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The genetics of competitive ability in spring wheat

by

Todd Andrew Reid

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Examining Committee

Dean Spaner, Agricultural, Food and Nutritional Science

Donald Salmon, Alberta Agriculture and Rural Development

James Cahill, Department of Biological Sciences

Rong-Cai Yang, Agricultural, Food and Nutritional Science

Edward Bork, Agricultural, Food and Nutritional Science

Stephen Jones, Department of Crop and Soil Sciences, Washington State University

Abstract

Competition with weeds decreases crop yields globally. Some traits are known to confer a competitive advantage to spring bread wheat (*Triticum aestivum* L.), but complex relationships between the competitive traits makes breeding for competitive ability difficult. Prairie organic producers use spring wheat cultivars which have been bred for conventional management systems or heritage cultivars released before the widespread use of synthetic fertilizers and pesticides. Breeding spring wheat specifically for organic production has been suggested.

The International Triticeae Mapping Initiative (ITMI) population was used to study the genetics of traits associated with competitive ability. Grain yield without weed competition and under experimentally sown cultivated oat competition exhibited similar heritability. Similar heritability estimates between competition treatments suggest that selection in a weed free environment can lead to improvements in a weedy environment, but some high yielding lines under competition would be eliminated during selection. Quantitative trait loci (QTL) analysis of the population found QTL associated with vigour, days to heading, anthesis, and maturity, and cultivated oat grain yield suppression on chromosome 5A. The genetic correlations support the idea that early maturity provides a competitive advantage in northern grain growing regions.

To investigate the feasibility of organic wheat breeding we used a random population of 79 F6-derived recombinant inbred sister lines from a cross between the Canadian hard red spring wheat cultivar AC Barrie and the CIMMYT derived cultivar Attila. The population, including the parents, was grown on conventionally and organically managed land in 12 environments over three years. Six environments had detailed agronomic data and heritability estimates differed between systems for five of the 14 traits recorded. Direct selection in each management system (10% selection intensity) resulted in 50% or fewer lines selected in common for four of the traits. Over all 12 environments direct selection within management system resulted in three lines retained specific to

each system. The results of the management studies suggest that selection differences occur across multi-location tests, and selection for grain yield in organic systems should be conducted within organic systems. However, data garnered from conventional yield trials does have some relevance towards breeding for organic environments.

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1.1 Introduction

Three main staple crops feed the world; rice (*Oryza sativa* L.), corn (*Zea mays* L.), and wheat (*Triticum aestivum* L. em. Thell.). In Canada, wheat is the most commonly grown crop of the three, and is exported globally. Plant breeders in Canada work to improve wheat through improved disease and lodging resistance, earlier maturity, and increased yield (DePauw and Hunt 2001). Breeding improvements are most effective when coupled with improved agriculture practices, but actual yields do not increase without increases in genetic yield potential (Cook and Veseth 1991).

Breeders have used genetic tools to map the wheat genome (Paillard *et al.* 2003; Song *et al.* 2005). Knowing the location of genes may result in the use of molecular marker assisted breeding (Davies *et al.* 2006). Such techniques have the potential to enable breeders to pyramid many genes of small effect for a specific quantitatively inherited trait in a single cultivar. Some breeders in Canada screen for specific genes controlling traits of economic importance, such as cadmium uptake in durum wheat (*Triticum turgidum* L. subsp. *durum* (Desf.) Husn.) (Penner *et al.* 1995), and grain protein content in bread wheat (Distelfeld *et al.* 2004).

Environmental concerns have some people questioning modern agriculture practices including the widespread use of chemical fertilizers and pesticides. Alternative methods of farming, including organic agriculture, are gaining in popularity (Macey 2006). Organic producers reject the use of transgenic crops and chemical inputs, relying instead on crop rotation and mechanical methods for weed and disease management (Wyss *et al.* 2001).

Organic cereal farmers often make use of cultivars bred before the wide spread use of chemical fertilizers and pesticides, although this practice is not supported by the scientific literature (Mason *et al.* 2007b). Though some organic producers may desire organically bred cultivars (Degenhardt *et al.* 2005), it has been suggested that stressful environments are not useful selection environments (Fasoula and Fasoula 1997). However recent evidence suggests that selecting for

yield under organic conditions can result in genotypic rank changes in wheat (Murphy *et al.* 2007).

The use of mechanical weed control methods in organic agriculture implies an organic field may have high weed populations, because there are limited weed control options once the crop is estabilished (Agha and Pallutt 2006). A competitive cultivar may be better suited to such a weedy environment and could potentially enable organic farmers to increase yields.

In the following literature review, I will provide a brief overview of wheat production, organic agriculture, genetic tools for modern plant breeding, and wheat breeding methodology. The various attributes of a competitive cultivar will be discussed, along with potential approaches to breeding for competitive ability.

1.2 Wheat History and Production

Common bread wheat is grown globally. It is an allohexaploid derived from a spontaneous cross of wild emmer wheat (*Triticum turgidum* subsp. *dicoccoides* (Korn. ex Asch. & Graebn.) Thell.) with the wild grass *Aegilops tauschii* Coss. (Salamini *et al.* 2002). Wheat and wheat cultivation originated in the area of Southwest Asia known as the Fertile Crescent (Armelagos and Harper 2005).

Wheat is an annual grass with dense spikes and erect culms (Gleason 1968). The unbranching tillers end in spikes which can be awned or awnless (Bailey 1951). Grains are oblong, naked, and pubescent at the top (Bailey 1951).

In Canada wheat is divided into classes depending on the growth habit, seed colour and size, kernel hardness, and the protein content of the grain (CGC 2007b). There are specific requirements to visually distinguish kernels of each class from each other (CGC 2007a) (Table 1.1). Proposed changes to the classification system will see a partial removal of the visual requirements which should open new avenues for wheat breeders in Canada (CGC 2007a).

Growth habit refers to either spring types, which are planted after the last frost and harvested at the end of the growing season, or winter types, which are planted prior to the first frost and require exposure to cold temperatures to initiate

flowering (Cook and Veseth 1991). Wheat grains are red, white, or amber in color, and can have high or low protein content (Cook and Veseth 1991). Wheat is termed either hard or soft depending on how the endosperm fractures during milling; with hard wheat breaking at the cell wall and soft wheat breaking through the cell wall (Campbell *et al.* 2001).

World cereal production in 2003 was 2081 Mt of which 560 Mt was wheat (FAO 2005). In 2007, 5.3% of farms in Canada reported producing wheat, with a total yield of 20.1 Mt (Statistics Canada 2007b). In Alberta, 5.7% of farms in 2007 reported wheat production with an estimated 6.1 Mt of grain harvested (Statistics and Data Development Unit 2007).

1.2.1 Green Revolution and Sustainable Agriculture

The Green Revolution is a term used to describe the dramatic increase in yield of wheat and rice which occurred in the mid 1960's (Brush 1992). For wheat, this was primarily accomplished through the use of dwarfing genes from the Norin 10 winter wheat cultivar (Reeves and Cassaday 2002) which had *Rht-B1b* and *Rht-D1b* height reducing genes (Zhang *et al.* 2006). These genes lower sensitivity to endogenous gibberellins (GA) in vegetative tissue which reduces stem elongation (Rebetzke *et al.* 2001). Reduced stem length increased yield and decreased lodging even with increased fertilizer application (Khush 1999). One unfortunate side effect of the Green Revolution was an increased use of chemical fertilizers which, coupled with chemical pesticides, has led to a degradation of soil fertility in developing nations (Swaminathan 2006). Soil conservation concerns have led to changes in tillage practices, but these same changes have also increased farmers use of chemical fertilizers and their reliance on pesticides (Young *et al.* 2006).

Relying solely on chemical inputs has been reported to be unsustainable in that it degrades soil fertility and crop productivity (Wanjari *et al.* 2004). Plant breeders are working to develop cultivars with improved nutrient and water use efficiency to aid farmers, especially in poorer countries and those with an eroded land base (Trethowan *et al.* 2005). It has been suggested by many proponents of

the Green Revolution that further increasing production in a sustainable manor will require more technological input in areas previously marginalized and more intensive farming practices, *e.g.* precision farming practises (Swaminathan 2006).

1.2.2 Organic Agriculture

Organic agriculture is a system of farming that protects and enhances the agroecosystem (*i.e*. soil flora and fauna) (Bruinsma 2003). It began as a modern movement in 1940s in response to industrial agriculture's specialization and intensification (Glenna and Jussaume 2007). There is a set of guidelines for specific farming practices, but organic agriculture can be considered a set of ideas for a "better" way of farming (Seppanen and Helenius 2004). The guiding principles have been outlined by the International Federation of Organic Agriculture Movements (IFOAM 2005).

Farmers who adhere to a specific set of guidelines can opt to become certified, meaning a third party agency inspects the farmer's operation to ensure that only organic practises are conducted (Seppanen and Helenius 2004). This certification allows the farmer access to the certified organic market, often resulting in price premiums for their products (Glenna and Jussaume 2007).

Certified organic crops are grown in over 120 countries on approximately 31 Mha (Willer and Yussefi 2006). Oceania, including Australia, has the greatest total percentage of organic land (38%) with Europe second at 21%, but Europe has the highest percentage of organic land in relation to conventional agricultural land (Willer and Yussefi 2006). North America had 1.4 Mha under organic management in 2005 (Willer and Yussefi 2006).

In Canada in 2005 there were 3618 certified organic farms, with 2077 producing field crops, including grains and oilseeds (Macey 2006). Total organic food production in Alberta in 2006 came from 2629 farms (5.3% of farms in Alberta), but 91.5% of these were not certified by a Certifying Agency (Statistics Canada 2007a). In 2005 there were 238 certified organic producers in Alberta (0.5% of total farms) (Macey 2006). Certified organic wheat production in

Alberta in 2005 was on 8205 ha which represented 11% of the total land in certified organic wheat production in Canada (Macey 2006).

1.3 Basic Plant Genetics

Knowledge of genetics has given breeders access to powerful tools that aid in the creation of new cultivars (Poehlman and Sleper 1995). The way a trait is expressed (phenotype) is a function of the genes controlling the trait (genotype) and environmental influences (Bernardo 2002). Gregor Mendel discovered the segregation of pairs of hereditary traits (genes) through the hybridization of pea plants (Mendel 1901). Today, hybridization followed by selection of superior phenotypes forms the basis of modern plant breeding (Schneider 2002).

Plant traits can be considered to be either qualitatively or quantitatively inherited. A qualitatively inherited trait is considered to be controlled by few genes, separates plants in distinct types, and is not greatly influenced by the environment (Falconer and Mackay 1996). Quantitatively inherited traits considered to be expressed in degrees of variation between individuals, have a large numbers of genes influencing the trait, and show greater influence from the environment (Bernardo 2002). For example, awn inhibition (qualitative) is controlled by the B1, B2, and Hd genes (Sourdille *et al.* 2002) while grain yield in wheat (quantitative) is controlled by a great many genes of small effect and is highly environmentally dependent (Novoselovic *et al.* 2004). These distinctions are not as clear cut in nature, and are at the discretion of the researcher. Yield is considered a quantitatively inherited trait, but the presence or absence of a single gene (e.g. height reducing gene) can greatly affect the amount and weight of grain produced.

Traits controlled by a few genes, with alleles at the same locus, can interact in a dominant or additive manner (Acquaah 2007). Epistasis, the interaction of non allelic genes, is common in quantitatively inherited traits because of the many genes associated with them, and these traits are often described by their gene action (Acquaah 2007). Though based on the principles of mendelian genetics, quantitatively inherited traits are studied using populations,

not individuals, and measurements, not classifications, are required (Falconer and Mackay 1996). In addition, environmental influences cause quantitatively inherited traits to have continuous phenotypic variation within a population (Windig *et al.* 2004).

Heritability estimates are calculated from measured variation within a population and is an estimate of the genetic control of a trait (Fehr 1987). Broad sense heritability (H) is the proportion of phenotypic variation controlled by the genotype while narrow sense heritability (h^2) is the proportion of phenotypic variation controlled by additive gene action (Bernardo 2002).

Phenotypic correlations provide the association of two traits that can be directly measured, but the variance and covariance of these traits can also be portioned into genetic and environmental correlations (Falconer and Mackay 1996). Genetic correlations are the degree to which two traits are controlled by the same gene (pleiotropy) or by closely linked genes (Bernardo 2002). Pleiotropy also means that selection of the one trait will result in the indirect selection of the other trait (Falconer and Mackay 1996) and the genetic correlation is also the magnitude and the direction of change for the traits in response to selection (Holland 2006). Environmental correlations are the associations due to non-additive gene action combined with environmental deviations (Falconer and Mackay 1996).

1.3.1 Mating Designs for inbred crop species

Selecting parents for crossing can be done on the basis of the progeny test where the breeding value of a plant is based on the performance of it's progeny (Allard 1966). This breeding value can be defined in terms of general and specific combining ability (Acquaah 2007).

The diallel cross is used to investigate combining ability (Falconer and Mackay 1996), but can also be used to investigate the genetics of a quantitatively inherited trait (Ortiz *et al.* 2001). This method involves the crossing of all the inbred lines being evaluated, in all possible combinations, and evaluating the progeny of those crosses (Bernardo 2002). Different diallel designs and methods

of analyzing the data generated have been developed depending on the specific information desired (For review see Christie and Shattuck 1992). The diallel cross has been widely used with many crops. Recent studies with wheat include earliness in spring bread wheat (Iqbal *et al.* 2006), grain fill duration at high temperatures in bread wheat and durum (Budak 2001), and the effects of increased nitrogen fertilizer on winter wheat hybrids (Le Gouis *et al.* 2002).

Gene action can be studied using the generation means analysis (GMA) (Hayman 1960). Additive and dominance action can be calculated as well as epistatic effects (Viana 2000). These epistatic effects include additive x additive, additive x dominant, and dominant x dominant interactions (Bernardo 2002). A population of related lines is created from a cross between two homozygous parents (P_1 and P_2) and individuals in the F_1 generation are either self pollinated to produce F_2, or backcrossed to one of the parents (BC_1 and BC_2) (Hayman 1958).

This type of analysis has been used extensively in wheat to study heading date, plant height, and kernel weight (Bhatt 1972), grain fill duration (Przulj and Mladenov 1999), drought stress (Malik *et al.* 1999), water logging stress (Boru *et al.* 2001), temperature stress (Mladenov *et al.* 1998), and disease resistance (Hakizimana *et al.* 2004). The GMA has also been used to study the complexities of yield, and yield components, in spring bread wheat (Singh *et al.* 1984), winter wheat (Edwards *et al.* 1976; Novoselovic *et al.* 2004; Sidwell *et al.* 1976), durum (Singh *et al.* 1990), melon (Zalapa *et al.* 2006) and long bean (Rahman and Saad 2000).

A self pollinating population can also be evaluated after a sufficient level of homozygosity is achieved (Fehr 1987). Methods used to achieve homozygosity are discussed in section 1.4.1 of this chapter. The population of recombinant inbred lines (RILs) will be segregating for the traits of interest if the parent cultivars differed in those traits (Bernardo 2002). The random nature of the population allows for the calculation of heritabilities, phenotypic, genetic, and environmental correlations (Holland *et al.* 2003).

1.3.2 Plant Genomics

Genetic maps help explain relationships between observed traits and provide important information for the modern plant breeder (Poehlman and Sleper 1995). Maps are constructed using molecular markers which help breeders identify the location of genes within the genome (Song *et al.* 2005). Common types of molecular markers include restriction fragment length polymorphisms (RFLP), simple sequence repeats (SSR) (Bernardo 2002), random amplified polymorphic DNA (RAPD), and amplified fragment length polymorphism (AFLP) (Asins 2002).

Genetic maps are used to identify quantitative trait loci (QTL) (Song *et al.* 2005). QTLs are regions of the genome that are associated with a certain quantitatively inherited trait, and though the QTL itself is often not the gene in question, the two are closely linked (Bernardo 2002). For self pollinating plants, RILs are phenotyped for the trait of interest, genotyped with various molecular markers, and then analysed statistically to identify the loci (Falconer and Mackay 1996). A map with a high marker density is better able to reliably detect QTLs (Asins 2002). This technique has become standard operating procedure when studying quantitative genetics (Salvi and Tuberosa 2005).

1.3.3 International Triticeae Mapping Initiative

A group of researchers in 1989 established the International Triticeae Mapping Initiative (ITMI) with the goal of developing maps for the major Triticeae species (Sorrells *et al.* 2005). For wheat, a detailed map was created from a population derived from a cross between the synthetic wheat W7984 and the bread wheat Opata 85 and is referred to as the ITMI population (ITMI*pop*) (Langridge *et al.* 2001). This map is updated as new technology allows (Langridge *et al.* 2001). The current ITMI population map has 1410 markers detected with RFLP probes and SSR microsatelites (Song *et al.* 2005) and represents the most complete map of the population to date. It has been used to investigate wheat quality traits (Nelson *et al.* 2006), tillering, growth habit, spike morphology, gross morphology (Li *et al.* 2002), heading, maturity, plant height,

leaf color (Kulwal *et al.* 2003), as well as many diseases and pests (eg. Friesen and Faris 2004; Sardesai *et al.* 2005; Zwart *et al.* 2006).

1.4 Breeding Crops

Wheat production worldwide has increased dramatically since the early 1960's despite a marginal increase in land area in production (Marshall *et al.* 2001). The release of high yielding, semi dwarf, "Green Revolution", wheat and rice cultivars along with increased availability and use of inorganic fertilizers and irrigation systems is primarily responsible for this increase (Khush 1999). Genetic gains in yield potential are attributed to the accumulation of quantitative genes of small effect in the germplasm (Austin 1999). An analysis of the average yield of potential new varieties grown in cooperative tests in the southern Canadian prairies shows an increase in yield from the 1950's to the 1990's (McCaig and DePauw 1995) though not all released cultivars fit this trend (Mason *et al.* 2007b).

Plant breeding has been a part of agriculture since the first domestication of plants (Evans 1980). The selection of new varieties from available high performance landraces has long been the domain of farmers (Schneider 2002). The rediscovery of Mendelian genetic principles in the early 20th century sparked the creation of professional scientific plant breeders, who then performed specific crosses to manipulate the traits of interest (Schneider 2002). Improved methods have hastened the breeding process and breeding is one of the main causes of the increase in crop productivity over the past century (Duvick 2002).

Plant breeders often produce a small number of cultivars suited to optimal conditions over a wide geographic area; whereas farmers often desire cultivars suited to more marginal environments in a geographically small area (Cleveland and Soleri 2002). Farmers in developing countries continue to adapt local cultivars and land races to suit their specific needs and microenvironments (Hawtin *et al.* 1996).

Despite the different goals, collaboration between farmers and professional plant breeders often produce improved cultivars more suited to farmers needs (Dawson *et al.* 2008). The most popularly grown cultivars are often incorporated into breeding material and improved agronomic practices can change breeding goals (Duvick 2002). Increased planting rates by farmers have led to the development of maize cultivars with increased tolerance to stress and intra-specific competition in Canada (Tollenaar and Wu 1999) and the United States (Duvick and Cassman 1999). The adoption of organic agricultural methods by farmers may necessitate the development of organic specific breeding programs for wheat (Mason and Spaner 2006; Murphy *et al.* 2007) and other field crops (van Bueren *et al.* 2003a).

Participatory plant breeding is a more involved form of collaborative breeding where the farmers themselves make crosses, selections, and help set goals for the breeding program (Sperling *et al.* 2001). Canadian regulations work against this form of breeding, however supporters feel this type of breeding will make modern cultivars more responsive to end users in marginal environments (Morris and Bellon 2004). Participatory plant breeding has been suggested for low input agriculture systems (Dawson *et al.* 2008), and can result in an increased cost to both farmers and scientists, as well as an overall increase in the number of required cultivars (Sperling *et al.* 2001).

1.4.1 Breeding Techniques for Wheat

Wheat is a self pollinated crop with minimal cross pollination occurring under field conditions (Hucl 1996). A large scale gene flow study in Saskatchewan found an average cross pollination rate of 0.44% which decreased to 0.01% at a distance of 100m from the pollinator (Matus-Cadiz *et al.* 2004). Factors contributing to the low rate of cross pollination are cultivar specific and include the amount of time and degree to which the floret is open during anthesis, and pollen viability (Hucl 1996).

Self-pollination is inbreeding and this reduces, by half, the heterozygosity of each successive generation (Fehr 1987). Cultivars of wheat are not released

until they have reached a significant level of homozygosity, usually in the F_8 or later generation (Poehlman and Sleper 1995). Three common methods of generation advance are pedigree selection, single seed descent, and bulk population (Poehlman and Sleper 1995).

Pedigree selection is the most labour intensive of the selection methods and requires detailed note taking with selection occurring in every generation until homozygosity (Poehlman and Sleper 1995). Single seed descent (SSD) or modified pedigree method (Brim 1966) and bulk selection methods have lower labour requirements by removing the note taking and selection until a reasonable level homozygosity is reached (Fehr 1987).

Comparisons between SSD and pedigree methods suggest lines generated from SSD are often as good as or superior to wheat lines developed by pedigree methods (Srivastava *et al.* 1989), however non-competitive high yielding lines may be lost in SSD (Roy 1976). Loss of lines can also occur with bulk selection, but within line variation is maintained in bulk breeding, while it is lost in single seed descent (Kervella and Fouilloux 1992). Though no specific information is maintained during the advancement of the generations in SSD, methods exist which facilitate selection for specific genes (Jansen and Jansen 1990). Simulation studies suggest SSD is most effective for traits with low heritabilities (Casali and Tigchelaar 1975).

Most breeding programs employ a mixture of these methods depending on the goals of the program and the resources available. The International Maize and Wheat Improvement Centre (CIMMYT) uses a modified pedigree/bulk method (Wang *et al.* 2003) and a modified bulk/pedigree system, which is beneficial in participatory plant breeding with local producers (Witcombe and Virk 2001).

Recent developments in biotechnology have somewhat altered traditional breeding methods, though artificial hybridization remains the most popular breeding method (Baenziger *et al.* 2006). Biotechnology enables the wheat breeder to produce doubled haploid lines (Graf *et al.* 2003), conduct genetic transformation (Tarinejad *et al.* 2007), use marker assisted selection (Wang *et al.* 2008), and create hybrid wheat (Zhou *et al.* 2008).

Doubled haploid production has greatly increased the rate of cultivar release for self pollinated crops (Poehlman and Sleper 1995) and is widely accepted in many crop species (Tenhola-Roininen *et al.* 2006). Different methods exist for producing doubled haploid wheat cultivars including anther culture, microspore culture, and maize hybridization techniques (Guzy-Wrobelska and Szarejko 2003). In Canada, the cultivar McKenzie was the first hard red spring wheat released from doubled haploidy (Graf *et al.* 2003).

Plant transformation, the insertion of new genes directly into a plant's genome, gives the plant breeder access to a limitless range of genes from any organism (Baenziger *et al.* 2006). Some transformed wheat cultivars have been found to perform as well as their non-transformed parents, suggesting that transformed wheat can be as stable as their conventional counterparts (Shewry *et al.* 2006). Transgenic, herbicide tolerant, wheat may have a low human health risk, with no toxicity level found for the transformed wheat protein (Peterson and Shama 2005).

Marker assisted selection (MAS) uses molecular markers to select lines for advancement in breeding programs. If phenotypic evaluation is costly or difficult then MAS is a valuable tool (Bernier *et al.* 2007), but phenotypic selection can be as effective as MAS when the trait is controlled by few genes of major effect (Davies *et al.* 2006). Marker assisted selection is currently being used to monitor changes in genomic regions with an unidentified effect, but are still retained and selected for in a pedigree breeding program (Christopher *et al.* 2007).

Wheat hybrids have been created using male sterile lines, but low seed set was recorded under field conditions, with 10% of the seeds coming from self pollination (Marais *et al.* 2000). Other male sterility genes have been identified in wheat, and though self pollination has been eliminated, hybrid seed set remains low (5.5% to 8.2%) (Zhou *et al.* 2008).

1.4.2 Organic Breeding

Modern plant breeding occurs in close to ideal growing conditions with low abiotic stresses, using high fertilizer inputs (Atlin and Frey 1989). Organic

grain farmers mainly use cultivars bred under such conventional management systems; or older cultivars released before the widespread use of chemical fertilizers or pesticides (Carr *et al.* 2006). Organic producers are interested in organic-specific cultivars (Carr *et al.* 2006; Degenhardt *et al.* 2005) and the development of breeding programs specific for organic farming systems may be warranted (Mason and Spaner 2006; Murphy *et al.* 2007).

Genetic transformation enables the plant breeder to take a gene from virtually any organism and incorporate it into a plants genome (Baenziger *et al.* 2006). These procedures are perceived to have an inherent lack of respect for the plant, as a living entity, resulting in a rejection of transformation technology by the organic community (van Bueren and Struik 2004). The methods involved in genetic transformation require the breeder to view plants, or any organism, solely as a collection of genes. The principles of organic agriculture imply a respect for the integrity of plants outside the usefulness of the species for human beings (van Bueren *et al.* 2003b).

Plant breeding for organic agricultural systems employs natural plant fertility to enhance genetic diversity in sustainable cultivar development (IFOAM 2004) while protecting the integrity of the plant species (van Bueren *et al.* 2003b). The general requirements for organic agriculture differ from conventional agriculture, with specific breeding techniques considered more appropriate than others for use in organic plant breeding (for review see Wyss *et al.* 2001).

Organic agricultural systems generally have greater weed pressures (Agha and Pallutt 2006), have a slow release of nutrients (Barberi 2002), an increased soil microbial biomass (Fliessbach and Mader 2000), and limited treatments for disease (Scheuerell and Mahaffee 2002). An organic cultivar should be able to develop a large root base with beneficial interactions with soil biota, efficiently utilize available soil nutrients and water, suppress or tolerate weed pressure, and be tolerant of disease and pests (van Bueren *et al.* 2001).

Ethical considerations aside, breeding theory holds that selection for specific traits in any breeding program should be conducted in environments with appropriate selection pressure (Boyer 1982). The ability to interact beneficially

with soil biota means that selection should take place in an environment where such interactions are necessary (Drinkwater and Snapp 2007). Organic agriculture provides such an environment, suggesting that organic breeding should take place under organic conditions (van Bueren *et al.* 2002) and genotypic rank changes have been reported between conventional and organic systems (Murphy *et al.* 2007).

Breeders utilizing a participatory approach in conjunction with organic farmers have had some success in producing high performance bulk populations of wheat specific to the needs of the farmer (Murphy *et al.* 2005). Participatory approaches have also been employed with maize and wheat under low input conditions in the tropics (Banziger and Cooper 2001). Programs investigating breeding in less than ideal conditions focus on low input agriculture (Atlin and Frey 1989; Bramel-Cox *et al.* 1991; Ceccarelli 1996; Li *et al.* 1995) or compare performance of released cultivars under organic and conventional systems (Carr *et al.* 2006; Mason *et al.* 2007b).

1.5 Competitive Crops

The study of competitive crops can be problematic as the concept is vague, difficult to measure, and depends on how competition is defined (Goldberg 1996). It has been suggested that a separation between crop tolerance, measured in percent yield loss due to weeds (competitive response), and weed suppression (competitive effect), is important in understanding competitive relationships (Didon 2002; Jordan 1993). However, wheat cultivars can also suppress weed growth while maintaining yield (Lemerle *et al.* 2001b).

Increased competitiveness in wheat, both tolerance and suppression, is a desirable goal for breeders globally (Lemerle *et al.* 2001b; Vandeleur and Gill 2004). Specific traits are more strongly associated with competitive ability than others and a competitive ideotype has been developed for a number of geographic regions, though no single set of traits work in all situations (Lemerle *et al.* 2006; Mason *et al.* 2007b).

1.5.1 Competitive Advantage of Tall Plants

Increased height has been linked to increased weed suppression. The reason for this is shading effects. The taller the plant, the more light it will intercept, which is detrimental to shorter plants growing below (Lemerle *et al.* 2001a). This trait appears to have a threshold and yield losses can occur if a strongly competitive weed, such as wild oat (*Avena fatua* L.), overtops the crop at maturity (Cousens *et al.* 1991). Greater height has also been linked to increased lodging, resulting in yield loss (Lemerle *et al.* 2001a).

Challaiah *et al.* (1986) studied the effects of downy brome (*Bromus tecorum* L.) on various winter wheat cultivars. They reported taller cultivars reduced downy brome yield, but the tallest plants measured in the study were the lowest yielding in both weed free and weed infested plots.

Seefeldt *et al.* (1999) compared the common height reducing genes *Rht-B1b* and *Rht-D1b* and their influence on the ability of winter wheat to compete with *Aegilops cylindrical* Host. They reported that the weed reduced the yield of the dwarf plants, containing both *Rht-B1b* and *Rht-D1b* genes by 28%, and recommended breeding for taller plants. Despite this, the negative impact of plant height, with regards to decreased harvest index and increased lodging, means breeding wheat for increased height is unlikely in many breeding programs (Lemerle *et al.* 1996).

1.5.2 Competitive Advantage of Vigorous Plants

A species that achieves greater biomass early in the growing season will be a better competitor throughout (Cousens *et al.* 2003). A fast growing plant can make use of available water and nutrients before a slower growing competitor. Researchers often describe early vigour in terms of leaf growth (Botwright *et al.* 2002; Lopez Castaneda and Farquhar 1995; Rebetzke and Richards 1999) and as such this trait has been limited in wheat through the use of GA-insensitive dwarfing genes *Rht-B1b* and *Rht-D1b* (Ellis *et al.* 2004). Early vigour in wheat, as measured by leaf area, is altered by seed size and cultivar (Richards and Lukacs 2002), and the presence and size of a coleoptile tiller (Liang and Richards 1994).

A study on the early growth of corn reported increased vigour was associated with a larger endosperm (Wann 1980). The same study reported that the most vigorous cultivar (Truckers Favorite) had the lowest respiration rate and the highest starch content, while the least vigorous cultivar (Florida Sweet) had the highest respiration rate and highest sugar content (Wann 1980). This suggests that respiration rate can be limited by enzymatic activity, but such a limit may not result in decreased seedling vigour. Kernel respiration rate in corn has been used as an indication of seedling growth potential (Cantrell *et al.* 1972).

Seed size is an important aspect of seedling vigour (Richards and Lukacs 2002), however in tall fescue, the benefits of larger seed size disappear beyond the early stages of growth (Lewis and Garcia 1979). Larger seed size improved spring wheat competition with wild oats resulting in decreased wild oat (*Avena fatua* L.) seed production and decreased wild oat plant density (Xue and Stougaard 2002). The effect was more pronounced when plants with increased seed size were seeded at greater seeding rates (Stougaard and Xue 2004).

Field studies generally focus on above ground growth in vigour testing and vigour relationships (Lopez Castaneda and Farquhar 1995; Rebetzke and Richards 1999; Spitters and Kramer 1985). This is largely due to the relative ease of measurement of above ground material (Richards and Lukacs 2002). Above ground biomass is an important aspect of wheat competitive ability. Rapid leaf development ensures a large crop canopy which provides a greater area for photosynthesis as well as shading out younger competing species (Lemerle *et al.* 2001a).

1.5.3 Competitive Advantage of Large Leaf Size

Leaf size is considered a trait that contributes to the competitiveness of a plant (Lemerle *et al.* 2001a). Larger leaves capture more light, providing greater photosynthetic capacity for dry matter production, but plants must maintain a balance in leaf area to maximize light capture without creating problems from self shading (Peltonen-Sainio *et al.* 1997; Wall and Kanemasu 1990). Lemerle *et al.* (2001a) suggest a competitive ideotype with larger leaves and greater leaf area.

Leaf area is often reported as the ratio of green leaf area to ground area, referred to as the leaf area index (Peltonen-Sainio *et al.* 1997). Coleman *et al.* (2001) reported that wheat plants with larger leaf area index, and short stature, had greater yield without weeds and greater weed suppression when compared to taller plants.

Many factors can affect the leaf area index of cereals, including soil fertility and fertilizer application rates (Peltonen-Sainio *et al.* 1997), row spacing (Wall and Kanemasu 1990), and year of release (Vandeleur and Gill 2004).

Seavers and Wrights (1999) found a wheat cultivar (Avalon) with leaves that were wider and had a greater tip angle had reduced yield loss due to weeds than a cultivar with a more erect growth habit (Spark). This ability to suppress the weed was directly related to the health of the weed itself. In a dry year the weed was less vigorous and more susceptible to shade effects whereas no differences were observed between the two wheat cultivars in a year with adequate water (Seavers and Wright 1999). Low water potential has been found to alter perennial ryegrass (*Lolium perenne* L.) leaf growth, with leaf width being reduced while leaf extension was unchanged (van Loo 1992).

In general, taller crops with less erect leaves and a larger leaf area index, or ground cover, are considered more competitive (Fischer *et al.* 2000; Huel and Hucl 1996; Richards and Whytock 1993). In spite of this, Vandeleur and Gill (2004) found a decrease in leaf area index from older to modern wheat varieties in Australian varieties of wheat. They associate this with the introduction of GA insensitive dwarfing genes *Rht-B1b* and *Rht-D1b*, which reduced cell size in leaves. Gibberellins have been found to control leaf shape and development in sweet pea (*Lathyrus odoratus* L.) (Ross *et al.* 1993). Larger leaves confer their competitive advantage only if the canopy is closed early in the season, causing the weeds to be smothered (Pavlychenko and Harrington 1934).

1.5.4 Competition and Root Mass

A cultivar with a large root mass is able to take up more water and nutrients leaving less nutrients for their competitors (Bingham 1995). Pioneering

work in the area was conducted by Pavlychenko and Harrington (1934) and they concluded that a successful competitor is one with a large root mass close to the soil surface in addition to deep penetrating main roots. Recent research has demonstrated that annual ryegrass (*Lolium multiflorum* Lam.) is a better competitor than wheat for fertilizer nitrogen which subsequently leads to yield losses in the wheat (Palta and Peltzer 2001).

Bingham (1995) found modern wheat varieties had greater root length and a greater number of seminal axis's, each with a larger compliment of lateral roots, than wild oats. These findings suggest wheat is a better competitor than wild oats and are contrary to the findings of Pavlychenko and Harrington (1935) who reported wild oats as the better competitor.

Stone *et al.* (1998) reported wheat growth was reduced to a greater extent when competition from Italian ryegrass (*Lolium multiflorum* Lam.) included below ground competition instead of above ground competition alone. Satorre and Snaydon (1992), studying cereal competition with wild oats, reported no differences in below ground competitive ability of wheat, barley (*Hordeum vulgare* L.), and oats, but they did find differences in above ground competitive ability.

1.5.5 Breeding for Competitive Ability

The interplay of the large number of factors influencing competitive ability makes improvement through breeding problematic. Breeding efforts have focused on improving one trait at a time (Lemerle *et al.* 1996) or trying to define competitive ability solely on the basis of yield (Cousens *et al.* 2003; Lemerle *et al.* 2006). Alternatively, indirect selection of competitive ability through the selection of known competitive traits has been suggested for upland rice (Zhao *et al.* 2006b). Selection of these traits in a weed free environment is thought to improve competitive ability within a weedy environment (Zhao *et al.* 2006a).

Selection for multiple traits can be enhanced through the use of selection indices (Baker 1986). Different methods of creating indices exist (Baker 1986; Ceron-Rojas *et al.* 2006; Van Sanford *et al.* 1993) but only minor differences exist

in the effectiveness of different index types (Bernardo 2002). Selection indices have been widely used by plant breeders for a number of crops including oats (Holland and Munkvold 2001), and rice (Zhao *et al.* 2006b). In wheat, selection indices have been used for drought (Sio-Se Mardeh *et al.* 2006), disease resistance (Sharma and Duveiller 2006), and early maturing high protein wheat (Iqbal *et al.* 2007).

The negative relationship between yield and competitive ability, and decreased heritability estimates from increased environmental variation, may suggest that selection should not be done in a competitive environment (Fasoula and Fasoula 1997). However, specific breeding lines that yielded the greatest without competition may not be the greatest yielding lines in a competitive environment (Huel and Hucl 1996; Mason *et al.* 2007a; Mason *et al.* 2007b). Ranking wheat cultivars for competitive ability is often not consistent between sites due to genotype by environment (G×E) interactions (Lemerle *et al.* 2001b; Vandeleur and Gill 2004). Despite rank changes, weed free yield can be the best predictor of competitive yield (Cousens and Mokhtari 1998).

Rank changes for competitive ability shows that phenotype is influenced by the environment, or plastic, and the presence of G×E implies selection for plasticity may be possible (Windig *et al.* 2004). The plasticity of an individual cultivar may give the best indication of their competitive ability (Hucl and Baker 1993).

Much of our understanding of the genetics of competitive ability is through the associations of competitive ability with specific, measurable, morphological features. Coleman *et al.* (2001) identified QTLs for competitive traits in wheat and correlated them to weed dry matter at maturity, but they did not identify specific QTLs for crop tolerance or weed suppression. Identifying these genes may help improve breeding for competitive response through marker assisted selection.

Organic producers in central Alberta do not feel new methods of weed control are necessary despite citing competition from weeds as a major constraint to production (Degenhardt *et al.* 2005). The use of competitive crops is one

method in a long list of weed control measures in organic agriculture (Barberi 2002; Mason *et al.* 2007b). Breeding for competitiveness in organic agriculture cannot be separated from the other important traits required for successful organic cultivars (Murphy *et al.* 2007) and interactions between crops and weeds in organic agriculture must allow for a longer time frame than in conventional agriculture due, in part, to slower nutrient release rates (Barberi 2002).

1.6 Summary and Objectives

The different opinions expressed by researchers between which environments are best suited for the breeding of competitive ability affects the organic industry, and organic plant breeders. Investigating differences in the heritability of traits between competitive and non-competitive environments could provide further insight into this problem. Uncovering specific genes or QTLs which alter competitive response may provide more tools for the breeding of competitive ability.

The soil composition, nutrient levels and release rates, and weed pressure in organic agriculture systems differ from conventional agriculture systems, which suggest organic specific breeding may be required. Directly testing this suggestion and investigating the heritability of organic specific traits could provide further evidence for the development of organic specific breeding programs. This may aid in identifying traits suitable for selection.

Based on the preceding literature review I propose the following thesis objectives:

1) Determine if heritabilities, genotypic rank, and genotypic and environmental correlations differ between weedy and non weedy environments.
2) Determine if there are QTL associated with competitiveness in wheat and estimate their location and effect.
3) Determine if heritabilities, genotypic rank, and response to selection differ between organic and conventional management systems.

4) Determine which morphological traits are correlated with any genotypic rank change observed between conventional and organic systems.

These objectives will be tested with the following hypothesis:

1) Morphological traits will not differ for heritability and genotypic correlation between weedy and weedy free environments.
2) No specific QTL exist for crop tolerance to weeds.
3) Heritabilities, genotypic rank, and response to selection do not differ between organic and conventional management systems.
4) Morphological traits are not correlated with genotypic rank change between conventional and organic systems.

1.7 Table

Table 1-1: Descriptions of the Canadian wheat classes and their kernel visual distinguishability (KVD). [z]

Class	Description	KVD
Canada Prairie Spring Red (CPSR)	Medium hard kernels used for making hearth breads, flat breads, or steamed breads and noodles. Mean grain protein content of 11.8 in 2006.	Ovate to elliptical kernels are midsize to large, have an incurved base, small to midsize brush, and are opaque red to orange. The germ is small to midsize and oval.
Canada Prairie Spring White (CPSW)	Suitable for flat breads, noodles, chapattis, this white spring wheat has medium dough strength.	White kernels, midsize to large, ovate to elliptical, with small to midsize bush, and an incurved base. The germ is midsize and oval.
Canada Western Amber Durum (CWAD)	This wheat has excellent pasta-making quality from a high yield of semolina and a mean grain protein content of 12.8 in 2006.	The amber coloured large to midsize elliptical kernels have a large, wide oval to rectangular germ and angular cheeks.
Canada Western Extra Strong (CWES)	This hard red spring wheat with extra strong gluten is suitable for use in frozen dough, blending, or specialty breads.	Dark to medium red, large, ovate kernels, s-shaped base, round cheeks, and large collared brush. Germ is typically round, large wide.
Canada Western Hard White Spring (CWHWS)	Suitable wheat for bread and noodle production. The flour has excellent colour. Mean grain protein content of 13.2 in 2006.	White, small to midsize kernels are oval to ovate in shape with a round, midsize to large germ.
Canada Western Red Spring (CWRS)	This hard wheat with high protein content (13.4 in 2006) is the most widely grown class of wheat in Canada.	Small to midsize kernels are translucent red, and oval to ovate in shape. The germ is round and ranges from midsize to large.
Canada Western Red Winter (CWRW)	Hard wheat with a mean protein content of 10.4 in 2006. Used for French breads, flat breads, steamed breads, and noodles.	Orange to opaque red kernels are small to midsize and elliptical with a small brush and round cheeks. The small germ is oval to round.
Canada Western Soft White Spring (CWSWS)	Low protein content (10.8 in 2006) makes this wheat suitable for cookies, cakes and pastry.	Small to midsize kernels are white, and ovate to oval with a small, oval germ.

[z](CGC 2007b; Edwards *et al.* 2006)

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2.0 A genetic analysis of weed competitive ability in spring wheat. [1]

2.1 Introduction

Competition with weeds is known to decrease crop yields (Oerke 2006). The study of competitive crop cultivars can be problematic as the concept is vague, difficult to measure, and depends on how competition is defined (Goldberg 1996; Hager 2004). Wheat (*Triticum aestivum* L.) cultivars can suppress weed growth while maintaining their yield (Lemerle et al. 2001b). It has been suggested that a separation between crop tolerance, measured in percent yield loss due to weeds (competitive response), and weed suppression (competitive effect), is important in understanding competitive relationships (Didon 2002; Jordan 1993).

Increased competitiveness in wheat, both tolerance and suppression, is a goal for some wheat breeding programs, including those directed to low-input environments (Lemerle et al. 2001b; Vandeleur and Gill 2004). Some specific traits are more strongly associated with competitive ability than others, and competitive ideotypes have been developed for a number of geographic regions, though no single set of traits apply in all situations (Lemerle et al. 2006; Mason et al. 2007b).

Taller crops with less erect leaves and a high leaf area index, or ground cover, are considered more competitive (Fischer et al. 2000; Huel and Hucl 1996; Richards and Whytock 1993). Plant height has been widely studied (Challaiah et al. 1986; Lemerle et al. 2001a; Seefeldt et al. 1999; Thomas et al. 1994), with less attention placed on other traits. Early maturity and greater early season vigour have been identified specifically for organic agriculture (Mason et al. 2007b).

The interplay of the large number of factors influencing competitive ability makes improvement through breeding problematic. Breeding efforts have focused on improving one trait at a time (Lemerle et al. 1996) or trying to define competitive response solely on the basis of yield (Cousens et al. 2003a; Lemerle

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et al. 2006). Alternatively, indirect selection for competitive ability through the selection of known competitive traits has been suggested for upland rice (Zhao et al. 2006c). Selection for these traits in a weed free environment may result in the improvement of competitive ability in a weedy environment (Zhao et al. 2006a). There may be certain traits which can not be directly measured in a competitive environment, but would still offer a competitive advantage in weedy situations. For example, improved light interception (*i.e.* reduced percent transmittance) may provide a competitive advantage to crops (Harbur and Owen 2004). Measuring such a trait in a dense weedy canopy may be biased (Park et al. 2003).
The negative relationship between yield and competitive ability and decreased heritability estimates from increased environmental variation, suggest that selection should not be done in naturally weedy environments (Fasoula and Fasoula 1997). However, Huel and Hucl (1996) reported that specific breeding lines which yielded the highest without competition from weeds are not necessarily the highest yielding under competition from weeds. Further to this, ranking wheat cultivars for weed competitive ability may be inconsistent between sites due to site-specific yield limitations and weed density (Lemerle et al. 2001b; Vandeleur and Gill 2004). Despite rank changes between sites, weed-free grain yield may be the best predictor of wheat grain yield under weedy conditions (Cousens and Mokhtari 1998).

The objective of the present study was to determine if genetic parameters associated with competitive ability in spring wheat differed when grown with and without a controlled competitive weed treatment.

2.2 Materials and Methods

2.2.1 Plant Material

One hundred and eight random recombinant inbred lines (RILs) from the International Triticeae Mapping Initiative (ITMI) mapping population, provided by Dr. C. O. Qualset (University of California, Davis), and 12 check cultivars (Table 2-1) were used in this study. The ITMI population was established in 1989 with the goal of developing linkage maps for the major Triticeae species (Sorrells

et al. 2005) This population came from a cross between a conventional hexaploid wheat ('Opata 85'= Bluejay / Jupateco F 73) and a synthetic hexaploid wheat accession W7984. The synthetic hexaploid wheat is an amphiploid developed from a cross between the tetraploid Mexican durum wheat cultivar 'Altar 84' (*Triticum turgidum*) and an accession of diploid goat grass *Aegilops tauschii* (Coss.) Schmal. (Song et al. 2005). The population is genetically diverse for many agronomic traits and has been used to investigate wheat quality traits (Nelson et al. 2006), tillering, growth habit, spike morphology, gross morphology (Li et al. 2002), heading, maturity, plant height, leaf color (Kulwal et al. 2003), as well as many diseases and pests (Friesen and Faris 2004; Sardesai et al. 2005; Zwart et al. 2006). Several of these traits are thought to contribute to competitive ability (Lemerle et al. 2001a).

2.2.2 Experimental Design

The population was grown at two sites in each of two years (2005 and 2006) with two competition treatments in two replications per site. In 2005, the experiment was grown at the University of Alberta Edmonton Research Station (ERS), Edmonton, Alberta, Canada (53° 34′ N, 113° 31′ W), (Michener field) and the University of Alberta Ellerslie Research Station, located 10 km south of ERS. The Ellerslie site was planted on May 25th 2005, 15 days later than the Michener site. In 2006, the experiment was grown on two different fields at the ERS (Michener and W240 fields, 1 km distance). The Michener site was planted on May 29th 2006, 13 days later than the W240 site. Soil at all sites is classified as a Black Chernozem which is typical of central Alberta (Alberta Agriculture Food and Rural Development 2002). Granular fertilizer (11-52-0: N-P-K) was banded with the seed, during sowing, at a rate of 140 kg ha^{-1}. Competition ranges were cross seeded with 'Grizzly' tame oats (McKenzie and Harder 1995) at a rate of 60 seeds m^{-2}, with no additional fertilizer placed with the oats. Broad leaf weeds were controlled, in both treatments, using a commercial mixture of dicamba + MCPA (Dyvel®, BASF Canada, Mississauga, ON.) at a rate of 92 and 397 g ai ha^{-1}, respectively.

A nested split plot randomized complete block design with two replications was used at each site. Each replication consisted of eight ranges of 30 subplots, where four of the ranges were cross seeded with tame oats and four were not (main plot). Within each replication, 20 subplots (10 subplots each over two ranges), formed 12 incomplete blocks which were later employed in statistical modelling to adjust for within-replication environmental variation. Subplots consisted of two rows of wheat, two meters long, 22.5 cm apart, planted at a rate of 250 seeds m^{-2}. Individual subplots were separated within ranges by an empty crop row, while ranges were separated by a two-meter pathway.

2.2.3 Data Collection

Data recorded for each subplot included early season vigour, plant height, number of spikes m^{-2}, grain yield, harvest index, and days from seeding to heading, anthesis, and physiological maturity. Proportion of light captured was recorded for the non-competition treatment only and oat grain yield was recorded for the competition treatment.

Early season vigour was rated visually at the 3 to 4 leaf stage, which is Zadok's growth stage 13 to 14 (Zadoks et al. 1974), using a 1 to 5 scale based on plant leaf size, number, and overall plant growth habit, with 1 being the least vigorous and 5 the most (Mason et al. 2007b). Spikes m^{-2} was determined by counting fertile stems from a 0.5 m length of the two subplot rows. Days to heading was recorded when approximately 75% of the plants in a subplot had spikes emerged from the boot. Likewise, days to anthesis was recorded when 75% of the plants had anthers extruded. Physiological maturity was determined visually as the number of days from seeding to when 75% of the peduncles in a subplot had lost green color.

A 0.5 m length of the two crop rows was cut near ground level after physiological maturity and each plot was collected into labelled cotton bags. Both wheat and oats were cut and collected in the weed competition treatment. Samples were dried, weighed and threshed to calculate harvest index and yield. Samples from

the weed competition treatment were first separated by crop before weighing and threshing each crop.

Photosynthetically active radiation (PAR) levels were recorded for the non-competition subplots using a LI-COR LI-191SA Line Quantum Sensor (LI-COR Biosciences, Lincoln, Nebraska). After heading was complete, from Zadok's growth stages 58 to 69 (Zadoks et al. 1974), the sensor was held level between the two rows at ground level and above the subplot with PAR recorded in μmol s^{-1} m^{-2}. The proportion of light captured was calculated as:

$$Light\ Captured = 1 - \frac{PAR\ Below\ Canopy}{PAR\ Above\ Canopy} \quad (1)$$

2.2.4 Data Analyses

All data were analysed using the mixed procedure of SAS v9.1 (SAS Institute 2003). Each environment (site × year) was subjected to analysis of variance in the mixed model by considering competition as fixed effect and genotype and genotype × competition as random effects. All multi-location-year data were then subjected to a combined analyses of variance as a mixed model by considering competition as the fixed effect and genotype, environment, genotype × competition, genotype × environment, competition × environment, genotype × competition × environment, rep(environment), and incomplete-block(rep × environment) as random effects. Best linear unbiased predictions (BLUPS) were then estimated for genotype × competition, across environments, using the estimate statement in the mixed procedure (Littell et al. 2006).

These BLUP values were used to calculate population means, 95% confidence limits, and observed response to a 10% selection intensity for each environment. The observed response to selection was estimated as the difference between the mean of the selected lines and the population mean. Significance between the two means was determined using proc TTest in SAS (SAS Institute 2003). Least-square mean values of genotype × competition were calculated for the check cultivars for comparison of means, and 95% confidence limits. The terms in the model were the same for the check cultivars as for the random

genotypes, except genotype and genotype × competition were considered fixed effects for the check cultivars.

For analyses requiring a separation of competition treatments (heritabilities, and genetic correlations) a random model of genotype, genotype × environment, rep(environment), and incomplete-block(rep × environment) was used. Random effects estimated to have zero variance were removed from the model for the specific trait being analysed.

Broad sense heritabilities were then estimated for each trait across environments, with and without competition, using:

$$H = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2 + \sigma_e^2} \tag{2}$$

where σ_G^2, σ_{GE}^2, and σ_e^2 are the genotype, genotype × environment, and error variances, respectively. The standard errors of the heritabilities were calculated using the delta method (Holland et al. 2003). Expected genetic gain was estimated as:

$$R_e = iH\sigma_P \tag{3}$$

where σ_P is the phenotypic standard deviation, *H* is the broad sense heritability and *i* is the selection intensity (1.755 for 10% selection), (Falconer and Mackay 1996).

Genetic correlations were calculated for all traits within and between competition treatments using:

$$r_{Gij} = \frac{Cov_{Gij}}{\sigma_{Gi}\sigma_{Gj}} \tag{4}$$

(Bernardo 2002), where r_{Gij} is the genetic correlation between the *i*th and *j*th traits, Cov_{Gij} is the genotypic covariance between the *i*th and *j*th traits, σ_{Gi}, and σ_{Gj} are the genetic standard deviations of the *i*th and *j*th traits, respectively. Environmental correlations were calculated within and between competition treatments using environmental variance and covariance in equation four. Variance and covariance were estimated using restricted maximum likelihood in the mixed procedure, and the standard errors of the correlations were calculated

via the delta method (Holland 2006). For each correlation, 95% confidence intervals were constructed as $r_{gij} \pm z_{(0.05)}\sigma_e$ where r_{gij} is the correlation coefficient, $z_{(0.05)}$ is the ordinate of the standard normal distribution such that the area under the curve from $-\infty$ to $z_{(0.05)}$ equals $1-0.05$, and σ_e is the standard error of the correlation. Correlations were considered significantly different from zero if the confidence interval did not include zero (Holland et al. 2003). The differences between correlation coefficients of interest were considered significant where

$z_{(0.05)} < (r_1 - r_2)/\sigma_{r1-r2}$ (Zar 1996).

2.3 Results

The check cultivars, on average, yielded 22-30 % more grain, had greater early season vigour, and flowered and matured earlier ($P < 0.05$) than the experimental population (Table 2-2). The presence of a cultivated oat weed analogue in the experimental population furnished an adequate selection screen as a competition treatment, in that the weed analogue treatment reduced grain yield (1.64 t/ha), spikes m^{-2} (25%) and days to maturity (2 d) ($P < 0.05$) in the random population (Table 2-2).

Heritability estimates were similar ($P > 0.05$) with and without weed competition for all recorded traits except plant height ($P < 0.01$) (Table 2-2). Observed response to a 10% selection intensity differed ($P < 0.05$) from the population mean for all measured traits, in both treatments. Observed response to selection was greater ($P < 0.01$) in the weed free treatment for grain yield, spikes m^{-2}, early season vigour, days to heading and grain fill duration. As well, environmental correlations between competition treatments for grain yield, spikes m^{-2}, early season vigour, and harvest index were all strong ($r > 0.7$) (Table 2-3).

For the genetic correlations, grain yield and spikes m^{-2} were not related to early season vigour in the weed-free treatment ($P>0.05$), but were in the weed analogue treatment ($P < 0.01$) (Table 2-4). The proportion of light captured was positively related to grain yield, plant height, and spikes m^{-2}, but not to early

season vigour. Oat grain yield was negatively related to wheat grain yield and spikes m^{-2}, but the correlation was stronger ($P < 0.05$) in the weed analogue treatment. Flowering times were also negatively related to grain yield and spikes m^{-2} in the presence of oats, but not in the weed free treatment ($P < 0.01$) (Table 2-5).

The population genotypes were ranked for all recorded traits in both competition treatments. There was very little rank change for plant height, early season vigour, grain fill duration, and days to maturity in the top 10% of ranked lines (Figure 2-1). Many of the highest yielding lines in the non competitive treatment also yielded highly under competition, and though there was some genotypic rank change, the two highest yielding lines were the same for both competition treatments (Figure 2-1). However, lines with the lowest oat grain yield were not among the top 10% of lines for yield.

2.4 Discussion

The check cultivars in this study yielded higher, tillered more, and flowered earlier than the ITMI recombinant inbred line population. This was expected because many of the check cultivars used are locally adapted while the ITMI population is not. Even so, the heritability estimates we report are the same between competition treatments for all traits except plant height. These results differ from those of Fasoula and Fasoula (1997) and Zhao et al. (2006b) who report decreased heritability estimates under competition. For yield, the actual yield of the recombinant inbred line population, and subsequent selection response, was lower under competition than in the weed free treatment, but the percent increase was higher.

The similar ranking of lines, and the similar heritability estimates, suggests that selection in a weed free environment may provide advancement in a weedy environment. The use of a weed free environment for selection has been suggested for rice (Zhao et al. 2006c). However, while there was some overlap in selected lines, our results suggest that the use of a weed free environment would result in discarding some lines which yielded better under competition.

The complexity of competitive ability itself does not allow for direct selection as it cannot be explained by a single trait (Lemerle et al. 1996). Oat competition in this experiment reduced wheat yield, which has been reported previously (Harker 2001). Defining competitive ability as decreased yield loss under weedy conditions puts breeding for it on familiar ground, *i.e.* single trait selection, without removing the possibility for weed suppression (Huel and Hucl 1996; Lemerle *et al*. 2001b). However in this study, the top two yielding lines were the same for both treatments, but these lines were not among the top 10% of lines for reduced oat yield.

We found a strong negative relationship between wheat grain yield and oat grain yield, but the correlation alone does not provide an explanation of the underlying mechanisms involved (Fasoula and Fasoula 1997; Mason and Spaner 2006). Light capture is considered an important aspect of competitive success with other competitive traits often related to the increased capture of light (Coleman et al. 2001; Cousens et al. 2003b; Harbur and Owen 2004). In this study, light capture measured in the weed free treatment was negatively related to oat grain yield, suggesting that lines able to capture more light may be more competitive. Measuring light capture in a weedy environment is not practical (Park et al. 2003), but the trait, though difficult to measure directly, can still confer a competitive advantage (Harbur and Owen 2004).

Tillering capacity is one of the more plastic traits in wheat, and genotypes with a higher tillering capacity are considered more competitive (Hucl and Baker 1993) though this is still debated (Mason et al. 2007a). We found a positive relationship between spikes m^{-2} and grain yield under competition and negative relationship between spikes m^{-2} and oat yield. Interestingly, early season vigour was related to increased wheat grain yield and spikes m^{-2} under competition only and also negatively related to oat grain yield. Rapid early growth is associated with competitive ability (Huel and Hucl 1996; Lemerle et al. 2001a). The near simultaneous emergence of the oats and wheat in this study may highlight the importance of early season vigour to wheat competitive ability, because cultivated oats have a high suppressive ability during early growth (Seavers and Wright

1999). Rapid early growth in wheat could increase light capture, conferring a competitive advantage (Coleman et al. 2001, Harbur and Owen 2004), but a relationship between rapid early growth and light capture was not observed in this study.

In addition, we found the flowering times and maturity of wheat were negatively correlated with wheat grain yield under competition and positively correlated with oat grain yield. Early maturing wheat has been correlated with increased yield in competitive organic farming systems (Mason et al. 2007b) and early heading associated with competitive ability (Huel and Hucl 1996). Flowering in wheat is influenced by photoperiod, vernalization, and earliness *per se* genes (Iqbal et al. 2006). Cousens et al. (2003a) reported reduced time to flower did not increase competitive ability. This study supports the idea of early maturing wheat aiding in both the suppressive and tolerant aspects of competitive ability in wheat, but how flowering times assist in the suppression of weeds is still not clear (Mason et al. 2007a).

In this study similar heritability estimates between competition treatments suggest that selection in a weed free environment can lead to improvements in a weedy environment, but some high yielding lines under competition would be eliminated during selection. Use of a weed free environment allows for the selection of traits which cannot be measured in a weedy environment, *e.g.* light capture. Early season vigour and early maturity both help wheat escape the negative effects of weed pressure in a northern grain growing region. Our study is somewhat limited as it cannot be related to field scale crop competitive conditions, due to the small plot size employed. A similar study using a population derived from locally adapted cultivars employing a larger plot size is warranted.

2.5 Tables and Figure

Table 2-1: Check cultivars employed and their attributes of interest / reason for their inclusion in this study.

Variety	Attributes of Interest[z] / Reason for Inclusion
Opata	Bread wheat parent in original ITMI population cross
M6	Synthetic parent in original ITMI population cross
Attila	Semi-dwarf, high yield, CIMMYT cultivar (CIMMYT 2008)
AC[x] Barrie	Tall, high yield, Canadian hard red spring wheat[y] (McCaig et al. 1996)
CDC[w] Go	Semi-dwarf, early, high yield, Canadian hard red spring wheat (Hucl 2003)
AC Intrepid	High yield, early, Canadian hard red spring wheat (DePauw et al. 1999)
McKenzie	Tall, high tillering, Canadian hard red spring wheat (Graf et al. 2003)
Park	Tall, commonly used in organic production systems, early maturing, Canadian hard red spring wheat (Kaufmann and McFadden 1968)
Saar	Taller semi-dwarf, high tillering, CIMMYT bread wheat
Sapphire	Semi-dwarf, low tillering, late maturing, New Zealand bread wheat
AC Splendor	Tall, low tillering, Canadian hard red spring wheat (Fox et al. 2007)
Superb	High yield, Semi-dwarf, Potentially competitive, Canadian hard red spring wheat (Secan 2006)

[z] Attributes such as yield potential, tillering capabilities, maturity characters of the cultivars were determined previously by our research group over various studies.

[y] For a discussion of the attributes of Canada hard red and Canada prairie spring wheat see (CGC 2007)

[x] AC: Agriculture Canada

[w] CDC: Crop Development Center, University of Saskatchewan, Saskatoon SK Canada

Table 2-2: Mean values, 95% confidence intervals (CI), estimates of heritability and selection response (SR) for 10 traits measured on 108 lines of the ITMI population and on 12 spring wheat check cultivars grown in four environments with (C) and without (N) weed analogue competition during 2005-2006. Treatment means, heritabilities, and selection response were tested for equality between treatments using T-tests.

		Non-Competition		Competition		Heritability Estimates		SR_e[z]		SR_o[z]	
Variable		Mean	95% CI	Mean	95% CI	N[y]	C	N	C	N	C
Grain Yield (t/ha)	Lines	4.87**	0.18	3.23**	0.15	0.42 (0.05)[x]	0.42 (0.05)	1.22	0.77	1.73**	1.31**
	Checks	6.25**	0.58	4.62**	0.37	–[w]	–	–	–	–	–
Height (cm)	Lines	79	1.2	81	1.2	0.73 (0.03)**	0.58 (0.04)**	10	8	11	11
	Checks	81	5.2	81	4.4	–	–	–	–	–	–
Spikes m^{-2} (n)	Lines	446**	9.0	335**	8.0	0.33 (0.04)	0.29 (0.04)	53	42	84**	75**
	Checks	557**	69.1	471**	43.7	–	–	–	–	–	–
Early Season Vigour	Lines	3.3	0.1	3.2	0.1	0.42 (0.05)	0.47 (0.05)	0.6	0.7	0.9**	0.8**
	Checks	4.2	0.2	4.1	0.3	–	–	–	–	–	–
Days to Heading	Lines	54	0.7	54	0.7	0.91 (0.01)	0.90 (0.01)	-6	-6	-5**	-6**
	Checks	51	1.5	50	1.5	–	–	–	–	–	–
Days to Anthesis	Lines	57	0.7	57	0.7	0.89 (0.02)	0.84 (0.02)	-6	-6	-5	-5
	Checks	54	1.6	53	1.7	–	–	–	–	–	–
Days to Maturity	Lines	100*	1.0	98*	1.0	0.77 (0.03)	0.78 (0.03)	-8	-7	-9	-8
	Checks	95	3.6	94	3.5	–	–	–	–	–	–
Grain Fill Duration (days)	Lines	42**	0.5	41**	0.4	0.44 (0.05)	0.31 (0.05)	3	2	5**	4**
	Checks	41	2.3	41	2.1	–	–	–	–	–	–
Harvest Index	Lines	0.42	0.01	0.42	0.01	0.40 (0.04)	0.39 (0.05)	0.07	0.06	0.11	0.11
	Checks	0.52	0.03	0.51	0.02	–	–	–	–	–	–
Proportion of Light Captured	Lines	0.86	0.01	–	–	0.24 (0.05)	–	0.05	–	0.08	–
	Checks	0.86	0.06	–	–	–	–	–	–	–	–
Oat Grain Yield (t/ha)	Lines	–	–	1.65	0.06	–	–	–	–	–	–
	Checks	–	–	1.09	0.17	–	–	–	–	–	–

*,** Significant at P = 0.05 and P = 0.01 respectively (T-Test).

[z] SR_e: expected response from 10% selection; SR_o: observed response from 10% selection;

[y] N: Non-competitive treatment. C: Competitive treatment.

[x] Standard error of the heritability estimate

[w] Dashes: Not estimated

Table 2-3: Environmental correlations (r_{env}) between treatments for traits measured in both treatments.

Trait	r_{env}
Grain Yield	0.74
Plant Height	0.96
Spikes m-2	0.79
Early Season Vigour	0.95
Harvest Index	0.76
Days to Heading	0.99
Days to Anthesis	0.99
Days to Maturity	0.97
Grain Fill Duration	0.90

Table 2-4: Genetic correlations ($P < 0.05$) made within and between competitive treatments for six agronomic traits measured on 108 lines of the ITMI population for four locations in Alberta, Canada.

		Grain Yield		Plant Height		Spikes m^{-2}		Early Season Vigour		Harvest Index		Light Capture
		N[z]	C	N	C	N	C	N	C	N	C	N
Plant Height	N	0.31	0.31									
	C	0.29	0.26									
Spikes m^{-2}	N	0.42	0.42	NS[y]	NS							
	C	0.43	0.61	NS	NS							
Early Season Vigour	N	NS	0.44	NS	NS	NS	0.61					
	C	NS	0.48	NS	NS	NS	0.68					
Harvest Index	N	0.75	0.65	NS	NS	NS	NS	NS	NS			
	C	0.66	0.57	-0.24	-0.24	NS	NS	NS	NS			
Light Capture	N	0.67	0.47	0.53	0.45	0.77	0.38	NS	NS	NS	NS	
Oat Grain Yield	C	-0.33	-0.75	-0.24	NS	-0.36	-0.89	-0.77	-0.78	NS	NS	-0.58

[z] N: Non-competitive treatment. C: Competitive treatment.
[y] NS: Not significantly different from zero ($P = 0.05$)

Table 2-5: Genetic correlations made within and between competitive treatments using the 108 lines of the ITMI population for four locations in Alberta, Canada. Six agronomic traits and oat grain yield are correlated to flowering times and grain fill duration.

		Days to Heading		Days to Anthesis		Days to Maturity		Grain Fill Duration	
		N[z]	C	N	C	N	C	N	C
Grain Yield	N[z]	NS[y]	NS	NS	NS	NS	NS	NS	NS
	C	-0.33	-0.35	-0.39	-0.38	-0.27	-0.35	NS	NS
Plant Height	N	0.33	0.34	0.26	0.30	0.30	0.28	0.25	NS
	C	0.32	0.32	0.25	0.28	0.27	0.25	0.22	NS
Spikes per m^2	N	NS	NS	NS	NS	NS	NS	NS	NS
	C	-0.56	-0.57	-0.62	-0.62	-0.54	-0.61	-0.29	-0.41
Early Season Vigour	N	-0.84	-0.85	-0.86	-0.86	-0.83	-0.9	-0.57	-0.71
	C	-0.86	-0.88	-0.86	-0.85	-0.89	-0.93	-0.67	-0.79
Light Capture Oat Grain Yield	N	0.44	0.42	0.30	0.30	0.36	0.36	NS	NS
	C	0.64	0.66	0.70	0.69	0.60	0.64	0.30	0.32

[z] N: Non-competitive treatment. C: Competitive treatment.
[y] NS: Not significantly different from zero (P = 0.05)

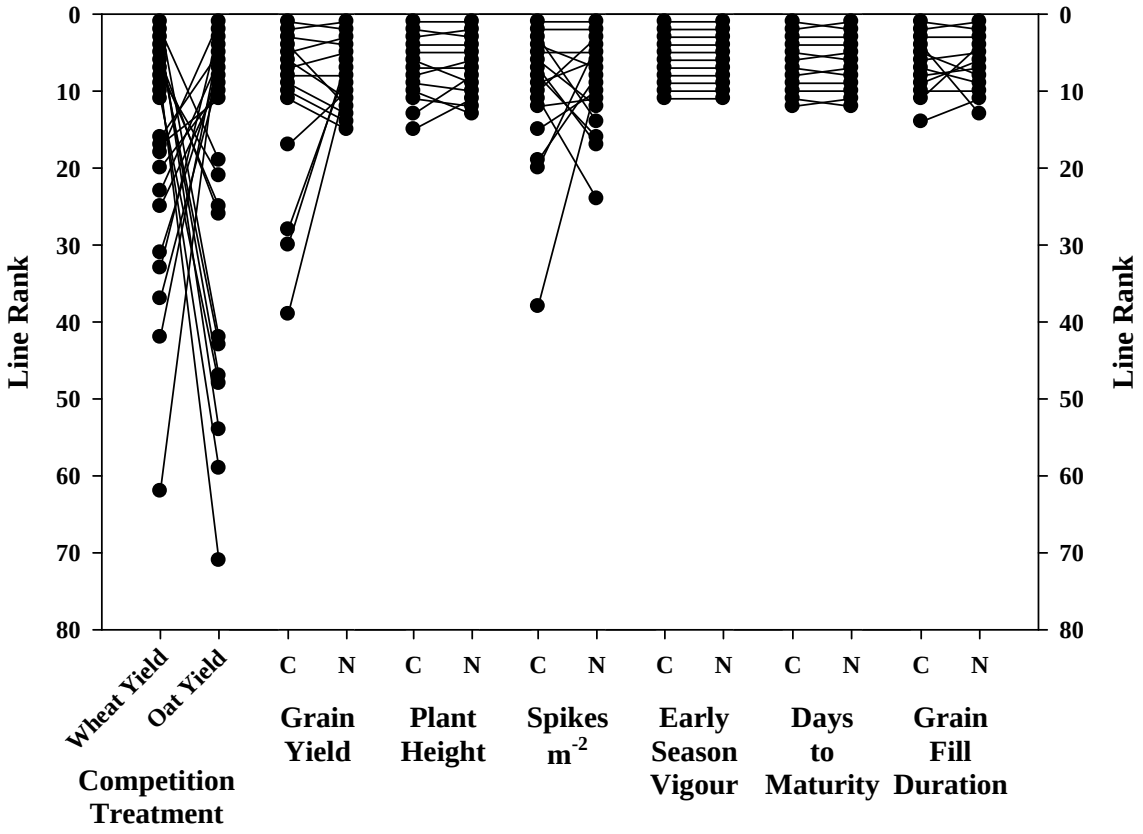

Figure 2-1: Genotypic ranks changes observed in the top 10% of lines ranked under each treatment condition (C: Competitive treatment N: Non-competitive treatment) for selected traits measured in both treatments and between wheat yield and oat yield suppression in the competition treatment. Rank was assigned according to the desired direction of selection (*e.g.* rank one for grain yield was the highest yielding whereas rank one for oat yield was the lowest yielding)

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3.0 Genetic evidence of a relationship between earliness and competitive ability in wheat.

3.1 Introduction

Competition from weeds reduces crop yields. A species that achieves greater biomass in an early growth stage will be a better competitor throughout the growing season (Cousens et al. 2003). Fast growing plants can make use of available water and nutrients before a slower growing competitor. Rapid leaf development also ensures a large crop canopy, providing greater photosynthetic area, and can shade younger competing species (Lemerle et al. 2001).

Early flowering and early maturity are important goals for wheat breeders in high latitude grain growing regions (Iqbal et al. 2007a). In such regions, earliness helps wheat escape droughts during grain fill and late summer frosts (Iqbal et al. 2007b). Early maturity is related to increased wheat yield in competitive organic farming systems (Mason et al. 2007). Using tame oats (*Avena sativa* L.) as a weed analogue, we found oat grain yield was lower in early maturing spring wheat lines and there was a genetic correlation (0.64) between increased time to maturity and increased oat grain yield (Reid et al. 2009).

Quantitative trait loci (QTL) analysis links phenotypic and genotypic data, and is a reliable statistical tool in studying the genetic mechanism underlying complex traits. Molecular markers that are linked to a QTL influencing the trait of interest will be associated more frequently with the data on the trait. Unlinked markers will not show statistically significant association with the phenotype. Coleman *et al.* (2001) identified QTL for competitive traits in wheat, and related them to weed dry matter at maturity, but they did not identify QTL specifically associated with the suppression of weeds. The purpose of this study was to detect QTL associated with competitive ability in wheat in a northern grain growing region.

3.2 Materials and Methods

One hundred and eight random recombinant inbred lines (RILs) from the International Triticeae Mapping Initiative (ITMI) mapping population, provided

by Dr. C. O. Qualset (University of California, Davis) were employed in this study. This population is derived from a cross between a Mexican hexaploid wheat ('Opata 85'= Bluejay / Jupateco F 73) and a synthetic hexaploid wheat (*Triticum aestivum* L.) cultivar accession W7984 (Song et al. 2005). The synthetic hexaploid wheat is an amphiploid developed from a cross between the tetraploid Mexican durum wheat cultivar 'Altar 84' (*Triticum turgidum*) and an accession of diploid goat grass (*Aegilops tauschii* (Coss.) Schmal.) (Song et al. 2005).

The population was grown at two sites in each of two years (2005 and 2006) with two replications (rep) per site. In 2005, the experiment was grown at the University of Alberta Edmonton Research Station (ERS), Edmonton, Alberta, Canada (53° 34′ N, 113° 31′ W), (Michener field) and the University of Alberta Ellerslie Research Station, located 10 km south of ERS. The Ellerslie site was planted on May 25th 2005, 15 days later than the Michener site. In 2006, the experiment was grown on two different fields at the ERS (Michener and W240 fields, 1 km distance). The Michener site was planted on May 29th 2006, 13 days later than the W240 site. Soils at all sites are classified as Black Chernozems, which is typical of central Alberta (Alberta Agriculture Food and Rural Development 2002). Granular fertilizer (11-52-0: N-P_2O_5-K_2O) was banded with the seed, during sowing, at a rate of 140 kg ha^{-1}. Competition was created through the use of a weed analogue. Specifically, 'Grizzly' tame oats (*Avena sativa* L.) (McKenzie and Harder 1995) was cross seeded at a rate of 60 seeds m^{-2}, with no additional fertilizer placed with the oats. Broad leaf weeds were controlled using Dyvel® (BASF Canada, Mississauga, ON.) at a rate of 1.1 L ha^{-1}.

A randomized incomplete block design with two replications was used at each site. Each replication consisted of four ranges of 30 plots. Within each replication, groups of 10 plots (three groups per range) formed 12 incomplete blocks which were later employed in statistical modelling to adjust for within-replication environmental variation. Plots consisted of two rows of wheat, two meters long, 22.5 cm apart, planted at a rate of 250 seeds m^{-2}. Individual plots were separated within ranges by an empty crop row, while ranges were separated by a two-meter pathway. Data collected from the population included early season

vigour, oat grain yield, and days to heading, anthesis, and maturity, in addition to a number of other agronomic traits. Quantitative genetic population parameters (apart from QTL analyses), including heritability, and genetic and environmental correlations have, been reported elsewhere (Reid et al. 2009)

Early season vigour was rated visually at the 3 to 4 leaf stage, (Zadok's growth stage 13 to 14) (Zadoks et al. 1974), using a 1 to 5 scale based on plant leaf size, number, and overall form (with 1 being the least vigorous) (Mason et al. 2007). Days to heading, anthesis, and maturity were recorded when approximately 75% of the plants in a subplot had spikes emerged from the boot, anthers extruded, and a loss of green color in the peduncle, respectively.

All data were analysed using the mixed procedure of SAS (SAS® Institute 2003). Each environment (site × year) was subjected to analysis of variance in a random model

$$P_{ijk} = \mu + G_i + R_j + B_k(R_j) + \varepsilon_{ijk} \quad (1)$$

where P_{ijk} is the measurement taken, μ is the grand mean, and G, R, B, and ε refer to genotype, replicate, incomplete block, and error respectively. All multi-location-year data were then subjected to a combined analysis of variance in a random model

$$P_{ijklm} = \mu + G_i + Y_l + GY_{il} + S_m(Y_l) + R_l(SY_{ml}) + B_k(RSY_{jml}) + \varepsilon_{ijklm} \quad (2)$$

where Y and S refer to year and site respectively. Best linear unbiased predictions (BLUPS) were then estimated for genotype across all environments and for each year across sites using the estimate statement in the mixed procedure (Littell et al. 2006).

Mapping data for the ITMI population was obtained from the GrainGenes database (Graingenes 2.0 2008). The map consists of 1410 loci and includes 222 microsatellite markers giving an average of one marker every 2.8 cM (Song et al. 2005). Allelic frequencies for each marker genotype were tested against the expected 0.5 frequencies using Chi square, and markers showing segregation distortion ($P < 0.05$) were removed, resulting in 1229 markers used. All QTL analyses were completed in R/QTL version 1.08-56 (Broman et al. 2003), using the Haley-Knott regression method (Haley and Knott 1992). The BLUPs of the

phenotypes were then used to locate QTL. Genome wide analyses (using interval mapping) were employed, followed by a chromosome specific (5A) interval mapping analyses. Genome wide composite interval mapping was then performed with one covariate, large effect QTL detected from the previous analysis, were then selected for each phenotype to determine if any smaller effect QTL were being masked. Log of odds (LOD) threshold levels were determined empirically for each phenotype using 1000 permutations (Churchill and Doerge 1994).

To estimate the proportion of the genetic variance explained by each peak detected, the genotype effect from eq. (2) was partitioned into a component due to marker *(M)*, and residual genetic variation among genotypes (*G(M)*), changing the model to:

$$P_{ijklmn} = \mu + M_n + Y_l + MY_{nl} + G_i(M_n) + G_i(MY_{nl}) + S_m(Y_l) + R_l(SY_{ml}) + B_k(RSY_{jml}) + \varepsilon_{ijklmn} \quad (3)$$

Variance components in this model were estimated using the REML option in PROC VARCOMP of SAS (SAS® Institute 2003).

3.3 Results and Discussion

Flowering times, early season vigour and weed suppression QTL were all detected in a similar region (65-89 cM) on chromosome 5A (Table 1). The peak for weed suppression accounted for 56% of the genetic variance overall (Table 1). Multiple peaks occurred in interval mapping (Figure 1), however only single peaks were detected through composite interval mapping of chromosome 5A. The QTL for flowering times and weed suppression all had negative additive effects; these QTL decrease flowering times and result in weed suppression. This region also contains Vrn-A1 (Galiba et al. 1995), but this gene was not segregating in this population and we therefore could not test the influence of this gene directly. Canadian spring wheat cultivars primarily contain Vrn-A1a singly or in combination with Vrn-B1 (Iqbal et al. 2007c) and combinations of Vrn-A1 and Vrn-B1 are preferred in Canada for providing early flowering times in Canadian spring wheat cultivars (Iqbal et al. 2007b). Kirkland and Hunter (1991) reported increased suppression of wild oat grains in an early maturing Canadian

wheat cultivar, ‘Neepawa’ (Campbell 1970). This locally adapted cultivar is known to have the Vrn-A1a gene (Iqbal et al. 2007c). Our research group has found, and reported, earliness was correlated with reduced weed biomass in organic systems in central Alberta, Canada (Mason et al. 2007). In conventional systems, using the same ITMI population, we have reported a genetic correlation of 0.64 between days to maturity of spring wheat and oat grain yield (weed analogue) (Reid et al. 2009). The same study found early season vigour to be negatively related to both days to maturity (-0.90) and oat grain yield (-0.78).

Thus breeding for earliness, a goal of breeders in northern grain growing regions (Iqbal et al. 2007a; McCaig and DePauw 1995), may also improve competitive ability. This study provides genetic support for the idea that cultivars with early flowering and maturity have a competitive advantage in a northern grain growing region, and that this advantage may result in weed suppression. The region of the genome on chromosome 5A in proximity to the Vrn-A1 gene is of interest, but because the ITMI population is not segregating for the gene, further work using a locally adapted population may provide more evidence of this theory.

3.4 Table and Figure

Table 3-1. The additive effect, R^2 values, and proportion of the genetic variance (%) of the QTLs detected on chromosome 5A, from composite interval mapping of the ITMI population, grown in the presence of a weed analogue, for five traits, across environments, for each year, and over both years.

Trait	QTL Interval	Marker Closest to LOD peak	Position of LOD Peak (cM)	Genes in proximity (<20 cM)	2005				2006				Overall			
					LOD*	Add†	R^2	% of σ^2_G	LOD	Add	R^2	% of σ^2_G	LOD	Add	R^2	% of σ^2_G
Early Season Vigour	Xfba190 - Xbarc230	Xrz395	77	*Vrn-A1*‡	4.18	0.38	16	34					4.53	0.47	18	37
	Xfba68-Xbarc319	Xfba68	84	*Vrn-A1*					5.96	0.68	22	26				
Days to Heading	Xfba190 - Xbarc230	Xrz395	77	*Vrn-A1*									4.49	-3.25	17	33
	Xfba68-Xbarc319	Xfba68	84	*Vrn-A1*	5.54	-3.89	21	49	5.64	-3.48	21	47				
Day to Anthesis	Xfba190 - Xbarc230	Xrz395	77	*Vrn-A1*									5.08	-3.47	19	38
	Xfba68-Xbarc319	Xfba68	84	*Vrn-A1*	5.30	-3.74	20	52								
	Xfbb199-Xfba351	Xfbb199	89	*Vrn-A1*					4.49	-3.18	17	36				
Days to Maturity	Xfba190 - Xbarc230	Xrz395	77	*Vrn-A1*					4.83	-4.09	19	34				
	Xfbb199-Xfba351	Xfbb199	89	*Vrn-A1*	3.91	-4.28	13	20					4.00	-4.60	16	23
Weed Suppression	Xfbb255 - Xfba166	Xfbb255	65	*Vrn-A1*	3.61	-0.21	14	64	3.84	-0.28	15	43	3.88	-0.24	15	56

* Log of odds score.
† Additive effect of the QTL
‡ Vrn-A1, vernalization response gene, proximity inferred from known position of gene on other maps

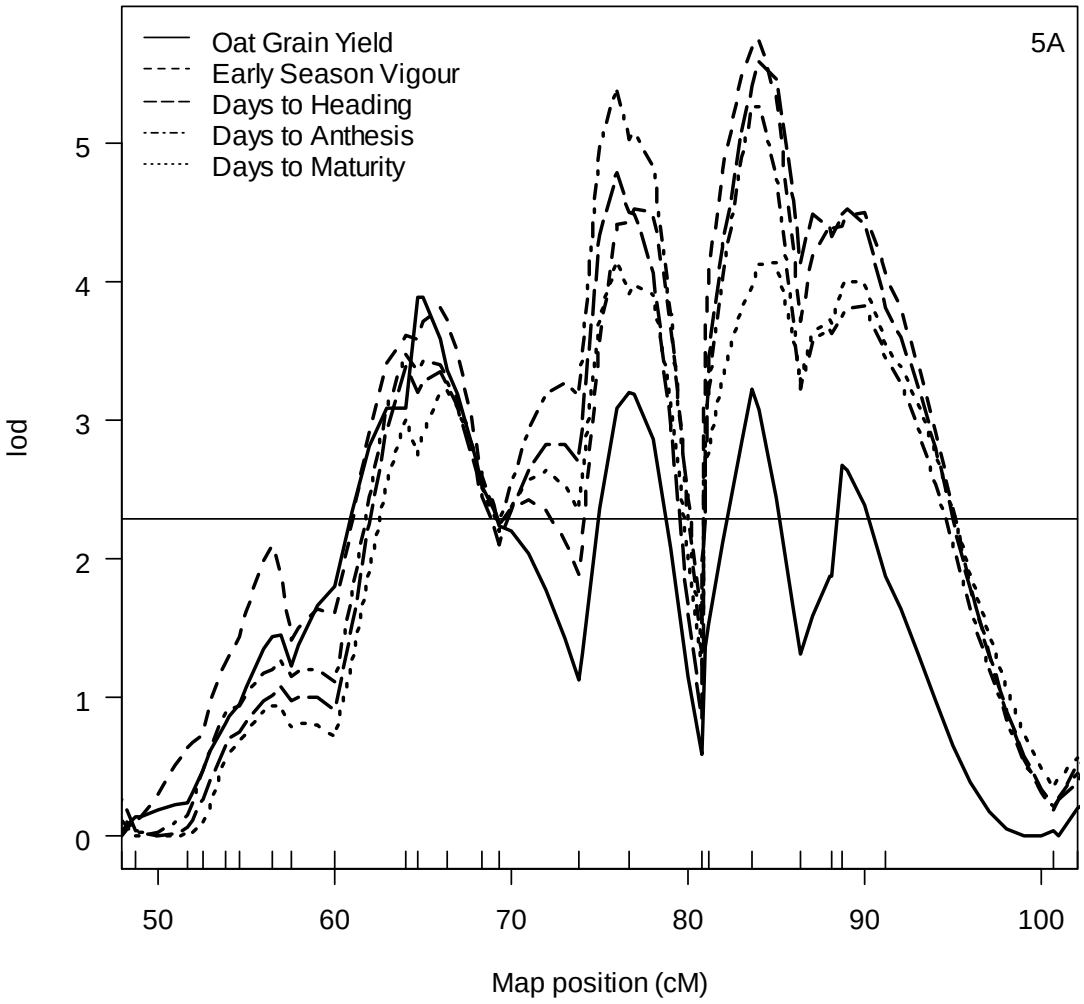

Figure 3-1: LOD peaks of QTLs on chromosome 5A for weed suppression, early season vigour, days to heading, days to anthesis, and days to maturity overall environments in the competition treatment. A 50 cM region of the chromosome is shown, and peaks above the chromosome based LOD threshold (horizontal line) are in the region of *Vrn-A1* (< 20 cM distant).

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4.0 Should spring wheat breeding for organically managed systems be conducted on organically managed land?[2]

4.1 Introduction

The term "organic agriculture" describes production systems that aim to promote and enhance agro-ecosystem health while discouraging the use of off-farm inputs. Globally, interest in organic agriculture is increasing due to concerns over a number of factors, including environmental health, agricultural sustainability, pesticide residues, human health, and input costs. Long term market projections indicate that the North American demand for organic products will continue to grow, eventually overtaking Europe to become the world's largest organic market (Sahota 2006).

Scientific research involving organic production systems is relatively limited. Long-term research relating to soil fertility and biology in various organic cropping systems has been conducted in Europe (Fleissbach et al. 2007; Gosling and Shepherd 2005; Mader et al. 2000), and to a lesser extent in the United States (Harris et al. 1994) and Canada (Entz et al. 2004). Interest in crop breeding and agronomic research for organic production is growing in Canada and the United States. Nonetheless, there are still very few published scientific reports relative to those concerned with conventionally managed cropping systems.

Researchers and farmers often cite weeds as one of the greatest impediments to organic crop production (Barberi 2002; Degenhardt et al. 2005). Studies in Canada and elsewhere have reported higher weed populations, greater aboveground weed biomass, and a greater diversity of weed species in organic cereal crops than in their conventional counterparts (Entz et al. 2001; Leeson et al. 2000; Mason et al. 2007d). In a study of 32 Canadian spring bread wheat (*Triticum aestivum* L.) cultivars, increased weed abundance on organically managed land contributed to grain yield reductions of ~40% compared to yields

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on conventionally managed land (Mason et al. 2007d). Increasing crop competitive ability against weeds could be an effective strategy for controlling weeds and improving crop yields in organic grain production systems (Barberi 2002). Several research trials have found competitive ability to differ among wheat genotypes (Lemerle et al. 2001; Wicks et al. 1986), including cultivars registered in Canada (Huel and Hucl 1996; Mason et al. 2007a).

Several research trials have identified plant traits associated with increased competitive ability in wheat, the most compelling of which may be increased plant height (Cousens et al. 2003; Mason et al. 2007a). In contrast, global wheat breeding efforts over the past 50 years have largely been aimed at increasing grain yield, leading to the introduction of height-reducing (*Rht*) genes and the subsequent development of "semi-dwarf" cultivars. Semi-dwarf wheat cultivars exhibit reduced cell size, contributing to smaller root systems, shorter coleoptile lengths and/or smaller leaf areas than traditional cultivars (Gale and Youssefian 1985; Vandeleur and Gill 2004). Thus, semi-dwarf cultivars may not be well-suited for out-competing weeds. Greater yield losses (Cousens et al. 2003) and less weed suppression (Mason et al. 2007b) have been reported in semi-dwarf wheat cultivars under weed competition compared to conventional height cultivars. In Canada, the use of semi-dwarf wheat cultivars is increasing. The semi-dwarf cultivar Superb (released in 2003, Secan 2006) is currently the most widely grown cultivar, representing close to one fifth of the prairie wheat acreage only three years after its release (CWB 2007).

Other plant traits such as crop biomass, ground cover, flag leaf length, tillering capacity and early season growth have been reported to be associated with competitive ability in wheat genotypes from around the world (Hucl 1998; Huel and Hucl 1996; Lemerle et al. 1996). However, these studies were conducted in controlled environments, where plant responses to competition may differ from natural or native conditions. Our research (conducted on organically managed land in central Alberta) suggests that tall plants, fast early season growth, early heading and maturity, and a greater number of fertile tillers are important competitive plant traits for organic environments; where aboveground

weed biomass is typically higher and soil fertility is more variable (Mason et al. 2007a; Mason et al. 2007d).

The selection of cultivars for low-input and/or organic environments has not been a priority of past breeding programs. Ceccarelli (1996) suggested that breeders justify selection under optimum conditions because greater environmental variability of low-input conditions reduces heritability. Nevertheless, there have been reports of similar rankings for disease resistance and quality traits in conventional and organic cropping trials (Mader et al. 2000; Mason et al. 2007c), and similar heritability estimates between systems in maize (*Zea mays* L.) (Burger et al. 2008).

The reduction in environmental variability through the wide-spread use of chemical inputs means individual cultivars can be successful over a large geographic area (Wolfe et al. 2008). In a review, Wolfe et al. (2008) report that the selection of some traits are similar between organic and conventional breeding programs, but some more complex traits are specific to organic management. For example, Baresel et al. (2008), reported genetic variability in the nitrogen use efficiency of winter wheat. They suggested that cultivars with improved nitrogen uptake during early growth stages, and subsequent efficient translocation, would be more adapted to the timing of nitrogen mineralization on organically managed soils.

Banziger and Cooper (2001) suggested that cultivars developed through formal crop breeding have not been adopted for low-input conditions because few programs have focused on low-input conditions. They further reported that optimally managed on-station experimental trials may be used for assessing highly heritable qualitative traits such as grain size, texture, color or maturity, but that they would not be useful for most quantitative traits (hence most important agronomic traits) affected by genotype by environment interactions. Our initial studies (eg. Mason et al. 2007d) provide some evidence of the existence of genotype by environment interaction between organic and conventional conditions.

The applicability to organic agriculture of trials conducted under conventional conditions is questionable. Several studies have reported differences in the performance of wheat cultivars in organic and conventional management systems, with some cultivars better suited to organic management in northern North America (Carr et al. 2006; Mason et al. 2007d; Nass et al. 2003). Murphy et al. (2007) reported selecting for yield under organic management resulted in genotypic ranks different from conventional management. Przystalski et al. (2008) reported high genetic correlations between management systems, but the authors identified specific cultivars which exhibited cross-over interactions between systems. They concluded that selection of cultivars should be conducted under conditions which closely match commercial organic farms and should include traits important to organic farmers.

The objective of the present study was to determine if a breeding population of spring wheat exhibited different heritabilities and/or other genetic parameters for agronomic traits under conventionally and organically managed agricultural systems. We were further interested in determining whether selection results would be different between systems.

4.2 Materials and Methods

A randomly derived recombinant inbred population was created from a cross between the spring wheat cultivar AC Barrie and the CIMMYT spring wheat cultivar Attila. AC Barrie is an awnless, high yielding, high protein, hard red spring wheat (CWRS) cultivar (McCaig et al. 1996) and was the most commonly grown spring wheat cultivar on the Canadian Prairies in the 1990s. Results from the Western Canadian cooperative tests show AC Barrie to be lodging resistant, medium height (93 cm), high yielding (4.05 t ha^{-1}) with high protein (14.0%) and average maturity (108 days) (McCaig et al. 1996). Attila is an awned semi-dwarf bread wheat cultivar widely grown in Southeast Asia (Rosewarne et al. 2008). The 2004 CIMMYT international bread wheat trials report Attila to be high yielding (5.34 t ha^{-1}) and semi-dwarf (84 cm) with average maturity for the regions tested (135 days) (CIMMYT 2008). The original

population consisted of 79, F4 derived F6 genotypes, which were advanced to F4 by single seed descent. The population and the two parents were planted in double head rows the year prior in order to multiply seed for experimental use.

The experimental study was conducted from 2005 to 2007 at the University of Alberta Edmonton Research Station (ERS), Edmonton, Alberta, Canada (53º 34' N, 113º 31' W), with the conventionally managed site less than 1 km from the organically managed site. Different areas of each site were used in subsequent years, in keeping with the research station crop rotation. Plots were seeded on May 6th, 5th, and 14th, on the conventional site and on May 30th, June 1st, and May 24th, on the organic site for 2005, 2006 and 2007, respectively. On the conventional site, granular fertilizer (11-52-0: N-P_2O_5-K_2O) was banded with the seed during sowing, at a rate of 140 kg ha^{-1}, and broad leaf weeds were controlled using Dyvel® (BASF Canada, Mississauga, ON.) at a rate of 1.1 L ha^{-1}. No fertilizer or herbicides have been used on the organically managed site since 1999. The four year rotation on the conventional site consisted of canola research plots, field pea, triticale/field pea mixture, and cereal research plots. The three year rotation on the organic site consisted of barley, triticale/field peas, and cereal research plots. Composted dairy manure had been applied to the organic field in the fall of each year prior to the start of this study, but was not applied during the years of the study because soil nutrient levels were adequate according to soil tests performed (optimal in 2006, only nitrogen was marginal in 2007) (data not shown) . Soil at both sites are classified as Black Chernozemics, which is typical of central Alberta (Alberta Agriculture Food and Rural Development 2002). Weather data for Edmonton, for each year, were obtained from the Environment Canada data archive at the conclusion of the study (Environment Canada 2008). Plots were seeded with 250 seeds m^{-2} in a randomized complete block design within management system. In 2005, because of seed limitations, two blocks were grown in the two trials grown that year, and plots were 2 m long by four rows of 23.5-cm row spacing. Three blocks per trial were planted in subsequent years and plot size increased to 6 rows of 4 m length with similar row spacing.

4.2.1 Data Collection

Data recorded for each plot included early season vigour, plant height, number of spikes m^{-2}, grain yield, 1000 kernel weight, kernels $spike^{-1}$, test weight, harvest index, grain protein, flag leaf area, weed biomass, and days from seeding to anthesis, and physiological maturity.

Early season vigour was rated visually at the 3 to 4 leaf stage, (Zadok's growth stage 13 to 14) (Zadoks et al. 1974), using a 1 to 5 scale based on plant leaf size, number, and overall form, with 1 being the least vigorous (Mason et al. 2007d). Spikes m^{-2} was determined by counting fertile stems from a randomly chosen 0.5 m length of the center two plot rows. Grain protein content (%) was determined using Near-infrared Reflectance (NIR) spectroscopy using a Monochromator NIR Systems model 6500 (NIRSystems, Inc., Silver Springs, MD, USA). Flag leaf area was recorded using an LI-3000A portable area meter (LI-COR Biosciences, Lincoln, Nebraska) with five different flag leaves selected at random and the mean area recorded. To estimate weed suppressive ability, weed biomass was sampled at wheat physiological maturity from a 625 cm^2 area of the plot. The weed samples were dried for three days at 50ºC and dry weight was recorded.

The confounding effect of the natural weed population in organic trials meant three traits (leaf area index, mean tip angle, and light capture) were recorded only in conventionally managed trials. Leaf area index and mean tip angle were recorded with an LAI-2000 Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, Nebraska). Photosynthetically active radiation (PAR) was recorded using a LI-COR LI-191SA Line Quantum Sensor (LI-COR Biosciences, Lincoln, Nebraska). The sensor was held in the center of a plot, at ground level and above the canopy, with PAR recorded in μmol s^{-1} m^{-2}. The proportion of light captured was calculated as:

$$Light\ Capture = 1 - \frac{PAR\ below\ canopy}{PAR\ above\ canopy} \qquad (1)$$

Days to anthesis were recorded when 75% of the plants had anthers extruded. Physiological maturity was determined visually as the number of days from

seeding to the point in time when 75% of the peduncles in a plot had lost green color. Grain fill duration was then calculated as the time from anthesis to physiological maturity.

4.2.2 Statistical Analysis

All data were analysed with the mixed procedure of SAS v9.1 (SAS® Institute 2003). The experimental trials were initially analysed separately, with block and genotype considered random. Thereafter, for the purposes of comparing genetic parameters within the two management systems, all 6 site-years (environments) were considered as one experiment. Each year was considered to be a complete block, comprised of replications within each block and the experiment was replicated in time (over years). The data were thus analysed as a split plot, with the fixed effect of management system considered the whole plot, and the random effect of genotype considered the subplot. The data were modeled to:

$$y_{ijk} = \mu + M_i + Y_j + MY_{ij} + G_k + GM_{ik} + GY_{jk}(M_i) + \varepsilon_{ijk} \qquad (2)$$

where M, Y, and G are the management system, year, and genotype, respectively. Only management was considered a fixed effect for the model. The parental cultivars were analysed with the same model, but both management and genotype along with their interaction, were considered fixed effects. For instances where a term resulted in a zero variance estimate, the term was removed from the model. Estimates of variance for the within block replications were always zero and thus are not presented in the model above.

Best linear unbiased predictions (BLUPs) were then estimated for genotype × management, across years, using the estimate statement in the mixed procedure (Littell et al. 2006), and these were used for estimating observed response to selection for the population, and Spearman rank correlations using the Spearman option of the corr procedure in SAS v9.1 (SAS® Institute 2003). Best linear unbiased predictions were also estimated separately for the genotypes for each year and each management system. These BLUPs were used to construct

histograms, which were fitted with a three parameter Gaussian curve, to approximate the population distribution using SigmaPlot 10.0 (Sigmaplot 2006). Heritabilities were estimated for each trait pooled over environments, for both organically and conventionally managed environments separately. The variance components were estimated using:

$$y_{ijk} = \mu + E_i + R_j(E_i) + G_k + GE_{ik} + \varepsilon_{ijk} \quad (3)$$

Broad sense heritability was then calculated on a plot basis using:

$$H = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2 + \sigma_e^2} \quad (4)$$

where σ^2_G, σ^2_{GE}, and σ^2_e are the genotype, genotype × environment, and error variances, respectively. The standard errors of the heritabilities were calculated using the delta method (Holland et al. 2003). Expected genetic gain was estimated as:

$$R_e = iH\sigma_P \quad (5)$$

where σ_P is the phenotypic standard deviation, H is the broad sense heritability and i is the selection intensity (1.755 for 10% selection) (Falconer and Mackay 1996).

Genetic correlations were calculated for all traits within and between competition treatments using:

$$r_{Gij} = \frac{Cov_{Gij}}{\sigma_{Gi}\sigma_{Gj}} \quad (6)$$

(Bernardo 2002), where r_{Gij} is the genetic correlation between the ith and jth traits, Cov_{Gij} is the genotypic covariance between the ith and jth traits, σ_{Gi}, and σ_{Gj} are the genetic standard deviations of the ith and jth traits, respectively. Prior to calculating the correlations, data were standardized within management system and year, to minimize differences in scale between traits (Zar 1996), using:

$$Z = \frac{X_i - \mu}{\sigma} \quad (7)$$

where Z is the standardized data point, X_i is the ith observation, μ and σ is the population mean and standard deviation within each year and management

system. Variance and co-variance were then estimated using restricted maximum likelihood in the mixed procedure, and the standard errors of the correlations were calculated via the delta method (Holland 2006). For each correlation, 95% confidence intervals were constructed as $r_{gij} \pm z_{(0.05)}\sigma_e$ where r_{gij} is the correlation coefficient, $z_{(0.05)}$ is the ordinate of the standard normal distribution such that the area under the curve from $-\infty$ to $z_{(0.05)}$ equals $1-0.05$, and σ_e is the standard error of the correlation. Correlations were considered significantly different from zero if the confidence interval did not include zero (Holland et al. 2003). Results are considered and reported as different only when $P < 0.05$.

4.3 Results

Temperature levels were consistent with normals for the area over the three years of the study. Highest temperatures occurred in late July and early August (Figure 4-1). Water is the major limiting factor for agriculture production in central Alberta and rainfall over the three study years was variable (Figure 4-1), but consistent with normal rainfall patterns. Nevertheless, the month with the highest average rainfall is normally July, which was not the case for any of the years in this study.

On average, the parental genotypes AC Barrie and Attila yielded less grain with greater protein content under organic than under conventional management (Table 4-1). In the conventional system, AC Barrie had similar grain yield, had 30% more spikes m^{-2}, was 15 cm taller and had 10% greater protein content than Attila. In the organic system AC Barrie had 28% greater yield, had similar spikes m^{-2} was 17 cm taller, and had 5% greater protein content than Attila.

Each year on average, the AC Barrie × Attila population yielded less grain under organic than under conventional management ($P < 0.01$). However, in conventional management, the population distributions were narrower, and were less variable over years (Figure 4-2). In 2006, decreased precipitation after planting on the organically managed land created increased weed pressure (data not shown) which reduced wheat growth and yields. In 2007, the organic plots had low weed competition (data not shown) which resulted in increased growth

and yield for the organic wheat. Interestingly, Attila consistently yielded less grain than AC Barrie in organically managed trials while the reverse was true under conventional management. In contrast to grain yield, the population distributions for protein content were similar between systems (Figure 4-3).

Conventionally managed trials, on average, yielded double the amount of grain, and with less recorded weed biomass, than organic trials (Table 4-1). No other traits differed statistically between the systems. The ranges of measured variables tended to be greater in conventional with the exception of harvest index, weed biomass, and flowering times (Table 4-1).

The experimental population exhibited statistically similar heritability estimates for grain yield, kernel spike^{-1}, harvest index, flag leaf area, weed biomass, early season vigour, days to maturity, and grain fill duration under both management systems (Table 4-2). Lower heritability estimates occurred in the organic system for spikes m^{-2}, plant height, test weight, thousand kernel weight, and protein content (Table 4-2). Where the observed response to selection did differ (harvest index, and weed biomass), there was no observed difference in heritability estimates between systems for those traits.

Spearman rank correlations were high between the management systems with grain fill duration showing the lowest correlation (0.56) of the measured traits (Table 4-3). Direct selection in each management system (10% selection intensity) resulted in 50% or fewer lines selected in common for four traits, including grain yield, grain protein, spikes m^{-2}, and grain fill duration (Table 4-3). If the top yielding 8 lines (10 %) of the population were selected from each management system (based on our results) 3 lines would be in common. Selecting the top 12 (15%) and 16 (20%) lines based on yield resulted in 7 and 10 lines in common, respectively. This suggests that selecting in the two management systems would result in large differences between systems for lines retained for further yield trials in a breeding program. The difference in the relative ranking of lines between systems was also large for other agronomically important traits (Table 4-3; Figure 4-4).

Among yield components, grain yield was moderately correlated ($0.4 < r < 0.8$) to 1000 kernel weight in organically managed land. Alternately, in conventionally managed land, grain yield was moderately correlated to kernels spike^{-1} (Table 4-4). Spikes m^{-2} was negatively correlated to kernels spike^{-1} in both systems.

Heritability estimates for weed biomass suppressive ability, and early season vigour did not differ from zero in either conventionally or organically managed systems (Table 4-1). This suggests that the environmental and statistically unaccounted variation in weed biomass suppressive ability and compensation for increased weed biomass was far greater than the genotypic variation to suppress or withstand weed pressure. Perhaps as a result of this, under organic management, weed biomass levels were not correlated to any of the eight measured traits. However, under conventional management, weed biomass levels were negatively correlated with grain yield, plant height, test weight, and flag leaf area (Table 4-5). Days to maturity in organically managed trials was negatively correlated with grain yield, kernels spike^{-1}, and flag leaf area. In conventionally managed trials, the correlations were positive.

Three traits, measured in conventional trials only (leaf area index, mean tip angle, and light capture), were not correlated to grain yield under organic management. However, grain protein in organically managed land was correlated to light capture and leaf area index (Table 4-6).

4.4 Discussion

Our study employed an experimental wheat population at the developmental stage, within a single seed descent breeding program, where a preliminary yield trial would normally occur to select lines for replicated multi-location trials. To the best of our knowledge, there has been no direct comparison of a random recombinant inbred spring wheat breeding population between conventional and organic management in North America.

We found heritability estimates for various agronomic traits were either similar between the two systems or lower in the organic system. This suggests

that, at best, breeding under organic conditions would produce similar genetic gains to conventional breeding. Nevertheless, breeding directly within organically managed systems would result in lower genetic gains than on conventionally managed land for some traits. Burger et al. (2008) reported heritability estimates for yield that were similar between organic and conventional systems for populations of maize. Reduced heritability estimates have been predicted for plants grown in competitive or stressful environments (Fasoula and Fasoula 1997), but there have been exceptions to this under both artificially induced weed competition in spring wheat (Reid, unpublished data) and under imposed drought stress in rice (Bernier et al. 2007).

Direct selection in each management system (up to 20% selection intensity) resulted in 50% or fewer lines selected in common for four traits, including grain yield, grain protein, spikes m^{-2}, and grain fill duration. These four traits also had Spearman rank correlations below 0.80. This suggests that selecting in the two management systems would result in large differences between systems for lines retained for further yield trials in breeding programs. The difference in the relative ranking of lines between systems was also large for other agronomically important traits. Loschenberger et al. (2008) recommended growing conventional and organic trials in parallel, on advanced breeding material, to obtain a more accurate analysis. In our study, observed response to selection did not differ between systems for traits with differing heritability estimates. This suggests that genetic gain may not differ between the two systems, but would be more difficult to predict under organic conditions. Over years, the mean and population distributions for grain yield were more variable in organic trials. Variable cultivar performance differences have been observed between organic farms in Europe (Przystalski et al. 2008).

Nass et al. (2003) reported that AC Barrie performed well under organic management. Therefore, AC Barrie was a logical choice as a parent to initiate breeding for organic agriculture. Parental selection is an important first step for breeding in organic systems (Wolfe et al. 2008). The introduction of height reduction genes is common in conventional wheat breeding (Worland and Snape

2001) and the population used in this study was segregating for height. Mason et al. (2007b) reported that semi-dwarf cultivars of wheat were not as competitive against weeds as tall cultivars. In this study, AC Barrie yielded higher in organic systems while Attila, a semi-dwarf cultivar, yielded more grain in the conventional system.

Weed biomass was much greater in the organic trials of this experiment. However, in our trials weed biomass suppressive ability and early season vigour were not heritable traits in both management systems. This could have been the result of inherent field variability, especially in an uncontrolled organic system. In the conventional system weeds were largely controlled through herbicide application making genetic variation difficult to estimate. Higher weed biomass levels in organic systems have been reported previously (Leeson et al. 2000). Different levels of natural weed pressure can affect which competitive traits are more important (Mason et al. 2007a). In this study, plant height was the most important trait for reducing weed biomass levels. This suggests that breeding for semi-dwarf wheat may not be prudent for organic farming systems.

In this study four traits had a low number of lines selected in common between management systems with three traits having similar heritability estimates between systems. The similar heritability estimates suggests there will be similar genetic gain in both systems, however the selection of different lines between systems implies the genetic gain is being achieved though different paths. Breeding programs, whether in conventional or organic systems, do not make selections based on only one trait (Wolfe et al. 2008). Organic breeding will require selections based on traits specifically required for organic agriculture, and selecting in an environment requiring the expression of those traits (Loschenberger et al. 2008; Murphy et al. 2007; Przystalski et al. 2008).

The negative relationship between flowering time and grain yield under organic management in the present study suggests that earliness is an advantage in organic systems. This agrees with previous reports which concluded that earliness confers a competitive advantage to spring wheat in central Alberta (Mason et al. 2007d), even when seeding dates are the same (Reid, unpublished data).

4.5 Conclusions

The results of this study show that for certain agronomic traits, variability in organic management systems may reduce the precision of genetic parameters commonly estimated in breeding programs. This makes predicting the potential gains from selection difficult in organically managed fields; but direct selection should result in observable gains. This study demonstrates that selection in conventionally managed land for the purposes of developing cultivars for organic production does not result in the same genotypes being selected for each system for all traits. Based on the results of this study, we believe the selection of spring wheat cultivars for organic production systems should be done on organically managed land. Creating a population from parents exhibiting traits necessary for success in organic agriculture could result in greater differences in selection results between the two systems.

4.6 Tables and Figures

Table 4-1: Least square means of AC Barrie and Attila and the population derived from a cross between the two, grown under organic and conventional management in Edmonton, AB Canada from 2005 to 2007, and the range of the population for 17 agronomic traits.

	AC Barrie[a]		Attila[a]		Diff Between Parents[b]		Population Mean[a]		SE of Diff	Conventional		Organic	
Variable	Conv[c]	Org	Conv	Org	Conv	Org	Conv	Org		Min	Max	Min	Max
Grain Yield (t ha^{-1})	4.54*	2.68*	4.83**	2.09**	-0.29	0.59*	3.88*	1.85*	0.67	4.19	5.22	1.80	2.63
Spikes m^{-2}	536	322	414	336	122*	-14	454	343	83	387	520	303	396
Plant Height (cm)	86	84	71	67	15*	17**	76	74	7.2	64	92	66	88
Test Weight (kg hl^{-1})	81	79	81	77	0	2	80	76	2.5	76	82	73	79
Kernels spike^{-1}	31	28	39**	32**	-8**	-4	40	32	3.0	32	48	25	39
1000 Kernel Weight (g)	37*	40*	38	38	-1	2**	36	36	1.2	31	41	30	41
Harvest Index (%)	45	45	49	42	-4	3	47	42	2.3	42	50	33	49
Flag Leaf Area (cm^{2})	19	15	16	10	3	5	18	14	3.4	13	22	9	17
Grain Protein (%)	14.1**	15.2**	12.8**	14.4**	1.3**	0.8**	13.0	14.8	0.58	11.6	15.1	13.7	16.1
Weed Biomass (g m^{-2})	0	10	1**	20**	-1	-10	1*	13*	3.5	0.2	2	12	16
Early Season Vigour	4	4	3	3	1	1*	3	3	0.1	3	4	3	3
Days to Anthesis	59	53	58	53	1	0	59	53	3.3	56	63	48	58
Days to Maturity	90	90	95	90	-5	0	94	92	3.5	88	100	85	101
Grain Fill Duration (Days)	32*	37*	37	37	-5*	0	35	39	3.9	29	38	34	44
Leaf Area Index	2.93	–[d]	2.44	–	0.49	–	2.58	–	–	1.75	3.73	–	–
Mean Tip Angle	60.7	–	58.5	–	2.25	–	59.0	–	–	50.1	65.9	–	–
Light Capture	0.88	–	0.91	–	0.03	–	0.81	–	–	0.79	0.81	–	–

*,** Significant at P = 0.05 and P = 0.01 respectively.

[a] Statistical differences tested between management systems.

[b] Statistical differences tested between AC Barrie and Attila.

[c] Conv: Conventionally managed system; Org: Organically managed system.

[d] Trait not measured in the organically managed system.

Table 4-2: Estimates of heritability, their standard error, and selection response (SR) for 14 agronomic traits in a population derived from a cross between AC Barrie and Attila grown under organic and conventional management in Edmonton, AB Canada from 2005 to 2007.

	Heritability Estimate (%)				SR_e[a]		SR_0[a]	
Variable	Conv[b]	SE[c]	Org[b]	SE	Conv	Org	Conv	Org
Grain Yield (t ha^{-1})	22	5	14	5	0.25	0.13	0.31	0.30
Spikes m^{-2}	22**	5	4**	4	30	6	53**	34**
Plant Height (cm)	67**	4	43**	5	9	7	12	11
Test Weight (kg hl^{-1})	51**	5	26**	6	1.4	1.0	1.5	1.6
Kernels $spike^{-1}$	47	5	37	6	5	4	6	5
1000 Kernel Weight (g)	59**	5	39**	5	3	3	4	4
Harvest Index (%)	31	5	37	6	2	5	3**	4**
Flag Leaf Area (cm^2)	36	5	32	6	11	9	3	3
Grain Protein (%)	62**	6	31**	8	0.83	0.45	1.2	0.9
Weed Biomass (g m^{-2})	7	4	2	2	-0.13	-0.45	-0.3**	-0.8**
Early Season Vigour	6	3	4	3	0.1	0.1	0.2	0.2
Days to Anthesis	37*	6	53*	5	-1	-3	-2*	-3*
Days to Maturity	35	5	44	5	-2	-4	-4	-5
Grain Fill Duration (Days)	21	6	27	5	1	2	3	4

*,** Significant at P = 0.05 and P = 0.01 respectively (T-Test).

[a]SR_e: expected response from 10% selection; SR_0: observed response from 10% selection

[b] Conv: Conventionally managed system; Org: Organically managed system.

[c]SE: Standard error of the heritability estimate.

Table 4-3: Spearman rank correlation (r_s) and the number of lines in common at three selection intensities, for 14 agronomic traits in a population derived from a cross between AC Barrie and Attila grown under organic and conventional management in Edmonton, AB Canada from 2005 to 2007.

		Lines selected in common		
Trait	Rank (r_s)	10%[a] (8)[b]	15% (12)	20% (16)
Grain Yield	0.75	3	7	10
Spikes m^{-2}	0.63	4	7	8
Plant Height	0.86	7	9	10
Test Weight	0.98	7	11	14
Kernel $spike^{-1}$	0.96	6	12	12
1000 Kernel Weight	0.97	6	9	13
Harvest Index	0.84	5	7	8
Flag Leaf Area	0.63	5	10	12
Grain Protein	0.77	3	6	7
Weed Biomass	0.95	7	10	13
Early Season Vigour	0.96	7	9	12
Days to Anthesis	0.96	6	11	12
Days to Maturity	0.95	7	11	14
Grain Fill Duration	0.57	2	4	6

[a]Selection intensity applied within each system

[b] Maximum number of lines selected from the population of 79 lines at the given selection intensity (10, 15, 20 %).

Table 4-4: Genetic correlations (r) for eight agronomic traits, calculated using data standardized within management system, measured in a population derived from a cross between AC Barrie and Attila grown under organic and conventional management in Edmonton, AB Canada from 2005 to 2007.[a]

	Grain Yield	Spikes m^{-2}	Kernel $spike^{-1}$	1000 Kernel Weight	Plant Height	Harvest Index	Flag Leaf Area	Grain Protein
Grain Yield		–[b]	–	0.45	–	0.72	0.53	-0.38
Spikes m^{-2}	–		-0.94	–	-0.61	–	–	–
Kernel $spike^{-1}$	0.33	-0.56		–	–	0.58	0.59	-0.91
1000 Kernel Weight	–	–	–		–	–	0.29	0.31
Plant Height	0.27	-0.38	–	0.68		-0.44	–	–
Harvest Index	–	–	0.33	-0.40	-0.65		0.71	-0.79
Flag Leaf Area	0.58	-0.41	0.42	–	0.53	-0.26		-0.55
Grain Protein	–	–	-0.67	0.62	0.56	-0.60	–	

[a]Values above the diagonal represent organically managed system; values below the diagonal represent conventionally managed system

[b]Correlation not different from zero ($P > 0.05$).

Table 4-5: Genetic correlations (r) between eight agronomic traits and each of weed biomass, early season vigour, days to anthesis, days to maturity, and grain fill duration, all calculated using standardized data within management system, measured in a population derived from a cross between AC Barrie and Attila grown under organic and conventional management in Edmonton, AB Canada from 2005 to 2007.

	Grain Yield		Plant Height		Test Weight		Kernel spike^{-1}		1000 Kernel Weight		Harvest Index		Flag Leaf Area		Grain Protein	
	Conv[a]	Org	Conv	Org	Conv	Org	Conv	Org	Conv	Org	Conv	Org	Conv	Org	Conv	Org
Weed Biomass	-0.72	–[b]	-0.52	–	-0.32	–	–	–	–	–	0.41	–	-0.45	–	–	–
Early Season Vigour	–	–	0.35	–	0.41	–	-0.61	–	–	0.81	–	0.42	–	0.49	0.83	–
Days to Anthesis	0.57	-0.28	0.23	–	–	–	–	–	–	–	-0.55	-0.70	0.41	-0.57	–	0.31
Days to Maturity	0.84	-0.28	–	–	–	–	0.41	-0.31	–	–	–	-0.74	0.53	-0.60	–	0.29
Grain Fill Duration	0.75	–	–	–	–	–	0.64	-0.40	–	–	–	-0.55	0.43	-0.43	-0.42	–

[a] Conv: Conventionally managed system; Org: Organically managed system.
[b] Correlation not different from zero ($P > 0.05$).

Table 4-6: Genetic and phenotypic correlations, between 17 traits measured in the conventionally managed system, and grain yield and grain protein measured in the organically managed system, calculated using data standardized within management system, on a population derived from a cross between AC Barrie and Attila grown under organic and conventional management in Edmonton, AB Canada from 2005 to 2007.

	Organic Grain Yield		Organic Grain Protein	
Conventional	Genetic	Phenotypic	Genetic	Phenotypic
Grain yield (t ha^{-1})	0.56	0.10	–[a]	–
Spikes m^{-2}	–	–	0.36	–
Plant Height (cm)	–	–	0.28	0.20
Test Weight (kgHl)	0.44	–	–	–
Kernel $spike^{-1}$	–	–	-0.72	-0.28
1000 Kernel Weight	–	–	0.53	0.25
Harvest Index (%)	0.29	0.18	-0.81	-0.27
Flag Leaf Area (cm^2)	–	–	–	–
Grain Protein (%)	–	-0.13	1	0.47
Early Season Vigour	–	0.08	0.47	–
Weed Biomass (g)	-0.43	-0.08	–	–
Days to Anthesis	–	-0.20	0.29	0.17
Days to Maturity	–	–	–	–
Grain Fill Duration	–	–	–	-0.14
Leaf Area Index	–	–	0.38	0.14
Mean Tip Angle	–	–	–	–
Light Capture	–	–	0.90	–

[a]Correlation not different from zero ($P > 0.05$).

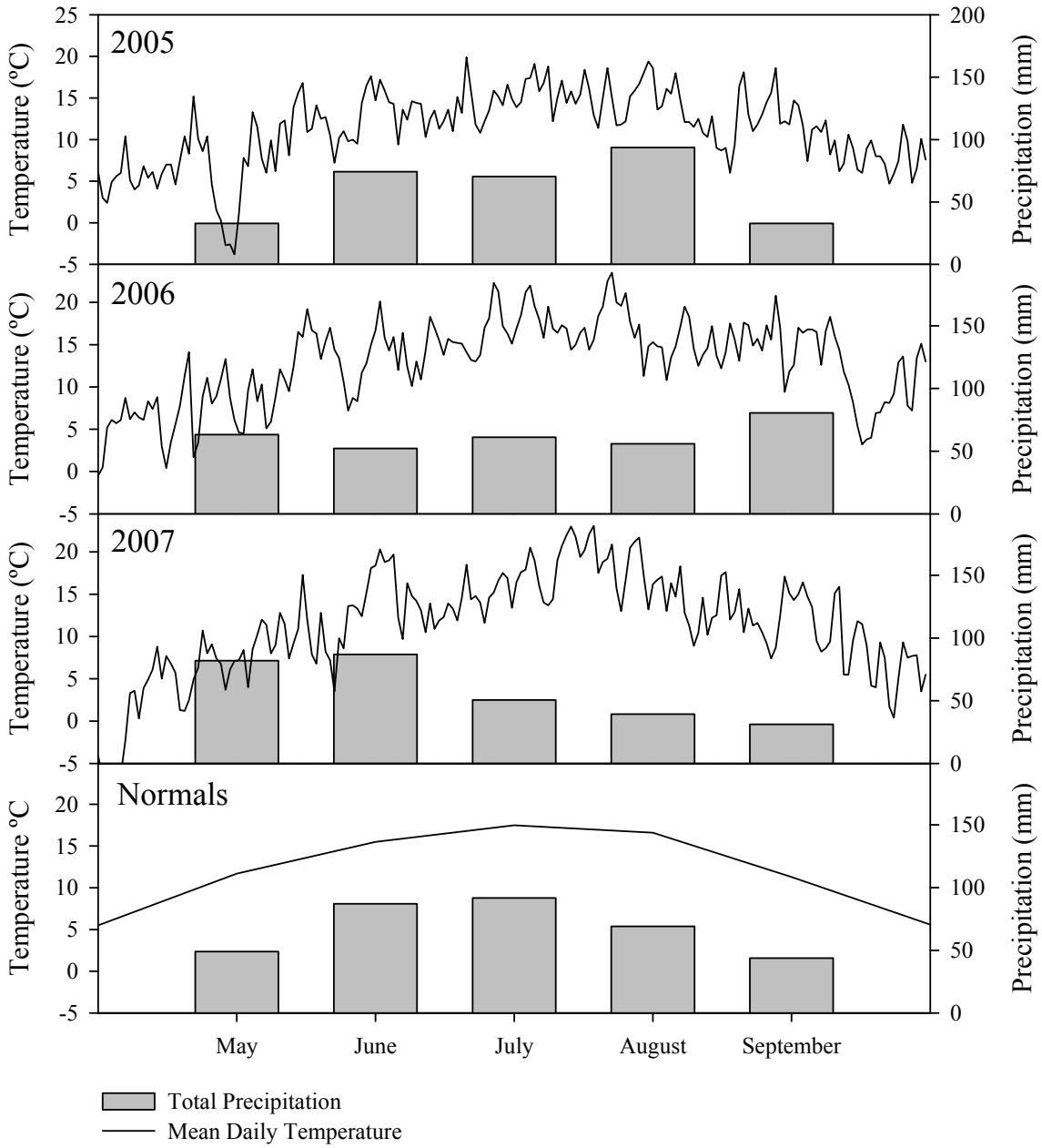

Figure 4-1: Weather data from the Edmonton International Airport for each year of the experiment and the 40 year normal for the months of the growing season. Data obtained from the Environment Canada weather data archive (Environment Canada 2008)

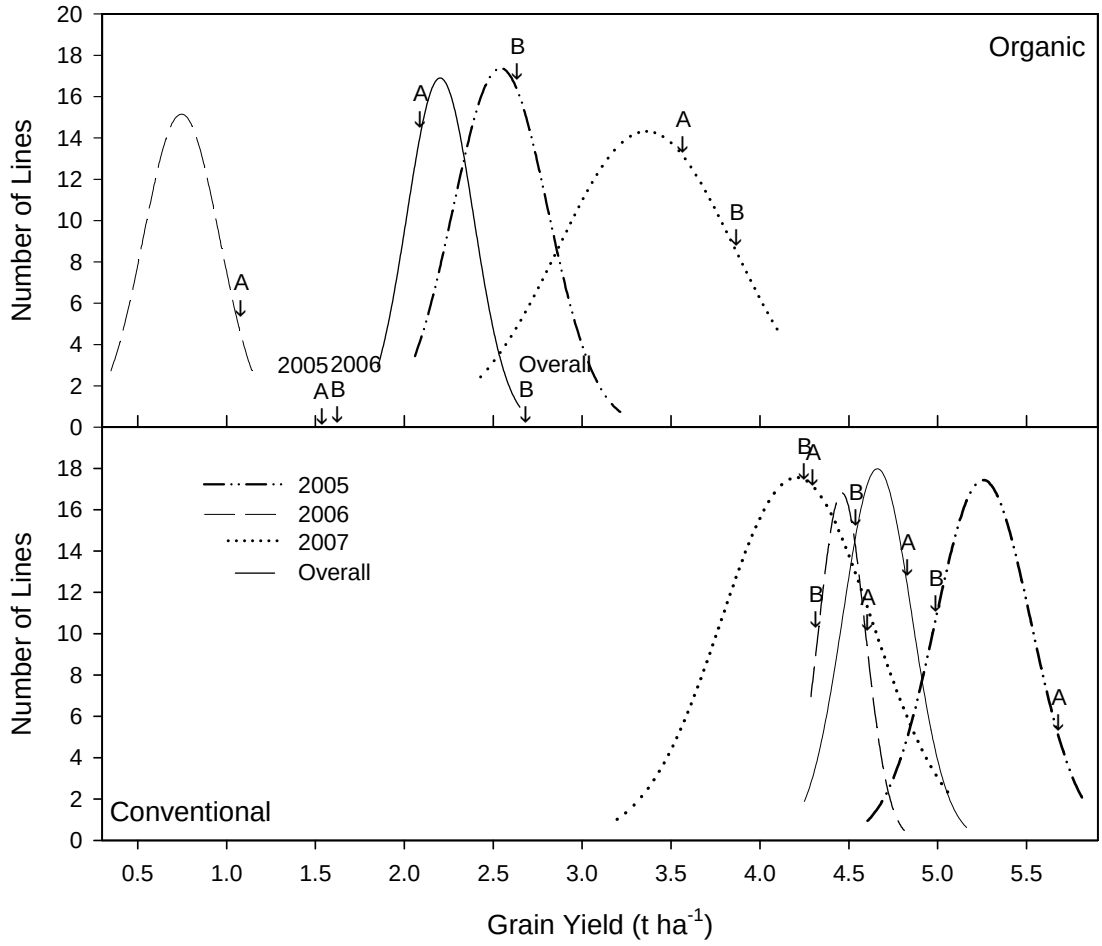

Figure 4-2: Population distribution of grain yield for both management systems for each year and across years, with arrows showing the position of each parent (A: Attila, B: AC Barrie) for each distribution

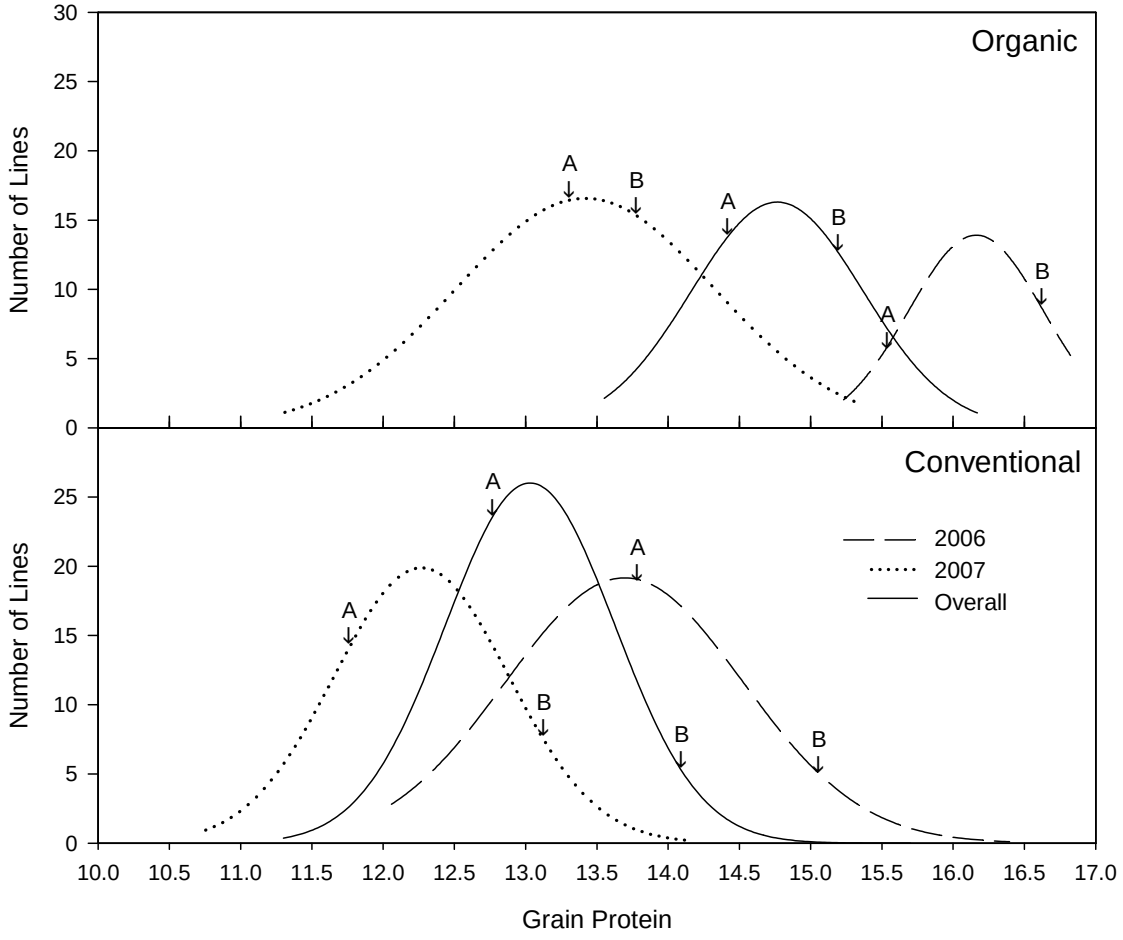

Figure 4-3: Population distribution of grain protein levels for both management systems for each year and across years, with arrows showing the position of each parent (A: Attila, B: AC Barrie) for each distribution

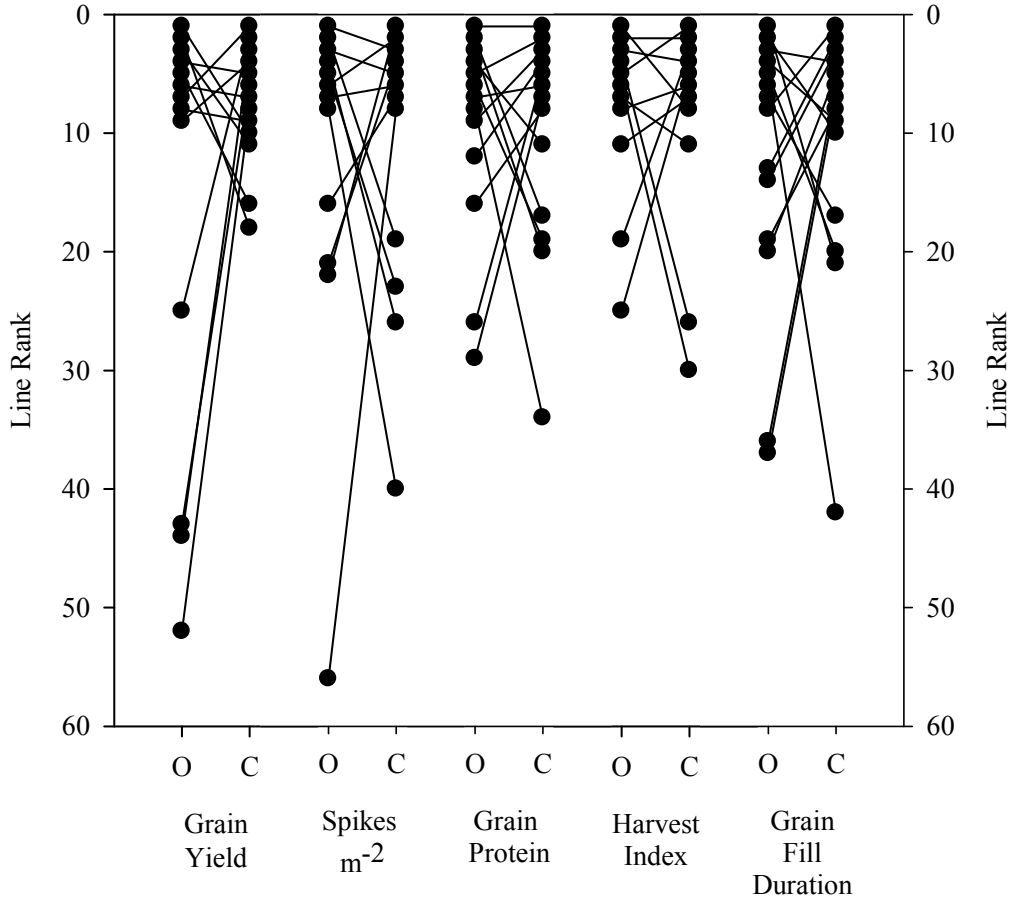

Figure 4-4: Genotypic ranks changes observed in the top 10% lines ranked under each management system (O: Organic; C: Conventional) for five traits measured in both systems. Rank was assigned according to the desired direction of selection (e.g.
rank one for grain yield was the highest yielding)

4.7 Literature Cited

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5.0 Realized gains from selection for spring wheat grain yield are different in conventional and organically managed systems

5.1 Introduction

Globally, the market for organic food products doubled between 2002 and 2007, to more than $46 billion (USD) (Sahota 2004; Willer 2009), with North America representing one of the fastest growing markets in the sector. Canadian sales of organic products exceeded an estimated $1 billion in 2006 (Macey 2007). In 2009, Canada enacted new federal regulations for organic production, requiring mandatory certification to a revised national standard for all products represented as organic in inter-provincial or international trade. These regulations replace a previously voluntary certification process and address issues of regulatory equivalency between major trading partners (Canadian Food Inspection Agency 2009).

The reduction in environmental variability in conventional agriculture through the widespread use of chemical inputs implies that individual cultivars can be successful over a large geographic area (Wolfe et al. 2008). Organic grain farmers in Canada must make use of cultivars bred before the wide-spread use of chemical fertilizers and pesticides or cultivars bred under conventional agricultural systems. Breeding bread wheat (*Triticum aestivum* L.) specifically for organic systems has been suggested for Europe (Wolfe et al. 2008), the United States (Murphy et al. 2007) and Canada (Reid et al. 2009b). In a review, Wolfe et al. (2008) reported that the selection of some traits are similar between organic and conventional breeding programs, but some more complex traits are specific to organic management.

Breeding efforts coupled with increased inputs, in conventional agriculture, have provided a continuous increase in bread wheat yields globally over the past 40 years (FAO 2005). The selection of cultivars for low-input and/or organic environments has not been a priority of past breeding programs. Ceccarelli (1996) suggested that breeders justify selection under optimum conditions because greater environmental variability of low-input conditions reduces heritability. Nevertheless, there have been reports of similar rankings for

disease resistance and quality traits in conventional and organic cropping trials (Mader et al. 2000; Mason et al. 2007b). Reid et al. (2009b) reported lower or similar heritability estimates for 13 agronomic traits, including grain yield, in a population of recombinant inbred spring wheat lines grown in both organically and conventionally managed systems.

Several studies have reported differences in the performance of wheat cultivars in organic and conventional management systems, with some cultivars better suited to organic management in northern North America (Carr et al. 2006; Mason et al. 2007c; Nass et al. 2003). Przystalski et al. (2008) found specific cultivars which exhibited cross-over interactions between management systems despite high genetic correlations between systems. They concluded that selection of cultivars should be conducted under conditions which closely mimic commercial organic farms and should include traits important to organic farmers. Direct selection for yield under organic management resulted in genotypic ranks different from conventional management (Murphy et al. 2007), and the use of yield stable cultivars for low input or highly weedy environments has been suggested (Mason et al. 2008).

Cultivars responsive to favourable environments may not be yield stable across a wide geographic area (Navabi et al. 2006). Early attempts to capitalise on introducing dwarfing genes in durum wheat (*Triticum durum* Desf.) resulted in a decrease in the yield stability of released cultivars in Italy (De Vita and Maggio 2006). When researchers in that area made yield stability a breeding priority, it was restored without a subsequent drop in yield potential (De Vita and Maggio 2006).

Common spring wheat breeding strategies in Canada include single seed descent with or without selection, or modified bulk breeding with selection in the Canadian summer and shuttle breeding in a Southern location (with or without selection) in the winter. At about the F^5 or F^6 generation, single heads are grown in rows to obtain enough seed for un-replicated preliminary yield and quality trials. Selection occurs within these preliminary yield trials at intensities of about 10 to 20 %. Replicated multi-location (five or six sites) yield trials are conducted on the

F^7 to F^{10} prior to prairie wide cooperative trialing and eventual release (Fox et al. 2007).

We originally used a random population of 79 F_6-derived recombinant inbred sister lines from a cross between the Canadian hard red spring wheat cultivar AC Barrie and the CIMMYT derived cultivar Attila to examine differences in quantitative genetic parameters for many agronomic traits in paired organic and conventionally managed trials (Reid et al. 2009b). The population, including the parents, was grown on conventionally and organically managed land in Edmonton AB Canada (where we could record detailed measurements on 14 agronomic traits) for three years. We also grew this entire population in replicated yield trials on an additional three organic and three conventional sites (F^7 and F^8 generations) in diverse locations where we could not obtain detailed agronomic data beyond grain yield, test weight and some protein and days to maturity. These data (all twelve locations of grain yield), when combined, allow us to examine the differences between realized yield gains from selection in advanced generation yield trials when grown in organic and conventionally managed environments. This experiment follows actual breeding methodology but uses the entire population throughout (rather than eliminating lines through selection) to examine the central underlying hypothesis that selection in the two systems would yield different results. The objective of the present study was therefore to investigate the effects of direct selection within organic and conventional management, evaluating the actual performance of the selected lines over multiple locations.

5.2 Materials and Methods

A population was created from a cross between the spring wheat cultivar AC Barrie and the CIMMYT spring wheat cultivar Attila. AC Barrie is an awnless high yielding, high protein, hard red spring wheat cultivar adapted to the Canadian Prairies (McCaig et al. 1996). The experimental materials and methods are discussed in detail by Reid et al. (2009b). In brief, the population itself consisted of 79, F4 derived F6 genotypes, which were advanced to F4 by single seed descent. The population and the two parents were planted in double head

rows, the year prior, to multiply the seed for experimental use. Three check cultivars were also grown for comparison. They were AC Intrepid (DePauw et al. 1999) a high yielding early cultivar, AC Superb (Secan 2006), a high yielding semi-dwarf, and Park (Kaufmann and McFadden 1968), a tall, early maturing cultivar commonly used in organic agriculture,

Field trials were conducted at two locations in 2005, at six locations in 2006, and at four locations in 2007 (Table 5-1). In all three years, the trial was conducted at the Edmonton Research Station, Edmonton, Alberta (53° 34′ N, 113° 31′ W), on one organically managed site and one conventionally managed site, located approximately 1 km apart. In 2006 and 2007, the trial was also conducted in conventionally managed fields at the Alberta Agriculture, Food, and Rural Development Field Crop Development Centre Research Farm in Lacombe, Alberta (52° 28′ N, 113° 44′W), as well as at a certified organic farm near New Norway, Alberta (52° 52′ N, 112° 56′ W). An additional two sites were used in 2006; an organic farm near Namao, Alberta (53° 43' N, 113°30' W) and a conventionally managed field at Ellerslie, Alberta, located 10 km south of Edmonton.

Soils at the New Norway sites were Eluviated Black Chernozems (Albic Argicryolls), while soils at Edmonton, Ellerslie, Lacombe, and Namao were classified as Orthic Black Chernozems (Typic Haplustolls), typical of central Alberta (Alberta Agriculture Food and Rural Development 2002). Different areas of each site were used in subsequent years in keeping with the crop rotation used on the research stations, or farms.

On the conventionally managed Edmonton site and the Ellerslie site, granular fertilizer (11-52-0: N-P_2O_5-K_2O) was banded with the seed, during sowing, at a rate of 36 kg ha^{-1}, and broad leaf weeds were controlled using Dyvel® (BASF Canada, Mississauga, ON.) at a rate of 1.1 L ha^{-1}. On the Lacombe site, fertilizer (11-52-0: N-P_2O_5-K_2O) was banded with the seed at a rate of 112 kg ha^{-1}, and weeds were controlled using Mextrol® (Nufarm Agriculture Inc. Calgary, Alberta, Canada) at a rate of 1.2 L ha^{-1} in 2006 and 1.0 L ha^{-1} in 2007.

No fertilizer or herbicides were used on the organically managed sites. The organic sites, outside of Edmonton, were managed according to Organic Crop Improvement Association International Certification Standards (Organic Crop Improvement Association 2000), but only the New Norway site was certified organic. The Edmonton site has been managed as such since 1999. The three year rotation on the Edmonton organic site consisted of barley, triticale/field peas, and cereal research plots. Composted dairy manure had been applied to the organic field in the fall of each year prior to the start of this study, but was not applied during the years of the study because soil nutrient levels were adequate according to soil tests performed (optimal in 2006, only nitrogen was marginal in 2007) (data not shown).

Plots were seeded at 250 seeds m^{-2} in a randomized complete block design within each site. In 2005, because of seed limitations, two replications were used per site, and plots were two meters long by four rows wide, with 23.5 cm row spacing. Subsequent years had three replicates in the Edmonton and Namao sites, and plot size was increased to four meter long, six row plots. The New Norway and Lacombe sites had two replicates each due to land constraints and the New Norway site had the same plot size as the other sites. Lacombe had eight row plots with 14 cm row spacing, planted over 4.5 m, with 2.5 m harvested.

Data recorded included grain yield, test weight, grain protein, and days to maturity. Grain protein content (%) was recorded in 2006 and 2007 only, and was determined using Near-Infrared Reflectance (NIR) spectroscopy using a Monochromator NIR Systems model 6500 (NIRSystems, Inc., Silver Springs, MD, USA). Physiological maturity was determined visually as the number of days from seeding to the point in time when 75% of the peduncles in a plot had lost green color, at the Edmonton sites only. To estimate competition in each environment, weed biomass was sampled on 10 randomly selected plots within each environment, near physiological maturity of the wheat, from a 625 cm^2 area of the plot. The weed samples were dried for three days at 50ºC and dry weight was recorded.

5.2.1 Statistical Analysis

All data were analysed with the MIXED procedure of SAS v9.1 (SAS® Institute 2003). Sites and years were considered as 12 environments, six organic and six conventional. Data were first analyzed by year and management system using:

$$y_{ijk} = \mu + E_j + R_k\left(E_j\right) + G_i + GE_{ij} + \varepsilon_{ijk} \quad (1)$$

where G, E, and R, are the genotypes, including the inbred lines, population parents, and check cultivars, environment, and replicate respectively. All terms were analysed as fixed effects except for $R_k(E)_j$ which was considered a random effect. Least squared means were calculated from the model for the genotypes. These least squared means were used to construct histograms, which were fitted with a three parameter Gaussian curve, to approximate the population distributions using SigmaPlot 11.0 (Sigmaplot 2008).

To simplify the analysis and presentation of the large and complex data set, the data were also grouped by selection year (2005) and test years (2006-2007). These groups were then analysed separately, within management system, using equation (1), and least squared means were again calculated for genotype. Selections were made at 10% selection intensity, within each management system in 2005, based on grain yield. The least squared means for the test group were also used to construct histograms, and then fitted with a three parameter Gaussian curve in Sigmaplot (Sigmaplot 2008).

Data were standardized within management system and year, to minimize differences in scale between traits (Zar 1996), using:

$$Z = \frac{X_i - \mu}{\sigma} \quad (2)$$

where Z is the standardized data point, X_i is the ith observation, μ and σ is the population mean and standard deviation within each year and management system. Selection differential was calculated on this standardized data, for each trait individually using:

$$I = \overline{X}_s - \overline{X} \quad (3)$$

where I is the selection differential, X_S is the mean of the selected lines for the specific trait, and X is the mean of the population excluding checks and parents (St. Martin and McBlain 1991).

Genotype stability was determined using a Finlay-Wilkinson analysis (Finlay and Wilkinson 1963) within each management system. An index of the yield potential of each environment was created by subtracting the grand mean yield of all environments, within management system, from the mean yield of each environment. Each genotype was then regressed on the index, to obtain the regression coefficient. Cultivar adaptation was visualized by plotting the regression coefficient of each cultivar against the cultivar mean yield across all environments, within management system. Regression analyses were conducted using the reg procedure of SAS (SAS® Institute 2003). Grain yield data were log transformed prior to analysis (Finlay and Wilkinson 1963), and back transformed for presentation.

5.3 Results

In 2005 we grew the trial in smaller plots (because of seed limitations) at Edmonton only, while the multi-site trials of 2006 and 2007 were grown with full plot sizes and over a wide range of environments. Our study therefore employed an experimental wheat population at the developmental stage, within a single seed descent breeding program, where a preliminary yield trial would normally occur to select lines (2005) for replicated multi-site trials (2006 and 2007). Thus we considered 2005 as the 'selection year' and 2006-2007 as 'multi-site yield trials'.

Two of the 2006 organic trials had intense weed competition, suffered from mild drought and had low average grain yield (Table 5-1). On average, the organic environments yielded 53% less, with a great deal more weed competition, than the conventional environments (Table 5-1). Grain yield was 10% lower across all management systems in 2006-2007 compared to the 'selection year' of 2005 (Table 5-2). In the years of the multi-site yield trials, lines grown under conventional management matured 6 days later, yielded 2.4 times more grain with

test weights 1.8 kg hl^{-1} greater, with 0.6 % less grain protein, on average, than the organically managed trials (Table 5-2).

AC Superb, a modern Canadian semi-dwarf bread wheat, was the highest yielding and latest maturing check cultivar in the experiment, and in both organic and conventional management (Table 5-3). Grain protein content of the check cultivars was 4% lower, on average, in the conventional test environments. The CIMMYT-derived semi-dwarf high-yielding parental cultivar of the population (Attila) was much higher yielding and matured later than the population in the conventional trials, but was lower yielding and earlier maturing than the average of the population in the organic trials (Tables 5-3 and 5-4). AC Barrie, the Canadian adapted bread wheat parent, yielded and matured within the range of the population under the differing management strategies (Tables 5-3 and 5-4).

We selected the top eight yielding lines (10% selection intensity) in both conventional and organic management following the 2005 selection year. These selected lines were 34 and 24 % greater yielding, with 3.3 and 2.1 % greater test weight, and 12 and 8 days earlier maturing than the general population, on average, when grown organically and conventionally in 2005, respectively (Table 5-4). Two lines (BA 05 and BA 36) were in the top 10 % in both organic and conventionally managed trials in that 2005 selection year. Following multi-site yield trials of 2006 and 2007, the chosen 10% averaged more grain yield in both systems with slightly greater test weights and 3 days longer maturity than the average of the entire population (Table 5-4; Figures 5-1 and 5-2). The selection differentials for the lines selected in each management for grain yield were similar in the first year, but lines selected under conventional management had double the selection differential in the test years (Table 5-4). The two lines (BA 05 and BA 36) ranked in the top 10% of both the conventional and organic selection trial of 2005, remained ranked 2nd and 1st, respectively, under conventional management in multi-site yield trials. However, these lines ranked 53 and 21st, respectively, for grain yield in the multi-site organic yield trials.

Three of the highest yielding lines (in the top 10% of the population) selected in the conventional ‘selection’ trial (BA 05, BA 27, BA 36) were also in

the highest 10% of the population following multi-site yield trials of 2006 and 2007. The remaining five lines selected remained within the highest yielding 1/3 of the population following multi-site conventional trials (Table 5-5). The organic selection environment also retained three lines (BA 9, BA 31, BA 41) in the top 10% of the population based on multi-site organic yield trials (Table 5-4), and these three lines were the earliest maturing of the selected lines in the organic test environments (Table 5-3). The remaining five lines selected yielded within the lower 2/3 of the population following multi-site organic trials (Table 5-4).

Growing the entire population in replicated yield trials on six organic and six conventional sites in diverse locations allowed us to examine real yield differences and ranking between organic and conventionally managed environments. Following replicated multi-location yield trials, three lines from the population (BA02, 29 and 58) ranked within the highest 10 % yielding lines in both conventional and organic systems (Table 5-5). The Kendall τ rank correlation coefficient for genotype least square mean yield between the organic and conventional systems for the selection year of 2005 was $\tau = 0.21$ ($P < 0.01$) and for the multi-site trials of 2006-2007 was $\tau = 0.28$ ($P < 0.01$).

Lines selected as the top 10% grain yield in either the organic or the conventional environment had greater stability in their respective environments (Figure 5-3). The lines selected in common between the two systems (BA 05, BA 36, and BA 74) were stable in the conventional system, but they were more responsive to environments with higher yield potential under organic management (Figure 5-3).

5.4 Discussion

We originally used a random population of 79 F_6-derived recombinant inbred sister lines from a cross between the Canadian hard red spring wheat cultivar AC Barrie and the CIMMYT derived cultivar Attila to examine differences in quantitative genetic parameters for many agronomic traits in paired organic and conventionally managed trials (Reid et al. 2009b). We then grew this entire population in replicated yield trials on six organic and six conventional sites

in diverse locations where we obtained data on grain yield, test weight and some protein and days to maturity. These data allowed us to examine the differences between realized yield gains from selection in advanced generation yield trials when grown in organic and conventionally managed environments. This experiment follows actual breeding methodology but uses the entire population throughout (rather than eliminating lines through selection) to examine the central underlying hypothesis that selection in the two systems would yield different results. To the best of our knowledge, there has been no direct comparison of an entire random recombinant inbred spring wheat breeding population grown over such a large range of environments comparing conventional and organic management in North America.

In the present study, organically managed trials showed less than half the gains from 10 % selection for grain yield in a 'selection' year compared to the conventional multi-site yield trials. Two lines (BA 05 and BA 36) ranked in the top 10% of both the conventional and organic selection trial of 2005, remained ranked 2nd and 1st, respectively, under conventional management in multi-site yield trials. However, these lines ranked 53rd and 21st, respectively, for grain yield in the multi-site organic yield trials. Following replicated multi-location yield trials, three lines from the population (BA02, 29 and 58) ranked within the highest 10 % yielding lines in both conventional and organic systems.

It thus appears that conducting multi-location yield trials in the two management systems would result in large differences between lines selected from breeding programs. It is evident, however, that data garnered from conventional yield trials does also have some relevance towards breeding for organic environments. Of the eight highest yielding lines (10%) in the multi-site organic trials, five were also in the top 15% of the multi-site conventional trials. The converse did not occur. In addition, the Kendall τ rank correlation coefficient for genotype least square mean yield between the organic and conventional systems for the selection year and for the multi-site trials of 2006-2007 was low, but indeed positive and significant ($0.21 < \tau < 0.28$).

Loschenberger et al. (2008) recommended growing conventional and organic trials in parallel, on advanced breeding material, to obtain a more accurate analysis. In our study, realized genetic gain for grain yield was less under organic conditions. Over years, the mean and population distributions for grain yield were more variable in organic trials. Variable cultivar performance differences have been observed between organic farms in Europe (Przystalski et al. 2008).

Our results suggest that direct selection for yield in organic systems, and testing those selected lines in organic systems, may not improve yields as quickly as in conventional systems. Increased complexity in organic systems has implications in breeding cultivars specifically adapted to organic systems. A lack of breeding specifically for organic management has meant that yield gains, in this sector, have been limited (Wolfe et al. 2008). We previously reported similar heritability estimates between conventional and organic systems, suggesting the potential for similar genetic gains (Reid et al. 2009b). However, reduced heritability estimates have been predicted for plants grown in competitive or stressful environments (Fasoula and Fasoula 1997). Results from the present study demonstrate that selection in conventionally managed land for the purposes of developing cultivars for organic production does not result in the same genotypes being selected for each system. Based on the results of this study, we believe the selection of spring wheat cultivars for organic production systems should be done on organically managed land.

Differences are known to exist, between management systems, in the relative performance of registered cultivars and advanced breeding lines (Carr et al. 2006; Mason et al. 2007c; Murphy et al. 2007; Nass et al. 2003). Cultivars also differ in their stability across different levels of natural weed competition (Mason et al. 2008). Cereal breeders work with large populations of sister lines, but only release a few specific lines, considered elite lines following selection and multi-site performance testing. By retaining the entire population in the present study, we were able to observe the relative performance of selected lines to their sister lines. Despite some lines selected in common between the two management systems, direct selection for grain yield did result in three different lines retained

within each management system over the test environments. Those lines remained among the top performing lines within the population in the environment they were selected, implying the potential for management-system-specific advancement within the population. Further, each set of three lines retained in each system exhibited increased yield stability within their respective management systems.

The level of weed competition has been reported to be an important determining factor for the direction (positive or negative) of the relationship between yield and maturity (Mason et al. 2008). The authors report that high levels of weed pressure, regardless of the management system, resulted in a negative relationship between yield and maturity; whereas moderate to low levels of weed pressure engendered a positive relationship between yield and maturity. Previous reports concluded that earliness confers a competitive advantage to spring wheat in central Alberta (Mason et al. 2007c; Reid et al. 2009a). In this study, increased weed pressure was apparent in the organic environments, with weeds nearly absent in all the conventional environments. We found increased time to maturity was associated with increased yield in the check cultivars under conventional management. Selection based on yield in the conventional environments did not necessarily increase maturity times, however the three top yielding lines in the organic test environment were also the earliest maturing lines of the selected lines.

Nass et al. (2003) reported that AC Barrie performed well under organic management. Therefore, AC Barrie was a logical choice as a parent to initiate breeding for organic agriculture. Parental selection is an important first step for breeding in organic systems (Wolfe et al. 2008). The introduction of height reduction genes is common in conventional wheat breeding (Worland and Snape 2001) and the population used in this study was segregating for height. Mason et al. (2007a) reported that semi-dwarf cultivars of wheat were not as competitive against weeds as tall cultivars. In this study, AC Barrie yielded higher in organic systems while Attila, a semi-dwarf cultivar, yielded more grain in the conventional system.

Wheat breeders routinely select for protein content depending on the end use of the line being developed, high protein for bread wheat and low protein for feed wheat (Shewry 2009). Different environments have been shown to have differential effect upon grain quality (Ikic et al. 2008), and grain protein content in wheat is greatly influenced by the environment (Shewry 2009). Protein levels for the population used in this study were either similar between the systems or higher in the organic system.

5.5 Conclusion

In the present study, gains from 10 % selection for grain yield in a 'selection' year were 3.4 times greater in conventional multi-site yield trials than in organically managed trials. Following replicated multi-location yield trials, only one line from the population (BA29) ranked within the highest 10 % yielding lines following both conventional and organic trials. Specific line selection differences exist between conventional and organic management systems. These differences imply that cultivars specific for organic management systems could be created by selecting under organic management. Yield stability within organic management systems maybe an important selection tool for the development of organic specific cultivars because the specific top performing lines were also yield stable across organic environments. The results of this study suggest that selection differences occur across multi-location tests, and that selection for grain yield in organic systems should be conducted within organic systems. It is evident, however, that data garnered from conventional yield trials does also have some relevance towards breeding for organic environments. Of the eight highest yielding lines (10%) in the multi-site organic trials, five were also in the top 15% of the multi-site conventional trials. In addition, the Kendall τ rank correlation coefficient for genotype least square mean yield between the organic and conventional systems for the selection year and for the multi-site trials of 2006-2007 was low ($0.21 < \tau < 0.28$), but indeed positive and significant.

5.6 Tables and Figures

Table 5-1: Average, minimum, and maximum grain yield, and the average weed pressure, of each location in central Alberta, from 2005 to 2007.

Location	Management	North Latitude	West Longitude	Year	Grain Yield (t ha^{-1}) Mean	Min	Max	Mean Weed (g m^{-2})
Edmonton	Organic	53º 29′	113º 32′	2005	2.55	1.26	4.09	152
Edmonton	Conventional	53º 29′	113º 32′	2005	5.24	2.38	7.55	8
Edmonton	Organic	53º 29′	113º 32′	2006	0.80	0.07	2.34	307
Camrose	Organic	52º 51′	112º 45′	2006	1.16	0.20	2.13	347
Namao	Organic	53º 43′	113º 24′	2006	2.84	1.66	4.83	189
Edmonton	Conventional	53º 29′	113º 32′	2006	4.47	2.66	6.01	2
Lacombe	Conventional	52º 26′	113º 44′	2006	6.45	2.78	8.48	0
Ellerslie	Conventional	53º 25′	113º 32′	2006	2.74	1.18	4.28	6
Edmonton	Organic	53º 29′	113º 32′	2007	3.40	1.62	5.11	148
Camrose	Organic	52º 51′	112º 45′	2007	1.98	0.92	2.84	212
Edmonton	Conventional	53º 29′	113º 32′	2007	4.23	2.55	5.86	17
Lacombe	Conventional	52º 26′	113º 44′	2007	6.73	4.75	9.48	0

Table 5-2: Population mean, standard deviation (SD) and range, for four traits measured on a spring wheat population derived from a cross between AC Barrie and Attila grown under organic and conventional management in central Alberta, Canada from 2005 to 2007.

	2005		2006-2007	
	Organic	Conventional	Organic	Conventional
Grain Yield (t ha^{-1})				
Mean (SD)	2.54 (0.51)	5.23 (0.65)	2.02 (0.25)	4.93 (0.37)
Range	1.26-3.93	3.69-6.69	1.49-2.57	4.02-5.98
Test Weight (kg hl^{-1})				
Mean (SD)	82.2 (1.1)	75.1 (1.6)	76.2 (1.4)	78.0 (1.3)
Range	78.7-84.4	70.3-78.0	71.8-79.4	73.5-80.7
Days to Maturity (days)				
Mean (SD)	106 (7)	101 (5)	85 (4)	91 (2)
Range	91-111	91-108	78-96	85-96
Grain Protein (%)				
Mean (SD)			14.0 (0.67)	13.4 (0.63)
Range			12.4-15.7	12.0-14.9

Table 5-3: Grain yield, test weight, days to maturity, and grain protein content measured on five check cultivars and the lines selected in the 2005 selection environment, based on grain yield within management system at a 10% selection intensity, from a spring wheat population derived from a cross between AC Barrie and Attila grown under organic and conventional management in central Alberta, Canada from 2005 to 2007.

Conventional Management					Organic Management				
	Grain Yield (t ha^{-1})	Test Weight (kg hl^{-1})	Days to Maturity (days)	Grain Protein (%)		Grain Yield (t ha^{-1})	Test Weight (kg hl^{-1})	Days to Maturity (days)	Grain Protein (%)
Checks					*Checks*				
2005 Selection Environment					2005 Selection Environment				
Attila	5.68	83.5	102	-	Attila	1.52	78.7	99	-
AC Barrie	4.99	83.1	97	-	AC Barrie	2.63	79.4	105	-
AC Intrepid	4.89	82.0	93	-	AC Intrepid	2.53	79.1	98	-
Park	4.62	81.4	94	-	Park	2.87	79.1	95	-
AC Superb	5.56	83.6	101	-	AC Superb	3.17	78.7	111	-
SE diff	0.67	0.65	3.5	-		0.49	1.42	6.7	-
2006-2007 Test Environments					2006-2007 Test Environments				
Attila	5.33	78.8	92	13.1	Attila	2.23	77.1	86	13.9
AC Barrie	4.68	79.6	87	14.0	AC Barrie	2.36	78.4	83	14.3
AC Intrepid	5.21	78.2	85	13.7	AC Intrepid	2.1	75.3	80	14.3
Park	4.28	78.0	85	13.9	Park	1.96	76.8	81	14.8
AC Superb	5.42	80.6	92	13.5	AC Superb	2.55	78.3	83	13.9
SE diff	0.22	0.41	1.2	0.21		0.15	0.41	0.9	0.21
Selected Lines (10 %)					*Selected Lines* (10 %)				
2005 Selection Environment					2005 Selection Environment				
BA 03	6.11	82.3	103	-	BA 05	3.18	78.4	114	-
BA 05	6.66	83.0	105	-	BA 09	3.93	79.0	112	-
BA 17	6.24	80.2	107	-	BA 28	3.26	76.9	119	-
BA 27	6.69	82.9	107	-	BA 31	3.62	78.3	112	-
BA 36	6.52	82.6	107	-	BA 36	3.48	78.3	109	-
BA 44	6.42	81.5	103	-	BA 41	3.32	75.7	115	-
BA 49	6.32	82.6	107	-	BA 56	3.26	78.3	104	-
BA 74	6.23	82.1	105	-	BA 74	3.15	77.0	116	-
SE diff	0.67	0.65	3.5	-		0.49	1.42	6.7	-
2006-2007 Test Environments					2006-2007 Test Environments				
BA 03	5.27	78.6	92	12.1	BA 05	1.94	75.3	94	15.3
BA 05	5.71	79.6	94	13.4	BA 09	2.49	77.3	83	13.8
BA 17	5.18	77.1	96	13.8	BA 28	1.62	77.4	95	14.7
BA 27	5.43	78.4	95	13.2	BA 31	2.39	78.3	84	14.1
BA 36	5.98	78.4	93	12.1	BA 36	2.27	77.1	89	13.1
BA 44	5.27	77.5	96	13.6	BA 41	2.41	75.9	85	14.2
BA 49	5.17	78.4	91	13.3	BA 56	2.16	77.0	85	14.4
BA 74	5.13	77.7	93	12.8	BA 74	1.98	75.6	91	13.5
SE diff	0.22	0.41	1.2	0.21		0.15	0.41	0.9	0.21

Table 5-4: Selection differential and genetic gains from direct select within management system separately for three traits measured on a spring wheat population derived from a cross between AC Barrie and Attila grown under organic and conventional management in central Alberta, Canada from 2005 to 2007.

	Grain Yield (t ha^{-1})		Test Weight (kg hl^{-1})		Days to Maturity (days)		Grain Protein (%)	
	Org[a]	Conv	Org	Conv	Org	Conv	Org	Conv
Selection Year 2005								
$\bar{x}_c$ = *Mean of checks*	2.52	5.19	79.2	82.8	102	97	-	-
$\bar{x}$ = *Mean of population*	2.54	5.24	78.5	82.2	106	101	-	-
$\bar{x}_s$ = *Mean of selected lines* (10%)	3.40	6.40	81.1	83.9	94	93	-	-
I = Selection differential	1.41	1.50	1.3	1.4	-1	-2	-	-
Combined Multi-location Test 2006-2007								
$\bar{x}'_c$ = *Mean of checks*	2.28	4.92	77.3	79.1	82	87	14.2	13.7
$\bar{x}'$ = *Mean of population*	2.02	4.93	76.2	78.0	85	91	14.0	13.4
$\bar{x}'_s$ = *Mean of selected lines* (10%)	2.16	5.39	76.7	78.2	88	94	14.1	13.1
I = Selection differential	0.30	0.72	0.7	0.9	-1	-1	-	-
Means of lines selected for performance in either organic or conventional systems 2006-2007								
BA05 (Conventional)	1.94	5.70	75.3	79.6	94	94	15.3	13.5
BA09 (Organic)	2.49	4.97	77.3	79.7	83	90	13.8	13.6
BA36 (Conventional)	2.27	5.98	77.1	78.4	89	93	13.1	12.1
BA41 (Organic)	2.41	5.36	75.9	76.9	85	91	14.2	14.0
BA79 (Organic)	2.57	5.08	77.4	77.7	85	89	12.8	12.9
BA 02 (Organic + Conventional)	2.37	5.45	76.4	78.2	84	93	14.7	14.8
BA 29 (Organic + Conventional)	2.37	5.50	78.9	80.7	85	89	13.7	13.6
BA 58 (Organic + Conventional)	2.47	5.37	79.4	80.4	84	93	12.7	12.5

Table 5-5: The rank of selected lines, within a spring wheat population derived from a cross between AC Barrie and Attila grown under organic and conventional management in central Alberta, Canada from 2005 to 2007, at a 10% selection intensity based on yield in 2005 (forward selection) and relative ranking of the top 10% in multi-site yield trials over 2006-2007.

Selection (10%) in 2005					Relative performance of top 10% in production years (2006-2007)				
	Rank in Conventional		Rank In Organic			Rank in Conventional		Rank In Organic	
Line No.	2005	2006-2007	2005	2006-2007	Line No.	2006-2007	2005	2006-2007	2005
Selection in Conventional									
BA 03	8	12	46	5	BA 02	5	13	8	25
BA 05	2	2	7	48	BA 05	2	2	48	7
BA 17	6	17	41	49	BA 27	6	1	65	18
BA 27	1	6	18	65	BA 29	4	23	7	31
BA 36	3	1	3	19	BA 36	1	3	19	3
BA 44	4	11	20	73	BA 38	7	42	17	63
BA 49	5	20	27	18	BA 58	8	14	3	21
BA 74	7	24	8	40	BA 78	3	73	23	53
Selection in Organic									
BA 05	2	2	7	48	BA 02	5	13	8	25
BA 09	10	38	1	2	BA 03	12	8	5	46
BA 28	47	25	6	77	BA 09	38	10	2	1
BA 31	65	28	2	6	BA 29	4	23	7	31
BA 36	3	1	3	19	BA 31	28	65	6	2
BA 41	55	9	4	4	BA 41	9	55	4	4
BA 56	58	55	5	24	BA 58	8	14	3	21
BA 74	7	24	8	40	BA 79	31	16	1	24

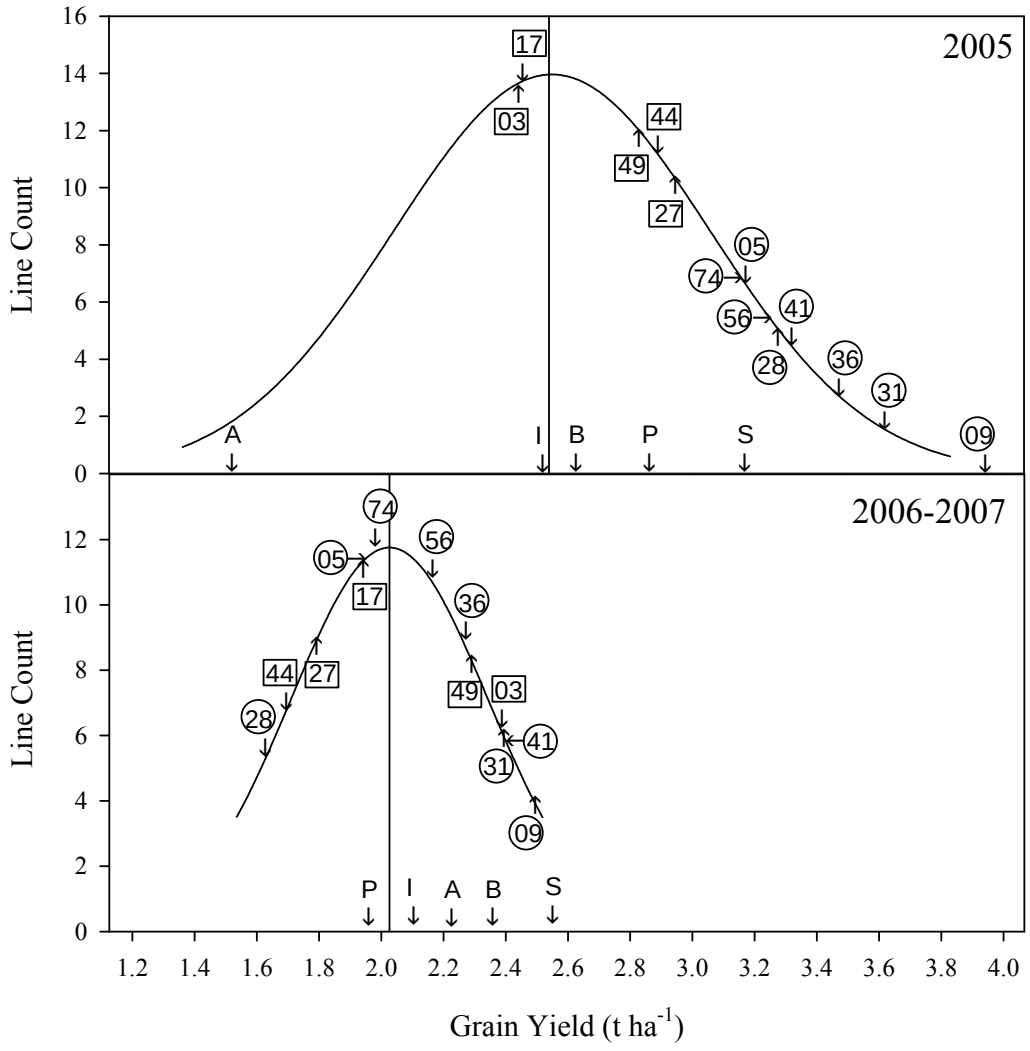

Figure 5-1: Distribution of recombinant inbred lines, based on grain yield, derived from a cross between AC Barrie and Attila grown on various organically managed sites analyzed for 2005, and combined across test years (2006-2007). The relative position of the lines selected in 2005 from the organic and conventional sites, based on 10% selection intensity, are shown. The squares indicate the lines selected in the conventional site only and the circles show the lines selected in the organic site. The relative position of five check cultivars, Attila (A), AC Barrie (B), Intrepid (I), Park (P) and Superb (S), are also indicated. The vertical line indicates the population mean.

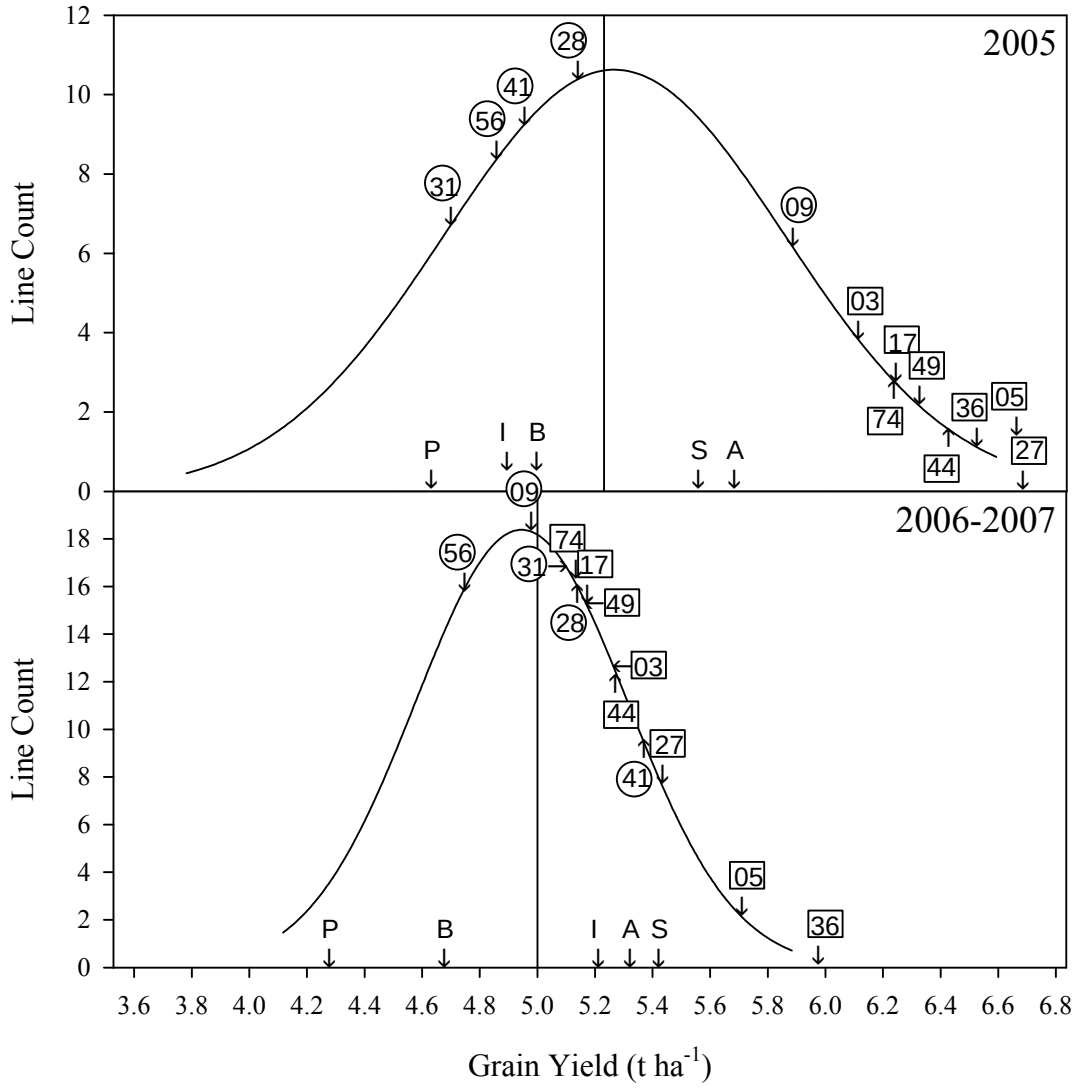

Figure 5-2: Distribution of recombinant inbred lines, based on grain yield, derived from a cross between AC Barrie and Attila grown on various conventionally managed sites analyzed for 2005, and combined across test years (2006-2007). The relative positions of the lines selected in 2005 from the organic and conventional sites, based on 10% selection intensity, are shown. The circles indicate the lines selected in the organic site only and the squares show the lines selected in the conventional site. The relative position of five check cultivars, Attila (A), AC Barrie (B), Intrepid (I), Park (P) and Superb (S), are also indicated. The vertical line indicates the population mean.

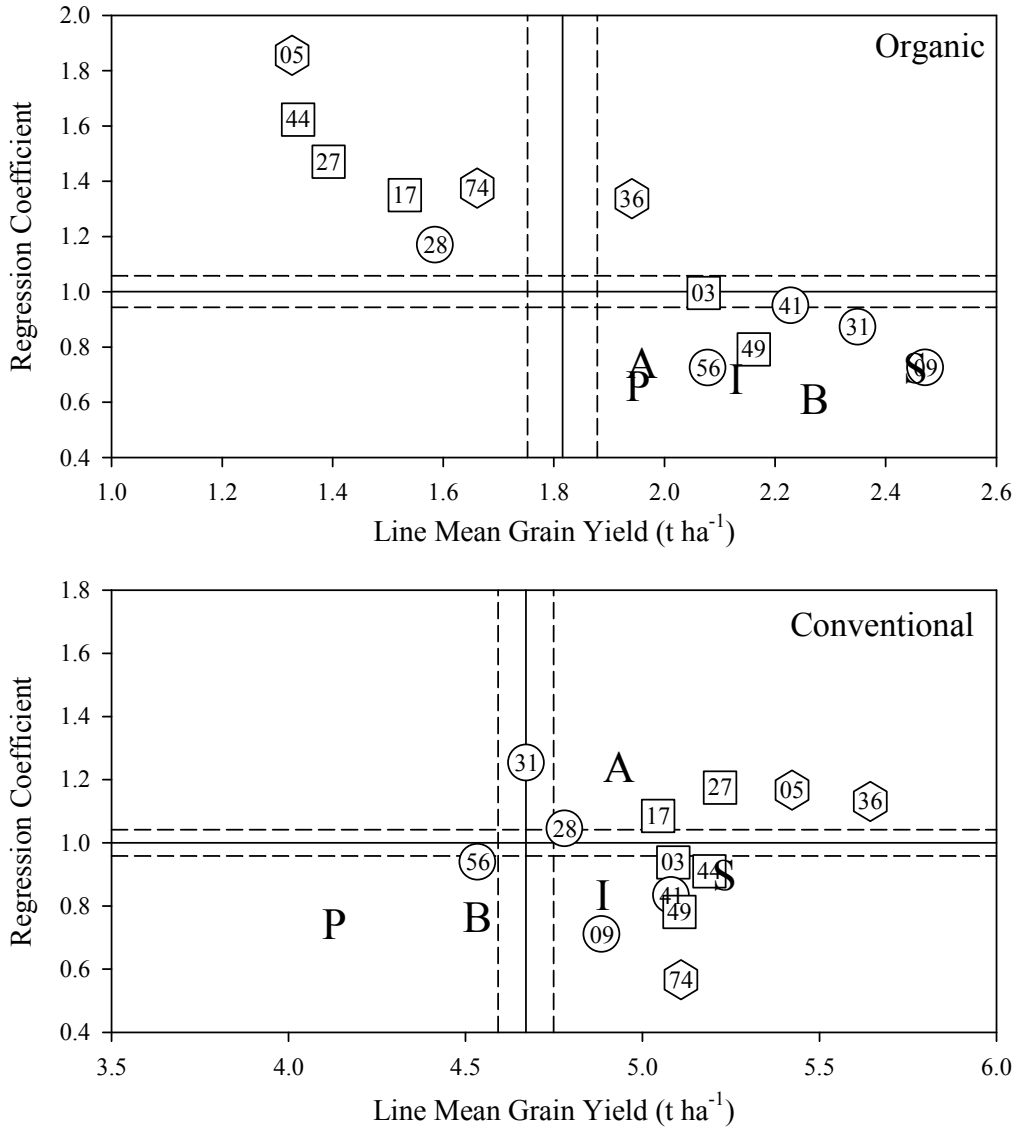

Figure 5-3: Stability analysis for the 79 members of the population derived from a cross between AC Barrie and Attila grown under organic and conventional management in central Alberta, Canada from 2005 to 2007, resulting in six site years for each management system. The relative positions of the lines selected in 2005 from the organic and conventional sites, based on grain yield at 10% selection intensity, are indicated. The circles indicate the lines selected in the organic site only, the squares show the lines selected in the conventional site only and the hexagons show the lines selected in both conventional and organic sites. The relative position of five check cultivars, Attila (A), AC Barrie (B), Intrepid (I), Park (P) and Superb (S), are also indicated. Solid lines indicate the population mean values and dashed lines represent the 95% confidence limits for the population. Scales are different between the two figures to increase separation of the individual lines presented, and to highlight relative line position within each figure.

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6.0 General Discussion and Conclusions

6.1 Introduction

Environmental concerns have some people questioning modern agriculture practices, including the widespread use of chemical fertilizers and pesticides stemming from the Green Revolution (Swaminathan 2006). Perhaps as a result of this, organic agriculture and other alternative methods of farming are gaining in popularity (Macey 2006). Organic producers use crop rotation and mechanical methods for weed and disease management, while rejecting the use of chemical inputs and transgenic crops (Wyss *et al.* 2001). This rejection can result in a rejection of all modern plant breeding; and organic cereal farmers often make use of cultivars bred before the wide spread use of chemical fertilizers and pesticides. However, some organic producers may desire organically bred cultivars (Degenhardt *et al.* 2005).

Modern breeding methods use statistics, among other tools, to obtain a greater understanding of the level of genetic control, and thus the breeding potential for certain traits. By understanding the underlying quantitative genetics of a given trait and how this relates to other traits, a breeder can more efficiently reach the goals of a given breeding program. This has helped breeding become a major source of increased crop productivity over the past century (Duvick 2002).

The selection of new varieties from available landraces was the domain of farmers (Schneider 2002), but collaboration between farmers and professional plant breeders often produce improved cultivars more suited to farmers needs (Dawson *et al.* 2008). The most popularly grown cultivars are often incorporated

into breeding material and improved agronomic practices can change breeding goals (Duvick 2002), including the adoption of organic agricultural methods by farmers (Mason and Spaner 2006; Murphy *et al.* 2007). Organic breeding methods employ natural plant fertility to enhance genetic diversity in sustainable cultivar development (IFOAM 2004). The traits required by organic specific cultivars may be different from those their conventional counterparts and include a large root base with beneficial interactions with soil biota, efficient utilization of available soil nutrients and water, and the suppression or tolerance of weeds, diseases, and pests (van Bueren *et al.* 2001).

Increased competitiveness in wheat, both tolerance and suppression, is a desirable goal for breeders globally (Lemerle et al. 2001; Vandeleur and Gill 2004). Some traits, including plant height, vigorous growth, large leaf size, and larger root mass, are more strongly associated with competitive ability. Breeding efforts have focused on single trait selection, defining competitive ability on the basis of yield, or the indirect selection of competitive ability through the selection of known competitive traits (Cousens et al. 2003; Lemerle et al. 2006; Lemerle et al. 1996; Zhao et al. 2006).

The different opinions expressed by researchers on which environments are best suited for breeding for competitive ability affects the organic industry, and organic plant breeders. Investigating differences in the heritability of traits between competitive and non-competitive environments could provide further insight into this problem. Uncovering specific genes or quantitative trait loci (QTL) which alter competitive response may provide more tools for the breeding

of competitive ability. The soil composition, nutrient levels and release rates, and weed pressure in organic agriculture systems differ from conventional agriculture systems, which suggest organic specific breeding may be required. Directly testing this suggestion and investigating the heritability of organic specific traits could provide further evidence for the development of organic specific breeding programs. The goal of my thesis was to examine the genetic control of competitive ability and test the effects of breeding wheat on organically managed land.

The specific objectives of this thesis were 1) determine if heritabilities, genotypic rank, and genotypic and environmental correlations differ between weedy and non weedy environments, 2) determine if there are QTL associated with competitiveness in wheat and estimate their location and effect, 3) determine if heritabilities, genotypic rank, and response to selection differ between organic and conventional management systems, 4) determine which morphological traits are correlated with any genotypic rank change observed between conventional and organic systems.

6.2 A genetic analysis of weed competitive ability in spring wheat

One hundred and eight random recombinant inbred lines from the widely studied International Triticeae Mapping Initiative (ITMI) population were grown in two locations over two years, with and without tame oats cross seeded to act as a weed analogue. Tame oats were used in this study primarily because it was the seed on hand. Gizzly oats has been used by our research group to investigate the

potential of growing mixed species cereal blends on organic land (Kaut 2008). That study found differences between the wheat to oat ratio planted and the wheat to oat ratio that was harvested, but the differences were variety specific. This meant that varietal differences exist in wheat for tame oat competition and it was thus concluded that tame oats would be a valid weed analog for our study.

This allowed us to study the genetics of traits associated with competitive ability in a high latitude (52–53ºN) wheat-growing environment in central Alberta, Canada (Chapter 2). Competitive stress from the weed analogue treatment reduced grain yield, spikes m^{-2}, and days to maturity in the random population.

Heritability estimates and relative ranking of the random lines were similar between the two competition treatments for most of the traits measured. These similarities suggest that selection in a weed free environment may provide advancement in a weedy environment. While this antagonistic selection has been suggested for rice (Zhao et al. 2006) our results suggest that the use of a weed free environment would result in discarding some lines which yielded better under competition.

Competitive ability cannot be explained by a single trait (Lemerle et al. 1996) and this complexity does not lend itself to direct selection. Defining competitive ability as decreased yield loss under weedy conditions puts breeding for it on familiar ground, *i.e.* single trait selection, without removing the possibility for weed suppression (Huel and Hucl 1996; Lemerle et al. 2001). However, our results show that the top two yielding lines in both competition

treatments were not among the top 10% of lines for reduced oat yield despite a strong negative relationship between wheat grain yield and oat grain yield.

Light capture, tillering capacity, early season vigour were all related to increased grain yield under competition. The flowering and maturity times of wheat were also found to be negatively correlated with wheat grain yield under competition and positively correlated with oat (weed) grain yield. Early maturing wheat has been correlated with increased yield in competitive organic farming systems (Mason et al. 2007b) and early heading is also associated with competitive ability (Huel and Hucl 1996). This study supports the idea of early maturing wheat aiding in both the suppressive and tolerant aspects of competitive ability in wheat. How flowering times assist in the suppression of weeds is still not clear (Mason et al. 2007a). We suggest that early season vigour and early maturity both help wheat escape the negative effects of weed pressure in a northern grain growing region.

6.3 Genetic evidence of a relationship between earliness and competitive ability in wheat.

Quantitative trait loci analysis of the 108 lines from the ITMI population, grown in two locations over two years with and without tame oats acting as a weed analogue, showed regions of the genome associated with decreased tame oat yield. Flowering times, early season vigour and weed suppression QTL were all detected in a similar region on chromosome 5A (Chapter 3.0). This region is also known to contain *Vrn-A1* (Galiba et al. 1995), but this gene was not segregating in

this population and we therefore could not test this hypothesis. This gene is important in that Canadian hard red spring wheat cultivars primarily contain *Vrn-A1a* singly or in combination with *Vrn-B1* (Iqbal et al. 2007b). Thus breeding for earliness, a goal of breeders in northern grain growing regions (Iqbal et al. 2007a; McCaig and DePauw 1995), may also improve the competitive ability. This study provides some genetic support for the idea that cultivars with early flowering and maturity have a competitive advantage in a northern grain growing region, and that this advantage may result in weed suppression. We suggest that further work using a locally adapted population, segregating for the *Vrn-A1* gene may provide more evidence of this theory.

6.4 Should spring wheat breeding for organically managed systems be conducted on organically managed land?

To study, at the genetic level, the feasibility of breeding organic wheat cultivars on organically managed land, a random population of 79 F_6-derived recombinant inbred sister lines, from a cross between the Canadian hard red spring wheat cultivar AC Barrie and the CIMMYT derived cultivar Attila, was grown on conventionally and organically managed land for three years (Chapter 4.0). This population was at the developmental stage where line selection, through preliminary yield trials, for replicated multi-location trials would normally occur to.

Heritability estimates for various agronomic traits were either similar between the organic and conventional systems or lower in the organic system,

suggesting that, breeding directly within organically managed systems would result in lower genetic gains than on conventionally managed land for some traits. However, observed response to selection did not differ between systems for traits with differing heritability estimates. This then suggests that genetic gain may not differ between the two systems, but would be more difficult to predict under organic conditions.

Direct selection in each management system did result in 50% or fewer lines selected in common for some economically important traits such as grain yield, and grain protein. Low Spearman rank correlations between the two management systems suggest that selecting in each management system would result in large differences between systems for lines retained in a breeding program. Growing conventional and organic trials in parallel, on advanced breeding material, has been suggested (Loschenberger et al. 2008).

AC Barrie was a logical choice as a parent to initiate breeding for organic agriculture because it has been reported to perform well under organic conditions (Nass et al. 2003). The introduction of height reduction genes is common in conventional wheat breeding (Worland and Snape 2001). However, plant height was the most important trait for reducing weed biomass levels in this study. This suggests that semi-dwarf wheats may not be appropriate for organic farming systems. Organic breeding will require selections based on traits specifically required for organic agriculture, and therefore selection in an environment requiring the expression of those traits (Loschenberger et al. 2008; Murphy et al. 2007; Przystalski et al. 2008)

6.5 Realized gains from selection for spring wheat grain yield following advanced generation multi location yield trials are different for conventional and organically managed systems.

The same random population used in chapter four, consisting of 79 F_6-derived recombinant inbred sister lines from a cross between the Canadian hard red spring wheat cultivar AC Barrie and the CIMMYT derived cultivar Attila, was grown on multiple conventionally and organically managed sites for three years (Chapter 5.0) following actual breeding methodology. However, the entire population was used throughout rather than eliminating lines through selection, to examine the central underlying hypothesis that selection in the two systems would yield different results.

We found gains from selection were greater in conventional multi-site yield trials than in organically managed trials. Lines selected in common between organic and conventional management systems in a 'selection' year did not always perform similarly in the multi-location tests. It thus appears that conducting multi-location yield trials in the two management systems would result in large differences between systems of lines selected from breeding programs. It is evident, however, that data garnered from conventional yield trials does also have some relevance towards breeding for organic environments.

Differences are known to exist, between management systems, in the relative performance of registered cultivars and advanced breeding lines (Carr et al. 2006; Mason et al. 2007b; Murphy et al. 2007; Nass et al. 2003). Cultivars also

differ in their stability across different levels of natural weed competition (Mason et al. 2008). Cereal breeders only release a few lines, from large populations of sister lines, following selection and multi-site performance testing. In this study the relative performance of selected lines to their sister lines was observed by retaining the entire population and, despite some lines selected in common between the two management systems, direct selection for grain yield did result in three different lines retained within each management system over the test environments. Those lines remained among the top performing lines within the population in the environment they were selected, implying the potential for management-system-specific advancement within the population. Further, each set of three lines retained in each system exhibited increased yield stability within their respective management systems

The level of weed competition is known to effect the direction (positive or negative) of the relationship between yield and maturity (Mason et al. 2008). In this study it was evident that increased competition fostered a negative relationship between grain yield and time to maturity. We found competition from weeds primarily in the organic environments, but selection based on yield in the conventional environments did not necessarily increase maturity times. Interestingly in this study, the three top yielding lines in the organic test environment were also the earliest maturing lines of the selected lines. This agrees with previous reports that concluded that earliness confers a competitive advantage to spring wheat in central Alberta (Mason et al. 2007b; Reid et al. 2009a).

A lack of breeding specifically for organic management has meant that yield gains have been limited (Wolfe et al. 2008), but the reported similar heritability estimates between conventional and organic systems suggests the potential for similar genetic gains (Chapter 4.0, Reid et al. 2009b). In the present study, gains from 10 % selection for grain yield in a 'selection' year were 3.4 times greater in conventional multi-site yield trials than in organically managed trials. Following replicated multi-location yield trials, only one line from the population (BA29) ranked within the highest 10 % yielding lines following both conventional and organic trials. Specific line selection differences exist between conventional and organic management systems. These differences imply that cultivars specific for organic management systems could be created by selecting under organic management. The results of this study suggest that selection differences occur across multi-location tests, and that selection for grain yield in organic systems should be conducted within organic systems. It is evident, however, that data garnered from conventional yield trials does also have some relevance towards breeding for organic environments.

6.6 General Discussion

Breeding wheat for organic production is not a common practise in North America, though some breeders are starting to show interest. The basic assumption of breeding for organic agriculture is that modern conventionally bred cultivars will make good organic cultivars. This assumption is made despite observed differences between the two management systems, the most obvious of

which is the higher level of weed competition in organic environments. In this thesis weed measures were taken from a small area of the plot and no distinction was made between monocot and dicotyledonous weeds. Competitive ability can differ between the two weeds type, and the lack of distinction is a limitation in the weeds measures reported. Nonetheless, breeding for competitive ability could provide a non chemical way to manage weeds while maintaining yields. Unfortunately breeding for competitive ability can result in a reduction in yield potential.

In this thesis we report similar heritabilities for grain yield between a population grown in a weed free environment and the same population grown with a model weed analogue (tame oats). Despite the similar heritability estimates, specific line selection differed between the two populations, suggesting that selection in a weed free environment would result in high yielding competitive lines being missed.

Nevertheless, locating specific genes associated with competitive ability would be useful for breeders using marker assisted selection, enabling them to rapidly screen potentially competitive lines. Though no single specific large effect quantitative trait loci were identified in this thesis for competitive ability, regions of interest were identified in the genome in close proximity to the area associated with *Vrn-A1*. This suggests that early maturity is important in organic systems, perhaps as a way of avoiding weed pressure.

While it is an over-simplification to state that organically managed land is conventional land with more weeds, increased weed competition is common

under organic management. Growing the same population under both organic and conventional management allowed for the direct comparison of the effects of organic management on selection within the population. Like the ITMI population, the heritability estimates for yield for the random Barrie/Attila population were not different between the two environments; however selection within each environment resulted in different specific lines being selected.

Heritability estimates can provide the breeder with valuable information on the potential gains from selection and the potential genetic gain for yield under organic management is similar to the conventional systems. However the specific lines selected are the ones that get advanced and eventually released and the lines that achieve the genetic gain are different under the different management systems. This suggests a different genetic pathway achieving this yield. Selected lines are also retained within management system, over years in a multi-location multi-year trial.

Selecting for specific traits under specific selection pressure is not a new idea for plant breeders. The suggested different genetic pathway for yield under organic systems means selection for that pathway must take place in an environment that would allow for its expression. This thesis supports the idea of synergistic selection; selecting for organic cultivars under organic management.

6.7 Conclusions

The following provides a summary of the conclusions of this thesis:

- Heritability estimates were similar ($P > 0.05$) with and without weed competition for nine recorded agronomic traits, but not plant height ($P < 0.01$).
- The similar heritability estimates between competition levels are achieved despite genotype differences in performance.
- Grain yield and spikes m^{-2} were not genetically correlated, to early season vigour in the weed-free treatment ($P>0.05$), but were in the weed analogue treatment ($P < 0.01$)
- Selection in a weed free environment can lead to improvements in a weedy environment, but some high yielding lines under competition would be eliminated during selection.
- Competitive ability in wheat is associated with earliness in the northern Great Plains and also the long arm of chromosome 5A.
- The same population grown under organic and conventional management systems had similar heritability estimates for grain yield, kernel $spike^{-1}$, harvest index, flag leaf area, weed biomass, early season vigour, days to anthesis, days to maturity, and grain fill.
- The similar heritabilities estimates seen between management systems are achieved despite genotype differences in performance.
- Weed biomass was not correlated to grain yield, kernel $spike^{-1}$, harvest index, flag leaf area, early season vigour, days to anthesis, days to maturity, or grain fill under organic management, but weed biomass was

negatively correlated with grain yield, plant height, test weight, and flag leaf area under conventional management.

- Specific line selection differences exist between conventional and organic management systems.
- Selection differences occur across multi-location tests, and that selection for grain yield in organic systems should be conducted within organic systems.
- Breeding spring wheat for organic agriculture should be completed on organic land, but data garnered from conventional yield trials does also have some relevance towards breeding for organic environments.

6.8 Original Contributions to Knowledge

Breeding for organic management is a matter of some contention in both North America and Europe. While research had been ongoing in Europe, little work has been completed in North America. The original contributions to the knowledge of breeding spring wheat for organic agriculture are discussed in the following paragraphs:

It has been well established that the amount of weeds found in organic environments is greater than in a conventionally managed systems, and breeding for competitive ability has been suggested for both organic and conventional systems. Chapter 1.0 is a review of the literature which outlines what constitutes a competitive wheat plant, common breeding practices for wheat, and how the two can be combined under the principles of organic agriculture to breed for wheat

adapted to such a competitive environment. The review consolidates and summarizes the available knowledge on the subjects and will act as a reference for researchers wanting to investigate related topics.

Chapter 2.0 examines the effects of weeds alone on a population of wheat. The use of a model weed analogue is not uncommon in competition studies. However, reporting quantitative genetic parameters commonly used by breeders in population evaluation, and selection in a competitive environment, to my understanding, has not been reported in North America before. The study found that, for some traits, heritability estimates were similar under the two levels of weed competition. These results are contrary to the current breeding theory (Fasoula and Fasoula 1997) and could spark further investigation.

Attempting to uncover QTL associated with competitive ability has not been done in North America. Such a study was completed in Australia (Coleman et al. 2001), but the genetic map available for the population used in my study (Chapter 3.0) was the most detailed map of wheat created, comprising 1229 markers. The fact that no single large effect QTL was discovered demonstrates genetically the complexity of competitive ability in wheat.

Chapter 4.0 is a direct comparison of the effects of organic management on a random population of spring wheat that has been advanced to the stage where a preliminary yield trial would normally occur. It is my understanding that this kind of direct comparison has not been completed on such a population in North America. The study provides evidence that selection on organic land is different than selection on conventional land. This study also suggests that breeding

directly within organically managed systems would result in lower genetic gains than on conventionally managed land. Despite this, some traits may have similar heritability estimates between the two management systems. The heritability within each management system would follow different genetic paths because different genotypes are selected as top performers within each management system.

The final study of the thesis, Chapter 5.0, tests both the selections made, and the entire population, over multiple organic and conventional environments. To my knowledge, this type of testing has not been attempted previously. The study shows that despite some lines selected in common between management systems in a 'selection' year, multi-location yield trials in the two management systems could result in large differences between systems of lines selected from breeding programs. This provides evidence that breeding for organic management systems is possible, but data garnered from conventional yield trials does also have some relevance towards breeding for organic environments. Of the eight highest yielding lines (10%) in the multi-site organic trials, five were also in the top 15% of the multi-site conventional trials.

This thesis, as a whole, constitutes an "advancement of knowledge in the domains in which the research was conducted". Possibilities and limitations of organic spring wheat breeding were discussed and potential avenues of investigation into wheat competitive ability uncovered. Differences in line selection between organic and conventional management systems were identified and tested. In addition, I am very pleased that I was able to finish this thesis. I

have learned a great deal about perseverance, statistics, genetics and wheat breeding.

6.9 Literature Cited

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Appendix 1: BLUPS used in Chapter 2 and 3 sorted by year and location.

Table A1-1: BLUPS for each traits measured on the ITMI population grown without competition on the Ellerslie site in 2005 (See Chapter 2).

Line	Grain Yield (t ha^{-1})	Plant Height (cm)	Spike per m^{-2}	Grain fill Duration (days)	Days to Heading (days)	Days to Anthesis (days)	Days to Maturity (days)	Harvest index	Percent Trans-mittance
ITMI 001	4.22	93	101	52	55	59	111	0.42	0.26
ITMI 002	4.75	80	93	52	54	56	109	0.47	0.19
ITMI 003	4.54	94	78	54	54	56	111	0.43	0.32
ITMI 004	4.45	83	94	49	53	58	107	0.39	0.29
ITMI 005	5.38	98	98	54	61	63	117	0.44	0.22
ITMI 006	2.96	93	85	51	62	66	116	0.30	0.26
ITMI 009	2.93	77	79	48	56	60	109	0.39	0.36
ITMI 010	4.35	93	87	45	52	56	101	0.46	0.30
ITMI 011	3.66	84	85	56	57	61	118	0.40	0.23
ITMI 012	3.36	88	84	50	57	62	112	0.39	0.31
ITMI 013	3.27	94	104	50	62	66	117	0.34	0.26
ITMI 014	5.22	79	88	49	55	58	107	0.54	0.22
ITMI 015	5.32	97	90	52	63	67	118	0.38	0.26
ITMI 016	4.65	94	103	48	54	57	105	0.43	0.23
ITMI 017	4.62	93	100	48	54	57	105	0.43	0.23
ITMI 018	4.38	85	87	55	55	58	113	0.47	0.22
ITMI 019	3.24	89	75	48	56	62	109	0.38	0.26
ITMI 020	6.08	93	102	53	58	63	117	0.47	0.29
ITMI 021	3.60	84	103	55	59	63	118	0.41	0.26
ITMI 022	3.00	84	86	47	53	57	104	0.44	0.35
ITMI 023	3.60	80	101	48	54	57	105	0.33	0.32
ITMI 024	4.35	103	97	51	59	62	113	0.34	0.27
ITMI 025	5.98	91	96	50	56	58	109	0.52	0.26
ITMI 026	4.38	87	105	48	60	65	112	0.40	0.19
ITMI 027	5.10	81	90	49	56	59	109	0.50	0.23
ITMI 028	2.73	76	85	50	63	68	118	0.34	0.30
ITMI 029	5.10	90	83	51	52	56	108	0.48	0.25
ITMI 030	3.40	80	89	46	51	57	103	0.40	0.30
ITMI 031	2.52	88	66	49	58	64	112	0.32	0.32
ITMI 032	5.47	87	85	49	50	55	104	0.50	0.33
ITMI 033	4.31	88	78	47	51	57	104	0.49	0.32
ITMI 034	4.53	79	92	50	51	58	108	0.47	0.20
ITMI 035	2.89	86	80	49	64	68	116	0.41	0.34
ITMI 036	5.22	84	85	51	61	68	118	0.50	0.33
ITMI 037	2.28	93	69	47	61	67	113	0.30	0.30
ITMI 038	3.16	88	86	51	57	61	112	0.34	0.23
ITMI 039	2.46	81	83	44	53	58	102	0.30	0.32
ITMI 040	2.77	79	80	49	57	61	110	0.39	0.32
ITMI 041	4.67	79	81	51	52	55	106	0.52	0.29
ITMI 042	3.63	87	75	46	62	69	113	0.36	0.32
ITMI 044	3.71	86	104	45	51	54	99	0.32	0.22
ITMI 045	2.97	84	95	47	50	55	102	0.32	0.25
ITMI 046	3.82	87	67	51	67	69	120	0.41	0.24
ITMI 047	4.69	99	86	45	54	58	102	0.48	0.31
ITMI 048	2.90	81	83	49	53	56	105	0.39	0.33

ITMI 049	4.19	84	83	46	57	63	108	0.46	0.26
ITMI 050	4.34	97	93	53	67	69	122	0.44	0.27
ITMI 051	4.59	96	89	55	67	70	126	0.42	0.22
ITMI 052	2.80	89	64	46	55	60	106	0.42	0.39
ITMI 053	3.58	92	81	50	53	56	107	0.33	0.25
ITMI 054	4.47	101	92	46	55	58	103	0.39	0.23
ITMI 055	3.79	94	79	49	54	57	106	0.37	0.24
ITMI 056	4.34	94	82	54	64	66	120	0.44	0.22
ITMI 057	3.20	89	65	49	54	57	106	0.43	0.31
ITMI 058	2.84	81	75	48	57	61	109	0.39	0.31
ITMI 059	2.85	83	79	58	57	62	120	0.35	0.29
ITMI 060	3.81	84	91	50	51	55	105	0.37	0.26
ITMI 061	3.68	79	87	53	56	62	116	0.39	0.25
ITMI 062	5.35	89	98	50	52	56	106	0.50	0.30
ITMI 063	3.75	97	90	50	54	57	108	0.31	0.28
ITMI 064	4.54	79	113	45	51	55	100	0.44	0.32
ITMI 065	5.38	94	97	46	60	65	110	0.45	0.31
ITMI 066	3.29	86	87	55	65	69	125	0.38	0.25
ITMI 067	3.37	92	90	53	50	53	106	0.31	0.29
ITMI 068	3.85	87	81	60	66	68	130	0.38	0.26
ITMI 069	3.91	111	68	49	59	63	112	0.41	0.24
ITMI 070	4.51	88	112	49	55	57	105	0.41	0.18
ITMI 071	3.50	87	78	50	56	60	111	0.41	0.25
ITMI 072	2.90	80	90	44	51	55	98	0.45	0.28
ITMI 073	4.68	89	94	50	54	56	107	0.49	0.18
ITMI 074	5.64	87	97	49	54	56	105	0.48	0.20
ITMI 075	3.39	97	84	52	58	61	112	0.26	0.34
ITMI 076	3.98	102	103	57	57	61	119	0.35	0.24
ITMI 077	6.42	95	103	49	58	62	110	0.51	0.18
ITMI 078	2.97	87	88	48	56	61	109	0.27	0.30
ITMI 079	5.24	88	97	49	52	55	104	0.49	0.23
ITMI 080	3.11	94	80	48	58	65	112	0.29	0.23
ITMI 081	4.27	100	85	51	62	65	116	0.32	0.30
ITMI 082	4.97	84	92	53	59	63	117	0.48	0.31
ITMI 083	4.40	88	92	53	64	68	121	0.36	0.24
ITMI 084	4.05	90	85	57	67	69	127	0.34	0.26
ITMI 085	3.23	83	88	51	51	55	105	0.33	0.30
ITMI 086	2.57	92	74	47	57	65	111	0.27	0.26
ITMI 087	3.85	84	69	49	55	57	107	0.47	0.35
ITMI 088	4.26	88	98	46	57	61	107	0.40	0.26
ITMI 089	3.50	98	87	50	65	69	120	0.39	0.21
ITMI 090	3.12	91	71	52	66	69	121	0.36	0.24
ITMI 091	5.60	81	126	48	51	55	103	0.51	0.25
ITMI 092	5.89	94	93	54	56	60	114	0.51	0.30
ITMI 093	3.64	84	81	50	52	56	106	0.42	0.31
ITMI 094	3.76	75	73	51	56	60	111	0.52	0.33
ITMI 095	3.56	80	96	49	55	59	108	0.40	0.33
ITMI 096	5.03	91	82	49	60	67	116	0.45	0.34
ITMI 097	6.01	87	89	53	57	60	114	0.45	0.26
ITMI 099	3.24	92	76	47	57	61	108	0.43	0.32

ITMI 100	6.05	92	102	48	65	68	116	0.42	0.19
ITMI 101	3.34	89	78	50	55	63	113	0.39	0.37
ITMI 102	3.65	84	92	48	55	58	107	0.43	0.39
ITMI 103	3.83	80	85	53	56	59	113	0.46	0.37
ITMI 104	4.77	86	95	51	54	56	108	0.43	0.23
ITMI 105	3.77	80	96	47	55	59	106	0.41	0.32
ITMI 106	3.14	83	79	49	62	66	115	0.43	0.37
ITMI 109	3.25	92	89	53	57	61	113	0.35	0.30
ITMI 110	4.51	94	79	54	56	59	113	0.40	0.32
ITMI 111	5.47	103	87	54	63	65	119	0.40	0.24
ITMI 112	5.02	87	101	52	62	66	118	0.44	0.29
ITMI 114	4.90	86	106	53	65	67	120	0.40	0.16
ITMI 115	4.14	98	90	55	61	64	119	0.36	0.25

Table A1-2: BLUPS for each traits measured on the ITMI population grown with competition on the Ellerslie site in 2005 (See Chapter 2).

Line	Grain Yield (t ha^{-1})	Plant Height (cm)	Spike per m^{-2}	Grain fill Duration (days)	Days to Heading (days)	Days to Anthesis (days)	Days to Maturity (days)	Harvest index
ITMI 001	3.64	91	83	47	54	58	106	0.44
ITMI 002	3.46	79	81	47	53	56	103	0.49
ITMI 003	4.05	92	73	48	53	56	105	0.45
ITMI 004	3.73	82	81	45	53	58	102	0.41
ITMI 005	4.10	97	83	49	60	62	111	0.46
ITMI 006	2.36	91	72	45	61	65	110	0.32
ITMI 009	2.21	76	66	44	56	59	104	0.41
ITMI 010	3.88	91	76	41	51	55	96	0.49
ITMI 011	2.89	82	73	50	56	60	111	0.42
ITMI 012	2.54	87	70	45	56	62	107	0.42
ITMI 013	2.43	92	81	45	61	65	111	0.36
ITMI 014	4.03	78	81	45	54	57	102	0.56
ITMI 015	3.50	95	72	46	62	66	112	0.40
ITMI 016	3.47	93	87	44	53	56	100	0.45
ITMI 017	4.07	92	93	42	53	57	99	0.45
ITMI 018	3.56	84	76	49	54	58	108	0.49
ITMI 019	2.32	87	61	43	55	62	104	0.40
ITMI 020	4.77	91	81	48	57	63	110	0.49
ITMI 021	2.63	83	89	50	58	63	113	0.43
ITMI 022	2.07	82	71	42	52	57	98	0.47
ITMI 023	2.94	79	88	43	53	57	100	0.35
ITMI 024	3.40	101	83	46	58	62	108	0.36
ITMI 025	4.44	90	86	45	55	58	103	0.54
ITMI 026	3.32	87	85	43	59	64	107	0.42
ITMI 027	4.12	80	79	44	55	59	103	0.52
ITMI 028	1.74	74	66	45	62	67	113	0.36
ITMI 029	4.24	89	69	46	51	56	102	0.50
ITMI 030	2.90	79	80	41	50	56	98	0.42
ITMI 031	2.26	87	59	43	57	64	106	0.34
ITMI 032	4.21	86	78	44	49	54	99	0.53
ITMI 033	3.70	88	70	42	50	56	98	0.52
ITMI 034	3.82	78	82	46	50	57	103	0.49
ITMI 035	1.99	85	69	44	63	67	111	0.43
ITMI 036	3.38	83	71	46	60	67	113	0.52
ITMI 037	1.72	91	57	41	60	67	107	0.32
ITMI 038	2.53	87	72	46	56	61	106	0.36
ITMI 039	1.99	79	72	40	52	57	97	0.32
ITMI 040	1.96	78	60	45	56	60	105	0.41
ITMI 041	3.43	78	75	46	51	55	101	0.54
ITMI 042	2.51	86	65	41	61	68	108	0.38
ITMI 044	2.75	85	89	40	50	54	94	0.34
ITMI 045	2.45	83	88	43	49	54	97	0.34
ITMI 046	2.17	86	52	47	66	68	115	0.43
ITMI 047	3.73	98	78	40	53	57	97	0.50
ITMI 048	2.28	80	71	44	52	55	100	0.41

ITMI 049	3.09	83	73	42	56	63	103	0.48
ITMI 050	2.93	95	72	47	66	69	117	0.46
ITMI 051	3.09	94	68	50	66	69	120	0.44
ITMI 052	2.13	87	60	42	55	59	101	0.44
ITMI 053	3.29	91	78	46	52	55	102	0.35
ITMI 054	3.83	99	82	41	54	58	98	0.41
ITMI 055	3.36	92	69	44	53	57	101	0.39
ITMI 056	3.11	92	71	49	63	66	115	0.46
ITMI 057	2.79	87	61	44	54	56	101	0.45
ITMI 058	2.11	81	62	43	56	61	104	0.40
ITMI 059	2.04	82	64	52	57	62	114	0.37
ITMI 060	3.37	83	81	45	50	54	100	0.39
ITMI 061	3.09	78	71	49	56	61	110	0.41
ITMI 062	4.32	87	86	46	51	55	101	0.52
ITMI 063	2.90	96	77	45	54	57	102	0.33
ITMI 064	3.59	78	96	40	50	54	94	0.46
ITMI 065	4.27	93	84	41	59	64	104	0.48
ITMI 066	2.71	85	68	51	64	68	119	0.41
ITMI 067	3.05	91	82	47	49	53	100	0.33
ITMI 068	2.92	85	66	55	65	68	124	0.40
ITMI 069	3.20	109	60	44	59	63	107	0.43
ITMI 070	3.51	87	88	43	54	56	99	0.43
ITMI 071	2.88	86	73	45	55	60	105	0.43
ITMI 072	2.23	79	79	40	50	54	93	0.47
ITMI 073	4.13	88	81	46	54	56	102	0.51
ITMI 074	4.42	86	82	44	53	56	99	0.50
ITMI 075	2.18	95	71	47	57	60	107	0.28
ITMI 076	3.06	100	88	51	56	61	113	0.37
ITMI 077	4.91	94	90	43	57	61	105	0.53
ITMI 078	2.62	86	70	44	55	61	104	0.28
ITMI 079	4.19	86	82	44	52	55	98	0.52
ITMI 080	2.60	93	71	43	57	65	106	0.31
ITMI 081	3.24	99	77	47	61	64	111	0.34
ITMI 082	3.62	83	74	48	58	63	111	0.51
ITMI 083	2.92	87	75	48	63	67	115	0.37
ITMI 084	2.35	88	63	52	66	69	121	0.35
ITMI 085	2.67	82	80	46	51	54	100	0.35
ITMI 086	2.35	90	60	43	57	64	106	0.29
ITMI 087	2.82	83	59	44	54	57	102	0.49
ITMI 088	3.76	87	88	41	56	61	101	0.42
ITMI 089	2.22	96	64	44	64	69	114	0.41
ITMI 090	1.96	89	60	47	65	69	116	0.37
ITMI 091	4.07	80	113	43	50	55	98	0.53
ITMI 092	4.66	92	79	48	55	59	108	0.53
ITMI 093	3.03	83	68	45	51	55	101	0.45
ITMI 094	2.84	73	68	45	55	60	105	0.54
ITMI 095	2.77	79	89	44	54	59	103	0.42
ITMI 096	3.16	89	70	44	59	66	109	0.47
ITMI 097	4.55	86	84	48	56	59	108	0.47
ITMI 099	2.75	91	71	43	57	60	103	0.45

ITMI 100	4.15	91	85	43	64	68	111	0.44
ITMI 101	2.48	89	62	44	55	63	107	0.41
ITMI 102	2.78	83	77	44	54	58	102	0.45
ITMI 103	3.48	79	75	48	55	59	108	0.48
ITMI 104	3.53	85	81	46	54	56	102	0.45
ITMI 105	3.27	78	83	43	54	58	101	0.43
ITMI 106	2.82	82	67	44	61	66	109	0.45
ITMI 109	2.81	90	77	47	56	60	107	0.37
ITMI 110	3.63	93	69	48	55	58	107	0.42
ITMI 111	3.80	102	75	49	62	65	114	0.42
ITMI 112	3.98	86	85	47	61	66	113	0.46
ITMI 114	3.80	84	86	47	64	67	115	0.42
ITMI 115	3.10	97	80	50	60	64	114	0.38

Table A1-3: BLUPS for each traits measured on the ITMI population grown without competition on the Michner site in 2005 (See Chapter 2).

Line	Grain Yield (t ha^{-1})	Plant Height (cm)	Spike per m^{-2}	Grain fill Duration (days)	Days to Heading (days)	Days to Anthesis (days)	Days to Maturity (days)	Harvest index
ITMI 001	6.91	82	136	45	60	64	109	0.45
ITMI 002	7.13	74	123	44	57	61	106	0.47
ITMI 003	6.29	89	114	46	57	61	107	0.40
ITMI 004	5.29	77	126	42	57	62	104	0.32
ITMI 005	7.34	90	136	46	64	66	112	0.42
ITMI 006	4.74	83	122	44	63	68	113	0.29
ITMI 009	4.36	66	108	35	60	64	99	0.40
ITMI 010	5.99	85	116	35	58	62	96	0.44
ITMI 011	4.63	76	118	47	59	66	113	0.33
ITMI 012	5.32	80	123	46	60	64	110	0.38
ITMI 013	4.88	86	145	44	66	70	114	0.31
ITMI 014	7.13	76	112	45	58	61	107	0.53
ITMI 015	6.38	91	117	47	64	68	115	0.31
ITMI 016	6.87	86	138	41	57	61	103	0.42
ITMI 017	5.72	87	139	41	58	61	103	0.36
ITMI 018	6.13	79	120	47	58	63	110	0.43
ITMI 019	6.25	79	114	43	58	63	107	0.41
ITMI 020	6.95	83	130	45	62	66	111	0.43
ITMI 021	4.80	75	135	47	63	66	113	0.36
ITMI 022	5.13	77	126	41	57	62	103	0.44
ITMI 023	5.16	71	129	42	56	61	103	0.32
ITMI 024	5.28	91	134	42	62	65	106	0.29
ITMI 025	9.12	84	134	42	60	63	105	0.58
ITMI 026	6.45	78	135	40	64	69	108	0.44
ITMI 027	7.44	75	129	44	60	63	107	0.49
ITMI 028	4.59	68	123	45	65	71	116	0.35
ITMI 029	7.52	85	109	42	57	62	104	0.49
ITMI 030	4.77	74	122	39	55	62	100	0.36
ITMI 031	3.48	81	99	46	61	64	112	0.27
ITMI 032	7.03	80	116	39	55	60	99	0.44
ITMI 033	5.88	83	114	36	54	61	96	0.43
ITMI 034	6.64	73	117	35	55	68	101	0.47
ITMI 035	4.45	76	111	43	65	69	112	0.47
ITMI 036	7.88	74	116	45	61	67	112	0.54
ITMI 037	3.74	84	108	42	62	68	110	0.26
ITMI 038	4.60	77	118	44	59	64	108	0.34
ITMI 039	3.74	75	115	36	58	64	99	0.27
ITMI 040	4.16	72	111	42	62	65	106	0.42
ITMI 041	6.43	71	120	45	56	61	106	0.48
ITMI 042	5.51	77	110	42	64	75	115	0.34
ITMI 044	5.69	81	138	37	55	60	96	0.32
ITMI 045	4.61	79	129	36	56	62	97	0.30
ITMI 046	6.03	82	96	46	67	71	118	0.39
ITMI 047	7.51	91	128	38	57	61	99	0.46
ITMI 048	4.09	73	109	41	57	60	101	0.34

ITMI 049	6.62	77	127	42	60	63	108	0.44
ITMI 050	6.92	92	130	44	69	72	116	0.45
ITMI 051	6.82	92	129	45	69	73	119	0.41
ITMI 052	3.78	76	91	32	60	69	99	0.36
ITMI 053	5.26	85	116	44	57	61	106	0.33
ITMI 054	6.41	92	123	41	60	63	104	0.38
ITMI 055	5.91	88	114	43	56	61	105	0.36
ITMI 056	6.62	85	116	47	65	68	115	0.44
ITMI 057	3.88	79	97	34	57	62	96	0.36
ITMI 058	4.28	71	105	42	61	65	107	0.37
ITMI 059	4.97	78	111	52	61	65	117	0.38
ITMI 060	4.96	77	118	40	55	61	100	0.33
ITMI 061	6.03	73	120	49	60	66	116	0.40
ITMI 062	6.89	80	125	42	57	61	103	0.46
ITMI 063	4.88	87	125	45	58	61	106	0.30
ITMI 064	6.26	71	141	37	55	60	97	0.43
ITMI 065	7.07	86	127	42	63	67	109	0.48
ITMI 066	5.79	81	122	47	66	70	117	0.44
ITMI 067	4.63	88	123	44	55	58	102	0.24
ITMI 068	4.83	80	107	49	67	71	121	0.35
ITMI 069	6.28	99	101	41	62	67	108	0.45
ITMI 070	6.98	83	134	42	57	63	105	0.41
ITMI 071	5.49	77	115	44	59	64	108	0.42
ITMI 072	4.29	70	124	33	54	58	89	0.43
ITMI 073	6.17	81	123	42	57	61	103	0.45
ITMI 074	7.17	82	128	45	57	61	106	0.46
ITMI 075	4.79	91	121	46	63	66	112	0.23
ITMI 076	5.19	93	132	48	61	64	112	0.33
ITMI 077	8.76	86	142	43	62	66	109	0.54
ITMI 078	3.80	78	125	43	61	65	109	0.21
ITMI 079	7.13	80	129	44	56	60	105	0.49
ITMI 080	4.73	88	114	42	62	71	114	0.28
ITMI 081	6.07	89	116	46	64	67	113	0.33
ITMI 082	7.33	79	128	46	64	67	113	0.49
ITMI 083	5.39	82	121	46	64	67	113	0.34
ITMI 084	5.70	80	115	46	67	71	117	0.31
ITMI 085	4.72	77	124	44	57	61	105	0.30
ITMI 086	4.26	82	108	41	61	69	109	0.25
ITMI 087	5.53	72	103	39	58	62	101	0.50
ITMI 088	6.00	81	143	46	59	63	109	0.37
ITMI 089	5.94	94	124	42	66	74	116	0.42
ITMI 090	5.24	82	109	45	68	74	119	0.38
ITMI 091	7.48	73	157	43	56	61	104	0.46
ITMI 092	7.76	86	124	46	58	63	110	0.50
ITMI 093	4.95	81	111	37	56	60	95	0.39
ITMI 094	6.09	68	104	43	58	62	106	0.51
ITMI 095	5.08	75	130	41	57	62	103	0.37
ITMI 096	8.35	85	121	44	65	73	117	0.47
ITMI 097	8.32	79	128	47	61	64	111	0.46
ITMI 099	5.07	80	113	36	60	64	99	0.42

ITMI 100	6.91	87	121	44	67	70	115	0.36
ITMI 101	5.35	83	111	44	59	65	109	0.40
ITMI 102	4.74	72	120	38	59	63	100	0.42
ITMI 103	5.64	75	117	45	58	63	108	0.42
ITMI 104	6.02	77	131	41	58	62	102	0.40
ITMI 105	5.46	72	130	42	59	63	106	0.39
ITMI 106	6.04	78	113	45	64	68	113	0.46
ITMI 109	4.69	85	126	50	60	64	115	0.33
ITMI 110	5.77	85	114	44	58	62	107	0.36
ITMI 111	6.36	95	119	48	65	67	116	0.38
ITMI 112	6.53	78	133	45	62	65	111	0.40
ITMI 114	6.75	82	142	46	65	68	115	0.38
ITMI 115	6.39	89	128	49	63	66	116	0.37

Table A1-4: BLUPS for each traits measured on the ITMI population grown with competition on the Michner site in 2005 (See Chapter 2).

Line	Grain Yield (t ha^{-1})	Plant Height (cm)	Spike per m^{-2}	Grain fill Duration (days)	Days to Heading (days)	Days to Anthesis (days)	Days to Maturity (days)	Harvest index
ITMI 001	6.01	84	109	46	60	63	109	0.47
ITMI 002	4.95	77	102	45	56	60	105	0.48
ITMI 003	5.18	92	99	47	56	60	108	0.42
ITMI 004	3.80	80	104	43	56	62	104	0.33
ITMI 005	5.19	93	112	46	64	66	112	0.43
ITMI 006	3.36	86	100	45	62	68	113	0.30
ITMI 009	2.82	70	85	36	60	64	99	0.41
ITMI 010	4.72	88	96	37	57	61	98	0.46
ITMI 011	3.29	79	97	46	58	65	112	0.34
ITMI 012	3.78	84	100	47	59	63	110	0.39
ITMI 013	3.32	88	112	44	65	69	114	0.33
ITMI 014	4.99	79	96	46	58	61	107	0.54
ITMI 015	3.91	93	91	47	64	67	115	0.32
ITMI 016	4.89	90	113	43	56	61	104	0.43
ITMI 017	4.25	90	122	42	57	61	103	0.37
ITMI 018	4.29	82	101	48	57	62	110	0.44
ITMI 019	4.35	82	91	44	58	63	107	0.42
ITMI 020	5.24	86	99	45	61	65	110	0.44
ITMI 021	3.13	79	112	48	62	65	113	0.37
ITMI 022	3.32	80	102	42	56	61	103	0.45
ITMI 023	3.63	75	108	43	55	60	103	0.33
ITMI 024	3.74	94	112	42	61	65	107	0.30
ITMI 025	6.65	86	115	43	59	62	105	0.59
ITMI 026	4.51	82	105	40	63	68	108	0.45
ITMI 027	5.64	79	109	44	59	63	107	0.50
ITMI 028	2.73	72	94	45	64	70	116	0.36
ITMI 029	5.82	88	86	43	56	61	104	0.50
ITMI 030	3.40	77	104	40	54	61	101	0.37
ITMI 031	2.38	84	83	46	60	64	112	0.28
ITMI 032	5.04	84	100	40	55	60	99	0.45
ITMI 033	4.85	86	96	37	53	60	96	0.44
ITMI 034	5.00	76	98	37	55	67	102	0.48
ITMI 035	2.85	79	91	43	64	69	112	0.48
ITMI 036	5.07	77	93	46	60	66	113	0.55
ITMI 037	2.43	87	87	43	61	67	110	0.27
ITMI 038	3.37	80	96	45	58	64	108	0.35
ITMI 039	2.59	78	94	37	57	63	100	0.29
ITMI 040	2.60	76	82	43	61	64	107	0.43
ITMI 041	4.47	74	104	45	56	60	106	0.49
ITMI 042	3.55	81	91	43	63	74	115	0.35
ITMI 044	3.98	84	114	39	55	59	97	0.33
ITMI 045	3.32	82	113	38	55	61	98	0.31
ITMI 046	3.21	85	71	47	66	70	118	0.39
ITMI 047	5.48	95	111	39	56	60	99	0.47
ITMI 048	2.72	76	88	42	56	60	101	0.35

ITMI 049	4.65	80	107	43	59	62	108	0.45
ITMI 050	4.70	95	100	45	68	72	116	0.46
ITMI 051	4.62	95	99	45	68	73	118	0.42
ITMI 052	2.27	79	77	33	59	69	100	0.37
ITMI 053	4.37	88	104	45	57	61	107	0.34
ITMI 054	5.01	95	104	42	59	62	104	0.39
ITMI 055	4.75	91	95	44	55	61	105	0.37
ITMI 056	4.51	89	97	48	64	68	116	0.45
ITMI 057	2.70	82	84	36	57	62	97	0.38
ITMI 058	2.70	75	83	43	60	64	107	0.38
ITMI 059	3.37	81	87	52	60	65	117	0.39
ITMI 060	3.82	81	99	41	55	61	101	0.34
ITMI 061	4.69	76	95	51	59	65	117	0.41
ITMI 062	5.24	83	104	43	56	61	104	0.47
ITMI 063	3.39	90	104	45	58	61	106	0.31
ITMI 064	4.63	75	115	37	54	60	97	0.44
ITMI 065	5.40	90	104	42	63	67	109	0.50
ITMI 066	4.49	84	94	49	65	69	118	0.45
ITMI 067	3.55	91	106	44	54	58	102	0.25
ITMI 068	3.19	84	83	50	67	70	121	0.36
ITMI 069	4.70	102	85	42	61	67	108	0.46
ITMI 070	5.28	86	100	43	57	62	105	0.42
ITMI 071	3.99	81	101	44	58	63	108	0.43
ITMI 072	2.97	74	104	35	53	57	90	0.44
ITMI 073	4.95	84	101	44	56	61	104	0.46
ITMI 074	5.30	85	104	45	57	60	106	0.47
ITMI 075	2.92	93	99	47	62	65	112	0.24
ITMI 076	3.62	96	107	48	60	64	112	0.34
ITMI 077	6.57	89	120	43	62	66	110	0.55
ITMI 078	2.68	82	99	45	60	64	110	0.21
ITMI 079	5.28	83	105	45	56	60	106	0.50
ITMI 080	3.43	92	96	43	61	71	114	0.29
ITMI 081	4.25	91	99	47	63	66	113	0.34
ITMI 082	5.22	82	102	47	63	66	113	0.51
ITMI 083	3.33	85	96	47	63	66	114	0.35
ITMI 084	3.15	82	83	46	66	70	117	0.32
ITMI 085	3.42	80	107	45	57	60	105	0.31
ITMI 086	3.43	85	85	42	60	68	109	0.26
ITMI 087	3.76	76	85	40	57	61	101	0.51
ITMI 088	4.85	85	124	46	58	62	109	0.38
ITMI 089	3.67	97	92	42	66	74	116	0.43
ITMI 090	3.42	85	88	46	67	73	119	0.39
ITMI 091	5.07	76	135	44	55	61	104	0.47
ITMI 092	5.81	89	100	47	58	63	110	0.52
ITMI 093	3.56	84	89	38	55	59	96	0.40
ITMI 094	4.18	71	90	43	58	62	106	0.52
ITMI 095	3.44	77	113	43	56	61	104	0.38
ITMI 096	5.18	87	100	45	64	72	117	0.48
ITMI 097	5.88	82	115	48	61	63	111	0.47
ITMI 099	3.90	84	99	38	60	63	100	0.43

ITMI 100	4.15	90	95	45	66	70	115	0.36
ITMI 101	3.64	87	85	44	59	65	109	0.41
ITMI 102	3.19	76	96	39	58	62	101	0.43
ITMI 103	4.49	78	98	46	58	62	109	0.43
ITMI 104	4.19	81	108	42	57	61	103	0.41
ITMI 105	3.98	75	108	44	58	62	106	0.40
ITMI 106	4.86	82	93	46	63	67	113	0.48
ITMI 109	3.58	87	106	50	59	63	114	0.35
ITMI 110	4.09	89	96	45	58	62	106	0.37
ITMI 111	4.03	98	98	49	64	67	117	0.39
ITMI 112	4.80	81	108	46	61	65	111	0.41
ITMI 114	4.96	85	113	47	64	67	115	0.39
ITMI 115	4.51	92	109	50	62	66	116	0.38

Table A1-5: BLUPS for each traits measured on the ITMI population grown without competition on the Michner site in 2006 (See Chapter 2).

Line	Grain Yield (t ha^{-1})	Plant Height (cm)	Spike per m^{-2}	Grain fill Duration (days)	Days to Heading (days)	Days to Anthesis (days)	Days to Maturity (days)	Harvest index	Percent Trans-mittance
ITMI 001	3.75	78	125	40	57	61	100	0.31	0.29
ITMI 002	6.02	68	118	42	44	46	88	0.52	0.27
ITMI 003	5.12	84	97	42	44	46	88	0.46	0.40
ITMI 004	4.69	70	107	40	45	47	88	0.41	0.34
ITMI 005	7.09	83	122	44	53	54	98	0.52	0.29
ITMI 006	4.14	76	107	42	49	52	94	0.35	0.33
ITMI 009	3.66	59	94	39	47	49	89	0.46	0.38
ITMI 010	5.35	78	110	37	44	47	84	0.49	0.34
ITMI 011	4.37	70	107	45	48	50	96	0.42	0.27
ITMI 012	3.58	74	97	41	48	50	90	0.40	0.35
ITMI 013	3.33	81	122	39	58	61	100	0.28	0.25
ITMI 014	6.22	70	105	41	47	49	90	0.57	0.33
ITMI 015	4.88	80	100	44	51	53	97	0.36	0.36
ITMI 016	5.64	80	122	37	46	49	86	0.46	0.20
ITMI 017	4.65	78	113	39	45	48	88	0.41	0.26
ITMI 018	4.86	74	99	44	44	47	90	0.49	0.29
ITMI 019	4.63	76	100	40	46	48	88	0.44	0.26
ITMI 020	5.84	76	117	43	49	51	94	0.49	0.32
ITMI 021	4.31	70	120	43	49	51	94	0.46	0.36
ITMI 022	4.68	74	109	39	44	46	85	0.59	0.32
ITMI 023	3.87	64	110	41	44	47	88	0.37	0.32
ITMI 024	5.71	86	115	39	50	52	90	0.40	0.28
ITMI 025	7.18	78	115	39	47	49	88	0.56	0.27
ITMI 026	4.90	75	128	40	54	57	96	0.44	0.26
ITMI 027	6.29	71	107	40	49	51	90	0.53	0.30
ITMI 028	3.90	63	103	44	54	57	102	0.44	0.36
ITMI 029	6.27	80	103	40	44	46	86	0.54	0.34
ITMI 030	4.21	63	104	39	43	46	86	0.45	0.31
ITMI 031	4.48	75	95	43	43	45	89	0.42	0.34
ITMI 032	5.53	75	103	38	42	45	82	0.52	0.39
ITMI 033	5.70	76	101	37	42	45	82	0.56	0.32
ITMI 034	5.44	71	108	36	43	47	82	0.51	0.26
ITMI 035	3.81	70	97	45	47	50	96	0.45	0.45
ITMI 036	6.70	70	98	42	50	53	96	0.60	0.36
ITMI 037	2.83	81	83	41	54	56	97	0.32	0.30
ITMI 038	3.81	72	103	47	46	49	96	0.36	0.29
ITMI 039	3.30	63	102	35	46	50	85	0.36	0.37
ITMI 040	3.33	67	99	41	48	50	91	0.42	0.40
ITMI 041	6.09	67	111	40	44	47	86	0.56	0.38
ITMI 042	4.56	74	94	41	52	56	98	0.43	0.41
ITMI 044	4.49	74	126	37	43	45	82	0.36	0.23
ITMI 045	3.54	71	121	37	43	45	83	0.31	0.27
ITMI 046	5.75	77	92	43	57	60	102	0.47	0.29
ITMI 047	6.18	84	108	37	43	46	83	0.54	0.29
ITMI 048	3.93	71	102	40	44	46	86	0.41	0.43

ITMI 049	4.69	73	95	39	49	52	91	0.48	0.32
ITMI 050	5.40	84	114	39	55	58	97	0.48	0.30
ITMI 051	6.23	84	114	43	56	59	101	0.47	0.23
ITMI 052	3.43	72	79	37	48	52	89	0.47	0.45
ITMI 053	5.22	79	104	40	44	46	86	0.40	0.24
ITMI 054	5.31	86	107	37	47	50	86	0.43	0.28
ITMI 055	4.51	80	100	38	46	49	86	0.36	0.26
ITMI 056	4.98	79	98	43	53	56	98	0.46	0.28
ITMI 057	3.98	74	82	38	46	49	87	0.47	0.40
ITMI 058	3.20	67	88	40	52	55	95	0.42	0.42
ITMI 059	3.86	72	97	46	50	53	98	0.40	0.35
ITMI 060	4.01	72	106	41	42	45	86	0.36	0.27
ITMI 061	3.99	66	111	43	49	52	96	0.40	0.34
ITMI 062	5.15	75	110	39	44	47	85	0.52	0.28
ITMI 063	4.06	82	108	40	45	47	87	0.31	0.32
ITMI 064	4.93	64	126	36	43	45	81	0.48	0.38
ITMI 065	5.41	82	110	39	52	56	94	0.47	0.33
ITMI 066	3.71	73	103	44	54	57	101	0.42	0.26
ITMI 067	3.69	80	112	41	42	43	84	0.28	0.32
ITMI 068	3.89	73	89	46	56	58	104	0.41	0.28
ITMI 069	5.41	89	86	38	51	53	91	0.49	0.31
ITMI 070	5.52	73	120	40	46	48	88	0.46	0.22
ITMI 071	4.48	74	103	41	45	50	91	0.45	0.29
ITMI 072	3.22	63	101	40	42	44	85	0.44	0.35
ITMI 073	5.31	74	116	42	44	45	88	0.53	0.25
ITMI 074	6.33	75	115	42	43	45	87	0.51	0.28
ITMI 075	4.27	83	106	41	49	51	92	0.29	0.30
ITMI 076	4.69	87	111	43	48	51	93	0.41	0.27
ITMI 077	6.99	79	123	39	49	52	91	0.56	0.27
ITMI 078	2.89	72	109	41	50	53	93	0.25	0.37
ITMI 079	5.18	76	112	40	44	47	86	0.49	0.42
ITMI 080	4.48	82	99	42	50	53	96	0.35	0.20
ITMI 081	4.39	83	97	41	52	54	95	0.34	0.26
ITMI 082	5.46	74	105	43	54	56	100	0.52	0.28
ITMI 083	4.39	74	101	42	50	53	95	0.38	0.29
ITMI 084	5.25	77	101	44	51	54	98	0.43	0.34
ITMI 085	3.41	71	103	41	44	47	88	0.31	0.33
ITMI 086	3.45	77	93	42	49	52	95	0.30	0.29
ITMI 087	4.70	69	85	38	46	50	87	0.52	0.38
ITMI 088	4.79	74	120	41	48	50	90	0.41	0.27
ITMI 089	4.88	87	106	42	58	60	102	0.40	0.25
ITMI 090	4.32	74	93	42	56	60	102	0.42	0.28
ITMI 091	5.66	65	145	40	44	46	86	0.50	0.27
ITMI 092	6.43	79	111	42	48	50	92	0.54	0.31
ITMI 093	4.36	74	96	39	44	46	85	0.44	0.36
ITMI 094	5.07	64	92	42	49	52	94	0.58	0.37
ITMI 095	4.58	67	117	40	47	49	89	0.45	0.36
ITMI 096	6.27	78	101	43	51	55	98	0.51	0.29
ITMI 097	6.45	73	103	42	48	50	91	0.49	0.27
ITMI 099	4.17	76	97	37	47	50	87	0.49	0.39

ITMI 100	6.61	79	116	42	55	56	98	0.47	0.19
ITMI 101	4.29	77	95	44	46	52	97	0.44	0.41
ITMI 102	3.85	69	105	38	46	49	87	0.45	0.42
ITMI 103	3.95	67	90	40	46	49	89	0.48	0.42
ITMI 104	5.92	71	118	40	45	46	86	0.57	0.30
ITMI 105	4.24	69	118	38	44	47	86	0.45	0.29
ITMI 106	3.79	71	93	43	53	54	97	0.45	0.35
ITMI 109	4.76	78	109	43	46	49	92	0.44	0.35
ITMI 110	4.97	79	96	40	46	49	88	0.44	0.35
ITMI 111	5.70	87	98	44	54	56	100	0.41	0.21
ITMI 112	5.75	71	112	42	50	53	95	0.50	0.30
ITMI 114	5.18	75	132	44	55	57	102	0.38	0.25
ITMI 115	5.35	80	115	44	52	54	98	0.38	0.26

Table A1-6: BLUPS for each traits measured on the ITMI population grown with competition on the Michner site in 2006 (See Chapter 2).

Line	Grain Yield (t ha^{-1})	Plant Height (cm)	Spike per m^{-2}	Grain fill Duration (days)	Days to Heading (days)	Days to Anthesis (days)	Days to Maturity (days)	Harvest index
ITMI 001	2.46	79	84	41	57	60	101	0.32
ITMI 002	3.83	71	83	42	44	46	89	0.52
ITMI 003	3.75	85	68	43	43	46	89	0.46
ITMI 004	3.11	72	70	42	45	47	89	0.41
ITMI 005	4.89	85	84	44	52	54	98	0.52
ITMI 006	2.58	78	71	42	49	51	94	0.35
ITMI 009	1.97	62	56	40	47	49	90	0.45
ITMI 010	3.95	79	74	39	44	47	86	0.49
ITMI 011	2.71	71	72	45	48	50	95	0.42
ITMI 012	1.95	76	60	41	48	50	91	0.40
ITMI 013	1.68	82	75	40	58	61	100	0.28
ITMI 014	4.18	72	75	42	47	49	91	0.57
ITMI 015	2.33	81	58	44	51	53	98	0.36
ITMI 016	3.60	82	82	39	46	48	87	0.46
ITMI 017	3.22	79	82	40	45	48	88	0.41
ITMI 018	3.10	76	65	45	43	47	91	0.48
ITMI 019	2.79	77	63	41	45	48	89	0.44
ITMI 020	3.86	78	72	43	48	51	94	0.49
ITMI 021	2.41	72	82	43	49	51	94	0.46
ITMI 022	2.87	75	71	40	44	46	86	0.59
ITMI 023	2.37	66	75	42	44	46	88	0.37
ITMI 024	3.69	87	77	39	50	52	91	0.40
ITMI 025	4.73	80	82	40	47	49	88	0.55
ITMI 026	2.98	77	84	40	53	57	97	0.45
ITMI 027	4.33	73	73	41	48	51	91	0.53
ITMI 028	1.98	65	60	45	54	57	103	0.45
ITMI 029	4.43	82	65	41	44	46	87	0.54
ITMI 030	2.86	65	71	41	43	46	87	0.45
ITMI 031	3.20	77	65	43	43	46	90	0.42
ITMI 032	3.61	77	73	38	42	45	83	0.52
ITMI 033	4.24	78	69	38	42	45	83	0.56
ITMI 034	3.79	72	75	37	42	46	84	0.51
ITMI 035	2.05	73	63	46	47	50	97	0.45
ITMI 036	3.72	72	61	43	49	53	97	0.60
ITMI 037	1.41	82	47	41	54	56	98	0.33
ITMI 038	2.38	75	66	47	46	48	96	0.37
ITMI 039	1.98	65	67	37	46	49	86	0.36
ITMI 040	1.65	69	55	43	48	50	93	0.42
ITMI 041	4.04	69	81	40	44	47	87	0.56
ITMI 042	2.51	76	60	43	52	55	98	0.43
ITMI 044	2.74	76	88	38	43	45	83	0.36
ITMI 045	2.27	73	90	38	42	45	83	0.31
ITMI 046	3.02	79	53	44	57	59	103	0.47
ITMI 047	4.25	86	76	38	43	46	84	0.54
ITMI 048	2.28	73	66	41	44	45	86	0.41

ITMI 049	2.56	75	61	40	48	52	92	0.48
ITMI 050	3.02	86	69	40	55	58	98	0.48
ITMI 051	3.82	86	69	43	56	59	101	0.47
ITMI 052	1.77	73	51	39	48	52	90	0.47
ITMI 053	4.05	81	77	41	44	46	87	0.40
ITMI 054	3.82	88	74	38	47	50	87	0.43
ITMI 055	3.43	81	66	39	45	48	87	0.37
ITMI 056	2.79	81	64	43	53	55	99	0.46
ITMI 057	2.51	75	55	39	46	49	88	0.47
ITMI 058	1.59	69	51	41	52	55	96	0.42
ITMI 059	2.06	73	58	46	50	52	98	0.40
ITMI 060	2.72	73	72	42	42	45	87	0.36
ITMI 061	2.57	68	71	45	49	52	97	0.40
ITMI 062	3.30	77	74	40	44	47	86	0.52
ITMI 063	2.46	84	72	41	45	47	88	0.31
ITMI 064	3.23	66	86	36	42	45	81	0.48
ITMI 065	3.59	84	73	39	52	56	95	0.47
ITMI 066	2.20	75	60	45	53	56	101	0.43
ITMI 067	2.44	82	81	41	42	43	85	0.28
ITMI 068	2.07	75	51	47	56	58	105	0.41
ITMI 069	3.61	90	55	39	50	53	91	0.49
ITMI 070	3.66	76	72	40	46	48	88	0.46
ITMI 071	2.87	76	75	42	45	49	92	0.45
ITMI 072	1.74	65	66	42	42	44	86	0.44
ITMI 073	3.77	76	79	44	43	45	89	0.53
ITMI 074	4.20	76	77	42	43	45	87	0.51
ITMI 075	2.20	84	69	42	49	51	92	0.29
ITMI 076	2.84	88	72	43	48	50	93	0.41
ITMI 077	4.49	81	86	39	49	52	91	0.56
ITMI 078	1.67	74	68	42	50	53	95	0.25
ITMI 079	3.34	78	73	41	44	47	87	0.49
ITMI 080	3.02	84	67	42	50	53	96	0.35
ITMI 081	2.50	84	65	42	52	54	96	0.34
ITMI 082	3.18	75	64	44	54	56	100	0.52
ITMI 083	2.20	76	61	43	50	53	96	0.38
ITMI 084	2.68	78	54	45	51	53	99	0.43
ITMI 085	2.01	73	72	42	44	46	88	0.30
ITMI 086	2.35	78	56	43	49	52	95	0.30
ITMI 087	2.85	71	52	39	46	49	88	0.52
ITMI 088	3.46	76	86	41	47	50	91	0.41
ITMI 089	2.52	89	60	41	58	61	102	0.40
ITMI 090	2.31	75	58	43	56	59	103	0.41
ITMI 091	3.30	67	108	41	44	46	87	0.50
ITMI 092	4.39	81	73	42	48	50	92	0.54
ITMI 093	2.82	76	59	40	43	46	86	0.45
ITMI 094	3.06	65	63	42	49	52	94	0.58
ITMI 095	2.81	69	86	41	47	49	90	0.45
ITMI 096	3.49	79	66	44	51	54	98	0.50
ITMI 097	4.17	74	75	42	48	50	92	0.49
ITMI 099	2.70	78	68	38	47	50	88	0.49

ITMI 100	3.90	81	75	42	55	56	99	0.47
ITMI 101	2.46	79	55	44	46	52	97	0.44
ITMI 102	2.19	72	66	39	46	49	88	0.45
ITMI 103	2.64	68	56	41	46	49	90	0.48
ITMI 104	4.13	73	80	41	44	46	87	0.57
ITMI 105	2.71	70	81	40	44	47	87	0.45
ITMI 106	2.61	74	58	43	52	54	97	0.45
ITMI 109	3.37	79	74	43	46	49	92	0.45
ITMI 110	3.17	81	63	40	46	48	88	0.44
ITMI 111	3.19	89	62	45	54	56	101	0.41
ITMI 112	3.73	73	73	43	50	53	96	0.50
ITMI 114	3.16	77	88	45	55	57	102	0.38
ITMI 115	3.29	82	81	45	52	54	99	0.38

Table A1-7: BLUPS for each traits measured on the ITMI population grown without competition on the West 240 site in 2006 (See Chapter 2).

Line	Grain Yield (t ha^{-1})	Plant Height (cm)	Spike per m^{-2}	Grain fill Duration (days)	Days to Heading (days)	Days to Anthesis (days)	Days to Maturity (days)	Harvest index	Percent Trans-mittance
ITMI 001	5.17	78	111	37	51	51	51	0.44	0.28
ITMI 002	5.85	68	105	36	48	48	49	0.52	0.24
ITMI 003	4.93	83	85	35	49	49	49	0.46	0.35
ITMI 004	4.60	70	101	35	49	49	49	0.38	0.32
ITMI 005	6.23	84	108	36	54	54	55	0.50	0.25
ITMI 006	3.57	73	92	36	52	53	53	0.33	0.28
ITMI 009	3.52	60	84	31	51	51	50	0.45	0.40
ITMI 010	5.46	79	101	31	49	49	47	0.50	0.37
ITMI 011	4.23	71	90	37	52	52	53	0.42	0.26
ITMI 012	3.90	74	90	36	51	51	51	0.42	0.35
ITMI 013	4.17	82	116	34	57	57	57	0.37	0.24
ITMI 014	6.12	68	95	36	50	50	49	0.56	0.27
ITMI 015	5.00	81	91	36	53	53	54	0.36	0.36
ITMI 016	5.45	80	117	32	51	51	50	0.47	0.22
ITMI 017	4.84	78	107	34	50	50	50	0.41	0.26
ITMI 018	5.63	74	95	40	50	50	51	0.56	0.24
ITMI 019	4.69	75	94	35	50	50	50	0.44	0.30
ITMI 020	5.90	76	106	37	52	52	53	0.47	0.33
ITMI 021	4.62	70	103	38	52	52	53	0.46	0.31
ITMI 022	4.44	73	103	33	47	47	47	0.51	0.34
ITMI 023	3.35	64	110	34	49	49	49	0.30	0.33
ITMI 024	4.66	86	104	37	52	52	52	0.36	0.24
ITMI 025	6.84	78	100	34	51	50	50	0.56	0.27
ITMI 026	4.94	71	108	34	54	54	54	0.48	0.31
ITMI 027	6.29	70	96	37	50	50	50	0.53	0.28
ITMI 028	3.80	61	95	34	58	58	58	0.43	0.32
ITMI 029	5.92	79	88	35	48	48	48	0.54	0.35
ITMI 030	4.18	66	91	32	47	48	47	0.50	0.36
ITMI 031	3.98	74	80	35	48	48	48	0.40	0.37
ITMI 032	5.73	74	95	32	47	47	47	0.52	0.34
ITMI 033	5.47	76	88	32	48	48	47	0.53	0.33
ITMI 034	5.21	67	99	28	47	48	47	0.52	0.31
ITMI 035	3.88	73	88	35	54	54	54	0.48	0.38
ITMI 036	6.12	67	86	36	52	52	52	0.60	0.36
ITMI 037	2.87	79	77	35	53	53	53	0.32	0.36
ITMI 038	3.97	72	91	39	49	49	50	0.38	0.33
ITMI 039	3.63	63	93	31	49	49	48	0.39	0.38
ITMI 040	3.52	65	83	36	52	52	51	0.48	0.34
ITMI 041	5.64	64	93	36	48	48	48	0.55	0.31
ITMI 042	4.69	72	79	35	54	54	54	0.42	0.42
ITMI 044	4.48	76	116	33	47	47	46	0.34	0.21
ITMI 045	3.67	73	106	35	47	47	46	0.31	0.27
ITMI 046	4.95	77	76	36	58	58	59	0.48	0.29
ITMI 047	5.68	84	99	34	48	48	47	0.53	0.27
ITMI 048	3.83	69	94	34	48	48	48	0.42	0.46

ITMI 049	5.18	70	88	33	52	52	51	0.52	0.32
ITMI 050	5.52	80	100	35	56	56	56	0.51	0.33
ITMI 051	5.80	83	99	37	56	56	57	0.51	0.21
ITMI 052	3.51	69	70	31	49	49	48	0.47	0.43
ITMI 053	4.58	78	92	34	49	49	49	0.39	0.31
ITMI 054	5.11	85	103	34	51	51	50	0.42	0.28
ITMI 055	4.72	79	85	33	49	49	49	0.43	0.31
ITMI 056	5.00	76	82	37	54	54	54	0.51	0.30
ITMI 057	3.81	70	73	32	50	50	49	0.45	0.34
ITMI 058	3.38	65	78	34	52	52	52	0.44	0.37
ITMI 059	3.69	70	84	41	52	52	54	0.41	0.35
ITMI 060	4.52	74	101	35	47	47	47	0.38	0.33
ITMI 061	4.13	66	97	36	52	52	53	0.39	0.30
ITMI 062	5.75	74	102	34	49	49	48	0.56	0.34
ITMI 063	4.01	81	98	35	49	49	49	0.31	0.32
ITMI 064	5.36	66	118	31	47	47	46	0.46	0.38
ITMI 065	5.70	80	102	33	53	53	53	0.49	0.34
ITMI 066	3.80	70	90	37	55	55	55	0.43	0.31
ITMI 067	3.54	82	94	36	47	47	47	0.27	0.32
ITMI 068	3.97	70	80	38	57	57	58	0.43	0.32
ITMI 069	5.14	88	72	35	53	53	53	0.47	0.28
ITMI 070	5.34	74	109	35	49	49	49	0.45	0.21
ITMI 071	4.62	73	90	35	50	51	51	0.47	0.27
ITMI 072	3.84	63	98	33	47	47	45	0.51	0.44
ITMI 073	5.49	75	103	35	48	48	48	0.53	0.23
ITMI 074	6.31	73	106	35	48	48	48	0.52	0.27
ITMI 075	4.07	84	96	37	52	52	52	0.30	0.28
ITMI 076	4.18	86	104	37	52	52	53	0.38	0.27
ITMI 077	6.75	80	110	35	52	52	52	0.56	0.22
ITMI 078	3.14	72	98	36	51	51	51	0.27	0.46
ITMI 079	6.12	75	105	35	49	49	49	0.56	0.27
ITMI 080	4.17	79	92	37	50	51	51	0.35	0.31
ITMI 081	4.59	83	86	37	53	53	53	0.37	0.36
ITMI 082	6.06	71	95	36	53	53	54	0.56	0.29
ITMI 083	4.51	74	91	37	53	53	53	0.37	0.33
ITMI 084	4.55	71	84	37	53	53	54	0.40	0.35
ITMI 085	4.01	72	97	37	47	47	47	0.34	0.35
ITMI 086	3.56	75	83	35	52	53	52	0.32	0.29
ITMI 087	4.43	67	76	33	50	49	49	0.50	0.35
ITMI 088	4.78	74	103	37	53	53	53	0.41	0.32
ITMI 089	4.99	86	93	34	57	57	57	0.46	0.25
ITMI 090	3.99	74	81	33	58	59	59	0.45	0.26
ITMI 091	6.69	65	131	34	48	48	48	0.57	0.30
ITMI 092	6.39	78	102	37	52	52	53	0.54	0.34
ITMI 093	4.27	72	87	35	47	47	46	0.46	0.37
ITMI 094	4.58	62	76	35	51	51	51	0.60	0.35
ITMI 095	4.58	66	108	35	52	52	51	0.45	0.45
ITMI 096	5.79	77	86	35	53	53	54	0.49	0.31
ITMI 097	5.98	72	100	36	51	51	52	0.46	0.29
ITMI 099	3.75	76	87	32	51	51	50	0.43	0.39

ITMI 100	6.21	78	98	36	57	57	57	0.45	0.24
ITMI 101	3.85	69	80	33	51	51	52	0.44	0.39
ITMI 102	3.81	68	93	31	50	50	49	0.46	0.38
ITMI 103	4.09	65	81	37	51	50	51	0.51	0.39
ITMI 104	5.15	70	104	36	49	49	48	0.47	0.30
ITMI 105	5.25	69	104	32	49	49	48	0.49	0.32
ITMI 106	4.38	71	84	36	54	54	54	0.53	0.38
ITMI 109	4.61	77	98	38	50	50	51	0.43	0.28
ITMI 110	4.60	76	84	37	50	50	51	0.43	0.32
ITMI 111	4.94	88	85	37	54	54	55	0.36	0.25
ITMI 112	4.95	71	96	36	53	53	53	0.48	0.34
ITMI 114	5.04	73	110	35	56	56	57	0.41	0.18
ITMI 115	5.30	82	99	38	53	53	54	0.41	0.27

Table A1-8: BLUPS for each traits measured on the ITMI population grown with competition on the West 240 site in 2006 (See Chapter 2).

Line	Grain Yield (t ha^{-1})	Plant Height (cm)	Spike per m^{-2}	Grain fill Duration (days)	Days to Heading (days)	Days to Anthesis (days)	Days to Maturity (days)	Harvest index
ITMI 001	3.52	78	75	36	51	51	51	0.42
ITMI 002	3.31	70	74	34	48	48	48	0.49
ITMI 003	3.23	83	61	34	49	49	49	0.43
ITMI 004	2.73	71	69	34	49	49	49	0.36
ITMI 005	3.73	85	74	35	54	54	54	0.48
ITMI 006	1.72	73	61	34	52	52	52	0.31
ITMI 009	1.58	62	51	31	51	51	50	0.42
ITMI 010	3.76	80	71	31	48	48	48	0.48
ITMI 011	2.21	72	60	35	52	52	52	0.39
ITMI 012	1.94	75	58	34	51	51	51	0.39
ITMI 013	2.10	82	74	33	57	57	57	0.34
ITMI 014	3.65	69	70	35	49	49	50	0.54
ITMI 015	2.09	80	55	35	53	53	53	0.33
ITMI 016	3.12	81	83	32	50	50	50	0.45
ITMI 017	2.98	79	81	33	50	50	49	0.39
ITMI 018	3.49	75	66	38	50	50	50	0.53
ITMI 019	2.51	75	62	34	50	50	50	0.41
ITMI 020	3.48	77	66	35	52	52	52	0.44
ITMI 021	2.45	71	70	36	52	52	52	0.44
ITMI 022	2.24	73	70	32	47	47	47	0.48
ITMI 023	1.58	65	79	33	49	49	49	0.27
ITMI 024	2.51	87	72	36	52	52	52	0.33
ITMI 025	4.12	78	72	33	50	50	50	0.53
ITMI 026	2.58	72	69	33	54	54	54	0.45
ITMI 027	3.85	71	68	36	50	50	50	0.51
ITMI 028	1.56	62	57	33	57	57	58	0.41
ITMI 029	3.72	80	56	34	48	48	48	0.51
ITMI 030	2.48	67	64	31	47	47	47	0.47
ITMI 031	2.47	75	55	33	48	48	48	0.38
ITMI 032	3.46	75	69	31	47	47	46	0.49
ITMI 033	3.60	77	61	31	47	48	47	0.50
ITMI 034	3.20	68	70	27	47	48	47	0.49
ITMI 035	1.76	74	58	34	54	54	54	0.45
ITMI 036	2.93	68	54	35	52	52	53	0.57
ITMI 037	1.12	79	46	33	53	53	53	0.30
ITMI 038	2.19	73	60	37	49	48	49	0.36
ITMI 039	1.96	64	64	30	49	49	48	0.36
ITMI 040	1.43	67	45	36	52	51	52	0.46
ITMI 041	3.31	65	68	35	48	48	48	0.52
ITMI 042	2.23	73	51	34	53	53	54	0.40
ITMI 044	2.39	76	83	32	47	47	46	0.32
ITMI 045	1.94	75	80	34	47	47	46	0.29
ITMI 046	2.00	78	42	35	58	58	58	0.45
ITMI 047	3.33	85	72	33	48	48	47	0.50
ITMI 048	1.92	70	63	33	48	48	48	0.39

ITMI 049	2.79	71	60	32	51	52	52	0.50
ITMI 050	2.74	81	61	33	56	56	56	0.49
ITMI 051	3.06	84	59	35	56	56	56	0.49
ITMI 052	1.54	70	47	31	49	49	48	0.44
ITMI 053	3.11	79	71	34	49	49	49	0.36
ITMI 054	3.27	86	75	33	50	50	50	0.40
ITMI 055	3.19	79	57	32	49	49	49	0.41
ITMI 056	2.44	77	53	36	54	53	54	0.48
ITMI 057	2.07	70	51	31	50	50	49	0.42
ITMI 058	1.48	67	47	33	52	52	52	0.41
ITMI 059	1.65	70	50	39	52	52	53	0.39
ITMI 060	2.79	75	73	34	47	47	47	0.36
ITMI 061	2.25	67	62	36	52	52	53	0.37
ITMI 062	3.57	75	72	33	49	49	48	0.54
ITMI 063	2.00	81	67	34	49	49	49	0.29
ITMI 064	3.18	68	83	30	47	47	46	0.44
ITMI 065	3.51	81	70	32	53	53	53	0.46
ITMI 066	1.95	71	53	36	54	54	55	0.41
ITMI 067	1.95	83	68	34	47	47	47	0.25
ITMI 068	1.85	71	47	37	57	57	58	0.41
ITMI 069	3.04	88	46	34	53	53	53	0.44
ITMI 070	3.16	75	66	34	49	49	48	0.43
ITMI 071	2.62	74	67	34	50	50	50	0.45
ITMI 072	2.01	64	69	33	47	47	46	0.48
ITMI 073	3.59	76	72	35	48	48	48	0.51
ITMI 074	3.89	74	73	34	48	48	47	0.49
ITMI 075	1.77	84	65	36	52	52	52	0.28
ITMI 076	2.13	86	70	35	52	52	52	0.36
ITMI 077	4.01	80	78	34	52	52	52	0.54
ITMI 078	1.56	73	62	36	51	51	52	0.25
ITMI 079	3.86	76	71	34	49	49	49	0.53
ITMI 080	2.40	80	65	35	50	50	50	0.33
ITMI 081	2.37	83	60	36	53	53	53	0.34
ITMI 082	3.51	72	59	34	53	53	53	0.53
ITMI 083	1.90	75	56	36	53	53	53	0.35
ITMI 084	1.73	71	43	35	53	53	54	0.38
ITMI 085	2.19	73	71	36	47	47	47	0.31
ITMI 086	2.15	76	51	35	52	52	52	0.30
ITMI 087	2.19	68	48	32	49	49	49	0.47
ITMI 088	3.01	75	74	35	53	52	52	0.38
ITMI 089	2.36	86	51	32	57	57	57	0.43
ITMI 090	1.70	74	51	32	58	58	59	0.42
ITMI 091	3.91	65	99	33	48	48	48	0.54
ITMI 092	3.98	79	69	36	52	52	52	0.51
ITMI 093	2.38	73	56	34	47	47	47	0.43
ITMI 094	2.36	62	52	34	50	50	50	0.57
ITMI 095	2.43	66	82	35	52	52	52	0.42
ITMI 096	2.73	77	56	34	52	53	53	0.46
ITMI 097	3.35	72	77	35	51	51	51	0.43
ITMI 099	2.08	77	63	32	51	51	50	0.40

ITMI 100	3.04	78	63	35	57	56	57	0.42
ITMI 101	1.76	70	45	31	51	51	51	0.41
ITMI 102	1.80	69	60	30	50	50	49	0.43
ITMI 103	2.29	66	52	35	50	50	51	0.49
ITMI 104	2.93	72	72	35	49	49	49	0.44
ITMI 105	3.30	69	73	32	49	49	49	0.46
ITMI 106	2.75	72	55	34	54	54	54	0.50
ITMI 109	2.93	77	68	36	50	50	50	0.40
ITMI 110	2.41	77	56	36	50	50	50	0.40
ITMI 111	2.11	89	54	36	54	54	55	0.34
ITMI 112	2.69	72	61	35	53	53	53	0.45
ITMI 114	2.79	73	72	34	56	56	56	0.38
ITMI 115	2.94	83	70	37	53	53	54	0.38

Appendix 2: Grain yield LSMeans of the breeding population used in Chapter 4 and 5, grouped by management system.

Table A2-1: LS Means of grain yield (t ha^{-1}) of a spring wheat population derived from a cross between AC Barrie and Attila, and seven check varieties, grown on various organically managed sites from 2005 to 2007.

	2005	2006			2007		2006	2007	
Line	West240	West240	Camrose	Namao	West240	Camrose	Overall	Overall	Overall
Attila	1.52	1.07	1.29	3.34	3.57	1.89	1.90	2.73	2.46
Barrie	2.63	1.62	1.26	3.20	3.87	1.87	2.03	2.87	2.75
CDCGo	2.78	1.32	1.94	2.95	4.40	2.12	2.07	3.26	2.92
Intrepid	2.53	1.28	0.98	2.89	3.59	1.77	1.72	2.68	2.53
McKenzie	2.16	1.24	1.19	2.76	4.18	1.73	1.73	2.96	2.48
Park	2.87	1.05	1.59	2.34	3.35	1.47	1.66	2.41	2.49
Superb	3.17	1.31	1.76	3.21	4.52	1.95	2.10	3.24	3.10
BA-01	2.39	0.53	0.89	2.85	3.62	2.02	1.42	2.82	2.63
BA-02	2.83	1.08	1.13	3.29	4.19	2.14	1.83	3.17	2.99
BA-03	2.43	0.83	1.24	3.41	3.98	2.52	1.82	3.25	2.99
BA-04	2.24	0.98	0.82	2.83	3.00	2.48	1.55	2.74	2.57
BA-05	3.18	0.29	0.47	3.48	2.97	2.47	1.42	2.73	3.17
BA-06	2.77	0.53	1.35	2.61	2.99	2.00	1.50	2.50	2.66
BA-07	3.04	0.73	1.22	2.47	3.82	1.63	1.47	2.72	2.67
BA-08	2.24	1.06	0.84	3.31	4.32	2.21	1.74	3.27	2.80
BA-09	3.93	1.29	1.98	3.17	3.75	2.28	2.14	3.01	3.36
BA-10	1.97	0.72	1.61	2.78	3.65	1.97	1.70	2.81	2.51
BA-11	3.09	0.78	1.45	2.60	2.65	1.59	1.61	2.12	2.62
BA-12	3.03	0.60	0.84	2.43	3.08	1.67	1.29	2.38	2.56
BA-13	2.44	0.70	1.22	2.33	2.86	1.26	1.42	2.06	2.24
BA-14	2.88	1.01	1.06	3.44	3.80	2.38	1.84	3.09	3.06
BA-15	2.67	0.68	1.14	2.34	2.77	1.78	1.39	2.28	2.43
BA-16	1.98	0.28	0.56	2.57	3.10	1.85	1.14	2.48	2.30
BA-17	2.46	0.40	0.85	2.86	3.07	2.50	1.37	2.78	2.73
BA-18	2.96	1.11	1.03	3.01	3.18	2.14	1.72	2.66	2.82
BA-19	2.44	0.37	1.02	2.66	3.16	2.10	1.35	2.63	2.57

BA-20	2.45	0.61	1.12	2.47	3.67	1.95	1.40	2.81	2.54
BA-21	2.82	1.17	1.31	3.02	3.90	2.05	1.83	2.98	2.85
BA-22	2.44	0.59	1.37	2.97	3.45	1.81	1.65	2.63	2.67
BA-23	2.52	0.70	1.12	2.31	3.70	2.06	1.38	2.88	2.52
BA-24	2.38	0.48	0.77	2.35	3.76	1.91	1.20	2.83	2.45
BA-25	2.04	0.49	1.35	2.54	3.20	1.74	1.46	2.47	2.36
BA-26	1.26	1.16	1.31	3.37	3.67	2.08	1.95	2.88	2.43
BA-27	2.94	0.34	0.62	3.33	2.78	1.85	1.43	2.32	2.85
BA-28	3.26	0.57	0.47	3.11	2.07	1.86	1.38	1.97	2.77
BA-29	2.75	1.39	1.70	3.28	3.65	1.82	2.12	2.73	2.85
BA-30	1.90	0.75	1.27	2.66	3.27	1.99	1.56	2.63	2.48
BA-31	3.62	1.05	1.53	3.07	4.42	1.88	1.88	3.15	3.34
BA-32	2.37	0.23	0.87	2.78	2.12	2.05	1.29	2.08	2.49
BA-33	2.18	0.53	0.84	2.16	2.90	2.42	1.18	2.66	2.35
BA-34	3.05	0.59	0.85	2.90	3.02	2.03	1.45	2.52	2.87
BA-35	2.68	0.75	1.31	3.26	3.48	2.23	1.78	2.85	2.93
BA-36	3.48	0.45	1.31	3.28	3.80	2.53	1.68	3.16	3.33
BA-37	2.30	0.82	1.16	3.08	3.12	1.79	1.69	2.46	2.57
BA-38	2.16	1.03	1.62	2.66	3.77	2.31	1.77	3.04	2.60
BA-39	2.54	1.03	1.39	2.91	3.86	2.49	1.78	3.17	2.84
BA-40	2.07	0.88	1.33	3.52	3.86	1.97	1.91	2.91	2.74
BA-41	3.32	1.23	0.76	3.68	4.20	2.17	1.89	3.19	3.23
BA-42	1.71	0.91	0.78	2.08	3.43	1.85	1.26	2.64	2.04
BA-43	2.41	0.61	1.48	3.48	4.17	1.85	1.86	3.01	2.92
BA-44	2.90	0.23	1.03	2.64	2.66	1.88	1.30	2.27	2.65
BA-45	1.95	0.64	0.87	2.79	2.68	1.49	1.44	2.08	2.24
BA-46	2.50	0.53	1.24	2.39	3.36	1.99	1.39	2.68	2.52
BA-47	1.80	0.68	0.88	2.40	3.37	1.68	1.32	2.52	2.17
BA-48	1.84	1.09	1.04	2.36	2.55	1.88	1.49	2.22	2.11
BA-49	2.82	1.23	1.22	3.70	3.61	1.61	2.05	2.61	2.93
BA-50	2.98	0.28	0.53	3.35	2.78	1.60	1.38	2.19	2.81

BA-51	2.40	0.48	1.04	2.70	2.75	1.83	1.40	2.29	2.46
BA-52	2.89	0.92	0.67	2.31	3.04	2.04	1.30	2.54	2.51
BA-53	2.62	0.75	1.14	3.25	3.94	2.28	1.72	3.11	2.94
BA-54	1.73	0.60	1.66	3.15	4.10	1.89	1.81	3.00	2.61
BA-55	2.66	0.25	0.72	2.65	3.03	1.70	1.21	2.36	2.54
BA-56	3.26	1.18	1.38	2.81	3.45	1.99	1.79	2.72	2.85
BA-57	3.01	1.00	1.38	2.92	3.47	1.37	1.76	2.42	2.70
BA-58	2.90	1.25	1.61	3.02	4.08	2.38	1.96	3.23	2.99
BA-59	3.09	0.93	1.06	2.58	3.42	1.96	1.52	2.69	2.72
BA-60	2.92	0.77	1.13	2.72	3.58	2.02	1.54	2.80	2.76
BA-61	2.27	0.79	1.08	2.22	3.27	2.47	1.36	2.87	2.45
BA-62	2.95	0.75	1.01	2.99	3.23	2.11	1.58	2.67	2.84
BA-63	2.82	0.94	1.46	2.97	2.78	2.05	1.79	2.41	2.76
BA-64	1.83	0.73	1.11	2.45	3.22	1.60	1.43	2.41	2.18
BA-65	2.19	0.53	1.50	2.93	3.29	1.54	1.65	2.42	2.51
BA-66	2.19	0.77	1.28	3.01	3.21	2.16	1.69	2.68	2.63
BA-67	2.36	0.96	1.10	3.42	3.07	1.59	1.83	2.33	2.64
BA-68	1.58	0.78	1.21	2.45	3.53	2.13	1.48	2.83	2.26
BA-69	2.04	0.65	1.73	2.77	3.87	2.15	1.71	3.01	2.62
BA-70	1.50	0.68	1.29	2.63	3.88	1.38	1.53	2.63	2.17
BA-71	2.76	1.01	0.84	2.70	2.78	1.85	1.52	2.32	2.53
BA-72	2.10	0.62	1.08	2.78	2.69	2.26	1.49	2.47	2.48
BA-73	2.69	0.54	0.83	2.31	3.54	2.44	1.23	2.99	2.64
BA-74	3.15	0.34	1.30	3.16	3.03	2.09	1.60	2.56	3.01
BA-75	2.16	0.33	0.61	2.42	2.40	1.67	1.12	2.03	2.20
BA-76	2.65	0.84	1.45	2.53	4.06	1.74	1.61	2.90	2.62
BA-77	2.32	0.69	1.13	2.74	2.95	2.01	1.52	2.48	2.51
BA-78	2.35	0.93	1.31	3.03	3.06	2.66	1.76	2.86	2.78
BA-79	2.84	1.36	1.53	3.30	4.18	2.47	2.06	3.32	3.08

Table A2-2: LS Means of grain yield (t ha^{-1}) of a spring wheat population derived from a cross between AC Barrie and Attila, and seven check varieties, grown on various conventionally managed sites from 2005 to 2007.

	2005	2006			2007		2006	2007	
Line	Michener	Michener	Ellersli	Lacombe	Michener	Lacombe	Overall	Overall	Overall
Attila	5.68	4.60	2.59	7.24	4.29	7.92	4.81	6.10	5.32
Barrie	4.99	4.32	2.99	6.09	4.25	5.77	4.47	5.01	4.63
CDCGo	5.74	4.65	2.40	6.84	4.53	6.44	4.63	5.48	4.91
Intrepid	4.89	4.56	3.38	7.07	4.21	6.82	5.00	5.52	5.05
McKenzie	4.87	4.06	2.14	5.41	3.89	7.08	3.87	5.48	4.54
Park	4.62	3.87	2.97	5.67	3.54	5.36	4.17	4.45	4.34
Superb	5.56	5.05	2.99	7.15	5.27	6.65	5.06	5.96	5.16
BA-01	5.22	4.21	2.63	6.06	3.73	5.89	4.30	4.81	4.57
BA-02	5.82	5.19	2.93	7.49	4.26	7.39	5.20	5.83	5.33
BA-03	6.11	4.84	3.20	6.86	4.25	7.21	4.97	5.73	5.44
BA-04	5.03	4.13	2.34	6.15	3.60	5.98	4.20	4.79	4.44
BA-05	6.66	4.55	2.82	7.80	5.39	7.98	5.06	6.68	5.91
BA-06	3.91	4.79	2.58	5.87	3.69	7.02	4.41	5.36	4.30
BA-07	5.71	4.42	2.01	6.50	3.76	6.76	4.31	5.26	4.76
BA-08	5.29	4.14	2.82	6.47	4.67	6.64	4.48	5.66	4.98
BA-09	5.88	4.73	3.41	6.46	4.37	5.90	4.87	5.14	5.11
BA-10	5.43	4.95	2.87	6.89	4.13	7.19	4.90	5.66	5.08
BA-11	5.83	4.29	2.48	6.53	4.31	7.28	4.43	5.79	5.15
BA-12	4.96	4.67	2.57	6.84	3.79	7.46	4.69	5.63	4.87
BA-13	4.83	3.90	2.51	5.39	2.84	5.67	3.93	4.26	4.23
BA-14	5.55	4.13	2.81	8.09	4.52	6.17	5.01	5.34	5.10
BA-15	5.50	4.33	2.88	5.94	3.72	6.63	4.39	5.18	4.90
BA-16	4.74	4.54	2.37	7.27	4.52	6.61	4.73	5.56	4.66
BA-17	6.24	4.70	2.49	6.76	5.19	6.75	4.65	5.97	5.23
BA-18	5.25	4.38	2.35	6.93	4.56	7.62	4.55	6.09	5.05
BA-19	4.54	3.75	1.44	5.86	3.46	6.66	3.68	5.06	4.13

BA-20	5.04	4.55	2.51	6.76	4.17	7.42	4.61	5.80	4.91
BA-21	3.69	4.38	2.28	6.70	3.94	6.52	4.46	5.23	4.16
BA-22	5.24	4.55	2.93	4.73	3.94	6.61	4.07	5.28	4.70
BA-23	5.63	3.78	2.58	6.19	3.48	7.34	4.18	5.41	5.06
BA-24	4.48	4.05	2.30	6.60	4.03	6.67	4.32	5.35	4.50
BA-25	4.83	4.03	2.95	5.50	3.47	5.90	4.16	4.69	4.49
BA-26	5.31	4.89	3.09	6.06	4.29	5.85	4.68	5.07	4.74
BA-27	6.69	4.44	2.59	7.12	5.34	7.68	4.72	6.51	5.71
BA-28	5.13	4.16	2.81	6.36	4.91	7.38	4.44	6.15	5.10
BA-29	5.60	4.78	2.45	7.15	4.88	8.25	4.80	6.56	5.36
BA-30	4.92	4.47	2.90	6.55	4.09	6.56	4.64	5.32	4.78
BA-31	4.70	4.55	2.24	6.87	4.60	7.26	4.55	5.93	4.72
BA-32	5.22	4.14	2.36	7.19	5.15	6.77	4.56	5.96	4.95
BA-33	3.94	4.10	2.22	4.60	4.03	6.30	3.64	5.17	4.00
BA-34	5.12	4.27	2.11	5.77	4.60	6.84	4.05	5.72	4.64
BA-35	4.81	4.36	2.90	7.26	4.61	6.43	4.84	5.52	4.84
BA-36	6.52	5.68	3.01	8.12	4.88	8.22	5.60	6.55	5.85
BA-37	5.10	4.63	3.50	7.43	4.02	6.71	5.19	5.37	5.14
BA-38	5.24	4.87	3.02	6.61	4.19	8.27	4.83	6.23	5.30
BA-39	5.36	5.22	3.03	5.80	4.33	6.45	4.68	5.39	4.82
BA-40	5.36	5.08	2.80	5.23	4.34	5.79	4.37	5.06	4.54
BA-41	4.95	4.86	3.18	6.95	4.97	6.83	5.00	5.90	5.04
BA-42	4.04	4.11	2.25	6.21	3.96	6.22	4.19	5.09	4.18
BA-43	5.93	4.06	3.23	6.32	4.44	7.32	4.54	5.88	5.46
BA-44	6.42	4.73	3.05	7.17	4.93	6.49	4.98	5.71	5.43
BA-45	4.62	3.96	2.71	5.92	3.70	5.95	4.20	4.83	4.42
BA-46	4.10	4.48	2.61	6.07	3.69	6.42	4.39	5.06	4.29
BA-47	4.67	4.19	2.54	5.88	3.45	6.30	4.20	4.87	4.41
BA-48	5.21	4.65	3.19	5.42	3.94	6.09	4.42	5.02	4.72
BA-49	6.32	4.77	3.35	6.75	4.65	6.31	4.96	5.48	5.38
BA-50	4.58	3.85	2.39	5.96	4.61	7.28	4.07	5.95	4.72

BA-51	4.51	4.77	2.62	6.08	3.63	5.64	4.49	4.64	4.21
BA-52	5.31	4.52	3.20	6.25	3.67	6.51	4.66	5.09	4.92
BA-53	5.47	4.66	3.10	6.30	4.04	7.40	4.69	5.72	5.18
BA-54	5.85	4.66	2.39	6.86	3.82	7.43	4.63	5.63	5.11
BA-55	5.62	4.39	2.79	6.85	4.48	6.49	4.68	5.48	5.04
BA-56	4.85	4.72	2.55	6.11	4.33	5.97	4.46	5.15	4.46
BA-57	5.27	4.19	2.61	6.10	4.04	6.17	4.30	5.11	4.69
BA-58	5.81	5.24	2.99	7.45	4.39	6.76	5.23	5.58	5.20
BA-59	4.98	4.26	3.04	6.52	4.49	6.17	4.61	5.33	4.81
BA-60	5.57	4.53	2.28	7.10	3.85	7.06	4.64	5.46	4.93
BA-61	5.16	4.35	3.11	7.05	4.52	6.84	4.84	5.68	5.10
BA-62	5.07	4.62	2.89	7.23	4.00	7.37	4.91	5.68	5.06
BA-63	5.40	5.18	3.33	6.30	4.72	6.25	4.93	5.48	4.98
BA-64	5.62	3.96	2.70	4.80	3.47	6.40	3.82	4.94	4.72
BA-65	4.03	4.19	2.67	5.91	3.92	6.28	4.26	5.10	4.29
BA-66	5.81	4.26	2.40	7.08	4.20	6.78	4.58	5.49	5.04
BA-67	5.69	4.40	2.56	7.56	4.53	7.15	4.84	5.84	5.21
BA-68	4.70	4.23	3.49	5.39	4.27	7.34	4.37	5.81	5.01
BA-69	4.86	5.01	2.74	6.30	4.29	7.49	4.68	5.89	4.86
BA-70	4.78	4.21	1.43	5.24	3.94	5.27	3.63	4.61	3.82
BA-71	5.44	4.48	2.83	6.13	4.45	6.34	4.48	5.39	4.87
BA-72	5.57	4.13	3.87	7.25	4.14	7.32	5.08	5.73	5.61
BA-73	5.57	4.20	2.34	6.43	3.77	7.01	4.32	5.39	4.90
BA-74	6.23	4.63	3.90	6.20	4.76	6.17	4.91	5.47	5.48
BA-75	4.40	4.03	2.73	5.79	3.22	5.59	4.18	4.40	4.21
BA-76	5.64	4.17	2.48	6.46	4.25	6.79	4.37	5.52	4.97
BA-77	5.38	4.81	2.38	6.37	4.52	6.52	4.52	5.52	4.74
BA-78	4.13	4.91	3.31	7.01	5.35	7.13	5.08	6.24	4.91
BA-79	5.74	4.67	2.87	6.09	4.29	7.47	4.54	5.88	5.21