework for finding the balance between modeling simplicity and the complexity of the process being modeled, and helps bridge the gap between making inferences from experimental or observational studies and ecological management decisions.

2. Introduction

In many designed experiments the response variable depends not just on the treatment, but also on measurable covariates. When a covariate is independent of the treatment, its inclusion in the statistical model reduces variance of the experimental

error terms and improves inference. However, in the absence of independence, the effects of treatments and covariates are confounded. A similar problem is encountered with inferences from observational studies when collinearity between columns of the design matrix inflates standard errors. Non-independence due to causal links between treatments and covariates, i.e. the treatment affects the covariate, is common in ecological field experiments (Norris, 2005) and may result in poor coverage of the data space.

Covariances between non-independent pairs of variables can be included in path analysis (Wright, 1920), assuming an underlying causal structure (Mitchell, 2001). Defining and graphing the causal relations helps to better conceptualize the system and interpret effects of confounding variables. Solving the graph, i.e. estimating its coefficients, may allow causal inferences from observational studies (Shipley, 2002) and was suggested as an alternative to removing collinear predictors from multiple regression models in ecology (Graham, 2003). Framed in a path analysis context, treatments or management schemes in natural resources will not only have a direct effect on the response, but also an indirect effect along paths of interacting covariates in the ecological system (Mitchell, 2001). Estimating the total effect for a given treatment, defined as a composite of all direct and indirect effects in the model graph, may therefore be of interest to improve natural resource management decision process for future projections.

Studies of path analysis and related variants of multiple regression such as structural equations models (SEM) often focus on the structural model, its causal implications (Pearl, 2010; Shipley, 2002), and the decomposition of direct effects through latent (unobserved) variables. The measurement model of fully observed networks, where the final objective is to derive the total effects, has received little attention. As a result, the problem of collinearity between variables in the path model remains

unresolved (Petraitis *et al.*, 1996; Pugesek and Grace, 1998). The goal of this paper is to describe an algorithm we termed "annihilation" which is a procedure to derive estimates and standard errors of all total effects in the causal graph during model fitting. We do not attempt to define hypothesis tests of the structural model or infer causality, but restrict ourselves to improving the estimation of total effects in recursive models, i.e. measurement models of *apriori* specified directed acyclic graphs (DAG, hereafter). Therefore, annihilation may be well suited for parameter estimation in complex ecological networks where interest lies in accounting for multiple causal relationships between organisms.

We introduce the difficulty in the analysis of natural resource management problems in the absence of independence of treatments and covariates in section 3. In sections 3.1 and 3.2 we present the DAG networks and discuss the problem of collinearity in the current approach to deriving total effects. Section 4 presents the annihilator and its justification based on an intuitive result of linear regression that seems to have been mostly overlooked in this context. A similar proof can be found in the covariance adjustment procedure of Sengupta and Jammalamadaka (2003), but without application. Our analytical result is of ordinary least squares (OLS) and therefore can be viewed as frequentist in nature, but we opted a Bayesian approach as there are several advantages to doing so in the context of annihilation, path analysis, and SEM (Arhonditsis *et al.*, 2006; Congdon, 2003). Ando and Zellner (2010) discuss error propagation between equations for SEM and seemingly unrelated regression (SUR) in a Bayesian context. In section 5.1 we analyze the properties of the annihilator when conducted by Gibbs sampling. Finally, section 5.2 is a complete worked out example of a natural resources management problem, a pest management decision in agricultural settings, where the annihilator is applied.

3. Motivating Problem

Consider an agronomy experiment on the addition of a fertilizer to improve crop yield. While much research has been conducted on the response of crops to resource availability, the fertilizer treatment also affects the growth of non-target species such as weeds (Kristensen *et al.*, 2008) which, in turn, compete for resources and reduce yield of the targeted crop. When evaluating natural resources management schemes, underlying ecological processes such as crop-weed competitive interactions need to be accounted for to inform the decision process for future projections. For example, the presence of weeds influences the observed response and should be incorporated in the statistical model as a covariate. However, because weed abundance and productivity also depends on resource availability, higher weed pressures are expected at elevated fertilizer levels. Thus, the covariate is not independent but is partially nested in the treatment and modeling solutions such as analysis of covariance or mixed effects models still suffer from low coverage of the data space, which may result in poor model fits and less than optimal estimates as in an unbalanced design. Moreover, when multiple predictors of a response are themselves linked through causal relationships, information stemming from classical statistical inference cannot be fully interpreted without violating an inherent assumption. Specifically, assuming predictors i and j that have a causal relationship between them are applied. The expected response $E(Y)$ is described by the vector of parameters $\boldsymbol{\beta}$. In a main effects model, an estimator $\hat{\beta}_i$ is then the effect of a one unit increase in the i^{th} predictor, with all other predictors in the model held fixed. Statistical inference requires accepting that j can be constant for varying levels of i, which introduces a paradox because there can be no causal link between them as by the first assumption (Freedman, 2005). Inclusion of an interaction term $\hat{\beta}_{ij}$, interpreted as the adjustment to the increase in i for different

levels of j, does not resolve this problem because causality implied the levels of i and j varied together regardless of their combined effect on Y at different levels, and the paradox persists.

In the previous example, the confounding of the covariate weed pressure may be mitigated in the design and execution stages of the experiment by applying a management practice such as continuous selective weeding or herbicide applications to generate a range of weed pressures, creating a balanced design with respect to covariate levels. While this approach allows investigation of the effect of the interaction between the covariate and the treatment on the response variable, it does not solve the paradox described above but redefines the scope of inference for the experiment. In essence, the covariate now becomes a treatment and interpretation of the estimated expectations, i.e. evaluation of the treatment as a potential crop management scheme, is only possible conditional on the level of weed control.

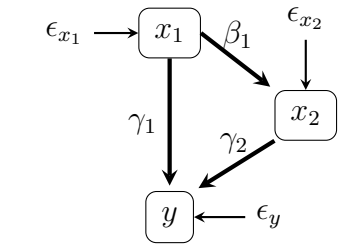
Analysis of the experiment described above could be conducted in several ways. First, the main effects of the treatment and covariate on yield, independent of each other can be estimated by adding the covariate, centered around its mean, to the model. Second, the direct impact of the covariate under different management scenarios can be modeled by the interaction term between the unscaled covariate and the treatments. However, while these models allow assesing the impacts of variables in the system on the target (yield), neither fully describes the biological system as the relationship between the treatments and covariate is not incorporated in the model. Hypotheses about multiple processes operating in the ecosystem may be better investigated with alternative approaches to data modeling such as path analysis and SEM that emphasize estimating causal effects through the study of path relations, where the focus is on understanding direct and indirect effects (Grace *et al.*, 2010). A path analysis would involve estimating all edges in a DAG (defined below) constructed

from the non-independent observations, where the hypothesized causal links between variables determine the structure of the graph. The total effect for the treatment or management scenario is the composite of the direct and indirect paths to the response and accounts for the possible biological interactions which may have resulted from the treatments. As such, the total effect can be used for decision support in natural resources without reducing the scope of inference of ecological field experiments through explicit control of confounding variables.

3.1. Structural Model and Notation

The graphical models of path analysis are a DAG where first, all edges are unidirectional so two variables cannot cause each other simultaneously. Second, there are no cycles where a variable causes itself indirectly through one or more intermediaries. Most applied ecological problems will fit under these restrictions (Shipley, 2009), including some density dependent processes where time steps in the life cycle or yearly cohorts are considered. A hierarchy in the structural equations describing the graph follows immediately from the properties of a DAG. A DAG of three observed variables x_1, x_2, and y, where x_1 causes x_2 and both x_1 and x_2 are causes of y can be solved simultaneously or by a recursive system of two seemingly unrelated structural equations (Fig. 2.1a).

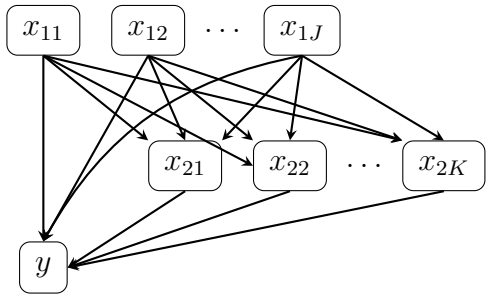
For clarity of presentation we dropped the intercept terms β_0 and γ_0 from the graphical model and the error term ϵ_{x_1} from the structural equations. We view the latter as a minor issue, where although we treat x_1 as measured without error, measurement error models can easily be incorporated in the framework described below. Finally, for the purpose of estimating total effects it is not imperative to distinguish between continuous and categorical variables as in standard path analysis and the models discussed here may be viewed as the special case of Fig. 2.1 where



(a) Univariate

$$x_2 = \beta_0 + \beta_1 x_1 + \epsilon_{x_2} \tag{2.1}$$

$$y = \gamma_0 + \gamma_1 x_1 + \gamma_2 x_2 + \epsilon_y \tag{2.2}$$



(b) Multivariate

$$\boldsymbol{X_{2k}} = \boldsymbol{X_1}\boldsymbol{\beta}_k + \boldsymbol{\Psi}_k \quad \text{where } \boldsymbol{\Psi}_k \sim N(\mathbf{0}, \mathbf{I}\sigma_k^2)$$

$$\mathbf{y} = \begin{bmatrix} \boldsymbol{X_1} & \boldsymbol{X_2} \end{bmatrix} \boldsymbol{\gamma} + \boldsymbol{\epsilon} \quad \text{where } \boldsymbol{\epsilon} \sim N(0, \boldsymbol{I}\sigma^2)$$

Figure 2.1: Common graphical representation (left) and corresponding structural equations (right) used for path analysis. (a): Three variables of interest (x_1, x_2, y). Endogenous (observed) nodes are bounded by squares while their corresponding exogenous variables (ϵ) are unbounded. Directed arrows imply a causal relationship and the graph is acyclic, i.e. no indirect paths lead from any node back on to itself. (b): The same DAG as the top but expanded such that $\boldsymbol{X_1}$ is a matrix of of J top level variables, $\boldsymbol{X_2}$ is a matrix of K intermediate variables, and $\mathbf{y}$ is a single vector representing a response or a variable of interest effected by variables in both $\boldsymbol{X_1}$ and $\boldsymbol{X_2}$. Matrix $\boldsymbol{\beta}$ is composed of K vectors $\boldsymbol{\beta}_k$. $\boldsymbol{\Sigma_k}$ is a matrix of $\sigma_k^2 \quad k = 1, \ldots, K$ on the diagonal and zero off diagonal. Such a network structure is more commonly found in ecological applications for e.g. trophic food-webs.

$\boldsymbol{X_1}$ is a design matrix of dummy variables corresponding to treatments and $\boldsymbol{X_2}$ may be continuous covariates.

A single variable may play both the roles of a response and a predictor in different equations, but it can only occur as a response on the left hand side once in the system. Thus, even when fit simultaneously, any system of structural equations describing a

path model can be stacked to form the general structure:

$$\left.\begin{aligned} x_1 &= \epsilon_{x_1} \\ -\beta x_1 + x_2 &= \epsilon_{x_2} \\ -\gamma_1 x_1 - \gamma_2 x_2 + y &= \epsilon_y \end{aligned}\right\} \text{Fig. 2.1a} \quad \Rightarrow \begin{pmatrix} 1 & 0 & 0 \\ -\beta & 1 & 0 \\ -\gamma_1 & -\gamma_2 & 1 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ y \end{pmatrix} = \begin{pmatrix} \epsilon_{x_1} \\ \epsilon_{x_2} \\ \epsilon_y \end{pmatrix} \tag{2.3}$$

While the matrix of parameters does not have to be square, the free edges are always at the lower triangle, where the upper triangle is zero. For this reason, in the absence of any latent variables and undirected edges, path analysis is a simplified special case of SEM or LISREL (linear structural relations) models. Thus, while path analysis can be conducted using dedicated SEM software, using maximum likelihood to simultaneously solve (2.3), it can also be done by directly fitting equations (2.1) and (2.2) as a series of unrelated models (Fox, 2002).

The model in Fig. 2.1b is a direct extension of Fig. 2.1a to matrix notation. Although it is $i(j-1)(k-1)$ larger, it is of the same complexity of the triangle path model described by two structural equations. The network in Fig. 2.1b is saturated but some directed arrows can be dropped by assigning values of zero in the appropriate location in $\boldsymbol{\beta}$.

We use the more general matrix notation for (2.1) and (2.2) in Fig. 2.1b and interchangeably throughout to emphasize that while we provide simplified examples for clarity, our discussion is not constrained to the univariate case. Fig. 2.1 can be viewed as the building block for more complex path models. Additional biological processes or organisms at different trophic levels can be added to Fig. 2.1b at intermediate layers ($\boldsymbol{X_3}$,$\boldsymbol{X_4}$,...), or related environmental variables as parents ($\boldsymbol{X_0}$) to $\boldsymbol{X_1}$ without loss of generality, as long as the DAG rules are kept. For example, the fertilizer experiment case where one treatment was applied and one covariate consid-

ered can be readily extended to several species or organisms which interact and are affected by multiple environmental variables or management treatments. Therefore, while ecological networks and management problems may have a large number of variables they can be sufficiently described by DAG.

3.2. Inflated Variance In Bottom Level Equations

Assume only direct effects were used as a model to describe the system depicted in Fig. 2.1. Despite the causal relationships presented in Fig. 2.1 the model in (2.2) is misspecified as information in (2.1) is not utilized even in (2.3) due to the zeros on the upper triangle of the matrix. In the context of causality, this model may be viewed as a partially over-specified model since by (2.1) part of $\boldsymbol{X_2}$ is explained by $\boldsymbol{X_1}$. It is readily demonstrated that over-specification results in inflated standard errors for the estimated treatment effects apparent when considering the OLS solution $\hat{\boldsymbol{\gamma}}$ (see Appendix A):

Letting $\hat{\boldsymbol{\Psi}} = (\mathbf{I} - \mathbf{P_1})\boldsymbol{X_2}$

$$\begin{pmatrix} \hat{\gamma}_1 \\ \hat{\gamma}_2 \end{pmatrix} = \begin{pmatrix} (\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1}\boldsymbol{X_1}^T - \hat{\boldsymbol{\beta}}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\Psi}}^T \\ (\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\Psi}}^T \end{pmatrix} \begin{pmatrix} y_1 \\ \vdots \\ y_n \end{pmatrix} \tag{2.4}$$

$$Var(\hat{\boldsymbol{\gamma}}) = \begin{pmatrix} (\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1} + \hat{\boldsymbol{\beta}}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\beta}}^T & -\hat{\boldsymbol{\beta}}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1} \\ -(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\beta}}^T & (\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1} \end{pmatrix} \sigma^2 \tag{2.5}$$

The causal structure $\boldsymbol{X_1} \rightarrow \boldsymbol{X_2}$ determines the form of (2.4) and (2.5) that are the familiar result for over-specified or collinear models, but where the effect is apparent in $\hat{\gamma}_1$ only. The estimates are unbiased (2.4), and prediction intervals will be correct given the off-diagonal covariances in (2.5), but the standard error for $\hat{\gamma}_1$ is inflated. More specifically, $\hat{\boldsymbol{\gamma}}$ is the vector of direct effects of $\boldsymbol{X_1}$ and $\boldsymbol{X_2}$. Note, if $\boldsymbol{\beta} = \mathbf{0}$ then $\boldsymbol{X_2} = \hat{\boldsymbol{\Psi}}$ in (2.1). Thus, $\hat{\gamma}_1 = (\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1}\boldsymbol{X_1}^T\mathbf{y}$ and $\hat{\gamma}_2 = (\boldsymbol{X_2}^T\boldsymbol{X_2})^{-1}\boldsymbol{X_2}\mathbf{y}$ in (2.4). The OLS solution to a linear model in partitioned form. Moreover, if $\boldsymbol{\beta} \neq \mathbf{0}$

$$\hat{\boldsymbol{\Psi}} \perp\!\!\!\perp \boldsymbol{X_1}\hat{\boldsymbol{\beta}} \quad \text{by the construction of (2.1)}$$

$$\Rightarrow \hat{\gamma}_2 = (\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\Psi}}^T\mathbf{y} \quad \text{is still the direct effect of } \boldsymbol{X_2}$$

$$\Rightarrow \hat{\gamma}_1 = (\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1}\boldsymbol{X_1}^T(\mathbf{I} - \underbrace{\boldsymbol{X_2}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\Psi}}^T}_{X_2\gamma_2 \rightarrow \text{direct effect on } y})\mathbf{y} \quad \text{is the direct effect of } \boldsymbol{X_1}$$

However, $\hat{\boldsymbol{\beta}}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\beta}}^T > 0$ for any $\hat{\boldsymbol{\beta}}$ in $Var(\hat{\gamma}_1)$, generally inflating the standard error for $\hat{\gamma}_1$ in (2.5).

In full information SEM, likelihood is maximized simultaneously to estimate the parameters. However, from (2.3) clearly there is no difference between path analysis conducted by full information maximum likelihood (FIML), OLS, or two stage least squares (2SLS). The zero values on the upper triangle of (2.3) imply $\hat{\boldsymbol{\gamma}}$ is (2.4) with variance (2.5) irrespective of the methodology, and the advantages of full-information estimations are lost on DAG (Fox, 2002). Being more general, SEM methodology has for the most part replaced Wrightian path analysis in the literature (Mitchell, 1992; Pugesek and Grace, 1998). In practice there is no need to construct (2.3) because to conduct path analysis, a variety of dedicated SEM packages such as LISREL, SAS's CALIS procedure, R libraries and more, can provide a convenient wrapper. Since $\hat{\boldsymbol{\beta}}$ and its variance is quantified in the full network covariance matrix, this form of collinearity may not pose a problem for testing many ecological hypotheses using the

SEM approach (Pugesek and Grace, 1998). However, when the emphasis in analysis is on indirect or total effects, deriving the correct precision of the total effect from the estimated direct effects suffering from collinearity is not a straight forward task. While this problem has received some attention in the literature for other fields of science (see example in mediation models Ato and Vallejo, 2011; Cheung, 2009; Fritz *et al.*, 2012; Preacher and Kelley, 2011), it seems to have been mostly overlooked in biology (Petraitis *et al.*, 1996).

4. Annihilation

We use the term "annihilation" in the context of statistical analysis to refer to the process of eliminating linear dependencies between columns of the design matrix. Letting $\mathbf{P} = \boldsymbol{X_1}(\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1}\boldsymbol{X_1}^T$, the hat matrix of $\boldsymbol{X_1}$, (2.2) can be written as

$$\mathbf{y} = \boldsymbol{X_1}\gamma_1 + (\mathbf{P}\boldsymbol{X_2} + (\mathbf{I}-\mathbf{P})\boldsymbol{X_2})\gamma_2 + \boldsymbol{\epsilon}$$

The error terms for intermediate nodes $\hat{\boldsymbol{\Psi}} = (\mathbf{I}-\mathbf{P})\boldsymbol{X_2}$ are orthogonal to the parents and therefore replacing all observed intermediate nodes in the graph with their corresponding error terms, yields an *annihilated path model*. In this model, the parent ($\boldsymbol{X_1}$) is not included with the collinear child ($\boldsymbol{X_2}$) in the bottom level equation for the descendant ($\mathbf{y}$) since $\mathbf{y} = \begin{bmatrix}\boldsymbol{X_1} & \hat{\boldsymbol{\Psi}}\end{bmatrix}\boldsymbol{\alpha} + \boldsymbol{\epsilon}$ and the cross products of the inverse covariance matrix are now $\boldsymbol{X_1}^T\hat{\boldsymbol{\Psi}} = \underbrace{\boldsymbol{X_1}^T(\mathbf{I}-\mathbf{P})}_{\mathbf{0}}\boldsymbol{X_2} = \mathbf{0}$. Thus, the estimates are:

$$\hat{\boldsymbol{\alpha}} = \begin{pmatrix}(\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1}\boldsymbol{X_1}^T \\ (\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\Psi}}^T\end{pmatrix}\mathbf{y} \tag{2.6}$$

$$Var(\hat{\boldsymbol{\alpha}}) = \begin{pmatrix} (\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1} & \mathbf{0} \\ \mathbf{0} & (\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1} \end{pmatrix} \sigma^2 \tag{2.7}$$

The result corresponds to that of multiple regression with $\boldsymbol{X_1} \perp\!\!\!\perp \boldsymbol{X_2}$. However, $\boldsymbol{X_1}$ is still causally linked to $\boldsymbol{X_2}$. Comparing (2.6) and (2.7) to (2.4) and (2.5) it is apparent that while $\hat{\alpha}_2 = \hat{\gamma}_2$,

$$\hat{\alpha}_1 = \hat{\gamma}_1 + \hat{\boldsymbol{\beta}}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\Psi}}^T\mathbf{y} \tag{2.8}$$

where $\hat{\boldsymbol{\beta}}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\Psi}}^T$ account for the indirect paths from $\boldsymbol{X_1}$ to $\mathbf{y}$ via $\boldsymbol{X_2}$. The estimate given by $\hat{\boldsymbol{\alpha}}_1$ is intuitively interpreted as "the unit increase in $\mathbf{y}$ for every unit increase in $\boldsymbol{X_1}$ and $\hat{\boldsymbol{\beta}}$ units of $\boldsymbol{X_2}$, which *must* change along with $\boldsymbol{X_1}$", solving the paradox described in the first paragraph of section 3.

A common approach to the problem of collinearity is dropping whole terms from the design matrix, yet this results in a misspecified (underfit) model which has biased coefficient estimates and inflated var($\hat{\mathbf{y}}$). However, what is considered bias in misspecified models, relates to direct effect estimates such as $\hat{\gamma}_1$, where the magnitude of the bias is in fact the term determining the total effects $\hat{\boldsymbol{\alpha}}_1$. Annihilating can be viewed as dropping only the part of $\boldsymbol{X_2}$ which is in the column space of $\boldsymbol{X_1}$ from the design matrix rather than the full term $\boldsymbol{X_2}$. Thus, the annihilator provides the same point estimates of $\boldsymbol{X_1}$ as if $\boldsymbol{X_2}$ was dropped from the model altogether, but in contrast to the misspecified model, retains the correct variance estimate for σ^2 and variance of $\hat{\alpha}_1$.

5. Results

5.1. Simulation

Methods of SEM can be divided into two general categories: full information methods where the likelihood of the measurement model under the structural model is maximized for all equations simultaneously, and partial information methods such as two-stage least squares (IISLS), where the structural equations are evaluated sequentially. While in path analysis both methods provide the same outcome (Fox, 2002), in annihilation partial information methods can not be easily used to derive the correct variances of $\hat{\boldsymbol{\alpha}}$. This is because by passing $\hat{\boldsymbol{\Psi}}$ to the later stages as data, the error associated with estimation of $\hat{\boldsymbol{\beta}}$ in the first stage is not accounted for. However, using iterative procedures such as MCMC, samples can be drawn from the joint posterior distribution of all parameters, and the correct variance estimates are produced.

We simulated 60 standard normal variates for x_1, x_2 and y in Fig. 2.1a where β, γ_1 and $\gamma_2 = 1$. Total effects were calculated in replicated MCMC runs using JAGS 2.1.0 (Plummer, 2003). First, we fit all direct edges in the path model and calculated total effects post-hoc, and second, by annihilation where the intermediate node was replaced with its corresponding error terms. The main loops of the two models are presented in code snippets below where lines 4 and 6 in the direct effects model with post hoc calculations, are substituted by line 4 only in the annihilated model.

Total effects from path analysis

```
for(i in 1:N){                                                    1
 x2[i] ~ dnorm(mu.x2[i] , tau.x2)                                 2
  mu.x2[i] <- beta * x1[i]                                        3
 y[i] ~ dnorm(gamma1 * x1[i] + gamma2 * x2[i] , tau.y)            4
}                                                                 5
 total <- gamma1 + gamma2 *  beta                                 6
```

Path analysis by annihilation

```
for(i in 1:N){                                                              1
 x2[i] ~ dnorm(mu.x2[i] , tau.x2)                                           2
  mu.x2[i] <- beta * x1[i]                                                  3
 y[i] ~ dnorm(alpha1 * x1[i] + alpha2 * (x2[i]-mu.x2[i]) , tau.y)           4
}                                                                           5
```

In the annihilated model, the hypothesized structure need only be specified once (line 4), subtracting the means of all intermediate variables from their corresponding observed values. In the BUGS language, the order of equations entered into the model is arbitrary, but a consistent naming convention makes the substitution of `x2[i]` with its error term straight forward for any set of structural equations. In the common path analysis model, all sub models (line 4) need to be considered when calculating total effects post hoc (line 6). This makes total effects estimates cumbersome and prone to error especially in complex multilevel networks, since the graphical model (here, Fig. 2.1a) is separate from the code used for fitting the structural equations in a software package. In a meta analysis of path analysis use in ecology, Petraitis *et al.* (1996) found simple oversights in incorporating all indirect effects when constructing total effect estimates to be a major cause of error. This is not surprising given that most path analysis is performed on complex network graphs, where deriving appropriate total effects post hoc requires careful matching of model output and the hypothesized structural model. The annihilator makes this last step redundant, where by monitoring a single set of bottom level coefficients, the correct total effects for all variables in $\boldsymbol{X_1}$ are returned.

Trace plots for the first 50 iterations and posterior densities of total effects are presented in Fig. 2.2. Both models were fit with noninformative independent normal priors for all parameters and while both eventually converged to the correct posterior distribution, convergence was achieved almost immediately for the annihilated model

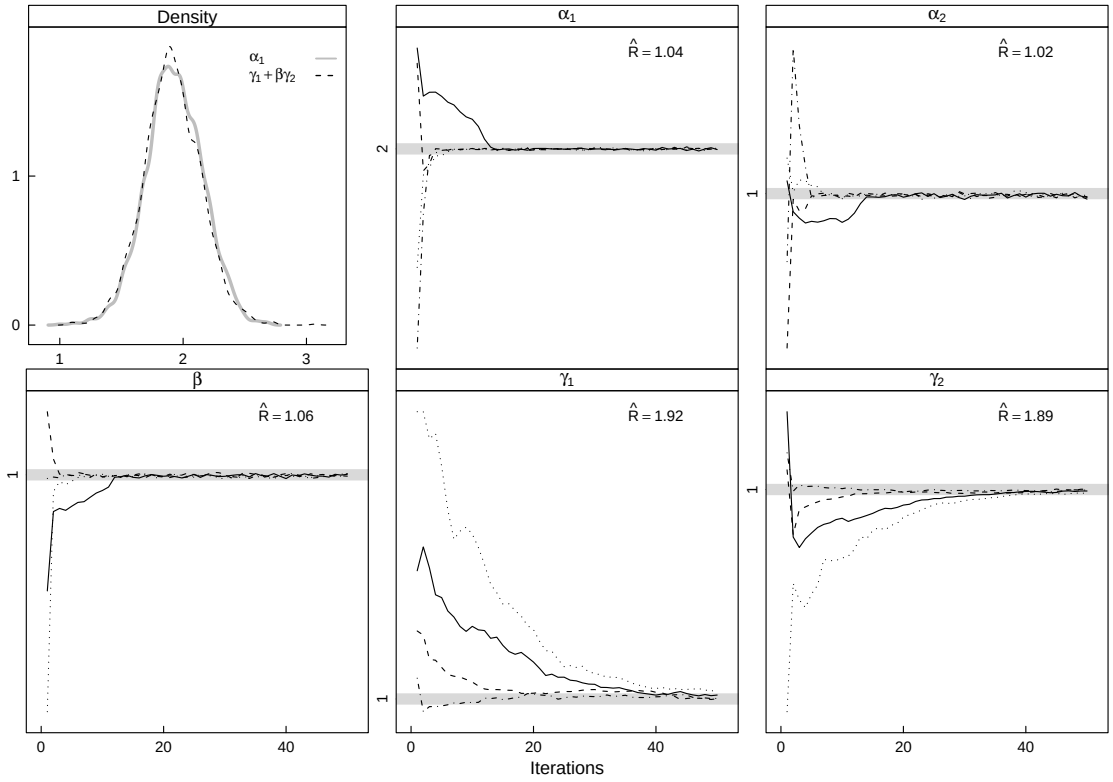


Figure 2.2: Posterior density of the total effect (top left) and convergence of the first 50 iterations for the parameters of 60 simulated standard normal variates of x_1, x_2 and y in Fig. 2.1a. Total effects were calculated by annihilation (solid) or post-hoc from direct effects (dashed). Density estimates are based on 500 draws after a burnin period of 500. $\hat{R}$ is the between- to within- chain variance diagnostic measure for 50 iterations (Gelman and Rubin, 1992).

with $\hat{R}$ values of the within to between chain variance ratio (Gelman and Rubin, 1992) close to 1. The faster convergence reflects the more desirable properties of (2.7) compared with (2.5) when estimated via MCMC methods (Gelman and Hill, 2007). Furthermore, evident in the patterns traced by the Markov chains (Fig. 2.2) is the fact that substitution on line 4 of the annihilated model linked $\beta^\star$ with $\boldsymbol{\alpha}^\star$ internally at every step of the random walk (Choi and Dulikravich, 1995; Jespersen and Buning, 1983). In the context of statistical inference this is more than a technical detail of the mechanics of the Gibbs sampler. As noted in section 3.1, the structure of (2.3)

implies full information methods are reduced in DAG to a series of partial information equations which are not truly simultaneous. By annihilation we in essence constructed a full information method for (2.3). In MCMC, samples from the joint posterior distribution of all parameters are drawn at every step which ensures propagation of the errors through the network. Thus, the variability associated with $\hat{\boldsymbol{\beta}}$ is accounted for in the total effects calculated from $\hat{\boldsymbol{\gamma}}_{\mathbf{1}}$ as in Fig. 2.2. In contrast, $\hat{\boldsymbol{\alpha}}$ already represents the total effect estimated from a full information method, allowing $\boldsymbol{\Psi}$ rather than $\hat{\boldsymbol{\Psi}}$ in (2.7) and making the estimation of (2.3) more efficient.

5.2. Example Application

During the growing seasons of 2008-2010, we conducted a study assessing ecologically-based pest management strategies in small grain systems (Chapter 4). This study was carried out in a production field near Amsterdam Montana (45°45.0250 N, 111°25.1900 W, 1490 m elevation). We applied path analysis by annihilation to a portion of the data to illustrate how this approach to data analysis aids in the development of decision models. Specifically, we assessed the impact of crop variety, seeding rate, and the presence of a grassy weed [downy brome (*Bromus tectorum* L.)] on spring wheat (*Triticum aestivum* L.) grain yield performance.

Downy brome is an increasingly problematic grassy weed in range, wildlands, and cropping systems of the Northern Great Plains. While typically a winter annual, downy brome could exhibit summer annual life history traits with seedlings capable of emerging through the winter and into spring and plant height reaching 40-50 cm by early June (Hulbert, 1955). In crop lands, the life form similarities of wheat and downy brome are responsible for the existence of strong crop-weed competitive relations (Mack, 2011; Zimdahl, 2007). Yield reductions due to downy brome infestations range between 28% and 92% (Rydrych and Muzik, 1968), with a strong dependency

on weed density, time of emergence, and distance to crop (Stahlman and Miller, 1990). Increased adoption of conservation tillage, enhanced reliance on broadcast nitrogen fertilizer, and use of narrow-spectrum herbicides have been cited as contributing to the increased spread and impact of downy brome in wheat cropping systems (Blackshaw, 1991).

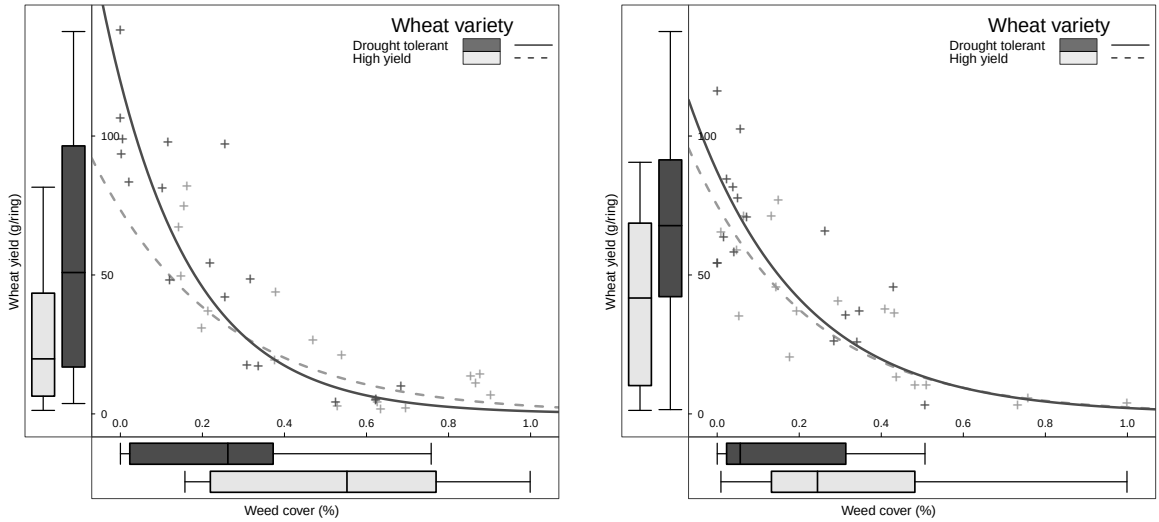
The emergence of herbicide resistant downy brome biotypes (Ball *et al.*, 2007; Menendez *et al.*, 2006) and associated economic and environmental impacts have spurred increased interest in reducing the reliance on herbicides (Berti *et al.*, 2003; Prato and Woo, 2008). One alternative to excessive chemical control is their integration with other management approaches that utilize the crop's competitive potential against weeds. Among them, crop seeding rate has been shown to be an important factor in determining weed biomass and seed production (Olsen *et al.*, 2006; Weiner *et al.*, 2001). Also, it has been suggested that in semiarid environments, such as those dominating the Northern Great Plains, variety traits such as drought tolerance can increase competition with weeds for water and nutrients (Lemerle *et al.*, 2001, 2004; Quarrie *et al.*, 1999).

Treatments that represented alternative crop management practices were established in 2008 and repeated during the growing seasons of 2009 and 2010. A detailed description of the study design and data collection procedures is available in Chapter 4. The data presented here is of the 2009 growing season where annual temperature averaged $13°C$ and total precipitation for the duration of the growing season was 270.51 mm. Two wheat cultivars were included in the study 1) drought tolerant (DT) McNeal (MSU,1994): semidwarf, red chaffed variety, and 2) a high yielding with available moisture (HY) Reeder (ND,1999): semidwarf variety with a longer grain-fill period. The two cultivars were seeded at half and double the recommended initial seeding rate (125 and 500 plants m^{-2}, respectively) with a 7 double disc openers,

no-till drill, spaced 25.4 cm apart at a seeding depth of 3.8-5 cm. Sulfosulfuron was applied at 0.014, and 0.007 Kg ha^{-1} of active ingredient, which is 0.4 and 0.2 of the label rate, to allow for a range of downy brome pressure. Eighteen metal rings, 0.475 m in diameter, were randomly placed in each of the four wheat variety by seeding rate treatment combinations. Rings where anchored to the ground, centered between two wheat rows, covering an area of 0.18 m^2 and 80.3 cm of crop rows. When downy brome reached peak biomass, its percent cover in the rings was visually estimated and all above ground downy brome biomass in the rings was clipped, dried to a constant weight and weighted. These measures were standardized and combined for each ring to form a downy brome pressure index on a $[0, 1)$ scale which is percent cover, adjusted for biomass. At harvest, all wheat within the rings was uprooted and threshed for grain yield. Yield, measured in grams for every ring, was log transformed to linearize the relationship with downy brome pressure.

Wheat yield was higher for the DT variety than the HY variety and increased with seeding rate for both varieties (Fig. 2.3). However, for each variety and seeding rate, variability in mean yield was high probably due to the impact of downy brome. While the rate of yield loss due to downy brome pressure was similar for the different treatment combinations, wheat varieties and seeding rates differently affected downy brome pressure. Specifically, the DT variety at high seeding rates suppressed more effectively downy brome pressure. Downy brome pressure was greater than 0.142 in the low-seeded HY variety, an order of magnitude higher than all other treatment combinations.

Three approaches were used to evaluate the outcomes of crop variety and seeding management choices with respect to wheat grain yield: by fitting the standardized main effects (a design matrix of treatments and downy brome centered around its mean), by fitting unstandardized direct effects (intercept and slope-by-downy brome



(a) Low seeding rate (b) High seeding rate

Figure 2.3: Results of an agroecology experiment evaluating spring wheat grain yields after two seasons under a range of downy brome pressure. Two varieties at two seeding rates are evaluated: a drought tolerant (solid black) and high-yielding-with-available-moisture (dashed gray), each seeded at (a) half and (b) double the recommended target of 250 plants m^{-2}. Curves are based on maximum likelihood estimates from a linear model after a natural log transformation of yield. Plots are for untransformed grain weight for 80.3 cm of crop row.

for wheat yield at every treatment), and by annihilation. Identical beta regression models for the effect of treatment on downy brome pressure were fit in all three approaches, followed by models differing in the design matrix of treatment and downy brome impact on yield:

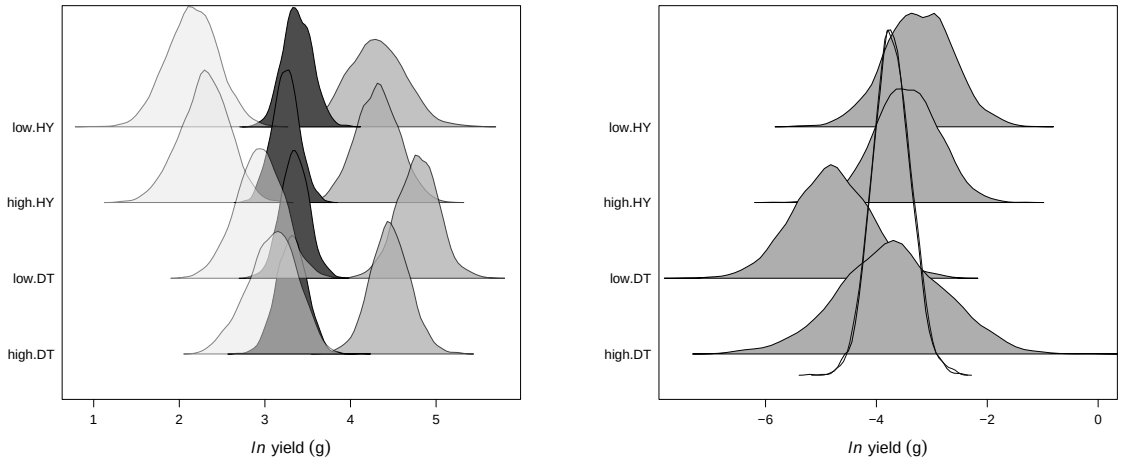
$$\text{Main: } \left[\mathbf{T} \quad \mathbf{d} - \bar{\mathbf{d}}\right]$$

$$\text{Direct: } \left[\mathbf{T} \quad \mathbf{T_{ij}}(\mathbf{d^T} \otimes \mathbf{1_n})_{\mathbf{ij}}\right]$$

$$\text{Annihilator: } \left[\mathbf{T} \quad (\mathbf{I} - \mathbf{P_T})\mathbf{d}\right]$$

where $\mathbf{T}$ is a matrix of dummy variables of the 4 treatments, $\mathbf{P_T}$ is the "hat" matrix for $\mathbf{T}$, and $\mathbf{d}$ is a vector of downy brome pressure. All models were fit with JAGS 2.1.0 (Plummer, 2003) and analysis conducted in R 2.12.0 (R Development Core Team, 2010).

The distributions in Fig. 2.4a represent different estimable functions for the dif-



(a) Intercepts (b) Slopes

Figure 2.4: **a.** Posterior distributions of the treatment effects on wheat yield for three models: Main effects model (dark gray), Direct effects (medium gray), and Annihilated (light color). **b.** Posterior distributions of the downy brome effects on wheat yield for the Main effects model (Dark gray line), Direct effects (filled gray), and Annihilated (black line). The estimated downy brome effect is virtually identical in the annihilated and main effects models and distributions overlap. Densities are based on 2,000 draws from 4 $t = 10,000$ MCMC simulations with a burn in period of 5,000 thinned every 10 iterations.

ferent approaches. For the main effect model, estimates are of mean wheat yield when grown under downy brome pressure and can be viewed as ANCOVA, where the direct effects of the treatment are independent of downy brome pressure. In this scenario, low seeded-HY is estimated as the highest yielding distribution, but because

variability in the expectations between treatments is confounded by the inclusion of downy brome, the analysis is poor in comparison to the raw data in the left most boxplots of Fig. 2.3. The direct effects approach can be described as an interaction model, where intercepts represent treatment effects in the absence of downy brome, while the direct effect of downy brome for every treatment presented in Fig. 2.4b. The higher intercepts for the DT variety compared with the HY variety, especially at low seeding rates is the result of poor data coverage at low downy brome pressure for HY. In the annihilation approach, estimates are interpreted as the joint impact of treatment and downy brome on wheat given the relative of ability of the treatment to suppress downy brome pressure. Thus, mean estimates incorporate in them the effect of downy brome pressure (Fig. 2.4b) and are generally lower than the estimates of the main effects model.

All three approaches to analysis (main effects, direct effects, and annihilation) resulted in equivalent model fits with residual standard error of 0.68 ± 0.06 for the effects of treatments on yield, and a precision parameter (ϕ) 1.24 ± 0.18 for the effects of treatments on downy brome pressure (Table 2.1). Downy brome pressure was affected by wheat variety, more than by seeding rate, with no significant interaction in all three models (Table 2.1).

While downy brome had a strong negative impact on wheat yield using all three approaches (Table 2.1, Fig. 2.4b), estimated impact of treatments on wheat yield differed between approaches (Fig. 2.5). In the main effects model, management scenarios did not differ in mean wheat yield. The only contrast showing a trend in this model was towards higher yields in the low-seeded-HY variety combination (Fig. 2.5a). Similarly, no differences were detected between varieties or seeding rates with the direct effects approach, where paradoxically the strongest effect was towards a descision of DT variety at low seeding rates in the absence of downy brome (Fig. 2.5b). Moreover,

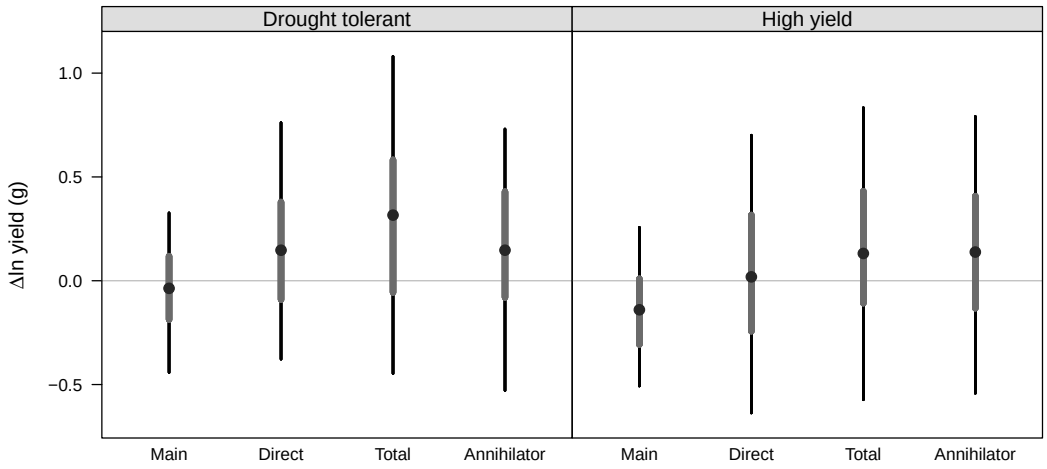
Table 2.1: Medians, Standard deviation and 90% credible intervals for all other parameters in the model other than the effect of treatment on yield. Estimates from all three models are reported.

	Annihilated				Main				Direct			
	Est.	SD	Lower	Upper	Est.	SD	Lower	Upper	Est.	SD	Lower	Upper
$^{\dagger}\beta_{HY.low}$	0.639	0.065	0.537	0.751	0.643	0.063	0.540	0.747	0.644	0.064	0.541	0.752
$\beta_{DT.low}$	0.422	0.058	0.329	0.519	0.417	0.057	0.328	0.514	0.416	0.056	0.327	0.509
$\beta_{HY.high}$	0.565	0.059	0.473	0.663	0.568	0.059	0.477	0.667	0.568	0.060	0.473	0.668
$\beta_{DT.high}$	0.369	0.061	0.269	0.469	0.365	0.058	0.276	0.469	0.367	0.057	0.278	0.463
ϕ	1.235	0.183	0.958	1.548	1.237	0.179	0.947	1.521	1.247	0.180	0.971	1.557
$^{\dagger\dagger}\alpha_{cg}$	-3.733	0.342	-4.253	-3.152	-3.737	0.348	-4.256	-3.127	-3.713	0.95	-5.45	-2.376
σ	0.678	0.061	0.579	0.772	0.680	0.061	0.594	0.792	0.676	0.064	0.580	0.783

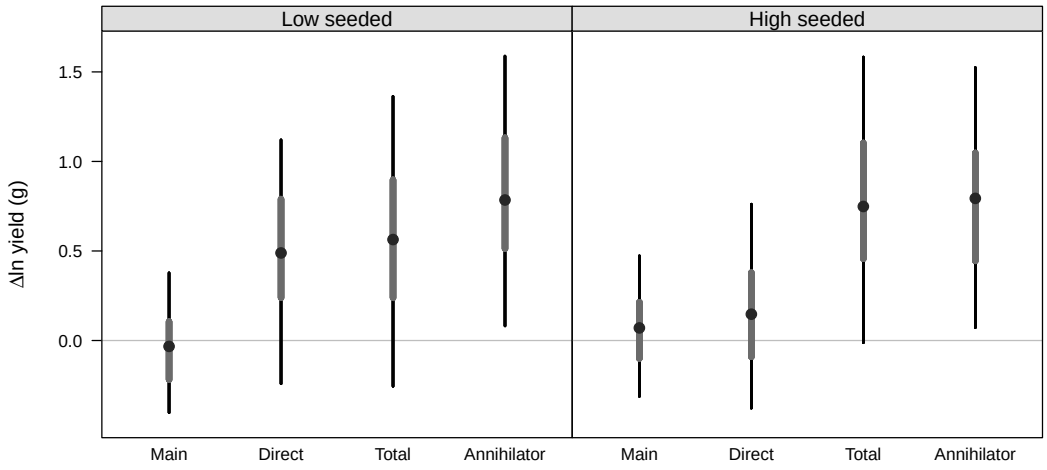
† Coefficients from a Beta regression of treatments on downy brome cover. β_i is the mean of the treatment, ϕ is the precision parameter of a Beta distribution parametrized $Beta(\mu\phi, (1-\mu)\phi)$.

†† Slope (α_{cg}) and residual standard error (σ) of the regression model for downy brome on yield. For the direct effects model α_{cg} was averaged across treatments.

this model can only be fully interpreted in conjunction with the downy brome effect for different treatments (Fig. 2.4b), which was lowest in the low seeded-DT variety combination as well. In a management recommendation context these results imply that for the DT variety, a low seeding rate represents the best management decision even under increasing downy brome pressure. In contrast to the main and direct effects approaches, significant differences between varieties were detected using the annihilated approach (Fig. 2.5b). The DT variety was higher yielding than the HY variety, at low and high seeding rates. Interpreted as the total effect of the treatment on downy brome and wheat, the high-seeded-DT variety was estimated to be the highest yielding decision of the four scenarios (Fig. 2.4a). Calculated total effects from the direct effects model represent a common approach to modeling of natural resources management problems, where predictions are made based on the results of the statistical analysis. While these estimates have the same interpretation as the annihilated estimates, the issues encountered in estimation of direct effects propagated to the post-hoc calculations with two implications. First, credible intervals are somewhat wider than in the annihilated model. Second, this model implies that choice of variety was more important under high seeding rates (Fig. 2.5b), and its converse, that seeding rate has more of an impact on the DT variety (Fig. 2.5a).



(a) Contrasts for High-Low seeding rates



(b) Contrasts for Drought tolerant-High yielding variety

Figure 2.5: Means, 50%, and 90% highest posterior density contrasts of choice between seeding rates for each variety (**a.**), or choice of variety at each seeding rate (**b.**). Contrasts were derived for the three models (Main, Direct, and Annihilated), where Direct are the intercepts only of the Direct effects model, and Total are calculated post-hoc from the intercepts and slopes of the direct effects model.

6. Discussion

Rather than being a statistical technique, path analysis and SEM provide a framework to evaluate complex multivariate hypotheses about ecological systems where clear experimental control of multiple intercorrelated variables may not be achieved (Grace *et al.*, 2010; Lamb *et al.*, 2011; Shipley, 2002). In this paper we argued, supported by the results obtained with annihilation, that for path analysis to be useful as a natural resources management tool, total effects and their correct standard errors must be further calculated from the model graph (Grace and Bollen, 2008; Mitchell, 2001). While total effects do not reflect the current state of the system ($\hat{\mathbf{y}}$), they hold the advantage of quantifying the realistic impact of management without the need for further "what if" simulations. In our results, yield estimates obtained by annihilation accounted for the underlying process of plant competition, given the impact of the treatment on both the crop and the weed.

By deriving total effects for each node during the model fitting process, the annihilator rendered post-hoc calculations from direct edge estimates redundant, simplifying the task of accounting for error propagation through complex networks, and mitigated the problem of collinearity (Petraitis *et al.*, 1996). In our example application, all three approaches resulted in the same fitted values and therefore the direct and main effects approaches could also be considered from a path analysis perspective. Yet, they resulted in poor precision of the estimates which may lead to erroneous conclusions even when total effects are derived. This fact, together with the analytical result of section 4 and simulations (Fig. 2.2), suggests that annihilation is advantageous to the current techniques when deriving total effects. When applied through MCMC, annihilation retained the benefits of a full information method but can be applied to a wide range of structural models, not limited to continuous multivariate Gaussian

distributions. However, we make no claims as to its use in the presence of latent variables, random effects or nonlinear models, where the matrix of free parameters cannot be described by the recursive form of (2.3). While we illustrated the advantages of annihilation using simple networks of only three variables, we demonstrated analytically it is generalizable to more complex designs/scenarios. With the modeling flexibility of many available software packages, annihilation is easy to apply through MCMC in a Bayesian or maximum likelihood framework.

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CHAPTER 3

ASSESSMENT OF THE VISUAL SCORING METHOD FOR *FUSARIUM SPP.* IN THE PRESENCE OF WHEAT STEM SAWFLY (*CEPHUS CINCTUS*).

1. Abstract

Root infecting fungi such as *Fusarium spp.* causing crown rot of wheat (FCR) are long-time persistent problems in many semi-arid regions of the world. Recent advances in molecular techniques such as real-time quantitative polymerase chain reaction (qPCR) assays introduced new ways to quantify disease severity of plant pathogens such as FCR. These new approaches are free of some of the limitations of traditional cell culture and visual estimation techniques. We revisited the problem of developing an accurate and consistent disease severity index for FCR by visual scoring discoloration of the lower internodes of wheat stems. We compared visual scores to the number of DNA copies of naturally occurring (uninoculated) FCR in three cultivars of spring wheat grown in North-central Montana. Results indicated that visual symptoms of FCR differed between wheat varieties and were affected by the presence of the wheat stem sawfly (*Cephus cinctus*), a major insect pest of the region. A model for developing disease severity indices for different wheat varieties based on Bayesian Markov-Chain-Monte Carlo (MCMC) sampling of an objective measure, such as qPCR, is proposed and compared to the traditional approach of assigning linear weights to visual score categories. Our approach improved both interpretation and correlations between visual scores of disease severity and FCR copy numbers and allowed new insights into the resistance and tolerance of different wheat varieties to FCR and its impact on WSS. Our work has implications in improving both research and joint management of these important agricultural pests.

2. Introduction

In the Northern Great Plains (NGP) members of the *Fusarium spp.* fungi causing crown rot (FCR hereafter) and the wheat stem sawfly [*Cephus cinctus* Norton (Hymenoptera: Cephidae), WSS hereafter] form a multitrophic pathogen-insect pest complex which is a major burden to wheat (*Triticum aestivum* L.) cropping systems (Sun, 2008; Wenda-Piesik *et al.*, 2009). A critical first step in the study, monitoring, and management of these pests is to identify and determine their levels of co-occurrence. However, accurately quantifying FCR levels in field conditions presents a challenge (Moya-Elizondo *et al.*, 2011) which could be further complicated by the presence of WSS. Traditional methods to quantify FCR are based on subjective visual evaluations of wheat stems for intensity and height of discoloration (Chełkowski, 1989). These estimates are often followed by a weighted average of stem counts in prechosen categories which are then used to develop a single disease severity index (DSI). However, disease scores may diverge between evaluators and disease symptoms may also vary by wheat variety, strains of *Fusarium spp.*, and environmental conditions (Cook and Christen, 1976; Paul *et al.*, 2005; Paulitz *et al.*, 2002). As such, there is no universal index of FCR or a common convention for the number of categories and their assigned weights in visual scores (see example Beddis and Burgess, 1992; Dyer *et al.*, 2009; Klein *et al.*, 1991). In addition, to our knowledge, no study has formally evaluated how other biological stressors, such as WSS infestations, can impact these estimates.

In small grain systems, strong correlations between visual FCR indices and different crop damage types have been shown, but inconsistencies in FCR measurements may obscure the relationship between FCR levels and pathogenicity (Hogg *et al.*, 2007; Smiley *et al.*, 2005). Isolates from infected plants can be identified and quan-

tified with genetic and culturing methods and used as a quantitative alternative to visual scores (Moya and Jacobsen, 2008; Moya *et al.*, 2009; Nelson *et al.*, 1983). These methods allow a more accurate distinction between disease levels and pathogen populations, but require field samples to be rigorously processed by expensive and time-consuming methodologies. In Montana, FCR is caused primarily by *Fusarium culmorum* and *Fusarium pseudograminearum* and has become a wide-spread problem as the popularity of no-till methods grows (Moya-Elizondo *et al.*, 2011). Infective propagules of FCR overwinter in the crop residue or in the soil surface and infect newly sown plants, colonizing their crowns and lower internodes as they develop (Hogg *et al.*, 2010). Symptoms of FCR include stand and grain yield reduction, and rotting of root, crown and stem tissues (Chełkowski, 1989; Smiley *et al.*, 2005) that take on a distinctive brown color (Nelson *et al.*, 1983). Under drought conditions plant defenses weaken and FCR can also invade and obstruct vascular tissue (Beddis and Burgess, 1992; Cook and Christen, 1976). As there is no viable chemical solution, management of FCR is based on cultural practices such as lowering seeding rates to conserve soil moisture and minimize crop residue to reduce disease pressure and infection rates over time (Paulitz *et al.*, 2002).

WSS is a widely distributed and destructive insect pest of wheat production in the NGP (Beres *et al.*, 2011). WSS completes one life cycle per year, where all immature stages are spent inside protective plant stems, synchronized with the physiological development of the host. In the NGP, females typically oviposit in the uppermost internode of wheat stems from late May to mid-July. WSS development includes four or five larval instars feeding on parenchyma and vascular tissues causing up to 22% reduction in number and size of wheat kernels (Holmes, 1977). As the wheat plants start to senesce, the surviving larvae move toward the bottom of the stems, cutting a notch at the base and constructing a diapause chamber to overwinter in the crop

residue. The notch weakens the stem which is subsequently lodged. Lodging reduces harvest efficiency and increases volunteer wheat in the fall and following spring. While lodging causes loss of mature wheat plants, boring larvae also cause dark spots below the nodes in infested stems (Morrill *et al.*, 1992).

Three lines of logic make the joint management of FCR and WSS imperative. First, in the absence of effective conventional insecticides, reduction of WSS populations and damage is best achieved through solid-stem wheat cultivars (Holmes and Peterson, 1962). However, lodging tolerant solid-stem varieties (SFLT hereafter) tend to be lower yielding and have reduced disease and drought resistance, while FCR tolerant varieties may be more susceptible to WSS infestation and lodging. Second, in the time spent inside the plant stem the living WSS larva becomes vulnerable to pathogenic invasion by micro-organisms. In the past, *Fusarium spp.* have been isolated from pink-colored WSS larva cadavers (Sun, 2008; Wenda-Piesik *et al.*, 2009). Third, wheat lodging and boring by WSS larva may discolor stems, reducing the number of stems available for visual estimation and compromising assessment and monitoring of FCR in field settings.

To shortcut the above-mentioned limitations, it is necessary to develop a better index of FCR disease levels. An approach that combines visual scoring and quantitative methods may allow developing economically and logistically viable methods for large scale FCR evaluations. To assess the impact of WSS on FCR measurement and improve on available FCR disease severity index, we first evaluated FCR levels in standing and lodged spring wheat stems both visually and with real-time quantitative polymerase chain reaction (qPCR), an approach that is not confounded by WSS cutting. Second, we assessed the presence of WSS in wheat stems and their disease status. Finally, we developed a model to quantify disease severity for different wheat varieties based on an objective measure of FCR status. Our objectives were to 1)

assess the accuracy of FCR level estimates in the presence of WSS lodging, 2) expand on the work of Hogg *et al.* (2007) on visual disease indices of FCR, and 3) assess the variability of FCR measurements for different wheat varieties and in the presence of WSS.

3. Materials and Methods

This study was conducted during the 2010 growing season as part of a larger project assessing ecologically based pest management strategies in small grain systems that was carried out during the growing seasons of 2008-2010 in a 1 ha production field near Ulm, MT (47°26.1326 N 111°32.0578 W). Our previous observations at the site indicated high FCR levels, low history of weed pressure, and high abundance of WSS. Average daily temperatures for the months of March to Sept. 2010 were 12 C and total precipitation of 350 mm, with 67-70 mm occurring each month from April to June.

The experimental design followed a split-split-plot design with 3 replications, wheat variety being the whole plot (7 m x 63 m), seeding rates the sub-plot (7 m x 21 m), and weed management approach the sub-sub-plot (7 m x 7 m). Broadleaf weeds were controlled at the entire site with bromoxynil + MCPA applied at 0.274 Kg ai ha^{-1}. To generate a range of grassy weed pressure, Sulfosulfuron was applied to the sub-sub-plots at either 0.028, 0.014, or 0.007 Kg ai ha^{-1}. Ten and 5 m buffers separated plots and subplots, respectively, and were kept weed free through an application of glyphosate and 2,4-D.

On March 26, 2010, we planted three wheat cultivars: 1) WSS lodging tolerant (SFLT) Choteau (MSU, 2004) MT9929: semidwarf, solid-stem variety with good sawfly resistance rating, 2) Drought tolerant (DT) McNeal (MSU, 1994): semidwarf,

hollow-stem variety with good lodging resistance but less resilient straw that is prone to breaking, and some tolerance to dryland root rot, and 3) High yielding with available moisture (HY) Reeder (ND, 1999): semidwarf hollow-stem variety with a longer grain-fill period. All three wheat varieties were seeded at three rates targeting 125, 250, 500 plants/m^2, respectively. All seeding was performed with a Fabro no-till drill at 3.8-5 cm depth. Broadcast urea 46-0-0 NPK was added at varying rates based on 54 soil samples obtained to a depth of 61 cm, two in each sub-plot, the previous fall to achieve 150 Kg N/ha across the field.

On August 12, 2010, forty-six paired samples of approximately 10 consecutive standing and 10 consecutive lodged wheat stems were collected from different locations in the field. The field was not inoculated with *Fusarium spp.* and at the time of data collection, naturally occurring FCR levels were unknown. To secure a range of FCR in the data set, samples were obtained based on 2009 FCR observations. Our attempt to balance number of samples in treatments with creating an effective range of disease severity resulted in an unbalanced design with respect to the number of samples obtained in each variety and seeding rate treatments combination (Table 3.1). Each standing stem in a sample was visually scored on a 3-point scale, i.e. the first internode categorized as having low (healthy, no discoloration), medium (light brown) or high (dark brown) FCR levels (Dyer *et al.*, 2009). Then, stems were dissected for evidence of WSS activity by noting the number and color of larvae cadavers in the sample. Finally, FCR levels in these 10 stems and 10 adjacent stubs (stems lodged by WSS) were assessed with qPCR following the protocol described in Hogg *et al.* (2007), with the number of FCR copies $CP = 10^{sct}$ where sct is a standardized threshold cycle $12.5 - 0.3ct$.

Table 3.1: Number of samples for each wheat variety and seeding rate. Wheat varieties are wheat stem sawfly lodging tolerant (SFLT), drought tolerant (DT), and high yielding (HY). Low, medium and high seeding rates were established targeting 125, 250, 500 plants m^{-2}, respectively.

	seeding rate			
	low	medium	high	Total
SFLT	4	8	4	16
DT	4	4	4	12
HY	10	4	4	18
Total	18	16	12	46

4. Statistical Analysis

We took a Bayesian approach to data analysis, using R 2.13.0 (R Development Core Team, 2010) and JAGS 3.0 (Plummer, 2003). In Bayesian statistics interest lies in the posterior, the probability distribution of the parameter of interest, given the observed data and a prior belief (Berger, 1985). When analysis is conducted with completely diffused or non-informative priors, the parameter estimates or modes of the posterior distribution are not biased by the prior distribution and are essentially maximum likelihood estimates. However, an important distinction is that the probabilistic framework of Bayesian statistics does not rely on the long-term frequency interpretation of the estimates and their standard errors, allowing inference based on small sample sizes. Bayesian p-values reported are posterior probabilities for the observed or more extreme values, given the size and variability of data. The Bayesian framework was better suited to our sample size and design, and allowed greater flexibility in modeling than the frequentist approach (Gelman and Hill, 2007; Robert, 1994). We used the available closed form posterior distributions for multiple comparisons of FCR levels between varieties and between standing and lodged stems.

Due to the observational nature of this study, we utilized naturally occurring FCR levels and no individual plants could be considered *a priori* as healthy controls. Since stems exhibiting low levels of FCR are visually indistinguishable from discolored healthy stems, we derived two measures of FCR occurrence based on the number of stems in each of the three visual score categories:

$$\text{Incidence} = \frac{n_m + n_h}{n} = 1 - \frac{n_l}{n} \qquad \epsilon \quad [0,1] \tag{3.1}$$

$$\text{Severity} = \frac{n_h}{n_m + n_h} = \frac{n_h}{n}\text{Incidence}^{-1} \qquad \epsilon \quad [0,1] \tag{3.2}$$

where n is number of stems and the subscripts l, m, and h correspond to the low, medium and high categories respectively. Incidence represents the proportion of stems containing FCR with a high degree of confidence. Severity is the relative proportion of stems with high FCR infection from stems scored medium and high and reflects the strength of infection conditional on non-zero Incidence of FCR.

For the standing wheat stems that were both visually scored and processed with qPCR, a measurement error regression model was fit to the natural log of DNA copy numbers of FCR determined by qPCR (lnCopy) as the response, and a weighted average of Incidence and Severity as a predictor. For every one of three wheat varieties, a hierarchical model was fit by Gibbs sampling where:

$$\text{Visual}_i \sim \mathcal{M}ulti(n_i, \theta_i^{low}, \theta_i^{medium}, \theta_i^{high}) \qquad \text{where } \boldsymbol{\theta_i} \sim \mathcal{D}irichlet(a_0, b_0, c_0) \tag{3.3}$$

$$\text{Incidence}_i = 1 - \theta_i^{low} \tag{3.4}$$

$$\text{Severity}_i = \frac{\theta_i^{high}}{\text{Incidence}_i} \tag{3.5}$$

$$X_i = \text{Incidence}_i W + \text{Severity}_i(1 - W) \qquad \text{where } W \sim \mathcal{B}eta(a_0, b_0) \tag{3.6}$$

$$ln\text{Copy}_i = X\beta + \epsilon_i, \qquad \text{where } \epsilon_i \sim N(0, I\sigma^2) \tag{3.7}$$

In the above model, Incidence and Severity are derived from the parameter (θ) in equations (3.4) and (3.5) rather than the data (n) as in equations (3.1) and (3.2). This approach allowed us to account for the variability caused by the subjective nature of the visual score. The estimation of weights ($W, 1-W$) in (3.6) allowed us to simplify the two measures, Incidence and Severity, and combine them into a single index for FCR disease severity model (weighted Incidence Severity by variety, WISbV hereafter). The $\mathcal{D}irichlet$ and $\mathcal{B}eta$ distributions are the conjugate priors for the multinomial and binomial distributions respectively and were parametrized to represent a uniform distribution over the interval 0-1, i.e. a non informative prior. Finally, equation (3.7) is a simple linear regression model where diffuse priors were also placed on β and $ln(\sigma)$.

5. Results

This study investigated methodological aspects of FCR assessments and assessed the degree to which management practices and WSS infestations influence FCR measurements. Therefore, we did not collect samples randomly across the entire field, but purposefully targeted hypothesized areas of high FCR infection for each wheat seeding rate and variety combination. Results of an initial analysis of variance indicated that there were no significant differences in lnCopy values between seeding rates, nor did seeding rates significantly interact with wheat variety (results not shown), which did exhibit marginal differences (p-value = 0.083) in lnCopy values. Moreover, no pattern in the visual score of discoloration was detectable for seeding rate and seeding rate by variety interaction. Therefore, values for each variety were pooled across all seeding rates for the remainder of the analysis.

Mean estimates of FCR levels in wheat varieties depended on the method used to assess disease status, i.e. qPCR or visual scoring (Table 3.2). On average, the HY variety had higher *ln*Copy values than the SFLT and DT varieties (p-value = 0.078 and 0.043 respectively). However, all three visual score categories of the HY variety were comparable to those observed for the DT variety and higher than the SFLT variety only for the medium FCR category (p-value = 0.025). The SFLT variety was comparable to the DT variety in *ln*Copy, but had on average fewer stems scored as medium (p-value = 0.1007) and more stems scored high (p-value = 0.036) than the DT variety.

Table 3.2: Posterior* means and standard deviations of average *ln*Copy of FCR levels measured by qPCR and visual score categories by wheat variety. Wheat varieties are wheat stem sawfly lodging tolerant (SFLT), drought tolerant (DT), and high yielding (HY).

		Visual scores		
	*ln*Copy **	Low	Medium	High
SFLT	$6.6^{a} \pm 1.8$	0.5 ± 0.043	$0.27^{a} \pm 0.039$	$0.23^{a} \pm 0.034$
DT	$6.4^{a} \pm 1.7$	0.52 ± 0.052	$0.34^{ab} \pm 0.047$	$0.14^{b} \pm 0.037$
HY	$8.8^{b} \pm 1.3$	0.45 ± 0.047	$0.37^{b} \pm 0.038$	$0.18^{ab} \pm 0.036$

* Estimates are based on 10,000 draws from the posterior $P(\theta|y,\phi)P(\phi|I)$ where $I \sim \mathcal{M}ulti(n_j, \phi)$ represents the number of samples in each of three seeding rate categories for wheat variety j accounting for the unbalanced design.

** Means not sharing a common letter across columns differ at $\alpha = 0.1$.

Agreement between visual scores and *ln*Copy varied across wheat varieties (Fig. 3.1). For the SFLT variety, the rate of increase in *ln*Copy closely followed Incidence except for sample number 11/16 that was estimated as completely free

of FCR through qPCR but received a relatively high visual score. However, this variety showed poor agreement between lnCopy and Severity, with high variability in lnCopy for samples with equal Severity, as well as lnCopy increasing with a decreasing Severity (samples 5-10/16). For the DT variety, there was very low agreement between lnCopy and Incidence, which varied very little for this variety. However, Severity provided a good measure for distinguishing between medium and high levels of lnCopy for all but three samples (6,7 and 9/12). For the HY variety, lnCopy did not agree with either Incidence or Severity. For this variety, although Incidence seems to agree with lnCopy for several samples of mid to high-level visual scores (samples 9-13 /18), lnCopy remained relatively constant in samples 12-18/18 where Incidence showed a distinct increasing trend. Moreover, while Severity, like lnCopy, remained relatively constant in samples 12-18, high lnCopy were also measured by qPCR in samples 1,3,4, and 5/18 when Severity was zero, and only low to medium Incidence.

Pink colored WSS larva cadavers indicative of high FCR presence, were found in nine of the forty-six samples (Fig. 3.1). As a general rule we assumed higher accuracy of the objective lnCopy measure and attributed variability in agreement mostly to the visual scores. However, the relatively low lnCopy values in samples where WSS larvae was killed by FCR (15/16 in SFLT and 7/12 in DT) suggests that qPCR, which is only conducted on plant tissue, may be underestimating FCR levels in the presence of WSS.

The trends observed in the raw data were reflected in the posterior distribution of the WISbV model parameters (Fig. 3.2). The intercept (β_0) represents lnCopy at the low visual category (zero Incidence and Severity), and is a measure of the underestimation of FCR caused by treating low scored stems as uninfected (Fig. 3.2;β_0). Although all three varieties exhibit some degree of underestimation, it was substantially higher for HY than the other two varieties (Bayesian p-values for the underestimation of

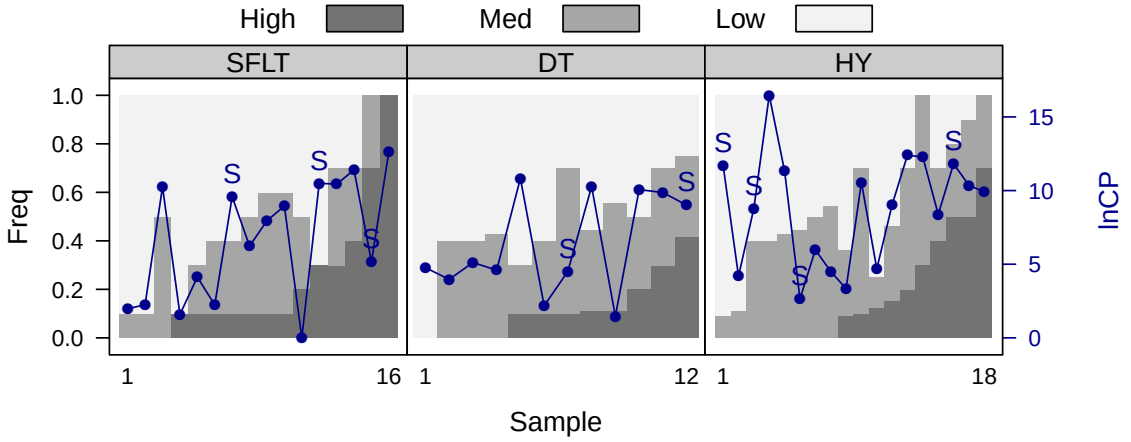


Figure 3.1: Agreement between *ln*Copy, *Fusarium* levels measured by qPCR, (continuous line) and number of stems in the low, medium, and high visual score categories (shaded bars). Two measures of visual scores are considered: Incidence is the relative area represented by medium and high categories, and Severity is the area represented by the area of the dark shaded bars relative to Incidence. A pink colored wheat stem sawfly larvae cadaver indicative of FCR infection of the larvae was found in nine of the samples, marked with an "S".

0.097, 0.082, and 0.003 for SFLT, DT and HY, respectively). A weak relationship between *ln*Copy and visual scores for the HY variety was apparent in the slope parameter β_1 (Fig. 3.2;β_1). While p-values for SFLT and DT were 0.035 and 0.054, respectively, p-value for HY was 0.134, i.e. two and a half to three and half times higher probability of having no relationship between visual estimates and *ln*Copy. Finally, the weights for Incidence and Severity in the combined visual score (Eq. 3.6) were, in accordance with Fig. 3.1, greater for Incidence relative to Severity in the SFLT variety, the opposite for the DT variety, and with relatively equal emphasis on Incidence and Severity for the HY variety (Fig. 3.2;*weights*).

A Bayesian analysis conditions on the whole probability model and can be misleading if the model is far from plausible. A posterior predictive check, where hypothetical replications of the data are expected to generate values similar in relevant ways to the

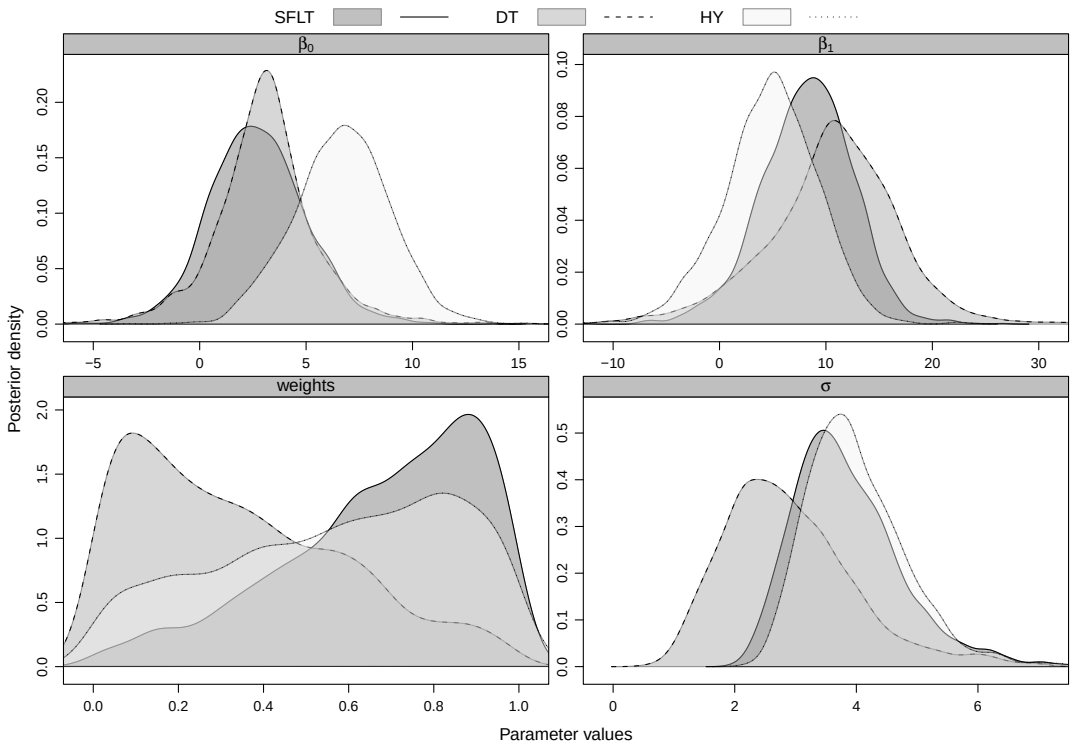


Figure 3.2: Posterior density distribution for the parameters of the Weighted Incidence Severity by Variety (WISbV) models for wheat stem sawfly lodging tolerant (SFLT), drought tolerant (DT), and high yielding (HY) wheat varieties. For each of three varieties, four MCMC chains, overdispersed at initialization, were run for 40,000 iterations, with a burnin period of 20,000 and thinning interval of 40 to retain 2,000 samples for density estimation. Each regression is of the form $lnCopy = \beta_0 + \beta_1 x^* + \epsilon$ where $x^* = wIncidence + (1 - w)Severity$ and $\epsilon \sim N(0, I\sigma^2)$.

original observations if model specifications are appropriate, allows detection of systematic differences between the proposed model and observed data (Rubin, 1984). A posterior predictive check confirmed that deriving a disease index by variety through the the WISbV model improved the accuracy of visual scores compared with those values derived from weighted average of visual scores (Fig. 3.3). For both the SFLT and DT varieties, 95% highest posterior density intervals of the WISbV model captured the value of lnCopy eight times, compared with only three for the weighted

average model. For the HY variety, the WISbV model captured lnCopy ten times, twice as many as the linear weights model. There were no instances where lnCopy values that were not captured by the WISbV model were captured by the weighted average model.

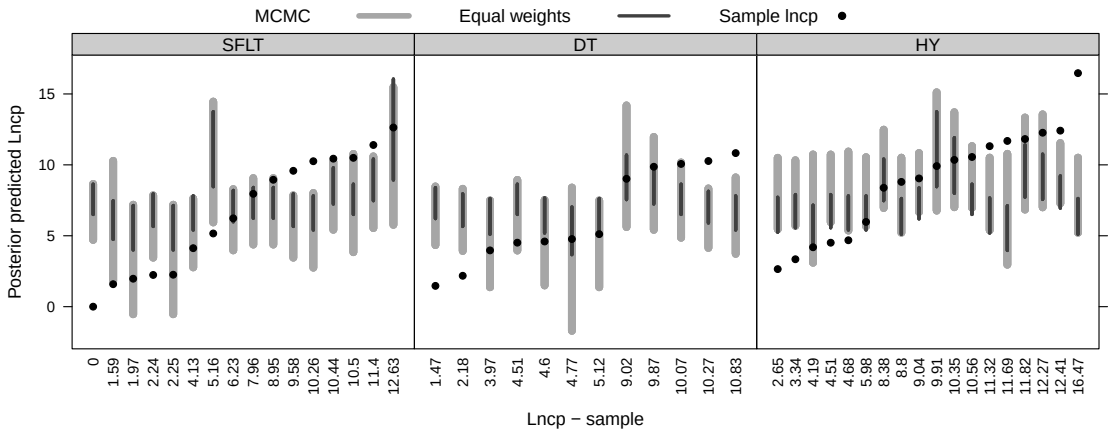


Figure 3.3: Posterior predictive check of the weighted Incidence Severity by variety (WISbV) disease index. For each of 46 samples, we generated 2,000 values of lnCopy from the posterior of the WISbV model, and from a multivariate normal distribution for the coefficients of a linear model $lnCopy = X\beta + \epsilon$ where disease severity $X = (0.25n_{Low} + 0.5n_{Med} + n_{High})/n$. 95% prediction intervals for WISbV (thick gray bars) and the common linear weights model (thin black bars) are plotted for each sample.

It is possible that the wider prediction intervals that resulted from the variability in the weights of the WISbV model, as compared to the single weight values utilized in the weighted average model were responsible for the fact the WISbV always performed better in a predictive check. Yet, to develop an economically and logistically feasible disease severity index for large scale evaluations, it may not be possible to develop a range of weights values and a single estimate needs to be used. To assess the applicability of this approach, we utilized the modes of the posterior $\pi(w_j|y)I_j(\text{variety})$ presented in Fig. 3.2;w in a regression settings, and compared the results to the

results obtained from a weighted average model. Regression models of predicted vs. observed *ln*Copy had higher r^2, lower BIC, and lower standard errors for the estimated regression coefficients compared with predictions from the weighted average model developed with constant weights across varieties (Table 3.3). The intercept $\hat{\beta}_0$ for the across-variety weighted average model was not significantly different than zero, implying that assigning a weight of 0.25 to the low visual score mitigates the underestimation of low FCR levels observed in the WISbV model whose intercept was 70% higher. This result suggests a large FCR underestimation could occur in wheat varieties where symptoms are not as apparent. The slope of the regression line was significant in both models but lower for the WISbV model compared with the across variety weighted average model, suggesting the inclusion of the low FCR category in the latter disease severity index may underestimate FCR at high levels compared with WISbV.

It is possible that the relative contribution of FCR to increased WSS larvae mortality differed among wheat varieties. Overall, the SFLT variety had more dead larvae in the stems than the other two varieties (p-values = 0.245, 0.031 for DT and HY, respectively). However, of the samples containing dead larvae, pink colored cadavers indicative of FCR related mortality where found in only 20% of SFLT samples compared with 33%, and 31% for DT and HY respectively. FCR levels as measured by *ln*Copy in standing wheat stems were 2.45 (p-value = 0.073) times greater than in WSS lodged stems with no discernible pattern among wheat varieties or seeding rates. To evaluate the existence of a FCR threshold level required to impact WSS viability, we conducted a series of repeated paired t-tests on our sample, successively removing the lowest mean *ln*Copy for both cut and uncut stems from the data. An evaluation of the 95% credible intervals resulting from these successive tests suggests that at *ln*Copy higher than 7.64 the FCR levels in standing stems was 3.6 (p-val=0.0105,

Table 3.3: Comparison of linear regression models* for lnCopy by disease index calculated with linear†, or posterior†† weights.

	Coeff.	Estimate	Std. Error	t value	Pr(>|t|)	r^2	BIC**
Linear	β_0	2.4	1.4	1.7	0.1	0.27	234.70
	β_1	10.65	2.85	3.73	< 0.001		
Post.	β_0	4.1	0.84	4.9	< 0.001	0.35	229.26
	β_1	7.8	1.7	4.61	< 0.001		

* Models are generalized least squares regression fit by Maximum likelihood.

** Bayesian Information Criteria. Similar to AIC it is the likelihood penalized for the number of parameters, k, in the model: $-2ln(Likelihood) + kln(n)$ such that lower is better.

† Disease index is $\sum w_j \frac{n_j}{n}$ where $j = \{Low, Med, High\}$ and $w = (0.25, 0.5, 1)^T$.

†† Disease index is $w_k \frac{n_{Med}+n_{High}}{n} + (1 - w_k)\frac{n_{High}}{n_{Med}+n_{High}}$ where $k = \{SFT, DT, HY\}$, and $w = (0.88, 0.093, 0.82)^T$ are the modes of the posterior for each variety.

n = 21) times higher than lodged Fig. 3.4, indicating that relatively high pathogen levels were required to effectively kill WSS.

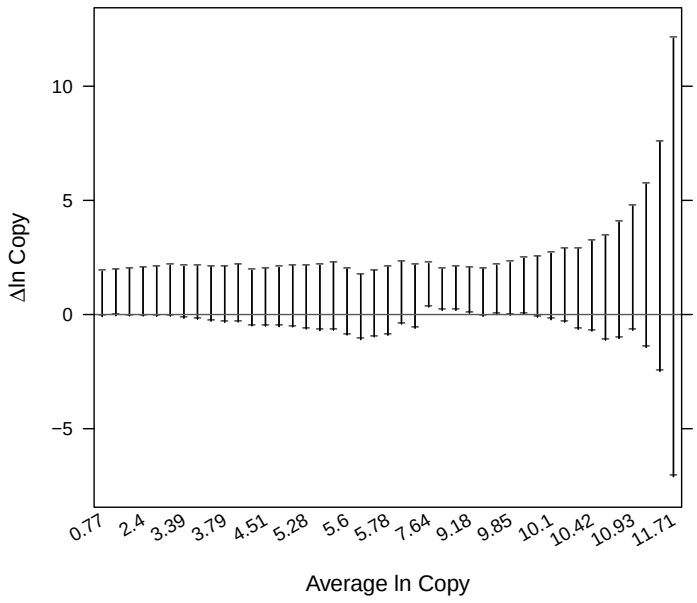


Figure 3.4: 95% credible intervals for the difference in lnCopy, FCR levels measured by qPCR, between wheat standing stems and stems lodged by WSS.

6. Discussion

The importance of choices made in the construction of a visually-based disease severity index to assess *Fusarium spp.* pathogenicity has long been recognized (Browne, 2007; Smiley *et al.*, 2005; Yi *et al.*, 2000). A common practice is to use a single index, often a weighted average of the visual categories (Hogg *et al.*, 2007). Our results indicated that wheat stem discoloration due to FCR varies across varieties and in response to potential confounding factors such as the presence of WSS. Therefore, interpreting correlations between visual scores of disease status and yields as a causal effect of FCR while ignoring the potential impact of confounding factors, may introduce measurement error (Powell and Swanton, 2008). The advent of new methodologies such as qPCR provides accurate quantification of FCR population size

and allows revisiting the visual scoring methodology to gain new insights regarding crop resistance and tolerance to FCR.

In plant pathology, genetic resistance describes the ability of a plant to retard or prevent infection by the pathogen, and sustain little tissue damage. By reducing pathogen spore production, disease resistance decreases the risk of future outbreaks. In contrast, genetic tolerance describes the ability of a plant to withstand infection and produce acceptable growth without reducing the numbers of reproductive spores or limiting the ability of the fungus to infect or damage tissue. While disease resistance can be measured by evaluating the presence or absence of infection or its relative severity, tolerance is evaluated by comparing growth attributes from plants grown under a range of imposed disease pressure (Smiley and Yan, 2009).

Lowering seeding rates and increasing crop resistance has been proposed as management approaches to mitigate FCR by reducing plant residue, decreasing volunteer inoculation (Hogg *et al.*, 2010), and conserving soil moisture (Cook and Christen, 1976). However, wheat resistance to FCR is only partial and disease outbreaks are common and can be severe when climatic conditions are favorable for the pathogens (Moya *et al.*, 2010). In this study, the HY variety showed less resistance to FCR than the DT and SFLT varieties. Three factors could have affected the differential response of wheat varieties to FCR. First, the inherent disease resistance of the tested varieties. Second, the faster tillering rate of the HY variety (Hansen *et al.*, 2005; Naruoka *et al.*, 2011) that may have increased inter-specific competition. Finally, the presence of grassy weeds and the associated intra-specific competition. While the entire area had relatively low weed pressure in 2008 and 2009, the differential herbicide treatments resulted in a range of downy brome (*Bromus tectorum* L.) pressure in 2010. Downy brome is a highly competitive grassy weed of winter and spring wheat cropping systems (Blackshaw, 1991) and may have a strong impact on the HY variety

(ref chapter 2, 4). This study was not conducted to assess the relative importance of these factors in mediating wheat responses to FCR, and future manipulative studies could be conducted to fill this knowledge gap.

Integrating visual scores with the results of the qPCR analysis allowed us to compare changes in disease tolerance across wheat varieties. This study showed the SFLT variety was less tolerant to FCR than the hollow stemed varieties, in particular the DT variety. The concentration of posterior weights on Incidence for the SFLT variety and to a lesser extent for the HY variety, compared with the high concentration on Severity for the DT variety, suggests that FCR symptoms became apparent in the SFLT and HY varieties at low disease levels. However at low numbers, FCR had little effect on DT, where only high levels were visually apparent and could be predicted almost exclusively by Severity. These results suggest that field observations, surveys, and monitoring schemes could benefit from pre-calibrating disease indices to account for specific crop's inherent resistance or tolerance (Paul *et al.*, 2005).

The enhanced performance of the WISbV model compared with a disease severity index based on assigning linear weights to the raw visual-score categories can be attributed to two factors. First, the utilization of Incidence and Severity as measures rather than the raw visual scores, and second, the assignment of weights by variety rather than utilizing a common across-variety value. In contrast to the raw visual scores, Incidence and Severity are conditionally independent measures and information in Severity complements Incidence (Yi *et al.*, 2000). Incidence represents the proportion of stems containing FCR with a high degree of confidence and while it may underestimate the total amount of FCR in a given field because all stems ranked low are treated as healthy, it is useful for within field comparisons because it disregards observations that could lie below the economic threshold. Severity, on the other hand, is the relative proportion of stems with high FCR infection and represents the

disproportionality in which FCR at the highest rating may affect parameters of wheat vigor (Dyer *et al.*, 2009).

When integrated, Incidence and Severity also had better numerical properties than a weighted average model of the raw visual scores. Independence allows the measures to be combined to a weighted disease index without any additional assumptions on the total number of stems in the sample. We attempted to distinguish between the two sources of advantage in performance by recreating the 0.25, 0.5, 1.0 weights for the visual score categories for this data set, but did not achieve convergence for the raw visual scores after 140,000 iterations. A model using common across variety weights on Incidence and Severity had much wider 95% prediction intervals, but performed poorly when only the modes were used, with $r^2 = 0.17$ and a BIC of 240.4, further establishing the importance of distinguishing between varieties when developing a disease index.

In conclusion, our observations confirmed previous findings by Wenda-Piesik *et al.* (2009) of interactions between FCR and WSS. The proposed model appeared appropriate to assess how the impact of these interactions modify disease severity assessments. Despite the small sample size, our observations suggested that FCR was associated with increased WSS larva mortality in hollowed-stem wheat varieties. Previous studies suggest FCR actively infects WSS larva rather than colonizes it postmortem as a secondary host (Sun, 2008). Our observations of pink cadavers not only at high FCR levels but also at medium *ln*Copy and low Incidence, support this concept and suggest that FCR impact on the plant may be lessened when presented with a WSS larvae. This result may have far reaching implications towards management or use of certain less pathogenic endemic -*Fusarium spp.* in the biological control of wheat stem WSS as suggested by Wenda-Piesik *et al.* (2009). Yet, the FCR levels required

to achieve a meaningful impact on WSS lodging could be economically inviable given the damage FCR inflicts on wheat.

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CHAPTER 4

INTERACTING AGRICULTURAL PESTS AND THEIR EFFECT ON CROP YIELD: APPLICATION OF A BAYESIAN DECISION THEORY APPROACH TO THE JOINT MANAGEMENT OF THE WHEAT STEM SAWFLY AND DOWNY BROME

1. Abstract

This paper implements and discusses a framework for evaluating outcomes of crop management strategies that reflects a total-system approach to pest management. To do so, the direct and indirect interactions between a stem boring insect pest, a grassy weed, and spring wheat were modeled. Bayesian statistical inference and Decision theory were utilized in order to model complex behavior patterns of the insect in the presence of the weed, and the joint impact of the two pests on wheat yields. The information on the functional relationships between these organisms occurring at different trophic levels and under different crop management strategies was then incorporated in a decision-aid model by annihilation. Annihilation is a path analysis technique to derive total effects in a prespecified model of causal relationships and can therefore be used in predictive models that take advantage of the crop's attributes for tolerating a pest species. Our results suggested that complex and dynamic direct and indirect interactions between the two pests had significant impact on system outputs. Moreover, joint consideration of the effects of multiple pests in a decision model, rather than a combination of separate analyses can be essential for ecologically-sound pest management.

2. Introduction

Encouraging positive biotic interactions and reducing negative unintended consequences, while maintaining an acceptable level of production, is at the core of the integrated pest management (IPM) concept. Yet, many IPM programs are designed around a single category of pests and may not provide satisfactory solutions when confronted with the dynamic and complex interactions between pests occurring at different trophic levels (Capinera, 2005; Lewis *et al.*, 1997; Norris *et al.*, 2003). Replacement of single-pest, chemically-based control approaches with more sophisticated, biologically-based programs requires an understanding of the direct and indirect interactions between all categories of pests in the IPM decision-making process (Norris and Kogan, 2005). For example, the inherent preventive strengths of a crop to effectively compete with weeds or tolerate insect pests can be utilized as ecologically sound pest management tactics in IPM. However, the limitations and potential contradictions between the responses of different pest groups to specific crop attributes and the complexity of biological interactions challenge scientific research and predictive modeling. This challenge is further amplified when attempting to use knowledge of ecological dynamics to inform alternative management actions such as crop yield maximization in the presence of multiple, interacting pests (Colbach, 2010; Dorazio and Johnson, 2003).

In the Northern Great Plains (NGP), the high commodity specialization of conventional agriculture has resulted in vast monocultures of wheat (*Triticum aestivum* L.) and an increased reliance on off-farm synthetic inputs. However, an influx of a specialized pest complex compromises the requirements of robustness, resilience, and environmental integration required in sustainable farming systems (Cochran *et al.*, 2006; Gan *et al.*, 2010; NRC, 2010). Two members of this pest complex include the

wheat stem sawfly [*Cephus cinctus* Norton (Hymenoptera: Cephidae)] (WSS hereafter), a widely distributed, destructive, and one of the most economically important insect pests of wheat (Beres *et al.*, 2011a), and downy brome (*Bromus tectorum* L.), an increasingly problematic weed in range, wildlands, and cropping systems of the NGP (Mack, 2011). WSS and downy brome do not occur in isolation. Recent evidence suggests that levels of WSS infestation in downy brome are two-fold higher than for wheat (Perez-Mendoza *et al.*, 2006) indicating that interactions between these pests can play an important role in their joint survival and impact. Moreover, the lack of a viable insecticide for WSS management and the associated energy, environmental concerns, and health risk costs of excessive herbicide use, as well as the emergence of herbicide resistant weed biotypes, motivate recent attempts to reduce reliance on chemical control and a shift away from high-input-single-pest control methods (Grant, 1998; Shennan, 2008).

Utilizing management strategies to take advantage of the crop's attributes for tolerating a pest species, whether insects or grassy weeds within a cultivated grass cereal crop, is a complex task because of the dynamic nature of agroecological systems. For example, agronomic traits that increase crop's competitiveness against weeds including height, disease resistance, drought hardiness, and yield potential have the ability to decrease downy brome impacts (Beres *et al.*, 2010; Lemerle *et al.*, 2001). Yet, while increasing crop seeding rates has been suggested as an intuitive strategy to suppress weed emergence and growth, evidence suggests that intraspecific competition and environmental conditions may offset their usefulness (Blackshaw, 1994; Crawley, 2009; Lemerle *et al.*, 2004; Weiner *et al.*, 2001). Also, time spent inside protective stems make WSS less susceptible to external factors and in the absence of an effective conventional insecticide, mitigation of WSS populations and damage is best achieved through use of solid-stem wheat cultivars that have negative impacts

on the egg and restrict tunneling or cause mortality of young boring WSS larvae (Holmes and Peterson, 1962). However, solid stem varieties may not be as competitive and concerns exist regarding yield, efficacy, and market opportunities. Solid stem wheat varieties also exhibit mixed results as a WSS population control method, mostly due to inconsistent pith expression which may be affected by abiotic factors as well as intra- and inter-specific competition (Beres *et al.*, 2009; Weaver *et al.*, 2004). Residue management and increasing seeding rates also have potential for reducing WSS population and increasing yields, but may not be economically viable and have an inverse relation with pith expression (Beres *et al.*, 2011b, 2012).

Since pest management schemes do not affect just one species and trophic interactions exist between agricultural pests (Price *et al.*, 1980), ecologically-based pest management requires increased understanding of approaches to incorporate direct and indirect interactions into the management decision process. The WSS-downy brome-wheat complex represents a case study to assess such approaches in the design of holistic management recommendations. In this paper, we implemented and assessed a formal framework for evaluating outcomes of commonly used crop management practices to reflect a total-system approach to pest management. Specifically, we used a Bayesian decision theoretic approach to probabilistically model wheat grain yield while accounting for how wheat variety, seeding rate, and herbicide application rate jointly affect WSS and downy brome abundance and impact. This approach allowed us to incorporate the direct and indirect multiple biological interactions occurring within the agroecosystem in a predictive model of wheat yield, rather than individually evaluate the effect of any single pest- or crop-management tactic. To meet our objective, we developed our model based on empirical data of wheat yield and naturally occurring pest levels observed in a field experiment where the crop was grown under different management scenarios.

3. Materials and Methods

3.1. Site

This study was conducted as part of a main study assessing ecologically-based pest management strategies that was carried out during the growing seasons of 2008-2010 in a commercial farm near Amsterdam, Montana (45°45.0250 N, 111°25.1900 W, 1490 m elevation). Soil type at the area is classified as fine-silty, mixed Typic Haploborolls Amsterdam silt loam series (Chen *et al.*, 2006). Typical frost-free period at the site is 98 d with a 30-year (1981-2010) average annual precipitation of 500 mm. Annual temperatures for 2008-2010 averaged 12.4 C, 13 C, and 12.6 C with total precipitation for the duration of the growing season of 252 mm, 270.5 mm, and 302.8 mm, respectively.

We planted spring wheat in three blocks separated by 10 m buffers within a 1 ha area. Treatments (crop variety, seeding rate, and herbicide rate) were assigned in a randomized split-split plot design to the same sub-sub plots (7x7 m) in all three years to represent a variety of management practices (Fig. 4.1). Due to space constraints, there were no buffers between sub-sub plots in block 3, and the first two sub-sub plots in block 1. All other sub-plots were separated by a 5 m buffer. Broadleaf weeds in the whole experimental site and grassy weeds in the buffers were chemically controlled.

Whole plot treatment consisted of three wheat cultivars: 1) WSS lodging tolerant (SFLT) Choteau (MSU, 2004) MT9929: a semidwarf, solid stem variety with good resistance to lodging caused by WSS stem cutting at harvest, 2) Drought tolerant (DT) McNeal (MSU , 1994): a semidwarf, hollowed stem red chaffed variety with good lodging resistance, but less resilient straw, and 3) High yielding (HY) Reeder (ND, 1999): a semidwarf hollowed stem variety with a longer grain-fill period and high yielding, particularly with limited available moisture during grain fill. The first

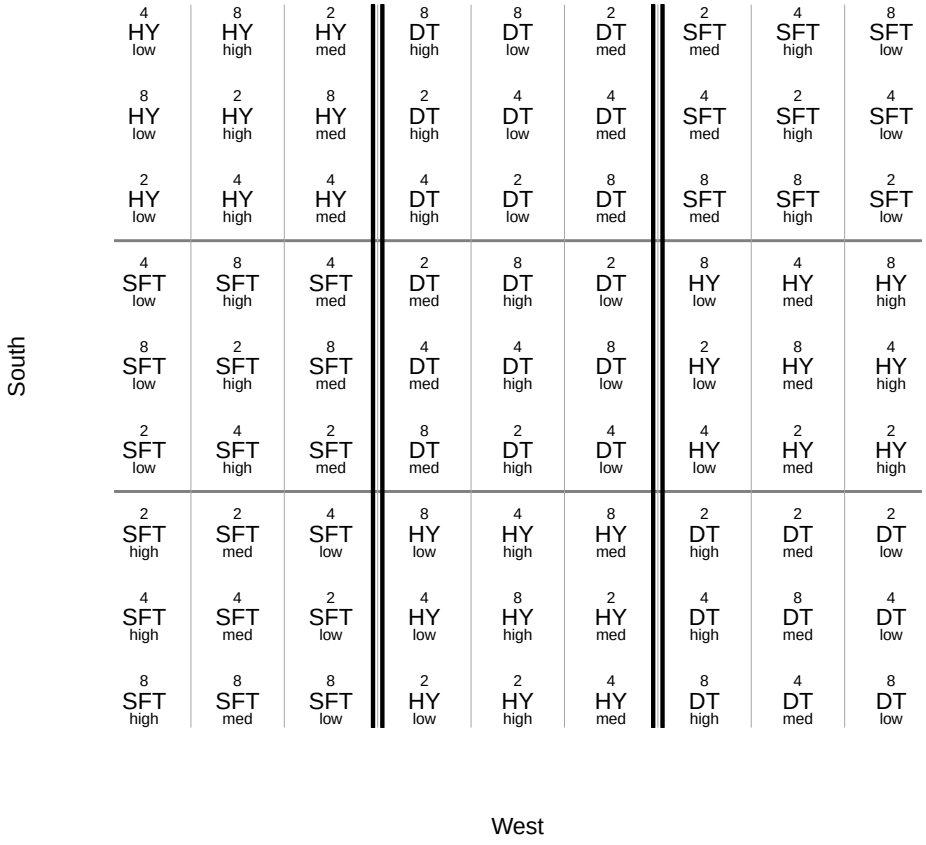


Figure 4.1: Arrangment of treatments in a randomized split-split plot design with three replications for field experiment conducted in Amsterdam, MT 2008-2010 to asses ecologically based approaches to multiple pest management. Blocks direction is East-West. Wheat variety SFLT (WSS tolerant), DT (drought tolerant), and HY (high yield potential) were planted as the whole plot treatment. Seeding rates low (half), med (recommended), and high (double) as a first split. Herbicide application rate, 8 (0.8x label), 4 (0.4x label), and 2 (0.2x label) as the second split.

split plot consisted of half, recommended, and double initial seeding rates to target 125, 250, and 500 plants m^{-2}, respectively. Plots were planted on April 11, 2008, April 20, 2009 and March 24, 2010 with a Fabro (Swift Current, SK, Canada) No-Till drill with 7 double disc openers spaced 25.4 cm apart and a seeding depth of 3.8-5 cm. At planting we used a starter fertilizer of a 50:50 mix of ammonium phosphate 11-51-0-

(0) and potassium sulfate 0-0-52-(18) at 100 Kg ha^{-1} for N-P-K-S rate of 5-25-26-9 Kg ha^{-1}. Broadcast urea 46-0-0 was added May 30, 2008, May 14, 2009 and May 27, 2010 to achieve 150 Kg N ha^{-1} across the field. Urea application rates were based on 54 soil samples obtained to a depth of 61 cm, two in each sub-plot, the previous fall. The second split treatment consisted of Sulfosulfuron application at 0.028, 0.014, and 0.007 Kg ha^{-1} of active ingredient respectively to correspond to herbicide application rates of 0.8, 0.4 and 0.2 of the label rate (Monsanto, 2009). These in-crop herbicide treatments were applied on May 20, 2008, May 6, 2009 and May 13, 2010 to generate a range of downy brome abundance.

Approximately one month after planting, three metal rings 0.475 m in diameter, were anchored to the ground for the duration of the growing season and used for WSS and downy brome data collection. Rings were randomly placed in the north half of each sub-sub-plot and were centered between two wheat rows, covering 80.3 cm of crop rows. Percent cover of downy brome, visually estimated by the same observer across the duration of the study, and downy brome height in each ring were measured twice during each growing season, at peak downy brome biomass, and at harvest. At peak biomass, two additional rings of the same dimensions were randomly placed in each sub-sub plot, visually estimated for downy brome cover and measured for height. After these measures above ground downy brome biomass was harvested, oven dried to a constant mass, and weighed. At harvest, visual percent cover and downy brome height were again determined before all plant biomass within each ring was uprooted and downy brome separated from wheat, oven dried to a constant mass and weighed. Downy brome pressure on a 0-1 scale was calculated from volume (cover x height) and biomass. Biomass regression on volume in the two additional rings was used to predict biomass from observed volume at harvest. The average of predicted values

and observed biomass at harvest was rescaled to 0-1, to create a measure of downy brome pressure which was volume at harvest adjusted to peak biomass.

All wheat stems harvested within each ring were taken to the laboratory for examination. The number of WSS cut wheat stubs per ring was counted to determine WSS lodging. All remaining intact stems were dissected lengthwise and inspected under magnification for evidence of WSS infestation. These intact stems were categorized as 1) Infested - frass, indicative that WSS larval boring occurred, but an unknown mortality factor prevented cutting of the stem, 2) Parasitoids - evidence that a WSS parasitoid was found, either a cocoon or an emergence hole that the parasitoid chewed when exiting the stem, and 3) Uninfested - no evidence of frass, larvae or parasitoid. For each ring, wheat stems were grouped by category, counted, and their heads threshed to estimate grain yield.

3.2. Biology and Ecology of Modeled Species

Sawfly completes one life cycle per year, where all immature stages are spent inside protective plant stems and crop residue, synchronized with the physiological development of the host. Over their 7 day lifespan during an approximately 28-42 day period in the spring, individual female adults oviposit mostly in the upper internodes of larger plant stems to encourage success of the larvae (Buteler *et al.*, 2009). In extensive monoculture, host population densities are high and infestation can reach 80% of available stems with females exhibiting strong preferences between wheat cultivars (Buteler *et al.*, 2010; Weaver *et al.*, 2009). Larvae feed on host parenchyma and vascular tissues. As wheat plants start to senesce, a single larva moves toward the bottom of the stems cutting a v-shape notch at the base and constructing a diapause chamber to overwinter in the crop residue. Herbivory can cause up to 22% reduction in number and size of wheat kernels (Holmes, 1977). Stem cutting weakens the tillers,

which subsequently lodge, causing irretrievable loss of mature stems, reduced harvest efficiency and yield, increased volunteer wheat pressure in the fall and following spring, and loss of anchored residue which may result in greater vulnerability to soil erosion and snow retention capabilities.

With increased adoption of conservation tillage, enhanced reliance on broadcast nitrogen fertilizer, and increased use of narrow-spectrum herbicides, downy brome has become a major weed in winter and spring wheat cropping systems (Blackshaw, 1991). The similar life forms of the two species allows downy brome to effectively compete for resources (Zimdahl, 2007) with yield reductions ranging between 28% and 92% (Rydrych and Muzik, 1968) with a strong dependency on weed density, time of emergence, and distance to crop (Stahlman and Miller, 1990). Downy brome is typically a winter annual but also exhibits summer annual life history traits with seedlings capable of emerging through the winter and into spring and plant height reaching 40-50 cm by early June (Hulbert, 1955).

4. Statistical Analysis

4.1. Decision Theory

In natural resource management an optimal course of action should be chosen from a predefined set of available options and this process can be considered a decision problem because it is made under conditions of uncertainty, i.e. future scenarios and exact outcomes are unknown. For example, in agricultural settings decisions such as choice of crop variety, seeding rate, or pesticide application rate while chosen to improve a desired outcome, have a risk of potential losses associated with them (Anderson *et al.*, 1977). To reduce uncertainty and minimize risk, the decision maker identifies parameters which may influence the outcome, collects information through

experiments or observations, and decides on the best course of action, given the most likely outcome in light of new information (Robert, 1994).

To make ecologically sound managerial decisions based on statistical knowledge, experimental results or observations should be evaluated, interpreted, and related back to the set of choices. Under a frequentist strategy, statistical inference reflects the likelihood of an observed phenomena (data) under a null hypothesis, and therefore a decision protocol such as "if p-value $< \alpha$ for $\hat{\mu}$, then take action A", must be specified in advance. In this context, the statistical result is not a statement about the unknown parameter or subsequent action, but about the long-term expectation, under infinite repeated sampling, that data reflects the true parameter. Relating the estimates and their standard errors to the unknown parameter value is not intuitive or straightforward. Also, if the parameter estimate is near the significance threshold, the decision is not robust and may be altered by small variations in the sample. Moreover, the protocol may not cover the eventuality of p-value $\geq \alpha$ because non-significance implies there is not enough information to choose any decision (Stauffer, 2008). Finally, the uncertainty in the implementation of the selected action is not accounted for which may cause a St.Petersburg type paradox (Bernoulli, 1954) where consideration of the long-term expectation only, as provided by the frequentist parameter estimate, could lead to an irrational decision. For example, a given recommendation in a decision support system for natural resources, while based on a statistically significant result, can have only occasional net positive return and be misleading from a biological (Real, 1996) or management perspective (Dorazio and Johnson, 2003).

In contrast to frequentist analysis, Bayesian inference can be described as statistical decision theory, implementing the same logic of a decision making process to the statistical analysis procedures (Berger, 1985). Under the Bayesian paradigm, the likelihood of the data is combined with a prior distribution, the probability distribu-

tion that describes the uncertainty about the unknown parameter before the data was obtained, to produce a posterior, a direct probabilistic statement about the unknown parameter. The posterior reflects previous knowledge that has been updated with empirical observations. Statistical inference from a Bayesian perspective comprises evaluation of a loss function, such as the mean squared error function in use also by frequentists. However, the Bayes estimator minimizes expected posterior loss and therefore selecting a particular model, rejecting a hypothesis, and deriving estimates and predictions are all regarded as decisions on the most likely parameter value (Robert, 1994). As such, Bayesian analysis provides a coherent framework for combining all sources of uncertainty in the decision making process, overcomes the problem of discontinuity between the analysis and the managerial decision (Larocque *et al.*, 2011), and fits naturally into our intuitions about that process in the physical world (Ellison, 1996).

A common criticism of the Bayesian approach is that by relying on subjective probabilities through prior specification, it may mislead researchers by confirming inaccurate predespositions (Dennis, 1996). This may be a reason the Bayesian approach has not been widely adopted in the construction of pest management decision models, despite its advantages of overcoming some of the shortcomings of frequentist methods and the growing availability of computing power and designated software (Dorazio and Johnson, 2003; Prato, 2005; Stauffer, 2008). However, knowledge of many aspects of the functional relationships between crops, insect pests, weeds, and management practices exists (Capinera, 2005; de la Fuente *et al.*, 2003; Norris and Kogan, 2000) and implementation of a Bayesian pest management model that combines this knowledge with ecologically sound logic in the incorporation of prior information can improve inference and predictions without compromising objectivity (Fabre *et al.*, 2006; Tari, 1996; Thackray *et al.*, 2009).

4.2. Model Development

To derive a forecasting tool suitable for decision-making under the presence of an interacting pest complex, prior biological and ecological knowledge of WSS and downy brome in wheat-fallow systems was used to construct a structural causal model of hypothesized interactions (Choy *et al.*, 2009). The causal, or structural model was considered a prior because final yield predictions from the model were conditional on the biological interactions between pests determining, in part, the outcomes.

4.2.1. Oviposition Behavior of WSS

Oviposition behavior complicates the characterization of the impact that WSS injury has on wheat yield as females prefer larger stem diameter and height (Buteler *et al.*, 2009), which tend to have larger heads and yields, confounding observed yield reduction estimates (Macedo *et al.*, 2005). This may be further complicated by WSS preference for different hosts such as grassy weeds compared to wheat cultivars (Perez-Mendoza *et al.*, 2006). To incorporate these uncertainties, a prior was constructed as follows (Fig. 4.2). For a large collection of wheat stems which the WSS female encounters, we assumed a bell shaped distribution of grain yield. For this distribution, there is a minimum value for a stem to be considered suitable for oviposition and discarded stems are represented by the shaded area under the distribution curve. Observed uninfested stems have mean yield represented by solid black arrows. Two possible scenarios were evaluated under the condition of reduced wheat yield due to lower yield potential, or inter- or intraspecific competition (dashed gray curve). First, WSS maintained the same cutoff value (solid gray arrows), or second, WSS responds to the lower overall potential yields by lowering the cutoff value (dashed gray arrows). In the first case, there are more stems below the cutoff value that are discarded, and WSS infestation will be

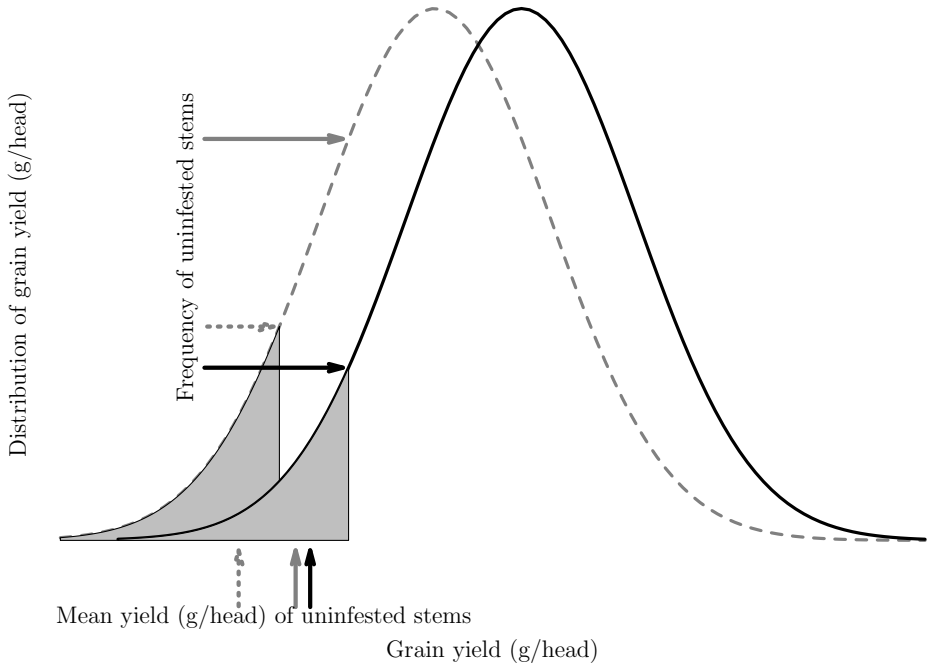


Figure 4.2: Hypothesized WSS choice mechanism. Standardized grain yield of wheat heads is represented by a $N(0,1)$ distribution (solid black curve). Dashed gray curve represents wheat which is 25% lower yielding than the standard and shaded areas represent stems discarded by WSS. Solid black arrows correspond to observed frequency and mean weight of grain in the uninfested category due to WSS attacking appropriate wheat stems only (greater than a particular yield) - or discarding stems lower than that value. Solid gray arrows represent observed value's under the same choice mechanism, i.e. the same grain yield value is considered appropriate despite overall lower yields. Dashed gray arrows represent a modification of the choice mechanism where stems which could have been considered inappropriate under higher overall yields are now oviposited in.

reduced while yields associated with uninfested stems will not change. Under the second scenario, WSS responds to the lower overall yields by modifying their choice mechanism and oviposits on a higher proportion of low yielding stems. Under the latter scenario, there may be lower or no significant change in the rate of infestation, but mean yield in the uninfested category will be reduced. These two scenarios can

be viewed as competing and testable hypotheses of WSS oviposition behavior that draw on existing knowledge.

4.2.2. Model Parametrization In this non-manipulative study, the first two years (2008 and 2009) were used to generate a pest response to the applied management practices. Field collected data from the third year (2010) was used to update diffuse priors on model parameters, where the prior distribution had a large enough variance to reflect a high degree of uncertainty in the estimated value. Thus the contribution of the prior relative to the likelihood of the data can be considered non-informative where, if the data did not support the prior model specification, no trends will be evident in the posterior. An annihilated Bayesian decision model was utilized to asses outcomes of management decisions (Fig. 4.3, Eq.1-4). Annihilation is a path

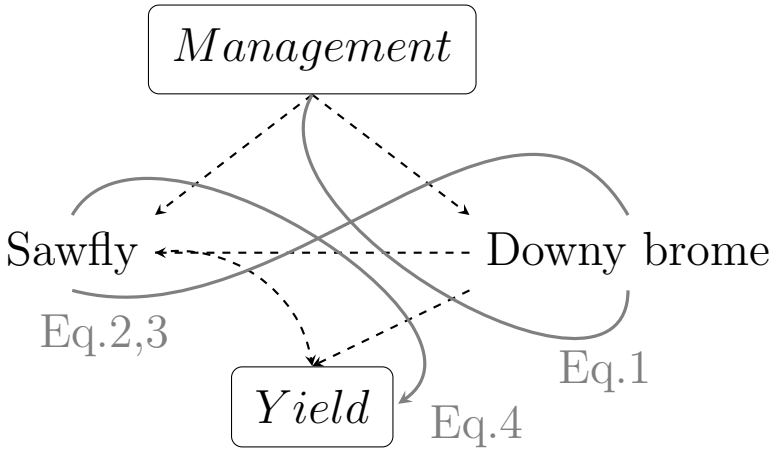


Figure 4.3: Graphical depiction of the annihilated Bayesian decision model described by structural equations 1-4. Dahed arrows represent direct causal effects, or estimated coefficients of equations 1-4 whose total (direct and indirect) effect is represented by the curved gray line path.

analysis technique to derive total effects, all direct and indirect paths between two

variables, in a prespecified model of causal relationships (Chapter 2). When applied to management schemes as predictors of wheat yield, parameter estimates from an annihilated model incorporate in them all hypothesized biological interactions occurring within the agroecosystem. Thus, p_i, downy brome pressure in ring i measured on a scale of 0-1, is distributed as a Beta random variable with β the logit mean effects of treatment X (variety, seeding rate, and herbicide application rate) on downy brome and precision parameter ϕ

$$ln\left(\frac{\mu_i}{1-\mu_i}\right) = X\boldsymbol{\beta} \qquad \text{where } p_i \sim Beta(\mu_i\phi, (1-\mu_i)\phi) \tag{4.1}$$

Given downy brome pressure and mean effect in every ring $\hat{p}_i = \mu_i$, the number of stems in each of $j = 1-4$ categories (uninfested , lodged , mined/not lodged, parasitized) in each ring (n_{ij}) is a Multinomial variable with rates θ_j

$$ln(\theta_i)_j = X\boldsymbol{\Gamma}_j + (p_i - \mu_i)\boldsymbol{\gamma}_j \qquad \text{where } n_{ij} \sim Multi(\boldsymbol{\theta}_i, n_i) \tag{4.2}$$

Therefore, $\hat{\boldsymbol{\Gamma}}_j$ is the estimate of the mean logit rates of the WSS categories in the treatment combinations which also accountes for the impact of the expected downy brome in the treatment on these rates. The yields per head in the different categories j are also correlated within a given ring because of the WSS choice of Eq. (4.2), and are therefore a multivariate normal

$$Y_{ij} = X\boldsymbol{\Delta}_j + (p_i - \mu_i)\boldsymbol{\delta}_j + \epsilon_{ij} \qquad \text{where } (\epsilon_{i1}, \epsilon_{i2}, \epsilon_{i3}, \epsilon_{i4})^T \sim N(0, \boldsymbol{\Omega}) \tag{4.3}$$

The product of estimates from (4.2) and (4.3), summed over j provides a weighted average yield per head for every treatment T with weights being the rates of WSS categories. Predicted posterior yield ($\hat{Y}_T^*$) are then the product of average yield per

head and n_T^*, the number of stems, assumed to be Poisson

$$\hat{Y}_T^* = n_T^* \sum_j \mathbf{\Delta}_j \frac{e^{\mathbf{\Gamma}_j}}{\sum_j e^{\mathbf{\Gamma}_j}} \qquad \text{where } n_T^* \sim Pois(\lambda_T) \tag{4.4}$$

Posterior means from the annihilation model account for the effect of treatment on WSS and the effect of downy brome, which is also impacted by the treatment, on WSS. Estimated mean yields of the different WSS categories were then collected to provide an estimate of wheat yield as impacted by WSS. Therefore, while results of this model reflect WSS management recommendations that may be modified in the presence of downy brome, we did not annihilate these predicted yields in a model of treatment effects on wheat yield, i.e. there is no direct dashed arrow from treatments to yield in Fig. 4.3. In this sense this model is not a complete predictive management model but a proof of concept for decision support analysis. The biological processess modeled, i.e. weed-crop competition and yield lossess of individual stems due to WSS mining, is at the scale of the observation rings placed across the field. Variability related to these processess between rings within a sub-sub plot was assumed to be as large as between treatment replications across the field and the 9 rings in each variety, seeding rate, herbicide application rate treatment combinations were treated as independent replicates with no sub-sub, sub, or whole plot effects fitted. The last level (annihilation of these results on yield) of a complete predictive management model should be fit as a heirarchical model accounting for the split-split plot design of the experiment to avoid issues with pseudoreplication.

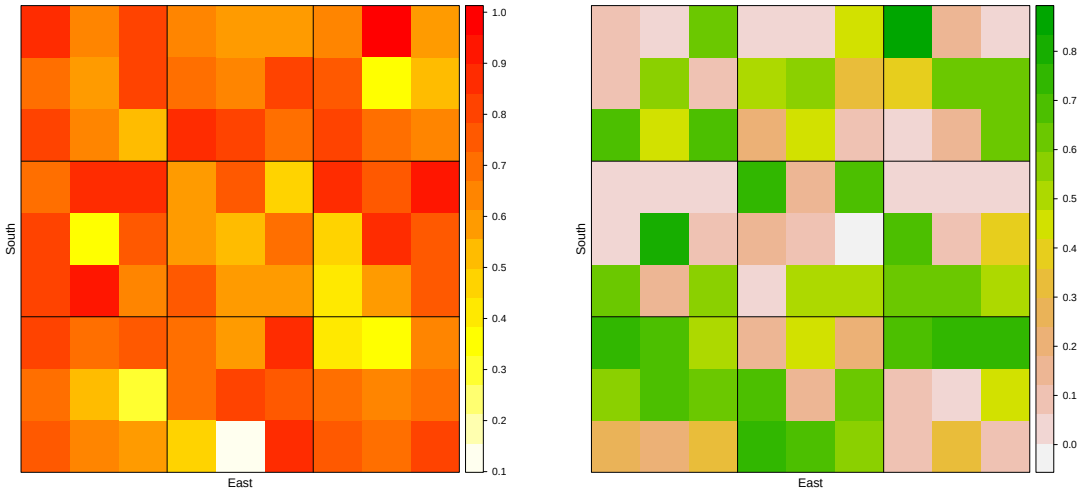
Parameter estimates from the joint posterior of Equations (4.1 - 4.4) were derived by Gibbs sampling (Markov Chain Monte Carlo - MCMC) with JAGS 3.2.0 (Plummer, 2003) via package rjags (Plummer, 2010) in R 2.13
(R Development Core Team, 2010). All MCMC simulations consisted of 10 thousand

iterations of four chains at overdispersed starting values. After a burnin period of 5 thousand, two thousand values for every parameter were retained at a thinning interval of 10. Convergence and uni-modality of the distributions for all parameters were assessed visually and run until a $\hat{R} < 1.1$ was achieved (Gelman and Rubin, 1992). Independence of MCMC draws was confirmed by qualitative comparison of naive standard error to a time-series corrected one.

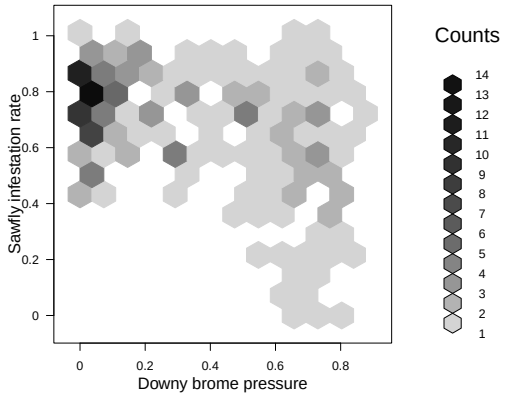
5. Results

In 2010 and after three years of consecutively applying the same management practices to each sub-subplot, WSS infestation ranged between 62.4±19.3% to 76.6±18.5% in the low seeded-SFLT and recommended seeded HY subplots respectively. While WSS relative abundance was not uniformly distributed across the field (Fig. 4.4a), no significant spatial pattern could be identified. Also, parasitism by *B. cephi* and *B. lissogaster* averaged 13%±9.5% over the entire field, but with no detectable spatial pattern.

As expected, herbicide applications modified downy brome pressure with values ranging from $9.1 \pm 8.2\%$ at 0.8x herbicide rate to $64.5 \pm 23\%$ at 0.2x herbicide rate (Fig. 4.4b). Crop's seeding rate also affected downy brome pressure, most noticeably at the 0.4x herbicide rate, ranging from $44 \pm 24.6\%$ at low seeding rates to $29 \pm 20.5\%$ at high seeding rates. Results of the Bayesian decision model on the impact of management practices on downy brome abundance (Eq. 4.1) allowed us to compare treatments more precisely and confirmed the above observations. Specifically, reduced herbicide rates resulted in significant increase in downy brome pressure, with high seeded-DT remaining the most competitive and effective in suppressing downy brome, particularly in the 0.4x herbicide application rate (Fig. 4.5).



(a) Sawfly (b) Downy brome



(c) Hexagon binned joint histogram

Figure 4.4: Mean WSS infestation rate (a) and downy brome pressure (b) in each treatment sub-sub plot across the field, and joint frequency of observations by levels of WSS and downy brome (c) showing decreasing WSS infestation of wheat in the presence of a downy brome alternative.

When evaluated together, it was possible to detect a negative association between WSS infestation of wheat and downy brome pressure (Fig. 4.4c). In accordance with previous research (Perez-Mendoza *et al.*, 2006), WSS appeared to prefer downy brome

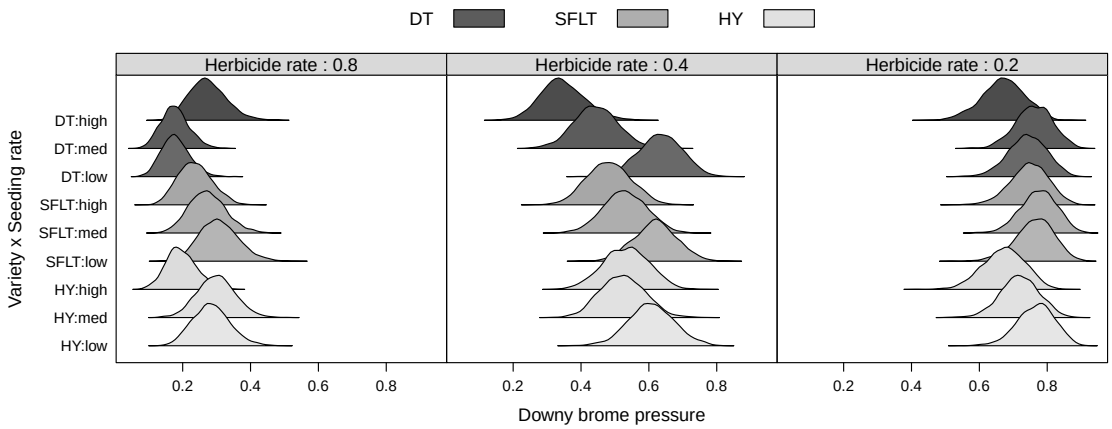
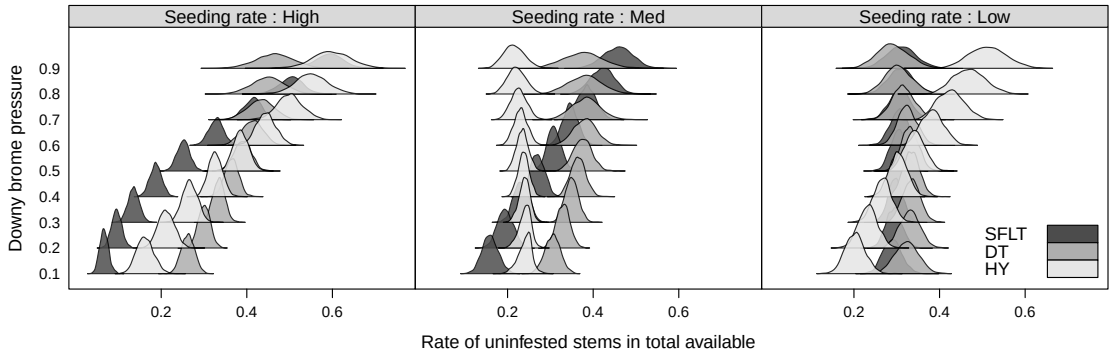


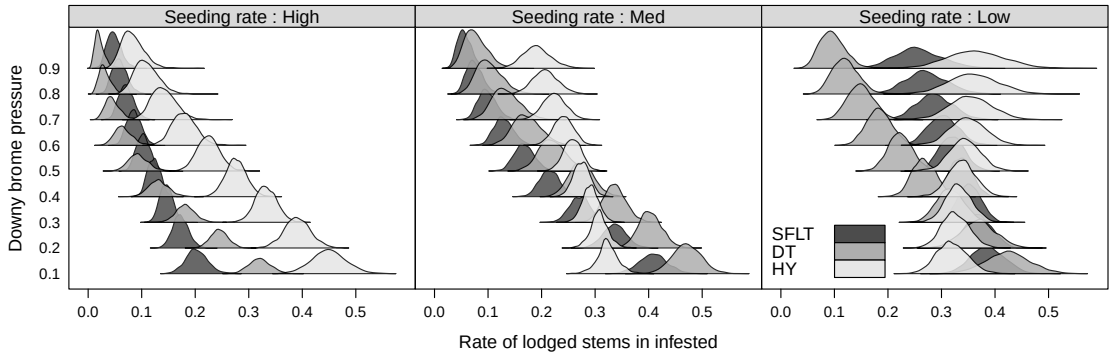
Figure 4.5: Posterior distribution of downy brome pressure by wheat variety and seeding rate treatments under three years of 0.8x (left), 0.4x (center), or 0.2x (right) herbicide application rates.

to wheat. This behavioral pattern resulted in having areas of low WSS infestation on wheat associated with high downy brome abundance. Furthermore, downy brome pressure interacted with wheat variety and seeding rate in determining WSS oviposition behavior (Eq. 4.2, Eq. 4.3). When the crop was seeded at a high seeding rate, increasing downy brome pressure was associated with decreased sawfly infestation for all varieties with no significant mean grain yield reductions in the uninfested category for the SFLT and DT varieties (Fig. 4.6a, Table 4.1). In contrast, the impact of downy brome on WSS oviposition behavior increased at the recommended and low seeding rates for the DT variety and at the low seeding rate for the SFLT variety. Significant mean grain yield reductions in the uninfested category associated with increased downy brome pressure (Table 4.1) were observed together with no significant change in infestation rates (Fig. 4.6a). For the HY variety, increased downy brome pressure was associated with reduced infestation rates also at low seeding rates, and with increased infestation levels at the recommended rate. However, for this variety these

effects were not strong and significant yield reductions were observed at all but the recommended seeding rate.



(a) Uninfested stems



(b) Lodging rate

Figure 4.6: Posterior predictions of the impact of downy brome pressure on (a) WSS fraction of uninfested stems, and (b) lodged wheat stems presented as a fraction out of total infested stems only. Likelihood was a multinomial distribution of four infestation categories (uninfested, lodged, mined - not lodged, and parasitied) for all observations in 0.2x and 0.4x herbicide treatments.

Wheat lodging due to WSS oviposition generally decreased with downy brome pressure and the functional shape of this relationship depended on crop seeding rate and crop variety (Fig. 4.6b). Lodging was generally lower at high seeding rate com-

Table 4.1: Posterior mode, standard deviation and Bayesian p-value for the effect of downy brome on the yield per head (g) of wheat in four† WSS categories.

		Uninfested		Lodged		Mined		Parasitoid	
Seeding rate	Variety	Est.	p-value	Est.	p-value	Est.	p-value	Est.	p-value
Low	HY	-0.23 ± 0.18	**0.10**	-0.02 ± 0.19	0.45	-0.61 ± 0.20	**0.00**	-0.30 ± 0.18	**0.05**
	SFLT	-0.45 ± 0.17	**0.00**	-0.65 ± 0.17	**0.00**	-0.59 ± 0.21	**0.00**	-0.52 ± 0.18	**0.00**
	DT	-0.85 ± 0.18	**0.00**	-0.08 ± 0.62	0.45	-0.32 ± 0.65	0.30	-0.32 ± 0.67	0.32
Med	HY	0.07 ± 0.61	0.45	0.00 ± 0.58	0.50	2.18 ± 0.58	**0.00**	-0.10 ± 0.74	0.44
	SFLT	0.30 ± 0.58	0.30	-0.08 ± 0.65	0.45	-0.03 ± 0.17	0.44	0.05 ± 0.17	0.39
	DT	-0.46 ± 0.18	**0.01**	-0.16 ± 0.16	0.15	-0.19 ± 0.15	**0.10**	-0.30 ± 0.15	**0.02**
High	HY	-0.58 ± 0.21	**0.00**	0.14 ± 0.16	0.18	-0.33 ± 0.15	**0.02**	0.04 ± 0.19	0.42
	SFLT	-0.07 ± 0.19	0.36	-0.74 ± 0.24	**0.00**	-0.01 ± 0.18	0.48	-0.06 ± 0.17	0.37
	DT	-0.13 ± 0.20	0.27	-0.33 ± 0.24	**0.09**	0.04 ± 0.19	0.42	-0.42 ± 0.18	**0.01**

† The four categories are conditional and therefore must be considered as: Uninfested-"avoided", Lodged-"suitable", Mined/Parasitoid-"suitable at oviposit but pest did not survive to lodging".

pared to the recommended and low rates for the SFLT and DT varieties, with no clear trend for the HY variety. As for WSS infestation, these results must be assessed in conjunction with the yields values observed in each seeding rate and crop variety combination (Table 4.1). At the low seeding rate, when SFLT maintained a constant lodging rate of 0.3-0.4, yield per head was significantly reduced by 0.65 grams for every unit increase in downy brome pressure. In contrast, yields for DT remained constant as lodging decreased from 0.45 to 0.15. Yields for these two varieties also remained unchanged as lodging rates decreased in the recommended rate, but were significantly reduced by downy brome at high seeding rates, where the reduction was twice as large in SFLT, with 0.74 grams per head, compared with DT with 0.33 grams per head mean yield reduction (Fig. 4.6b, Table 4.1).

The impacts of downy brome on WSS described above and the responses of these two pests to management practices were jointly modeled (Equations 1-3) and collected (Eq. 4.4) to derive an estimate of crop yield that reflects the underlying process of multi-pest effects under contrasting management scenarios. This information in turn allowed the determination of the best management decisions given the most probable outcome in terms of yield (Fig. 4.7). At low downy brome pressure (0.8x herbicide rate), the low seeding rate SFLT variety had highest yields, 12.3% higher on average than DT at low seeding rates. However, the advantage of the SFLT variety decreased with increasing crop seeding rates to yields lower than the DT variety when both were planted at high seeding rates. A significant seeding rate by variety interaction became apparent at increased downy brome pressure (lower herbicide rates): while yield remained negatively associated with higher seeding rates in SFLT wheat, increasing seeding rates of DT wheat had a positive effect on yield due to its increased competitiveness against downy brome. Thus, at a 0.4x herbicide level, high seeded-DT was the highest yielding management decision while high-seeded SFLT was

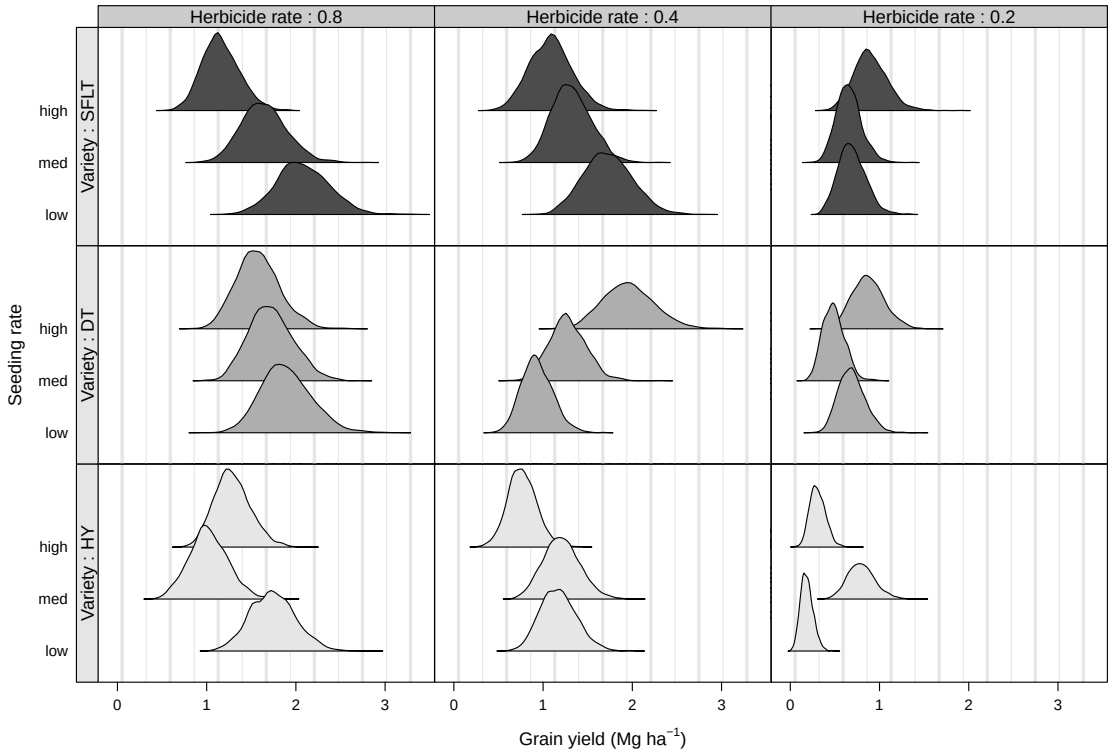


Figure 4.7: Posterior predicted yields for SFLT, DT, and HY wheat varieties (rows) at three seeding densities and under 0.8x, 0.4x, and 0.2x herbicide rate treatments (columns).

the lowest yielding one. As expected, at very high downy brome pressure (reduced herbicide rate of 0.2x), weed competition had a significant and overriding negative effect on crop yields with a slight advantage of higher seeding rates compared with low and recommended, in both SFLT and DT. At intermediate and high downy brome pressure, yields for the HY variety were generally lower than SFLT and DT with no clear pattern across seeding rates.

6. Discussion

Current pest management strategies typically consider problems in isolation from each other, potentially leading to undesirable responses by other pests (Lewis *et al.*,

1997). As such, non-integrative single-pest management approaches are not sustainable and do not meet the needs of producers to develop system-based programs. This system-level understanding must include the linkages among biophysical processes, human activities, and socioeconomic goals (Robertson *et al.*, 2008). Our study demonstrated that even in the relatively low diversity agricultural system that dominates the NGP, interactions between pest groups belonging to different trophic levels could complicate the outcome of otherwise seemingly simple management decisions. Our experiment and analysis are consistent with applying a systems approach to modeling: by developing hypotheses of causal relationships from key structural and functional aspects of the system, we were able to generalize relevant system dynamics from available data and represent them in a simple manner consistent with management goals (Grant, 1998).

Norris and Kogan (2005) classified the interactions between weeds and insect pests according to three driving mechanisms: direct and indirect trophic interactions, alteration of the physical habitat by the presence of weeds, and control tactics in the context of multidisciplinary IPM. Our observations of the interactions between WSS, downy brome, crop attributes, and management decisions suggest that aspects belonging to each classification could play a significant role in the net outcome of pest interactions. Observed WSS infestation levels in wheat were generally high across the entire field, yet they were locally reduced in areas with high downy brome pressure, particularly in those adjacent to relatively low weed pressure areas. In wheat-fallow systems, overwintering sawflies emerge from the stubble to infest wheat growing in the adjacent field, typically exhibiting a clear edge effect (Weaver *et al.*, 2004). In this study wheat was replanted for a third consecutive year and infesting WSS populations would have emerged from each sampled sub-sub-plot. The observed pattern of reduced infestation of wheat in areas with high downy brome pressure agrees with previous

observations that suggested WSS responded to the presence of downy brome as a preferred alternative host, presumably because the quality of the available wheat was compounded (Buteler *et al.*, 2010; Perez-Mendoza *et al.*, 2006; Weaver *et al.*, 2009).

Evaluating WSS infestation rates and grain yield reductions in the presence of weeds provided insights into WSS oviposition behavior. At high crop densities, consistent with the first hypothesized scenario of hypothesized sawfly choice mechanism (Fig. 4.2), increasing downy brome pressure was associated with increased rates of uninfested stems of similar grain yield in both SFLT and DT varieties. This suggests there was no change in the behavioral pattern of WSS females discarding unsuitable hosts. However, at lower seeding rates and greater downy brome pressure, WSS seemed to compromise offspring-performance (Jaenike, 1978) by ovipositing in significantly lower yielding stems, and maintaining a relatively constant level of infestation in the crop, consistent with the second hypothesized scenario (Fig. 4.2).

Wheat variety also played a role in determining WSS ovipositing behavior. Downy brome had a greater effect in reducing WSS infestation rates in the less competitive SFLT variety, as compared with the DT variety at high and recommended seeding rates. Being less competitive with respect to both pests, the HY variety exhibited a complete breakdown of the trend, with significantly lower yields despite greater numbers of discarded stems when deviating from the recommended seeding rate.

It is possible that the presence of downy brome indirectly increased WSS larva mortality, as suggested by the reduction in lodged wheat stems relative to infested ones associated with increasing weed pressure. Reduced lodging in DT wheat compared with a weaker effect in SFLT may be have been caused by reduced plant resources available to the larva instars to complete the stem boring stage in DT (Delaney *et al.*, 2010; Macedo *et al.*, 2005), whereas mechanical pressure and other factors in the solid stem are causes of larvae mortality in SFLT wheat. In the absence

of downy brome, Beres *et al.* (2011c) found that solid stem wheat sown at 150 seeds m^{-2} had higher but inconsistent pith expression compared with densities of 250-450 seeds m^{-2}, suggesting a negative effect of interspecific competition on pith expression and sawfly control. In our study, reduced seeding rates of the SFLT variety in the presence of downy brome was associated with increased mean lodging rates from 0.1 to 0.35 suggesting that intraspecific competition may also reduce pith expression. However, the negative association between wheat lodging and downy brome pressure in the recommended seeded-SFLT treatment contradicts this interpretation. We did not specifically measure pith expression which does not perfectly correlate to lodging rate as both may be affected by other factors. More detailed experiments on the effects of intra- and inter-specific competition on plant characteristics and subsequent WSS impact are needed to fully interpret these results.

The joint evaluation of stem counts and grain yield is essential given the interactions of stem boring insects and weeds in agricultural systems, but it is often conducted for each measure separately (Michaud *et al.*, 2009; Qureshi *et al.*, 2007). Statistical results from this approach can still be interpreted and contribute to the understanding of the ecological system and to informing management. However, the Bayesian approach utilized in this study allowed us to jointly model these two measures of WSS impact and formally quantify the management implications. We treated our hypothesis on WSS choice as an informative prior because we utilized prior knowledge of the functional relationships in the system to construct a meaningful model (Choy *et al.*, 2009) that ensured correct interpretation of seemingly conflicting results (Real, 1996). By using diffused distributions as priors for parameter estimates, our results describing WSS behavior under increasing downy brome pressure are, therefore, an objective confirmation of the modeled process. Our results exemplify the fact that behavioral aspects such as WSS maternal oviposition decisions often

result in outcomes that can only be understood within the context of a certain model rationality (Real, 1996).

An important property of the decision theoretic approach utilized in this study was the seamless propagation of sources of variation from descriptive models of the underlying biological process to the assessment of the outcome of applied management decisions. Under the standard approach, results of statistical inference only describe the current state of pest levels and crop yields. To inform management decisions statistical results must be qualitatively assessed under perceived future risks. For example, in the absence of downy brome and with seeding rates comparable to the ones used in our study, Beres *et al.* (2011c) reported slightly higher grain yields for a hard-red spring wheat variety compared with a solid stem variety, a negative correlation between grain yield and pith expression, and high coefficients of variation at low seeding rates for all measures. Noting that considerations other than grain yield performance and factors not included in the study influenced the conclusion, Beres *et al.* (2011c) suggested a low to recommended seeding rate for solid stem varieties at WSS infestation prone regions, and a high seeding rate for hollow stem varieties for others. In our model, the 0.8x herbicide application rate mitigated the risk of downy brome and is representative of a single-pest (WSS) decision problem. Average yields for the 0.8x herbicide - DT management option in our study were comparable to those reported in Beres *et al.* (2011c): 2.8 ± 1.16 Mg ha^{-1} and 3.94 ± 0.73 Mg ha^{-1} for the low and high seeding rates, respectively, and not significantly higher than 2.22 ± 1.08 Mg ha^{-1} and 3.05 ± 0.72 Mg ha^{-1} observed for the low and high SFLT seeding rates, respectively.

An advantage in the annihilated models proposed here is that the effects of a particular management scheme on pest interaction and subsequent impact on the crop are formally incorporated in the estimates of predicted yields under the poste-

rior. While the implication in yield losses may be over-estimated for all management decisions in the model output (Chapter 2), this property becomes advantageous in an IPM context because the estimates reflect a risk aversion strategy given the effect that any single management decision will have on pest levels, their interactions, and subsequent impact. For the observed mean yields described above, our model predicted yields in the range of 1-2 Mg ha^{-1} with low seeded-SFLT being the highest and best decision. At high seeding rates, the SFLT variety lost the insect-pest control advantage, probably due to lack of pith expression, and the DT variety that did not show major yield penalties was higher yielding and became the best decision at high seeding rates. Thus, our model promoted a decision to plant a solid stem cultivar based on the quantification of the impact of management practices on the direct and indirect effects of sawfly and downy brome on wheat as well as on their interactions.

Furthermore, despite the low downy brome pressure observed at the high herbicide application rate (0.8x), the risk of yield losses due to weed competition drives the decision at high seeding rates where stem solidness is less effective. Weed populations are often present in agroecosystems, even under intense management as they may require fewer resources than the crop to persist in the presence of a pest complex (Schroeder *et al.*, 2005). In our study, the importance of a joint consideration of the risk from multiple pests was most pronounced at intermediate downy brome pressure (0.4x herbicide treatment). Here, the competitiveness of the DT variety at increasing seeding rates gave it a greater advantage to become the highest yielding option. Increasing seeding rates at the 0.4x herbicide level had less of a negative effect on the SFLT variety, reflecting that the increased competitiveness against downy brome mitigated WSS damage due to loss of stem solidness. The lower competitiveness of the SFLT variety compared with the DT variety and net impact of the interactions

between the two pests made the decision to use a high seeded SFLT combination the lowest yielding management option.

7. Conclusion

In this paper, we provided a framework for development of decision support models through an example of the joint management of two agricultural pests. Our approach utilizes the benefits of Bayesian analysis to allow decision makers to evaluate consequences of management actions that reflect the variability of ecosystem dynamics. The ability to combine sources of prior knowledge on the interactions between pests and their respective responses to management actions provided insights that a standard model would not have revealed. Our work exemplifies the necessity of accounting for direct and indirect interactions between multiple pests in the agroecosystem, and propagating this information from the statistical analysis stage to the management model. This work may help to further advance the incorporation of scientific knowledge as a decision-aid tool in the integrated management of agricultural pests.

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CHAPTER 5

CONCLUSION

> "*Once the statistician has selected a procedure, Nature selects the state of nature (i.e., the parameter) that maximizes the loss of the statistician.*"
>
> Christian Robert criticizing *minimax*,
> The Bayesian Choice

This dissertation presented a framework for scientific research and analysis that informs natural resources management decisions. The value of pest management programs that reflect the variability of ecosystem dynamics has long been recognized. Yet, complex direct and indirect interactions between the components of agroecosystems, challenge attempts to reduce uncertainty in the outcomes of management actions. The two separate but related aspects of this work, developing the "annihilator" and taking a Bayesian approach, address in part these challenges.

Despite considerable control efforts and accumulated knowledge on the population dynamics and incurred damage of wheat stem sawfly, downy brome, and *Fusarium spp.*, these pests continue to pressure wheat cropping systems in the Northern Great Plains. Rather than investigating these pests in isolation, we took a total-systems approach and quantified the joint impact of this interacting, multitrophic pest complex in response to management. Overall, our results highlighted the importance of generating ecologically based knowledge for the integration of simple crop management practices that allow producers to increase their ability to mitigate pest pressure while at the same time reducing dependence on off-farm chemical inputs.

In order to take full advantage of the interdisciplinary information collected in this study, its evaluation (statistical analysis) also reflected the total systems approach. This work demonstrated that given the causal aspect of the interrelations between

producer decisions, pests, and crops, it is imperative to consider the total effects of management for making agronomically sound decisions. We discussed the technical aspects of analysis by annihilation. Yet, the foremost advancement of this approach over current statistical methods is in the intuitive interpretation of parameter estimates as total effects. Currently, the dominating modus operandi for knowledge-based management of natural resources is comprised of two main stages. First, assessing the natural variability in the components of the system. Then, quantitatively or qualitatively projecting the result of statistical inference to the future of the system. The discontinuity in this approach leaves a potential for error in what is perceived as the "best" management decision. By annihilating, we combined and quantified the biological interactions of the WSS-downy brome-FCR-wheat complex to estimate the total-system implications of simple crop management decisions in the statistical inference step, revealing new insights for integrated management solutions.

The unknown consequences of management decisions can be viewed as a random variable that depends on a composite of biological and environmental factors. Therefore, the annihilator fits naturally into the Bayesian decision theoretic framework. Our prior belief that pest levels and their interactions will be affected by the management scheme, consequently impacting wheat yield, was updated with empirical data to provide a probability distribution for yields. The posterior expectation brings us closer to answering the question of interest to producers: the expected wheat yields from crop management practices, given the reality of potential damage from multiple pests. Furthermore, the Bayesian approach allows greater flexibility in modeling, incorporating prior knowledge to complement short-term observations of long-term ecological processes, and combining sources of information about different biological processes associated with multitrophic organisms, thus completing the modeling framework.

This work does not completely resolve all management challenges presented by natural systems and in particular the WSS-downy brome-FCR pest complex. Opportunities for further study can be found in almost every aspect of this dissertation. First, while the technical advantages in annihilation as laid out in Chapter 2 can be generalized to increasingly complex networks, they may not be applicable to models with non-trivial error structures (such as spatial or time-series dependence). Further study on estimation procedures of total effects is needed in order to make the concept applicable to a wide range of problems. Second, the advent of molecular technologies such as quantitative PCR can give scientists insights and allow development of new hypotheses on disease prevalence and crop tolerance previously unattainable. The relatively small side experiment described in Chapter 3, left several unanswered questions regarding the potential for differential effects of FCR in wheat varieties and different field conditions, as well as the role of *Fusarium spp.* in contributing to wheat stem sawfly larvae mortality. Third, we did not directly manipulate pest levels in the field which limited our modeling capacity. For example, while FCR levels have been increasing over the three years of the study, they did not reach a level where they can be incorporated into a management model and presented here. Further study of this system under the full range of FCR in field settings is required. Finally, the significant and complex WSS-FCR and WSS-downy brome two-way interactions and their joint impact on simple crop management recommendations exposed in Chapters 3 and 4, suggest continuous investigation of these pests as a three-way multitrophic complex, and higher resolution of whole-farm management practices may help update single-pest recommendations and mitigate pest pressure to wheat cropping systems. Missing from this dissertation is an important aspect of decision making in natural systems, namely the influence of abiotic environmental variables on all components of the system. However, the implications of our field observations and more so the con-

cepts laid out, may help further understanding and management of ecological systems, design of integrated pest management programs, and enhance the environmental and economic sustainability of the farming enterprise of the Northern Great Plains.

APPENDIX A

DERIVATION OF $\hat{\gamma}$ AND ITS VARIANCE

Note first Eq. (2.1)

$$\boldsymbol{X_2} = \boldsymbol{X_1}\boldsymbol{\beta} + \boldsymbol{\Psi}$$

$$\hat{\boldsymbol{\Psi}} = (\mathbf{I} - \mathbf{P})\boldsymbol{X_2}$$

$$\hat{\boldsymbol{\beta}} = (\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1}\boldsymbol{X_1}^T\boldsymbol{X_2}$$

and from Eq. (2.2)

$$\mathbf{y} = \mathbf{V}\boldsymbol{\gamma} + \boldsymbol{\epsilon_y} \qquad \boldsymbol{\epsilon_y} \sim N(0, \mathbf{I}\sigma^2)$$

$$\mathbf{V} = \begin{bmatrix} \boldsymbol{X_1} & \boldsymbol{X_2} \end{bmatrix}$$

$$\hat{\boldsymbol{\gamma}} = (\mathbf{V}^T\mathbf{V})^{-1}\mathbf{V}^T\mathbf{y}$$

$$Var(\hat{\boldsymbol{\gamma}}) = (\mathbf{V}^T\mathbf{V})^{-1}\sigma_y^2$$

To derive $\hat{\boldsymbol{\gamma}}$ we can invert

$$\mathbf{V}^T\mathbf{V} = \begin{pmatrix} \boldsymbol{X_1}^T\boldsymbol{X_1} & \boldsymbol{X_1}^T\boldsymbol{X_2} \\ \boldsymbol{X_2}^T\boldsymbol{X_1} & \boldsymbol{X_2}^T\boldsymbol{X_2} \end{pmatrix}$$

by the following (Searle, 1971):

$$\begin{bmatrix} A & B^T \\ B & D \end{bmatrix}^{-1} = \begin{bmatrix} A^{-1} + A^{-1}B^TE^{-1}BA^{-1} & -A^{-1}B^TE^{-1} \\ -E^{-1}BA^{-1} & E^{-1} \end{bmatrix} \text{ where } E = D - BA^{-1}B^T$$

Note,

$$\begin{aligned} E &= \boldsymbol{X_2}^T\boldsymbol{X_2} - \boldsymbol{X_2}^T\boldsymbol{X_1}(\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1}\boldsymbol{X_1}^T\boldsymbol{X_2} \quad \text{for } \mathbf{V}^T\mathbf{V} \\ &= \boldsymbol{X_2}^T(\mathbf{I}-\mathbf{P})\boldsymbol{X_2} \end{aligned}$$

$(\mathbf{I}-\mathbf{P})$ is idempotent and symmetric

$$\begin{aligned} &= \boldsymbol{X_2}^T(\mathbf{I}-\mathbf{P})^T(\mathbf{I}-\mathbf{P})\boldsymbol{X_2} \\ &= \hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}} \end{aligned}$$

Therefore

$$(\mathbf{V}^T\mathbf{V})^{-1} = \begin{pmatrix} (\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1} + \hat{\boldsymbol{\beta}}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\beta}}^T & -\hat{\boldsymbol{\beta}}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1} \\ -(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\beta}}^T & (\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1} \end{pmatrix}$$

$$\begin{aligned} \hat{\boldsymbol{\gamma}} = (\mathbf{V}^T\mathbf{V})^{-1}\mathbf{V}^T\mathbf{y} &= \begin{pmatrix} (\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1}\boldsymbol{X_1}^T + \hat{\boldsymbol{\beta}}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\beta}}^T\boldsymbol{X_1}^T - \hat{\boldsymbol{\beta}}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\boldsymbol{X_2}^T \\ -(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\beta}}^T\boldsymbol{X_1}^T + (\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\boldsymbol{X_2}^T \end{pmatrix}\mathbf{y} \\ &= \begin{pmatrix} (\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1}\boldsymbol{X_1}^T + \hat{\boldsymbol{\beta}}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}(\hat{\boldsymbol{\beta}}^T\boldsymbol{X_1}^T - \boldsymbol{X_2}^T) \\ (\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}(\boldsymbol{X_2}^T - \hat{\boldsymbol{\beta}}^T\boldsymbol{X_1}^T) \end{pmatrix}\mathbf{y} \end{aligned}$$

$$\begin{aligned} \text{But } \boldsymbol{X_2}^T - \hat{\boldsymbol{\beta}}^T\boldsymbol{X_1}^T &= (\boldsymbol{X_2} - \boldsymbol{X_1}\hat{\boldsymbol{\beta}})^T = ((\mathbf{I}-\mathbf{P})\boldsymbol{X_2})^T = \hat{\boldsymbol{\Psi}}^T \\ &= \begin{pmatrix} (\boldsymbol{X_1}^T\boldsymbol{X_1})^{-1}\boldsymbol{X_1}^T - \hat{\boldsymbol{\beta}}(\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\Psi}}^T \\ (\hat{\boldsymbol{\Psi}}^T\hat{\boldsymbol{\Psi}})^{-1}\hat{\boldsymbol{\Psi}}^T \end{pmatrix}\mathbf{y} \end{aligned}$$

$$\text{with } Var(\hat{\boldsymbol{\gamma}}) = (\mathbf{V}^T\mathbf{V})^{-1}\sigma_y^2$$

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