Genetic variation for nitrogen use efficiency in Canada Western Red Spring wheat (*Triticum aestivum* L.) under conventional and organic management systems

by

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Abstract

Improved nitrogen use efficiency in cereal-based agricultural systems can contribute to increasing grain production while reducing agriculture-related pollution caused by nitrogen leaching, volatilization and denitrification. Organic agriculture differs to conventional systems in terms of in management practice, fertilization regimes, and the nature of nitrogen cycling. These differences affect nitrogen use efficiency and its associated traits. Therefore, breeding for improved nitrogen use efficiency in spring wheat (*Triticum aestivum* L.) requires adequate genetic variability for the traits according to the farming practice employed. Studies were carried out from 2010 to 2015 to evaluate differences in agronomic traits and genetic variation for nitrogen use efficiency traits in Canada Western Red Spring wheat cultivars under conventional and organic systems, and identified specific genotypes of high nitrogen use efficiency. Organically grown grain was earlier flowering, and had lower test weight grain yield compared to its conventional counterpart. Earlier maturity associated *Vrn* genes did not translate to any yield advantage under organic field conditions. There was a cross-over interaction of the genotypes between managements in grain protein content, indicating a necessity of specific cultivar choice/breeding for organic system. Under high and low nitrogen levels in conventional practices, genotype × fertilizer interaction was shown to be significant for important yield and nitrogen use efficiency traits. Correlations among traits were more pronounced under high nitrogen than low nitrogen treatment. The significant positive correlations between total dry matter at harvest and nitrogen uptake efficiency suggested that vigorous biomass production is an important driver for increased nitrogen uptake. Prominent effects of the *Rht* alleles on agronomic and nitrogen use efficiency traits were identified under high N conditions. However, the effect of the *Rht-1b* alleles on cultivar nitrogen uptake efficiency is inconsistent under high nitrogen condition, indicating that dwarfing *Rht* alleles have indirect mechanisms associated with nitrogen uptake. Genetic improvements were observed for grain yield, nitrogen use efficiency, and nitrogen utilization efficiency over the last century only in high nitrogen condition. These increases were mainly attributed to improved harvest index, suggesting an improvement in assimilate partitioning efficiency. Between conventional and organic farming systems, analysis of variance revealed significant effects of genotype, environment, and their interactions on grain and stem nitrogen yield, and nitrogen utilization efficiency under organic systems. Modern genotype, Superb, CDC Kernen, and CDC Stanley were superior and stable across the tested organic environments in several important traits including grain yield, and nitrogen use efficiency relative to other modern genotypes. These cultivars seemed to obtain high grain yield by different strategies. Breeding cultivars that possess characteristics of high grain and stem nitrogen yield with nitrogen use efficiency may be achievable by using potential genotypes such as Superb for organic cultivation systems to optimize the system sustainability while maintaining grain yield.

Preface

Improving nitrogen use efficiency (NUE) is necessary for the globally successful and sustainable production of wheat. Therefore, understanding the impact of farming practice on genetic variability is important for developing efficient breeding programs for the improvement of NUE. I participated in all steps of planning, sowing, harvesting, of all the studies in this thesis with the cereal research group members at Edmonton Research Station (ERS), St. Albert Research Station (SARS) at the University of Alberta from 2010 to 2015. I also had the same responsibilities at Lamont Organic farm from 2012 to 2015.

I had ultimate responsibility for the collection and critical interrogation of all the scientific articles reviewed as part of Chapter 1. Drs. Muhammad Iqbal Dean Spaner provided kind guidance throughout the writing process. Drs. Miles Dyck and Sylvie Quideau also provided valuable comments. The review article: Agronomic and physiological aspects of nitrogen use efficiency in conventional and organic cereal-based production systems was published in Renewable Agriculture and Food Systems. 2017. Hiroshi Kubota, Muhammad Iqbal, Sylvie Quideau, Miles Dyck and Dean Spaner. Renewable Agriculture and Food Systems. DOI: https://doi.org/10.1017/S1742170517000163.

Agronomic data included in the breeder seed collection study presented in Chapter 2, on Canadian germplasm studied in organic and conventional fields was generously provided by Klaus Strenzke. I took field notes for plant height, final grain yield, thousand kernel weight, test weight, NIR analysis for protein from 2010 to 2012 in this study. Dr. Atif Kamran was responsible for cultivar genotyping to determine their vernalization gene composition. I also contributed to data analysis and interpretation, and manuscript writing. A modified version of Chapter 2 was previously published as: Relative performance of Canadian spring wheat cultivars under organic and conventional field conditions. 2014. Atif

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I was responsible for experimental design, seed preparation, taking field notes, yield data collection, and nitrogen analysis in the experiments carried out from 2012 to 2015 presented in chapter 3 and 4. Members of the cereal research group assisted with sample preparation for nitrogen analysis. I had ultimate responsibility for all data analysis and interpretation presented in all the studies in Chapter 3 and Chapter 4. Chapter 3 is accepted to Crop Science. Chapter 4 is submitted to Agroecology and Sustainable Food System under review for publication.

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Completing my Ph.D. degree, I recalled my life at the University of Alberta for eight years. It has been a period of long and intense learning for me, not only in the scientific arena but also on a personal level. I would never have been able to finish my dissertation without the support of many people. I would like to reflect on the people who have supported and helped me so much throughout my Ph.D. program.

I would first like to thank my supervisor Dean for providing me this opportunity. You believed me and guided me when I needed. I failed your first assignment (you know what I mean), but I am still here with this degree. This is because of your patient and generosity. It is difficult to find the word to express my gratitude. Thank you very much, Dean. I also would like to thank my supervisory committee Dr. Sylvie Quideau and Dr. Miles Dyck for their guidance and support to develop my background knowledge in soil science. I thank Dr. Martin Entz and Dr. Guillermo Hernandez Ramirez who were willing to participate in my defense as an arm-length and an external examiners, providing me a lot of inputs. I thank Dr. Muhammad Iqbal for his valuable inputs during my writing process. I also thank Dr. Kassa Fentaye for his valuable suggestions. Also, I would like to thank Dr. Kelvin Lien for his support of my nitrogen analysis.

Agricultural research requires a team effort. During my Ph.D. research, I have received a lot of help from my research group members. First of all, a special thanks go to Klaus who oversaw field activities and provided the necessary support in a field. Thank you, Fabiana, Joe, Izabela, Russell, Alex, Atif, Asif, Khang, Susan, Carla, Lindsay, Katherine, RongRong, Briana, Tom, Krista, Darcy, Michaela, Graham, Marika, Jun for technical assistant and support.

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In the end, I would also like to thank my parents and wife, especially Hiroko for your patient and support on this long journey. You are always here with me. Thank you.

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1.0 Agronomic and physiological aspects of nitrogen use efficiency in conventional and organic cereal-based production systems[1]

1.1 Introduction of Nitrogen Use Efficiency (NUE) in Conventional and Organic Agriculture

Nitrogen (N) fertilization is integral to the steady increase in global cereal production since the Green Revolution. The global demand for N fertilizer was 115 million metric tons (MMT) in 2015, and the fertilizer use is projected to increase to 236 MMT by 2050 to meet global demands (Pathak et al., 2011; Food and Agriculture Organization of the United Nations [FAO], 2015). Despite increased application of N fertilizer, a large amount is lost and/or unavailable to crop plants in most current agricultural systems. The estimated N recovery in crops during the first year of fertilizer application ranges from 25 to 50%. Applied N losses include loss into ground water, gaseous loss through volatilization and denitrification, immobilization within the soil system, or limits of plant uptake capacity (Figure 1-1) (Robertson, 1997; Raun and Johnson, 1999; Pathak et al., 2011). These N losses into the environment result in serious problems such as water pollution, increased greenhouse gas emissions, altered global N cycles and consequent vegetative alteration (Frink et al., 1999; Horrigan et al., 2002). Also, the production of synthetic N fertilizer requires a significant amount of non-renewable natural gas (Vance, 2001). Transportation and application of the synthetic fertilizer add extra non-renewable energy consumption. Additionally, the use of synthetic fertilizer on the soil over a longer period of time may affect its ability to sustain healthy plant growth and crop production (Lim et al., 2015). Therefore, our continuing overdependence on synthetic N for cereal

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production is not sustainable.

Accordingly, there is a growing interest in improving nitrogen use efficiency (NUE) in modern agriculture to reduce associated problems without adversely affecting grain yield. Increased NUE would also benefit primary producers as nitrogen fertilization is one of the major costs in crop production, especially in developing countries (Masclaux-Daubresse et al., 2010). According to one estimate, a 1% improvement in cereal NUE could save more than $ 200 million in N fertilizer costs globally (Raun and Johnson, 1999). Organic agriculture has become a major food production system over the last few decades partly because of the perceived environmental and health concerns related to high-input conventional agricultural practices. Organic agriculture is “a production system that sustains the health of soils, ecosystems, and people. It relies on ecological processes, biodiversity and cycles adapted to local conditions, rather than the use of inputs with adverse effects” (International Federation of Organic Agriculture Movement [IFOAM], 2008). Therefore, organic systems primarily rely on nutrition supplied from natural agroecosystems, which are highly variable in their N supply capability and dynamic. Organic soils often have low N levels, despite high N retention capability on a long-term basis due to higher soil organic matter (SOM) and soil microbial diversity, than soils in conventional systems (Mäder et al., 2002; Pimentel et al., 2005).

One of the overall goals of NUE improvement in grain production is to increase grain yield per unit of N in soil. Variation of grain yield associated with NUE may be altered through genotypic selection (Van Sanford and MacKown, 1986; Huggins and Pan, 1993; Sinebo et al., 2004; Muurinen et al., 2007), agricultural management (Spargo et al., 2008; Khalil et al., 2009a; Sainju et al., 2009), rates, kinds, and timing of N applied (Ortiz-Monasterio et al., 1997), climate conditions (Sinebo et al., 2004; Muurinen et al., 2007) and soil properties (Meisinger et al., 1985; Spargo et al., 2008). Some studies suggest that NUE can be improved to obtain higher grain yield in both conventional and organic systems. Several reviews on different aspects of NUE have been published (Raun and Johnson, 1999; Bassirirad, 2006; Dawson et al., 2008; Pathak et al., 2011).

Despite the significant contribution of NUE to crop productivity and the environment, understanding of the detailed mechanisms to improve NUE is relatively limited due to inherent complexity (Basra and Goyal, 2002). Especially, there is limited knowledge on the comparison of various aspects of NUE in conventional and organic production systems. Therefore, the purpose of this review is to present an overall examination of genetic, physiological and agronomical aspects of NUE and related traits under conventional and organic systems. We also propose a possible integrated approach of breeding and agronomic practices to improve NUE in both systems.

1.2 Definition and Concept of NUE

The N cycle in agricultural systems is affected by many factors such as soil N concentration, soil chemical, physical and biological properties, crop species and climatic conditions. The manipulation of N movement between N sinks and sources within a plant and an entire ecosystem is a critical component of NUE improvement. Moll et al. (1982) defined the basic concept of NUE as the plant's ability to take up N efficiently from the soil and to partition absorbed N for grain production. Thus, NUE is expressed as the ratio of grain dry matter (Gw) to all N supplied from all available N sources (Ns) (Moll et al., 1982). Applied N fertilizer is often used as Ns because of the difficulties associated with measuring plant available N from mineralization through soil microbial activities. The amount of N loss is also often not accounted for in the calculation. The notion of N source and sink is interchangeable depending on research areas on NUE improvement. For instance, considering soil systems as N sources and crops as N sinks negates the non-linear reality that crops eventually become N sources, etcetera. In addition, a soil system itself could simultaneously become both sink and source; soil microbial immobilization as N sink and inorganic N release from SOM as N source (Havlin, 2014). Nitrogen exchange between N sink and source in the individual plant also exists in N metabolic processes according to plant growth (Figure 1-1). Owing to the involvement of complex traits in the concept of NUE, several parameters, which support the explanation of NUE, have been proposed (Table 1-1). First, NUE has been further divided into two primary components to illustrate the plant's ability to absorb available soil N and to partition N (Moll et al., 1982). N uptake efficiency (NUpE) reflects a crop's ability to absorb N and is defined as the ratio of total aboveground N (Nt) in the plant at maturity to supplied N (Ns) during the growing season. Nitrogen utilization efficiency (NUtE) is an index of the N partitioning ability in the plant, defined as the ratio of grain yield (weight) (G_w) to total N (N_t) in the plant (Moll et al., 1982). For these parameters, the N sink is the entire plant for NUpE and grain for NUtE, whereas the N source is all plant available N, including applied fertilizer and SOM degradation for both NUpE and NUtE.

Variation in NUpE is caused by genetic, soil, climatic and several agronomic factors (e.g. tillage, irrigation, timing and placement of N fertilizer) and their interaction (Huggins and Pan, 2003; Sinebo et al., 2004). Huggins and Pan (1993) reported the importance of applied soil N levels to NUpE. For instance, the contribution of applied N to grain N yield became less as the amount of the applied N increased, even though NUpE increased with increased N application. Huggins and Pan (2003) reviewed results of several previous studies and concluded that the decreased contribution of increased N use to NUpE was unsynchronized crop N demand and N supply of N fertilizer and N mineralization. In other words, when N is applied over the soil storing capacity, N is lost from the system unless N demand of crop is high and synchronized with crop N demand to utilize an optimum quantity of applied N.

The NUtE is another important parameter describing NUE. In a broader sense, NUtE explains the plants' ability to produce grain per unit of the total N in a plant, and cultivars with high NUtE are ideal for cereal crops grown in low fertility where plant-available N is limited. Several studies report that the contribution of NUtE to overall NUE is not well understood and may not be as significant as NUpE in wheat, barley, oats and maize (Presterl et al., 2002; Sinebo et al., 2004; Muurinen et al., 2006; Sylvester-Bradley and Kindred, 2009). In general, a crop species or cultivar has a unique N optimum utilization threshold, and crop internal N and grain yield do not increase in direct proportion to applied N (Sylvester-Bradley and Kindred, 2009). In addition, quality traits such as grain protein are very important for wheat and barley producers. Increased NUtE may lead to lower grain protein concentration due to N dilution effects when nitrogen harvest index (NHI: N in grain/ N in total biomass) remains the same (Huggins and Pan, 2003). Isfan (1993) suggested that increased NUtE may be an important trait to consider when developing high NUE cultivars for limited N conditions typically found on organic farms. Greater NUtE might be achieved through either improvement of N remobilization efficiency (NrE) or maintaining active photosynthesis (Masclaux-Daubresse et al., 2010). Fertilization rates and regimes also affect wheat NrE which is affected by specific enzymatic activity (Habash et al., 2001; Miflin and Habash, 2002; Forde and Lea, 2007; Bancal, 2009). Therefore, the effects of fertilizer management on NUtE cannot be ignored. Similar to NUtE, NHI represents the translocation efficiency of acquired N for grain protein accumulation (Dawson et al., 2008). This parameter is of particular importance in choosing parental cultivars for wheat breeding because the protein content in wheat grain directly affects grain price, and is of great importance to producers. High NHI levels indicate an efficient N utilization/translocation; thus cultivars with high NHI requires less N to produce similar yield as those with low NHI (Spiertz and De Vos, 1983).

1.3 Improvement of NUE for Mitigating Environmental Issues

The highly productive cereal production systems have negatively impacted environment through exploitation of non-renewable resources, ground fresh water pollution and eutrophication (Glibert et al., 2006). The relationship between yield and consumption of N fertilizer is non-linear (Sowers et al., 1994). Thus, the challenge in most of the agricultural systems is to find the means to improve efficiency of N fertilizer for sustainable food production. Mitigating the inefficiency of N fertilization has also a potential to slow down climate change through reducing emission of major greenhouse gases. Among these, nitrous oxide (N_2O) emission from soil is mainly related to the excess amount of N fertilizer (Figure 1-1); therefore, improved NUE in agriculture would reduce N_2O emission. Liu et al. (2016) wrote a comprehensive review on the sustainable farming practices that could impede climate change through reducing carbon (C) footprints. In Brazil, direct and indirect N2O emission from cereal production was found to be 12 times higher in 2011 compared with 1970, while NUE decreased by approximately 74% in that period (Amanullah et al., 2016). The authors attributed these results to increased consumption of N fertilizer and predicted that an increase in NUE by 2.4% from current figure would reduce use of N fertilizer worth $21 million, resulting in reduced N2O emission (Amanullah et al., 2016). A meta-analysis of 19 published studies indicated that N2O emission per unit of harvested product, called yield-scaled N_2O emission, reduced 12.7 to 7.1 g

N_2O-N/kg N uptake with an increase of NUE from 19 to 75% (Sowers et al., 1994). It is challenging to breed genotypes with 50 % greater NUE than current genotypes in a short time; however, it may be realistic to improve crop NUE up to 50% with minimizing yield loss as NUE is largely controlled by phenotypic variations (Table 1-2).

Inorganic fertilizer or manure application is prone to leaching or runoff, resulting in the environmental issues, when not properly applied under water and tillage managements. For instance, in Canadian agricultural soil, more than 1 million ton of N that are derived from N fertilization, biological fixation, and atmospheric deposition is prone to loss or build-up in environment (Janzen et al., 2003). In a semi-arid irrigation practice, increasing N fertilization over 150 kg ha^{-1} did not increase maize yield due to reduction in NUE, and increased the risk of N leaching under irrigation (Gholamhoseini et al., 2013). These facts indicate that oversupply of N fertilizer in soil may occur around the world. N inputs such as N fertilizer and manure are vulnerable to loss in the environment when not incorporated into the soil (Eghball and Gilley, 1999).

1.4 NUE in Conventional and Organic Agriculture

1.4.1 Physiology and genetics of NUE

To overcome the complex and quantitative manner of endogenous and exogenous mechanisms in NUE-related traits, understanding the genetic basis of N metabolism is essential for improving NUE. All components involved in NUE-related gene expression and metabolic pathways, controlling N uptake, utilization, partitioning and recycling are the subject of physiology, genetic and molecular studies. Most grain crops store a large pool of absorbed N during the vegetative stage and recycle pooled N during the reproductive stage when post-anthesis N uptake declines. In wheat, 50 to 90% of N in grain is derived from pooled N in stems and leaves (Spiertz and De Vos, 1983; Kichey et al., 2007). Therefore, systems in the pathways of N assimilation, remobilization and re-assimilation must be regulated according to external and internal N status to improve NUE. These metabolic pathways are controlled by complex genomic and consequent physiological steps in association with environmental factors that result in phenotypic characteristics. While N availability is mostly determined by environmental conditions and agronomic practices, the quantity of N intake into the root cytoplasm is regulated by passive and active uptake mechanisms controlled by several plant genes (Schenk, 1996; Tinker and Nye, 2000). Passive absorption usually refers to mass flow and diffusion, occurring along transpiration and energy gradients, respectively (Havlin, 2014). Active uptake occurs against concentration gradients through energy-required enzymatically driven actions. Thus, attempts to improve NUpE through modifying root kinetics have been proposed (Bassirirad, 2006). The nature of uptake kinetics is mediated by genetically regulated active membrane transporters. Nitrate transporters (NRT) from the NRF and NRT2 gene families, and ammonium transporters (AMT) have been identified for absorption and translocation of nitrate and ammonium (Dechorgnat et al., 2011; Nacry et al., 2013; Léran et al., 2014). Plants selectively use these transporter systems to absorb nitrate and ammonium, depending on their concentration in soil solutions. A high-affinity transporter system (HATS) works when nitrate and ammonium concentrations are lower than 1mM, while a low-affinity transporter system (LATS) becomes predominant when concentrations are higher than 1mM (Dechorgnat et al., 2011; Nacry et al., 2013).

Extensive studies have been conducted to characterize genes involved in these transporter systems as well as the functions of those genes (Vidmar et al., 2000; Orsel et al., 2002; Plett et al., 2010; Léran et al., 2014). Exploring functional mechanism of gene families NRF and NRT2, which are responsible for the activities of LATS and HATS, respectively, is the first step toward improving N uptake and specifically nitrate uptake in plants. The HATS system is further divided into constitutive HATS (cHATS) and inducible HATS (iHATS) (Behl et al., 1988; Aslam et al., 1992). Attempts to increase N uptake through overexpressing these gene families resulted in improved nitrate influx under some conditions but failed to improve NUE in *Arabidopsis thaliana* and tobacco plants (Fraisier et al., 2000; Pathak et al., 2008). This may suggest that improvement of NUE is not always source limited and improved N uptake can be successful to improve NUE when polygenetic functions involved in N metabolism pathways are taken into account for NUE enforcement.

During the vegetative stage, a large pool of absorbed nitrate is assimilated into roots and shoots. During this process of assimilation, nitrate is firstly reduced to nitrite in the cytoplasm by an enzyme called nitrate reductase (NR), and then further reduced to ammonium by nitrite reductase (NiR) in the chloroplast (Dechorgnat et al., 2011). The ammonium produced by NiR and ammonium from soil solutions and photorespiration is finally transported through phloem sap in the phloem and stored in each part of the plant's body as different forms of amino acids. The amount and the place for storing these amino acids depend on the plant species and the amount of available nitrate in soil solutions (Christophe et al., 2011). Assimilated N is stored as some form of amino acid or protein in plant organelles, which later becomes a source for N remobilization. Because NR is the first enzyme involved in N assimilation where nitrate is the N source, it was thought that the variability of NR activity is rate limiting and a key to increasing NUE in maize and growth of tobacco (Sherrard et al., 1986; Quilleré et al., 1994; Hirel et al., 2001; Masclaux et al., 2001). In maize, a high variability of NR activity was observed and was used to increase grain yield through traditional breeding techniques (Sherrard et al., 1986). In transformed *Nicotiana plumbaginifolia*, which overexpresses NR, NR activity in leaves increased 25 to 150% than that of the wild type while there was no difference in total N protein and dry matter production between the two types (Quilleré et al., 1994). Since NR is just responsible for the first step of N, increased expression of NR genes in plants with little uptake or storage pool of nitrate may not be an ideal strategy. The enzymes involved in the further assimilation process need to be considered to improve nitrate assimilation.

The second candidate enzyme in the process of nitrate assimilation is glutamine synthetase (GS) (Andrews et al., 2004). Ammonium derived from nitrite reduction and photorespiration is finally synthesized into glutamine by GS. Together with 2-oxoglutarate, glutamine is further catalyzed by the glutamine 2-oxoglutarate aminotransferase (GOGAT) to form glutamate in the plastid and cytoplasm (Masclaux-Daubresse et al., 2010). In major cereal crops, assimilation and remobilisation of N have been widely studied in relation to GS activity (Miflin and Habash, 2002; Masclaux-Daubresse et al., 2010; Bao et al., 2015). Since the failure of improving crop yield through single enzyme overexpression of NR/NiR (Quilleré et al., 1994; Masclaux et al., 2001; Hirel et al., 2001), GS has been studied to understand the entire enzymatic involvement for improving NUE in cereal crops. Together with glutamate synthetase, GS forms a GS-GOGAT cycle that is responsible for the central role of ammonium assimilation and remobilization from vegetative parts to developing grain in cereal crops (Miflin and Lea, 1977; Miflin and Habash, 2002). Multiple isoforms of GS exist in plants. The number of genes encoding cytosolic GS isoforms varies in wheat (*TaGS1a, TaGS1b* and *TaGS1c* for GS1;1*, TAgsR1* and *TaGSr2* for GS1;2 or GSr, *TaGSe1,* and *TaGSe2* for GS1;3 or GSe) (Bernard et al., 2008), rice (*OsGS1;1, OsGS1;2* and *OsGS1;3*) (Tabuchi et al., 2005) and maize (*Gln1-1, Gln1-2, Gln1-3, Gln1-4* and *Gln1-5*) (Martin et al., 2006), while a gene encoding chloroplast GS has been found in wheat (*TaGS2a, TaGS2b* and *TaGS2c* for GS2) (Bernard et al., 2008; Wang et al., 2015), maize (*Gln2*) (Martin et al., 2006) and rice (*OsGS2*) (Tabuchi et al., 2005). Improvement of reverse genetic techniques and availability of mutant plants have led to our increased knowledge of the specific gene functions related to the GS isoform family (Martin et al., 2006). In maize, double- and single-mutants of *Gln1-3* and *Gln1-4* reduced the expression of GS mRNA in leaves, kernel number per ear and kernel weight, respectively, while not exhibiting a significant reduction of vegetative biomass (Martin et al., 2006). This implies that these two GS isoforms are specifically responsible for grain development but not vegetative growth (Martin et al., 2006). The knockout mutant of *OsGS1;1* showed a severe decline in the total growth of a rice stand and grain filling (Tabuchi et al., 2005). Although the presence of other GS1 genes *OsGS1;2* and *OsGS1;3* in the mutant did not compliment this phenotypic result, re-introduction of *OsGS1;1* cDNA in the mutant led to complementation of these phenotypes (Tabuchi et al., 2005). Therefore *OsGS1;1* could be a pivotal gene for the assimilation of ammonium and the translocation of glutamine to developing rice grains.

Nitrogen remobilization occurs in the process of senescence. During this process, photosynthetic cellular components (e.g. chloroplast) and enzymes (e.g. Rubisco) are mainly dismantled into amino acids, amides and ammonium (Hörtensteiner and Feller, 2002; Gooding et al., 2005). Degraded ammonium is reduced by GS into glutamine. Glutamine is the major amino acid exported through both phloem and xylem to developing grain in barley and wheat. Therefore, the GS gene family plays a critical role in remobilizing necessary N to grain development during leaf senescence in cereal crops (Habash et al., 2001; Miflin and Habash, 2002; Forde and Lea, 2007). At this growth stage, leaves become an N source for protein synthesis in grain while N uptake from roots gradually reduces (Masclaux-Daubresse et al., 2010). Therefore, efficient N recycling in leaves influences N yield in final harvest products. A positive correlation between GS activity in leaves and grain protein content has been reported in both rice and wheat (Yang et al., 2005; Habash et al., 2007). Therefore, cytosolic GS1 and chloroplast GS2 activities in the flag leaf are considered useful characteristics to evaluate when selecting potential parents for breeding (Obara et al., 2001; Kichey et al., 2007; Fontaine et al., 2009). These three studies suggest that enzymes involved in N assimilation pathways (i.e. NR, NiR, GS, and GOGAT) are all coordinated, and a single approach will not efficiently enhance NUE and final yield. However, GS activity appears to play a pivotal role during leaf senescence contributing to increasing NUE (Jain et al., 2011).

1.4.2 Aspects of Management Systems

1.4.2.1 Strategies to reduce N losses in conventional agriculture

Nitrogen fertilization is the primary source of N leaching and atmospheric nitrogen oxides (NOx) emissions and is estimated to exceed 50% of the global NOx budget by 2025 (Yienger and Levy, 1995). Understanding the proper application of N fertilizer is, therefore, critical to reducing its environmental loading and to improve NUE in the system (Yienger and Levy, 1995). To achieve optimum results, a fertilization strategy, also called the 4Rs of N nutrient management or Best Management Practices (BMPs) for N fertilization, has been proposed (Griffith and Murphy, 1991; Matson et al., 1998; Alva et al., 2011; Ruidisch et al., 2013). The BMPs is a combination of four different concepts of fertilization practices. The practices emphasize a fertilization regime with the right rate and the right timing from the right sources at the right place (Griffith and Murphy, 1991; Alva et al., 2011). Nitrogen dynamics vary with production systems such as organic and conventional, or dry and humid environments. Thus, operation of BMPs requires substantial understanding of on-site N mineralization, immobilization, cycling and N requirement of growing crops (Dawson et al., 2008). Recent studies demonstrate that precision agricultural technologies based on BMPs offer a promising approach to improve NUE (Khosla et al., 2002; Zebarth et al., 2009; Ahrens et al., 2010). A study at a site-specific N management indicated that the key for successful on-farm precision N management is the right choice and timing of N application while taking into account on-farm residual N (Ahrens et al., 2010).

Selection and rate of N fertilizers, placement depth (Khalil et al., 2009a) and timing of application (Malhi et al., 2010) all influence N losses from soil. Different forms of inorganic N fertilizer cause different rate of N loss (Table 1-3). Urea is one of the most widely applied N fertilizers accounting for 55% of global N fertilizer consumption due to minimum risk of explosion under storage conditions, easy handling and low cost (Glibert et al., 2006; International Fertilizer Industry Association [IFA], 2011). The share of urea consumption to total N consumption is higher in developing countries than in developed countries (IFA, 2011). Urea is also responsible for a greater amount of ammonia and N_2O emissions than other N fertilizer because of its rapid and easily hydrolyzed nature after application (Khalil et al., 2002; San Francisco et al., 2011). This characteristic causes a significant amount of ammonia to be volatilized and a percentage of nitrate from the ammonia to be denitrified. Application of urea over large physical areas also results in severe N loss.

Nitrogen sources affect crop morphological root development differently. For instance, nitrate promotes elongation of lateral roots, whereas ammonium promotes initiation of lateral roots (Zhou et al., 2009; Lima et al., 2010). Due to this differential response, plants can extend specific roots and efficiently explore different N sources, which selectively promote root development in a large volume of soil. Wang and Below (1992) studied the effect of mixture of nitrate and ammonium fertilizers on morphology of two wheat cultivars. Although no causal relationship of treatment-induced differences was found, they observed a substantial increase in vegetative dry weight and the number of tillers of cultivars with the mixture of these fertilizers (i.e. 75/25, 50/50 and 25/ 75, NO3/NH4), compared with that of cultivars receiving only one form. The two wheat cultivars also responded differently to the different forms of N fertilizer for tiller development; one cultivar produced more tillers with nitrate, whereas the other produced more tillers with ammonium (Wang and Below, 1992). Similarly, yield, development of leaf area, chlorophyll and plant height differed with N sources in maize (Abbasi et al., 2013; Amanullah et al., 2016). Yield and the growth response of these traits were greater with application of either calcium ammonium nitrate or ammonium sulfate than with urea. These studies indicate that crops and N sources interact to cause various growth responses, thus further studies are needed to take full advantage of choice of N fertilizers for achieving better NUE.

Critical periods of N demand vary in crops and adjusting fertilization timing according to crop N requirements may reduce the risk of N loss and excessive N fertilizer application (Fageria and Baligar, 2005). For instance, the critical timing of N demand in spring wheat is between double ridge to terminal spikelet phases (between 20 to 45 days after seeding) (Limon-Ortega and Villaseñor-Mir, 2006), while in maize it ranges from 35 to 45 days after seeding (Richie, 1986). In malting barley, adjusting the amount of split-N application is necessary to ensure good malting quality (Baethgen et al., 1995). López-Bellido et al. (2005) reported that recovery of split- ^{15}N fertilizer application in wheat was, on average, 55% in three different N rates when fertilizer was applied as topdressing at terminal spikelet and stem-elongation stages; compared with 14% recovery for one-time application at pre-sowing. Under a winter wheat cultivation system, the plant recovery of ^{15}N-labeled N at booting was greater when applied with split-N fertilization than with one-time fall application (57.4 and 46.0 %, respectively) (Sowers et al., 1994). In many cereal production areas, N application practices are based on soil N analysis at seeding. Although one-time application of all required N at seeding is a common and relatively effective practice for winter wheat production in drier areas (McKenzie et al., 2010), several studies indicated that split-application of N fertilizer (e.g. at seeding, tillering and stem elongation) improved NUE, the total N yield and grain yield in various growing conditions (Spiertz and De Vos, 1983; Limaux et al., 1999; López-Bellido et al., 2005). These results clearly show that the extent of plant N uptake is associated with N demands at different plant growth stages where N is used for cell division and growth, and thus the timing of fertilizer application needs to be synchronized with the timing of crop N requirement.

Besides split-fertilization, application of polymer coated N fertilizers is another useful strategy to synchronize N supply and demand, and reduce N losses (Yanai et al., 1997; Khalil et al., 2009b; Malhi et al., 2010). These fertilizers are covered with different types of polymer coats such as controlled- release compounds or urease and nitrification inhibitors (Havlin, 2014). Several studies reported the positive effects of polymer coated controlled-release N (CRN) on grain yield, NUE (McKenzie et al., 2007; Malhi et al., 2010) and N leaching (Yanai et al., 1997). The release timing of CRN is designed to synchronize N requirement in the plant (Malhi et al., 2010), thereby minimizing the risk of N leaching under normal conditions. For instance, urea is nitrified within two weeks under favorable conditions, whereas anhydrous ammonia is converted to nitrate slower than urea (Nielsen, 2006). The critical timing for N requirement in winter wheat is at the double ridge stage and from tillering to stem elongation, which occurs at the beginning of the spring. Therefore, regular fertilization at the time of seeding does not provide the appropriate amount of N at the proper time in winter wheat. Moreover, a considerable amount of

N is lost to the environment during the winter. Therefore, the application of CRN at seeding is especially effective in winter wheat to prevent N loss under wet winter conditions, which tend to result in increased denitrification and N leaching (Malhi et al., 2010). Nevertheless, negative or negligible influence of CRN on NUE has also been reported in the literature (McKenzie et al., 2010). Such inconsistent responses may be caused by year-to-year variation in weather (Malhi et al., 2010; McKenzie et al., 2010). Split-banded application of urea in spring wheat and barley (half each at seeding and tillering) and canola (at bolting stages) was as effective as the spring-banded application of CRN as a single dose (Malhi et al., 2010). Use of CRN to pots with and without crop reduced the concentration of nitrate in soil solutions at all sampling times, indicating that CRN reduces N leaching (Yanai et al., 1997). These results suggest that CRN and split applications of fertilizer may have theoretically similar effects of reducing N loss and, therefore, improving NUE.

To mitigate soil enzymatic factors affected by environmental variation, the combination of urease and nitrification inhibitors has been tested (Gioacchini et al., 2002; Boeckx et al., 2005). These types of inhibitors are responsible for limiting the enzymatic activities of urea hydrolysis and ammonium nitrification. The use of urease inhibitors leads to increased urea content in the soil, and the use of a nitrification inhibitor increases soil ammonium content (San Francisco et al., 2011). In general, nitrate is more readily lost in the environment than ammonium. Usage of several urease and nitrification inhibitors resulted in some suppression of N losses (Weber et al., 2004). In general, these inhibitors are more effective in reducing N loss when the fertilizers along with inhibitors are applied, under conditions that are prone to volatilization, denitrification and N leaching (Barth et al., 2001). Therefore, results depend on soil and environmental variation (Gioacchini et al., 2002; Boeckx et al., 2005; Khalil et al., 2009b; San Francisco et al., 2011).

In addition to fertilization regimes, the diversification of crops/cropping practices in crop rotation plays a significant role in improving NUE in conventional systems. Diversified crop rotations with leguminous crops take biologically fixed N into the N cycle in situ, resulting in the reduction of N fertilizer use. When legume crops were included as preceding crops in a no-till crop rotation, N fertilizer accounted for 42 to 55% of the total N input in wheat and canola compared to 52 to 60% of total N input derived from N fertilizer when preceding crops were non-legumes (Luce et al., 2016). N derived from the decomposition of preceding leguminous crops compensated for a portion of the N fertilizer input. When a large volume of N is required for cereal crops, selection of N-fixing crops as preceding crops could reduce N fertilizer application amount, minimizing the risk of N loss in the environment. When succeeding crops were fertilized with the recommended amount of N, increased yield of the following crops are greater than those following non-leguminous crops (Badaruddin and Meyer, 1994; Yadav et al., 2003; O'Donovan et al., 2014; Luce et al., 2015). The amount and timing of available N in legumes depends on factors such as the C/N ratio, tillage practices, soil microbial diversity and climate. Greater care is needed when legumes are incorporated in rotations for reducing N fertilizer.

The inclusion of post-harvest cover crops in crop rotations has been successfully practised throughout the world. Cover crops maintain favorable soil conditions for improving NUE such as adding and conserving N, optimizing the C/N ratio of residues and preventing soil erosion (Dabney et al., 2010). In summer crop farming regions, the use of two winter cover crops affected yield and N uptake of the following maize crop (Gabriel et al., 2016). Barley as a winter cover crop grew faster than common vetch; however, vetch finally covered more ground than barley in winter, resulting in high N content in yield biomass (Gabriel et al., 2016). Thus, barley may be used as a means of N conservation in this system as it minimizes the risk of post-harvest N loss and soil erosion. On the other hand, vetch has a greater N contribution to the following crop than barley. A meta-analysis of N dynamics between the diversified rotations and the conventional simple rotations with bare fallow demonstrated that legume-based crop rotations reduced nitrate leaching up to 40% relative to conventional fertilizer- based rotations, indicating that the replacement of bare fallow with legume cover crops provide dual benefits of conserving and adding N (Tonitto et al., 2006). The authors also reported that inclusion of cover crops prevented post-harvest N volatilization and denitrification. In the Northern Plain semiarid area, summer fallow used to be a common practice to store sufficient soil moisture for succeeding crop germination despite the risk of soil erosion and denitrification (Aulakh et al., 1982). Studies of crop diversification in rotations in semiarid regions reported that diversification with pulse/green manure in rotation had the additional benefit of increased water availability for succeeding crops (Gan et al., 2015; Gan et al., 2016). Such a finding provides farmers an alternative practice to conserve soil moisture, replacing summer fallow. Although, long-term studies investigating the direct effect of diversified crop rotations on NUE are few, these studies suggest the importance of crop sequences and diversification of crops in rotations for potential improvement of NUE.

1.4.2.2 Strategies to reduce N loss in organic agriculture

Organic agriculture is based on using the existing ecological system and recycling processes. Unlike conventional counterparts, practices in organic agriculture must be agreed to the inter-connected ethical principles that preclude any means that improved NUE but do not fit organic regulations (IFOAM). For instance, genetically engineered cultivars, specially designed slow-release N fertilizer or herbicide use in no-till for improved NUE are not allowed in organic management. The primary approach for improving NUE in organic agriculture is to maintain potential N mineralization reserves in the soil and to recycle on-farm materials through green manure, and incorporating plant residues on a surface of the field from previous crops (Spiertz and De Vos, 1983; Drinkwater, 2004; IFOAM, 2008). The centre of N cycle in organic management is N mineralization that is a biological process. The quantity of N released from SOM largely depends on the chemical compound of SOM, soil environment and the biological properties of decomposers (Masunga et al., 2016). Therefore, diverse knowledge, techniques and strategies are required to optimize the utilization of various N reservoirs. Sources of N are mainly derived from on-farm materials, and can be limited, especially in extensive organic farming systems. Therefore, proper management of these reserves in soils is a key management strategy to provide the necessary amount of N to crops. This can be achieved through a combination of crop rotation, incorporation of legume crops as a source of biologically fixed N in the rotation, tillage practices and use of catch crops (Lupwayi et al., 2006; Constantin et al., 2010; Snyder and Spaner, 2010; Doltra and Olesen, 2013). Although these practices are also observed in conventional systems, the contribution of these practices towards NUE is greater in organic systems than in conventional systems (Huggins and Pan, 1993; Drinkwater, 2004).

Organic practices tend to cause less N loss than conventional systems; a combined result attributed to inherent low concentrations of plant available inorganic N, the incorporation of legumes and catch crops and diverse crop rotations (Stopes et al., 2002; Syswerda et al., 2012). For example, annual nitrate loss under organic management was 19 kg N ha^{-1} yr^{-1} compared to 62 kg N ha^{-1} yr^{-1} in conventional systems in one study (Syswerda et al., 2012), and 36 kg N ha^{-1} yr^{-1} in organic systems versus 57 kg N ha^{-1} yr^{-1} in conventional systems in another (Stopes et al., 2002). It may, therefore, be more difficult to increase NUE in organic systems than in conventional. This suggests that it is even more important to understand the mechanisms contributing to increase NUE in organic systems.

Crop rotation is one of the most important management practices for organic farmers to maintain soil fertility (López-Bellido and López-Bellido, 2001; Eriksen et al., 2004). In western Canada, the typical organic rotation includes legumes and pulses in a several-year rotation that appears to maintain soil N levels due to N fixation of these crops (Degenhardt et al., 2005; Snyder and Spaner, 2010). The choice of crops in rotation depends on weather, soil condition, plant adaptation, and market demands but the inclusion of legumes is obviously beneficial to maintain soil N levels. The relationship between crop rotation and NUE/N loss has been extensively studied (Porter et al., 1996; López-Bellido and López-Bellido, 2001; Sainju et al., 2009; Askegaard et al., 2011).

Legumes and their associated N-fixing bacteria are critical components of N supply in organic crop rotation systems. Inclusion of leguminous crops provides atmospheric N to the host plants which eventually store N as SOM for long term. Several studies have reported improvement of soil N status, including potentially mineralizable N, total N and plant available N in legume-based rotation practices (Marriott and Wander, 2006; Kayser et al., 2010). Ammonia fixed through biological means such as legume and N-fixing bacteria provides an important portion of plant required N, partially obviating the need for industrial fertilizers. For instance, endophytic N-fixing bacteria can provide 10–25% of required N in maize and rice (Okon and Labandera-Gonzalez, 1994; Mano and Morisaki, 2008; Figueiredo et al., 2010; Amiri and Rafiee, 2013). Moreover, biologically fixed N is less susceptible to loss than synthetic N fertilizer on a short-term basis due to direct translocation of ammonia from bacteria to their host plants (Ondersteijn et al., 2002). The fixed N is immediately converted into organic forms as amino acids, which assimilate into plant cells and become stable. A study reported that unfertilized wheat following a grain legume crop yields almost the same as wheat with 75kg N ha^{-1} fertilization although grain N concentration varies according to weather conditions (Badaruddin and Meyer, 1994). Wheat NUE, NUpE and NUtE were greater after cowpea compared with rice (Yadav et al., 2003). This was caused by the better root growth and crop establishment of wheat coupled with the increase of the soil organic C and available N in the cowpea–wheat rotation. These results demonstrated that including legumes in rotation ensures N availability to succeeding crops. Although availability in legume residual N in rotation is unpredictable and difficult to manage; plough-in legumes or other plant residues are eventually decomposed by soil microorganisms, and released N from these residues is prone to loss when N supply and crop demand are asynchronous (Crews and Peoples, 2005). A key for the rate of N mineralization in plowed legumes is the C/N ratio, weather and soil microbial conditions. Thus timing of plowing, which provides favorable conditions to decomposers, must be considered (Herridge et al., 2008; Kayser et al., 2010). Much of the N pool of grain legumes is removed during harvesting, whereas green manure or cover crop legumes are not grown for grain and inclusion of these non-grain legumes is a better choice for keeping all fixed N within the system.

Planting legumes with overlapping life cycle of main crops, also called relay intercropping, is found to be an agronomically and ecologically feasible practice for improving NUE (Jeranyama et al., 1998). Although competition between legumes and winter wheat for resources caused reduction of grain protein in wheat grain after relay intercropping, the yield of subsequent crops increased due to leguminous soil N enrichment (Amossé et al., 2013; Amossé et al., 2014).

Tillage remains necessary in organic systems especially for weed control. Tillage provides necessary aeration and optimum moisture and is, therefore, very important to the microbial decomposition of SOM. However, tillage may cause severe N losses through N leaching or soil erosion (Kessavalou et al., 1998; Sainju et al., 2009). Due, in part, to N conservation awareness and increased fuel costs, no-till has been widely implemented in conventional systems to conserve N pools (Porter et al., 1996; Spargo et al., 2008). Organic matter derived from plant residues accumulates on the surface. Plant available N is immobilized into organic forms by diverse soil microorganisms around the surface soil under no-till managements (Doran et al., 1998), whereas an increase in N loss through leaching, volatilization and denitrification was observed as the frequency and intensity of tillage increased (Sainju et al., 2009). Another study noted that no-till maintained a larger amount of soil nitrate concentration than conventional tillage system (Lupwayi et al., 2006). This may be because long-term conservation (reduced or no) tillage systems preserve habitat for soil microbial communities and promote accumulation of soil enzymes responsible for N dynamics. Since most soil enzymes are of microbial origin (Gianfreda et al., 2011), maintaining soil microbial communities in no-till systems has a great impact on soil enzyme activities, thus affecting N mineralization (Muruganandam et al., 2009). Nitrate and ammonium produced through microbial mineralization may simultaneously immobilize due to the rapid turnover of microbial biomass under the high C/N ratio in soil (Muruganandam et al., 2010). Immobilization of N caused by no-till is in balance with N mineralization; thus no-tillage practice may be more efficient from a sustainable standpoint (House et al., 1984; Muruganandam et al., 2010). Franzluebbers (2004) estimated the amount of soil organic N in several tillage treatments in the previous studies and found that the total organic N in no-till managements is 23 kg N ha^{-1} yr^{-1} higher compared to plow tillage.

However, the effect of no-till on limiting N losses is mostly controlled by soil and weather conditions (Hansen and Djurhuus, 1997), and may be less effective in limiting N loss than catch crops or timing of tillage (Constantin et al., 2010). Finding mechanisms to incorporate no or limited tillage systems into organic management strategies is needed.

Depending on soil fertilization regimes, the rate of N uptake during the crop growing season is generally higher than the rate of N mineralization in organic fields and the risk of N loss is low in most cases (Watkins and Barraclough, 1996; Masunga et al., 2016). However, a high risk of N leaching could become a problem in bare fields after harvest, especially when the temperature in a fallow season is relatively high and the field is left uncropped (Stopes et al., 2002; Eriksen et al., 2004). This leaching is due to a combination of increased activity of decomposers and the absence of crop to trap N. The use of a catch crop after the main crop harvest has a potential role in reducing the risk of N leaching during the off-season (i.e. fall and winter). Catch crops absorb N in the soil and store N, thus preventing N leaching. The stored N as SOM is eventually decomposed in the next crop season. A long-term study was conducted to evaluate the effect of cover crop on the reduction of soil N loss from the system (Constantin et al., 2010). Using cover crops in the off-season resulted in a reduction of 36-62% of N loss from the system compared to no-cover crop in three different locations. However, the large variability in the reduction of N loss by cover crops in three different locations also indicated that other factors such as precipitation, soil types and crop rotation also affect the amount of N leaching (Constantin et al., 2010). To test the effectiveness of cover crops in reducing N loss under different cropping practices, Lemaire and Meynard (1997) investigated 6-year average annual N leaching loads among three cultivation systems. The conventional system received an appropriate amount of N fertilizer and two organic systems treated with and without animal manure. Mean N leaching loads between the three systems were not statistically significant when catch crops were grown. They concluded that the use of catch crop after the main crop had a potential role in reducing the risk of N leaching during off-season under different amount and quality of external inputs. Similar results were reported by Stopes et al. (2002). Catch crops absorb N in the soil and store N, thus preventing N leaching. Therefore, the ability to store a large quantity of N and the turnover rate of the stored N in catch crops may be important subjects to consider for the selection of catch crops. These studies highlight the importance of cover crops for reduction of N loss between growing seasons for both organic and conventional cultivation systems.

One of the distinctive differences of organically managed soils from conventionally managed soils is the diversity and quantity of functional microbial population (Mäder et al., 2002; Pimentel et al., 2005; Braman et al., 2016). Besides N-fixation, all other N cycling processes are governed by the quality and quantity of substrate and microbial activity. Organic farming, which relies on ecosystem service, essentially has the potential to increase crop NUE through its cultivation practices (Veresoglou et al., 2012). For instance, the rapidly available fraction of SOM, particulate organic matter (POM), is 30 to 40 % higher in organic systems than in conventional system and functional soil microbial community that decompose the POM may be more active and diverse in species and abundance (Lavelle and Spain, 2001; Marriott and Wander, 2006; Reilly et al., 2013). Microbial contribution to plant N acquisition is estimated to be 0-20% or more through N-fixing bacteria including free-living bacteria, and 0 to 80% through mycorrhizal symbiosis (Van Der Heijden et al., 2008). Ubiquitous soil symbiotic fungi, arbuscular mycorrhizal fungi (AMF) are able to transport N from soil to the host plant, although this does not appear to contribute to increasing plant biomass or total plant N content (Hawkins and George, 1999; Hawkins et al., 2000). These studies indicated that the hyphae of AMF uptake both inorganic (NO_3- and NH_4+) and organic (Glycine and Glutamic acids) N. The quantity of acquired N through AMF varied depending on AMF isolated and species, but the organically managed pasture had higher ability to uptake organic N than conventional (Hamilton III and Frank, 2001). A comprehensive review of the mechanism of N acquisition through AMF is elsewhere (Jin et al., 2012; Veresoglou et al., 2012). Recent studies suggest that the degree of N mineralization in mixed crop-livestock farming systems is partly controlled by carbon excretes from plant roots, which stimulate activities of the soil microbial community (De Nobili et al., 2001; Hamilton III and Frank, 2001). Promoted carbon exudates by grazed grass stimulate microbial activity, resulting in increase of soil inorganic N as well as plant N uptake (Hamilton III and Frank, 2001).

1.4.2.3 Predicting N recovery from soil organic matter

Unpredictable rate and timing of mineralization of N source (i.e. green manure, farmyard manure, compost, residual SOM) also impede synchronization of N sink and source in both conventional and organic agriculture. Organic N materials tend to release a form of plant available N in various manners depending on the materials, environment and agronomical practices. N recovery in crops from SOM varies due to environment and characteristics of SOM (Amlinger et al., 2003; Crews and Peoples, 2005). The recovery rates from different SOM are variable and are generally less than 30% of the total recovery at first year of SOM incorporation and several percent in subsequent years (Amlinger et al., 2003; Crews and Peoples, 2005).

Nitrogen mineralization models from various SOM provide rough estimates of SOM mineralization and may help to optimize N sink/source synchrony in both systems. The details of several proposed models are reviewed by Benbi and Richter (2002). Mineralization during crop growth has been estimated through nonlinear equations using the separated or the total active SOM (Benbi and Richter, 2002). The common limitation of the N models under organic systems is that the active organic N pools are larger in size and variety than the inorganic pools, thus causing a significant error variance in the models (Tanji et al., 1979; Camargo et al., 1997). However, meta-analyses of accumulated laboratory data have proven that exponential models are useful to predict N dynamics when site-specific calibration is possible. These models, however, don't take into account the mineralization/immobilization reverse cycles occurring simultaneously in various N pools (Benbi and Richter, 2002; Dijkstra et al., 2009).

Exponential models are based on mathematical fitting techniques to predict N mineralization as a function of time (Benbi and Richter, 2002). The models consider existing N pools as separated fractions of soil N pools and estimate the total N mineralization from each fraction with different mineralization rates. Benbi and Richter (2002) suggested that multiple N fraction models provide better estimations of N mineralization. Therefore, the double-N-pool model (i.e. labile and recalcitrant SOM) would be the best to calculate parameters for N mineralization modelling compared to other N pool models (Benbi and Richter, 2002). By using data sets from several previous studies, Gilmour and Mauromoustakos (2011) found that the rate of N mineralization of labile N pool and accumulated N from labile N pool are correlated with the rate of labile N mineralization during the first week. These labile N mineralization rate and accumulated N could be estimated using total soil N, CO_2 release during first 3-day incubation, clay content in soils, soil temperature and moisture (Gilmour and Mauromoustakos, 2011). The environmental factors affecting N mineralization vary with the C/N ratio and biochemical quality of organic residue, soil moisture and temperature and the frequency of soil rewetting events

(Cabrera et al., 2005); therefore, calibration and validation of the models are necessary for reliable prediction (Cabrera et al., 2005; Zhao et al., 2011).

1.5 Breeding for Integration of Physiological and Agronomic Strategies to Improve NUE

1.5.1 Genetic improvement to maximize NUE for target conditions

Genetic improvement in NUE through breeding relies on the availability of genetic variation and heritability of the morphological and physiological traits associated with NUE. Genetic variability in N uptake and utilization has been reported in several grain crops (Table 1-2) including wheat (Ortiz-Monasterio et al., 1997; Gaju et al., 2011; Swain et al., 2014), maize (Barbieri et al., 2008; Kalinova et al., 2014; Li et al., 2015), rice (Cassman et al., 1996; Sun et al., 2012) and barley (Sinebo et al., 2004; Anbessa et al., 2009). Existing variation in grain/ total N concentration in different genotypes under the same amount of fertilization indicate the potential genotypic improvement of both NUpE and NUtE through breeding. Many of these studies did not focus on root traits. Roots are an interface where crops absorb N and are essential functional traits for synchrony of N supply and demand. Several positively correlated overlapping quantitative trait loci (QTLs) for root traits and N uptake have been reported (Table 1-4).

Functional root traits responsible for optimizing N uptake are key subjects to improve NUE. Since roots have multiple roles, improvement of a single trait in the root function is not likely to enhance N uptake and NUE (Lynch, 1995). Positive correlations among QTL for root traits, some physiological traits and N uptake in maize, wheat, and rice have been reported (Gallais and Hirel, 2004; An et al., 2006; Coque et al., 2008; Namai et al., 2009; Gaju et al., 2011). For instance, QTLs for NUpE and root dry weight under low N conditions were reported linked in a Chinese doubled haploid wheat population (An et al., 2006). In a QTL meta-analysis, QTLs for NUpE, traits of root architecture (root depth, surface area, diameter) and leaf stay-green positively coexisted in eight clusters of QTLs, while QTLs for N remobilization coincided with QTLs for leaf senescence in maize (Coque et al., 2008). While referring to the results in the meta-analysis, the authors hypothesized that NUpE and N remobilization (or NUtE) are independently inherited traits, and traits associated with these two NUE sub-components may, therefore, be combined through breeding to further improve NUE (Dawson et al., 2008).

Although the final goal of breeding for both organic and conventional agriculture converges at increasing productivity through improvement of crop potential, biotic and abiotic resistance, in terms of root function for improved NUE, breeding approaches depend on soil N levels where intended bred cultivars grow. Root traits for conventional agriculture require an early vigorous development of roots. Such roots are robust and uptake N when N comes available depending on whether applied as conventional, slow-released or split fertilizer regime. In contrast, proliferation of root system and root biomass could be more important under organic or low available N conditions. Wheat breeding lines with early vigorous root branching resulted in a higher N uptake and biomass production in sandy soil where nitrate leaching and runoff are major problems (Wu et al., 1997; Liao et al., 2004; Liao et al., 2006). As a consequence, the final amount of N per plant was greater in these vigorous wheat lines than in conventional cultivars (Liao et al., 2006). This trait can, therefore, reduce N leaching into the environment when fertilizer is applied at seeding as a single dose. The authors also highlighted the significance of the root branching pattern for early N uptake. The contribution of branched root system in the upper and middle soil profile (0 to 0.7 m) to N fertilizer recovery was greater than the deeper root system. This greater contribution was related to larger root length density at shallower soil profiles, although nitrate is soluble and easily moves into roots by mass flow in transpiration and diffusion so that roots do not need to have a physical interface with N (Liao et al., 2006). This result agrees with another study in maze (Wiesler and Horst, 1994). Cultivars with this trait may be more versatile for any cultivation strategies to reduce N loss if the capacity of N storage in their vegetative parts is high.

For crops grown in limited N condition, the proliferation of roots is advantageous where there is irregular and unpredictable soil N availability. Increased proliferation of roots is considered adaptability to the spatial and temporal heterogeneity of soil N concentration in several crops, including maize, wheat and barley in response to the localized high N availability (Drew et al., 1973; Drew and Saker, 1975; Hong-Bo et al., 2012; Jing et al., 2012; Shen et al., 2013). The proliferation of lateral roots in high N concentration patch and consequent increased N inflow into crops logically increase NUE under soil conditions of uneven SOM. The benefit of lateral root proliferation can be expected not only in organic but also conventional fields with band placement of N fertilizer. Although there appears to be a small contribution of the root proliferation to total N uptake in some studies (Wiesler and Horst, 1994; Van Vuuren et al., 1996), the mechanism underlying this root proliferation within the soil zone of localized high N concentration has been only validated on the basis of single plant inter-C/N economy (Robinson, 2001). In the plant inter- specific competition model, the author found that the extra C required for the proliferation of roots was just 0.2% of daily C gain from photosynthesis under 12 h photoperiod, which is much less than that for establishment of AM symbiosis (e.g. 4 to 20 %) (Douds Jr et al., 2000; Graham, 2000; Robinson, 2001). The ability of carbon assimilation and allocation that is governed by the gradient of labile C in shoots and leaves is assumed to have an influence on root biomass production (Andrews et al., 2001; Chun et al., 2005). Therefore, as long as the sacrifice of C to promote root proliferation is at a reasonable cost and compensates the benefit of extra N inflow, it can be beneficial to choose any means of fertilization that promote root proliferation. The gene responsible for this reaction is well- described in a review (Walch-Liu et al., 2006a).

An investigation of the genetic relationship between the height reducing *Rht* genes and root traits using doubled-haploid and near-isogenic lines in wheat found coincidence of QTLs for plant height and root traits (Bai et al., 2013). Dwarfing genes (*Rht-B1c*, *Rht-D1c*, and *Rht12*) reduced root related traits including root length, total root surface area, root dry weight, and some *Rht* genes controlled both height and root traits (Bai et al., 2013). We may need to take into account this relationship between *Rht* genes and root traits. The introduction of *Rht* dwarfing genes may have a negative impact on root proliferation traits that can be useful characteristics for improving NUE (Bai et al., 2013; Hawkesford, 2014) although a study reported no difference in thr rooting patterns between semi-dwarf and tall wheat cultivars (Entz et al., 1992).

Walch-Liu et al. (2006b) proposed a novel theory that the presence of L-glutamate in organic N-rich soil induces shorter but branched root system in *Arabidopsis* to efficiently acquire N, while inhibiting primary root growth. They observed natural variation for L-glutamate sensitivity among different ecotypes, suggesting that this initiation of root branching is genotype-dependent. This finding suggests that breeders might take advantage of this trait to develop new cultivars with branched roots. This trait may be more advantageous for crops grown in organic fields because, in general, soil under organic management contains more SOM thus is likely to have more L-glutamate than in conventional management. Further detailed studies of genes involved in the response of L-glutamate are needed. As a result of significant interaction between genotypic profiles and soil N availability, selection for elite NUE traits adapting given N levels should take place at several levels of soil N concentrations in order to devise their potentials toward appropriate agronomic practices (Poorter and Nagel, 2000; Trachsel et al., 2013; Obara et al., 2014).

1.5.2 Optimization of N supply and demand

The observed genetic variation for NUE in various grain crops under different spatial and temporal soil N availability suggests a possibility to optimize NUE by filling the gaps in these environmental- and cultivar-specific variations (Scharf et al., 2005; Coque et al., 2008; Anbessa et al., 2009; Bancal, 2009; Cui et al., 2009; Gaju et al., 2011).

The breeding strategy for improved morphological and physiological N efficiency is mainly based on knowledge of functions of crop organs and enzymatic activities involved in N metabolism of absorption, assimilation, translocation and remobilization by considering the crop itself or cereals as N sink (Figure 1-1) (Simpson et al., 1982; Cormier et al., 2013). Thus the characterization of related traits needs to be explored. Contrarily, agronomic strategies for better NUE are based on strategies that reduce N loss from soil systems and efficiently supply N according to crop demand. Although theoretical mechanisms of each NUE component have been studied for decades, improvement of a single crop trait or cultivation technique does not necessarily result in increased crop NUE (Fraisier et al., 2000; Pathak et al., 2008). Several NUE studies emphasize the importance of synchrony between N supply from N sources and plant N demand as an N sink (Sandhu et al., 2000; Crews and Peoples, 2005; Shanahan et al., 2008). Asynchronous events could happen spatially and temporally when N supply exceeds plant demands or when N supply is insufficient to meet crop demands (Crews and Peoples, 2005). Although, the former often occurs in conventional systems and the latter is more prominent in many low input/organic production systems, improvement of synchrony between N demand and supply, and reduction of N loss from agricultural systems, maybe achieved through a combination of several different approaches (Table 1-5). The integration of knowledge from breeding and agronomic strategies, therefore, may provide useful information to improve NUE although the lack of on-farm studies about optimization of N supply and demand will require long-term commitments.

As a result of significant interaction between genotypic profiles and soil N availability, selection for elite NUE traits should take place at several levels of soil N concentrations in order to devise appropriate agronomic practices (Poorter and Nagel, 2000; Trachsel et al., 2013; Obara et al., 2014). The scarcity of N in the soil solution results in greater biomass partitioning in roots than in shoots (Poorter and Nagel, 2000; Chun et al., 2005). In this situation, a cultivar with improved stay-green trait may not display its ability toward NUE. It has also been reported that root growth angles of maize inbred lines become steeper (i.e. deeper) in N deficit condition (Trachsel et al., 2013). The total root length in rice increases in high soil ammonium concentration (Obara et al., 2014). Through these responses to soil N concentration, crops modify their root systems. It has been demonstrated that the relative contribution of NUpE and NUtE on NUE depends upon the soil N levels (Moll et al., 1982; Le Gouis et al., 2000). The contribution of NUpE towards NUE is greater than that of NUtE in low soil N concentrations in spring wheat (Ortiz-Monasterio et al., 1997; Le Gouis et al., 2000; Muurinen et al., 2006). The contributions of both NUpE and NUtE are same at moderate soil N concentrations, and that of NUtE is greater than NUpE under high soil N levels (Ortiz-Monasterio et al., 1997). In a study of genetic variability among ancestral and modern cultivated wheat, Gorny and Garczyński (2008) found that under low soil N level, the primitive polyploid species had higher NUpE, whereas the modern cultivated hexaploid species had better NUtE. Generally, a low soil N level decreases biomass and grain yield but improves NUtE in wheat (Gorny and Garczyński, 2008). Therefore, selection from a wide range of germplasm under low soil N levels may be useful in breeding cultivars for different management systems (Reid et al., 2009). Although results of these studies varied, they did indicate genetic variability with differences in soil N concentration. Therefore, performance of new cultivars may not meet breeders' expectation when grown under conditions different than those where breeding was practised. In addition, heritability of NUE related traits seems to vary with N levels, which complicates selection for these traits (Presterl et al., 2002; Laperche et al., 2006; Coque et al., 2008; Reid et al., 2009). Heritability is largely associated to genetic variation and its interaction with environment. Therefore, it is useful to have more information about the behavior of important NUE related traits under different soil N concentration to breed ideal cultivars for specific N management practices.

The concept of N dilution curve has been studied as a crop N status indicator. This curve is a plant-based diagnostic tool providing an estimation of the crop total N requirement under given N conditions for optimum biomass production (Greenwood et al., 1990). N concentration in crop aboveground biomass declines according to growth stages even under optimal soil N levels (Justes et al., 1994; Hoogmoed, 2015). This N dilution phenomenon is commonly shared in any species and genotypes of crops grown in any climatic conditions and is related to plant above ground biomass production (Lemaire and Meynard, 1997; Lemaire et al., 2007). The curve is, therefore, a useful decision- making tool for N fertilization. Crop specific nitrogen dilution curves have been proposed in wheat (Justes et al., 1994; Ziadi et al., 2010; Hoogmoed, 2015), rice (Ata-Ul-Karim et al., 2014a; Ata-Ul-Karim et al., 2014b; Sheehy et al., 1998) and maize (Herrmann and Taube, 2004). Utilization of the curve to evaluate a critical point of the best balance between crop N concentration and biomass may be another approach for improving crop NUE.

Application of NUE knowledge is more challenging in organic production systems due to a number of uncontrollable biotic- and abiotic factors, which result in significant phenotypic variation. Therefore, synchronization in N sink and source in organic fields is more challenging. From sink's perspective, for instance, the prediction of expected genetic gain in spring wheat by direct selection in an organic field is difficult because genetic parameters cannot be precisely estimated due to variability in some agronomic traits (Reid et al., 2009). A low heritability for grain protein content is reported in organically grown wheat, while others reported high heritability for NUpE, NUtE and NrE in wheat and maize under organic conditions (Presterl et al., 2002; Coque and Gallais, 2007; Reid et al., 2009). Struik and Yin (2009) concluded that polygenic control, environmental variation (e.g. plant available N concentration, timing and amount of mineralization, weed, and disease pressure) and their interaction with NUE related traits cause inconsistencies and hinder improvement of crop NUE through conventional breeding. Therefore, QTL mapping and marker-assisted selection for traits associated with NUE and the interaction of these genes/QTLs with environment and management practices may provide breeders with tools to improve NUE for target management systems (Struik and Yin, 2009; van Bueren et al., 2010).

1.6 Summary

Raising concerning for environmental issues caused by N management in agriculture brings a necessity for improved NUE in cereal-based farming systems. Major breeding programs are currently conducted under the condition where N fertilizer is controlled to ensure optimum crop performance. Contrarily, organic farming systems are usually low in soil N and rely on on-farm materials and natural cycles for maintain crop productivity. Due to the notable differences between two systems in terms of spatial and temporal N availability, biotic and abiotic stress, management practices, important traits/cultivar choice for improving NUE may differ. Effective approaches for improved NUE should be an integration of knowledge in physiological, genetics and agronomic studies. This will provide a key selection criterion for breeders to develop suitable genotypes according to environments.

NUE is a complex trait to improve with many potential interactions and trade-offs with other factors controlling final yield. Key genotypic factors for improving crop NUE seem to be common traits between conventional and organic agriculture. Those traits capture and utilize N when it is available for grain production. However, those regulations and responses vary according to genotypes, environmental and agronomic regimes. Therefore, a genetic, environmental and N-level interaction should be taken into consideration in breeding programs for intended production systems. The agronomic approach requires considering ways to synchronize N supply with crop N demand besides optimizing N utilization in a system. Implementation of BMPs for N fertilization has great potential to fill the gap between optimum and the actual current practices, and thus in the improvement of NUE in conventional production systems. Organic practices put more emphasis on incorporation of legumes and crop residues in crop rotation and diversification of cropping practices. Factors controlling crop NUE and the efficiency in crop production management are intertwined in both organic and conventional systems. The challenge for maintaining crop yield and improving NUE needs emphasis globally. While theoretical approaches to improving NUE by altering single traits related to N efficiency are necessary, studies covering holistic approaches will lead to improvement of NUE within the entire agroecosystem.

1.7 How my Ph.D. study arose

During my M.Sc. program at the University of Alberta, I studied wheat agronomy in organic agriculture, focusing on a study of the effects of a weed community on wheat yield and soil microbiota. During this time, I participated in a study for comparing performance of the breeder seed collection on Canadian germplasm at organic and conventional fields. This study showed the presence of cross-over interactions between CWRS cultivars and management systems (i.e., organic vs. conventional) for protein (Chapter 2). Improving sustainable food production has been my main research goal, and I have kept a research topic for improved nitrogen use efficiency in cereal-based systems. Therefore, this cross-over interaction of protein raised a big question of cultivar choice for NUE between two systems. If the cross-over interaction presents in different organic environments/locations, it would be necessary to explore genetic variability and cultivar performance for improvement of NUE in CWRS wheat, because NUE affects cereal yield-protein relationships. This led me to continue my study in a Ph.D. program under Dr. Dean Spaner to explore a genetic variation of NUE in CWRS wheat in different management systems. I was also eager to develop my fundamental agronomy and statistics skills during a Ph.D. program, preparing for my future career where I would like to contribute to developing sustainable food production systems. I started my Ph.D. program in September 2012, conducting two experiments. The first experiment was carried out under two N levels (high and low) with fifteen CWRS cultivars to evaluate cultivar response to N fertilizer and their genetic progress during 1910 to 2009 (Chapter 3). The second study was designed to evaluate genetic variability and cultivar choices in organic practices for improved NUE in CWRS wheat (Chapter 4). This study also evaluated cultivar difference of stem N yield for selecting wheat cultivar with high N residue that is ideal for long-term sustainability in organic farming systems.

1.8 Objectives and hypotheses of the entire thesis

The objectives of the entire thesis were to:

1. Investigate agronomic performance of Canada Western Red Spring cultivars in conventional and organic management systems.
2. Evaluate the grain yield advantage, if any, to the reduction in days to maturity due to insensitive *Vrn* gene under organic farming systems.
3. Determine the cultivars that yield better under organic conditions.
4. Assess genetic variability for agronomic and NUE traits existing in CWRS wheat cultivars under high and low N conditions in conventional management.
5. Estimate genetic progress of grain yield and NUE in CWRS cultivars made during the last century.
6. Assess genetic variability for agronomic and NUE traits existing in CWRS wheat cultivars under organic management.
7. Assess the relative performance among fifteen CWRS wheat cultivars for grain yield, NUE and stem N yield and identify cultivars that suite in organic farming practices.

The underlying null hypotheses tested were:

1. Agronomic performance of Canada Western Red Spring cultivars in organic system does not differ from that in conventional system.
2. There is no grain yield advantage due to the reduction in days to maturity that results from insensitive *Vrn* alleles under organic conditions.
3. All CWRS cultivars yield/rank the same in grain yield across organic and conventional systems

4. All CWRS cultivars perform the same, and there is no genetic variation for agronomic and NUE traits among them under high and low N conditions in conventional systems.
5. No rate of genetic progress for grain yield and NUE traits in CWRS wheat cultivars has been achieved over the last century.
6. There is no genetic variation for grain yield, NUE and stem N yield in CWRS wheat cultivars in organic systems.
7. Grain yield, NUE, and stem N yield are the same among fifteen CWRS wheat cultivars in organic systems.

1.9 Tables

Table 1-1. Common parameters used for describing Nitrogen use efficiency.

NUE parameter	Description
Nitrogen Use Efficiency (NUE)[a]	Grain dry biomass at harvest per plant available N (applied N fertilizer + plant available soil N)
Nitrogen Uptake Efficiency (NUpE)[a]	Total aboveground N per plant available N (applied N fertilizer + plant available soil N)
Nitrogen Utilization Efficiency (NUtE)[a]	Grain weight per the total aboveground N
Nitrogen Harvest Index (NHI)[a]	Grain N per the total aboveground N
Nitrogen Remobilization Efficiency (NrE)[b]	The ratio of the total N remobilized to grain from vegetative part (the total vegetative N at anthesis – the total vegetative N at maturity) to the total vegetative N at anthesis

[a] Dawson et al., 2008, [b] Bancel 2009

Table 1- 2. Examples of nitrogen use efficiency[a], uptake and utilization efficiency in cereals.

Crops	NUE kg kg^{-1}		NUpE kg kg^{-1}		NUtE kg kg^{-1}		N fertilization	Tested materials	References
	High N	**Low N**	**High N**	**Low N**	**High N**	**Low N**			
Wheat	18-38	41-101	0.74-0.92	1.14-1.35	27-39	41-59	Two levels	Registered and advanced breeding line winter variety	Gaju et al., 2011
	Conventional 27	Organic 19	NA		NA		fertilized in conventional and legume-based rotation in organic	Registered winter variety	Swain et al., 2014
	26-44		NA		31-42		Four N levels	CIMMYT historical variety	Ortize-Monasterio et al., 1997
Maize	5-32	21-110	0.17-0.99	0.75-2.59	11-54	16-59	Two levels	Recombinant inbred lines and Parents	Li et al., 2015
	33-52		NA		NA		Five N levels including foliar fertilization and control	Hybrid	Kalinova et al., 2014
	25-44		0.36-0.58		110-167[b]		Two N levels and control with different row spacing	Hybrid	Pablo et al., 2008
Rice	9-15		0.27-0.53		8-19		Four different split-plot combinations with the same total N and control	Hybrid	Sun et al., 2012
	12-18		0.34-0.53		8-20		Three different panicle N application with the same basal N application and control		
	Dry season crop: 29	Wet season crop: 64	NA		NA		No fertilization	IRRI variety	Cassman et al., 1996
Barley	13-31		0.38-0.92		26-43		One level with split-application and control	Breeding lines	Sinebo et al., 2004
	35-58		NA		NA		Fertilized	Multiple crosses + registered variety	Anbessa et al., 2009

[a] These NUE values are obtained from only studies in which NUE was calculated as Gw/Na (N applied +/or initial soil N)

[b] The values are obtained as the ratio between the total above ground DM and N in the DM

Table 1-3. Estimation of nitrogen loss by volatilization for various N source and application methods[ab].

Fertilizer	Application method	% ammonia loss by volatilization
Urea/Urea-ammonium Nitrate	Surface broad cast	0 to 44
	Deep point placement	0 to 12
Ammonium Sulfate	Surface broad cast	0 to 60
	Deep point placement	0 to 30
Ammonium Nitrate	Surface broad cast	0 to 30
	Deep point placement	0 to 20
Anhydrous Ammonia	Injected	0 to 5

[a] Cai et al., 2002, [b] Havlin et al., 2014

Table 1-4. Co-localized QTL for GS or root traits and NUE related traits in three major cereals.

Crops	Co-localized QTL	Population	N treatment	References
Wheat	Grain fill duration and plant height (4B)[a], days to anthesis (5D)	DHLs[c]	Mixed with a peat-based compost and slow release fertilizer	Habash et al., 2007
	Flag leaf weight, flag leaf GS activity and flag leaf soluble protein (2A, 2B, 3A, 5A, 5D, 7A)			
	Peduncle at the grain fill and flag leaf GS[b] activity (2B, 3A, 5A, 5D, 7A)			
	Flag leaf protein content and GS activity in flag leaf and in peduncle (5D)	DHLs	Optimal N fertilization	Fontaine et al., 2009
	N uptake and root dry weight (1B)	DHLs	High N condition	An et al., 2006
Maize	GS activity and TKS (5)	RILs[d]	Regardless of N condition	Hirel et al., 2001
	GS activity and kernel number per plant (1)	RILs	High N condition	
	Leaf GS1 activity and remobilization from stem (1)	RILs	Low N condition	Chun et al., 2005
	Leaf GS1 activity and remobilization from whole plant, post-anthesis N uptake (1)			
	Leaf GS1 activity and grain yield, Kernel number (1)	RILs	Regardless of N condition	
	Deep and thin root development and N uptake and N remobilization (2)	RILs	High N condition	Scharf et al., 2005
	Number of secondary roots and N utilization efficiency (3)			
	Number of secondary roots and leaf senescence (3)			
	Root diameter and N uptake (5)			
	Root diameter and N remobilization (5)			
	GS activity and ^{15}N uptake (4)			
	GS activity and N remobilization (8)	RILs	Low N condition	
Rice	GS1 content in 9th leaf and one spikelet weight (2)	BILs[e]	Slow-release fertilizer	Obara et al., 2001
	GS1 content in 9th leaf and spiklet number per panicle on the main stem (2)			
	GS1 content in 9th and Panicle weight on the main stem (2)			
	GS1 content in 9th and rates of full-discololaration (8)			
	GS1 content in 9th leaf and Panicle weight on the main stem (11)			
	GS1 content in 9th leaf and spiklet number per panicle on the main stem (11)			
	GS1 content in 9th leaf and rates for half-discoloration (11)			
	GS1 content in 9th leaf and rates of full-discoloaration (11)			

[a] The numbers in parentheses indicate co-localized QTL locations of chromosome numbers, [b] Glutamine synthetase, [c] Doubled haploid lines, d Recombinant inbred lines, [e] Backcross inbred lines

Table 1-5. Factors controlling synchrony between nitrogen supply and crop demand in conventional and organic agriculture [a].

Variables	Interaction with N	Strategies	Consideration	N source/sink
Crop	•Absorption of N •N storage in biomass	•Improvement of 1) the total crop N demand; 2) root function to absorb existing N; 3) N metabolisms to develop grain •Monitoring crop N status to optimize fertilization •Diversification of crop cultivars and species	•The amount and timing of N requirement in growth stage •Crop yield response to the amount of applied N •Growing season,	N source/ sink
Fertilizer	•Supplementation of N in soils •N loss in environment	•Choice and timing of N fertilization according to crop N demand (e.g. manure, compost, split-application, topdressing, slow-releasing) •Soil N analysis before seeding •4R practice	•Behavior of mineral N •Cost and return of application	N source
Tillage	•Promotion (tillage)/depression (no-till) of SOM decomposition •Weed (N pool) management	•Increased aeration to promote decomposition of SOM where N supply is limited (e.g. organic agriculture) •Reducing tillage practice to increase SOM accumulation to maintain a capacity of soil to prevent N loss from systems	• Proper type and timing of tillage practices	
Crop choice	•Absorption of N •N storage in biomass	•Increased SOM and N storage capacity	•Biomass production •C/N ratio	N source/ sink
Water management	•Movement of labile N in systems	•Monitoring and assessing N loss due to water movement	•Rainfed or irrigated	
Biological N-fixation	•Contribution to providing N to plants and systems	•Incorporation of leguminous plants in rotations •Inoculation of legumes	•Crop and rhizobia interaction •Antagonism between inorganic fertilizer and efficiency of N-fixation by rhizobia	N source
Soil microorganisms	•Control of decomposition and mineralization •Enhancement of crop N absorption	•Maintaining a favorable environment for diverse soil microbial communities •Refrain from excessive use of synthetic fertilizer, fungicide, and pesticide	•The rate of decomposition, mineralization, immobilization, volatilization, ammonification, and denitrification •Carbon source for respiration and growth	N source/ sink

(Continued)

(Continued)

Variables	Interaction with N	Strategies	Consideration	N source/sink
Other agricultural practices	•Prevention of erosion, runoff, leaching •N storage in biomass	•Incorporating several different practices (e.g. crop rotation, cover cropping, relay cropping, alley cropping, catch cropping) to reduce N loss from systems •Utilization of decision-making tools (e.g. N dynamics prediction, crop N requirement prediction)	•The quality of cover cropping, relay cropping as temporary N storage and N source to be decomposed •Cost and application of advanced	
Soil property, characteristics	•A temporal (short and long terms) N storage	•Amending factors that restrict plant root growth •Amending soil pH, moisture, aeration •Remote sensing of soil N dynamics	•Physical, chemical, and biological properties that affect N dynamics for short and long term perspectives	N source/sink
Climate	•Affecting N loss, SOM decomposition, and crop development	•Referring to a local weather forecast (e.g. temperature, precipitation)	•Rainy season, annual temperature, growing degree days	

[a] Information is obtained from Crews and Peoples, 2005.

1.10 Figure

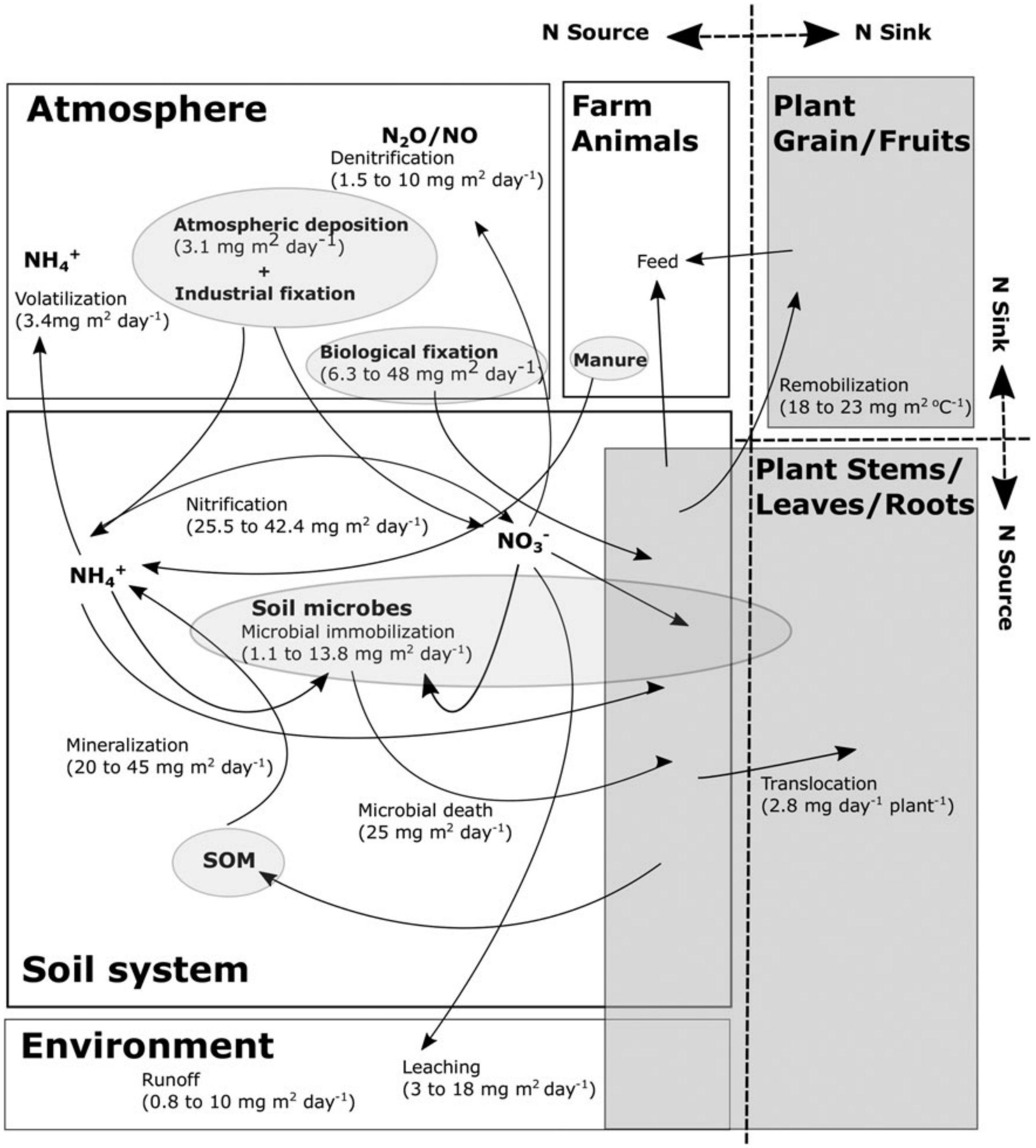

Figure 1-1. Schematic diagram of nitrogen dynamics in agroecosystems.

An example of the amount of nitrogen dynamics in each nitrogen reserve is indicated in parentheses. Boxes with white color indicate environment, whereas dark gray ones refer to plant. Example values are obtained from previous studies (Simpson et al., 1982; Wu et al., 1997; Cabrera et al., 2005; Gooding et al., 2005; Herridge et al., 2008; Dijkstra et al., 2009; Zhao et al., 2011).

References

Abbasi, M. K., Tahir, M. M., and Rahim, N. 2013. Effect of N fertilizer source and timing on yield and N use efficiency of rainfed maize (*Zea mays* L.) in Kashmir–Pakistan. Geoderma 195:87-93.

Ahrens, T., Lobell, D., Ortiz-Monasterio, J., Li, Y., and Matson, P. 2010. Narrowing the agronomic yield gap with improved nitrogen use efficiency: A modeling approach. Ecological Applications 20:91-100.

Alva, A., Fan, M., Qing, C., Rosen, C., and Ren, H. 2011. Improving nutrient-use efficiency in Chinese potato production: Experiences from the United States. Journal of Crop Improvement 25:46-85.

Amanullah, Iqbal, A., Ali, A., Fahad, S., and Parmar, B. 2016. Nitrogen source and rate management improve maize productivity of smallholders under semiarid climates. Frontiers in Plant Science 7.

Amiri, A., and Rafiee, M. 2013. Effect of soil inoculation with azospirillum and azotobacter bacteria on nitrogen use efficiency and agronomic characteristics of corn. Annals of Biological Research 4:77-79.

Amlinger, F., Götz, B., Dreher, P., Geszti, J., and Weissteiner, C. 2003. Nitrogen in biowaste and yard waste compost: Dynamics of mobilisation and availability-a review. European Journal of Soil Biology 39:107-116.

Amossé, C., Jeuffroy, M.-H., and David, C. 2013. Relay intercropping of legume cover crops in organic winter wheat: Effects on performance and resource availability. Field Crops Research 145:78-87.

Amossé, C., Jeuffroy, M.-H., Mary, B., and David, C. 2014. Contribution of relay intercropping with legume cover crops on nitrogen dynamics in organic grain systems. Nutrient Cycling in Agroecosystems 98:1-14.

An, D., Su, J., Liu, Q., Zhu, Y., Tong, Y., Li, J., Jing, R., Li, B., and Li, Z. 2006. Mapping QTLs for nitrogen uptake in relation to the early growth of wheat (*Triticum aestivum* L.). Plant and Soil 284:73-84.

Anbessa, Y., Juskiw, P., Good, A., Nyachiro, J., and Helm, J. 2009. Genetic variability in nitrogen use efficiency of spring barley. Crop Science 49:1259-1269.

Andrews, M., Lea, P. J., Raven, J., and Lindsey, K. 2004. Can genetic manipulation of plant nitrogen assimilation enzymes result in increased crop yield and greater N-use efficiency? An assessment. Annals of Applied Biology 145:25-40.

Andrews, M., Raven, J., and Sprent, J. 2001. Environmental effects on dry matter partitioning between shoot and root of crop plants: Relations with growth and shoot protein concentration. Annals of Applied Biology 138:57-68.

Askegaard, M., Olesen, J. E., Rasmussen, I. A., and Kristensen, K. 2011. Nitrate leaching from organic arable crop rotations is mostly determined by autumn field management. Agriculture, Ecosystems and Environment 142:149-160.

Aslam, M., Travis, R. L., and Huffaker, R. C. 1992. Comparative kinetics and reciprocal inhibition of nitrate and nitrite uptake in roots of uninduced and induced barley (*Hordeum vulgare* L.) seedlings. Plant Physiology 99:1124-1133.

Ata-Ul-Karim, S. T., Yao, X., Liu, X., Cao, W., and Zhu, Y. 2014a. Determination of critical nitrogen dilution curve based on stem dry matter in rice. PloS One 9:e104540.

Ata-Ul-Karim, S. T., Zhu, Y., Yao, X., and Cao, W. 2014b. Determination of critical nitrogen dilution curve based on leaf area index in rice. Field Crops Research 167:76-85.

Aulakh, M., Rennie, D., and Paul, E. 1982. Gaseous nitrogen losses from cropped and summer-fallowed soils. Canadian Journal of Soil Science 62:187-196.

Badaruddin, M., and Meyer, D. 1994. Grain legume effects on soil nitrogen, grain yield, and nitrogen nutrition of wheat. Crop Science 34:1304-1309.

Baethgen, W. E., Christianson, C. B., and Lamothe, A. G. 1995. Nitrogen fertilizer effects on growth, grain yield, and yield components of malting barley. Field Crops Research 43:87-99.

Bai, C., Liang, Y., and Hawkesford, M. J. 2013. Identification of QTLs associated with seedling root traits and their correlation with plant height in wheat. Journal of Experimental Botany 64:1745-1753.

Bancal, P. 2009. Decorrelating source and sink determinism of nitrogen remobilization during grain filling in wheat. Annals of Botany 103:1315-1324.

Bao, A., Zhao, Z., Ding, G., Shi, L., Xu, F., and Cai, H. 2015. The stable level of glutamine synthetase 2 plays an important role in rice growth and in carbon-nitrogen metabolic balance. International Journal of Molecular Sciences 16:12713-12736.

Barbieri, P. A., Echeverría, H. E., Saínz Rozas, H. R., and Andrade, F. H. 2008. Nitrogen use efficiency in maize as affected by nitrogen availability and row spacing. Agronomy Journal 100:1094-1100.

Barth, G., Von Tucher, S., and Schmidhalter, U. 2001. Influence of soil parameters on the effect of 3, 4-dimethylpyrazole-phosphate as a nitrification inhibitor. Biology and Fertility of Soils 34:98-102.

Basra, A. S., and Goyal, S. S. 2002. 18 mechanisms of improved nitrogen-use efficiency in cereals. Quantitative Genetics, Genomics, and Plant Breeding: 269.

Bassirirad, H. 2006. Root system characteristics and control of nitrogen uptake. Journal of Crop Improvement 15:25-51.

Behl, R., Tischner, R., and Raschke, K. 1988. Induction of a high-capacity nitrate-uptake mechanism in barley roots prompted by nitrate uptake through a constitutive low-capacity mechanism. Planta 176:235-240.

Benbi, D. K., and Richter, J. 2002. A critical review of some approaches to modelling nitrogen mineralization. Biology and Fertility of Soils 35:168-183.

Bernard, S. M., Møller, A. L. B., Dionisio, G., Kichey, T., Jahn, T. P., Dubois, F., Baudo, M., Lopes, M. S., Tercé-Laforgue, T., and Foyer, C. H. 2008. Gene expression, cellular localisation and function of glutamine synthetase isozymes in wheat (*Triticum aestivum* L.). Plant Molecular Biology 67:89-105.

Boeckx, P., Xu, X., and Van Cleemput, O. 2005. Mitigation of N_2O and CH_4 emission from rice and wheat cropping systems using dicyandiamide and hydroquinone. Nutrient Cycling in Agroecosystems 72:41-49.

Braman, S., Tenuta, M., and Entz, M. H. 2016. Selected soil microbial parameters measured in the 19th year of a long term organic-conventional comparison study in Canada. Agriculture, Ecosystems and Environment. 233:343-351.

Cabrera, M., Kissel, D., and Vigil, M. 2005. Nitrogen mineralization from organic residues. Journal of Environmental Quality 34:75-79.

Camargo, F. D. O., Gianello, C., and Vidor, C. 1997. Comparative study of five hydrolytic methods in the determination of soil organic nitrogen compounds. Communications in Soil Science and Plant Analysis 28:1303-1309.

Cassman, K., Gines, G., Dizon, M., Samson, M., and Alcantara, J. 1996. Nitrogen-use efficiency in tropical lowland rice systems: Contributions from indigenous and applied nitrogen. Field Crops Research 47:1-12.

Christophe, S., Jean-Christophe, A., Annabelle, L., Alain, O., Marion, P., and Anne-Sophie, V. 2011. Plant n fluxes and modulation by nitrogen, heat and water stresses: A review based on comparison of legumes and non- legume plants. Abiotic Stress in Plants–Mechanisms and Adaptations. Intech Open Access Publisher, Rijeka, Croatia: 79-118.

Chun, L., Mi, G., Li, J., Chen, F., and Zhang, F. 2005. Genetic analysis of maize root characteristics in response to low nitrogen stress. Plant and Soil 276:369-382.

Constantin, J., Mary, B., Laurent, F., Aubrion, G., Fontaine, A., Kerveillant, P., and Beaudoin, N. 2010. Effects of catch crops, no till and reduced nitrogen fertilization on nitrogen leaching and balance in three long-term experiments. Agriculture, Ecosystems and Environment 135:268-278.

Coque, M., and Gallais, A. 2007. Genetic variation for nitrogen remobilization and postsilking nitrogen uptake in maize recombinant inbred lines: Heritabilities and correlations among traits. Crop Science 47:1787-1796.

Coque, M., Martin, A., Veyrieras, J., Hirel, B., and Gallais, A. 2008. Genetic variation for N-remobilization and postsilking n-uptake in a set of maize recombinant inbred lines. 3. QTL detection and coincidences. Theoretical and Applied Genetics 117:729-747.

Cormier, F., Faure, S., Dubreuil, P., Heumez, E., Beauchêne, K., Lafarge, S., Praud, S., and Le Gouis, J. 2013. A multi-environmental study of recent breeding progress on nitrogen use efficiency in wheat (*Triticum aestivum* L.). Theoretical and Applied genetics 126:3035-3048.

Crews, T. E., and Peoples, M. B. 2005. Can the synchrony of nitrogen supply and crop demand be improved in legume and fertilizer-based agroecosystems? A review. Nutrient Cycling in Agroecosystems 72:101-120.

Cui, Z., Zhang, F., Mi, G., Chen, F., Li, F., Chen, X., Li, J., and Shi, L. 2009. Interaction between genotypic difference and nitrogen management strategy in determining nitrogen use efficiency of summer maize. Plant and Soil 317:267-276.

Dabney, S. M., Delgado, J. A., Meisinger, J. J., Schomberg, H. H., Liebig, M. A., Kaspar, T., Mitchell, J., and Reeves, W. 2010. Using cover crops and cropping systems for nitrogen management. Advances in Nitrogen Management for Water Quality: 231-282.

Dawson, J. C., Huggins, D. R., and Jones, S. S. 2008. Characterizing nitrogen use efficiency in natural and agricultural ecosystems to improve the performance of cereal crops in low-input and organic agricultural systems. Field Crops Research 107:89-101.

De Nobili, M., Contin, M., Mondini, C., and Brookes, P. 2001. Soil microbial biomass is triggered into activity by trace amounts of substrate. Soil Biology and Biochemistry 33:1163-1170.

Dechorgnat, J., Nguyen, C. T., Armengaud, P., Jossier, M., Diatloff, E., Filleur, S., and Daniel-Vedele, F. 2011. From the soil to the seeds: The long journey of nitrate in plants. Journal of Experimental Botany 62:1349-1359.

Degenhardt, R., Martin, R., and Spaner, D. 2005. Organic farming in central Alberta: Current trends, production constraints and research needs. Journal of Sustainable Agriculture 27:153-173.

Dijkstra, F. A., Bader, N. E., Johnson, D. W., and Cheng, W. 2009. Does accelerated soil organic matter decomposition in the presence of plants increase plant n availability? Soil Biology and Biochemistry 41:1080-1087.

Doltra, J., and Olesen, J. E. 2013. The role of catch crops in the ecological intensification of spring cereals in organic farming under Nordic climate. European Journal of Agronomy 44:98-108.

Doran, J., Elliott, E., and Paustian, K. 1998. Soil microbial activity, nitrogen cycling, and long-term changes in organic carbon pools as related to fallow tillage management. Soil and Tillage Research 49:3-18.

Douds Jr, D. D., Pfeffer, P. E., and Shachar-Hill, Y. 2000. Carbon partitioning, cost, and metabolism of arbuscular mycorrhizas. In: Kapulnik, Y., and Douds Jr, D. D. (eds.) Arbuscular mycorrhizas: Physiology and function. Springer. pp.107-129.

Drew, M., and Saker, L. 1975. Nutrient supply and the growth of the seminal root system in barley II. Localized, compensatory increases in lateral root growth and rates op nitrate uptake when nitrate supply is restricted to only part of the root system. Journal of Experimental Botany 26:79-90.

Drew, M., Saker, L., and Ashley, T. 1973. Nutrient supply and the growth of the seminal root system in barley I. The effect of nitrate concentration on the growth of axes and laterals. Journal of Experimental Botany 24:1189-1202.

Drinkwater, L. E. 2004. Improving fertilizer nitrogen use efficiency through an ecosystem-based approach. In: Mosier, A. R., Syers, J. K., and Freney, J. R. (eds.) Agriculture and the nitrogen cycle: Assessing the impacts of fertilizer use on food production and the environment. Island Press, Washington. pp.93-102.

Eghball, B., and Gilley, J. E. 1999. Phosphorus and nitrogen in runoff following beef cattle manure or compost application. Journal of Environmental Quality 28:1201-1210.

Entz, M. H., Gross, K. G., and Fowler, D. B. 1992. Root growth and soil-water extraction by winter and spring wheat. Canadian Journal of Plant Science 72:1109-1120.

Eriksen, J., Askegaard, M., and Kristensen, K. 2004. Nitrate leaching from an organic dairy crop rotation: The effects of manure type, nitrogen input and improved crop rotation. Soil Use and Management 20:48-54.

Fageria, N., and Baligar, V. 2005. Enhancing nitrogen use efficiency in crop plants. Advances in Agronomy 88:97-185.

Figueiredo, M. D. V. B., Seldin, L., De Araujo, F. F., and Mariano, R. D. L. R. 2010. Plant growth promoting rhizobacteria: Fundamentals and applications. Plant growth and health promoting bacteria. Springer. p.21-43.

Fontaine, J.-X., Ravel, C., Pageau, K., Heumez, E., Dubois, F., Hirel, B., and Le Gouis, J. 2009. A quantitative genetic study for elucidating the contribution of glutamine synthetase, glutamate dehydrogenase and other nitrogen-related physiological traits to the agronomic performance of common wheat. Theoretical and Applied Genetics 119:645-662.

Food and Agriculture Organization of the United Nations [FAO]. World fertilizer trends and outlook to 2018. 2015 Rome.

Forde, B. G., and Lea, P. J. 2007. Glutamate in plants: Metabolism, regulation, and signalling. Journal of Experimental Botany 58:2339-2358.

Fraisier, V., Gojon, A., Tillard, P., and Daniel-Vedele, F. 2000. Constitutive expression of a putative high-affinity nitrate transporter in nicotiana plumbaginifolia: Evidence for post-transcriptional regulation by a reduced nitrogen source. The Plant Journal 23:489-496.

Franzluebbers, A. 2004. Tillage and residue management effects on soil organic matter. In: Magdoff, F., and Weil, R. R. (eds.) Soil organic matter in sustainable agriculture. CRC Press, Washington, D.C. p.227-268.

Frink, C. R., Waggoner, P. E., and Ausubel, J. H. 1999. Nitrogen fertilizer: Retrospect and prospect. Proceedings of the National Academy of Sciences 96:1175-1180.

Gabriel, J., Alonso-Ayuso, M., García-González, I., Hontoria, C., and Quemada, M. 2016. Nitrogen use efficiency and fertiliser fate in a long-term experiment with winter cover crops. European Journal of Agronomy 79:14-22.

Gaju, O., Allard, V., Martre, P., Snape, J., Heumez, E., Legouis, J., Moreau, D., Bogard, M., Griffiths, S., and Orford, S. 2011. Identification of traits to improve the nitrogen-use efficiency of wheat genotypes. Field Crops Research 123:139-152.

Gallais, A., and Hirel, B. 2004. An approach to the genetics of nitrogen use efficiency in maize. Journal of Experimental Botany 55:295-306.

Gan, Y., Hamel, C., O'donovan, J. T., Cutforth, H., Zentner, R. P., Campbell, C. A., Niu, Y., and Poppy, L. 2015. Diversifying crop rotations with pulses enhances system productivity. Scientific Reports 5.

Gan, Y., Mooleki, S., Lemke, R. L., Zentner, R. P., and Ruan, Y. 2016. Durum wheat productivity in response to soil water and soil residual nitrogen associated with previous crop management. Agronomy Journal 108:1468-1478.

Gholamhoseini, M., Aghaalikhani, M., Sanavy, S. M., and Mirlatifi, S. 2013. Interactions of irrigation, weed and nitrogen on corn yield, nitrogen use efficiency and nitrate leaching. Agricultural Water Management 126:9-18.

Gianfreda, L., Rao, M., and Mora, M. 2011. Enzymatic activity as influenced by soil mineral and humic colloids and its impact on biogeochemical processes. In: Huang, P. M., Li, Y., and Sumner, M. E. (eds.) Handbook of soil science resource of management and environmental impacts. CRC Press, New York.

Gilmour, J. T., and Mauromoustakos, A. 2011. Nitrogen mineralization from soil organic matter: A sequential model. Soil Science Society of America Journal 75:317-323.

Gioacchini, P., Nastri, A., Marzadori, C., Giovannini, C., Antisari, L. V., and Gessa, C. 2002. Influence of urease and nitrification inhibitors on N losses from soils fertilized with urea. Biology and Fertility of Soils 36:129-135.

Glibert, P. M., Harrison, J., Heil, C., and Seitzinger, S. 2006. Escalating worldwide use of urea–a global change contributing to coastal eutrophication. Biogeochemistry 77:441-463.

Gooding, M. J., Gregory, P. J., Ford, K. E., and Pepler, S. 2005. Fungicide and cultivar affect post-anthesis patterns of nitrogen uptake, remobilization and utilization efficiency in wheat. The Journal of Agricultural Science 143:503-518.

Gorny, A., and Garczyński, S. 2008. Nitrogen and phosphorus efficiency in wild and cultivated species of wheat. Journal of Plant Nutrition 31:263-279.

Graham, J. 2000. Assessing costs of arbuscular mycorrhizal symbiosis in agroecosystems. In: Podila, G. K., and Douds Jr., D. D. (eds.) Current advances in mycorrhizae research. The American Phytophathological Society Press, St. Paul. pp.111-126.

Greenwood, D., Lemaire, G., Gosse, G., Cruz, P., Draycott, A., and Neeteson, J. 1990. Decline in percentage n of C3 and C4 crops with increasing plant mass. Annals of Botany 66:425-436.

Griffith, W., and Murphy, L. 1991. The development of crop production systems using best management practices. Potash & Phosphate Institute, Norcross, USA.

Hörtensteiner, S., and Feller, U. 2002. Nitrogen metabolism and remobilization during senescence. Journal of Experimental Botany 53:927-937.

Habash, D., Massiah, A., Rong, H., Wallsgrove, R., and Leigh, R. 2001. The role of cytosolic glutamine synthetase in wheat. Annals of Applied Biology 138:83-89.

Habash, D. Z., Bernard, S., Schondelmaier, J., Weyen, J., and Quarrie, S. A. 2007. The genetics of nitrogen use in hexaploid wheat: N utilisation, development and yield. Theoretical and Applied Genetics 114:403-419.

Hamilton III, E. W., and Frank, D. A. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

Hansen, E. M., and Djurhuus, J. 1997. Nitrate leaching as influenced by soil tillage and catch crop. Soil and Tillage Research 41:203-219.

Havlin, J. L., Tisdale, S.L., Nelson, W.L., and Beaton, J.D. 2014. Soil fertility and fertilizers, Upper Saddle River, N.J.

Hawkesford, M. J. 2014. Reducing the reliance on nitrogen fertilizer for wheat production. Journal of Cereal Science 59:276-283.

Hawkins, H.-J., Johansen, A., and George, E. 2000. Uptake and transport of organic and inorganic nitrogen by arbuscular mycorrhizal fungi. Plant and Soil 226:275-285.

Hawkins, H. J., and George, E. 1999. Effect of plant nitrogen status on the contribution of arbuscular mycorrhizal hyphae to plant nitrogen uptake. Physiologia Plantarum 105:694-700.

Herridge, D. F., Peoples, M. B., and Boddey, R. M. 2008. Global inputs of biological nitrogen fixation in agricultural systems. Plant and Soil 311:1-18.

Herrmann, A., and Taube, F. 2004. The range of the critical nitrogen dilution curve for maize (*Zea mays* L.) can be extended until silage maturity. Agronomy Journal 96:1131-1138.

Hirel, B., Bertin, P., Quilleré, I., Bourdoncle, W., Attagnant, C., Dellay, C., Gouy, A., Cadiou, S., Retailliau, C., and Falque, M. 2001. Towards a better understanding of the genetic and physiological basis for nitrogen use efficiency in maize. Plant Physiology 125:1258-1270.

Hong-Bo, L., Zhang, F.-S., and Jian-Bo, S. 2012. Contribution of root proliferation in nutrient-rich soil patches to nutrient uptake and growth of maize. Pedosphere 22:776-784.

Hoogmoed, M. 2015. Development of nitrogen dilution curves for current Australian wheat varieties. In: AcuñA, T., Moeller, C., Parsons, D., and Harrison, M. (eds.) Building productive, diverse and sustainable landscapes: Proceedings of the 17th Australian agronomy conference 2015. Warragul.

Horrigan, L., Lawrence, R. S., and Walker, P. 2002. How sustainable agriculture can address the environmental and human health harms of industrial agriculture. Environmental Health Perspectives 110:445.

House, G. J., Stinner, B. R., Crossley, D., Odum, E. P., and Langdale, G. W. 1984. Nitrogen cycling in conventional and no-tillage agroecosystems in the southern piedmont. Journal of Soil and Water Conservation 39:194-200.

Huggins, D., and Pan, W. 1993. Nitrogen efficiency component analysis: An evaluation of cropping system differences in productivity. Agronomy Journal 85:898-905.

Huggins, D., and Pan, W. 2003. Key indicators for assessing nitrogen use efficiency in cereal-based agroecosystems. Journal of Crop Production 8:157-185.

International Federation of Organic Agriculture Movement [IFOAM]. 2008. The principals of organic agriculture. http://www.ifoam.org/about_ifoam/principles/index.html (accessed May 26 2014).

International Fertilizer Industry Association [IFA]. 2011. Available: http://ifadata.fertilizer.org/ucSearch.aspx (accessed July 8 2014).

Isfan, D. 1993. Genotypic variability for physiological efficiency index of nitrogen in oats. Plant and Soil 154:53-59.

Janzen, H. H., Beauchemin, K. A., Bruinsma, Y., Campbell, C. A., Desjardins, R. L., Ellert, B. H., and Smith, E. G. 2003. The fate of nitrogen in agroecosystems: an illustration using Canadian estimates. Nutrient Cycling in Agroecosystems. 67: 85-102.

Jain, V., Khetarpal, S., Das, R., and Abrol, Y. P. 2011. Nitrate assimilation in contrasting wheat genotypes. Physiology and Molecular Biology of Plants 17:137-144.

Jeranyama, P., Hesterman, O. B., and Sheaffer, C. C. 1998. Medic planting date effect on dry matter and nitrogen accumulation when clear-seeded or intercropped with corn. Agronomy Journal 90:616-622.

Jin, H., Liu, J., Liu, J., and Huang, X. 2012. Forms of nitrogen uptake, translocation, and transfer via arbuscular mycorrhizal fungi: A review. Science China Life Sciences 55:474-482.

Jing, J., Zhang, F., Rengel, Z., and Shen, J. 2012. Localized fertilization with P plus N elicits an ammonium-dependent enhancement of maize root growth and nutrient uptake. Field Crops Research 133:176-185.

Justes, E., Mary, B., Meynard, J.-M., Machet, J.-M., and Thelier-Huché, L. 1994. Determination of a critical nitrogen dilution curve for winter wheat crops. Annals of Botany 74:397-407.

Kalinova, S., Kostadinova, S., and Hristoskov, A. 2014. Nitrogen use efficiency and maize yield response to nitrogen rate and foliar fertilizing. Bulgarian Journal of Agricultural Science 20:178-181.

Kayser, M., Müller, J., and Isselstein, J. 2010. Nitrogen management in organic farming: Comparison of crop rotation residual effects on yields, N leaching and soil conditions. Nutrient Cycling in Agroecosystems 87:21-31.

Kessavalou, A., Mosier, A. R., Doran, J. W., Drijber, R. A., Lyon, D. J., and Heinemeyer, O. 1998. Fluxes of carbon dioxide, nitrous oxide, and methane in grass sod and winter wheat-fallow tillage management. Journal of Environmental Quality 27:1094-1104.

Khalil, M., Buegger, F., Schraml, M., Gutser, R., Richards, K., and Schmidhalter, U. 2009a. Gaseous nitrogen losses from a cambisol cropped to spring wheat with urea sizes and placement depths. Soil Science Society of America Journal 73:1335-1344.

Khalil, M. I., Gutser, R., and Schmidhalter, U. 2009b. Effects of urease and nitrification inhibitors added to urea on nitrous oxide emissions from a loess soil. Journal of Plant Nutrition and Soil Science/Zeitschrift für Pflanzenernährung und Bodenkunde 172:651.

Khalil, M., Rosenani, A., Van Cleemput, O., Boeckx, P., Shamshuddin, J., and Fauziah, C. 2002. Nitrous oxide production from an ultisol of the humid tropics treated with different nitrogen sources and moisture regimes. Biology and Fertility of Soils 36:59-65.

Khosla, R., Fleming, K., Delgado, J., Shaver, T., and Westfall, D. 2002. Use of site-specific management zones to improve nitrogen management for precision agriculture. Journal of Soil and Water Conservation 57:513-518.

Kichey, T., Hirel, B., Heumez, E., Dubois, F., and Le Gouis, J. 2007. In winter wheat (*Triticum aestivum* L.), post-anthesis nitrogen uptake and remobilisation to the grain correlates with agronomic traits and nitrogen physiological markers. Field Crops Research 102:22-32.

Laperche, A., Brancourt-Hulmel, M., Heumez, E., Gardet, O., and Le Gouis, J. 2006. Estimation of genetic parameters of a DH wheat population grown at different n stress levels characterized by probe genotypes. Theoretical and Applied Genetics 112:797-807.

Lavelle, P., and Spain, A. 2001. Soil ecology, Dordrecht: Kluwer Academic Publishers.

Le Gouis, J., Béghin, D., Heumez, E., and Pluchard, P. 2000. Genetic differences for nitrogen uptake and nitrogen utilisation efficiencies in winter wheat. European Journal of Agronomy 12:163-173.

Lemaire, G., and Meynard, J. 1997. Use of the nitrogen nutrition index for the analysis of agronomical data. In: Lemaire, G. (ed.) Diagnosis of the nitrogen status in crops. Springer, Heidelberg. pp.45-55.

Lemaire, G., Van Oosterom, E., Sheehy, J., Jeuffroy, M. H., Massignam, A., and Rossato, L. 2007. Is crop n demand more closely related to dry matter accumulation or leaf area expansion during vegetative growth? Field Crops Research 100:91-106.

Léran, S., Varala, K., Boyer, J.-C., Chiurazzi, M., Crawford, N., Daniel-Vedele, F., David, L., Dickstein, R., Fernandez, E., and Forde, B. 2014. A unified nomenclature of nitrate transporter 1/peptide transporter family members in plants. Trends in Plant Science 19:5-9.

Li, P., Chen, F., Cai, H., Liu, J., Pan, Q., Liu, Z., Gu, R., Mi, G., Zhang, F., and Yuan, L. 2015. A genetic relationship between nitrogen use efficiency and seedling root traits in maize as revealed by QTL analysis. Journal of Experimental Botany 66:3175-3188.

Liao, M., Fillery, I. R., and Palta, J. A. 2004. Early vigorous growth is a major factor influencing nitrogen uptake in wheat. Functional Plant Biology 31:121-129.

Liao, M., Palta, J. A., and Fillery, I. R. 2006. Root characteristics of vigorous wheat improve early nitrogen uptake. Crop and Pasture Science 57:1097-1107.

Lim, S. L., Wu, T. Y., Lim, P. N., and Shak, K. P. Y. 2015. The use of vermicompost in organic farming: Overview, effects on soil and economics. Journal of the Science of Food and Agriculture 95:1143-1156.

Lima, J. E., Kojima, S., Takahashi, H., and Von Wirén, N. 2010. Ammonium triggers lateral root branching in arabidopsis in an ammonium transporter1; 3-dependent manner. The Plant Cell 22:3621-3633.

Limaux, F., Recous, S., Meynard, J.-M., and Guckert, A. 1999. Relationship between rate of crop growth at date of fertiliser n application and fate of fertiliser n applied to winter wheat. Plant and Soil 214:49-59.

Limon-Ortega, A., and Villaseñor-Mir, E. 2006. Nitrogen fertilizer management and recommendations for wheat production in central Mexico. Crop Management 5.

Liu, C., Cutforth, H., Chai, Q., and Gan, Y. 2016. Farming tactics to reduce the carbon footprint of crop cultivation in semiarid areas. A review. Agronomy for Sustainable Development 36:69.

López-Bellido, L., López-Bellido, R. J., and Redondo, R. 2005. Nitrogen efficiency in wheat under rainfed mediterranean conditions as affected by split nitrogen application. Field Crops Research 94:86-97.

López-Bellido, R., and López-Bellido, L. 2001. Efficiency of nitrogen in wheat under mediterranean conditions: Effect of tillage, crop rotation and n fertilization. Field Crops Research 71:31-46.

Luce, M. S., Grant, C. A., Zebarth, B. J., Ziadi, N., O'donovan, J. T., Blackshaw, R. E., Harker, K. N., Johnson, E. N., Gan, Y., and Lafond, G. P. 2015. Legumes can reduce economic optimum nitrogen rates and increase yields in a wheat–canola cropping sequence in western Canada. Field Crops Research 179:12-25.

Luce, M. S., Grant, C. A., Ziadi, N., Zebarth, B. J., O'donovan, J. T., Blackshaw, R. E., Harker, K. N., Johnson, E. N., Gan, Y., and Lafond, G. P. 2016. Preceding crops and nitrogen fertilization influence soil nitrogen cycling in no-till canola and wheat cropping systems. Field Crops Research 191:20-32.

Lupwayi, N., Clayton, G., O'donovan, J., Harker, K., Turkington, T., and Soon, Y. 2006. Soil nutrient stratification and uptake by wheat after seven years of conventional and zero tillage in the northern grain belt of Canada. Canadian Journal of Soil Science 86:767-778.

Lynch, J. 1995. Root architecture and plant productivity. Plant Physiology 109:7.

Mäder, P., Fliessbach, A., Dubois, D., Gunst, L., Fried, P., and Niggli, U. 2002. Soil fertility and biodiversity in organic farming. Science 296:1694-1697.

Malhi, S., Soon, Y., Grant, C., Lemke, R., and Lupwayi, N. 2010. Influence of controlled-release urea on seed yield and n concentration, and n use efficiency of small grain crops grown on dark gray luvisols. Canadian Journal of Soil Science 90:363-372.

Mano, H., and Morisaki, H. 2008. Endophytic bacteria in the rice plant. Microbes and Environments 23:109-117.

Marriott, E. E., and Wander, M. M. 2006. Total and labile soil organic matter in organic and conventional farming systems. Soil Science Society of America Journal 70:950-959.

Martin, A., Lee, J., Kichey, T., Gerentes, D., Zivy, M., Tatout, C., Dubois, F., Balliau, T., Valot, B., and Davanture, M. 2006. Two cytosolic glutamine synthetase isoforms of maize are specifically involved in the control of grain production. The Plant Cell 18:3252-3274.

Masclaux-Daubresse, C., Daniel-Vedele, F., Dechorgnat, J., Chardon, F., Gaufichon, L., and Suzuki, A. 2010. Nitrogen uptake, assimilation and remobilization in plants: Challenges for sustainable and productive agriculture. Annals of Botany 105:1141-1157.

Masclaux, C., Quilleré, I., Gallais, A., and Hirel, B. 2001. The challenge of remobilisation in plant nitrogen economy. A survey of physio-agronomic and molecular approaches. Annals of Applied Biology 138:69-81.

Masunga, R. H., Uzokwe, V. N., Mlay, P. D., Odeh, I., Singh, A., Buchan, D., and De Neve, S. 2016. Nitrogen mineralization dynamics of different valuable organic amendments commonly used in agriculture. Applied Soil Ecology 101:185-193.

Matson, P. A., Naylor, R., and Ortiz-Monasterio, I. 1998. Integration of environmental, agronomic, and economic aspects of fertilizer management. Science 280:112-115.

Mckenzie, R., Bremer, E., Middleton, A., Pfiffner, P., and Dowbenko, R. 2007. Controlled-release urea for winter wheat in southern Alberta. Canadian Journal of Soil Science 87:85-91.

Mckenzie, R. H., Middleton, A., Pfiffner, P., and Bremer, E. 2010. Evaluation of polymer-coated urea and urease inhibitor for winter wheat in southern Alberta. Agronomy Journal 102:1210-1216.

Meisinger, J., Bandel, V., Stanford, G., and Legg, J. 1985. Nitrogen utilization of corn under minimal tillage and moldboard plow tillage. I. Four-year results using labeled N fertilizer on an Atlantic coastal plain soil. Agronomy Journal 77:602-611.

Miflin, B., and Lea, P. 1977. Amino acid metabolism. Annual Review of Plant Physiology 28:299-329.

Miflin, B. J., and Habash, D. Z. 2002. The role of glutamine synthetase and glutamate dehydrogenase in nitrogen assimilation and possibilities for improvement in the nitrogen utilization of crops. Journal of Experimental Botany 53:979-987.

Moll, R., Kamprath, E., and Jackson, W. 1982. Analysis and interpretation of factors which contribute to efficiency of nitrogen utilization. Agronomy Journal 74:562-564.

Muruganandam, S., Israel, D. W., and Robarge, W. P. 2009. Activities of nitrogen-mineralization enzymes associated with soil aggregate size fractions of three tillage systems. Soil Science Society of America Journal 73:751-759.

Muruganandam, S., Israel, D. W., and Robarge, W. P. 2010. Nitrogen transformations and microbial communities in soil aggregates from three tillage systems. Soil Science Society of America Journal 74:120-129.

Muurinen, S., Kleemola, J., and Peltonen-Sainio, P. 2007. Accumulation and translocation of nitrogen in spring cereal cultivars differing in nitrogen use efficiency. Agronomy Journal 99:441-449.

Muurinen, S., Slafer, G. A., and Peltonen-Sainio, P. 2006. Breeding effects on nitrogen use efficiency of spring cereals under northern conditions. Crop Science 46:561-568.

Nacry, P., Bouguyon, E., and Gojon, A. 2013. Nitrogen acquisition by roots: Physiological and developmental mechanisms ensuring plant adaptation to a fluctuating resource. Plant and Soil 370:1-29.

Namai, S., Toriyama, K., and Fukuta, Y. 2009. Genetic variations in dry matter production and physiological nitrogen use efficiency in rice (*Oryza sativa* L.) varieties. Breeding Science 59:269-276.

Nielsen, R. N loss mechanisms and nitrogen use efficiency. Purdue Nitrogen Management Workshops, 2006. 1-5.

O'donovan, J. T., Grant, C. A., Blackshaw, R. E., Harker, K. N., Johnson, E., Gan, Y., Lafond, G. P., May, W. E., Turkington, T. K., and Lupwayi, N. Z. 2014. Rotational effects of legumes and non-legumes on hybrid canola and malting barley. Agronomy Journal 106:1921-1932.

Obara, M., Ishimaru, T., Abiko, T., Fujita, D., Kobayashi, N., Yanagihara, S., and Fukuta, Y. 2014. Identification and characterization of quantitative trait loci for root elongation by using introgression lines with genetic background of indica-type rice variety IR64. Plant Biotechnology Reports 8:267-277.

Obara, M., Kajiura, M., Fukuta, Y., Yano, M., Hayashi, M., Yamaya, T., and Sato, T. 2001. Mapping of QTLs associated with cytosolic glutamine synthetase and NADH-glutamate synthase in rice (*Oryza sativa* L.). Journal of Experimental Botany 52:1209-1217.

Okon, Y., and Labandera-Gonzalez, C. A. 1994. Agronomic applications of azospirillum: An evaluation of 20 years worldwide field inoculation. Soil Biology and Biochemistry 26:1591-1601.

Ondersteijn, C., Beldman, A., Daatselaar, C., Giesen, G., and Huirne, R. 2002. The Dutch mineral accounting system and the European nitrate directive: Implications for N and P management and farm performance. Agriculture, Ecosystems and Environment 92:283-296.

Orsel, M., Filleur, S., Fraisier, V., and Daniel-Vedele, F. 2002. Nitrate transport in plants: Which gene and which control? Journal of Experimental Botany 53:825-833.

Ortiz-Monasterio, R., Sayre, K., Rajaram, S., and Mcmahon, M. 1997. Genetic progress in wheat yield and nitrogen use efficiency under four nitrogen rates. Crop Science 37:898-904.

Pathak, R., Lochab, S., and Raghuram, N. 2011. Plant systems| improving plant nitrogen-use efficiency. In: Moo-Young, M. (ed.) Comprehensive biotechnology, 2nd edn. Elsevier, Amsterdam. pp.209-218.

Pathak, R. R., Ahmad, A., Lochab, S., and Raghuram, N. 2008. Molecular physiology of plant nitrogen use efficiency and biotechnological options for its enhancement. Current Science 94:1394.

Pimentel, D., Hepperly, P., Hanson, J., Douds, D., and Seidel, R. 2005. Environmental, energetic, and economic comparisons of organic and conventional farming systems. BioScience 55:573-582.

Plett, D., Toubia, J., Garnett, T., Tester, M., Kaiser, B. N., and Baumann, U. 2010. Dichotomy in the nrt gene families of dicots and grass species. PloS One 5:e15289.

Poorter, H., and Nagel, O. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: A quantitative review. Functional Plant Biology 27:1191-1191.

Porter, L. K., Follett, R. F., and Halvorson, A. D. 1996. Fertilizer nitrogen recovery in a no-till wheat-sorghum-fallow-wheat sequence. Agronomy Journal 88:750-757.

Presterl, T., Groh, S., Landbeck, M., Seitz, G., Schmidt, W., and Geiger, H. 2002. Nitrogen uptake and utilization efficiency of European maize hybrids developed under conditions of low and high nitrogen input. Plant Breeding 121:480-486.

Quilleré, I., Dufossé, C., Roux, Y., Foyer, C. H. F., Caboche, M., and Morot-Gaudry, J.-F. 1994. The effects of deregulation of nr gene expression on growth and nitrogen metabolism of nicotiana plumbaginifolia plants. Journal of Experimental Botany 45:1205-1211.

Raun, W. R., and Johnson, G. V. 1999. Improving nitrogen use efficiency for cereal production. Agronomy Journal 91:357-363.

Reid, T. A., Yang, R.-C., Salmon, D. F., and Spaner, D. 2009. Should spring wheat breeding for organically managed systems be conducted on organically managed land? Euphytica 169:239-252.

Reilly, K., Cullen, E., Lola-Luz, T., Stone, D., Valverde, J., Gaffney, M., Brunton, N., Grant, J., and Griffiths, B. S. 2013. Effect of organic, conventional and mixed cultivation practices on soil microbial community structure and nematode abundance in a cultivated onion crop. Journal of the Science of Food and Agriculture 93:3700-3709.

Richie, S. W., Hanway, J.J., and Benson, G.O. 1986. How a corn plant develops. Iowa: Iowa State University of Science and Technology. https://s10.lite.msu.edu/res/msu/botonl/b_online/library/maize/www.ag.iastate.edu/departments/agronomy/corngrows.html (accessed October 12 2015).

Robertson, G. P. 1997. Nitrogen use efficiency in row-crop agriculture: Crop nitrogen use and soil nitrogen loss. In: Jackson, L. E. (ed.) Ecology in agriculture. Academic press, New York. Academic Press, New York. pp.347-365.

Robinson, D. 2001. Root proliferation, nitrate inflow and their carbon costs during nitrogen capture by competing plants in patchy soil. Plant and Soil 232:41-50.

Ruidisch, M., Bartsch, S., Kettering, J., Huwe, B., and Frei, S. 2013. The effect of fertilizer best management practices on nitrate leaching in a plastic mulched ridge cultivation system. Agriculture, Ecosystems and Environment 169:21-32.

Sainju, U. M., Caesar-Tonthat, T., Lenssen, A. W., Evans, R. G., and Kolberg, R. 2009. Tillage and cropping sequence impacts on nitrogen cycling in dryland farming in eastern Montana, USA. Soil and Tillage Research 103:332-341.

San Francisco, S., Urrutia, O., Martin, V., Peristeropoulos, A., and Garcia-Mina, J. M. 2011. Efficiency of urease and nitrification inhibitors in reducing ammonia volatilization from diverse nitrogen fertilizers applied to different soil types and wheat straw mulching. Journal of the Science of Food and Agriculture 91:1569-1575.

Sandhu, K., Arora, V., Chand, R., Sandhu, B., and Khera, K. 2000. Optimizing time distribution of water supply and fertilizer nitrogen rates in relation to targeted wheat yields. Experimental Agriculture 36:115-125.

Scharf, P. C., Kitchen, N. R., Sudduth, K. A., Davis, J. G., Hubbard, V. C., and Lory, J. A. 2005. Field-scale variability in optimal nitrogen fertilizer rate for corn. Agronomy Journal 97:452-461.

Schenk, M. 1996. Regulation of nitrogen uptake on the whole plant level. Plant and Soil 181:131-137.

Shanahan, J., Kitchen, N., Raun, W., and Schepers, J. S. 2008. Responsive in-season nitrogen management for cereals. Computers and Electronics in Agriculture 61:51-62.

Sheehy, J., Dionora, M., Mitchell, P., Peng, S., Cassman, K., Lemaire, G., and Williams, R. 1998. Critical nitrogen concentrations: Implications for high-yielding rice (*Oryza sativa* L.) cultivars in the tropics. Field Crops Research 59:31-41.

Shen, J., Li, C., Mi, G., Li, L., Yuan, L., Jiang, R., and Zhang, F. 2013. Maximizing root/rhizosphere efficiency to improve crop productivity and nutrient use efficiency in intensive agriculture of China. Journal of Experimental Botany 64:1181-1192.

Sherrard, J., Lambert, R., Below, F., Dunand, R., Messmer, M., Willman, M., Winkels, C., and Hageman, R. 1986. Use of physiological traits, especially those of nitrogen metabolism for selection in maize. Biochemical Basis of Plant Breeding 2:109-130.

Simpson, R. J., Lambers, H., and Dalling, M. J. 1982. Translocation of nitrogen in a vegetative wheat plant (*Triticum aestivum*). Physiologia Plantarum 56:11-17.

Sinebo, W., Gretzmacher, R., and Edelbauer, A. 2004. Genotypic variation for nitrogen use efficiency in Ethiopian barley. Field Crops Research 85:43-60.

Snyder, C., and Spaner, D. 2010. The sustainability of organic grain production on the Canadian prairies-a review. Sustainability 2:1016-1034.

Sowers, K. E., Pan, W. L., Miller, B. C., and Smith, J. L. 1994. Nitrogen use efficiency of split nitrogen applications in soft white winter wheat. Agronomy Journal 86:942-948.

Spargo, J. T., Alley, M. M., Follett, R. F., and Wallace, J. V. 2008. Soil nitrogen conservation with continuous no-till management. Nutrient Cycling in Agroecosystems 82:283-297.

Spiertz, J., and De Vos, N. 1983. Agronomical and physiological aspects of the role of nitrogen in yield formation of cereals. Plant and Soil 75:379-391.

Stopes, C., Lord, E., Philipps, L., and Woodward, L. 2002. Nitrate leaching from organic farms and conventional farms following best practice. Soil Use and Management 18:256-263.

Struik, P., and Yin, X. 2009. QTL× E× M: Combining crop physiology and genetics. In: Østergård, H., Lammerts Van Bueren, E., and Bouwman-Smiths, L. (eds.) Proceedings of the bioexploit/eucarpia workshop on the role of marker assisted selection in breeding varieties for organic agriculture. BioExploit, Wageningen, The Netherlands. pp.18-21.

Sun, Y., Ma, J., Sun, Y., Xu, H., Yang, Z., Liu, S., Jia, X., and Zheng, H. 2012. The effects of different water and nitrogen managements on yield and nitrogen use efficiency in hybrid rice of china. Field Crops Research 127:85-98.

Swain, E. Y., Rempelos, L., Orr, C. H., Hall, G., Chapman, R., Almadni, M., Stockdale, E. A., Kidd, J., Leifert, C., and Cooper, J. M. 2014. Optimizing nitrogen use efficiency in wheat and potatoes: Interactions between genotypes and agronomic practices. Euphytica 199:119-136.

Sylvester-Bradley, R., and Kindred, D. R. 2009. Analysing nitrogen responses of cereals to prioritize routes to the improvement of nitrogen use efficiency. Journal of Experimental Botany 60:1939-1951.

Syswerda, S., Basso, B., Hamilton, S., Tausig, J., and Robertson, G. 2012. Long-term nitrate loss along an agricultural intensity gradient in the upper Midwest USA. Agriculture, Ecosystems and Environment 149:10-19.

Tabuchi, M., Sugiyama, K., Ishiyama, K., Inoue, E., Sato, T., Takahashi, H., and Yamaya, T. 2005. Severe reduction in growth rate and grain filling of rice mutants lacking *OSGS1*; 1, a cytosolic glutamine synthetase1; 1. The Plant Journal 42:641-651.

Tanji, K., Broadbent, F., Mehran, M., and Fried, M. 1979. An extended version of a conceptual model for evaluating annual nitrogen leaching losses from croplands. Journal of Environmental Quality 8:114-120.

Tinker, P. B., and Nye, P. H. 2000. Solute movement in the rhizosphere, Oxford University Press, New York.

Tonitto, C., David, M., and Drinkwater, L. 2006. Replacing bare fallows with cover crops in fertilizer-intensive cropping systems: A meta-analysis of crop yield and n dynamics. Agriculture, Ecosystems and Environment 112:58-72.

Trachsel, S., Kaeppler, S., Brown, K., and Lynch, J. 2013. Maize root growth angles become steeper under low n conditions. Field Crops Research 140:18-31.

Van Bueren, E. L., Backes, G., De Vriend, H., and Østergård, H. 2010. The role of molecular markers and marker assisted selection in breeding for organic agriculture. Euphytica 175:51-64.

Van Der Heijden, M. G., Bardgett, R. D., and Van Straalen, N. M. 2008. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters 11:296-310.

Van Sanford, D., and Mackown, C. 1986. Variation in nitrogen use efficiency among soft red winter wheat genotypes. Theoretical and Applied Genetics 72:158-163.

Van Vuuren, M., Robinson, D., and Griffiths, B. 1996. Nutrient inflow and root proliferation during the exploitation of a temporally and spatially discrete source of nitrogen in soil. Plant and Soil 178:185-192.

Vance, C. P. 2001. Symbiotic nitrogen fixation and phosphorus acquisition. Plant nutrition in a world of declining renewable resources. Plant Physiology 127:390-397.

Veresoglou, S. D., Chen, B., and Rillig, M. C. 2012. Arbuscular mycorrhiza and soil nitrogen cycling. Soil Biology and Biochemistry 46:53-62.

Vidmar, J. J., Zhuo, D., Siddiqi, M. Y., Schjoerring, J. K., Touraine, B., and Glass, A. D. 2000. Regulation of high-affinity nitrate transporter genes and high-affinity nitrate influx by nitrogen pools in roots of barley. Plant Physiology 123:307-318.

Walch-Liu, P., Ivanov, I. I., Filleur, S., Gan, Y., Remans, T., and Forde, B. G. 2006a. Nitrogen regulation of root branching. Annals of Botany 97:875-881.

Walch-Liu, P., Liu, L.-H., Remans, T., Tester, M., and Forde, B. G. 2006b. Evidence that l-glutamate can act as an exogenous signal to modulate root growth and branching in *arabidopsis thaliana*. Plant and Cell Physiology 47:1045-1057.

Wang, X., and Below, F. E. 1992. Root growth, nitrogen uptake, and tillering of wheat induced by mixed-nitrogen source. Crop Science 32:997-1002.

Wang, X., Wei, Y., Shi, L., Ma, X., and Theg, S. M. 2015. New isoforms and assembly of glutamine synthetase in the leaf of wheat (*Triticum aestivum* L.). Journal of Experimental Botany 66:6827-6834.

Watkins, N., and Barraclough, D. 1996. Gross rates of n mineralization associated with the decomposition of plant residues. Soil Biology and Biochemistry 28:169-175.

Weber, A., Gutser, R., Michel, H., Wozniak, H., Chen, G., Xu, H., and Niclas, H. Dicyandiamide and 1h-1, 2, 4-triazole–a new effective nitrification inhibitor for reducing nitrous oxide emissions from cultivated land. In: Weiske, A., ed. Greenhouse Gas Emissions from Agriculture–Mitigation Options and Strategies 2004 Leipzig, Germany. 273-275.

Wiesler, F., and Horst, W. 1994. Root growth and nitrate utilization of maize cultivars under field conditions. Plant and Soil 163:267-277.

Wu, J., Bernardo, D., Mapp, H., Geleta, S., Teague, M., Watkins, K., Sabbagh, G., Elliott, R., and Stone, J. 1997. An evaluation of nitrogen runoff and leaching potential in the high plains. Journal of Soil and Water Conservation 52:73-80.

Yadav, R., Singh, V., Dwivedi, B., and Shukla, A. K. 2003. Wheat productivity and n use-efficiency as influenced by inclusion of cowpea as a grain legume in a rice–wheat system. The Journal of Agricultural Science 141:213-220.

Yanai, J., Kosaki, T., Nakano, A., and Kyuma, K. 1997. Application effects of controlled-availability fertilizer on dynamics of soil solution composition. Soil Science Society of America Journal 61:1781-1786.

Yang, W., Xiang, Z., Ren, W., and Wang, X. 2005. Effect of S-3307 on nitrogen metabolism and grain protein content in rice. Chinese Journal of Rice Science 19:63-67.

Yienger, J., and Levy, H. 1995. Empirical model of global soil-biogenic noχ emissions. Journal of Geophysical Research 100:11447-11464.

Zebarth, B., Drury, C., Tremblay, N., and Cambouris, A. 2009. Opportunities for improved fertilizer nitrogen management in production of arable crops in eastern Canada: A review. Canadian Journal of Soil Science 89:113-132.

Zhao, G., Hörmann, G., Fohrer, N., Li, H., Gao, J., and Tian, K. 2011. Development and application of a nitrogen simulation model in a data scarce catchment in south china. Agricultural Water Management 98:619-631.

Zhou, C., Cai, Z., Guo, Y., and Gan, S. 2009. An arabidopsis mitogen-activated protein kinase cascade, MKK9-MPK6, plays a role in leaf senescence. Plant Physiology 150:167-177.

Ziadi, N., Bélanger, G., Claessens, A., Lefebvre, L., Cambouris, A. N., Tremblay, N., Nolin, M. C., and Parent, L.-É. 2010. Determination of a critical nitrogen dilution curve for spring wheat. Agronomy Journal 102:241-250.

2.0 Relative performance of Canadian spring wheat cultivars under organic and conventional field conditions[2]

2.1 Introduction

Crop production without the use of synthetic fertilizers and chemicals is called organic farming. International Federation of Organic Agriculture Movements (IFOAM) defines organic farming as “a production system that sustains the health of soils, ecosystems and people. It relies on ecological processes, biodiversity and cycles adapted to local conditions, rather than the use of inputs with adverse effects”. Extensive use of chemical inputs during the last century has raised numerous concerns over the human and environmental health, and agricultural sustainability. Due to the fact that, organic food production is safe and chemical-free, the demand for organic food has increased 4-5 times since 1990. Ever since, it has evolved as the most dynamic food industry worth $59 billion globally with approximately 37.2 million ha area under certified organic cultivation worldwide (Paull and Hennig, 2011). Canadian contribution towards organic food production is relatively small and approximately 0.7 million ha are organically managed and wheat is the number one Canadian organic crop grown on about 102, 434 ha of land (Agriculture Agri-Food Canada, 2009).

Organically managed lands differ substantially from their conventional counterparts for soil biodiversity, nitrogen level, soil moisture and retaining capacity, soil organic matter, weed intensity and types, and biotic and abiotic stresses (Hornick, 1992; Gruber et al., 2000; Barberi, 2002; Entz et al., 2001). This results in considerable differences in agronomic and quality traits of various crops grown and compared in organic and conventional management systems.

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[2] *This chapter is a slightly modified version of the published paper. Atif Kamran, Hiroshi Kubota, Rong-Cai Yang, Harpinder S. Randhawa, and Dean Spaner. 2014. Relative performance of Canadian spring wheat cultivars under organic and conventional field conditions. 2014.Euphytica, 196(1):13-24.*

Aside from the environmental stress, the cultivars exhibit significant genetic variation among each other to respond any biotic or abiotic stress (Romagosa and Fox, 1993). Therefore, several studies reported inconsistencies in crop and/or cultivar performance from one location to other (Peterson et al., 1992; Sial et al., 2000).

In organic management systems, the grain yields are generally low compared to conventional production systems when weed and nutritional constraints are prominent (Poutala et al., 1993; Mason et al., 2007; Reid et al., 2009) while a great deal of confusion exists around the quality of the produce. In fact the nutritionally important quality micronutrients are affected by a number of factors related to soil, environment and management (Davis et al., 2006). Nelson et al. (2011) concluded that the quality of the organic produce varies from one location to other and should not be universalized. A number of studies advocate organic production to be superior and rich in their nutritional value (Nelson et al., 2011; Reid et al., 2009); however, there are studies reporting significant loss in grain protein content under organic conditions (Starling and Richards, 1993; Ryan et al., 2004; Zorb et al., 2009). Mader et al. (2007) reported non-significant differences in nutritional value and baking quality in European germplasm studied over 21 years.

Across the Canadian Prairies, the growing season or the number of frost free days are limited to 95-125 days in total. Earlier flowering and maturity are desirable traits to avoid yield and quality losses in this region. Under organic field conditions, earliness with better early season vigour is beneficial to compete for limited nutrient supply. Mason et al. (2007) reported higher grain yield of the early maturing cultivars with better early season vigour under organic field conditions. Early maturity also confers adaptive advantage by avoiding abiotic stress conditions of early or late season frost, and hence, most of the Canadian spring wheat cultivars possess the most potent vernalization genes (Kamran et al., 2013). Iqbal et al. (2007) suggested that simultaneous selection for higher grain yield and early maturity is possible by identifying certain *Vrn* gene combinations. In this context, it is important to study how the different vernalization genes interact to induce early maturity without negatively affecting grain yield and whether early maturity confers any yield advantage under organic field conditions.

The objectives of the study were: a) to study how early flowering and maturity results in differential agronomic performance under organic and conventional management systems; b) if reduction in days to maturity due to insensitive *Vrn* genes confers grain yield advantage under organic field conditions; c) to identify the genotypes/cultivars that are better suited to organic production.

2.2 Materials and Methods

In this experiment we studied a set of 32 Canadian spring wheat cultivars in organic and conventional management systems. These cultivars were mostly released during the last ten years under the following four classes: Canada Western Red Spring (CWRS), Canada Western Soft White Spring (CWSWS), Canada Prairie Spring (CPS) and Canada Western Hard White spring (CWHWS). The four classes represent more than 96% of the area under cultivation in Canadian Prairies (Statistics Canada 2011).These cultivars were studied in 2010, 2011 and 2012 at the Edmonton Research Station (ERS) (53° 32'N, 113°32'W) University of Alberta, on conventional and organically managed fields located less than 1 km apart. The soil classification in this area is a black Chernozemic soil.

The organic field at ERS has been organically managed since 1999 and compost was applied at a rate of 50 to 62 t ha^{-1} (fresh weight) for five consecutive years from 1999 until 2005. The field has been rotationally managed with the crop sequence of wheat (*Triticum aestivium* L.) - fall rye (*Secale sereale* L.) - a mixture of triticale (×*Triticosecale* Wittmackand) - field pea

(*Pisum sativum* L.) until 2009, and fall rye - barley silage (*Hordeum vulgare* L.) - wheat until 2012. Weed control was carried out by tillage in fall and prior to seeding.

The experiment was laid out in alpha lattice design that increase homogeneity among tested cultivars by dividing replication into sub-blocks. The dimensions of each plot were 2 ×1.38 m with six rows spaced 23 cm apart. Harvested seeds in previous year were used and planted with 300 viable seeds m^{-2}. Data on days to flowering, days to anthesis and maturity, plant height, grain yield, test weight, and grain protein content were recorded. The organic field experiment in 2011 was overwhelmed with weeds and data were recorded for days to flowering, anthesis and maturity only. Days to flowering was recorded when 50% of the spikes emerged out of the flag leaf. Days to anthesis was recorded when 50% of the spikes in a plot have protruded out anthers. Days to maturity were recorded when 50% of the peduncles had completely lost their green color. Grain protein content was estimated using SpectraStar RTW apparatus by Unity Scientific by Near Infrared Reflectance (NIR) spectroscopy. Grain yield per plot was weighed and converted to yield t/ha dry basis. Grain fill duration (GFD) was estimated as the duration between anthesis and maturity and grain fill rate (GFR) was estimated by dividing the total gain yield to total grain fill days.

The cultivars were genotyped for vernalization (*Vrn-A1a, Vrn-A1b, Vrn-B1, Vrn-D1)* genes. 7-10 day old seedling leaf tissue was ground to extract DNA by standard CTAB protocol. Primer sequences for these *Vrn* genes were adopted from Yan et al., (2004) and Fu et al., (2005). PCRs were done in GeneAmp® 9700 PCR systems (Applied Biosystems). A total volume of 20µL of the reaction mixture was used for PCR containing: a) 1-4 µL of template DNA about at a concentration of 25-100 ng/µL, b) 0.5 µL of each forward and reverse primers at 5µM concentration, c) 10 µL of Extract-N-Amp™PCR ready mix (Sigma-Aldrich, Cat#E3004), and d) 5-8µL sterile water to make total reaction volume to 20µL. The PCR cycling conditions were followed exactly as described by Yan et al. (2004) and Fu et al. (2005). The PCR products were ran and visualized in a 3% agarose gel.

The cultivar LSMEANS were estimated in PROC MIXED of SAS by keeping cultivar as the only fixed effect, and year, block nested in year and incomplete block nested in block and year as random effects in each management. The LSMEANS were ranked from earliest to latest in term of time to flowering, anthesis, maturity and highest to lowest in terms of grain yield, grain protein content, test weight, grain fill duration and grain fill rate. To study the differential performance of the cultivars in the two managements (organic and conventional management systems), the data were analysed by using PROC MIXED in SAS by keeping the management as a fixed effect while year, block nested in year and incomplete block nested in block and year as random effects. To identify the better performance of a cultivar in either of the managements, cultivar ×management interactions were calculated by modelling the cultivar, management and cultivar ×management interaction as fixed effects. The identified significant interaction affects were further partitioned with SLICE command in PROC MIXED for both cultivars and managements. To account for the number of comparisons, the alpha values were adjusted by BONFERRONI correction (Dunn, 1961). The LSMEANS for the individual cultivar under each management were estimated by keeping the cultivars as fixed affect. The significance of difference between the conventional and organic management system was estimated by comparing it with the critical range estimate provided by Rayan-Einot-Gabrial-Welsh test which adjusts the alpha value ‘experiment-wise’. The cultivars were also sub-grouped based on their *Vrn* gene composition and class, and were considered as a treatment. To retain enough statistical power and to avoid the genetic background noise of the cultivars from different classes, only CWRS cultivars were taken into consideration for ranking and comparison under organic field conditions. The differences between the cultivars with single insensitive allele (*Vrn-A1a*) or two (*Vrn-A1a, Vrn-B1*) were estimated only in CWRS class. These treatments were dealt as a fixed effect to compare the organic and conventional environments.

2.3 Results

All the traits under study except days to maturity, plant height and grain protein content differed statistically between organic and conventional management in overall analysis of variance (Table 2-1). Generally, the cultivars under organic conditions were earlier flowering, lower yielding with a lower test weight compared to the conventional management system (Table 2-1). This trend was similar in sub-groups of cultivars belonging to CWRS class having either one or two insensitive alleles at *Vrn-1* locus (*Vrn-A1a-vrn-B1-vrn-D1 or Vrn-A1a-Vrn-B1-vrn-D1*) (Table 2-2). The only exception was the cultivars with single insensitive *Vrn* allele matured earlier under organic management compared to the cultivars having two insensitive vernalization alleles (*Vrn-A1a* and *Vrn-B1*) (Table 2-2). However, this reduction in days to maturity failed to translate into higher grain yields under organic field conditions.

Of the 22 CWRS cultivars, three out of the top six earliest maturing cultivars were among the lowest yielding (Lillian, Osler, and Alvena ranks: 21, 22 and 18); whereas, two out of the six latest maturing cultivars were higher yielding cultivars ranked as 6 and 5 (AC Barrie and Superb) (Table 2-3). These results suggest that there is no clear evidence to conclude whether earlier flowering and/or maturity have conferred any yield advantage. Rather, a strong positive correlation was found between grain yield and days to flowering and maturity (Table 2-6). These results also suggested that significant cultivar × management interaction is more likely to impact the grain yield, rather than the maturity times. Cultivar × management interaction effects were found significant for grain yield, grain protein content and grain fill rate (Table 2-4). The estimates of sliced LSMEANS of the cultivars and management for the traits were ranked according to the minimum and maximum differences between organic and conventional managements (Table 2-1). Maximum differences between organic and conventional conditions for days to flowering, anthesis and maturity were observed in Sadash and Superb. Sadash has the maximum acceleration under organic conditions by 3.3, 4.1 and 6.7d in flowering, anthesis and maturity, while Superb had the maximum delay of 0.6 and 3.7d in flowering and maturity (Table 2-1, 2-5). A low negative correlation between plant height and grain yield was found in organic and non-significant effect was found under conventional conditions (Table 2-6).

Marquis, the oldest studied cultivar, had higher yield and protein content under organic conditions than conventional. This was the only exception, as all other cultivars had lower yield under organic conditions. The minimum grain yield losses under organic conditions were incurred by Infinity (0.14 t ha^{-1}) while the maximum losses were noted in 5701PR (2.07 t ha^{-1}) (Table 2-1, 2-5). In terms of grain protein content, cross-over interaction among the cultivars and managements occurred: 15 of 32 cultivars studied exhibited higher grain protein content under organic conditions while 17 cultivars had higher grain protein under conventional conditions (Table 2-1, 2-5). The top six cultivars with higher grain protein (>1.85%) under organic conditions were: Andrew, Bhishaj, 5700PR, 5701PR, and 5702PR (Table 2-1, 2-5), however, all of these cultivars except 5702PR incurred maximum grain yield losses under organic field conditions (Table 2-1). The cultivars like Fieldstar, Infinity, AC Barrie, Stettler, and Katepwa had significant loss of grain protein (>1.05%) under organic grown conditions (Table 2-5). The trend for loss in grain filling rate was quite similar to the trend in grain yield. The cultivar Infinity had almost no difference (3.38) in grain fill rate while cultivar Lillian had substantially low (56.2) grain fill rate under organic conditions (Table 2-1).

Cultivars grown under organic field conditions generally flowered earlier as compared to conventional conditions. As the nutrient supply under organic conditions is not as abundant, the cultivars under organic field conditions produced 21% less grain yield on an average; however, the cultivars like Marquis, Infinity, Park, Unity, Harvest and Minnedosa had comparable grain yields in both management systems (Table 2-5).

2.4 Discussion and Conclusion

Three major findings of this study are as follows: *a*) cultivars having single insensitive *Vrn* alleles (i.e. *Vrn-A1a*) induced earlier maturity under organic conditions compared to *Vrn-A1a* and *Vrn-B1* in combination; however, this accelerated maturity did not confer any yield advantage; b) cultivars grown under organic management system were earlier flowering, lower yielding and had lower test weight compared to the conventional management system; and c) significant cultivar × management interactions were noted for grain yield, grain protein content and grain fill rate.

Mason et al. (2007) proposed a hypothesis that earlier flowering and maturity can help the plants outcompete weeds and produce better yields in organic systems. Based on this hypothesis, we studied modern Canadian germplasm to figure out if any of the particular *Vrn* genes or combination, governing the flowering and maturity time, is better suited for organic conditions. Based on the germplasm studied in this experiment, the proposed hypothesis does not stand true; the insensitive allele *Vrn-A1a* conferred earlier maturity compared to the two *Vrn* alleles *Vrn-A1a* and *Vrn-B1,* but this acceleration cannot be clearly attributed to any yield advantage. The earliest maturing cultivar Park (94 days to maturity) ranked 11 followed by Lovit (96.7 days to maturity) at 16th position (Table 2-3). A strong positive correlation was also found between days to flowering and/or maturity and grain yield (Table 2-6); which also suggests that the grain yield increases with longer growth duration and delayed maturity. Apparently, cultivar ×management interaction seems to be responsible for higher grain yield under organic field conditions rather than the delay in days to maturity or *Vrn* gene combination. Kirk et al. (2012) found significant effects of the managements (both organic and conventional) on grain yield and protein content; and reported higher grain yield of the lines selected in organic management. Another possible reason for this discrepancy could be due to the QTL responsible for accelerated grain filling rate (GFR) (Nass and Reisser 1975). GFR is a relatively less explored area of research, and is reported to play a significant role in determining wheat grain yield (Yang and Zhang, 2006). Wang et al. (2009) detected 17 QTL explaining 7.2-20.8% of the total phenotypic variation in GFR in a Chinese winter population. Kirigwi et al. (2007) also reported a QTL affecting the GFR on chromosome 4A. Therefore, a differential genetic background of the cultivars under study might have contributed towards a significant cultivar × management interaction for grain yield. A strong positive correlation between GFR and grain yield found in this study (Table 2-6) further justifies the differential behaviour of the cultivar under stress conditions. A low negative correlation between the grain yield and plant height found in organic conditions also suggest that the taller CWRS cultivars does not necessarily better compete with weeds for light interception. However, these results are not in agreement with Mason et al. (2007) and Wolfe et al. (2008), but support Wiebe et al. (2016). Similarly, a strong negative correlation between grain protein content and grain fill duration in organic conditions was found, and a moderate to low positive correlation between the same traits was found in conventional management systems (Table 2-6).

The significant cultivar × management interaction for grain yield found in this study suggests that some cultivars can manage to tolerate nutrient, weed and disease pressure are able to adapt stress conditions better than other cultivars. Overall, the cultivars exhibited significant interaction with the organic and conventional management systems for grain yield, grain protein content and grain fill rate.

Cultivar interaction with management for grain protein content was interesting, as some of the cultivars had higher grain protein content under organic conditions and some had higher grain protein content under conventional conditions. This may suggest a possibility that CWRS cultivars perform differently in nitrogen use efficiency (NUE) between organic and conventional systems (Giuliani et al., 2011). Some cultivars produced similar grain protein under both organic and conventional management systems (Table 2-5). As all the cultivars are flowering and maturing within the available growing time in Canadian Prairies, cultivars better suited to organic condition were selected based on minimum grain yield and grain protein losses. Selecting the top 6 cultivars (20%) that had minimum grain yield and grain protein losses among the systems resulted in three common cultivars (Table 2-5). These three cultivars (i.e. Marquis, Unity and Minnedosa) had comparable yield and grain protein contents in both production systems. Marquis, the oldest cultivar in the study, had higher yield and better protein content under organic conditions. Marquis was bred in early 20th century, and the selection was practiced under organic conditions. The other two cultivars that had minimum grain yield and grain protein losses under organic conditions, were released recently (Minnedosa 2008 and Unity 2009); and defy the particular hypothesis that older cultivars are better suited to organic breeding. In a micronutrient analysis of five Canadian spring wheat cultivars released during 1910 to 2000 Nelson et al. (2011) found no particular trend in cultivar performance in relation to their year of release.

Better performance of certain cultivars under organic field conditions has been reported previously (Mason et al., 2007). Nass et al. (2003) reported significant higher grain yield by AC Barrie under organic conditions compared to check AC Walton, which generally outcompeted AC Barrie for grain yields under conventional conditions. Kitchen et al. (2003) found higher grain yields in organic conditions at 3 of the 14 paired sites; and found significant cultivar × management interaction for grain yield. Carr et al. (2006) reported cultivar × management interactions for grain yield, grain protein content and test weights in fifteen spring wheat cultivars of northern Great Plains. Murphy et al. (2007) reported different genotypic ranks between the organic and conventional management systems. Przystalski et al. (2008) reported cross-over interaction of the cultivars between the management systems and suggested trait and stress oriented breeding for organic crop production.

Overall, we found significant interaction of the cultivars with management system; therefore, breeding for organic production should be conducted on organically managed lands. When grown under organic field conditions the cultivars generally earlier flowering; produced lower grain yields and had lower test weights. Four cultivars: Marquis, Minnedosa, Harvest and Unity had minimum losses under organic conditions and can potentially serve as parents for organic breeding.

2.5 Acknowledgements

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2.6 Tables

Table 2-1. Mean differences between the conventional and organic management system for days to flowering, anthesis, maturity, plant height (cm), grain yield (t ha^{-1}), test weight (Kg hL^{-1}), grain protein content (%), grain fill days and grain fill rate for all the cultivars under study grown at Edmonton Research station during 2010, 2011 and 2012.

Variety	Year of Registered	Class	Vrn-A1a	Vrn-B1	Vrn-D1	Flowering (Days)	Anthesis (Days)	Maturity (Days)	Height (cm)	Yield (t ha^{-1})	Test Weight (Kg hL^{-1})	Grain Protein	Grain Fill Duration	Grain Fill Rate
5700PR	2000	CPS[a]	Vrn-A1a	vrn-B1	vrn-D1	0	0.6	3.3	-2.5	1.77	2	-1.87	3.7	40.6
5701PR	2001	CPS	Vrn-A1a	vrn-B1	vrn-D1	1.2	1.5	6.5	-0.8	2.07	1.23	-1.87	6.4	36.7
5702PR	2010	CPS	Vrn-A1a	vrn-B1	vrn-D1	0.6	1.7	-0.4	-5.2	1.42	0.75	-1.85	-1.6	47.5
Ac Vista	1996	CPS	Vrn-A1a	vrn-B1	vrn-D1	0.9	0.4	2.7	-0.3	1.39	1.64	-1.11	3	33.1
Alvena	2007	CWRS[b]	Vrn-A1a	vrn-B1	vrn-D1	1.3	1.5	2.1	0.8	1.6	3.6	0.66	1.6	47.6
Andrew	2000	CWSWS[c]	vrn-A1	Vrn-B1	Vrn-D1	1.4	2.2	2.6	-1.5	1.85	1.68	-2.13	1.3	48.2
Attila	-	CIMMYT	vrn-A1	vrn-B1	Vrn-D1	0.9	1.2	2.7	-1.2	0.54	2.9	-0.82	2.6	14.6
AC Barrie	1994	CWRS	Vrn-A1a	vrn-B1	vrn-D1	0.5	0.9	-4.1	2.9	0.63	2.75	1.24	-2.9	33.8
Bhishaj	2002	CWSWS	Vrn-A1a	vrn-B1	vrn-D1	1.5	2	3.8	0.1	1.17	-0.52	-1.99	3.3	28.9
Bounty	-	CWRS	Vrn-A1a	Vrn-B1	vrn-D1	1	1.2	1.1	0	1.26	2.88	0.34	1.2	44.9
CDC Go	2004	CWRS	Vrn-A1a	Vrn-B1	vrn-D1	-0.4	0.4	1.4	-2.2	1.03	3.43	-0.15	1.9	28.3
Fieldstar	2009	CWRS	Vrn-A1a	vrn-B1	vrn-D1	1.4	2.7	5.4	-3.9	0.64	-0.38	1.05	3.5	19.5
Goodeve	2008	CWRS	Vrn-A1a	vrn-B1	vrn-D1	1.1	2.4	0.8	1.9	1.24	2.62	-0.1	-1	46.1
Harvest	2002	CWRS	Vrn-A1a	Vrn-B1	vrn-D1	0.8	1	0.3	0.7	0.34	1.51	-0.09	0.8	16.6
Infinity	2006	CWRS	Vrn-A1a	vrn-B1	vrn-D1	0.7	1.3	3.9	-2.4	0.14	0.46	1.1	3.9	3.4
Kane	2006	CWRS	Vrn-A1a	Vrn-B1	vrn-D1	0.1	0.6	-0.5	0.3	1.17	3.94	0.96	-0.4	37
Katepwa	1981	CWRS	Vrn-A1a	vrn-B1	vrn-D1	-0.5	0.1	1.1	-0.6	1.11	3.62	1.59	1.9	36
Lovit	2003	CWRS	Vrn-A1a	Vrn-B1	vrn-D1	1.3	1.5	2.7	-0.6	0.96	1.42	0.73	2	32.7
Marquis	1910	CWRS	Vrn-A1a	vrn-B1	vrn-D1	2.4	2.9	5.4	3.2	-0.41	2.25	-0.4	4	-6.3

(Continued)

(Continued)

Variety	Year of Registered	Class	Vrn-A1a	Vrn-B1	Vrn-D1	Flowering (Days)	Anthesis (Days)	Maturity (Days)	Height (cm)	Yield ($t\ ha^{-1}$)	Test Weight ($Kg\ hL^{-1}$)	Grain Protein	Grain Fill Duration	Grain Fill Rate
Minnedosa	2008	GP	Vrn-A1a	Vrn-B1	vrn-D1	1.6	2.1	3.1	-1.1	0.53	0.79	-0.34	1.8	12.5
Osler	2003	CWRS	Vrn-A1a	Vrn-B1	vrn-D1	0.2	1	2.7	2.1	2.01	3.64	0.89	2.9	53.2
Park	1963	CWRS	Vrn-A1a	Vrn-B1	vrn-D1	0.3	0.9	5.6	6.3	0.29	2.7	0.67	5.8	6.6
Sadash	2008	CWSWS	Vrn-A1a	vrn-B1	vrn-D1	3.3	4.1	6.7	-0.4	1.91	0.76	-0.73	4.2	41.8
Snowwhite 475	2004	CWHWS[d]	Vrn-A1a	vrn-B1	vrn-D1	0.7	2.6	2.1	-2.8	1.4	1.66	0.05	0.8	35.3
Snowwhite 476	2004	CWHWS	vrn-A1	Vrn-B1	vrn-D1	2.9	3.3	2.4	-1.8	1.09	1.14	0.14	0.6	31.6
Somerset	2005	CWRS	Vrn-A1a	vrn-B1	vrn-D1	2.2	2.1	1	5.1	1.07	3.52	0.49	0.6	33.5
Stettler	2008	CWRS	Vrn-A1a	Vrn-B1	vrn-D1	0.1	0.2	1	0	1.11	4.66	1.47	2.2	30.6
Superb	2001	CWRS	Vrn-A1a	Vrn-B1	vrn-D1	-0.6	0.2	-3.7	3.4	0.61	3.1	-1.12	-2.6	27.9
CDC Teal	1991	CWRS	Vrn-A1a	vrn-B1	vrn-D1	0.5	0.9	0.1	2.2	0.95	3.37	0.76	0.3	35.4
Unity	2009	CWRS	Vrn-A1a	Vrn-B1	vrn-D1	-0.4	1.4	2.8	3.6	0.32	1.17	-0.28	2	14.5
Waskada	2008	CWRS	Vrn-A1a	Vrn-B1	vrn-D1	1	1.5	0.1	-1.2	1.32	1.89	0.39	-0.2	42.4
			Mean (Conventional)			56.4	59.5	102.9	94.5	5.3	76	10.5	43.4	121.2
			S.E (Mean)			0.17	0.1	0.5	0.5	0.11	0.15	0.09	0.49	2.17
			Mean (Organic)			55.5	58	100.8	94.3	4.2	73.5	10.6	41.7	89.7
			S.E (Mean)			0.2	0.2	0.8	0.5	0.13	0.4	0.35	0.97	2.29
			***p* value**			***	***	n.s.	n.s.	***	***	n.s.	***	*

*** <0.001, **<0.01, *<0.05, n.s. not significant; Grain Fill Duration = Days to maturity – days to anthesis; Grain Fill Rate = (Toal Grain Yield) / (Grain Fill Duration); [a]Canadian Prairie Spring; [b]Canada Western Red Spring; [c]Canada Western Soft White spring; [d]Canada Western Hard White Spring.

Table 2-2. Differences in effects of vernalization genes in organic and conventional management systems for CWRS cultivars in the study, grown at Edmonton Research station during 2010, 2011 and 2012.

	Lines with *Vrn-A1a*			Lines with *Vrn-A1a* and *Vrn-B1*		
	Conventional	Organic	*p* value	Conventional	Organic	*p* value
Flowering (Days)	56.3 ± 0.3[a]	55.2 ± 0.4	**	55.8 ± 0.3	55.3 ± 0.3	n.s.
Anthesis (Days)	59.4 ± 0.2	57.8 ± 0.4	***	58.9 ± 0.2	57.9 ± 0.3	***
Maturity (Days)	100.7 ± 0.8	102.0 ± 1.2	n.s.	101.2 ± 0.8	103.5 ± 1.1	**
Height (cm)	97.8 ± 1.1	97.0 ± 0.9	n.s.	94.9 ± 0.7	94.2 ± 0.7	n.s.
Yield (t ha-1)	5.03 ± 0.2	4.04 ± 0.3	***	5.08 ± 0.2	3.99 ± 0.2	***
Test Weight (kg hL^{-1})	76.5 ± 0.3	72.6 ± 1.7	**	77.6 ± 0.2	73.9 ± 0.4	***
Protein Content (%)	10.94 ± 0.2	10.61 ± 0.3	n.s.	10.64 ± 0.1	10.56 ± 0.2	n.s.
Grain Fill Duration	41.25 ± 0.8	43.41 ± 0.9	*	42.4 ± 0.8	44.8 ± 0.9	**
Grain Filling rate	123.3 ± 4.7	89.6 ± 5.2	***	120.8 ± 3.5	85.7 ± 3.3	***

*** <0.001, **<0.01, *<0.05, n.s. not significant; [a] Standard error of the mean

Table 2-3. LSMEANS for the CWRS cultivars in organic management system and their relative ranks for days to flowering, anthesis, maturity, plant height (cm), grain yield (t ha^{-1}), test weight (Kg hL^{-1}), grain protein content (%), grain fill days and grain fill rate for the cultivars grown at Edmonton Research station during 2010, 2011 and 2012.

Variety	Flowering (Days)	Anthesis (Days)	Maturity (Days)	Yield (t ha^{-1})	Test Weight (Kg hL^{-1})	Grain Protein (%)	Grain Fill Duration	Grain Fill Rate
Park	53.2 (1)	56.1 (2)	94 (1)	4.1 (11)	73.9 (11)	10.4 (12)	36.8 (22)	98 (6)
Lovit	55.1 (10)	58.1 (14)	96.7 (2)	3.7 (16)	74.6 (8)	10.12 (14)	37.8 (19)	85 (15)
Lillian	56.7 (21)	59 (21)	97 (3)	3.3 (21)	73.4 (15)	11.02 (4)	37.2 (21)	82 (17)
Osler	55.6 (15)	58.3 (16)	97.3 (4)	3.1 (22)	72.7 (19)	10.32 (13)	37.8 (18)	77 (21)
Alvena	55.1 (11)	57.9 (11)	97.5 (5)	3.7 (18)	73.7 (22)	10.66 (7)	38.7 (16)	85 (14)
Marquis	55.5 (13)	57.5 (9)	97.6 (6)	4.3 (7)	75.4 (3)	11.57 (1)	38.7 (15)	101 (5)
Unity	54.7 (6)	56.8 (5)	97.7 (7)	4.6 (3)	76.1 (2)	10.84 (6)	40.3 (13)	105 (3)
Infinity	56.4 (19)	58.9 (20)	97.8 (8)	4.8 (2)	74.5 (9)	9.7 (19)	37.7 (20)	118 (1)
Fieldstar	53.5 (2)	56.1 (1)	97.9 (9)	4.3 (8)	76.7 (1)	9.87 (18)	41 (9)	93 (7)
Goodeve	54.8 (7)	57 (7)	98.5 (10)	4.2 (9)	73.8 (12)	11.02 (5)	40.8 (10)	90 (8)
Bounty	55.8 (17)	58.8 (18)	98.5 (11)	3.9 (12)	75.1 (4)	10.63 (9)	38.5 (17)	89 (9)
Harvest	54 (5)	56.4 (3)	98.6 (12)	4.6 (4)	75 (6)	10.63 (10)	40.7 (11)	103 (4)
Katepwa	55.7 (16)	58.2 (15)	99.8 (13)	3.5 (20)	72.7 (18)	9.6 (22)	40.7 (12)	78 (20)
Minnedosa	55.2 (12)	57.4 (8)	99.8 (14)	4.9 (1)	74.8 (7)	10.44 (11)	41.6 (7)	111 (2)
Somerset	56.2 (18)	58.8 (19)	100 (15)	3.7 (17)	72.4 (21)	11.12 (3)	39.5 (14)	86 (13)
CDC Teal	55 (8)	57.5 (10)	100 (16)	3.9 (14)	73.6 (14)	10.05 (16)	41.3 (8)	83 (16)
Kane	55 (9)	57.9 (12)	101.6 (17)	3.7 (19)	73.7 (13)	9.68 (21)	43.2 (5)	78 (19)
CDC Go	53.7 (4)	56.8 (6)	101.7 (18)	3.9 (13)	73.3 (16)	11.23 (2)	43.8 (3)	79 (18)
Waskada	53.6 (3)	56.6 (4)	102.2 (19)	3.8 (15)	75 (5)	10.09 (15)	44.3 (2)	72 (22)
Stettler	56.9 (22)	59.2 (22)	102.9 (20)	4.2 (10)	73.1 (17)	9.69 (20)	42.3 (6)	86 (12)
Barrie	55.5 (14)	58 (13)	103.8 (21)	4.3 (6)	74.4 (10)	9.95 (17)	43.7 (4)	89 (10)
Superb	56.6 (20)	58.6 (17)	105.7 (22)	4.5 (5)	72.5 (20)	10.65 (8)	45.8 (1)	88 (11)

The cultivars are ranked (parentheses) based on the days to maturity from earliest to latest maturing.

*** <0.001, **<0.01, *<0.05, n.s. not significant.

Table 2-4. ANOVA table of the probability of F-tests for genotype, environment (organic and conventional) and the interaction for the experiment grown at Edmonton Research Station during 2010, 2011 and 2012.

	Genotype	Environment	G × E
Flowering (Days)	***	***	n.s.
Anthesis (Days)	***	***	n.s.
Maturity (Days)	***	n.s.	n.s.
Height (cm)	***	n.s.	n.s.
Yield (t ha^{-1})	***	***	**
Test Weight (kg hL^{-1})	n.s.	***	n.s.
Protein Content (%)	***	n.s.	***
Grain Fill Duration	***	**	n.s.
Grain Filling rate	**	***	*

*** <0.001, **<0.01, *<0.05, n.s. not significant; G: genotype, E: environment.

Table 2-5. Relative ranking of the cultivars based on the differences between the conventional and organic management systems for grain yield (t ha^{-1}), grain protein content (%) for all the cultivars grown at Edmonton Research station during 2010, 2011 and 2012.

Rank		Yield (t ha^{-1})			Rank		Protein Content (%)		
	Cultivar	Con[a]	Org[b]	Diff[c]		Cultivar	Con	Org	Diff
1	Marquis	3.88	4.29	-0.41	1	Harvest	10.53	10.63	-0.09
2	Infinity	4.91	4.76	0.14	2	Goodeve	10.92	11.02	-0.1
3	Park	4.33	4.05	0.29	3	CDC Go	11.09	11.23	-0.15
4	Unity	4.94	4.62	0.32	4	Unity	10.55	10.84	-0.28
5	Harvest	4.88	4.55	0.34	5	Minnedosa	10.09	10.44	-0.34
6	Minnedosa	5.41	4.88	0.53	6	Marquis	11.17	11.57	-0.4
27	5700PR	5.9	4.12	1.77	27	Kane	10.64	9.68	0.96
28	Andrew	6.88	5.03	1.85	28	Fieldstar	10.92	9.87	1.05
29	Sadash	6.85	4.94	1.91	29	Infinity	10.8	9.7	1.1
30	Osler	5.14	3.13	2.01	30	AC Barrie	11.19	9.95	1.24
31	Lillian	5.39	3.34	2.05	31	Stettler	11.15	9.69	1.47
32	5701PR	5.71	3.64	2.07	32	Katepwa	11.19	9.6	1.59
	LSD[d] (0.05)	0.11	0.17				0.14	0.23	

[a]Conventional; [b]Organic; [c]Difference; [d] Least square differences

Table 2-6. Pearson correlation co-efficient for the conventional and organic management system for days to flowering, anthesis, maturity, plant height (cm), grain yield (t ha^{-1}), test weight (Kg hL^{-1}), grain protein content (%), grain fill days and grain fill rate for the CWRS cultivars only.

	Flowering	Anthesis	Maturity	Height	Grain yield	Test Weight	Protein	Grain Fill Duration	Grain Filling rate
Flowering		0.85	0.78		0.42	-0.41		-0.22	0.54
Anthesis	0.94		0.15		0.4	-0.34			0.47
Maturity	0.73	0.72		0.19	0.43	0.31	0.45	0.97	
Height	-0.16	-0.2	-0.23			0.47	0.47	0.17	
Grain yield	0.66	0.58	0.79	-0.2		0.42	0.33	0.32	0.84
Test Weight	0.2		0.19		0.21		0.26	0.38	0.19
Protein	-0.69	-0.67	-0.78	0.3	-0.76			0.43	
Grain Fill Duration	0.56	0.52	0.97	-0.21	0.76		-0.72		-0.22
Grain Filling rate	0.59	0.5	0.52		0.92	0.19	-0.63	0.46	

Values above diagonal are conventional and below are organic data coefficients.

Only *p* values <0.05 are presented.

References

Barberi, P. 2002. Weed management in organic agriculture: are we addressing the right issues? Weed Research 42:177–193. doi:10.1046/j.1365-3180.2002.00277.x.

Carr, P. M., Kandel, H. J., Porter, P.M., horsley, R. D., and Zwinger, S. F. 2006. Wheat cultivar performance on certified organic fields in Minnesota and North Dakota. Crop Science. 46:1963–1971.

Davis, J., and Abbott, L. 2006. Soil fertility in organic farming systems. In: Organic Agriculture: A Global Perspective, Kristiansen P, Taji A, Reganold J, (eds.) Comstock Publishing Associates, New York, pp 25-51.

Dunn, O. J. 1961. Multiple comparisons among means. Journal of the American Statistical Association 56:52-64.

Entz, M. H., Guilford, R., and Gulden, R. 2001. Crop yield and soil nutrient status on 14 organic farms in the eastern portion of the northern Great Plains. Canadian Journal of Plant Science 81:351-354.

Fu, D., Szucs, P., Yan, L., Helguera, M., Skinner, J.S., von Zitzewitz, J., Hayes, P. M., and Dubcovsky, J. 2005. Large deletions within the first intron in *VRN-1* are associated with spring growth habit in barley and wheat. Molecular Genetics and Genomics 273:54-65.

Gruber, H., Handel, K., and Broschewitz, B. 2000. Influence of farming system on weeds in thresh crops of a six-year crop rotation. Proceedings of the 20th German Conference on weed biology and weed control, Stuttgart- Hohenheim, Germany, March 14-16, Zeitschrift fur Pflanzenkrankheiten und Pflanzenschutz 17:33-40.

Giuliani, M. M., Giuzio, L., De Caro, A., and Flagella, Z. 2011. Relationships between nitrogen utilization and grain technological quality in durum wheat: I. nitrogen translocation and nitrogen use efficiency for protein. Agronomy Journal 103(5): 1487-1494.

Hornick, S. B. 1992. Factors affecting the nutritional quality of crops. American Journal of Alternative Agriculture 7:63-68.

Iqbal, M., Navabi, A., Salmon, D. F., Yang, R. C., and Spaner, D. 2007. Simultaneous selection early maturity, increased grain yield and elevated grain protein content in spring wheat. Plant Breeding 126:244-250.

Kamran, A., Randhawa, H.S., and Pozniak, C., and Spaner, D. M. 2013. Phenotypic effects of the flowering gene complex in Canadian spring wheat germplasm. Crop Science. 53:84-94.

Kirigwi, F. M., Ginkel, M. V., Guedira, G. B., Gill, B. S., Paulsen, G. M., and Fritz, A. K. 2007. Markers associated with a QTL for grain yield in wheat under drought. Molecular Breeding 20:401–413.

Kirk, A. P., Fox, S. L., Entz, M. H. 2012. Comparison of organic and conventional selection environments for spring wheat. Plant Breeding 131: 687-694.

Kitchen, J. L., McDonald, G. K., Shepherd, K. W., Lorimer, M. F., and Graham, R. D. 2003. Comparing wheat grown in South Australian organic and conventional farming systems. Australian Journal of Agricultural Research 54:889–901.

Mäder, P., Hahn, D., Dubois, D., Gunst, L., Alföldi, T., Bergmann, H., Oehme, M., Amadò, R., Schneider, H., Graf, U., Velimirov, A., Flieβbach, A., and Niggli, U. 2007. Wheat quality in organic and conventional farming: results of a 21 year field experiment. Journal of the Science of Food and Agriculture 87: 1826-1835.

Mason, H.E., A. Navabi, B.L. Frick, J.T. O'Donovan and D.M. Spaner. 2007. The weed-competitive ability of Canada western red spring wheat cultivars grown under organic management. Crop Science 47: 1167-1176.

Murphy, K.M., K.G. Campbell, S.R. Lyon and S.S. Jones. 2007. Evidence of varietal adaptation to organic farming systems. Field Crops Research 102: 172-177.

Nass, H. G., Reisser, B. 1975. Grain filling period and grain yield relationships in spring wheat. Canadian Journal of Plant Science 55:673–678.

Nass, H. G., Ivany, J. A., MacLeod, J. A. 2003. Agronomic performance and quality of spring wheat and soybean cultivars under organic culture. American Journal of Alternative Agriculture, 18, pp 164170.

Paull, J., Hennig, B. 2011. A world map of organic agriculture. European Journal of Social Science 24:360-369.

Peterson, C. J., Graybosch, R. A., Baenziger, P. S., and Grombacher, A. W. 1992 Genotype and environment effects on quality characteristics of hard red winter wheat. Crop Science. 38:98-103.

Poutala, R. T., Korva, J., Varis, E. 1993. Spring wheat cultivar performance in ecological and conventional cropping systems. Journal of Sustainable Agriculture 3:63–83.

Przystalski, M., Osman, A., Thiemt, E. M., Rolland, B., Ericson, L., Østergârd, H., Levy, L., Wolfe, M., Büchse, A., Piepho, H. P., and Krajewski, P. 2008. Comparing the performance of cereal varieties in organic and nonorganic cropping systems in different European countries. Euphytica 163:417–433. doi:10.1007/s10681-008-9715-4.

Romagosa, I., Fox, P. N. 1993. Genotype x environment interaction and adaptation. Plant breeding series, Plant breeding. pp:373-390.

Ryan, M., Derrick, J., and Dann, P. 2004. Grain mineral concentrations and yield of wheat grown under organic and conventional management. Journal of the Science of Food and Agriculture 84:207–216.

Sial, M. A., Arian, M. A., and Ahmed, M. 2000. Genotype × environment interaction on bread wheat grown over multiple sites and years in Pakistan. Pakistan Journal of Botany 32:85-91.

Starling, W., and Richards, M. C. 1993. Quality of commercial samples of organically-grown wheat. Aspects of Applied Biology 36:205–209.

Wiebe, L., Fox, S. L., and Entz, M. H. 2016. Organic selection may improve yield efficiency in spring wheat: a preliminary analysis. Canadian Journal of Plant Science. 97: 298-307.

Wolfe, M. S., Baresel, J.P., Desclaux, D., Goldringer, I., Hoad, S., Kovacs, G., Löschenberger, F., Miedaner, T., Østergârd, H., Lammerts van Bueren, E. T. 2008. Developments in breeding cereals for organic agriculture. Euphytica 163:323-346.

Yan, L., Helguera, M., Kato. K., Fukuyama, S., Sherman, J., and Dubcovsky, J. 2004. Allelic variation at the VRN-1 promoter region in polyploidy wheat. Theoretical and Applied and Genetics 109:1677-1686.

Yang, J. C., Zhang, J. H. 2006. Grain filling of cereals under soil drying. New Phytolgist 169:223–236.

Zorb, C., Niehaus, K., Barsch, A. 2009. Levels of compounds and metabolites in wheat ears and grains in organic and conventional agriculture. Journal of Agricultural and Food Chemistry 57:9555–9562.

3.0 Investigating genetic progress and variation for nitrogen use efficiency in spring wheat (*Triticum aestivum* L.)[3]

3.1 Introduction

Wheat (*Triticum aestivium* L.) is one of the three major staple cereal crops cultivated throughout the world for human consumption, with a projected global production of 751 million t in 2016/2017 (Bond and Liefert, 2017). As the world population is forecast to reach 9.7 billion, the demand of wheat production is expected to increase collinearly (UN-DESA, 2015). Under modern agricultural practices, soil nitrogen (N) is the common limiting plant nutrient for wheat production (Satorre and Slafer, 1999; Fageria et al., 2008). Thus, optimum use of N fertilizer plays a critical role in increasing wheat production to meet global demand. Increased application of synthetic N fertilizer has increased grain yield per unit area globally (Satorre and Slafer, 1999; Ladha et al., 2016). Since the 1950's, average wheat grain yield per unit area has increased steadily in Canada due to improvement in genetic potential and the availability of synthetic N fertilizers (DePauw and Hunt, 2001). Canadian producers use threefold higher synthetic N fertilizer (2.8 million t (MMT)) in 2014 than in the early 1980's (Dorff and Beaulieu, 2015; FAOSTAT, 2017). An estimated 50% increase in food production is required to sustain projected global demand in the coming 30 years (Gilland, 2006; Ray et al., 2013; FAO, 2016). Increasing production costs and environmental concerns due to inefficient and overuse of industrial N fertilizers are major concerns impeding future sustainable food production (Yadav et al., 1997; Kahrl et al., 2010; Kubota et al., 2017). Increased N use efficiency (NUE) in wheat production systems could be important to sustainably intensify wheat production without adverse environmental impacts on agricultural lands (Garnett et al., 2013).

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[3] *This chapter has been accepted to Crop Science.*

NUE is a complex term covering a range of components influenced by genetics and environmental interactions (Hirel et al., 2007; Xu et al., 2012). Since Moll et al. (1982) coined the term NUE as the ratio of plant output per N input, many studies examining different aspects of NUE have been published. With the rise in the challenges of sustainable intensification of the food production system, the need for further research has increased. Improved NUE is key to the success of the system due to the fact that N fertilizer, which accounted for most (60%) of total global fertilizer consumption in 2016 (FAO, 2016), has caused negative environmental impacts in many intensive agricultural systems in the world (UNEP, 2014). Global NUE has been estimated at around 48%, which indicates the necessity and possibility for improving NUE in current wheat production systems (Lassaletta et al., 2014).

As a complex trait, NUE is the net result of two important components: nitrogen uptake efficiency (NUpE) and nitrogen utilization efficiency (NUtE) (Moll et al., 1982). NUpE is the crop's ability to capture available N in the soil, while NUtE characterizes the assimilation and translocation efficiencies of absorbed N for grain or biomass production. Improvement of NUE through the enhancement of these two components is an attainable challenge in modern wheat breeding programs due to the fact that N assimilation and uptake ability in wheat cultivars has been improved over time, along with increased grain yield regardless of N supply levels (Ortiz-Monasterio et al., 1997; Guarda et al., 2004; Fageria and Baligar, 2005; Barraclough et al., 2010; Cormier et al., 2013).

The contributions of NUpE and NUtE to the genetic variability in NUE have been found variable. Some studies reported greater contribution of NUpE in the total variation of NUE at both high and low N (Le Gouis et al., 2000; Muurinen et al., 2006), while others reported that NUtE accounted for greater genetic variation in NUE under low N levels (Brancourt-Hulmel et al., 2003; Gaju et al., 2011). Ortiz-Monasterio et al. (1997) reported that the relative importance of these two components shifted from NUpE to NUtE as soil N levels increased. These results demonstrate the complexity of traits that control NUE. These traits have not been main breeding objectives, but rather genetic progress resulted from indirect selection for other traits (Ortiz-Monasterio et al., 1997; Sylvester-Bradley and Kindred, 2009; Cormier et al., 2013). Assessment of genetic progress in NUE varies with variety, growing environment and soil N levels. Under four different N fertilizer conditions, spring wheat cultivars bred between 1962 and 1985 in CIMMYT showed + 0.4 to 1.1 % annual increase in NUE (Ortiz- Monasterio et al., 1997). Cormier at al. (2013) also reported + 0.30 to 0.37% genetic gain in NUE between 1985 and 2010 in 195 European modern winter cultivars at two N levels.

Due to a very short growing season, western Canadian wheat breeding programs have prioritized their objective of developing early maturing wheat cultivars along with the main focus on increased grain yield and disease resistance (DePauw and Hunt, 2001; Kamran et al., 2014). During the last 75 years, Canada Western Red Spring (CWRS) wheat has also shown a remarkable improvement in harvest index (HI) due to reduction in plant height, suggesting efficient assimilate partitioning to grain development (Hucl and Baker, 1987). The contribution of introducing mutant alleles of the dwarfing *Rht* genes has been an important aspect of increasing yield in the CWRS wheat class (Flintham et al., 1997; Kamran et al., 2013). In a study investigating genetic variation, Chen et al. (2016) screened a set of 82 Canadian Western Spring Wheat cultivars, belonging to eight different classes, for *Rht*, photoperiod and vernalization response genes, and found that 37 cultivars released after 2000 had 6.9 cm shorter plants than those registered before 2000. They concluded that Canadian wheat breeding programs incorporated dwarfing *Rht* genes alongside desirable combinations of photoperiod and vernalization response genes to make wheat shorter, early heading and (relatively) later maturing, thereby increasing grain yield. This yield increase has successfully been achieved without significantly lowering grain protein concentration. This trend has also been observed in other parts of the world. For instance, simultaneous improvement in grain yield and end-use quality has been achieved over the last century in winter wheat cultivars due to a reduction in plant height and increases in N input (Guarda et al., 2004). The authors also speculated, based on their results, that modern wheat cultivars have genetic potential to improve N uptake and utilization simultaneously in low N conditions. This agrees with the results of Ortiz-Monasterio et al. (1997). The role of specific alleles and/or genes involved in improving NUE in wheat breeding has been investigated for European and American wheat germplasm, wherein the potential impact of flowering time (Bogard et al., 2011; Guttieri et al., 2017) and dwarf stature (Gooding et al., 2012; Loddo and Gooding, 2012; Guttieri et al., 2017) in improving NUE traits discussed.

The introduction of dwarfing genes in wheat resulted in the improvement of lodging resistance under high N conditions (Milach and Federizzi, 2001). These genes likely have a positive impact on NUE traits because the genes involved in controlling plant height and dry matter partitioning, appear to increase N partitioning to the grain (Hedden, 2003). Gooding et al. (2012), however, reported that the effect of the introduction of the dwarfing alleles on the aboveground N accumulation was less than on aboveground dry matter accumulation. This might suggest that dwarfing genes reduce either NUtE or NUpE (Gooding et al., 2012). The negative pleiotropic effect of *Rht* alleles on grain N concentrations was also discussed as a possible direct mechanism for reduced protein besides a dilution effect due to increased grain yield (Gale and Youssefian, 1985). These authors reviewed previous studies and found that *Rht* alleles reduced grain N content without increasing grain yield. The involvement of *Rht* alleles in root architecture, development and proliferation have also been investigated (Siddique et al., 1990; Wojciechowski et al., 2009; Gooding et al., 2012; Bai et al., 2013). These studies suggest a reduction in NUpE due to *Rht* alleles; however, few studies provided information about effects of this gene family on root systems, and it is not sufficient to conclude a relationship between NUE and dwarfing *Rht* alleles (Entz et al., 1992).

Due to readily available low-cost N fertilizers, major breeding programs have generally been conducted under optimum soil N levels. Consequently, genetic grain for important traits in commonly used modern CWRS wheat cultivars may differ between fertilized and low-input systems. This hypothesis has been tested for several traits such as weed competitiveness, plant height, early maturity and soil microbial community by our research group at the University of Alberta, Edmonton, Canada (Mason et al., 2007; Reid et al., 2009; Nelson et al., 2011; Kamran et al., 2014; Pswarayi et al., 2014; Asif et al., 2015). A general conclusion drawn from these studies was that advantageous traits/cultivars for high grain yield under low-input/organic systems differ from those in conventional systems. The increase in grain yield while maintaining grain protein contents in high yielding modern CWRS wheat cultivars may indicate a possibility to select ideal germplasm for improving NUE, although the beneficial alleles or genes related to NUE traits under low-input systems may be lost or limited through selection pressure (Feil, 1997; Hawkesford, 2017). Studies on identification and characterization of variability in wheat traits appear to suggest the presence of significant genotype × N fertilizer interaction effects, and the necessity of evaluating cultivars at different N levels for better selection (Barraclough et al., 2010; Gaju et al., 2011; Cormier et al., 2013; Hawkesford, 2017).

Studies for comparing genetic grain in different management systems can provide beneficial information of breeding progress as well as morpho-physiological and agronomical characteristics in wheat grown in different areas. Numerous studies reported genetic gain in grain yield, dry matter (DM) accumulation and partitioning among old and modern wheat cultivars grown in different geographical regions (Ortiz-Monasterio et al., 1997; Donmez et al., 2001; Brancourt-Hulmel et al., 2003; Guarda et al., 2004). To achieve better NUE in wheat requires efficient utilization of appropriate germplasm in breeding programs, but the information of the genetic progress in NUE in current bread wheat cultivars is limited. Therefore, the objectives of this study were 1) to assess genetic variation for NUE traits in CWRS wheat cultivars, and 2) to examine the change in NUE traits of CWRS cultivars released over the last century.

3.2 Materials and methods

This study was conducted in 2013, 2014 and 2015 under two levels of soil nitrogen (high: 200kg ha^{-1} with N fertilizer, low: ~50kg ha^{-1} without N fertilizer). Each year, the trial was conducted on a black Chernozemic soil (Spiess, 2015) in two locations - the University of Alberta Edmonton Research Station (ERS) (53°49’N, 113°55’W) and St. Albert Research Station (SARS) (53°49’N, 113°66’W) in Alberta, Canada. The long-term average annual precipitation excluding snowfall is 340 mm in the Edmonton area, and more than 90% of precipitation occurs during wheat growing season between April and September (Alberta Agriclture and Forestry, 2015). The average frost-free period of this area in last 30 years is 115 to 125 days (Alberta Agriclture and Forestry, 2015). The monthly temperature and precipitation during this study are presented in Figure 1. The experimental sites were managed with four-year rotations in the following order: canola-triticale (× *Triticosecale* Wittmack), pea (*Pisum sativum* L.) mixture (or only pea) for silage-wheat-barley (*Hordeum vulgare* L.) silage at ERS and canola-pea-wheat-barley at SARS. Prior to seeding, the initial soil nutrition levels were measured colorimetrically using a centrifugal analyzer after a potassium chloride extraction (Dorich and Nelson, 1983; Qian et al., 1994) every year at each location (Table 3-1). These initial soil N levels were used as a residual soil N (soil N) for calculations of NUE traits. In the high N treatment, the amount of N fertilizer required was calculated every year based on pre-seeding residual soil N and applied urea at seeding to achieve the total soil N levels of 200kg ha^{-1} to meet a local recommendation rate for optimal grain yield (McKenzie et al., 2013). No N fertilizer was applied to the low N treatment. Thus soil residual N was the only source of N for calculation of NUE traits. Weeds were controlled occasionally using Curtail^{TM} M according to the manufacture instruction. Fifteen genotypes were selected as representative samples of CWRS germplasm released in Western Canada from 1910 to 2010 (Table 3-2). Three of these cultivars namely, CDC Go, Carberry and Superb carry the semi-dwarfing mutant allele *Rht-B1b*; Harvest carries mutant allele *Rht-D1b,* whereas the rest carry wild-type alleles *Rht-B1a* and *Rht-D1a* at *Rht-1* loci.

Each field experiment for this study was laid out in a randomized incomplete block design (3 incomplete blocks per replication) with four-replications. The dimensions of each plot were 2 ×1.38 m with six rows spaced 23 cm apart. Seeds were planted using Pabro low disturbance plot seeder (Swift Current, SK, Canada) with the target planting density of 300 viable seeds m^{-2}. Agronomic data on days to flowering (flowering), and maturity, plant height (height) and lodging score (lodging) were recorded in-field. Flowering was recorded when 50% of the spikes reached anthesis. Maturity was recorded when 50% of peduncles turned yellow. Lodging was recorded at maturity with subjective scoring according to the severity of area and angle of lodging. The score ranged from 0 (no lodging) to 5 (entire plot with 90 degrees lodged).

Stem dry matter (StemDM) was obtained by hand harvesting plants in a 25 × 25 cm quadrat from each plot after maturity. Grain yield was obtained after harvesting each plot using a Wintersteiger Nursery Master Elite plot combine (Wintersteiger Inc., Salt Lake City, UT, USA). Grain and stemDM samples were stored in a dryer at 40°C for at least 24 h for stem DM and 48 h for grain yield. About 50g each of grain and stem samples were ground into powder for N estimation using a Cyclone Lab sample mill with 1 mm screen (Model 3010-030, UDY Corporation, Fort Collins, Co, USA). N contents of the ground samples were determined by combustion analysis using a LECO TruSpec CN Carbon/Nitrogen Determinator 200-288 (Leco Corporation, Saint Joseph, MI, USA). Obtained grain and stem N contents (GNper and SNper) were further used to determine total aboveground, grain and stem N yields per hectare (TotalNtha, GNtha and SNtha, respectively). Grain protein contents were calculated with a nitrogen to protein factor of 5.26 and the value of grain N content obtained from the LECO analyzer (Tkachuk, 1969).

The soil N level at SARS in 2014 was much higher than that of the other years/locations (Table 3-1) and the level was above the locally recommended amount (200kg ha^{-1}) without N fertilization. Therefore, we removed the data of the low and high N treatment at SARS in 2014 from the analysis.

NUE traits were calculated as proposed by Moll et al. (1982) using the following equations:

$$NUE = \frac{Grain\ \ yield}{Available\ \ N\ \ (low{:}soil\ \ residual\ \ N, high{:}soil\ \ residual\ \ N+N\ \ fertilizer)} \qquad (1)$$

$$NUtE = \frac{Grain\ \ Yield}{Total\ \ N_{tha}\ \ (SN_{tha} + \ GN_{tha})} \qquad (2)$$

$$NUpE = \frac{TotalNtha\ \ (SNtha + GNtha)}{Available\ \ N\ \ (low\text{: }soil\ \ residual\ \ N,\quad high\text{:}\,soil\ \ residual\ \ N + N\ \ fertilizer)} \tag{3}$$

We also calculated harvest index (HI) and nitrogen harvest index (NHI) using the following equations:

$$HI = \frac{Total\ \ Grain\ \ Yield}{Total\ \ Aboveground\ \ Biomass} \tag{4}$$

$$NHI = \frac{Grain\ \ Nitrogen\ \ (GNtha)}{Total\ \ \ Nitrogen\ \ (TotalNtha)} \tag{5}$$

In order to partition the total variation into different sources, analysis of variance (ANOVA) for individual N treatment was initially performed using GLM procedure in SAS version 9.4.1 (SAS Institute Inc. Cary, USA). Data for the agronomic, NUE traits were analyzed using the following model.

$T_{iklm}=\mu + E_i + G_k + R(E)_{il} + B(RE)_{ilm} + EG_{ik} + e_{ijklm}$ (6)

Where, T is the observation of the *k*th genotype G in the *i*th environment E in the *m*th block B within *l*th replication R in the environment. μ is the general mean and *e* is residual error term. In the analysis, genotypes were considered as fixed effects, whereas, environments (year × location), replications within environments, blocks within the environment and their interactions were treated as random effects.

Then, a combined ANOVA was conducted for the agronomic and NUE traits to test N treatment using the following model.

$T_{ijklm}=\mu + E_i + M_j + G_k + R(E)_{il} + B(RE)_{ilm} + EM_{ij} + EG_{ik} + MG_{jk} + EMG_{ijk} + e_{ijklm}$ (7)

Where, T is the observation of the *k*th genotype G in the *i*th environment E and *j*th management treatment M (high N and low N) in the *m*th block B within *l*th replication R in the environment. μ is the general mean and *e* is residual error term. In the analysis, genotypes, management treatments, and their interactions were considered as fixed effects. Environments, replications within the environments, blocks within environment and their interactions were treated as random effects. Significance levels for fixed and random effects were determined by PROC MIXED and PROC GLM, respectively. Cultivar LSMEANS for each trait were estimated by each N fertilizer treatment using PROC MIXED in SAS. Genotypes were treated fixed, whereas environment and its interaction were treated as random effects.

The effect of *Rht* alleles on different traits was evaluated using model (6) with PROC MIXED of SAS. To evaluate the response of these genes to N fertilizer, the analysis was conducted for each N fertilizer treatment individually. Genotypes were treated as fixed effect; environment and its interaction with genotypes were modeled as random effects.

Pearson correlation coefficients among all traits were estimated using the mean values of traits in SAS. Simple linear regression models were used to estimate genetic progress in agronomic and NUE traits over time using PROC REG in SAS. The four semi-dwarf wheat cultivars were excluded from the regression analysis to avoid any confounding effect of *Rht* alleles. The % change in a trait with year was calculated as the ratio of the coefficient of year to the LSMEAN of AC Barrie, which is often used as a reference cultivar.

3.3 Results

In combined analyses, environment contributed the most to the total sums of squares of the studied traits except grain yield, HI, lodging, Total Ntha, GNtha, NUE and NUtE; however, the effect of environment was statistically significant for only few of these traits (Table 3-3). The effect of N fertilization was significant (*$P<0.01$*) for maturity, grain yield, HI, lodging, TotalNtha, GNtha, TotalNper, SNper, NUE and NUpE. Cultivars differed for all traits except SNper and NUpE and contributed the most variation in grain yield, HI, lodging and NUtE (Table 3-3). Cultivars behaved differently under the two N treatments for all traits but flowering, maturity, height, TotalNtha, SNper and NUpE (Table 3-3). The interaction effect of E×M was significant for most of the traits but its contribution in the total phenotypic variation was greater for TotalDM, TotalNtha, SNtha, StemDM, NUE and NUpE. The effect of G×M interaction was also significant for several traits but its contribution was greater for grain yield, protein, HI, lodging, StemDM, NHI and NUtE. The contribution of G×E interactions was larger than that of genotypic source of variance for SNper and StemDM.

Overall, N fertilization significantly altered most of the traits studied (Table 3-3). Genotypes significantly matured later when fertilized. Plant height increased from 88 cm to 94 cm with N fertilization. Grain yield significantly (*$P<0.01$*) increased from 2.3 to 3.3 t ha^{-1} (68 %) with N fertilization (Table 3-3). HI and lodging scores increased from 0.28 to 0.35 and 0.12 to 0.28, respectively. TotalNtha, GNtha, SNtha and TotalDM also significantly increased in the studied genotypes when fertilized (Table 3-3). On the contrary, N fertilization decreased NUE and NUpE from 59 to 17.1 and 3.0 to 0.8, respectively. Time to flowering, height, grain protein content, SNtha, TotalDM, StemDM, NHI and NUtE of the studied genotypes didn’t change with N fertilization (Table 3-3). Under high N, GNtha increased mainly due to increased grain yield rather than increased grain N concentration (i.e. protein).

Cultivars differed for the effect of N fertilization (Tables 3-4, 3-5). CDC Stanley, CDC Kernen and CDC Go had the largest grain yield under high N while CDC Teal, Marquis and Sinton yield the highest in low N. For HI and NHI, CDC Teal, Carberry, and Harvest were the largest under low N, while CDC Stanley, Carberry, and Unity exhibited the highest for these two trait values under high N treatment. The cultivar rankings between NUE and NUtE were similar under the same N treatment.

Estimates of correlations of measured traits from each N treatment were positive between grain yield and all NUE traits in high N (Table 3-6). Negative correlations between protein contents and HI were found only in high N treatment. Stem DM showed negative correlations with NUE and NUtE at high N. NUpE was positively correlated with TotalDM in both N treatments.

Height reducing *Rht* alleles affected agronomic and NUE traits of the studied genotypes irrespective of N treatment, but the effects were more pronounced at high N (Tables 3-7, 3-8). Cultivars carrying the semi-dwarfing allele *Rht-1b* were early flowering (53.3days) and late maturity (95.3 days) compared to cultivars with *Rht-1a* (54.5 days and 94.2 days respectively) in high N. The semi-dwarfing cultivars were also shorter (84cm) with higher grain yield (3.78 t ha^{-1}) than cultivars with *Rht-1a* (height: 97 cm, grain yield: 3.19 t ha^{-1}) under high N treatment. The *Rht-1b* allele did not alter grain yield under the low N treatment (Table 3-7). Protein content was statistically different between cultivars carrying different *Rht-1* alleles only in high N (*Rht-1a*: 15.8%, *Rht-1b*: 15.4%). For NUE traits, cultivars carrying *Rht-1b* allele had significantly greater NHI, NUE, and NUtE in high N treatment; however, this was only the case under the low N condition for NHI and NUtE (Table 3-8). N fertilization decreased NUE and increased NUtE irrespective of wild and mutant *Rht* genes.

Due to the significant N fertilizer effect on several measured traits, the effect of registration year on agronomic and NUE traits was separately tested in the two N treatments. The registration year was regressed over the traits studied (Figure 3-2). Most of the important yield traits exhibited changes (either increase or decrease) over time in the high N treatment, while only plant height changed significantly with year of registration under the low N treatment (Table 3-10). Grain yield increased by 0.35 % year^{-1} and plant height decreased by 0.16% year^{-1} in the high N treatment. The changes in grain yield of the studied cultivars over time were not significant in the low N treatment. NUE and NUtE significantly increased by 0.34 % and 0.3 % year^{-1}, respectively only under the high N treatment. HI and NHI also increased under the high N treatment.

3.4 Discussion

Fifteen CWRS wheat cultivars were grown in six environments to evaluate genetic variation for NUE traits. We observed genetic variation for NUE and NUtE in the studied cultivars that reflect the genetic progress in CWRS class particularly under high N condition. Significant genetic and G×M interaction variation for grain yield, protein, HI, NHI, and NUtE reflected the diverse response of CWRS wheat to N fertilization. The effect of *Rht* alleles was significant under high N, contributing to increased NUE, NHI and NUtE. Significant genetic progress in grain yield and NUE traits observed under high N was mainly attributed to increased HI.

3.4.1 Genetic variation for NUE traits

The present study highlighted the genetic variation of NUE traits within the CWRS class. The G × E and G × M interaction effects showed a distinct pattern. There were highly significant G × E interaction effects on traits associated with vegetative growth (i.e. flowering, maturity, and height), while G × M interaction was highly significant for traits related to reproductive and post-reproductive development (i.e. grain yield, protein, HI, NHI, NUE, and NUtE). StemDM is one of the few traits that is significantly affected by G × E and G × M interactions. Seasonal precipitation, which fluctuates from year to year, is one of the major determinants of grain yield in Western Canaday. Accumulated precipitation during the vegetative growth stage (i.e. from May to June) in 2015 was only 30% and 36% of that in 2013 and 2014, respectively. Monthly average temperatures were relatively consistent among years in both locations except for April. In 2013, monthly average temperature in April was lower than the 30-year average temperature (0.44°C at ERS and -0.47°C at SARS compared to 5.3°C as 30-year average). The shortage of rainfall coupled with an annual variation in temperature during germination to double ridge and grain filling stages likely affected the response of CWRS wheat cultivars for the studied vegetative traits, resulting in significant G×E interaction as previously reported (Clarke et al., 1990; Guttieri et al., 2017). The high percentage contribution of M × E interaction in this study might be due to the lower moisture conditions in 2015 that caused the lower NUpE and mineralization of soil organic N, leading to consequent lower TotalNtha especially in the high N treatment. The soil moisture and N levels could be main factors in the variation of NUpE. Under drought conditions, although nitrate leaching and ammonia volatilization are rare events, immobilization and low mobility of N in soil solution could occur, resulting in the low amount of plant available N (Kubota et al., 2017). In addition, drought promotes deeper root growth instead of root growth in the shallower soil layers where plant available N is generally adequate (Barraclough et al., 1989).

The sum of G and G × M interaction was the largest source of variation for grain yield, HI, and NUtE, suggesting that development of grain and dry matter partitioning are more genotype dependent at high N condition in the absence of or in minimal levels of biotic and abiotic stresses (associated with the high-N treatment). Two winter wheat studies estimated the relative contribution of variance source for agronomic and NUE traits (Cormier et al., 2013;

Guttieri et al., 2017). Cormier et al. (2013) reported that the proportions of G, G × E and G × M was 60%, 36% and 5% for grain yield and 63%, 30% and 7% for NUtE in France, whereas Guttieri et al. (2017) reported these proportions to be 35% 62% and 0% for grain yield and 43%, 52% and 0% for NUtE in the USA. We estimated the proportion of variance sources including fixed and random terms in the model. Thus our values are not fully comparable to their results. However, when we re-calculated the relative contribution of variance sources of the genetic component of variance, our G, G × E, and G × M for grain yield were 56% 13% and 31%, respectively and 48%, 29% and 23% for NUtE, respectively. The major difference between our results and results of previous two studies is the large contribution of G × M interaction. One possible reason could be the greater quantity of N fertilizer in the high N treatment in our study (200 kg ha^{-1}) compared to the other two studies (100 to 150 kg ha^{-1}). Another reason may be the presence of large gaps (120 to 210 kg ha^{-1}) between two N treatments in our study relative to the other two (50 to 70kg). We could also expect large variation due to difference in growing seasons and germplasm tested. The previous studies used winter wheat as opposed to spring wheat in our study. These differences may have resulted in different interactions among studies. Theoretically, NUpE should be lower than 1.0 because it is estimated as the ratio of TotalNtha and the total plant available N. Above 1.0 mean values for NUpE under the low N treatment should be attributed to estimation errors of N availability derived from aerial N deposition, mineralization of residual soil N and organic matter over the wheat growing season. We estimated and used plant available N based on residual soil N at sowing plus applied N fertilizer. From a technical stand point, this estimation proxy was verified by Bingham et al. (2012) when comparing genotype rankings.

Maintaining grain protein content is as critical as improving grain yield potential for CWRS wheat to maintain superior end-use quality of bread-making flour. However, simultaneous improvement of these two traits is difficult due to negative correlation (Slafer et al., 1990; Simmonds, 1995; Feil, 1997). N dilution by increased carbon composition of grain (Acreche and Slafer, 2009) and internal energy cost balance between carbon and N (Munier-Jolain and Salon, 2005) have been proposed as probable explanations for this negative relationship. The present study demonstrated that application of N fertilizer increased grain yield, HI, and SNper but not protein and NHI, indicating that the dilution theory may be explained more as a factor limiting grain N content. Nevertheless, the presence of the significant G×F interaction for protein and NHI further suggests that it may be possible to improve grain protein together with NUE by selecting cultivars with better NHI. We also analyzed non-grain N content in our study using 50mg of the subsampled ground stem that included culms, leaves, rachis and glumes and did not take into account the variation of N content for each vegetative organ in our calculation and analysis.

Although improvements in NUtE and NUpE either alone or together are critical to increase NUE, these two traits are complex and greatly affected by environment. Wheat development is subject to water stress in Western Canada. Precipitation during vegetative growth in 2015 was very low in our study. This led to lower NUpE in that year and created large G × E interaction variation. We observed large variation for genetic and G× F interaction among the total source of variance for NUtE but no variation for N fertilizer treatment, suggesting the potential of efficiently improving NUtE in the CWRS class according to soil N levels.

3.4.2 Genotypic differences for NUE traits

In this study, a significant contribution of G × M interactions was observed for grain yield, NUE, and NUtE, indicating variation under high N response to NUE traits in tested cultivars (Appendix 3-1). In other words, cultivars performing well for these traits in high N may not perform well under low N conditions. CDC Teal, Carberry, and Harvest had the largest HI and NHI under low N, while CDC Stanley, Carberry, and Unity exhibited the highest HI and NHI under high N, resulting in the highest NUtE. Cultivars Carberry, CDC Go, and Superb possessed the gibberellin insensitive semi-dwarfing *Rht-B1b* allele. These three semi-dwarf cultivars showed higher grain yield and NUE under high N treatments but showed inconsistent results for these traits in low. Interestingly, CDC Go and Superb yielded the largest TotalNtha, but Carberry had one of the lowest TotalNtha under high N treatment. Superb, CDC Go, and AC Barrie also produced relatively large TotalDM and had the highest NUpE under high N. Contrarily, Carberry had the smallest TotalDM production with low NUpE under high N treatment. Studies have reported that the degree of TotalDM (N demand) is a major factor to control N uptake in high N conditions (Singh and Arora, 2001; Gastal and Lemaire, 2002). Significant positive correlations between TotalDM and NUpE in our study agree with these results.

Dry matter, and N partitioning and remobilization are important factors influencing final grain yield and protein contents. Dry matter and N for grain development are derived from pre- and post-anthesis sources (Dupont and Altenbach, 2003). Pre- and post-anthesis N uptake period is separated by date of flowering, at which time vegetative growth ceases and accumulated dry matter and N divert to reproductive organs, while N absorption and carbon fixation progress in active roots and leaves. The early flowering genotypes may have an advantage to uptake and translocate more N for grain development due to longer duration of the grain-filling stage under high N conditions. Conversely, traits associated with a longer vegetative period and a great N storing capacity might improve NUtE. The CWRS wheat cultivars we tested showed variation in flowering and maturity time. However, the three semi-dwarf cultivars Carberry, CDC Go and Superb that were early flowering and later maturing in high N treatments showed different NUpEs. The two highest yielding cultivars CDC Stanley and CDC Kernen had longer vegetative stage (0.6 and 2 days longer than the average, respectively) and higher NUtE in high N treatment.

However, we did not find significant correlations between pre-/post anthesis duration and NUE traits under high N. These results did not provide clear insights into the role of *Rht-1b* genes and pre-, post-anthesis durations in NUE. However, total dry matter production was significantly associated with N uptake capacity. Since we did not assess pre- and post-anthesis N uptake, the contribution of the rate of N uptake before and after anthesis associated with dry matter production is not clear. Previous studies have shown genotypic variability in the post-anthesis uptake of N (Cox et al., 1985; Monaghan et al., 2001). Up to 50% of the total N was found taken up after anthesis (Spiertz and Ellen, 1978; Van Sanford and MacKown, 1987). Moreover, post-anthesis N uptake has been found more strongly related to grain yield and grain N than to grain protein content (Cox et al., 1985). The influence of N remobilization on N uptake is also negligible. Therefore, investigating indirect mechanisms of dwarfism on root morphological traits, aboveground biomass production, functional and N metabolic activities and N sink - source interactions for NUpE may add valuable information for further improvement of NUE (Gooding et al., 2012).

3.4.3 Correlations among traits

Correlations between grain yield and NUE traits were expected to exhibit stronger association as grain /grain N yields are numerators in the calculation of NUE traits. In the present study, grain yield exhibited positive correlations for all NUE traits (i.e. NUE, NUtE, and NUpE), while there were strong negative correlations between grain yield and grain protein in both N treatments. We also observed significant positive correlations of NUtE with HI in both N treatments while there was a negative correlation between NUtE and StemDM under both N treatments. These two correlations indicated that increased partitioning of carbon and N assimilates to grain development at the expense of vegetative parts with N fertilization is associated with increased NUtE. Since negative correlation of HI with protein was found only in high N, increased N status in wheat by N fertilization resulted in more carbon assimilate partitioning to grain development than N assimilate partitioning from vegetative parts.

Nitrogen remobilization from stored N, and N uptake during post-anthesis are the two main sources of N for grain storage protein synthesis (Dupont and Altenbach, 2003). About 69 to 95 % of N for protein synthesis was derived from stored N (Sanford and MacKown, 1986; Palta and Fillery, 1995). Therefore, duration of the vegetative stage as well as the capacity of root to absorb N during that period are critical for further N remobilization for grain protein synthesis. In the present study, we found positive correlation only between NUpE and flowering (r=0.8) in low N. This indicated little or no importance of duration of the vegetative stage in improving NUpE. NUpE seems to be affected by soil moisture, soil N availability besides the characteristics of rapid and vigorous root growth, and capability of exploring a large area of soil (Palta et al., 2011). Genotypic variation for assimilate investments into roots has an impact on aboveground traits and uptake efficiency (Wojciechowski et al., 2009). Therefore, detailed physiological studies about carbon translocation and metabolism are needed to explain underlined mechanisms for improved NUpE. This study was not designed to investigate N and carbon assimilation and partitioning during pre- and post- anthesis as well as water availability. Therefore, further studies are needed to elucidate the mechanisms of NUpE.

NUtE should be a reliable criterion for selecting efficient cultivars in N use among CWRS class because of large genetic and G×F interaction variations. The magnitude and pattern of correlations between grain yield and NUE traits were generally similar between N treatments except NUpE that was positively correlated with TotalDM in both N treatments. Direct selection for NUE traits has not been the main subject of wheat breeding. Moreover, cultivar responses for NUtE and NUpE to N fertilizer were different according to the applied N levels, leading to variation in NUE under different N conditions (Ortiz-Monasterio et al., 1997). In wheat breeding, cultivars have been commonly selected under optimal/ high N conditions, suggesting that genetic progress under low-N fertility has been the result of indirect selection. This likely caused the significant G × M interaction as several studies reported the significant impact of G × M interaction (Ortiz-Monasterio et al., 1997; Barraclough et al., 2010; Górny et al., 2011; Cormier et al., 2013).Therefore, genotypic variation and cultivar choice under different N levels should be taken into account in breeding for improved NUE.

3.4.4 Genetic grain for NUE traits during the last century

The present study demonstrated that significant genetic progress for grain yield and NUE has been made under high N fertility in CWRS wheat cultivars released from 1910 to 2009 (Figure 3-2). Regression analysis showed that grain yield, HI, NHI, NUE, and NUtE increased, while plant height and grain protein decreased over time in the studied wheat cultivars under high N (Table 3-10). Genetic gain in these traits was 0.349% year^{-1} and 0.34% year^{-1}, respectively under the high N condition (p<0.01). By contrast, the genetic progress in grain yield and NUE was not statistically significant under the low N treatments. The larger genetic gain in grain yield and NUE compared with plant height may be due to the small number of tested cultivars with a higher number of those registered relatively in recent years. Such significant trend of genetic gain in grain yield was also observed by Pswarayi et al. (2014) who studied 27 CWRS wheat cultivars released in the last 114 years and concluded that improvement in disease resistance and producer involvement in breeding projects since the 1980's were the major reasons for this improvement. The patterns of genetic gain in these traits also agreed with other studies, suggesting that modern wheat cultivars have been bred in optimal soil N levels, thus outperform in such conditions (Brancourt-Hulmel et al., 2005; Muurinen et al., 2006; Pswarayi et al., 2014). Considering similar experimental conditions (location, environment, experimental methods and studied cultivars) of the present study and those of Pswarayi (2014), it may be concluded that genetic gain in NUE traits has increased in CWRS class over the last century.

Considering NUE as an integrated trait, its improvement could be the result of simultaneous alteration of several associated components. The genetic improvement in NUtE (0.3% year^{-1}) corresponded to that of grain yield (0.35 % year^{-1}) in the high N treatment. Several studies concluded that genetic gains in wheat grain yield over the last century were associated with increased HI (Gale and Youssefian, 1985; Waddington et al., 1986; Calderini et al., 1995; Sayre et al., 1997). However, due to the fact that grain yield in CWRS wheat cultivars significantly improved without significant reduction in grain protein content (DePauw et al., 2007), a significant genetic gain in NHI (0.244% year^{-1}) under high N in this study, which may be due to the effect of post-N uptake and subsequent improvement of NUtE as previously reported by Cormier et al. (2016), is worth noting. This explains how modern CWRS breeding programs have concurrently improved grain yield and NUE.

3.5 Conclusion

In the CWRS wheat class, modern cultivars generally exhibited greater NUE and NUtE; however, those rates of genetic gain were greater under high N treatment than the low N treatment. This is probably because the current genetic progress in NUE has been achieved due to direct selection for grain yield under optimum N conditions. This has improved dry matter and assimilates partitioning (i.e., HI and NUtE) as opposed to grain N concentration and N uptake. Additional improvement of NUE through increased NUpE could be possible but the large variation in E×F, probably due to low precipitation environments, may hinder enhancement through indirect selection. Among tested cultivars, the semi-dwarf cultivar, Carberry had high HI, NHI, and NUtE in high N treatment, suggesting it as possible donor for further improving NUE. However, Carberry was low in NUpE probably due to its low dry biomass production or probably to its root inability to efficiently uptake soil N. The other semi-dwarf cultivars, CDC Go and Superb exhibited higher NUpE and large total dry biomass. Further studies are required to fully elucidate the mechanisms underlying dwarfism, pre- and post-anthesis duration, dry matter and N accumulation pattern for improved NUE in wheat. In the meantime, future breeding programs should aim to improve NUE through optimizing N acquisition by a well ramified root system and N partitioning to grain using wheat genotypes that have better NUtE and NHI such as Carberry and those that exhibit large dry mass production in target environments.

3.6 Acknowledgments

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3.7 Tables

Table 3-1. Soil properties at 0 to 30 cm depth of the experimental sites at Edmonton Research Station (ERS) and St. Albert Research Station (SARS), Alberta in 2013, 2014 and 2015 at pre-seeding seasons.

	2013				2014				2015			
	ERS[a]		SARS[b]		ERS		SARS		ERS		SARS	
	High N	Low N	High N	Low N	High N	Low N	High N	Low N	High N	Low N	High N	Low N
NO_3-N (kg/ha)	54.9	38.1	72.9	26.9	37.0	39.2	235.4	242.1	23.5	54.9	47.1	82.9
P (kg/ha)	62.8	135	56.0	51.6	22.4	33.6	727	807	78.5	135	48.2	42.6
K (kg/ha)	1333	898	268	382	631	684	3571	3280	736	993	470	277
SO_4-S (kg/ha)	33.6	13.5	24.7	19.1	15.7	16.8	93.0	67.3	13.5	32.5	25.8	30.3
pH	6.6	6.6	7.6	7.6	6.3	6.1	8.1	8.1	6.4	6.4	7.6	7.6
EC (dS/m)	0.57	0.31	0.48	0.55	0.39	0.41	0.52	0.4	0.39	0.8	0.78	0.83
OM (g kg^{-1})	117	152	93	104	105	113	75	73	144	NA[c]	NA	NA

[a] Edmonton research station, [b] St. Albert research station, [c] Not obtained. We excluded the data obtained in low N at SARS 2014 (the location of grey colored) from analyses due to the excessive soil N level .

Table 3-2. Description of fifteen Canada Western Red Spring wheat cultivars tested during 2013 to 2015 in northern-central Alberta.

Genotype	**Year of Release**[a]	***Rht-B1***[a]	***Rht-Da***[a]
Marquis	1910	*Rht-B1a*	*Rht-D1a*
Garnet	1925	*Rht-B1a*	*Rht-D1a*
Red Bobs	1926	*Rht-B1a*[b]	*Rht-D1a*[b]
Park	1963	*Rht-B1a*	*Rht-D1a*
Sinton	1975	*Rht-B1a*[b]	*Rht-D1a*[b]
Katepwa	1981	*Rht-B1a*	*Rht-D1a*
CDC Teal	1991	*Rht-B1a*	*Rht-D1a*
AC Barrie	1994	*Rht-B1a*	*Rht-D1a*
Superb	2000	*Rht-B1b*	*Rht-D1a*
Harvest	2003	*Rht-B1a*	*Rht-D1b*
CDC Go	2004	*Rht-B1b*	*Rht-D1a*
Unity	2007	*Rht-B1a*	*Rht-D1a*
Carberry	2009	*Rht-B1b*	*Rht-D1a*
CDC Kernen	2009	*Rht-B1a*	*Rht-D1a*
CDC Stanley	2009	*Rht-B1a*	*Rht-D1a*

[a] Chen et al., 2016, [b] Iqbal et al., unpublished data.

Table 3-3. Relative contribution to the total sum of squares (SS) and the level of significance of source of variance for 19 traits[a] of 15 Canada Western Red Spring Wheat at two N levels during 2013-15.

Trait	Units	By N treatment		Source of Variance						
		Mean		E[b]	M[c]	G[d]	E*M	G*E	G*M	G*E*M
		Low N	High N	% contribution to the total SS						
Flowering	days	54.6	54.1	61.6 ***	0.184	9.6 ***	0.4 ***	3.3 ***	0.2	1.0 **
Maturity	days	91.3	94.5	66.0 ***	0.631 *	7.3 ***	0.6 ***	2.3 ***	0.2	0.9 **
Height	cm	88.3	93.6	32.6 *	0.8831	19.2 ***	2.7 ***	3.0 ***	0.2	0.6
Grain yield	t ha^{-1}	2.3	3.3	8.4	9.8819 **	13.5 ***	2.3 ***	3.1	7.5 ***	2.7 ***
Protein	%	15.4	15.7	21.5 *	0.8753	7.0 ***	1.8 ***	7.3 *	5.2 ***	4.6 **
HI	% DM	0.29	0.4	7.2	3.08 *	14.6 ***	1.7 **	6.8	9.7 ***	5.8
Lodging	0-5	0.12	0.28	1.2	0.34 **	34.5 ***	0.7	7.5	4.3 ***	4.8
TotalNtha	kg ha^{-1}	114	160	5.1	8.15 **	3.1 **	8.3 ***	4.1	1.4	2.8
GNtha	kg ha^{-1}	61	92.8	7.7	11.99 **	11.0 ***	2.4 ***	2.6	5.6 ***	2.4 ***
SNtha	kg ha^{-1}	52	67.5	9.4	0.97	6.1 ***	7.8 ***	6.6	5.1 ***	5.7
TotalNper	%	1.42	1.6	11.5	4.41 **	6.9 ***	1.9 ***	5.4 *	3.9 ***	3.1
SNper	%	0.89	1.0	21.6 **	1.55 **	3.0	0.8 *	7.7 **	0.6	3.6
TotalDM	t ha^{-1}	8.32	9.9	13.1	1.65	3.2 *	9.6 ***	5.9 *	2.7 ***	3.5
StemDM	t ha^{-1}	6.06	6.6	11.6	0.08	6.4 ***	8.1 ***	7.0 *	6.2 ***	4.1
NHI	% N	0.55	0.6	16.1	1.68	13.4 ***	1.3 **	6.9	7.8 ***	6.7 *
NUE	t ha^{-1}	59.0	17.1	10.9	12.37 **	1.4 ***	6.8 ***	1.1	0.6 **	0.9 ***
NutE	t Dm t^{-1} N	20.1	21.1	11.1	0.99	15.9 ***	0.8	7.7	9.5 ***	7.0 **
NupE	% N	3.01	0.8	12.7	12.58 **	0.4	8.6 ***	0.9	0.3	0.8 **

****P* value <0.001, ***P* value <0.01, **P* value <0.05, No asterisk indicate non-significant *P* value. [a] GNtha: grain N yield hectare-1, HI: harvest index, NHI: nitrogen harvest index, NUE: nitrogen use efficiency, NupE: nitrogen uptake efficiency, NutE: nitrogen utilization efficiency, SNtha: stem nitrogen yield hectare-1, StemDM: stem dry matter; SNper: stem nitrogen percentage, TotalNtha: total nitrogen yield hectare-1, TotalNper: total nitrogen percentage, [b] environment, [c] nitrogen fertilizer treatment, [d] genotype.

Table 3-4. Least squares means for agronomic traits[a] of 15 Canada Western Red Spring wheat genotypes under low N treatment during 2013 to 2015 in northern-central Alberta.

Genotype[b] (Year of registration)	Grain yield t ha^{-1}	Flowering days	Maturity days	Height cm	Protein %	HI % DM	TotalNtha kg ha^{-1}	StemDM t ha^{-1}	TotalDM t ha^{-1}	NHI % N
CDC Teal (1991)	2.54 (1) [c]	55 (5)	90 (12)	88 (8)	14.8 (15)	0.32 (1)	112 (10)	5.5 (13)	8.0 (9)	0.58 (3)
Marquis (1910)	2.45 (2)	58 (1)	95 (1)	105 (1)	15.1 (11)	0.29 (8)	121 (1)	6.2 (6)	8.7 (5)	0.54 (8)
Sinton (1975)	2.40 (3)	56 (3)	93 (5)	95 (4)	15.3 (10)	0.30 (5)	120 (3)	6.5 (4)	8.9 (3)	0.56 (4)
Harvest (2003)	2.40 (4)	53 (14)	88 (14)	81 (13)	15.6 (5)	0.32 (2)	110 (12)	5.3 (14)	7.7 (14)	0.60 (1)
Superb (2000)	2.38 (5)	54 (9)	94 (3)	82 (12)	15.0 (13)	0.31 (4)	118 (6)	5.9 (9)	8.3 (8)	0.55 (7)
CDC Stanley (2009)	2.34 (6)	55 (6)	91 (7)	84 (11)	15.0 (14)	0.27 (11)	119 (5)	6.7 (2)	9.1 (2)	0.53 (11)
AC Barrie (1994)	2.27 (7)	56 (4)	93 (6)	87 (9)	15.4 (9)	0.28 (10)	117 (7)	6.2 (7)	8.4 (7)	0.53 (12)
CDC Go (2004)	2.26 (8)	54 (10)	91 (10)	77 (14)	15.5 (7)	0.29 (9)	112 (9)	5.7 (12)	8.0 (10)	0.55 (5)
CDC Kernen (2009)	2.25 (9)	56 (2)	94 (4)	88 (7)	15.5 (8)	0.27 (12)	119 (4)	6.5 (3)	8.8 (4)	0.53 (9)
Red Bobs (1926)	2.21 (10)	55 (8)	90 (11)	99 (2)	15.1 (12)	0.29 (7)	116 (8)	6.4 (5)	8.6 (6)	0.53 (10)
Unity (2007)	2.21 (11)	54 (11)	91 (8)	87 (10)	15.5 (6)	0.25 (14)	120 (2)	6.9 (1)	9.1 (1)	0.51 (15)
Park (1963)	2.18 (12)	53 (13)	89 (13)	92 (5)	15.6 (4)	0.29 (6)	112 (11)	5.8 (11)	8.0 (13)	0.55 (6)
Carberry (2009)	2.18 (13)	53 (12)	94 (2)	74 (15)	15.7 (3)	0.32 (3)	106 (14)	5.2 (15)	7.4 (15)	0.59 (2)
Garnet (1925)	2.07 (14)	52 (15)	86 (15)	96 (3)	15.7 (2)	0.26 (13)	109 (13)	5.9 (10)	8.0 (12)	0.53 (13)
Katepwa (1981)	1.82 (15)	55 (7)	91 (9)	91 (6)	15.9 (1)	0.24 (15)	101 (15)	6.2 (8)	8.0 (11)	0.52 (14)
Ovweall mean	2.3	54.6	91.3	88.3	15.4	0.3	114	6.1	8.3	0.5
Standard error	0.28	2.30	4.31	8.64	0.42	0.03	12	0.91	1.11	0.04

[a] HI: harvest index, N: nitrogen, NHI: nitrogen harvest index, StemDM: stem dry matter, TotalNtha: total nitrogen yield hectare,

[b] Arranged in descending order of grain yield, [c] Numbers in parentheses indicate descending orders of each cultivar in each trait.

Table 3-5. Least squares means for agronomic traits[a] of 15 Canada Western Red Spring wheat genotypes under high N treatment during 2013-in northern-central Alberta.

Genotype[b] (Year of registration)	Grain yield t ha^{-1}	Flowering days	Maturity days	Height cm	Protein %	HI % DM	TotalNtha kg ha^{-1}	StemDM t ha^{-1}	TotalDM t ha^{-1}	NHI % N
CDC Stanley (2009)	3.92 (1)[c]	55 (6)	95 (7)	90 (11)	15.3 (13)	0.45 (1)	156 (6)	4.9 (15)	8.9 (14)	0.69 (1)
CDC Kernen (2009)	3.87 (2)	56 (3)	96 (4)	96 (7)	15.2 (14)	0.41 (4)	165 (5)	5.8 (12)	9.6 (8)	0.64 (4)
Superb (2000)	3.79 (3)	55 (8)	96 (3)	88 (12)	15.3 (12)	0.38 (5)	170 (2)	6.3 (9)	10.1 (5)	0.61 (6)
CDC Go (2004)	3.79 (4)	53 (12)	95 (6)	83 (14)	15.2 (15)	0.37 (7)	175 (1)	6.8 (6)	10.6 (3)	0.59 (7)
Carberry (2009)	3.73 (5)	53 (11)	97 (2)	82 (15)	15.4 (11)	0.43 (2)	152 (11)	5.0 (14)	8.7 (15)	0.67 (2)
Unity (2007)	3.59 (6)	54 (9)	93 (11)	92 (9)	15.4 (10)	0.41 (3)	150 (14)	5.1 (13)	8.9 (13)	0.65 (3)
Harvest (2003)	3.46 (7)	53 (13)	91 (14)	88 (13)	15.7 (8)	0.38 (6)	155 (9)	6.0 (11)	9.3 (10)	0.63 (5)
AC Barrie (1994)	3.37 (8)	55 (4)	94 (8)	92 (10)	15.6 (9)	0.34 (9)	169 (3)	7.1 (5)	10.4 (4)	0.56 (10)
Sinton (1975)	3.17 (9)	56 (2)	96 (5)	102 (2)	15.7 (7)	0.32 (11)	166 (4)	7.5 (2)	10.6 (2)	0.55 (12)
CDC Teal (1991)	3.16 (10)	55 (5)	94 (9)	96 (6)	15.9 (6)	0.33 (10)	153 (10)	6.6 (7)	9.7 (7)	0.59 (8)
Park (1963)	3.03 (11)	52 (14)	92 (13)	95 (8)	16.0 (5)	0.34 (8)	151 (13)	6.1 (10)	9.1 (12)	0.58 (9)
Marquis (1910)	2.80 (12)	57 (1)	97 (1)	111 (1)	16.1 (3)	0.30 (13)	156 (7)	7.2 (3)	10.1 (6)	0.52 (13)
Red Bobs (1926)	2.80 (13)	54 (10)	93 (12)	102 (3)	16.1 (4)	0.31 (12)	151 (12)	6.4 (8)	9.3 (11)	0.55 (11)
Katepwa (1981)	2.25 (14)	55 (7)	93 (10)	98 (5)	16.3 (2)	0.20 (15)	155 (8)	9.3 (1)	11.5 (1)	0.42 (15)
Garnet (1925)	2.22 (15)	52 (15)	87 (15)	100 (4)	16.4 (1)	0.24 (14)	138 (15)	7.2 (4)	9.6 (9)	0.48 (14)
Overall mean	3.3	54.3	93.9	94.4	15.7	0.3	157	6.5	9.8	0.6
Standard error	0.15	1.61	3.12	5.05	0.26	0.02	7	0.526	0.58	0.03

[a] HI: harvest index, N: nitrogen, NHI: nitrogen harvest index, StemDM: stem dry matter, TotalNtha: total nitrogen yield hectare,

[b] Arranged in descending order of grain yield, [c] Numbers in parentheses indicate descending orders of each cultivar in each trait.

Table 3-6. Least squares means for NUE traits[a] of 15 Canada Western Red Spring wheat cultivars under low and high N treatments during 2013 to 2015 in northern-central Alberta

Genotype (Year of registration)	**NUE**		**NUtE**		**NUpE**	
	Low N	**High N**	**Low N**	**High N**	**Low N**	**High N**
Marquis (1910) [b]	64.5 (2)[c]	13.6 (12)	20.1 (7)	18.3 (13)	3.22 (1)	0.75 (6)
Garnet (1925)	55.2 (14)	10.7 (15)	18.9 (13)	16.3 (14)	2.88 (12)	0.66 (15)
Red Bobs (1926)	57.3 (11)	13.5 (13)	19.9 (9)	19.3 (12)	3.12 (6)	0.73 (11)
Park (1963)	56.6 (12)	14.5 (11)	19.8 (10)	20.4 (9)	2.95 (10)	0.72 (13)
Sinton (1975)	62.5 (4)	15.2 (10)	20.6 (5)	19.5 (11)	3.18 (3)	0.79 (5)
Katepwa (1981)	47.1 (15)	10.8 (14)	18.3 (15)	14.6 (15)	2.68 (15)	0.74 (9)
CDC Teal (1991)	67.8 (1)	15.2 (9)	22.3 (1)	20.9 (8)	3.01 (9)	0.73 (10)
AC Barrie (1994)	58.3 (7)	16.2 (8)	19.4 (11)	20.2 (10)	3.06 (8)	0.81 (3)
Superb (2000)	61.3 (6)	18.2 (3)	20.6 (4)	22.6 (6)	3.11 (7)	0.81 (2)
Harvest (2003)	62.8 (3)	16.6 (7)	21.8 (2)	22.6 (5)	2.86 (13)	0.74 (8)
CDC Go (2004)	58.2 (8)	18.2 (4)	20.1 (6)	22.0 (7)	2.90 (11)	0.83 (1)
Unity (2007)	58.0 (9)	16.7 (6)	18.6 (14)	23.7 (3)	3.21 (2)	0.72 (14)
Carberry (2009)	61.4 (5)	18.8 (1)	19.9 (8)	25.3 (1)	3.14 (5)	0.75 (7)
CDC Kernen (2009)	57.7 (10)	18.6 (2)	19.4 (12)	23.6 (4)	3.15 (4)	0.79 (4)
CDC Stanley (2009)	56.4 (13)	17.8 (5)	20.9 (3)	24.6 (2)	2.79 (14)	0.73 (12)
Overall mean	59.0	15.6	20.0	20.9	3.0	0.8
Standard error	10.1	1.60	1.39	0.90	0.58	0.07

[a] HI: harvest index, N: nitrogen, NHI: nitrogen harvest index, StemDM: stem dry matter, TotalNtha: total nitrogen yield hectare^{-1}, [b] Arranged in descending order of grain yield, [c] Numbers in parentheses indicate descending orders of each cultivar in each trait.

Table 3-7. Pearson correlation coefficients for agronomic and NUE traits[a] of fifteen Canada Western Red Spring wheat genotypes in low N and high N treatments during 2013-15 in northern-central Alberta.

Traits		Fl	MT	HT	GY	HI	SDM	TDM
PRO	**Low**	-0.51	-0.34	-0.60	-0.60		-0.45	-0.53
	High	-0.56	-0.44	-0.38	-0.58	-0.23		-0.21
NUE	**Low**	0.72	0.76	0.79	0.81	-0.12	0.66	0.76
	High			-0.23	0.97	0.70	-0.36	
NUtE	**Low**	-0.18	-0.12		0.52	0.99	-0.39	-0.22
	High			-0.23	0.72	0.94	-0.78	-0.60
NUpE	**Low**	0.80	0.83	0.72	0.48	-0.49	0.83	0.83
	High				0.27	-0.38	0.61	0.74
NHI	**Low**	-0.37	-0.24	-0.15	0.33	0.90	-0.57	-0.42
	High	-0.18		-0.35	0.60	0.95	-0.86	-0.71

Only correlation coefficients significant at ($P<0.05$) are presented. [a] FL: flowering, GY: grain yield, HT: height, HI: harvest index, MT: maturity, NHI: nitrogen harvest index, NUE: nitrogen use efficiency, NUpE: nitrogen uptake efficiency, NUtE: nitrogen utilization efficiency, PRO: grain protein content; SDM: stem dry matter.

Table 3-8. Effect of *Rht-1* alleles on agronomic traits of fifteen Canada Western Red Spring cultivars at two N levels during 2013 to 2015 in northern-central Alberta.

Allele		**Grain Yield** t ha^{-1}	**Flowering** days	**Maturity** days	**Height** cm	**Tillers** m^{-2}	**Protein** %	**HI**[b] % DM	**Lodging**
					Low N				
Rht-1	**a**	2.25	55.0	91.1	91.9	504.8	15.3	0.28	0.17
	b	2.31	53.7	91.9	78.4	525.5	15.4	0.31	0
Difference		-0.06	1.3	-0.9	13.6	-20.7	-0.1	-0.03	0.17
SE[a]		0.05	0.5	0.7	2.7	14.8	0.1	0.01	0.06
F-test					**			**	
					High N				
Rht-1	**a**	3.1	54.6	93.6	97.8	571.9	15.8	0.33	0.43
	b	3.7	53.4	94.8	85.2	576.7	15.4	0.39	0.01
Difference		-0.6	1.2	-1.2	12.6	-4.8	0.4	-0.06	0.42
SE		0.07	0.3	0.4	1.7	15.7	0.1	0.01	0.08
F-test		***	**	**	***		***	***	***

***P* value <0.05, ***P* value <0.01, ****P* value <0.001, non-significant *P* value is not presented, [a] Standard error, [b] harvest index.**

Table 3-9. Effect of Rht-1 alleles on agronomic, and NUE traits[a] of fifteen Canada Western Red Spring Wheat cultivars at two N levels during 2013 to 2015 in northern-central Alberta.

Allele	**GNtha** kg ha^{-1}	**SNtha** kg ha^{-1}	**TotalDM** kg ha^{-1}	**StemDM** t ha^{-1}	**NHI**	**NUE**	**NUtE**	**NUpE**
				Low N				
Rht-1 **a**	61	54	8.50	6.25	0.54	58.8	19.7	3.05
b	63	49	7.86	5.55	0.57	59.8	20.9	2.91
Difference	-2	6	0.65	0.7	-0.04	-1	-1.1	0.14
SE[b]	1	3	1.02	0.32	0.01	1.1	0.4	0.14
F-test					**		**	
				High N				
Rht-1 **a**	87	69	9.79	6.66	0.57	14.89	20.20	0.75
b	101	62	9.69	6.03	0.63	17.76	23.00	0.78
Difference	-14	7	0.10	0.63	-0.06	-2.87	-2.80	-0.03
SE	2	4	0.46	0.29	0.01	0.41	0.50	0.01
F-test	***				**	**	***	*

******P* **value <0.05, *****P* **value <0.01, ******P* **value <0.001, non-significant** ***P*** **value is not presented, [a] GNtha: grain N yield hectare-1, NHI: nitrogen harvest index, NUE: nitrogen use efficiency, NUpE: nitrogen uptake efficiency, NUtE: nitrogen utilization efficiency, SNtha: stem nitrogen yield hectare^{-1}, StemDM: stem dry matter; SNper: stem nitrogen percentage, TotalDM: total dry matter hectare^{-1}, [b] Standard error.**

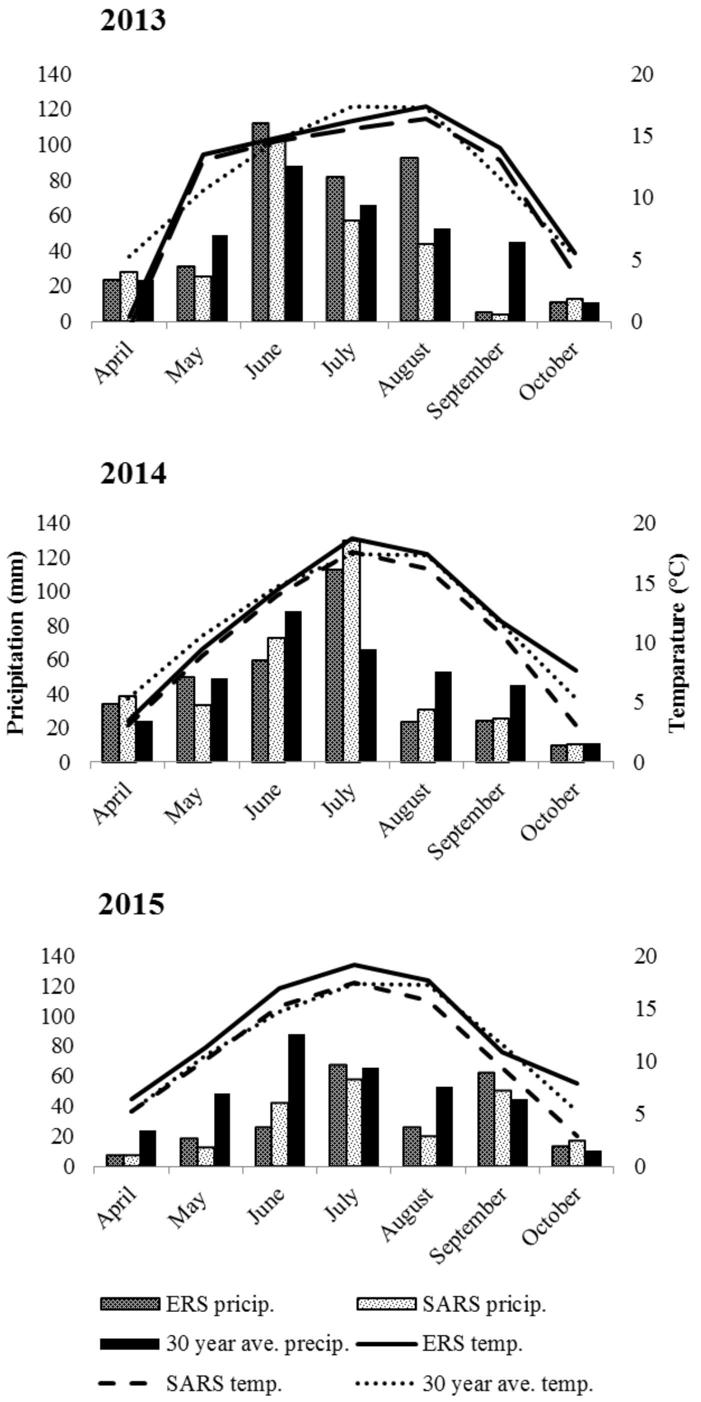
Table 3-10. Genetic gain over time in agronomic and NUE traits[a] of 15 CWRS wheat cultivars grown at two N levels during 2013-15 in northern-central Alberta.

Trait	Unit	Low N		High N	
		% year^{-1}	R^2	% year^{-1}	R^2
Flowering	days	0.004	0.003	0.019	0.052
Maturity	days	0.014	0.032	0.021	0.071
Height	cm	-0.179 ***	0.860	-0.158 **	0.706
Grain yield	kg ha^{-1}	0.024	0.022	0.349 ***	0.770
Protein	%	-0.002	0	-0.055 **	0.702
HI	% DM	-0.043	0.056	0.393 **	0.674
TotalNtha	kg ha^{-1}	0.027	0.077	0.054	0.152
StemDM	kg ha^{-1}	0.072	0.135	-0.219	0.382
NHI	% N	0.002	0	0.244 **	0.695
NUE	kg ha^{-1}	0.016	0	0.336 **	0.748
NUtE	kg ha^{-1}	0.002	0	0.299 **	0.727
NUpE	% N	0.023	0.051	0.054	0.152

****P* value <0.05, ***P* value <0.01, ****P* value <0.001, non-significant *P* value is not presented.[a] GNtha: grain N yield hectare^{-1}, HI: harvest index, NHI: nitrogen harvest index, NUE: nitrogen use efficiency, NUpE: nitrogen uptake efficiency, NUtE: nitrogen utilization efficiency, SNtha: stem nitrogen yield hectare^{-1}, StemDM: stem dry matter; TotalNtha: total nitrogen yield hectare^{-1}.**

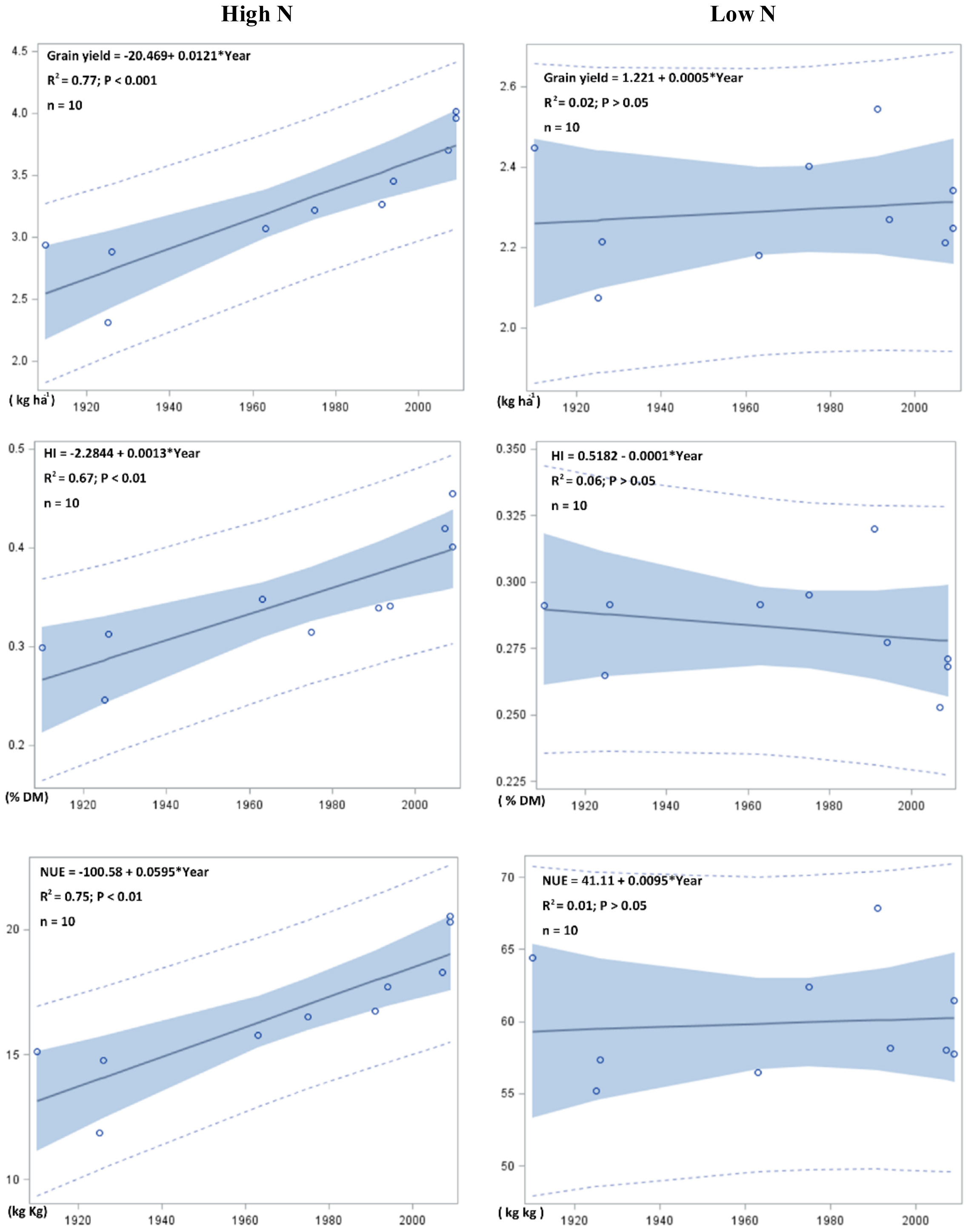
3.8 Figures

Figure 3-1. Weather data for three study years at two locations and the 30 years average during wheat growing season



ERS: Edmonton Research Station; SARS: St. Albert Research Station; precip.: precipitation; ave.: average; temp. temperature.

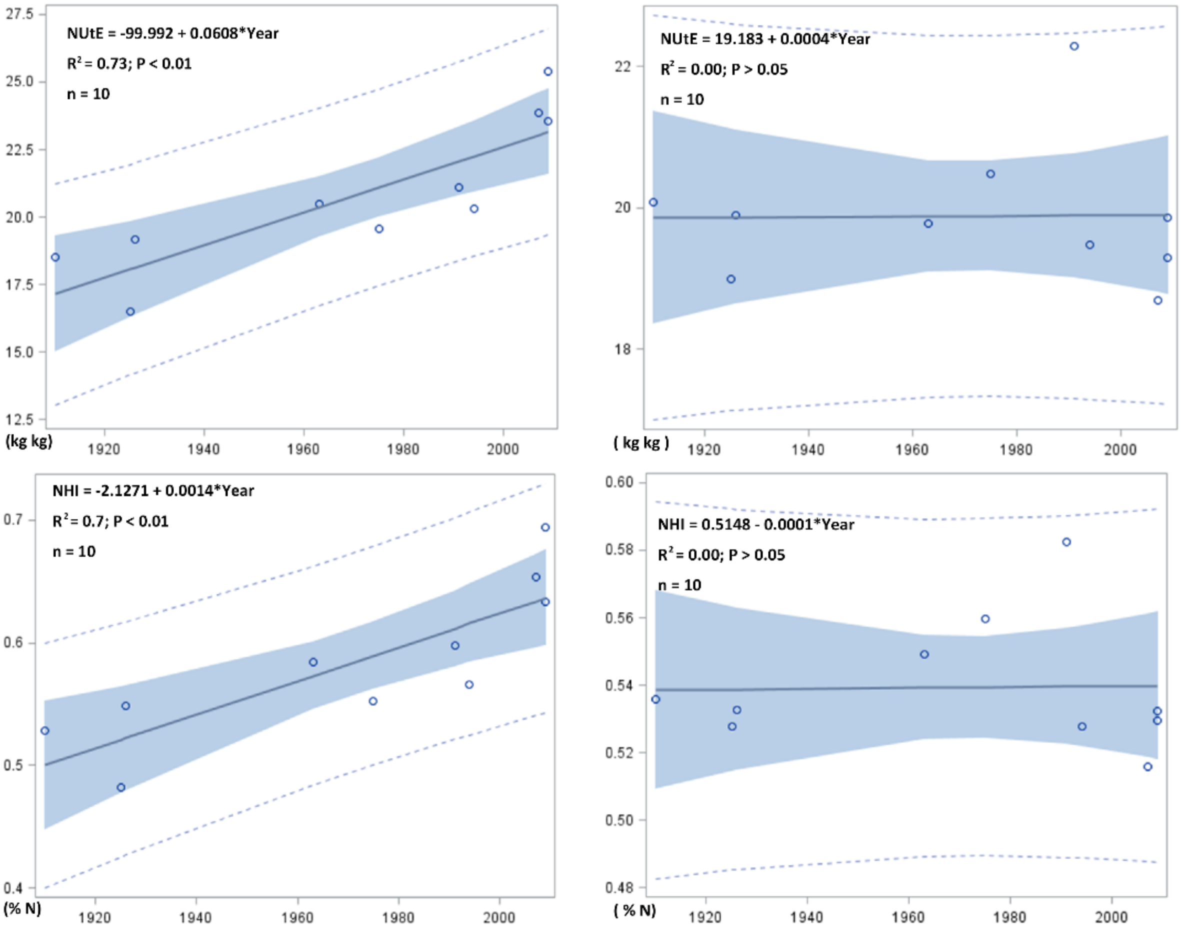
Figure 3-2. Regressions of fifteen Canada Western Red Spring Wheat cultivars grown in high N and low N treatments for grain yield, HI, NUE, NUtE, and NHI.



(Continued)

HI: harvest index, N: nitrogen, NUE: nitrogen use efficiency.

(Continued)



NHI: nitrogen harvest index, NUtE: nitrogen utilization efficiency.
See Table 3-10 for all regression statistics related to this figure.

References

Acreche, M.M. and G.A. Slafer. 2009. Variation of grain nitrogen content in relation with grain yield in old and modern Spanish wheats grown under a wide range of agronomic conditions in a Mediterranean region. Journal of Agricultural Science 147: 657-667.

Alberta Agriclture and Forestry. 2015. Agroclimatic Atlas of Alberta: Agricultural Climate Elements. Available http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/sag6301 (Accessed April 2, 2017).

Asif, M., R.-C. Yang, A. Navabi, M. Iqbal, A. Kamran, E. Lara, H. Randhawa, C. Pozniak and D. Spaner. 2015. Mapping QTL, selection differentials, and the effect of under organic and conventionally managed systems in the Attila× CDC go spring wheat mapping population. Crop Science 55: 1129-1142.

Bai, C., Y. Liang and M.J. Hawkesford. 2013. Identification of QTLs associated with seedling root traits and their correlation with plant height in wheat. Journal of Experimental Botany 64: 1745-1753.

Barraclough, P., H. Kuhlmann and A. Weir. 1989. The effects of prolonged drought and nitrogen fertilizer on root and shoot growth and water uptake by winter wheat. Journal Agronomy Crop Science 163: 352-360.

Barraclough, P.B., J.R. Howarth, J. Jones, R. Lopez-Bellido, S. Parmar, C.E. Shepherd and M.J. Hawkesford. 2010. Nitrogen efficiency of wheat: genotypic and environmental variation and prospects for improvement. European Journal of Agronomy 33: 1-11.

Bingham, I., A. Karley, P. White, W. Thomas and J. Russell. 2012. Analysis of improvements in nitrogen use efficiency associated with 75 years of spring barley breeding. European Journal of Agronomy 42: 49-58.

Bogard, M., M. Jourdan, V. Allard, P. Martre, M.R. Perretant, C. Ravel, E. Heumez, S. Orford, J. Snape and S. Griffiths. 2011. Anthesis date mainly explained correlations between post-anthesis leaf senescence, grain yield, and grain protein concentration in a winter wheat population segregating for flowering time QTLs. Journal of Experimental Botany 62: 3621-3636.

Bond, J. and O. Liefert. 2017. Wheat Outlook/WHS-17i. United States Department of Agriculture-Economic Research Service.

Brancourt-Hulmel, M., G. Doussinault, C. Lecomte, P. Bérard, B. Le Buanec and M. Trottet. 2003. Genetic improvement of agronomic traits of winter wheat cultivars released in France from 1946 to 1992. Crop Science 43: 37-45.

Brancourt-Hulmel, M., E. Heumez, P. Pluchard, D. Beghin, C. Depatureaux, A. Giraud and J. Le Gouis. 2005. Indirect versus direct selection of winter wheat for low-input or high-input levels. Crop Science 45: 1427-1431.

Calderini, D., M. Dreccer and G. Slafer. 1995. Genetic improvement in wheat yield and associated traits. A re ‐ examination of previous results and the latest trends. Plant Breeding 114: 108-112.

Clarke, J., C. Campbell, H. Cutforth, R. DePauw and G. Winkleman. 1990. Nitrogen and phosphorus uptake, translocation, and utilization efficiency of wheat in relation to environment and cultivar yield and protein levels. Canadian Journal of Plant Science 70: 965-977.

Cormier, F., S. Faure, P. Dubreuil, E. Heumez, K. Beauchêne, S. Lafarge, S. Praud and J. Le Gouis. 2013. A multi-environmental study of recent breeding progress on nitrogen use efficiency in wheat (*Triticum aestivum* L.). Theoretical Applied Genetics 126: 3035-3048.

Cormier, F., J. Foulkes, B. Hirel, D. Gouache, Y. Moënne ‐ Loccoz and J. Le Gouis. 2016. Breeding for increased nitrogen ‐ use efficiency: a review for wheat (*T. aestivum* L.). Plant Breeding 135: 255-278.

Cox, M.C., C.O. Qualset and D.W. Rains. 1985. Genetic variation for nitrogen assimilation and translocation in wheat. II. Nitrogen assimilation in relation to grain yield and protein. Crop Science 25: 435-440.

DePauw, R. and T. Hunt. 2001. Canadian wheat pool. In: A. P. Bonjean and W. J. Angus, editors, The world wheat book: a history of wheat breeding. Lavoisir, France. Lavoisier Publishing, Paris. p. 479-515.

DePauw, R., R. Knox, F. Clarke, H. Wang, M. Fernandez, J. Clarke and T. McCaig. 2007. Shifting undesirable correlations. Euphytica 157: 409-415.

Donmez, E., R. Sears, J. Shroyer and G. Paulsen. 2001. Genetic gain in yield attributes of winter wheat in the Great Plains. Crop Science 41: 1412-1419.

Dorff, E. and M.S. Beaulieu. 2015. Feeding the soil puts food on your plate. Available http://www.statcan.gc.ca/pub/96-325-x/2014001/article/13006-eng.htm (Accessed April 23, 2017)

Dorich, R. and D. Nelson. 1983. Direct colorimetric measurement of ammonium in potassium chloride extracts of soils. Soil Science Society of America Journal 47: 833-836.

Dupont, F. and S. Altenbach. 2003. Molecular and biochemical impacts of environmental factors on wheat grain development and protein synthesis. Journal of Cereal Science 38: 133-146.

Entz, M. H., Gross, K. G., Fowler, D. B. 1992. Root growth and soil-water extraction by winter and spring wheat. Canadian Journal of Plant Science 72:1109-1120.

Fageria, N. and V. Baligar. 2005. Enhancing nitrogen use efficiency in crop plants. Advances in Agronomy 88: 97-185.

Fageria, N., V. Baligar and Y. Li. 2008. The role of nutrient efficient plants in improving crop yields in the twenty first century. Journal of Plant Nutrition 31: 1121-1157.

FAO. 2016. World fertilizer trends and outlook to 2019. Available www.fao.org/3/a-i5627e.pdf (Accessed Nov. 28, 2017).

FAOSTAT. 2017. Available http://www.fao.org/faostat/en/ (Accessed April 10, 2017).

Feil, B. 1997. The inverse yield-protein relationship in cereals: possibilities and limitations for genetically improving the grain protein yield. Trends in Agronomy 1: e119.

Flintham, J., A. Börner, A. Worland and M. Gale. 1997. Optimizing wheat grain yield: effects of Rht (gibberellin-insensitive) dwarfing genes. Journal of Agricultural Science 128: 11-25.

Gaju, O., V. Allard, P. Martre, J. Snape, E. Heumez, J. LeGouis, D. Moreau, M. Bogard, S. Griffiths and S. Orford. 2011. Identification of traits to improve the nitrogen-use efficiency of wheat genotypes. Field Crops Research 123: 139-152.

Gale, M.D. and S. Youssefian. 1985. Dwarfing genes in wheat. Progress in Plant Breeding 1: 1-35.

Garnett, T., M. Appleby, A. Balmford, I. Bateman, T. Benton, P. Bloomer, B. Burlingame, M. Dawkins, L. Dolan and D. Fraser. 2013. Sustainable intensification in agriculture: premises and policies. Science 341: 33-34.

Gastal, F. and G. Lemaire. 2002. N uptake and distribution in crops: an agronomical and ecophysiological perspective. Journal of Experimental Botany 53: 789-799.

Gilland, B. 2006. Population, nutrition and agriculture. Population and Environment 28: 1-16.

Gooding, M.J., M. Addisu, R.K. Uppal, J.W. Snape and H.E. Jones. 2012. Effect of wheat dwarfing genes on nitrogen-use efficiency. Journal of Agricultural Science 150: 3-22.

Górny, A.G., Z. Banaszak, B. Ługowska and D. Ratajczak. 2011. Inheritance of the efficiency of nitrogen uptake and utilization in winter wheat (*Triticum aestivum* L.) under diverse nutrition levels. Euphytica 177: 191-206.

Guarda, G., S. Padovan and G. Delogu. 2004. Grain yield, nitrogen-use efficiency and baking quality of old and modern Italian bread-wheat cultivars grown at different nitrogen levels. European Journal of Agronomy 21: 181-192.

Guttieri, M.J., K. Frels, T. Regassa, B.M. Waters and P.S. Baenziger. 2017. Variation for nitrogen use efficiency traits in current and historical great plains hard winter wheat. Euphytica 213: 87.

Hawkesford, M.J. 2017. Genetic variation in traits for nitrogen use efficiency in wheat. Journal of Experimental Botany 68(10): 2627-2632.

Hedden, P. 2003. The genes of the Green Revolution. Trends in Genetics 19: 5-9.

Hirel, B., J. Le Gouis, B. Ney and A. Gallais. 2007. The challenge of improving nitrogen use efficiency in crop plants: towards a more central role for genetic variability and quantitative genetics within integrated approaches. Journal of Experimental Botany 58: 2369-2387.

Hucl, P. and R. Baker. 1987. A study of ancestral and modern Canadian spring wheats. Canadian Journal of Plant Science 67: 87-97.

Jaradat, A.A. 2009. Modeling biomass allocation and grain yield in bread and durum wheat under abiotic stress. Australian Journal of Crop Science 3: 237.

Kahrl, F., Y. Li, Y. Su, T. Tennigkeit, A. Wilkes and J. Xu. 2010. Greenhouse gas emissions from nitrogen fertilizer use in China. Environmental Science and Policy 13: 688-694.

Kamran, A., M. Iqbal, A. Navabi, H. Randhawa, C. Pozniak and D. Spaner. 2013. Earliness per se QTLs and their interaction with the photoperiod insensitive allele Ppd-D1a in the Cutler× AC Barrie spring wheat population. Theoretical and Applied Genetics 126: 1965-1976.

Kamran, A., H. Kubota, R.-C. Yang, H.S. Randhawa and D. Spaner. 2014. Relative performance of Canadian spring wheat cultivars under organic and conventional field conditions. Euphytica 196: 13-24.

Kubota, H., M. Iqbal, S. Quideau, M. Dyck and D. Spaner. 2017. Agronomic and physiological aspects of nitrogen use efficiency in conventional and organic cereal-based production systems. Renewable Agriculture and Food Systems.

Ladha, J., A. Tirol-Padre, C. Reddy, K. Cassman, S. Verma, D. Powlson, C. Van Kessel, D.d.B. Richter, D. Chakraborty and H. Pathak. 2016. Global nitrogen budgets in cereals: A 50-year assessment for maize, rice, and wheat production systems. Scientific Reports 6: 19355.

Lassaletta, L., Billen, G., Grizzetti, B., Anglade, J., and Garnier, J. 2014. 50 year trends in nitrogen use efficiency of world cropping systems: the relationship between yield and nitrogen input to cropland. Environmental Research Letters. 9: 105011.

Le Gouis, J., D. Béghin, E. Heumez and P. Pluchard. 2000. Genetic differences for nitrogen uptake and nitrogen utilisation efficiencies in winter wheat. European Journal of Agronomy 12: 163-173.

Loddo, S. and M. Gooding. 2012. Semi-dwarfing (Rht-B1b) improves nitrogen-use efficiency in wheat, but not at economically optimal levels of nitrogen availability. Cereal Research Communication 40: 116-121.

Mason, H.E., A. Navabi, B.L. Frick, J.T. O'Donovan and D.M. Spaner. 2007. The weed-competitive ability of Canada western red spring wheat cultivars grown under organic management. Crop Science 47: 1167-1176.

McKenzie, R.H., L. Kryzanowski and D. Pauly. 2013. Fertilizer requirements of irrigated grain and oilseed crops. Agri-Facts. Agdex 100/541-1 (Alberta Agriculture and Forestry).

Milach, S. and L. Federizzi. 2001. Dwarfing genes in plant improvement. Advances in Agronomy 73: 35-63.

Moll, R., E. Kamprath and W. Jackson. 1982. Analysis and interpretation of factors which contribute to efficiency of nitrogen utilization. Agronomy Journal 74: 562-564.

Monaghan, J.M., J.W. Snape, A.J.S. Chojecki and P.S. Kettlewell. 2001. The use of grain protein deviation for identifying wheat cultivars with high grain protein concentration and yield. Euphytica 122: 309-317.

Munier ‐ Jolain, N.G. and C. Salon. 2005. Are the carbon costs of seed production related to the quantitative and qualitative performance? An appraisal for legumes and other crops. Plant, Cell and Environment 28: 1388-1395.

Muurinen, S., G.A. Slafer and P. Peltonen-Sainio. 2006. Breeding effects on nitrogen use efficiency of spring cereals under northern conditions. Crop Science 46: 561-568.

Nelson, A., S. Quideau, B. Frick, D. Niziol, J. Clapperton and D. Spaner. 2011. Spring wheat genotypes differentially alter soil microbial communities and wheat breadmaking quality in organic and conventional systems. Canadian Journal of Plant Science 91: 485-495.

Ortiz-Monasterio, R., K. Sayre, S. Rajaram and M. McMahon. 1997. Genetic progress in wheat yield and nitrogen use efficiency under four nitrogen rates. Crop Science 37: 898-904.

Palta, J. and I. Fillery. 1995. N application enhances remobilization and reduces losses of pre-anthesis N in wheat grown on a duplex soil. Crop and Pasture Science 46: 519-531.

Palta, J.A., X. Chen, S.P. Milroy, G.J. Rebetzke, M.F. Dreccer and M. Watt. 2011. Large root systems: are they useful in adapting wheat to dry environments? Functional Plant Biology 38: 347-354.

Pswarayi, H., H. Kubota, H. Estrada and D. Spaner. 2014. Evaluation of Wheat Cultivars to Test Indirect Selection or Organic Conditions. Agronomy Journal 106: 441-451.

Qian, P., J. Schoenaru and R. Karamanos. 1994. Simultaneous extraction of available phosphorus and potassium with a new soil test: a modification of Kelowna extraction. Communications in Soil Science and Plant Analysis 25: 627-635.

Ray, D.K., N.D. Mueller, P.C. West and J.A. Foley. 2013. Yield trends are insufficient to double global crop production by 2050. PloS one 8: e66428.

Reid, T.A., R.-C. Yang, D.F. Salmon and D. Spaner. 2009. Should spring wheat breeding for organically managed systems be conducted on organically managed land? Euphytica 169:

239-252.

Sanford, D. and C. MacKown. 1986. Variation in nitrogen use efficiency among soft red winter wheat genotypes. Theoretical Applied Genetics 72: 158-163.

Satorre, E.H. and G.A. Slafer. 1999. Wheat: ecology and physiology of yield determination. The Haworth Press Inc., New York.

Sayre, K., S. Rajaram and R. Fischer. 1997. Yield potential progress in short bread wheats in northwest Mexico. Crop Science 37: 36-42.

Siddique, K., R. Belford and D. Tennant. 1990. Root: shoot ratios of old and modern, tall and semi-dwarf wheats in a Mediterranean environment. Plant and Soil 121: 89-98.

Simmonds, N.W. 1995. The relation between yield and protein in cereal grain. Journal of the Science of Food and Agriculture 67: 309-315.

Singh, V. and A. Arora. 2001. Intraspecific variation in nitrogen uptake and nitrogen utilization efficiency in wheat (*Triticum aestivum* L.). Journal of Agronomy and Crop Science 186: 239-244.

Slafer, G.A., F.H. Andrade and S.E. Feingold. 1990. Genetic improvement of bread wheat (*Triticum aestivum* L.) in Argentina: relationships between nitrogen and dry matter. Euphytica 50: 63-71.

Spiertz, J. and J. Ellen. 1978. Effects of nitrogen on crop development and grain growth of winter wheat in relation to assimilation and utilization of assimilates and nutrients. Netherlands Journal of Agricultural Science 26: 210-231.

Spiess, D. 2015. Soil group map of Alberta. Alberta Agriculture and Forestry. Available www1.agric.gov.ab.ca/soils/soils.nsf/soilgroupmap (Accessed Nov. 28, 2017)

Sylvester-Bradley, R. and D.R. Kindred. 2009. Analysing nitrogen responses of cereals to prioritize routes to the improvement of nitrogen use efficiency. Journal of Experimental Botany 60: 1939-1951.

Tkachuk, R. 1969. Nitrogen-to-protein conversion factors for cereals and oil-seed meals. Cereal Chemistry 46: 419-423.

UN-DESA, U.N.D.o.E.a.S.A. 2015. World Population Prospects: The 2015 Revision, Key Findings and Advance Tables. Working Paper, No. ESA/P/WP. 241.

UNEP. 2014. Air Pollution: World's Worst Environmental Health Risk. UNEP Year Book 2014 Emerging Issues Update.

Van Sanford, D. and C. MacKown. 1987. Cultivar differences in nitrogen remobilization during grain fill in soft red winter wheat. Crop Science 27: 295-300.

Waddington, S.R., J. Ransom, M. Osmanzai and D.A. Saunders. 1986. Improvement in the yield potential of bread wheat adapted to northwest Mexico. Crop Science 26: 698-703.

Wojciechowski, T., M. Gooding, L. Ramsay and P. Gregory. 2009. The effects of dwarfing genes on seedling root growth of wheat. Journal of Experimental Botany 60: 2565-2573.

Xu, G., X. Fan and A.J. Miller. 2012. Plant nitrogen assimilation and use efficiency. Annual Review of Plant Biology 63: 153-182.

Yadav, S.N., W. Peterson and K.W. Easter. 1997. Do farmers overuse nitrogen fertilizer to the detriment of the environment? Environmental and Resource Economics 9: 323-340.

4.0 Genetic differences for nitrogen use efficiency and stem nitrogen yield in spring wheat (*Triticum aestivum* L.) under organic management[4]

4.1 Introduction

A major problem in current conventional agriculture is inefficient use of nitrogen (N) fertilizer, a main source of ground and surface water contaminants derived from agricultural activities (Kubota et al., 2017; Peoples et al., 2012). Adoption of organic agricultural practices is considered a means to cope with agricultural derived environmental issues. Paulsen et al. (2002), for instance, noted that organic farming practices reduced nitrate leaching to half of conventional counterparts. The principle of organic agriculture is to maintain individual, community and ecosystem health through agricultural activities based on a function of the living ecosystem and its cycles (IFOAM, 2008). Numerous studies have reported that organic farming practices contribute to reducing N loss and increasing sustainability when compared to conventional management (Haas et al., 2001; Knudsen et al., 2006; Lynch 2009; Mäder et al., 2002). The positive aspects of organic agriculture accelerated the global increase in organically managed farmland, resulting in 300% increase of such land since 1999 (IFOAM, 2008). This trend is further stimulated by the market demand and growth, attracting more farmers to shift from conventional to organic practices. The remarkable increase in organically managed land accounting for 1% of the current total world arable land is predicted to increase continuously in the coming decades.

Despite increasing popularity, the question whether organic agriculture can serve as an alternative to conventional practices to sustainably feed the increasing world population needs to

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[4] *This chapter is submitted to Agroecology and Sustainable Food Systems and currently under review for publication.*

be carefully addressed (Tilman et al., 2002). Overall yields of organic agriculture have been reported 5 to 34 % lower than conventional counterparts (L-Baeckström et al., 2006; Mason et al., 2007; Nelson et al., 2011; Reid et al., 2009; Seufert et al., 2012). Although both systems have similar constraints for yields, organic farmers face substantial differences compared to their conventional counterparts for nutrition/weed management, and protection from biotic and abiotic stresses.

Soil nitrogen (N) limitation is a major challenge, among several constraints to organic farm management (Mäder et al., 2002; Mason and Spaner, 2006; Scow et al., 1994). In the absence of chemical N fertilizer, biological N fixation through legumes, incorporating preceding crop residues, livestock manure, and green manure are the primary N inputs in extensive organic agriculture (Berry et al., 2002). Organic farmers employ such on-farm N materials with a combination of cultivation practices (e.g. crop rotation, intercropping, and cover cropping) to optimize productivity (Eriksen et al., 2004; Kayser et al., 2010; Snyder and Spaner, 2010). Crops that are efficiently able to use limited N sources have a great advantage in organic agriculture. In addition, it is important for farmers to select crops/cultivars which contribute positively to N cycling in the whole rotation.

Improvement in wheat nitrogen use efficiency (NUE) has been reported in Europe and the USA in conventional systems (Cormier et al., 2013; Guttieri et al., 2017). Such improvement has not been reported in organic systems, perhaps due to the variation of cultivar performance under organic management. A study conducted under both conventional and organic systems reported significant genotypic (G) × management system (M) interaction for grain yield, indicating that cultivars that perform well under optimal conventional management may not perform similarly in organic conditions (Górny et al., 2011; Murphy et al., 2007). Complex G ×

Environment (E) interaction effects hinder the efficiency of breeding selection for target traits in organic systems (Baresel et al., 2008). Currently more than 95% of organic agriculture is practiced using crop cultivars bred specifically for high-input systems, and such cultivars are likely to lack important traits for organic systems (Mason et al., 2007; Murphy et al., 2007). Recent studies report the necessity of cultivar selection under organically managed land to develop ideal cultivars for organic systems (Asif et al., 2015; Reid et al., 2009). A significant G × soil N level interaction for important agronomic traits might also impede organic breeding progress for NUE (Cormier et al., 2013; Le Gouis et al., 2000; Ortiz-Monasterio et al., 1997). Inconsistency in cultivar performance at different soil N levels could be expected in organic systems (Mohammadi et al., 2015; Peterson et al., 1992).

Under the well-fertilized optimum growing condition in conventional systems, NUE has increased due, in part, to increased harvest index (HI) and Nitrogen harvest index (NHI) (Cormier et al., 2013; Guttieri et al., 2017). The yield and NUE improvement in conventional systems appear to result from incorporating dwarfing *Rht* alleles into modern cultivars coupled with easily available synthetic N fertilizer (Hay, 1995). When spring wheat genotypes were grouped into semi-dwarf and tall groups, the semi-dwarf group exhibited a greater partitioning of dry matter to grain, higher grain yield and greater NUE than the tall group (Singh and Arora, 2001). Semi-dwarf wheat, in general, exhibits reduced weed competitive ability maladapted to organic agriculture (Mason et al., 2007). Developing cultivars with better NUE characteristics specifically for organic systems would be desirable (Hirel et al., 2011). Although the main goal in the improvement of wheat NUE is to achieve high grain yield (Lin et al., 2016; Tilman et al., 2002), increased NUE in organic systems should also consider improving traits that could increase a potential for field N recycling.

Many organic cereal-based systems use an integrated approach to use and optimize on-farm nutrient cycling for maintaining grain production. In this context, returning as much as crop residues N (i.e. stubbles and chaff) to the soil is an important practice to improve soil N status and other physiological and biological properties (Hadas et al., 2004; Smith et al., 1993). In low-input or organic agriculture, the quantity of soil N largely relies on on-farm input, and crop sequences. Thus, a large volume of residual N in vegetative parts is of an important source of N for the subsequent crops although crop residues with high values of the C:N ratio (>41) resulted in the negative net N between mineralization and immobilization (Vigil and Kissel, 1991). Despite the fate of the immobilized soil labile N caused by returning wheat stem residues, its duration and remineralization vary depending on the test environment, residue management and timing (Unger, 1991).

In order to optimize the use of available N as well as maintain good N cycling in organic fields, it is necessary to have a better understanding of associated traits. However, little is known about genotype performance for NUE traits in Canada Western Red Spring (CWRS) wheat class under organic practices. Also, there is a lack of information on CWRS cultivars that are able to store a great volume of N in residual DM. In other words, cultivars with a good balance between NUE and vegetative N yield may be suitable for organic systems rather than the best NUE cultivars with low stem N yield for long-term sustainable management. The traits suited for organic farming might be the ones that efficiently uptake N from soil and store substantial N as the total N in biomass. However, these specific traits have not been studied extensively in the CWRS class in Western Canada although there are several studies about NUE in barley (Anbessa et al., 2009, Anbessa and Juskiw, 2012).

As improved NUE in wheat is aimed at increasing grain yield in organic agriculture, selection for stem N yield traits have an additional benefit for obtaining a long-term sustainable crop production in organic agriculture. Therefore, our objectives in the present study were to 1) analyze genetic variability for agronomic and NUE traits in organic management by comparing to those in conventional management, 2) to assess the relative performance of fifteen CWRS wheat cultivars for grain yield, NUE and stem N yield, and identify stable genotypes for these traits under organic management system. The information generated will be useful in identifying potential parents for improving NUE in future cultivars and in cultivar recommendation for organic producers.

4.2 Materials and Methods

Sixteen spring wheat cultivars were tested in conventional and organic systems in 2013, 2014 and 2015. However, we excluded one cultivar from analyses in this study because that belongs to a different wheat class from the other fifteen. Therefore, fifteen Canada Western Red Spring (CWRS) cultivars registered from 1910 to 2009 were analyzed. The fifteen cultivars were chosen based on a previous study (Kamran et al., 2014) and represent commonly grown cultivars of the CWRS class commonly grown in western Canada over the last 100 years (Table 4-1). Field trials were conducted at two conventional and two organic sites in three locations within a 100 km radius from Edmonton, AB Canada. At the University of Alberta Edmonton Research Station (ERS) (53°49’N, 113°55’W), the trials were conducted on paired organically and conventionally managed sites that were located approximately 0.5km apart. The organic site is not certified; however, it has been organically managed since 1999 and its management meets the organic certification standards. The other conventional trial was conducted at the University of Alberta St. Albert Research Station (SARS) (53°69’N, 113°64’W) and the other organic site is a certified organic farm near Lamont (53°85'N, 112°62'W). In total, twelve environments (year × location) were tested over the three years (6 in conventional and 6 in organic trials). The soil type in the studied area is classified as a black Chernozemic soil (Spiess, 2015). All trials were seeded in mid-to late May and harvested in mid-September when all plots were mature.

Each experiment was arranged in an incomplete block design with four replications. Each plot was 4 m by 1.38m with six rows spaced 23cm apart and seeded at 300 seeds m^{-2} using a six-row, no-till double –disk drill (Fabro Enterprises LtD., Swift Current, SK). Prior to seeding, 10 soil cores at depth of 30cm were sampled and mixed at each site and soil nutritional profiles were measured colorimetrically using centrifugal analyzer after a modified KCL extraction. These soil N levels were used as residual (initial) soil N to calculate NUE traits. In conventional sites, N fertilizer was applied to achieve the total soil N levels of 200kg ha^{-1} according to the residual soil N to meet a local recommendation rate for optimal grain yield (McKenzie et al., 2013). Weeds were controlled occasionally using Curtail^{TM} M according to the manufacture instruction only in conventional system.

The organic field at ERS has been organically managed since 1999 and compost was applied at a rate of 50 to 62 t ha^{-1} (fresh weight) for five consecutive years from 1999 until 2005. The field has been rotationally managed with the crop sequence of wheat (*Triticum aestivium* L.) - fall rye (*Secale sereale* L.) - a mixture of triticale (×*Triticosecale* Wittmackand) - field pea (*Pisum sativum* L.) until 2009, and fall rye - barley silage (*Hordeum vulgare* L.) - wheat until 2012. The sequence has changed to wheat - pea - triticale from 2013 onward. Plant residue from previous crops was disc harrowed before spring seeding. The organic site at Lamont was certified in 2000. The organic sites had no external inputs except compost. Weed control was carried out by tillage in fall and prior to seeding.

Agronomical data on days to flowering (flowering), days to maturity (maturity) and plant height (height) were recorded in field. Days to flowering were recorded when 50% of the spikes in a plot exhibited protruded anthers. Days to maturity were recorded when 50% of the peduncles lost their green color. Stem dry matter (StemDM) was obtained by hand harvesting sample using 25 × 25 cm quadrat from each plot at maturity. Grain yield was obtained after harvesting each plot. Grain and stemDM samples were stored in a dryer at 40°C for at least 24 h for stem DM and 48 h for grain. About 50g each of grain and stem samples were ground into powder for N estimation. N content of the ground samples were determined by combustion analysis using LECO TruSpec CN analyzer (Leco Corporation). Obtained grain and stem N contents (GNper and SNper) were further used to determine total, grain and stem N yields per hectare (TotalNtha, GNtha and SNtha respectively). Grain protein contents were then calculated by multiplying the value of grain N contents obtained by LECO analyzer with 5.26, which is nitrogen to protein conversion factor (Tkachuk 1969). NUE traits were calculated as proposed by Moll et al. (1982) using the following equations:

$$NUE = \frac{Grain\ yield}{Available\ N\ (low{:}soil\ residual\ N, high{:}soil\ residual\ N+N\ fertilizer)} \quad (1)$$

$$NUtE = \frac{Grain\ Yield}{Total\ N_{tha}\ (SN_{tha} + GN_{tha})} \quad (2)$$

$$NUpE = \frac{TotalNtha\ (SNtha + GNtha)}{Available\ N\ (low{:}\ soil\ residual\ N,\quad high{:} soil\ residual\ N + N\ fertilizer)} \quad (3)$$

We also calculated harvest index (HI) and nitrogen harvest index (NHI) using the following equations:

$$HI = \frac{Total\ \ Grain\ \ Yield}{Total\ \ Aboveground\ \ Biomass} \qquad (4)$$

$$NHI = \frac{Grain\ \ Nitrogen\ \ (GNtha)}{Total\ \ \ Nitrogen\ \ (TotalNtha)} \qquad (5)$$

In order to obtain the proportion of the total sum of squares for each source of variation, analysis of variance (ANOVA) for individual N treatment was initially performed with the PROC GLM procedure in SAS version 9.4.1 (SAS Institute Inc. Cary, USA). Data for the agronomic and NUE traits were analyzed using the following model.

$$T_{iklm}=\mu+E_i+G_k+R(E)_{il}+B(RE)_{ilm}+EG_{ik}+e_{ijklm}$$

(6)

where T is the observation of the *k*th genotype G in the *i*th environment E in the *m*th block B within *l*th replication R in the environment. μ is the general mean and *e* is residual error term. In the analysis, genotypes were considered as fixed effects, whereas, environments (year × location), replications within environments, blocks within environment and their interactions were treated as random effects.

Then, a combined ANOVA was conducted for the agronomic and NUE traits to test the effect of N treatment using the following model.

$$T_{ijklm}=\mu+E_i+M_j+G_k+R(E)_{il}+B(RE)_{ilm}+EM_{ij}+EG_{ik}+MG_{jk}+EMG_{ijk}+e_{ijklm} \qquad (7)$$

where T is the observation of the *k*th genotype G in the *i*th environment E and *j*th management treatment M in the *m*th block B within *l*th replication R in the environment. μ is the general mean and *e* is residual error term. In the analysis, genotypes, management treatments, and their interactions were considered as fix effects. Environments, replications within the environments, blocks within environment and their interactions were treated as random effects. Significance levels for fixed and random effects were determined by PROC MIXED and PROC GLM, respectively.

Cultivar LSMEANS for each trait were estimated for each N fertilizer treatment using PROC MIXED in SAS. Genotypes were considered fixed, whereas environment and its interaction were treated random effects. The stability analysis was performed to assess genotype stability for various traits under organic systems using Genotype × Environment analysis method (GEA-R) developed by Pacheco et al. (2015) in the software R. Eberhart and Russell (1966) described the model as

$$Y_{ij} = \mu + \beta_i I_i + \delta_{ij} + \varepsilon_{ij} \quad (8)$$

where Y_{ij} is the observation of i th genotypein the j th environment. μ is the general mean, β_i is the regression coefficient, I_j is the environmental index obtained by the difference among the mean of each environment and the general mean ($\sum_{j=1}^{n} I_j = 0$), δ_{ij} is the regression deviation of the i th cultivar in the j th environment and ε_{ij} is the experimental error. The coefficient of regression (bi) is a measure of stability in multi-environment trails. Genotypes with lower bi values than 1.0 indicate that those genotypes are above-average stability, while genotypes with higher bi values than 1.0 have below-average stability and perform well only under favorable conditions. The 0 value of the deviation from the regression line (S^2di) may be defined as stable. I also used mean values and coefficient of variation to assess cultivar stability for traits.

Pearson correlation coefficients among all traits were estimated using the mean values of traits in SAS. Simple linear regression models were used to estimate genetic progress in agronomic and NUE traits over time using PROC REG in SAS.

Our main purpose of this study was to elucidate genetic difference among CWRS wheat cultivars for improvement of NUE in organic systems; therefore, the data from conventional systems was used for mean value comparison and variance source contrast.

4.3 Results

Temperature trends during the study period were relatively consistent with the 30-year average except for relatively cooler April in 2013, whereas precipitation over the three years fluctuated (Figure 4-1). Soil N levels at seeding varied with experiment sites regardless of management system (Table 4-2). Limiting N (< 60kg ha^{-1}) occurred only on organic sites (e.g. 2014 Lamont and 2015 ERS Organic).

In the combined analyses over sites and years, grain yield, HI, NHI, GNtha, and NUtE were significantly lower (P<0.05) in organic than in conventional managements (Table 4-3). The G ×E interaction was not significantly different for all measured traits while the G × M interaction was significant for grain yield, protein, HI, NHI, GNtha, NUE, NUtE, and NUpE (Table 4-3, Appendix 4-1). Grain yield and NUtE were 50 % and 23% less in organic than conventional management (1.62 t ha^{-1} and 3.27 t ha^{-1} for grain yield and 16.2 t DM t^{-1} N and 20.9 t DM t^{-1} N for NUtE, respectively), while SNtha and NUE did not differ (Table 4-3).

Analysis by management showed significant effect (P<0.05) of genotype (G) and environment (E) on all measured traits in both management systems (Table 4-3). The contribution of E variance was the largest variance in all measured traits in organic systems, while G variance was the largest for grain yield, HI, NHI, StemDM, GNtha, and NUtE in conventional systems. The G × E interaction was also significant for several measured traits in both management systems; however, more traits showed this interaction in organic systems (i.e. grain yield, HI, TotalDM, StemDM, GNtha, SNtha, C:N ratio and NUtE) than in conventional systems (i.e. grain yield, GNtha and NUE). The relative contribution of the G × E interaction variance in both management systems were similar to or larger than G variance for TotalDM, StemDM, TotalNtha, SNtha, and NUpE.

The mean ranks of cultivars for studied traits were similar with management systems (Table 4-4). For example, CDC Stanley and CDC Kernen yielded the highest grain, and had greatest GNtha in both systems (Table 4-4). Superb, CDC Go, and AC Barrie yielded the highest TotalNtha in conventional, whereas Superb, AC Barrie and Katepwa in the organic managements. Katepwa had the highest SNtha in both management systems, followed by Sinton and AC Barrie in conventional and Superb and Sinton in organic systems. CDC Stanley, Unity, and Carberry had the highest NUtE under conventional, whereas Carberry, CDC Kernen, and Unity in organic systems. Superb, CDC Go and AC Barrie exhibited the greatest NUpE in conventional, while AC Barrie, Superb, and Sinton in organic systems (Table 4-4).

The values of the stability regression coefficient (bi) and deviation from regression (S^2di) were estimated for several important traits for each genotype under organic systems (Figure 4-2). Genotypes having high mean values, a regression coefficient close to 1 and deviation close to 0 were considered stable genotypes (Eberhart and Russell, 1966). CDC Kernen, CDC Stanley, Superb, and Unity exhibited high mean grain yield and NUE and low CV with good stability parameter values of bi and S^2di (Figure 4-2 a, b, c, d). Likewise, Unity, CDC Teal, CDC Stanley, and CDC Kernen had high mean NUtE values with good stability parameter values (Figure 4-2 e, f). Superb yielded the second highest stem N with small CV but stability parameters indicated this cultivar is not stable. However, Superb had above-average yield for StemDM and SNtha in all organic locations. CDC Stanley, CDC Go, Park, contrarily, showed the good values of stability parameters but their mean values were low.

NUE was positively correlated with GNtha but not with SNtha in organic management (Table 4-5). Grain yield was positively correlated with NUE and NUtE (Table 4-5). StemDM was negatively correlated with NUtE but positively correlated with NUpE. HI and NHI were also negatively correlated with NUpE. TotalDM was negatively correlated with NUtE, while positively correlated with NUpE.

4.4 Discussion

4.4.1 Effect of management systems

Results in studies for comparing grain and stem N yields, and NUE traits between organic and conventional systems vary with environment, crop species, NUE calculations, research methods, and management practices. Several studies of annual cereal grains over a range of soil N levels have shown that NUE increases as soil N levels decrease (Ortiz-Monasterio et al., 1997; Sing and Arora, 2001; Huggins and Pan, 2003). However, NUE was not statistically different between organic and conventional managements in our study. This disagreed with other studies (Ortiz-Monasterio et al., 1997; Sing and Arora, 2001; Huggins and Pan, 2003; L-Baeckström et al., 2006; Lin et al., 2016). Such contrasting results may partly be explained by the magnitude of the yield difference between organic and conventional systems in each study. A small reduction (20%) in spring and winter wheat yields was reported under organic systems (L-Baeckström et al., 2006). L-Baeckström's study were conducted under long-term organically managed fields where relatively intensive organic inputs were applied, showing good soil fertility levels with high N source utilization efficiency for crops. Several other long-term intensive organic studies also reported organic systems produced comparative grain yield to conventional systems (Lin et al., 2016; Mäder et al., 2002; Mäder et al., 2007). However, in our study, the mean grain yield in organic systems was 50% lower than that in the conventional counterpart. The value of NUE was computed as grain dry biomass per total plant available N. Therefore, the prominent grain yield reduction in organic systems resulted from elevated weed pressure and low soil N status may lead low NUE values (Clark et al., 1999; Mason et al., 2007). Although a study showed that the presence of interspecific competitor (barley [*Hordeum vulgare* L.]) significantly reduced NUE in durum wheat (*Triticum durum* Desf.) in varying soil N levels (Giambalvo et al. 2010), weed competitive ability and response to soil N depend on their species (Blackshaw and Brandt, 2008). Studies for comparing cultivar performance between organic and conventional agriculture, therefore, reported a wide range of yield reduction (Hildermann et al., 2009; Kamran et al., 2014; Mäder et al., 2007; Murphy et al., 2007; Nelson et al., 2011; Reid et al., 2011) and various NUE values (Bosshard et al., 2009; L-Baeckström et al., 2006; Lin et al., 2016; Musyoka et al., 2017) in organic agriculture. No significant difference in NUE between conventional and organic managements in our study may be explained as yield reduction by competition of resources against weeds.

4.4.2 Variance components for grain yield, stem N yield, and NUE traits

StemDM and SNtha were reduced 6% and 10% respectively in organic systems compared to conventional systems but this was not statistically significant at $p>0.05$ (Table 4-3). The proportions of each variance source for these two traits were inconsistent between two systems. Variance contribution under conventional managements for these two traits was similar among three variance components (E, G, and E×G), while the contribution of environment variance was several-fold larger than other two variance sources in organic management, suggesting additional environmental variation derived from spatial and seasonal soil N and weed variation existed in organic management (Hokazono and Hayashi, 2012; Wolfe et al., 2008). For instance, soil N levels under organic management in this study varied by locations and year, ranging from 32.5 kg ha^{-1} to 158 kg ha^{-1} while N levels in conventional fields were adjusted to 200 kg ha^{-1} with the application of synthetic N fertilizer. The key for successful weed management is level of soil moisture, which largely relies on weather condition. Mechanical weeding is more effective under air-dry soil condition where cut/tilled weeds are exposed to drying and thus, organic agriculture is more vulnerable to weather variability for weed management than conventional systems (Davies and Welsh, 2002). Contrarily, with sufficient soil moisture, N uptake by plant generally higher than under dried condition. Therefore, soil moisture levels have a significant impact on N uptake and weed competitive ability of wheat grown under organic systems. Such environmental dependence of traits that exhibited large E and G×E interaction variances in organic systems. G×E interactions in organic systems were statistically significant for grain yield, NUtE and stem traits that are sensitive to soil N levels and weed pressure.

Numerous studies suggest that direct selection in organic fields is necessary for improvement of quantitative traits because such traits are largely influenced by G×E interactions (Löschenberger et al., 2008; Murphy et al., 2007; Osman et al., 2016; Reid et al., 2009; Wolfe et al., 2008). The significant effect of G×E interactions for NUtE and stem traits in organic systems indicated the complexity of inherited quantitative manners for these traits. Therefore genetic materials with stable NUtE and stem traits in such environments are required for future breeding.

The quantity of N in the residues would be critical for the succeeding crops in many organic practices (Hadas et al., 2004; Hu et al., 2015; Smith et al., 1993). In the present study, we observed significant variability among G and G×E interaction effects for StemDM and SNtha under organic management. Significant G×M interactions for HI and NHI indicated that selection for these traits needs to be performed in each management system. We observed a significant difference in HI and NHI between cultivars in organic systems (HI=0.23, NHI=0.47) and in conventional systems (HI=0.35, NHI=0.6). Modern breeding programs have contributed to improving distribution of assimilates into grains, resulting in increased HI under optimum growing conditions (Austin et al., 1980; Rodrigues et al., 2007). Therefore, the reduction in grain yield, HI, and NHI under organic systems in the present study is most probably due to the reduced performance of assimilate partitioning derived from low soil N levels and growth competition against weeds as suggested previously (Mason et al., 2007).

4.4.3 Genotype differences for grain yield, stem N yield, and NUE traits

The ranks of cultivars in organic and conventional systems were generally similar for most of the measured traits except NUpE. Modern wheat cultivars CDC Stanley, CDC Kernen, CDC Go, and Superb performed well in both management systems for grain yield and NUE. Previous studies conducted on conventional lands also concluded that modern wheat cultivars have greater grain yield and NUE than old cultivars regardless of soil N levels (Cormier et al., 2013; Guttieri et al., 2017; Muurinen et al., 2007). Environmental factors (e.g. soil fertility and weed pressure) within organic systems significantly differ with locations and environments (Baresel et al., 2008). Therefore, selection of superior genotypes and comparison between organic and conventional systems is not simple and straight forward. However, in our study, CDC Stanley, CDC Kernen and Superb presented good stability for grain yield and NUE under organic systems, indicating that these cultivars have potential to perform consistently well under various organic field conditions, and suitable for both conventional and organic agriculture. This, in return, supports results of the previous studies that NUE mainly increased due to improvement in grain yield, which resulted from intensive selection for disease resistance and grain quality traits in CWRS class regardless of management systems (Baresel et al., 2008; Cormier et al., 2013; Guttieri et al., 2017; Pswarayi et al., 2014).

Interestingly, the above three modern CWRS cultivars have different characteristics. Superb is a semi-dwarf cultivar (Chen et al., 2016; Kamran et al., 2014) and has a large TotalDM in this study (8.7 t ha^{-1}), while CDC Kernen was bred for organic agriculture and has good competitive ability due to its tall statures (Kubota et al., 2015; Wiebe, 2015). CDC Stanley has a good package of disease resistance (i.e. leaf spot [*Phasosphaeria herpotrichoides*], leaf rust [*Puccinia triticina*] and stripe rusts [*Puccinia striiformis*], and fusarium head blight [*Fusarium*]) (Fedko, 2017). Although the improvement in grain yield and NUE has been mainly achieved by increased HI in modern wheat cultivars (Austin et al., 1980; Desai and Bhatia, 1978; Guttieri et al., 2017; Hay, 1995), the two of these CWRS cultivars have larger HI values (i.e. CDC Kernen: 0.3, CDC Stanley: 0.27), while Superb has lower value (i.e. 0.22) than the mean value of HI. Generally semi-dwarfing is an important trait for selection for obtaining high grain yield in conventional management due to their large sink size and lodging resistance (Iqbal et al., 2016). However, this trait has not been considered as important in organic systems as in conventional systems because cultivars require plasticity to variable soil N levels and weed pressure in organically managed conditions (Mason et al., 2007). Although Superb had high grain yield, Carberry and CDC Go, which are also semi-dwarf types (Chen et al., 2016), didn’t yield well under organic management in our study. Another high yielded cultivar, CDC Kernen is a tall cultivar, which agrees with another study (Mason et al., 2007). These results suggest that the ideotype approach may not be an ideal for breeding cultivars for organic management system.

Improvement in NHI, has been achieved concurrently with improved N partitioning (NUtE) in modern cultivars (Cormier et al., 2013) that is evident from the strong positive correlation between NHI and NUtE in the present study. Since the CWRS class has held constant grain protein contents (Kamran et al., 2014; Wang et al., 2003), genetic variation of GNtha in CWRS cultivars mainly depends on their variation of grain yield. In fact, grain yield and GNtha were strongly positively correlated with each other in both systems.

Amongst the tested CWRS cultivars, low NUtE and high NUpE value in Superb were distinctive compared to the other high yielding cultivars in organic systems. This suggested that the demand of vegetative growth for N may be an important determinant of nitrogen uptake (Singh and Arora, 2001). This assumption is further reinforced by the strong positive correlation between NUpE and TotalDM in organic systems. In other words, the sink (i.e. shoot) demand is more important for efficient capture of N than the ability to absorb N (i.e. root) under low N conditions (Clarkson, 1985; Kamiji et al., 2014). Therefore, aboveground biomass production (i.e. stem + leaf) should be included in the selection criteria for better NUpE (thus NUE) in organic breeding programs. This could simultaneously improve NUE and Stem N yield.

When using shoot biomass as criteria for selecting for better NUE, the trade-off effect in carbon and N investment due to an equilibrium metabolic cost for those resources between aboveground and root systems should be considered (Barraclough et al., 1989; Robinson, 2001). Breeding of CWRS class may have been successful to maintain this trade-off effect, obtaining high grain and grain protein contents due to the strict registration requirement of grain quality and yield in Canada. With all the above, we could postulate that Superb possesses either a characteristic of a deeper and well established root systems/vigorous vegetative growth or better affinity of roots for N ions and a beneficial soil microbial community that efficiently enable to absorb and transport N, thus maintaining high NUpE and NUE (Nelson et al., 2011; Pang et al., 2015). However, an investigation of root traits and vegetative growth stage in CWRS class is beyond the scope of our study and needs to be studied in future.

During the early stage of decomposition, incorporation of mature wheat stem residues causes soil microbial immobilization of plant available N due to its high carbon to nitrogen ratio (C/N ratio) (Shindo and Nishio, 2005). This event may be more prominently observed in organic systems where application of synthetic N fertilizers is not allowed. In addition, the fact that stem N yield generally reaches maximum at anthesis and decreases by about 70% during grain filling period through remobilization, leaf death, and ammonia volatilization. These may be a drawback for considering wheat shoot residues as a valuable N source for succeeding crops in the short-term (Morgan and Parton, 1989; Wang et al., 2003). However, incorporation of crop residues in organic fields is the primary practice to maintain soil organic matter and its resilience, and thereby increasing soil fertility levels in organic agriculture on a long-term basis (Smith et al., 1993). Therefore, it would have a significant impact on sustainable field management if great stem N yielding cultivars are planted into crop rotations. In the present study, CWRS cultivars, Katepwa produced the largest StemNtha (78kg ha^{-1}); however, its C:N ratio was slightly higher (51.7) than the average, indicating a higher risk of immobilization of N at the early stage of its decomposition. Also, its stability parameters for C:N ratio suggested it as unstable in organic conditions. Contrarily Superb exhibited the lowest C:N ratio (47) among the tested CWRS cultivars with the second largest SNtha (70kg ha^{-1}) under organic conditions. This indicates that the residues of this cultivar would be the best as a soil amendment (i.e. a long-term N cycling) among tested cultivars for incorporating into fields although its stability parameters were not good. The problem of temporal immobilization of soil N after the incorporation of wheat residues into organic fields could be mitigated by agronomical practices such as conservation tillage. Recent studies also demonstrated that the temporal problem of immobilization of crop residues with high C:N ratio may be remediated by a mixture of crop residues with low C, N and phosphorous ratio meaning incorporation of legumes crop as a cover crop or inter-seeding crops (Regehr et al., 2015; Wang et al., 2014). Moreover, delaying net N mineralization of legume may be ideal to synchronize succeeding crop N demand when legume is mixed with wheat straw. Therefore, further exploration for the best management practices where wheat residual N can be fully utilized, while minimizing the risk of immobilization, is necessary.

4.5 Conclusion

Important agricultural goals for improving NUE in organic wheat production systems are to 1) increase grain productivity, and 2) maintain an efficient N cycle in fields over time. Many environmental, biological and agronomical factors contribute to governing overall NUE in cereal-based agricultural systems. Therefore, selecting cultivars that present stable performance should be an ideal agronomic approach. In the present study, we have reported four major findings. 1) There was genetic variation for NUE and SNtha within tested CWRS genotypes. 2) Superb was a superior cultivar for grain yield, NUE, and stem N yield with relatively good stability parameters across the tested organic systems. 3) The ideotype approach may not be a best approach for organic wheat breeding due to the presence of different characteristics in high yield cultivars under organic management. 4) TotalDM could be possible selection criteria for improved NUpE. Although the presence of significant G × E interaction for several traits was likely due to variation in cultivar responses to variable temporal and spatial environments in organic fields, our findings could have practical implications for cultivar choice especially under organic systems where soil N availability and weed stress are often large constraints.

Using appropriate genetic material, simultaneous improvement of NUE and stem N yield for organic farming is possible. In our study, three cultivars with different characteristics (i.e. semi-dwarf, medium tall height, and a good disease resistance) presented stable grain yield and NUE in organic systems. This indicated that there are several potential approaches to improve grain yield and NUE through breeding such as semi-dwarf with extensive root systems, high affinity to beneficial soil microbial communities, tall height against weed stress, and disease resistance for organic farming. The selection of these traits should vary depending on target environments. Nitrogen recycling in organic agricultural practices could be improved by including wheat cultivars that return more N into soil. Therefore, a high stem N yielding trait should be included in selection criteria in organic breeding programs. One of the modern CWRS cultivars, Superb, was found to be superior and desirable genotype for this purpose. The coincidental improvement of NUpE and Stem N yield through breeding for organic farming might be possible using parental genotypes such as Superb.

4.6 Acknowledgments

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4.7 Tables

Table 4-1. Description of fifteen Canada Western Red Spring (CWRS) wheat (*Triticum aestivum* L.) cultivars

Cultivars	Released Years[a]	*Rht-B1*[b]	*Rht-D1*[b]	Days to maturity[d]	Origin[e]
Marquis	1910	*Rht-B1a*	*Rht-D1a*	+2	Agriculture Canada, Ottawa
Garnet	1925	*Rht-B1a*	*Rht-D1a*	-4	Agriculture Canada, Ottawa
Red Bobs	1926	*Rht-B1a*[c]	*Rht-D1a*[c]	-3	University of Alberta
Park	1963	*Rht-B1a*	*Rht-D1a*	-1	Agriculture Canada, Lacombe, AB
Sinton	1975	*Rht-B1a*[c]	*Rht-D1a*[c]	-2	Agriculture Canada, Regina and Swift Current, SK
Katepwa	1981	*Rht-B1a*	*Rht-D1a*	-3	Agriculture Canada, Winnipeg, MB
CDC Teal	1991	*Rht-B1a*	*Rht-D1a*	-1	Crop Development Center, Saskatoon, SK
AC Barrie	1994	*Rht-B1a*	*Rht-D1a*	0	Agriculture Canada, Swift Current, SK
Superb	2000	*Rht-B1b*	*Rht-D1a*	+2	Agriculture Canada, Winnipeg, MB
Harvest	2003	*Rht-B1a*	*Rht-D1b*	-2	Agriculture Canada, Winnipeg, MB
CDC Go	2004	*Rht-B1b*	*Rht-D1a*	+2	Crop Development Center, Saskatoon, SK
Unity	2007	*Rht-B1a*	*Rht-D1a*	-3	Agriculture Canada, Winnipeg, MB
Carberry	2009	*Rht-B1b*	*Rht-D1a*	+5	Agriculture Canada, Swift Current, SK
CDC Kernen	2009	*Rht-B1a*	*Rht-D1a*	+2	Crop Development Center, Saskatoon, SK
CDC Stanley	2009	*Rht-B1a*	*Rht-D1a*	0	Crop Development Center, Saskatoon, SK

[a] Iqbal et al., 2016, [b] Chen et al., 2016, [c] Iqbal et al., (Unpublished data), [d] based on AC Barrie, [e] Government of Alberta

Table 4-2. Soil properties prior to seeding at 0-30cm depth in each location during 2013 to 2015

	2013				2014				2015			
	ERS[a]		SARS[b]	Lamont	ERS		SARS	Lamont	ERS		SARS	Lamont
	Con.[c]	Org.[d]	Con.	Org.	Con.	Org.	Con.	Org.	Con.	Org.	Con.	Org.
NO_3-N (kg ha^{-1})	54.9	158.0	72.9	116.6	37.0	117.7	235.4	54.9	23.5	32.5	47.1	125.5
P (kg ha^{-1})	62.8	269.0	56.0	13.5	22.4	62.8	727.4	303.8	78.5	134.5	48.2	17.9
K (kg ha^{-1})	1332.7	1924.5	267.9	121.1	631.0	720.7	3571.0	2463.6	736.4	919.1	469.6	238.7
SO_4-S (kg ha^{-1})	33.6	72.9	24.7	84.1	15.7	20.2	93.0	67.3	13.5	30.3	25.8	654.6
pH	6.6	6.6	7.6	8.3	6.3	6.1	8.1	6.9	6.4	6.7	7.6	8
EC (dS/m)	0.57	0.57	0.475	0.65	0.39	0.68	0.52	0.09	0.39	0.6	0.78	1.88
OM (%)	11.7	9	9.3	6.9	10.5	12.9	7.5	4	14.4	NA[e]	NA	NA

[a] Edmonton research station, [b] St. Albert research station, [c] Conventional, [d] Organic, [e] Not obtained.

Table 4-3. Mean, variance and reduction of organic sites against conventional sites for agronomic and NUE traits.

Trait[d]		Conventional				Organic				Reduction (%)	Combined		
		Mean	E[a]	G[b]	E*G	Mean	E	G	E*G	*1-(Org/Con)*	G	M[c]	G*M
Grain yield	**t ha^{-1}**	3.3	14 ***	52 ***	9 ***	1.6	78 ***	6 ***	3 **	0.50	***	**	***
Protein	**%**	15.7	40 ***	18 ***	9	15.3	21 ***	9 ***	16	0.02	***		**
HI	**% DM**	0.35	8 ***	40 ***	8	0.23	48 ***	15 ***	9 **	0.35	***	**	***
NHI	**% N**	0.60	15 ***	36 ***	9	0.47	54 ***	14 ***	7	0.22	***	*	*
TotalDM	**t ha^{-1}**	9.7	28 ***	9 ***	14	7.6	61 ***	7 ***	7 *	0.21	***		
StemDM	**t ha^{-1}**	6.4	18 ***	18 ***	14	6.0	52 ***	10 ***	8 **	0.06	***		
GNtha	**kg ha^{-1}**	97	14 ***	50 ***	8 ***	47	82 ***	4 ***	3 ***	0.51	***	**	***
SNtha	**kg ha^{-1}**	64	20 ***	18 ***	12	58	56 ***	8 ***	8 **	0.10	***		
NUE	**kg ha^{-1}**	15.6	53 ***	26 ***	6 ***	19.8	90 ***	2 ***	1	-0.27	***		***
NutE	**t DM t^{-1} N**	20.9	11 ***	38 ***	9	16.2	50 ***	16 ***	7 *	0.23	***	*	**
NupE	**% N**	0.8	67 ***	4 ***	6	1.3	87 ***	1 ***	2	-0.70	***		**

*P value <0.05, **P value <0.01, ***P value <0.001, non-significant P value is not presented. [a] environment, [b] genotype, [c] management, [d] GNtha: grain N yield, HI: harvest index, NHI: nitrogen harvest index, NUE: nitrogen use efficiency, NupE: nitrogen uptake efficiency, NutE: nitrogen utilization efficiency, SNtha: stem nitrogen yield: StemDM: stem dry matter; SNper: stem nitrogen percentage, TotalNtha: total nitrogen yield, TotalDM: total dry matter.

Table 4-4. Means and relative ranks of fifteen CWRS wheat cultivars for grain yield, protein, carbon to nitrogen (C:N) ratio, Total N yield (TotalNtha), Grain N yield (GNtha), Stem N yield (SNtha), and Nitrogen use efficiency (NUE) traits in conventional and organic management systems during 2013 to 2015.

Cultivar	NUE (kg ha^{-1})			NUtE (t Dm t^{-1} N)			NUpE (% N)		
	Con	Org	Red %	Con	Org	Red %	Con	Org	Red %
AC Barrie	16.2 (8)	21.0 (6)	-0.30 (9)	20.2 (10)	14.9 (12)	0.26 (13)	0.81 (3)	1.45 (1)	-0.79 (10)
Carberry	18.8 (1)	19.6 (9)	-0.05 (1)	25.3 (1)	19.9 (1)	0.21 (7)	0.75 (7)	1.12 (15)	-0.49 (2)
CDC Go	18.2 (4)	20.0 (8)	-0.10 (2)	22.0 (7)	16.8 (6)	0.24 (10)	0.83 (1)	1.29 (7)	-0.55 (3)
CDC Kernen	18.6 (2)	22.2 (2)	-0.19 (4)	23.6 (4)	19.1 (2)	0.19 (4)	0.79 (4)	1.13 (14)	-0.42 (1)
CDC Stanley	17.8 (5)	23.4 (1)	-0.32 (11)	24.6 (2)	18.4 (4)	0.25 (12)	0.73 (12)	1.34 (5)	-0.84 (14)
CDC Teal	15.2 (9)	21.7 (4)	-0.42 (13)	20.9 (8)	17.1 (5)	0.18 (3)	0.73 (10)	1.33 (6)	-0.82 (12)
Garnet	10.7 (15)	16.2 (15)	-0.51 (14)	16.3 (14)	14.0 (13)	0.14 (1)	0.66 (15)	1.22 (11)	-0.83 (13)
Harvest	16.6 (7)	19.6 (10)	-0.18 (3)	22.6 (5)	16.5 (7)	0.27 (14)	0.74 (8)	1.23 (10)	-0.65 (5)
Katepwa	10.8 (14)	16.6 (14)	-0.55 (15)	14.6 (15)	12.0 (15)	0.18 (2)	0.74 (9)	1.42 (4)	-0.92 (15)
Marquis	13.6 (12)	16.8 (13)	-0.24 (6)	18.3 (13)	13.9 (14)	0.24 (11)	0.75 (6)	1.25 (8)	-0.66 (6)
Park	14.5 (11)	18.6 (11)	-0.28 (8)	20.4 (9)	15.6 (8)	0.24 (9)	0.72 (13)	1.23 (9)	-0.70 (8)
Red Bobs	13.5 (13)	17.7 (12)	-0.31 (10)	19.3 (12)	15.2 (10)	0.21 (6)	0.73 (11)	1.20 (13)	-0.64 (4)
Sinton	15.2 (10)	20.3 (7)	-0.34 (12)	19.5 (11)	15.1 (11)	0.23 (8)	0.79 (5)	1.42 (3)	-0.79 (11)
Superb	18.2 (3)	22.0 (3)	-0.21 (5)	22.6 (6)	15.5 (9)	0.32 (15)	0.81 (2)	1.44 (2)	-0.77 (9)
Unity	16.7 (6)	21.2 (5)	-0.27 (7)	23.7 (3)	18.9 (3)	0.20 (5)	0.72 (14)	1.20 (12)	-0.67 (7)
LSD[d] (0.05)	0.5	0.7	-	0.6	0.6	-	0.02	0.06	-

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	TotalNtha (kg ha^{-1})			GNtha (kg ha^{-1})			SNtha (kg ha^{-1})		
	Con	**Org**	**Red %**	**Con**	**Org**	**Red %**	**Con**	**Org**	**Red %**
AC Barrie	169 (3)	117.6 (2)	0.30 (6)	93.3 (8)	48.5 (7)	0.48 (9)	75.9 (3)	67.9 (4)	0.10 (4)
Carberry	152 (11)	85.9 (15)	0.44 (15)	101.8 (5)	47.6 (8)	0.53 (15)	50.3 (14)	37.3 (15)	0.26 (14)
CDC Go	175 (1)	105.1 (8)	0.40 (13)	102.1 (4)	50.2 (4)	0.51 (13)	72.3 (6)	55.4 (10)	0.23 (13)
CDC Kernen	165 (5)	93.8 (14)	0.43 (14)	104.3 (2)	52.3 (2)	0.50 (12)	60.5 (11)	42.0 (14)	0.31 (15)
CDC Stanley	156 (6)	110.0 (5)	0.30 (4)	106.3 (1)	56.6 (1)	0.47 (5)	49.8 (15)	52.9 (11)	-0.06 (1)
CDC Teal	153 (10)	107.1 (6)	0.30 (5)	89.1 (9)	50.2 (5)	0.44 (3)	63.6 (10)	56.4 (9)	0.11 (5)
Garnet	138 (15)	100.4 (11)	0.27 (2)	64.7 (15)	39.5 (14)	0.39 (1)	73.3 (5)	60.7 (7)	0.17 (11)
Harvest	155 (9)	98.5 (12)	0.36 (12)	96.3 (6)	47.3 (10)	0.51 (14)	58.6 (12)	51.9 (12)	0.11 (6)
Katepwa	155 (8)	117.1 (3)	0.25 (1)	65.2 (14)	37.9 (15)	0.42 (2)	90.1 (1)	78.1 (1)	0.13 (9)
Marquis	156 (7)	106.2 (7)	0.32 (10)	80.4 (12)	41.8 (13)	0.48 (8)	75.3 (4)	64.4 (5)	0.15 (10)
Park	151 (13)	104.4 (9)	0.31 (8)	86.4 (11)	45.2 (11)	0.48 (7)	64.4 (9)	59.4 (8)	0.08 (3)
Red Bobs	151 (12)	104.3 (10)	0.31 (9)	80.0 (13)	42.6 (12)	0.47 (6)	71.2 (7)	61.9 (6)	0.13 (8)
Sinton	166 (4)	115.5 (4)	0.30 (7)	88.8 (10)	47.6 (9)	0.46 (4)	77.5 (2)	68.3 (3)	0.12 (7)
Superb	170 (2)	120.2 (1)	0.29 (3)	103.2 (3)	52.1 (3)	0.50 (11)	66.5 (8)	70.0 (2)	-0.05 (2)
Unity	150 (14)	96.1 (13)	0.36 (11)	95.6 (7)	49.7 (6)	0.48 (10)	54.3 (13)	43.7 (13)	0.20 (12)
LSD (0.05)	3.9	4.6	-	2.3	1.6	-	3.4	4.8	-

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	NUE (kg ha^{-1})			NUtE (t Dm t^{-1} N)			NUpE (% N)		
	Con	**Org**	**Red %**	**Con**	**Org**	**Red %**	**Con**	**Org**	**Red %**
AC Barrie	16.2 (8)	21.0 (6)	-0.30 (9)	20.2 (10)	14.9 (12)	0.26 (13)	0.81 (3)	1.45 (1)	-0.79 (10)
Carberry	18.8 (1)	19.6 (9)	-0.05 (1)	25.3 (1)	19.9 (1)	0.21 (7)	0.75 (7)	1.12 (15)	-0.49 (2)
CDC Go	18.2 (4)	20.0 (8)	-0.10 (2)	22.0 (7)	16.8 (6)	0.24 (10)	0.83 (1)	1.29 (7)	-0.55 (3)
CDC Kernen	18.6 (2)	22.2 (2)	-0.19 (4)	23.6 (4)	19.1 (2)	0.19 (4)	0.79 (4)	1.13 (14)	-0.42 (1)
CDC Stanley	17.8 (5)	23.4 (1)	-0.32 (11)	24.6 (2)	18.4 (4)	0.25 (12)	0.73 (12)	1.34 (5)	-0.84 (14)
CDC Teal	15.2 (9)	21.7 (4)	-0.42 (13)	20.9 (8)	17.1 (5)	0.18 (3)	0.73 (10)	1.33 (6)	-0.82 (12)
Garnet	10.7 (15)	16.2 (15)	-0.51 (14)	16.3 (14)	14.0 (13)	0.14 (1)	0.66 (15)	1.22 (11)	-0.83 (13)
Harvest	16.6 (7)	19.6 (10)	-0.18 (3)	22.6 (5)	16.5 (7)	0.27 (14)	0.74 (8)	1.23 (10)	-0.65 (5)
Katepwa	10.8 (14)	16.6 (14)	-0.55 (15)	14.6 (15)	12.0 (15)	0.18 (2)	0.74 (9)	1.42 (4)	-0.92 (15)
Marquis	13.6 (12)	16.8 (13)	-0.24 (6)	18.3 (13)	13.9 (14)	0.24 (11)	0.75 (6)	1.25 (8)	-0.66 (6)
Park	14.5 (11)	18.6 (11)	-0.28 (8)	20.4 (9)	15.6 (8)	0.24 (9)	0.72 (13)	1.23 (9)	-0.70 (8)
Red Bobs	13.5 (13)	17.7 (12)	-0.31 (10)	19.3 (12)	15.2 (10)	0.21 (6)	0.73 (11)	1.20 (13)	-0.64 (4)
Sinton	15.2 (10)	20.3 (7)	-0.34 (12)	19.5 (11)	15.1 (11)	0.23 (8)	0.79 (5)	1.42 (3)	-0.79 (11)
Superb	18.2 (3)	22.0 (3)	-0.21 (5)	22.6 (6)	15.5 (9)	0.32 (15)	0.81 (2)	1.44 (2)	-0.77 (9)
Unity	16.7 (6)	21.2 (5)	-0.27 (7)	23.7 (3)	18.9 (3)	0.20 (5)	0.72 (14)	1.20 (12)	-0.67 (7)
LSD (0.05)	0.5	0.7	-	0.6	0.6	-	0.02	0.06	-

[a] Conventional, [b] Organic, [c] Reduction % based on 1- (organic/conventional), [d] Fisher's Least Significant Difference at $p<0.05$

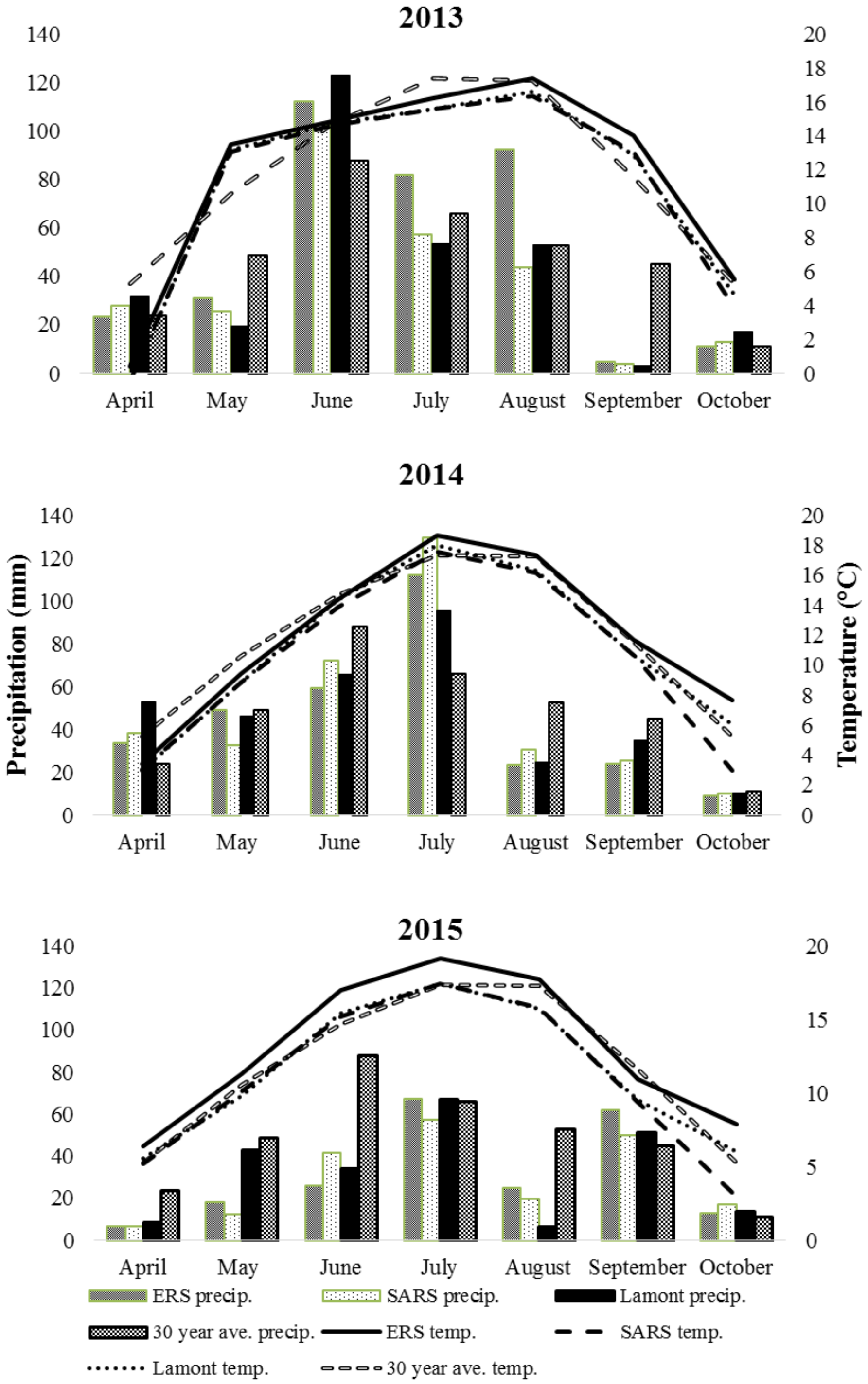
Table 4-5. Pearson correlation coefficients between Nitrogen use efficiency (NUE), nitrogen utilization efficiency (NutE), and nitrogen uptake efficiency (NupE) with agronomic traitsa in fifteen CWRS wheat cultivars in organic management systems during 2013 to 2015.

	NUE	NutE	NupE
Grain yield	0.22	0.30	0.15
Protein	-0.42	-0.23	-0.30
HI		0.86	-0.23
TotalDM	0.13	-0.58	0.40
StemDM		-0.71	0.38
TotalNtha		-0.37	0.28
NHI	0.11	0.92	-0.22

Only correlatValues only $p<0.05$ are shown, a HI: harvest index, TotalDM: total dry matter, StemDM: stem dry matter, NHI: nitrogen harvest index.

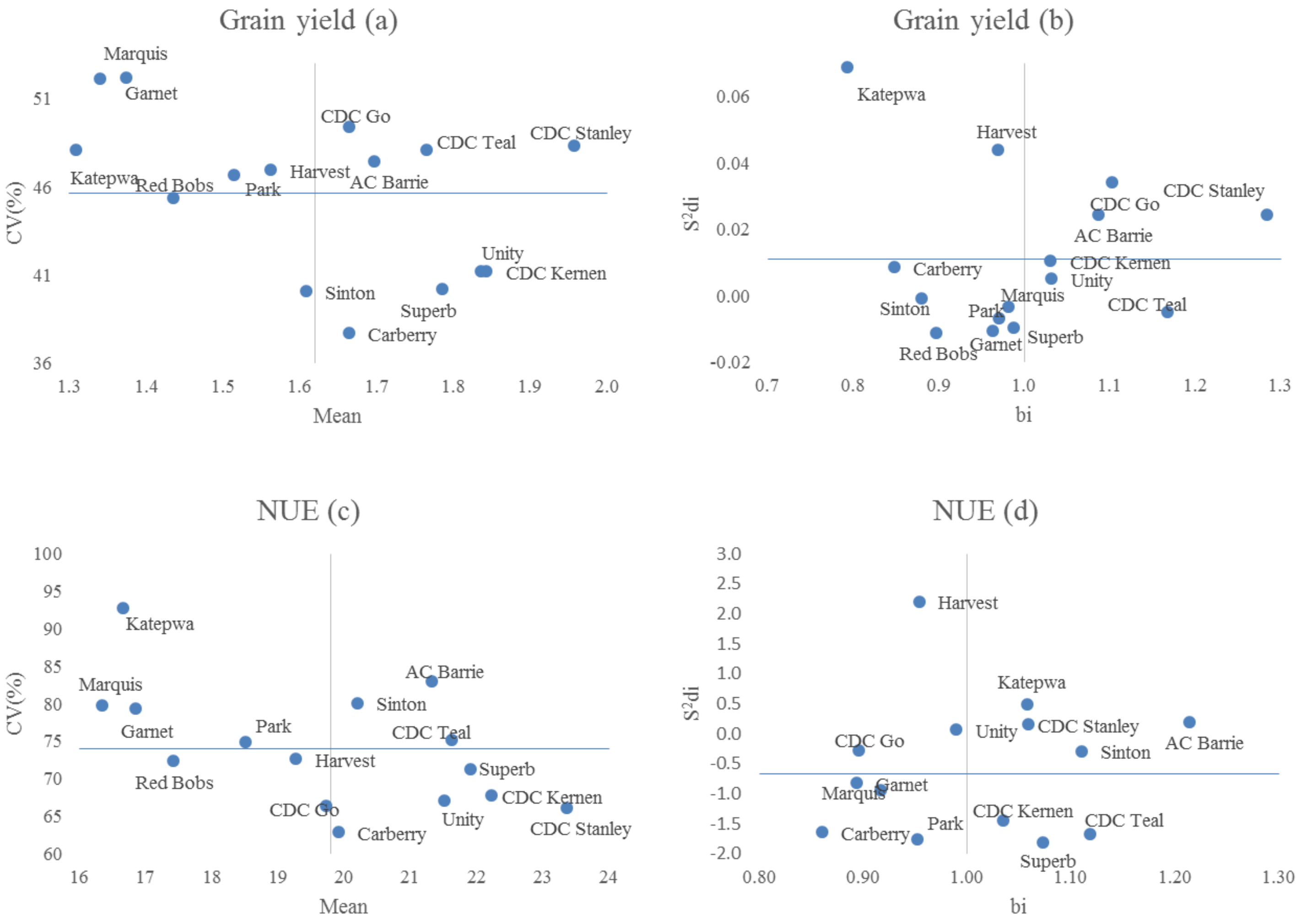
4.8 Figures

Figure 4-1. Weather data for three study years at three locations and the 30 years average during wheat growing season.



ERS: Edmonton Research Station, SARS: St. Albert Research Station, precip: precipitation, temp: temperature, ave: average.

Figure 4-2. Biplots for mean vs. coefficient of variation (CV) and joint regression coefficient (bi)^a vs. deviation from the regression line (s^{2}di)^b for grain yield, nitrogen use efficiency (NUE), nitrogen utilization efficiency (NUtE) and stem N yield (SNtha).



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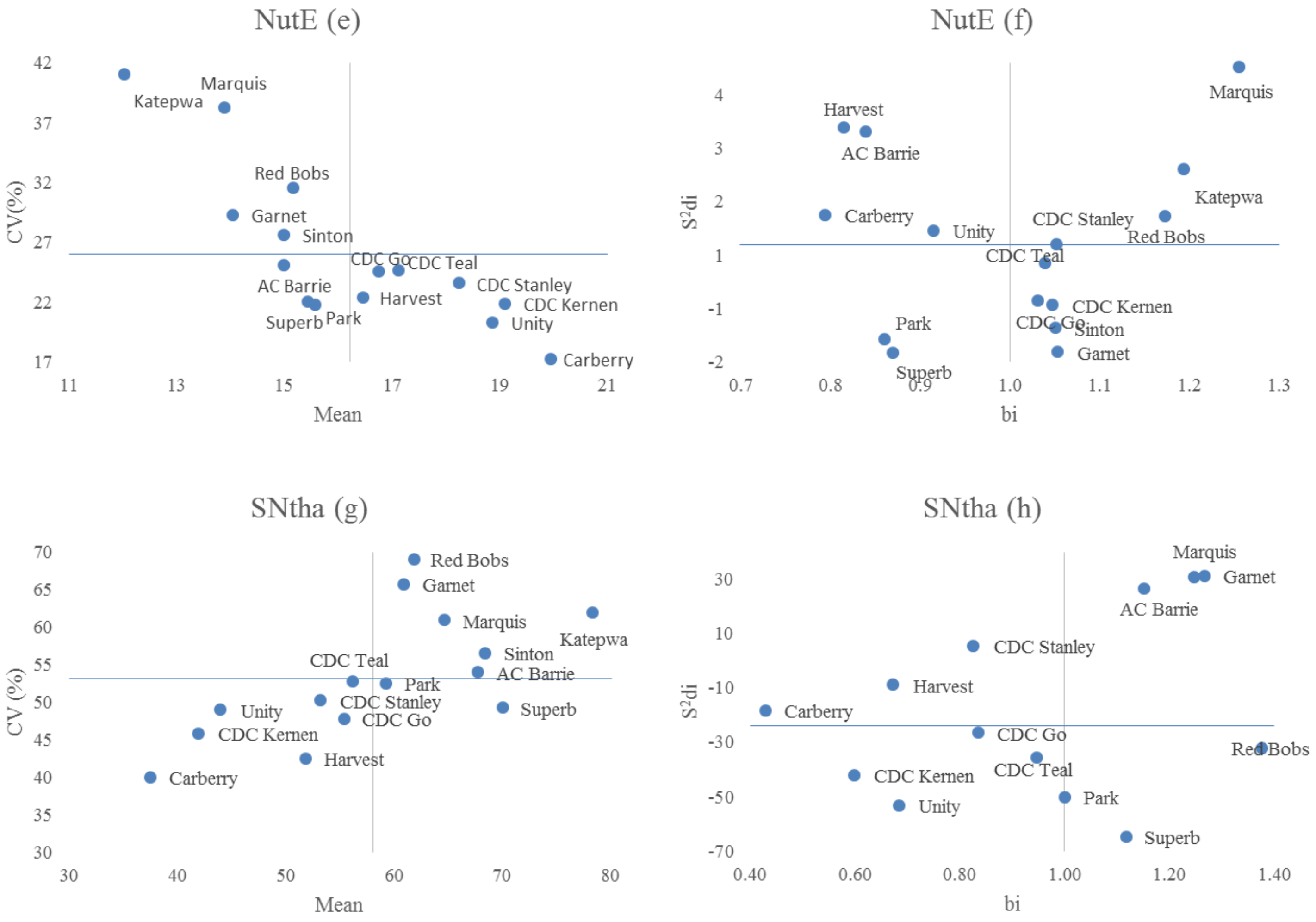


[a] regression coefficient, [b] regression deviation mean square. The lines in the figures are mean values except lines on x axes on the right figures (bi=1)

References

Anbessa, Y., Juskiw, P., Good, A., Nyachiro, J., and Helm, J. 2009. Genetic variability in nitrogen use efficiency of spring barley. Crop Science 49:1259-1269.

Anbessa, Y and Juskiw, P. 2012. Nitrogen fertilizer rate and cultivar interaction effects on nitrogen recovery, utilization efficincy, and agronomic performance of spring barley. ISRN Agronomy. 2012: 531647.

Anderson, W., M. Seymour and M. D'Antuono. 1991. Evidence for differences between cultivars in responsiveness of wheat to applied nitrogen. Australian Journal of Agricultural Research 42: 363-377.

Asif, M., R.-C. Yang, A. Navabi, M. Iqbal, A. Kamran, E. Lara, et al. 2015. Mapping QTL, selection differentials, and the effect of under organic and conventionally managed systems in the Attila× CDC go spring wheat mapping population. Crop Science 55: 1129-1142.

Austin, R., J. Bingham, R. Blackwell, L. Evans, M. Ford, C. Morgan, et al. 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. The Journal of Agricultural Science 94: 675-689.

Baresel, J., G. Zimmermann and H. Reents. 2008. Effects of genotype and environment on N uptake and N partition in organically grown winter wheat (Triticum aestivum L.) in Germany. Euphytica 163: 347-354.

Barraclough, P., H. Kuhlmann and A. Weir. 1989. The effects of prolonged drought and nitrogen fertilizer on root and shoot growth and water uptake by winter wheat. Journal of Agronomy and Crop Science 163: 352-360.

Berry, P., R. Sylvester-Bradley, L. Philipps, D. Hatch, S. Cuttle, F. Rayns, et al. 2002. Is the productivity of organic farms restricted by the supply of available nitrogen? Soil Use and Management 18: 248-255.

Bosshard, C., P. Sørensen, E. Frossard, D. Dubois, P. Mäder, S. Nanzer, et al. 2009. Nitrogen use efficiency of 15N-labelled sheep manure and mineral fertiliser applied to microplots in long-term organic and conventional cropping systems. Nutrient cycling in agroecosystems 83: 271-287.

Chen, H., N.P. Moakhar, M. Iqbal, C. Pozniak, P. Hucl and D. Spaner. 2016. Genetic variation for flowering time and height reducing genes and important traits in western Canadian spring wheat. Euphytica 208: 377-390.

Clark, S., K. Klonsky, P. Livingston and S. Temple. 1999. Crop-yield and economic comparisons of organic, low-input, and conventional farming systems in California's Sacramento Valley. American journal of alternative agriculture 14: 109-121.

Clarkson, D.T. 1985. Factors affecting mineral nutrient acquisition by plants. Annual review of plant physiology 36: 77-115.

Cormier, F., S. Faure, P. Dubreuil, E. Heumez, K. Beauchêne, S. Lafarge, et al. 2013. A multi-environmental study of recent breeding progress on nitrogen use efficiency in wheat (Triticum aestivum L.). Theoretical and Applied genetics 126: 3035-3048.

Davies, D. and J. Welsh. 2002. Weed control in organic cereals and pulses. Organic cereals and pulses. Papers presented at conferences held at the Heriot-Watt University, Edinburgh, and at Cranfield University Silsoe Campus, Bedfordshire, 6 and 9 November 2001, Chalcombe Publications.

Desai, R. and C. Bhatia. 1978. Nitrogen uptake and nitrogen harvest index in durum wheat cultivars varying in their grain protein concentration. Euphytica 27: 561-566.

Eberhart, S. A., and Russell, W. A. 1966. Stability parameters for comparing varieties. Crop Science 6(1): 36-40.

Eriksen, J., M. Askegaard and K. Kristensen. 2004. Nitrate leaching from an organic dairy crop rotation: the effects of manure type, nitrogen input and improved crop rotation. Soil Use and Management 20: 48-54.

Fedko, A. 2017. Varieties of cereal and oilseed crops for Alberta Agri-Fact. Alberta Agriculture and Forestry.

Górny, A.G., Z. Banaszak, B. Ługowska and D. Ratajczak. 2011. Inheritance of the efficiency of nitrogen uptake and utilization in winter wheat (Triticum aestivum L.) under diverse nutrition levels. Euphytica 177: 191-206.

Guttieri, M.J., K. Frels, T. Regassa, B.M. Waters and P.S. Baenziger. 2017. Variation for nitrogen use efficiency traits in current and historical great plains hard winter wheat. Euphytica 213: 87.

Haas, G., F. Wetterich and U. Köpke. 2001. Comparing intensive, extensified and organic grassland farming in southern Germany by process life cycle assessment. Agriculture, Ecosystems & Environment 83: 43-53.

Hadas, A., L. Kautsky, M. Goek and E.E. Kara. 2004. Rates of decomposition of plant residues and available nitrogen in soil, related to residue composition through simulation of carbon and nitrogen turnover. Soil Biology and Biochemistry 36: 255-266.

Hay, R. 1995. Harvest index: a review of its use in plant breeding and crop physiology. Annals of applied biology 126: 197-216.

Hildermann, I., A. Thommen, D. Dubois, T. Boller, A. Wiemken and P. Mäder. 2009. Yield and baking quality of winter wheat cultivars in different farming systems of the DOK long-term trial. Journal of the Science of Food and Agriculture 89: 2477-2491.

Hirel, B., T. Tétu, P.J. Lea and F. Dubois. 2011. Improving nitrogen use efficiency in crops for sustainable agriculture. Sustainability 3: 1452-1485.

Hokazono, S. and K. Hayashi. 2012. Variability in environmental impacts during conversion from conventional to organic farming: a comparison among three rice production systems in Japan. Journal of Cleaner Production 28: 101-112.

Hu, G., X. Liu, H. He, W. Zhang, H. Xie, Y. Wu, et al. 2015. Multi-Seasonal Nitrogen Recoveries from Crop Residue in Soil and Crop in a Temperate Agro-Ecosystem. PloS one 10: e0133437.

International Federation of Organic Agriculture Movement [IFOAM]. 2008. The principals of organic agriculture.

Iqbal, M., N.P. Moakhar, K. Strenzke, T. Haile, C. Pozniak, P. Hucl, et al. 2016. Genetic improvement in grain yield and other traits of wheat grown in western Canada. Crop Science 56: 613-624.

Kamiji, Y., J. Pang, S.P. Milroy and J.A. Palta. 2014. Shoot biomass in wheat is the driver for nitrogen uptake under low nitrogen supply, but not under high nitrogen supply. Field Crops Research 165: 92-98.

Kamran, A., H. Kubota, R.-C. Yang, H.S. Randhawa and D. Spaner. 2014. Relative performance of Canadian spring wheat cultivars under organic and conventional field conditions. Euphytica 196: 13-24.

Kayser, M., J. Müller and J. Isselstein. 2010. Nitrogen management in organic farming: comparison of crop rotation residual effects on yields, N leaching and soil conditions. Nutrient cycling in agroecosystems 87: 21-31.

Knudsen, M.T., I.S. Kristensen, J. Berntsen, B.M. Petersen and E.S. Kristensen. 2006. Estimated N leaching losses for organic and conventional farming in Denmark. The Journal of Agricultural Science 144: 135-149.

Kubota, H., M. Iqbal, S. Quideau, M. Dyck and D. Spaner. 2017. Agronomic and physiological aspects of nitrogen use efficiency in conventional and organic cereal-based production systems. Renewable Agriculture and Food Systems: 1-24.

Kubota, H., S.A. Quideau, P.J. Hucl and D.M. Spaner. 2015. The effect of weeds on soil arbuscular mycorrhizal fungi and agronomic traits in spring wheat (Triticum aestivum L.) under organic management in Canada. Canadian Journal of Plant Science 95: 615-627.

L-Baeckström, G., U. Hanell and G. Svensson. 2006. Nitrogen use efficiency in an 11-year study of conventional and organic wheat cultivation. Communications in soil science and plant analysis 37: 417-449.

Lassaletta, L., Billen, G., Grizzetti, B., Anglade, J., and Garnier, J. 2014. 50 year trends in nitrogen use efficiency of world cropping systems: the relationship between yield and nitrogen input to cropland. Environmental Research Letters. 9: 105011.

Le Gouis, J., D. Béghin, E. Heumez and P. Pluchard. 2000. Genetic differences for nitrogen uptake and nitrogen utilisation efficiencies in winter wheat. European Journal of Agronomy 12: 163-173.

Lin, H.-C., J.A. Huber, G. Gerl and K.-J. Hülsbergen. 2016. Nitrogen balances and nitrogen-use efficiency of different organic and conventional farming systems. Nutrient cycling in agroecosystems 105: 1-23.

Löschenberger, F., A. Fleck, H. Grausgruber, H. Hetzendorfer, G. Hof, J. Lafferty, et al. 2008. Breeding for organic agriculture: the example of winter wheat in Austria. Euphytica 163: 469.

Lynch, D. 2009. Environmental impacts of organic agriculture: A Canadian perspective. Canadian Journal of Plant Science 89: 621-628.

Mäder, P., A. Fliessbach, D. Dubois, L. Gunst, P. Fried and U. Niggli. 2002. Soil fertility and biodiversity in organic farming. Science 296: 1694-1697.

Mäder, P., D. Hahn, D. Dubois, L. Gunst, T. Alföldi, H. Bergmann, et al. 2007. Wheat quality in organic and conventional farming: results of a 21 year field experiment. Journal of the Science of Food and Agriculture 87: 1826-1835.

Mason, H. and D. Spaner. 2006. Competitive ability of wheat in conventional and organic management systems: a review of the literature. Canadian Journal of Plant Science 86: 333-343.

Mason, H.E., A. Navabi, B.L. Frick, J.T. O'Donovan and D.M. Spaner. 2007. The weed-competitive ability of Canada western red spring wheat cultivars grown under organic management. Crop science 47: 1167-1176.

McKenzie, R.H., L. Kryzanowski and D. Pauly. 2013. Agri-Fact: Fertilizer requirements of irrigated grain and oilseed crops. Government of Alberta.

Mohammadi, R., B. Sadeghzadeh, H. Ahmadi, N. Bahrami and A. Amri. 2015. Field evaluation of durum wheat landraces for prevailing abiotic and biotic stresses in highland rainfed regions of Iran. The Crop Journal 3: 423-433.

Moll, R., E. Kamprath and W. Jackson. 1982. Analysis and interpretation of factors which contribute to efficiency of nitrogen utilization. Agronomy Journal 74: 562-564.

Morgan, J.A. and W.J. Parton. 1989. Characteristics of ammonia volatilization from spring wheat. Crop Science 29: 726-731.

Murphy, K.M., K.G. Campbell, S.R. Lyon and S.S. Jones. 2007. Evidence of varietal adaptation to organic farming systems. Field Crops Research 102: 172-177.

Musyoka, M.W., N. Adamtey, A.W. Muriuki and G. Cadisch. 2017. Effect of organic and conventional farming systems on nitrogen use efficiency of potato, maize and vegetables in the Central highlands of Kenya. European Journal of Agronomy 86: 24-36.

Muurinen, S., J. Kleemola and P. Peltonen-Sainio. 2007. Accumulation and translocation of nitrogen in spring cereal cultivars differing in nitrogen use efficiency. Agronomy Journal 99: 441-449.

Nelson, A., S. Quideau, B. Frick, D. Niziol, J. Clapperton and D. Spaner. 2011. Spring wheat genotypes differentially alter soil microbial communities and wheat breadmaking quality in organic and conventional systems. Canadian Journal of Plant Science 91: 485-495.

Ortiz-Monasterio, R., K. Sayre, S. Rajaram and M. McMahon. 1997. Genetic progress in wheat yield and nitrogen use efficiency under four nitrogen rates. Crop Science 37: 898-904.

Osman, A., C. Almekinders, P. Struik and E.L. van Bueren. 2016. Adapting spring wheat breeding to the needs of the organic sector. NJAS-Wageningen Journal of Life Sciences 76: 55-63.

Pacheco, Á.V., Mateo; Alvarado, Gregorio; Rodríguez, Francisco; Crossa, José; Burgueño, Juan,. 2015. GEA-R (Genotype x Environment Analysis with R for Windows) Version 4.0. International Maize and Wheat Imrovement Center.

Pang, J., S.P. Milroy, G.J. Rebetzke and J.A. Palta. 2015. The influence of shoot and root size on nitrogen uptake in wheat is affected by nitrate affinity in the roots during early growth. Functional plant biology 42: 1179-1189.

Paulsen, H., U. Volkgenannt and E. Schnug. 2002. Contribution of organic farming to marine environmental protection. LANDBAUFORSCHUNG VOLKENRODE 52: 211-218.

Peoples, M.B., E.W. Boyer, K.W. Goulding, P. Heffer, V.A. Ochwoh, B. Vanlauwe, et al. 2012. Pathways of nitrogen loss and their impacts on human health and the environment.

Peterson, C., R. Graybosch, P. Baenziger and A. Grombacher. 1992. Genotype and environment effects on quality characteristics of hard red winter wheat. Crop Science 32: 98-103.

Pswarayi, H., H. Kubota, H. Estrada and D. Spaner. 2014. Evaluation of Wheat Cultivars to Test Indirect Selection or Organic Conditions. Agronomy Journal 106: 441-451.

Regehr, A., Oelbermann, M., Videla, C., and Echarte, L. 2015. Gross nitrogen mineralization and immobilization in temperate maize-soybean intercrops. Plant and Soil 391: 353-365.

Reid, T.A., R.-C. Yang, D.F. Salmon, A. Navabi and D. Spaner. 2011. Realized gains from selection for spring wheat grain yield are different in conventional and organically managed systems. Euphytica 177: 253-266.

Reid, T.A., R.-C. Yang, D.F. Salmon and D. Spaner. 2009. Should spring wheat breeding for organically managed systems be conducted on organically managed land? Euphytica 169: 239-252.

Robinson, D. 2001. Root proliferation, nitrate inflow and their carbon costs during nitrogen capture by competing plants in patchy soil. Plant and Soil 232: 41-50.

Rodrigues, O., J.C.B. Lhamby, A.D. Didonet and J.A. Marchese. 2007. Fifty years of wheat breeding in Southern Brazil: yield improvement and associated changes. Pesquisa Agropecuária Brasileira 42: 817-825.

Scow, K., O. Somasco, N. Gunapala, S. Lau, R. Venette, H. Ferris, et al. 1994. Transition from conventional to low-input agriculture changes soil fertility and biology. California

Agriculture 48: 20-26.

Seufert, V., N. Ramankutty and J.A. Foley. 2012. Comparing the yields of organic and conventional agriculture. Nature 485: 229-232.

Shindo, H. and T. Nishio. 2005. Immobilization and remineralization of N following addition of wheat straw into soil: determination of gross N transformation rates by 15 N-ammonium isotope dilution technique. Soil Biology and Biochemistry 37: 425-432.

Singh, V. and A. Arora. 2001. Intraspecific variation in nitrogen uptake and nitrogen utilization efficiency in wheat (Triticum aestivum L.). Journal of Agronomy and Crop Science 186: 239-244.

Smith, J., R. Papendick, D. Bezdicek and J. Lynch. 1993. Soil organic matter dynamics and crop residue management. Soil Microbial Ecology, Marcel Dekker, New York: 65-95.

Snyder, C. and D. Spaner. 2010. The sustainability of organic grain production on the Canadian Prairies—a review. Sustainability 2: 1016-1034.

Spiess, D. 2015. Soil group map of Alberta. Alberta Agriculture and Forestry. Available www1.agric.gov.ab.ca/soils/soils.nsf/soilgroupmap (Accessed Nov. 28, 2017)

Tilman, D., K.G. Cassman, P.A. Matson, R. Naylor and S. Polasky. 2002. Agricultural sustainability and intensive production practices. Nature 418: 671.

Tkachuk, R. 1969. Nitrogen-to-protein conversion factors for cereals and oil-seed meals. Cereal Chemistry.

Unger, P.W. 1991. Organic matter, nutrient, and pH distribution in no-and conventional-tillage semiarid soils. Agronomy Journal 83: 186-189.

Vigil, M. and D. Kissel. 1991. Equations for estimating the amount of nitrogen mineralized from crop residues. Soil Science Society of America Journal 55: 757-761.

Wang, H., T. McCaig, R. DePauw, F. Clarke and J. Clarke. 2003. Physiological characteristics of recent Canada Western Red Spring wheat cultivars: Components of grain nitrogen yield. Canadian journal of plant science 83: 699-707.

Wiebe, L. 2015. Examining the growth and nitrogen economy of organically selected spring wheat cultivars (Doctoral dissertation). The University of Manitoba, Manitoba, Canada.

Wolfe, M., J. Baresel, D. Desclaux, I. Goldringer, S. Hoad, G. Kovacs, et al. 2008. Developments in breeding cereals for organic agriculture. Euphytica 163: 323.

5.0 General discussions and Conclusion

5.1 Introduction

Wheat is an important cereal crop and has been incorporated in cereal-based cropping systems. There are two emerging challenges in the systems. First challenge is to increase food production to meet the immediate needs of the increased population. Second is to reduce negative impacts on environmental and human health caused by intensive agricultural practices specifically by excessive application of N fertilizer (Peoples et al., 2012; Hiroshi et al., 2017).

Conventional agricultural practices play a pivotal role in feeding the growing global population with high yielding cultivar and agrochemicals including synthetic N fertilizer. However, agricultural-related environmental issues are a major issue in sustainable future food production. Organic agriculture emerged as a counterpart to conventional but unsustainable agricultural practices, but inconsistent/low productivity in organic practices needs to be improved (Entz et al., 2001). Globally, cereal nitrogen use efficiency (NUE) including wheat was inefficient (i.e., 47% of the total available N) (Lassaletta et al., 2014). Thus, improved NUE should be a mean to solve these two challenges together in two management systems.

The distinctive differences between organic and conventional agriculture directly influence their N sources and cycling. Thus, important traits or superior cultivars for grain yield and NUE might also differ between them. Modern breeding programs may have restricted genetic diversity, and advantageous alleles or genes for valuable traits in improved grain yield and NUE may have been lost. Mason and colleagues (2007) found three important traits for grain yield under organic management; plant height, early maturity and tillering capacity. However, short plant stand is one of the important traits in modern wheat cultivars, contributing increased grain yield in conventional agriculture. This result suggests that traits that contribute to high grain yield in conventional systems may not be important for obtaining high grain yield under organic management systems. Therefore, the identification of genetic variability and important traits that are associated with NUE in each cultivation system is necessary for efficient improvement in wheat yield.

Therefore, the objectives of this thesis are to 1) determine the effect of days to flowering and maturity on grain yield and other agronomic traits in spring wheat germplasms grown under conventional and organic management, 2) to assess genetic variability for grain yield and NUE traits in Canada Western Red Spring (CWRS) cultivars grown under low and high N condition in conventional systems as well as in organic systems, 3) to assess the relative performance of CWRS for grain yield and NUE traits grown under high and low N condition in conventional management systems and select the best candidates as parents for further breeding programs, 4) to estimate genetic progress of grain yield and NUE traits 5) to assess the relative performance of CWRS cultivars for grain yield, NUE and stem N yield under organic management.

5.2 General discussions

5.2.1 Relative performance of Canadian spring wheat cultivars under organic and conventional field conditions

Producing higher yields under organic conditions is generally hampered by weeds and lower nutrient supply. In wheat, certain adaptive traits like early season vigour, tall height, and shorter life cycle have been reported to help plants to compete with weeds and produce satisfactory yields. In this experiment we tested the hypothesis that early flowering and maturity conferred by insensitive vernalization alleles *Vrn-A1a* and/or *Vrn-B1* confer a yield advantage under organic conditions in Canadian spring wheat germplasm. There were no differences between the cultivars having insensitive *Vrn* allele at either single locus (*Vrn-A1a*) or two (*Vrn-*

A1a, Vrn-B1) under organic and conventional field conditions; except for days to maturity, where cultivars having only *Vrn-A1a* allele matured earlier. This earlier maturity did not translate to any yield advantage under organic field condition. Overall, the cultivars grown under organic conditions were earlier flowering, lower yielding with lower test weight compared to the conventional management system. Significant cultivar × management interactions were found for grain yield, grain protein content and grain fill rate. For grain protein content, cross-over interactions of the cultivars between the management systems were observed. Three spring wheat cultivars (Marquis, Unity and Minnedosa) exhibited minimal comparative loss in grain yield and grain protein content under organic field conditions, and hence could potentially serve as parents for organic wheat breeding programs.

5.2.2 Investigating genetic progress and variation for nitrogen use efficiency in spring wheat (*Triticum aestivum* L.)

Improved nitrogen use efficiency (NUE) is required to increase wheat yields while reducing N losses to the evironment. This study was conducted to investigate genotypic variation and relationships among agronomic and NUE traits in Canada Western Red Spring (CWRS) wheat (*Triticum aestivum* L.) cultivars for further improvement of NUE. Trials were carried out over three years at two locations in central Alberta, Canada with two levels of N management (high and low N). Genotype (G) × environment (E) and G × Management (M) interactions showed a unique pattern. G × E interaction was statistically significant for traits associated with vegetative growth, while G × M interaction was significant for important yield and NUE traits. There were significant positive correlations between total dry matters at harvest and nitrogen uptake efficiency (NUpE). The effect of *Rht-1b* alleles was prominent under high N treatment and contributed to increasing NUE traits. However, cultivars with *Rht-1b* alleles presented inconsistent results in NUpE, indicating that dwarfing *Rht* alleles have pleiotropic mechanisms associated to N uptake. Grain yield, NUE, and nitrogen utilization efficiency (NUtE) exhibited genetic improvement over time only in high N. The result indicated increases in grain yield were mainly attributed to improved harvest index (HI), suggesting an improvement in assimilated carbon rather than N partitioning efficiency. Further progress in NUE is likely to be obtained by breeding lines that combine cultivars with high HI, NHI and NUtE with cultivars exhibiting good NUpE, using total dry matter production as a selection criterion.

5.2.3 Genetic differences for nitrogen use efficiency and stem nitrogen yield in spring wheat (*Triticum aestivum* L.) under organic management

High costs and environmental issues associated with the excessive usage of nitrogen (N) fertilizer have necessitated improving N use efficiency (NUE) in cereal-based organic systems. Also improvement in the N cycle in fields is critical to achieve the goal of sustainable crop production. Using fifteen spring wheat (*Triticum aestivum* L.) genotypes, we conducted a study in two organic and two conventional locations across the central Alberta region from 2013 to 2015 to determine the effect of management, genetic variability, and genotype on performance of agronomic and NUE traits. Average grain yield over the three years of testing was 50 % less in organic systems than in conventional systems, while Stem N yield and NUE were not statistically different between management systems. Analysis of variance revealed significant effects of genotype (G), environment (E), and G×E interactions on grain and stem N yield, and NUtE in organic sites. Modern genotype, Superb, CDC Kernen, and CDC Stanley were superior and stable across the tested organic environments in important traits including grain yield, and NUE compared to other modern genotypes. These cultivars had high grain yield by virtue of different traits. This result led an assumption that the ideotype approach may not be the best approach for organic wheat breeding. The semi-dwarf type cultivar Superb exhibited improved N uptake efficiency relative to tested modern cultivars, which is presumably associated with large stem biomass production. The tall modern cultivar, CDC Kernen produced more grain by overcoming weed pressure. On the other hand, Superb showed a large Total and stem N yield under organic management. Superb may, therefore, be used as donor parent for breeding cultivars with high grain and stem N yield with NUE for sustainable organic production systems.

5.3 General conclusion

Over the last half century, synthetic N fertilizer has been an essential input for increasing crop yield to meet growing demand. However, expecting increased production cost and contribution to negative environmental impact of inefficient N fertilizer application in conventional agriculture as well as typical low productivity in organic in organic agriculture raised necessity for improved crop NUE across agricultural systems.

Improvement of NUE while maintaining grain yield is possible under both conventional and organic management systems, but requires understanding of the complex traits associated with NUE. In a comparative study, we found a cross-over interaction of genotype × management system for grain protein. We also identified that earlier maturity associated to vernalization genes did not translate grain yield advantage in organic systems. The best three cultivars (i.e. Marquis, Unity and Minnedosa) for grain yield and protein content defied the particular hypothesis that old cultivars perform better under organic conditions. This indicated that cultivar choice have a significant impact on grain yield, protein content, thus NUE traits. As well, it is speculated that modern Canadian Western Spring wheat maintain important traits associated to improved NUE.

Under two soil N levels in conventional systems, grain yield and NUE traits had significant genotype × management (two N levels) interaction. Grain yield, NUE, and nitrogen utilization efficiency (NUtE) exhibited genetic improvement over time only under high N conditions. This indicated increases in grain yield were mainly attributed to improved harvest index (HI), suggesting an improvement in assimilated carbon rather than N partitioning efficiency for grain development. The positive correlation of total dry biomass production with NUpE in this study presented a possibility to further improved NUE by selecting lines with a large biomass production. This would enable breeders to concurrently improve grain yield and NUE in CWRS wheat class.

Under organic management, environmental variability (e.g. soil N levels, weed stress) is large and difficult to predict. Therefore, cultivars for organic farming should be stable for important yield and NUE traits. Also, a large stem N yield at harvest could be an advantageous trait to achieve long-term sustainable agriculture. The positive correlation of total dry biomass production with NUpE was also found in organic managements. This finding suggests that total biomass production may be an important tool for breeders to select cultivars with better NUpE regardless of cultivation systems. Result from the thesis indicated that modern CWRS cultivars has potential to improve grain yield and NUE through breeding lines that integrate the cultivars that have great dry biomass production, thus high NUpE with cultivars that are high in HI and NHI, thus high NUtE.

5.4 Future research areas

Improved NUE can contribute to increasing grain productivity and reducing environmental problems together in conventional and organic systems. Under organic management, cultivars had earlier flowering, lower grain yields, and lower test weights. We also found cross-over interaction of the cultivars for grain protein content with management systems. Improving NUE without the loss in grain yield and protein content in CWRS class is a critical goal for breeders. The amount of grain protein produced partly depends on wheat abilities to uptake and translocate assimilate nitrogen. Therefore, studies for evaluate pre- and post-anthesis dry mass production and N uptake in CWRS wheat as well as an ability of CWRS cultivars to translocate assimilated/absorbed N for grain in each management system are needed to achieve the goal.

N cycling in agroecosystem consists of several different elements. The studies in this thesis research mainly focused on the genetic variation for NUE and revealed potential parents/traits for improved NUE in CWRS wheat. However, environmental conditions play an important role in determining NUE, and future studies should be conducted under controlled conditions. For instance, mobility and availability of soil N is largely dependent on soil moisture, and therefore soil moisture-controlled greenhouse studies or irrigated/rainfed field studies to evaluate NUE in CWRS cultivars could provide valuable information to reduce environmental variation.

Total dry mass could be a good criterion for selecting cultivars that possess good NUpE in both systems. Under organic conditions, ability to compete resources against weeds should be an important factor for maintaining large dry mass production. Therefore, controlled field trials with artificially created homogenous weed density and species would help to concurrently evaluate wheat competitiveness and dry mass production thus NUpE under weed stress.

There has been a demand for developing wheat cultivars that suit to organic system due to its uncontrollable variability (e.g. weed pressure). This study found out that high grain yielding cultivars have different characteristics, which may make the ideotype breeding approach difficult. Therefore, detailed studies of performance in the three CWRS cultivars (CDC Kernen, CDC Stanley, Superb) are necessary to understand their strategies for obtaining high grain yield under organic management.

Studies presented in this thesis utilized the common calculation method to obtain nitrogen use efficiency (NUE) values, and interpreted the results for assessing genetic variation of NUE among cultivars in different management systems. As outlined in my literature review, there are different N sources and pathways in each management system. There are also some errors in the classical calculation formula used in this thesis research. Therefore, the choice of calculation formula employed depends on the research questions at hand. It is imperative that future studies adapt different approaches to assess wheat NUE from different angles.

5.5 Original contributions to knowledge

Threats to global food security associated with inefficiency and unsustainability in agricultural practices need immediate attention. Improved efficiency in nitrogen use in crops contributes to ensuring sustainable solutions. However, our understanding of nitrogen use efficiency in spring wheat that is bred for northern growing conditions is limited. The differences in approaches for improved nitrogen use efficiency (NUE) between conventional and organic agriculture are poorly understood. Therefore, we need to understand performance of grain yield and NUE in spring wheat under conventional and organic agriculture to select/breed cultivars suited in each management.

Chapter 1 in this thesis is a review of the literature on agronomic and physiological aspects of NUE in organic and conventional cereal-based systems. To the extent of my knowledge, this is the first review to discuss different strategies for improved NUE in cereal crops in two management systems (conventional and organic) highlighting characteristics of N cycling in each system. This review provides bridging knowledge between cereal physiological-and agronomic-based mechanisms of N cycle in each system. Reader can anticipate understanding research topics for improved NUE in cereal-based systems.

The study presented in Chapter 2 examined relative performance of Canadian spring wheat in organic and conventional agriculture systems. The importance of early maturity for grain yield in organic systems has been studied (Mason et al., 2008). However, the potentially advantageous effects of earlier maturity associated to vernalization genes on grain yield under organic systems had not been studied. The result presented that earlier maturity by vernalization genes had no advantageous effect on grain yield under organic systems. Rather significant cultivar × management system interaction for grain yield indicated the importance of the interaction effect for grain yield under organic conditions. We also found cross-over interactions of cultivars for grain protein between the management systems, suggesting a necessity of specific cultivar choice/breeding for organic agriculture for improved grain protein content and NUE.

The study in Chapter 3 investigated the genetic variation and genetic progress for grain yield and NUE in fifteen Canada Western Red Spring (CWRS) wheat cultivars under high and low N conditions in conventional agriculture. Several studies examined genetic variability and progress for NUE in winter wheat (Cormier et al., 2013; Guttieri et al., 2017), but information on NUE in spring wheat is little. We reported significant genetic variation for NUE among CWRS wheat cultivars. Genetic grain for NUE was only observed in high N. Genotype × fertilizer interactions were significant and more important than genotype × environment interactions for grain yield and NUE traits. The positive correlations between total dry matter and nitrogen uptake efficiency (NUpE) also suggested that the total biomass production may be a good selection criterion for selecting cultivars with high NUpE. Breeding for increasing grain yield of CWRS cultivars has simultaneously improved nitrogen utilization efficiency (NUtE). This study provided information about possible traits that can be used for improved NUE in CWRS wheat. Future breeding programs should utilize genetic materials that have great N partitioning and acquisition ability for improved NUE.

In Chapter 4, we conducted a study under organic and conventional systems to determine the effect of managements, genetic variability, and genotype performance on NUE traits and stem N yield. Analysis of variance revealed significant effects of genotype (G), environment (E), and G×E interactions on grain and stem N yield, and NUtE in organic systems. Modern wheat genotypes Superb, CDC Kernen, and CDC Stanley were superior and stable across the tested organic environments in grain yield and NUE, compared to other modern genotypes. These cultivars appeared to have high grain yields by virtue of different traits. The semi-dwarf type cultivar Superb exhibited great N uptake ability, which is presumably associated with large stem biomass production. The tall modern cultivar, CDC Kernen produced more grain by overcoming weed pressure and CDC Stanley has a good package of disease resistance. Superb also showed a large total and stem N yield under organic management. Superb may, therefore, be used as donor parent for breeding cultivars with high grain and stem N yield with NUE for sustainable organic production systems.

The significance of this thesis research is advancement on previously existing knowledge in the field of sustainable cereal production. The physiological- and agronomic-based mechanisms of N cycle in cereal-based cropping system in conventional and organic systems are reviewed. Effects of earlier maturity associated to vernalization genes on grain yield in organic systems and effect of genetic × management interactions in grain protein content were evaluated. Genetic progress for NUE in CWRS cultivars during 1910 to 2009 was identified. Possible traits/cultivars for improvement of N use in CWRS wheat cultivars in each system were proposed. Early maturity is advantageous for wheat to maintain high yield in the northern Great Plains; however, under organic conditions, acceleration in maturity does not reflect increased grain yield. Breeding could further improve wheat NUE through selecting lines that integrate a high N partitioning trait with large N uptake and stem dry matter production traits. The choice of cultivars could also be an important impact on soil N source for succeeding crops in organic systems.

References

Cormier, F., S. Faure, P. Dubreuil, E. Heumez, K. Beauchêne, S. Lafarge, et al. 2013. A multi-environmental study of recent breeding progress on nitrogen use efficiency in wheat (*Triticum aestivum* L.). Theoretical and Applied Genetics 126: 3035-3048.

Entz, M..H., Guilford, R., and Gulden, R. 2001. Crop yield and soil nutrient status on 14 organic farms in the eastern portion of the northern Great Plains. Canadian Journal of Plant Science 81:351-354.

Guttieri, M.J., K. Frels, T. Regassa, B.M. Waters and P.S. Baenziger. 2017. Variation for nitrogen use efficiency traits in current and historical great plains hard winter wheat. Euphytica 213: 87.

Kubota, H., M. Iqbal, S. Quideau, M. Dyck and D. Spaner. 2017. Agronomic and physiological aspects of nitrogen use efficiency in conventional and organic cereal-based production systems. Renewable Agriculture and Food Systems: 1-24.

Lassaletta, L., Billen, G., Grizzetti, B., Anglade, J., and Garnier, J. 2014. 50 year trends in nitrogen use efficiency of world cropping systems: the relationship between yield and nitrogen input to cropland. Environmental Research Letters. 9: 105011.

Mason, H.E., A. Navabi, B.L. Frick, J.T. O'Donovan and D.M. Spaner. 2007. The weed-competitive ability of Canada western red spring wheat cultivars grown under organic management. Crop science 47: 1167-1176.

Peoples, M.B., E.W. Boyer, K.W. Goulding, P. Heffer, V.A. Ochwoh, B. Vanlauwe, et al. 2012. Pathways of nitrogen loss and their impacts on human health and the environment.

References of the thesis

Abbasi, M. K., Tahir, M. M., and Rahim, N. 2013. Effect of N fertilizer source and timing on yield and N use efficiency of rainfed maize (*Zea mays* L.) in kashmir–pakistan. Geoderma 195:87-93.

Acreche, M.M., and G.A. Slafer. 2009. Variation of grain nitrogen content in relation with grain yield in old and modern Spanish wheats grown under a wide range of agronomic conditions in a Mediterranean region. Journal of Agricultural Science 147: 657-667.

Agriculture and Agri-Food Canada. 2009. Certified organic production statistics for Canada. http://www4.agr.gc.ca/AAFC-AAC/display-afficher.do?id=1312385802597&lang=eng (accessed June 13 2013).

Ahrens, T., Lobell, D., Ortiz-Monasterio, J., Li, Y., and Matson, P. 2010. Narrowing the agronomic yield gap with improved nitrogen use efficiency: A modeling approach. Ecological Applications 20:91-100.

Alberta Agriclture and Forestory. 2015. http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/sag6301 (accessed April 2 2017).

Alva, A., Fan, M., Qing, C., Rosen, C., and Ren, H. 2011. Improving nutrient-use efficiency in chinese potato production: Experiences from the United States. Journal of Crop Improvement 25:46-85.

Amanullah, Iqbal, A., Ali, A., Fahad, S., and Parmar, B. 2016. Nitrogen source and rate management improve maize productivity of smallholders under semiarid climates. Frontiers in Plant Science 7.

Amiri, A., and Rafiee, M. 2013. Effect of soil inoculation with azospirillum and azotobacter bacteria on nitrogen use efficiency and agronomic characteristics of corn. Annals of Biological Research 4:77-79.

Amlinger, F., Götz, B., Dreher, P., Geszti, J., and Weissteiner, C. 2003. Nitrogen in biowaste and yard waste compost: Dynamics of mobilisation and availability-a review. European Journal of Soil Biology 39:107-116.

Amossé, C., Jeuffroy, M.-H., and David, C. 2013. Relay intercropping of legume cover crops in organic winter wheat: Effects on performance and resource availability. Field Crops Research 145:78-87.

Amossé, C., Jeuffroy, M.-H., Mary, B., and David, C. 2014. Contribution of relay intercropping with legume cover crops on nitrogen dynamics in organic grain systems. Nutrient Cycling in Agroecosystems 98:1-14.

An, D., Su, J., Liu, Q., Zhu, Y., Tong, Y., Li, J., Jing, R., Li, B., and Li, Z. 2006. Mapping QTLs for nitrogen uptake in relation to the early growth of wheat (*Triticum aestivum* L.). Plant and Soil 284:73-84.

Anbessa, Y., Juskiw, P., Good, A., Nyachiro, J., and Helm, J. 2009. Genetic variability in nitrogen use efficiency of spring barley. Crop Science 49:1259-1269.

Anbessa, Y and Juskiw, P. 2012. Nitrogen fertilizer rate and cultivar interaction effects on nitrogen recovery, utilization efficincy, and agronomic performance of spring barley. ISRN Agronomy. 2012: 531647.

Anderson, W., M. Seymour and M. D'Antuono. 1991. Evidence for differences between cultivars in responsiveness of wheat to applied nitrogen. Australian Journal of Agricultural Research 42: 363-377.

Andrews, M., Lea, P. J., Raven, J., and Lindsey, K. 2004. Can genetic manipulation of plant nitrogen assimilation enzymes result in increased crop yield and greater N-use efficiency? An assessment. Annals of Applied Biology 145:25-40.

Andrews, M., Raven, J., and Sprent, J. 2001. Environmental effects on dry matter partitioning between shoot and root of crop plants: Relations with growth and shoot protein concentration. Annals of Applied Biology 138:57-68.

Askegaard, M., Olesen, J. E., Rasmussen, I. A., and Kristensen, K. 2011. Nitrate leaching from organic arable crop rotations is mostly determined by autumn field management. Agriculture, Ecosystems and Environment 142:149-160.

Asif, M., R.-C. Yang, A. Navabi, M. Iqbal, A. Kamran, E. Lara, et al. 2015. Mapping QTL, selection differentials, and the effect of under organic and conventionally managed systems in the Attila× CDC go spring wheat mapping population. Crop Science 55: 1129-1142.

Aslam, M., Travis, R. L., and Huffaker, R. C. 1992. Comparative kinetics and reciprocal inhibition of nitrate and nitrite uptake in roots of uninduced and induced barley (*Hordeum vulgare* L.) seedlings. Plant Physiology 99:1124-1133.

Ata-Ul-Karim, S. T., Yao, X., Liu, X., Cao, W., and Zhu, Y. 2014a. Determination of critical nitrogen dilution curve based on stem dry matter in rice. PloS One 9:e104540.

Ata-Ul-Karim, S. T., Zhu, Y., Yao, X., and Cao, W. 2014b. Determination of critical nitrogen dilution curve based on leaf area index in rice. Field Crops Research 167:76-85.

Aulakh, M., Rennie, D., and Paul, E. 1982. Gaseous nitrogen losses from cropped and summer-fallowed soils. Canadian Journal of Soil Science 62:187-196.

Austin, R., J. Bingham, R. Blackwell, L. Evans, M. Ford, C. Morgan, et al. 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. The Journal of Agricultural Science 94: 675-689.

Badaruddin, M., and Meyer, D. 1994. Grain legume effects on soil nitrogen, grain yield, and nitrogen nutrition of wheat. Crop Science 34:1304-1309.

Baethgen, W. E., Christianson, C. B., and Lamothe, A. G. 1995. Nitrogen fertilizer effects on growth, grain yield, and yield components of malting barley. Field Crops Research 43:87-99.

Bai, C., Liang, Y., and Hawkesford, M. J. 2013. Identification of QTLs associated with seedling root traits and their correlation with plant height in wheat. Journal of Experimental Botany 64:1745-1753.

Bancal, P. 2009. Decorrelating source and sink determinism of nitrogen remobilization during grain filling in wheat. Annals of Botany 103:1315-1324.

Bao, A., Zhao, Z., Ding, G., Shi, L., Xu, F., and Cai, H. 2015. The stable level of glutamine synthetase 2 plays an important role in rice growth and in carbon-nitrogen metabolic balance. International Journal of Molecular Sciences 16:12713-12736.

Barberi, P. 2002. Weed management in organic agriculture: are we addressing the right issues? Weed Research 42:177–193. doi:10.1046/j.1365-3180.2002.00277.x.

Barbieri, P. A., Echeverría, H. E., Saínz Rozas, H. R., and Andrade, F. H. 2008. Nitrogen use efficiency in maize as affected by nitrogen availability and row spacing. Agronomy Journal 100:1094-1100.

Baresel, J., G. Zimmermann and H. Reents. 2008. Effects of genotype and environment on N uptake and N partition in organically grown winter wheat (Triticum aestivum L.) in Germany. Euphytica 163: 347-354.

Barraclough, P., H. Kuhlmann and A. Weir. 1989. The effects of prolonged drought and nitrogen fertilizer on root and shoot growth and water uptake by winter wheat. Journal of Agronomy and Crop Science 163: 352-360.

Barraclough, P.B., J.R. Howarth, J. Jones, R. Lopez-Bellido, S. Parmar, C.E. Shepherd, and H., Malcolm J. 2010. Nitrogen efficiency of wheat: genotypic and environmental variation and prospects for improvement. European Journal of Agronomy 33: 1-11.

Barth, G., Von Tucher, S., and Schmidhalter, U. 2001. Influence of soil parameters on the effect of 3, 4-dimethylpyrazole-phosphate as a nitrification inhibitor. Biology and Fertility of Soils 34:98-102.

Basra, A. S., and Goyal, S. S. 2002. Mechanisms of improved nitrogen-use efficiency in cereals. Quantitative Genetics, Genomics, and Plant Breeding:269.

Bassirirad, H. 2006. Root system characteristics and control of nitrogen uptake. Journal of Crop Improvement 15:25-51.

Behl, R., Tischner, R., and Raschke, K. 1988. Induction of a high-capacity nitrate-uptake mechanism in barley roots prompted by nitrate uptake through a constitutive low-capacity mechanism. Planta 176:235-240.

Benbi, D. K., and Richter, J. 2002. A critical review of some approaches to modelling nitrogen mineralization. Biology and Fertility of Soils 35:168-183.

Bernard, S. M., Møller, A. L. B., Dionisio, G., Kichey, T., Jahn, T. P., Dubois, F., Baudo, M., Lopes, M. S., Tercé-Laforgue, T., and Foyer, C. H. 2008. Gene expression, cellular localisation and function of glutamine synthetase isozymes in wheat (*Triticum aestivum* L.). Plant Molecular Biology 67:89-105.

Berry, P., R. Sylvester-Bradley, L. Philipps, D. Hatch, S. Cuttle, F. Rayns, et al. 2002. Is the productivity of organic farms restricted by the supply of available nitrogen? Soil Use and Management 18: 248-255.

Bingham, I., A. Karley, P. White, W. Thomas and J. Russell. 2012. Analysis of improvements in nitrogen use efficiency associated with 75 years of spring barley breeding. European Journal of Agronpmy 42: 49-58.

Boeckx, P., Xu, X., and Van Cleemput, O. 2005. Mitigation of N_2O and CH_4 emission from rice and wheat cropping systems using dicyandiamide and hydroquinone. Nutrient Cycling in Agroecosystems 72:41-49.

Bogard, M., M. Jourdan, V. Allard, P. Martre, M.R. Perretant, C. Ravel, et al. 2011. Anthesis date mainly explained correlations between post-anthesis leaf senescence, grain yield, and grain protein concentration in a winter wheat population segregating for flowering time QTLs. Journal of Experimental Botany 62: 3621-3636.

Bosshard, C., P. Sørensen, E. Frossard, D. Dubois, P. Mäder, S. Nanzer, et al. 2009. Nitrogen use efficiency of 15N-labelled sheep manure and mineral fertiliser applied to microplots in long-term organic and conventional cropping systems. Nutrient cycling in agroecosystems 83: 271-287.

Braman, S., Tenuta, M., and Entz, M. H. 2016. Selected soil microbial parameters measured in the 19th year of a long term organic-conventional comparison study in Canada. Agriculture, Ecosystems and Environment. 233:343-351.

Brancourt-Hulmel, M., G. Doussinault, C. Lecomte, P. Bérard, B. Le Buanec and M. Trottet. 2003. Genetic improvement of agronomic traits of winter wheat cultivars released in France from 1946 to 1992. Crop Science 43: 37-45.

Brancourt-Hulmel, M., E. Heumez, P. Pluchard, D. Beghin, C. Depatureaux, A. Giraud, and J. Le Gouis. 2005. Indirect versus direct selection of winter wheat for low-input or high-input levels. Crop Science 45: 1427-1431.

Cabrera, M., Kissel, D., and Vigil, M. 2005. Nitrogen mineralization from organic residues. Journal of Environmental Quality 34:75-79.

Calderini, D., M. Dreccer and G. Slafer. 1995. Genetic improvement in wheat yield and associated traits. A re-examination of previous results and the latest trends. Plant breeding 114: 108-112.

Camargo, F. D. O., Gianello, C., and Vidor, C. 1997. Comparative study of five hydrolytic methods in the determination of soil organic nitrogen compounds. Communications in Soil Science and Plant Analysis 28:1303-1309.

Carr, P. M., Kandel, H. J., Porter, P.M., horsley, R. D., and Zwinger, S. F. 2006. Wheat cultivar performance on certified organic fields in Minnesota and North Dakota. Crop Science. 46:1963–1971.

Cassman, K., Gines, G., Dizon, M., Samson, M., and Alcantara, J. 1996. Nitrogen-use efficiency in tropical lowland rice systems: Contributions from indigenous and applied nitrogen. Field Crops Research 47:1-12.

Chen, H., N.P. Moakhar, M. Iqbal, C. Pozniak, P. Hucl and D. Spaner. 2016. Genetic variation for flowering time and height reducing genes and important traits in western Canadian spring wheat. Euphytica 208: 377-390.

Christophe, S., Jean-Christophe, A., Annabelle, L., Alain, O., Marion, P., and Anne-Sophie, V. 2011. Plant N fluxes and modulation by nitrogen, heat and water stresses: A review based on comparison of legumes and non legume plants. Abiotic Stress in Plants–Mechanisms and Adaptations. Intech Open Access Publisher, Rijeka, Croatia:79-118.

Chun, L., Mi, G., Li, J., Chen, F., and Zhang, F. 2005. Genetic analysis of maize root characteristics in response to low nitrogen stress. Plant and Soil 276:369-382.

Clark, S., K. Klonsky, P. Livingston and S. Temple. 1999. Crop-yield and economic comparisons of organic, low-input, and conventional farming systems in California's Sacramento Valley. American journal of alternative agriculture 14: 109-121.

Clarke, J., C. Campbell, H. Cutforth, R. DePauw and G. Winkleman. 1990. Nitrogen and phosphorus uptake, translocation, and utilization efficiency of wheat in relation to environment and cultivar yield and protein levels. Canadian Journal of Plant Science 70: 965-977.

Clarkson, D.T. 1985. Factors affecting mineral nutrient acquisition by plants. Annual review of plant physiology 36: 77-115.

Constantin, J., Mary, B., Laurent, F., Aubrion, G., Fontaine, A., Kerveillant, P., and Beaudoin, N. 2010. Effects of catch crops, no till and reduced nitrogen fertilization on nitrogen leaching and balance in three long-term experiments. Agriculture, Ecosystems and Environment 135:268-278.

Coque, M., and Gallais, A. 2007. Genetic variation for nitrogen remobilization and postsilking nitrogen uptake in maize recombinant inbred lines: Heritabilities and correlations among traits. Crop Science 47:1787-1796.

Coque, M., Martin, A., Veyrieras, J., Hirel, B., and Gallais, A. 2008. Genetic variation for N-remobilization and postsilking N-uptake in a set of maize recombinant inbred lines. 3. QTL detection and coincidences. Theoretical and Applied Genetics 117:729-747.

Cormier, F., S. Faure, P. Dubreuil, E. Heumez, K. Beauchêne, S. Lafarge, et al. 2013. A multi-environmental study of recent breeding progress on nitrogen use efficiency in wheat (*Triticum aestivum* L.). Theoritical and Applied Genetics 126: 3035-3048.

Cormier, F., J. Foulkes, B. Hirel, D. Gouache, Y. Moënne-Loccoz and J. Le Gouis. 2016. Breeding for increased nitrogen-use efficiency: a review for wheat (*T. aestivum* L.). Plant Breeding 135: 255-278.

Crews, T. E., and Peoples, M. B. 2005. Can the synchrony of nitrogen supply and crop demand be improved in legume and fertilizer-based agroecosystems? A review. Nutrient Cycling in Agroecosystems 72:101-120.

Cui, Z., Zhang, F., Mi, G., Chen, F., Li, F., Chen, X., Li, J., and Shi, L. 2009. Interaction between genotypic difference and nitrogen management strategy in determining nitrogen use efficiency of summer maize. Plant and Soil 317:267-276.

Dabney, S. M., Delgado, J. A., Meisinger, J. J., Schomberg, H. H., Liebig, M. A., Kaspar, T., Mitchell, J., and Reeves, W. 2010. Using cover crops and cropping systems for nitrogen management. Advances in Nitrogen Management for Water Quality:231-282.

Davis, J., and Abbott, L. 2006. Soil fertility in organic farming systems. In: Organic Agriculture: A Global Perspective, Kristiansen P, Taji A, Reganold J, (eds.) Comstock Publishing Associates, New York, pp 25-51.

Davies, D. and J. Welsh. 2002. Weed control in organic cereals and pulses. Organic cereals and pulses. Papers presented at conferences held at the Heriot-Watt University, Edinburgh, and at Cranfield University Silsoe Campus, Bedfordshire, 6 and 9 November 2001, Chalcombe Publications.

Dawson, J. C., Huggins, D. R., and Jones, S. S. 2008. Characterizing nitrogen use efficiency in natural and agricultural ecosystems to improve the performance of cereal crops in low-input and organic agricultural systems. Field Crops Research 107:89-101.

De Nobili, M., Contin, M., Mondini, C., and Brookes, P. 2001. Soil microbial biomass is triggered into activity by trace amounts of substrate. Soil Biology and Biochemistry 33:1163-1170.

Dechorgnat, J., Nguyen, C. T., Armengaud, P., Jossier, M., Diatloff, E., Filleur, S., and Daniel-Vedele, F. 2011. From the soil to the seeds: The long journey of nitrate in plants. Journal of Experimental Botany 62:1349-1359.

Degenhardt, R., Martin, R., and Spaner, D. 2005. Organic farming in central Alberta: Current trends, production constraints and research needs. Journal of Sustainable Agriculture 27:153-173.

DePauw, R., and T. Hunt. 2001. Canadian wheat pool. In: Bonjean, A. P., and Angus, W. J., editors, The world wheat book: a history of wheat breeding. Lavoisir, France. Lavoisier Publishing, Paris. p. 479-515.

DePauw, R., R. Knox, F. Clarke, H. Wang, M. Fernandez, J. Clarke, et al. 2007. Shifting undesirable correlations. Euphytica 157: 409-415.

Desai, R. and C. Bhatia. 1978. Nitrogen uptake and nitrogen harvest index in durum wheat cultivars varying in their grain protein concentration. Euphytica 27: 561-566.

Dijkstra, F. A., Bader, N. E., Johnson, D. W., and Cheng, W. 2009. Does accelerated soil organic matter decomposition in the presence of plants increase plant n availability? Soil Biology and Biochemistry 41:1080-1087.

Doltra, J., and Olesen, J. E. 2013. The role of catch crops in the ecological intensification of spring cereals in organic farming under Nordic climate. European Journal of Agronomy 44:98-108.

Donmez, E., R. Sears, J. Shroyer and G. Paulsen. 2001. Genetic gain in yield attributes of winter wheat in the Great Plains. Crop Science. 41: 1412-1419.

Doran, J., Elliott, E., and Paustian, K. 1998. Soil microbial activity, nitrogen cycling, and long-term changes in organic carbon pools as related to fallow tillage management. Soil and Tillage Research 49:3-18.

Dorff, E., and M.S. Beaulieu 2015. Feeding the soil puts food on your plate. http://www.statcan.gc.ca/pub/96-325-x/2014001/article/13006-eng.htm (accessed April 23 2017).

Douds Jr, D. D., Pfeffer, P. E., and Shachar-Hill, Y. 2000. Carbon partitioning, cost, and metabolism of arbuscular mycorrhizas. In: Kapulnik, Y., and Douds Jr, D. D. (eds.) Arbuscular mycorrhizas: Physiology and function. Springer. p.107-129.

Drew, M., and Saker, L. 1975. Nutrient supply and the growth of the seminal root system in barley II. Localized, compensatory increases in lateral root growth and rates op nitrate uptake when nitrate supply is restricted to only part of the root system. Journal of Experimental Botany 26:79-90.

Drew, M., Saker, L., and Ashley, T. 1973. Nutrient supply and the growth of the seminal root system in barley I. The effect of nitrate concentration on the growth of axes and laterals. Journal of Experimental Botany 24:1189-1202.

Drinkwater, L. E. 2004. Improving fertilizer nitrogen use efficiency through an ecosystem-based approach. In: Mosier, A. R., Syers, J. K., and Freney, J. R. (eds.) Agriculture and the nitrogen cycle: Assessing the impacts of fertilizer use on food production and the environment. Island Press, Washington. p.93-102.

Dunn, O. J. 1961. Multiple comparisons among means. Journal of the American Statistical Association 56:52-64.

Dupont, F., and S. Altenbach. 2003. Molecular and biochemical impacts of environmental factors on wheat grain development and protein synthesis. Journal of cereal science 38: 133-146.

Eberhart, S. A., and Russell, W. A. 1966. Stability parameters for comparing varieties. Crop Science 6(1): 36-40.

Eghball, B., and Gilley, J. E. 1999. Phosphorus and nitrogen in runoff following beef cattle manure or compost application. Journal of Environmental Quality 28:1201-1210.

Entz, M. H., Gross, K. G., and Fowler, D. B. 1992. Root growth and soil-water extraction by winter and spring wheat. Canadian Journal of Plant Science 72:1109-1120.

Entz, M..H., Guilford, R., and Gulden, R. 2001. Crop yield and soil nutrient status on 14 organic farms in the eastern portion of the northern Great Plains. Canadian Journal of Plant Science 81:351-354.

Eriksen, J., Askegaard, M., and Kristensen, K. 2004. Nitrate leaching from an organic dairy crop rotation: The effects of manure type, nitrogen input and improved crop rotation. Soil Use and Management 20:48-54.

Fageria, N., and Baligar, V. 2005. Enhancing nitrogen use efficiency in crop plants. Advances in Agronomy 88:97-185.

FAOSTAT. http://www.fao.org/faostat/en/ (accessed April 10 2017).

Fedko, A. 2017. Varieties of cereal and oilseed crops for Alberta Agri-Fact. Alberta Agriculture and Forestry.

Figueiredo, M. D. V. B., Seldin, L., De Araujo, F. F., and Mariano, R. D. L. R. 2010. Plant growth promoting rhizobacteria: Fundamentals and applications. Plant growth and health promoting bacteria. Springer. p.21-43.

Flintham, J., A. Börner, A. Worland and M. Gale. 1997. Optimizing wheat grain yield: effects of Rht (gibberellin-insensitive) dwarfing genes. Journal of Agricultural Science 128: 11-25.

Fontaine, J.-X., Ravel, C., Pageau, K., Heumez, E., Dubois, F., Hirel, B., and Le Gouis, J. 2009. A quantitative genetic study for elucidating the contribution of glutamine synthetase, glutamate dehydrogenase and other nitrogen-related physiological traits to the agronomic performance of common wheat. Theoretical and Applied Genetics 119:645-662.

Food and Agriculture Organization of the United Nations [FAO]. World fertilizer trends and outlook to 2018. 2015 Rome.

Food and Agriculture Organization of the United Nations [FAO]. 2016. World fertilizer trends and outlook to 2019. http://www.fao.org/3/a-i5627e.pdf (accessed March 12 2017).

Forde, B. G., and Lea, P. J. 2007. Glutamate in plants: Metabolism, regulation, and signalling. Journal of Experimental Botany 58:2339-2358.

Fraisier, V., Gojon, A., Tillard, P., and Daniel-Vedele, F. 2000. Constitutive expression of a putative high-affinity nitrate transporter in nicotiana plumbaginifolia: Evidence for post-transcriptional regulation by a reduced nitrogen source. The Plant Journal 23:489-496.

Franzluebbers, A. 2004. Tillage and residue management effects on soil organic matter. In: Magdoff, F., and Weil, R. R. (eds.) Soil organic matter in sustainable agriculture. CRC Press, Washington, D.C. p.227-268.

Frink, C. R., Waggoner, P. E., and Ausubel, J. H. 1999. Nitrogen fertilizer: Retrospect and prospect. Proceedings of the National Academy of Sciences 96:1175-1180.

Fu, D., Szucs, P., Yan, L., Helguera, M., Skinner, J.S., von Zitzewitz, J., Hayes, P. M., and Dubcovsky, J. 2005. Large deletions within the first intron in *VRN-1* are associated with spring growth habit in barley and wheat. Molecular Genetics and Genomics 273:54-65.

Gabriel, J., Alonso-Ayuso, M., García-González, I., Hontoria, C., and Quemada, M. 2016. Nitrogen use efficiency and fertiliser fate in a long-term experiment with winter cover crops. European Journal of Agronomy 79:14-22.

Gaju, O., Allard, V., Martre, P., Snape, J., Heumez, E., Legouis, J., Moreau, D., Bogard, M., Griffiths, S., and Orford, S. 2011. Identification of traits to improve the nitrogen-use efficiency of wheat genotypes. Field Crops Research 123:139-152.

Gale, M.D., and S. Youssefian. 1985. Dwarfing genes in wheat. Progress in Plant Breeding 1: 1-35.

Gallais, A., and Hirel, B. 2004. An approach to the genetics of nitrogen use efficiency in maize. Journal of Experimental Botany 55:295-306.

Gan, Y., Hamel, C., O'donovan, J. T., Cutforth, H., Zentner, R. P., Campbell, C. A., Niu, Y., and Poppy, L. 2015. Diversifying crop rotations with pulses enhances system productivity. Scientific Reports 5.

Gan, Y., Mooleki, S., Lemke, R. L., Zentner, R. P., and Ruan, Y. 2016. Durum wheat productivity in response to soil water and soil residual nitrogen associated with previous crop management. Agronomy Journal 108:1468-1478.

Garnett, T., M. Appleby, A. Balmford, I. Bateman, T. Benton, P. Bloomer, et al. 2013. Sustainable intensification in agriculture: premises and policies. Science 341: 33-34.

Gastal, F., and G. Lemaire. 2002. N uptake and distribution in crops: an agronomical and ecophysiological perspective. Journal of Experimental Botany 53: 789-799.

Gholamhoseini, M., Aghaalikhani, M., Sanavy, S. M., and Mirlatifi, S. 2013. Interactions of irrigation, weed and nitrogen on corn yield, nitrogen use efficiency and nitrate leaching. Agricultural Water Management 126:9-18.

Gianfreda, L., Rao, M., and Mora, M. 2011. Enzymatic activity as influenced by soil mineral and humic colloids and its impact on biogeochemical processes. In: Huang, P. M., Li, Y., and Sumner, M. E. (eds.) Handbook of soil science resource of management and environmental impacts. CRC Press, New York.

Gilland, B. 2006. Population, nutrition and agriculture. Population and Environment 28: 1-16.

Gilmour, J. T., and Mauromoustakos, A. 2011. Nitrogen mineralization from soil organic matter: A sequential model. Soil Science Society of America Journal 75:317-323.

Gioacchini, P., Nastri, A., Marzadori, C., Giovannini, C., Antisari, L. V., and Gessa, C. 2002. Influence of urease and nitrification inhibitors on N losses from soils fertilized with urea. Biology and Fertility of Soils 36:129-135.

Giuliani, M. M., Giuzio, L., De Caro, A., and Flagella, Z. 2011. Relationships between nitrogen utilization and grain technological quality in durum wheat: I. nitrogen translocation and nitrogen use efficiency for protein. Agronomy Journal 103(5): 1487-1494.

Glibert, P. M., Harrison, J., Heil, C., and Seitzinger, S. 2006. Escalating worldwide use of urea–a global change contributing to coastal eutrophication. Biogeochemistry 77:441-463.

Gooding, M. J., Gregory, P. J., Ford, K. E., and Pepler, S. 2005. Fungicide and cultivar affect post-anthesis patterns of nitrogen uptake, remobilization and utilization efficiency in wheat. The Journal of Agricultural Science 143:503-518.

Gooding, M.J., M. Addisu, R.K. Uppal, J.W. Snape and H.E. Jones. 2012. Effect of wheat dwarfing genes on nitrogen-use efficiency. Journal of Agricultural Science 150: 3-22.

Górny, A., and Garczyński, S. 2008. Nitrogen and phosphorus efficiency in wild and cultivated species of wheat. Journal of Plant Nutrition 31:263-279.

Górny, A.G., Z. Banaszak, B. Ługowska and D. Ratajczak. 2011. Inheritance of the efficiency of nitrogen uptake and utilization in winter wheat (*Triticum aestivum* L.) under diverse nutrition levels. Euphytica 177: 191-206.

Graham, J. 2000. Assessing costs of arbuscular mycorrhizal symbiosis in agroecosystems. In: Podila, G. K., and Douds Jr., D. D. (eds.) Current advances in mycorrhizae research. The American Phytophathological Society Press, St. Paul. p.111-126.

Greenwood, D., Lemaire, G., Gosse, G., Cruz, P., Draycott, A., and Neeteson, J. 1990. Decline in percentage N of C3 and C4 crops with increasing plant mass. Annals of Botany 66:425-436.

Griffith, W., and Murphy, L. 1991. The development of crop production systems using best management practices. Potash & Phosphate Institute, Norcross, USA.

Gruber, H., Handel, K., and Broschewitz, B. 2000. Influence of farming system on weeds in thresh crops of a six-year crop rotation. Proceedings of the 20th German Conference on weed biology and weed control, Stuttgart- Hohenheim, Germany, March 14-16, Zeitschrift fur Pflanzenkrankheiten und Pflanzenschutz 17:33-40.

Guarda, G., S. Padovan and G. Delogu. 2004. Grain yield, nitrogen-use efficiency and baking quality of old and modern Italian bread-wheat cultivars grown at different nitrogen levels. European Journal of Agronomy 21: 181-192.

Guttieri, M.J., K. Frels, T. Regassa, B.M. Waters and P.S. Baenziger. 2017. Variation for nitrogen use efficiency traits in current and historical great plains hard winter wheat. Euphytica 213: 87.

Haas, G., F. Wetterich and U. Köpke. 2001. Comparing intensive, extensified and organic grassland farming in southern Germany by process life cycle assessment. Agriculture, Ecosystems and Environment 83: 43-53.

Hadas, A., L. Kautsky, M. Goek and E.E. Kara. 2004. Rates of decomposition of plant residues and available nitrogen in soil, related to residue composition through simulation of carbon and nitrogen turnover. Soil Biology and Biochemistry 36: 255-266.

Hawkesford, M.J. 2017. Genetic variation in traits for nitrogen use efficiency in wheat. Journal of Experimental Botany 68(10):2627-2632.

Hay, R. 1995. Harvest index: a review of its use in plant breeding and crop physiology. Annals of applied biology 126: 197-216.

Hedden, P. 2003. The genes of the Green Revolution. Trends in Genetics 19: 5-9.

Habash, D., Massiah, A., Rong, H., Wallsgrove, R., and Leigh, R. 2001. The role of cytosolic glutamine synthetase in wheat. Annals of Applied Biology 138:83-89.

Habash, D. Z., Bernard, S., Schondelmaier, J., Weyen, J., and Quarrie, S. A. 2007. The genetics of nitrogen use in hexaploid wheat: N utilisation, development and yield. Theoretical and Applied Genetics 114:403-419.

Hamilton III, E. W., and Frank, D. A. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

Hansen, E. M., and Djurhuus, J. 1997. Nitrate leaching as influenced by soil tillage and catch crop. Soil and Tillage Research 41:203-219.

Havlin, J. L., Tisdale, S.L., Nelson, W.L., and Beaton, J.D. 2014. Soil fertility and fertilizers, Upper Saddle River, N.J.

Hawkesford, M. J. 2014. Reducing the reliance on nitrogen fertilizer for wheat production. Journal of Cereal Science 59:276-283.

Hawkins, H.-J., Johansen, A., and George, E. 2000. Uptake and transport of organic and inorganic nitrogen by arbuscular mycorrhizal fungi. Plant and Soil 226:275-285.

Hawkins, H. J., and George, E. 1999. Effect of plant nitrogen status on the contribution of arbuscular mycorrhizal hyphae to plant nitrogen uptake. Physiologia Plantarum 105:694-700.

Herridge, D. F., Peoples, M. B., and Boddey, R. M. 2008. Global inputs of biological nitrogen fixation in agricultural systems. Plant and Soil 311:1-18.

Herrmann, A., and Taube, F. 2004. The range of the critical nitrogen dilution curve for maize (*Zea mays* L.) can be extended until silage maturity. Agronomy Journal 96:1131-1138.

Hildermann, I., A. Thommen, D. Dubois, T. Boller, A. Wiemken and P. Mäder. 2009. Yield and baking quality of winter wheat cultivars in different farming systems of the DOK long-term trial. Journal of the Science of Food and Agriculture 89: 2477-2491.

Hirel, B., Bertin, P., Quilleré, I., Bourdoncle, W., Attagnant, C., Dellay, C., Gouy, A., Cadiou, S., Retailliau, C., and Falque, M. 2001. Towards a better understanding of the genetic and physiological basis for nitrogen use efficiency in maize. Plant Physiology 125:1258-1270.

Hirel, B., T. Tétu, P.J. Lea and F. Dubois. 2011. Improving nitrogen use efficiency in crops for sustainable agriculture. Sustainability 3: 1452-1485.

Hokazono, S. and K. Hayashi. 2012. Variability in environmental impacts during conversion from conventional to organic farming: a comparison among three rice production systems in Japan. Journal of Cleaner Production 28: 101-112.

Hong-Bo, L., Zhang, F.-S., and Jian-Bo, S. 2012. Contribution of root proliferation in nutrient-rich soil patches to nutrient uptake and growth of maize. Pedosphere 22:776-784.

Hoogmoed, M. 2015. Development of nitrogen dilution curves for current Australian wheat varieties. In: AcuñA, T., Moeller, C., Parsons, D., and Harrison, M. (eds.) Building productive, diverse and sustainable landscapes: Proceedings of the 17th australian agronomy conference 2015. Warragul.

Hornick, S. B. 1992. Factors affecting the nutritional quality of crops. American Journal of Alternative Agriculture 7:63-68.

Horrigan, L., Lawrence, R. S., and Walker, P. 2002. How sustainable agriculture can address the environmental and human health harms of industrial agriculture. Environmental Health Perspectives 110:445.

Hörtensteiner, S., and Feller, U. 2002. Nitrogen metabolism and remobilization during senescence. Journal of Experimental Botany 53:927-937.

House, G. J., Stinner, B. R., Crossley, D., Odum, E. P., and Langdale, G. W. 1984. Nitrogen cycling in conventional and no-tillage agroecosystems in the southern piedmont. Journal of Soil and Water Conservation 39:194-200.

Hu, G., X. Liu, H. He, W. Zhang, H. Xie, Y. Wu, et al. 2015. Multi-Seasonal Nitrogen Recoveries from Crop Residue in Soil and Crop in a Temperate Agro-Ecosystem. PloS one 10: e0133437.

Hucl, P., and R. Baker. 1987. A study of ancestral and modern Canadian spring wheats. Canadian Journal of Plant Science 67: 87-97.

Huggins, D., and Pan, W. 1993. Nitrogen efficiency component analysis: An evaluation of cropping system differences in productivity. Agronomy Journal 85:898-905.

Huggins, D., and Pan, W. 2003. Key indicators for assessing nitrogen use efficiency in cereal-based agroecosystems. Journal of Crop Production 8:157-185.

International Federation of Organic Agriculture Movement [IFOAM]. 2008. The principals of organic agriculture. http://www.ifoam.org/about_ifoam/principles/index.html (accessed May 26 2014).

International Fertilizer Industry Association [IFA]. 2011. http://ifadata.fertilizer.org/ucSearch.aspx (accessed July 8 2014).

Iqbal, M., Navabi, A., Salmon, D. F., Yang, R. C., and Spaner, D. 2007. Simultaneous selection early maturity, increased grain yield and elevated grain protein content in spring wheat. Plant Breeding 126:244-250.

Iqbal, M., N.P. Moakhar, K. Strenzke, T. Haile, C. Pozniak, P. Hucl, et al. 2016. Genetic improvement in grain yield and other traits of wheat grown in western Canada. Crop Science. 56(2):613-624.

Isfan, D. 1993. Genotypic variability for physiological efficiency index of nitrogen in oats. Plant and Soil 154:53-59.

Jain, V., Khetarpal, S., Das, R., and Abrol, Y. P. 2011. Nitrate assimilation in contrasting wheat genotypes. Physiology and Molecular Biology of Plants 17:137-144.

Janzen, H. H., Beauchemin, K. A., Bruinsma, Y., Campbell, C. A., Desjardins, R. L., Ellert, B. H., and Smith, E. G. 2003. The fate of nitrogen in agroecosystems: an illustration using Canadian estimates. Nutrient Cycling in Agroecosystems. 67: 85-102.

Jaradat, A.A. 2009. Modeling biomass allocation and grain yield in bread and durum wheat under abiotic stress. Australian Journal of Crop Science 3: 237.

Jeranyama, P., Hesterman, O. B., and Sheaffer, C. C. 1998. Medic planting date effect on dry matter and nitrogen accumulation when clear-seeded or intercropped with corn. Agronomy Journal 90:616-622.

Jin, H., Liu, J., Liu, J., and Huang, X. 2012. Forms of nitrogen uptake, translocation, and transfer via arbuscular mycorrhizal fungi: A review. Science China Life Sciences 55:474-482.

Jing, J., Zhang, F., Rengel, Z., and Shen, J. 2012. Localized fertilization with P plus N elicits an ammonium-dependent enhancement of maize root growth and nutrient uptake. Field Crops Research 133:176-185.

Justes, E., Mary, B., Meynard, J.-M., Machet, J.-M., and Thelier-Huché, L. 1994. Determination of a critical nitrogen dilution curve for winter wheat crops. Annals of Botany 74:397-407.

Kalinova, S., Kostadinova, S., and Hristoskov, A. 2014. Nitrogen use efficiency and maize yield response to nitrogen rate and foliar fertilizing. Bulgarian Journal of Agricultural Science 20:178-181.

Kamiji, Y., J. Pang, S.P. Milroy and J.A. Palta. 2014. Shoot biomass in wheat is the driver for nitrogen uptake under low nitrogen supply, but not under high nitrogen supply. Field Crops Research 165: 92-98.

Kamran, A., Randhawa, H.S., and Pozniak, C., and Spaner, D. M. 2013. Phenotypic effects of the flowering gene complex in Canadian spring wheat germplasm. Crop Science. 53:84-94.

Kamran, A., M. Iqbal, A. Navabi, H. Randhawa, C. Pozniak and D. Spaner. 2013. Earliness per se QTLs and their interaction with the photoperiod insensitive allele Ppd-D1a in the Cutler× AC Barrie spring wheat population. Theoreitical and Applied Genetics 126: 1965-1976.

Kamran, A., H. Kubota, R.-C. Yang, H.S. Randhawa and D. Spaner. 2014. Relative performance of Canadian spring wheat cultivars under organic and conventional field conditions.

Euphytica 196: 13-24.

Kayser, M., Müller, J., and Isselstein, J. 2010. Nitrogen management in organic farming: Comparison of crop rotation residual effects on yields, N leaching and soil conditions. Nutrient Cycling in Agroecosystems 87:21-31.

Kessavalou, A., Mosier, A. R., Doran, J. W., Drijber, R. A., Lyon, D. J., and Heinemeyer, O. 1998. Fluxes of carbon dioxide, nitrous oxide, and methane in grass sod and winter wheat-fallow tillage management. Journal of Environmental Quality 27:1094-1104.

Khalil, M., Buegger, F., Schraml, M., Gutser, R., Richards, K., and Schmidhalter, U. 2009a. Gaseous nitrogen losses from a cambisol cropped to spring wheat with urea sizes and placement depths. Soil Science Society of America Journal 73:1335-1344.

Khalil, M., Rosenani, A., Van Cleemput, O., Boeckx, P., Shamshuddin, J., and Fauziah, C. 2002. Nitrous oxide production from an ultisol of the humid tropics treated with different nitrogen sources and moisture regimes. Biology and Fertility of Soils 36:59-65.

Khalil, M. I., Gutser, R., and Schmidhalter, U. 2009b. Effects of urease and nitrification inhibitors added to urea on nitrous oxide emissions from a loess soil. Journal of Plant Nutrition and Soil Science/Zeitschrift für Pflanzenernährung und Bodenkunde 172:651.

Khosla, R., Fleming, K., Delgado, J., Shaver, T., and Westfall, D. 2002. Use of site-specific management zones to improve nitrogen management for precision agriculture. Journal of Soil and Water Conservation 57:513-518.

Kichey, T., Hirel, B., Heumez, E., Dubois, F., and Le Gouis, J. 2007. In winter wheat (*Triticum aestivum* L.), post-anthesis nitrogen uptake and remobilisation to the grain correlates with agronomic traits and nitrogen physiological markers. Field Crops Research 102:22-32.

Kirigwi, F. M., Ginkel, M. V., Guedira, G. B., Gill, B. S., Paulsen, G. M., and Fritz, A. K. 2007. Markers associated with a QTL for grain yield in wheat under drought. Molecular Breeding 20:401–413.

Kirk, A. P., Fox, S. L., Entz, M. H. 2012. Comparison of organic and conventional selection environments for spring wheat. Plant Breeding 131: 687-694.

Kitchen, J. L., McDonald, G. K., Shepherd, K. W., Lorimer, M. F., and Graham, R. D. 2003. Comparing wheat grown in South Australian organic and conventional farming systems. Australian Journal of Agricultural Research 54:889–901.

Knudsen, M.T., I.S. Kristensen, J. Berntsen, B.M. Petersen and E.S. Kristensen. 2006. Estimated N leaching losses for organic and conventional farming in Denmark. The Journal of Agricultural Science 144: 135-149.

Kubota, H., M. Iqbal, S. Quideau, M. Dyck and D. Spaner. 2017. Agronomic and physiological aspects of nitrogen use efficiency in conventional and organic cereal-based production systems. Renewable Agriculture and Food Systems: 1-24.

Kubota, H., S.A. Quideau, P.J. Hucl and D.M. Spaner. 2015. The effect of weeds on soil arbuscular mycorrhizal fungi and agronomic traits in spring wheat (*Triticum aestivum* L.) under organic management in Canada. Canadian Journal of Plant Science 95: 615-627.

Lassaletta, L., Billen, G., Grizzetti, B., Anglade, J., and Garnier, J. 2014. 50 year trends in nitrogen use efficiency of world cropping systems: the relationship between yield and nitrogen input to cropland. Environmental Research Letters. 9: 105011.

Lavelle, P., and Spain, A. 2001. Soil ecology, Dordrecht: Kluwer Academic Publishers.

L-Baeckström, G., U. Hanell and G. Svensson. 2006. Nitrogen use efficiency in an 11-year study of conventional and organic wheat cultivation. Communications in soil science and plant analysis 37: 417-449.

Le Gouis, J., Béghin, D., Heumez, E., and Pluchard, P. 2000. Genetic differences for nitrogen uptake and nitrogen utilisation efficiencies in winter wheat. European Journal of Agronomy 12:163-173.

Loddo, S., and M. Gooding. 2012. Semi-dwarfing (*Rht-B1b*) improves nitrogen-use efficiency in wheat, but not at economically optimal levels of nitrogen availability. Cereal Research Communications 40: 116-121.

López-Bellido, L., López-Bellido, R. J., and Redondo, R. 2005. Nitrogen efficiency in wheat under rainfed mediterranean conditions as affected by split nitrogen application. Field Crops Research 94:86-97.

López-Bellido, R., and López-Bellido, L. 2001. Efficiency of nitrogen in wheat under mediterranean conditions: Effect of tillage, crop rotation and n fertilization. Field Crops Research 71:31-46.

Löschenberger, F., A. Fleck, H. Grausgruber, H. Hetzendorfer, G. Hof, J. Lafferty, et al. 2008. Breeding for organic agriculture: the example of winter wheat in Austria. Euphytica 163: 469.

Léran, S., Varala, K., Boyer, J.-C., Chiurazzi, M., Crawford, N., Daniel-Vedele, F., David, L., Dickstein, R., Fernandez, E., and Forde, B. 2014. A unified nomenclature of nitrate transporter 1/peptide transporter family members in plants. Trends in Plant Science 19:5-9.

Laperche, A., Brancourt-Hulmel, M., Heumez, E., Gardet, O., and Le Gouis, J. 2006. Estimation of genetic parameters of a DH wheat population grown at different n stress levels characterized by probe genotypes. Theoretical and Applied Genetics 112:797-807.

Lemaire, G., and Meynard, J. 1997. Use of the nitrogen nutrition index for the analysis of agronomical data. In: Lemaire, G. (ed.) Diagnosis of the nitrogen status in crops. Springer, Heidelberg. p.45-55.

Lemaire, G., Van Oosterom, E., Sheehy, J., Jeuffroy, M. H., Massignam, A., and Rossato, L. 2007. Is crop n demand more closely related to dry matter accumulation or leaf area expansion during vegetative growth? Field Crops Research 100:91-106.

Li, P., Chen, F., Cai, H., Liu, J., Pan, Q., Liu, Z., Gu, R., Mi, G., Zhang, F., and Yuan, L. 2015. A genetic relationship between nitrogen use efficiency and seedling root traits in maize as revealed by QTL analysis. Journal of Experimental Botany 66:3175-3188.

Liao, M., Fillery, I. R., and Palta, J. A. 2004. Early vigorous growth is a major factor influencing nitrogen uptake in wheat. Functional Plant Biology 31:121-129.

Liao, M., Palta, J. A., and Fillery, I. R. 2006. Root characteristics of vigorous wheat improve early nitrogen uptake. Crop and Pasture Science 57:1097-1107.

Lim, S. L., Wu, T. Y., Lim, P. N., and Shak, K. P. Y. 2015. The use of vermicompost in organic farming: Overview, effects on soil and economics. Journal of the Science of Food and Agriculture 95:1143-1156.

Lima, J. E., Kojima, S., Takahashi, H., and Von Wirén, N. 2010. Ammonium triggers lateral root branching in arabidopsis in an ammonium transporter1; 3-dependent manner. The Plant Cell 22:3621-3633.

Limaux, F., Recous, S., Meynard, J.-M., and Guckert, A. 1999. Relationship between rate of crop growth at date of fertiliser n application and fate of fertiliser n applied to winter wheat. Plant and Soil 214:49-59.

Limon-Ortega, A., and Villaseñor-Mir, E. 2006. Nitrogen fertilizer management and recommendations for wheat production in central Mexico. Crop Management 5.

Lin, H.-C., J.A. Huber, G. Gerl and K.-J. Hülsbergen. 2016. Nitrogen balances and nitrogen-use efficiency of different organic and conventional farming systems. Nutrient Cycling in Agroecosystems 105: 1-23.

Liu, C., Cutforth, H., Chai, Q., and Gan, Y. 2016. Farming tactics to reduce the carbon footprint of crop cultivation in semiarid areas. A review. Agronomy for Sustainable Development 36:69.

Luce, M. S., Grant, C. A., Zebarth, B. J., Ziadi, N., O'donovan, J. T., Blackshaw, R. E., Harker, K. N., Johnson, E. N., Gan, Y., and Lafond, G. P. 2015. Legumes can reduce economic optimum nitrogen rates and increase yields in a wheat–canola cropping sequence in western Canada. Field Crops Research 179:12-25.

Luce, M. S., Grant, C. A., Ziadi, N., Zebarth, B. J., O'donovan, J. T., Blackshaw, R. E., Harker, K. N., Johnson, E. N., Gan, Y., and Lafond, G. P. 2016. Preceding crops and nitrogen fertilization influence soil nitrogen cycling in no-till canola and wheat cropping systems. Field Crops Research 191:20-32.

Lupwayi, N., Clayton, G., O'donovan, J., Harker, K., Turkington, T., and Soon, Y. 2006. Soil nutrient stratification and uptake by wheat after seven years of conventional and zero tillage in the northern grain belt of Canada. Canadian Journal of Soil Science 86:767-778.

Lynch, J. 1995. Root architecture and plant productivity. Plant Physiology 109:7.

Lynch, D. 2009. Environmental impacts of organic agriculture: A Canadian perspective. Canadian Journal of Plant Science 89: 621-628.

Mäder, P., Fliessbach, A., Dubois, D., Gunst, L., Fried, P., and Niggli, U. 2002. Soil fertility and biodiversity in organic farming. Science 296:1694-1697.

Mäder, P., Hahn, D., Dubois, D., Gunst, L., Alföldi, T., Bergmann, H., Oehme, M., Amadò, R., Schneider, H., Graf, U., Velimirov, A., Flieβbach, A., and Niggli, U. 2007. Wheat quality in organic and conventional farming: results of a 21 year field experiment. Journal of the Science of Food and Agriculture 87: 1826-1835.

Malhi, S., Soon, Y., Grant, C., Lemke, R., and Lupwayi, N. 2010. Influence of controlled-release urea on seed yield and n concentration, and n use efficiency of small grain crops grown on dark gray luvisols. Canadian Journal of Soil Science 90:363-372.

Mano, H., and Morisaki, H. 2008. Endophytic bacteria in the rice plant. Microbes and Environments 23:109-117.

Marriott, E. E., and Wander, M. M. 2006. Total and labile soil organic matter in organic and conventional farming systems. Soil Science Society of America Journal 70:950-959.

Martin, A., Lee, J., Kichey, T., Gerentes, D., Zivy, M., Tatout, C., Dubois, F., Balliau, T., Valot, B., and Davanture, M. 2006. Two cytosolic glutamine synthetase isoforms of maize are specifically involved in the control of grain production. The Plant Cell 18:3252-3274.

Masclaux-Daubresse, C., Daniel-Vedele, F., Dechorgnat, J., Chardon, F., Gaufichon, L., and Suzuki, A. 2010. Nitrogen uptake, assimilation and remobilization in plants: Challenges for sustainable and productive agriculture. Annals of Botany 105:1141-1157.

Masclaux, C., Quilleré, I., Gallais, A., and Hirel, B. 2001. The challenge of remobilisation in plant nitrogen economy. A survey of physio-agronomic and molecular approaches. Annals of Applied Biology 138:69-81.

Mason, H. and D. Spaner. 2006. Competitive ability of wheat in conventional and organic management systems: a review of the literature. Canadian Journal of Plant Science 86: 333-343.

Mason, H.E., A. Navabi, B.L. Frick, J.T. O'Donovan and D.M. Spaner. 2007. The weed-competitive ability of Canada western red spring wheat cultivars grown under organic management. Crop Science 47: 1167-1176.

Masunga, R. H., Uzokwe, V. N., Mlay, P. D., Odeh, I., Singh, A., Buchan, D., and De Neve, S. 2016. Nitrogen mineralization dynamics of different valuable organic amendments commonly used in agriculture. Applied Soil Ecology 101:185-193.

Matson, P. A., Naylor, R., and Ortiz-Monasterio, I. 1998. Integration of environmental, agronomic, and economic aspects of fertilizer management. Science 280:112-115.

Mckenzie, R., Bremer, E., Middleton, A., Pfiffner, P., and Dowbenko, R. 2007. Controlled-release urea for winter wheat in southern Alberta. Canadian Journal of Soil Science 87:85-91.

Mckenzie, R. H., Middleton, A., Pfiffner, P., and Bremer, E. 2010. Evaluation of polymer-coated urea and urease inhibitor for winter wheat in southern Alberta. Agronomy Journal 102:1210-1216.

McKenzie, R.H., L. Kryzanowski and D. Pauly. 2013. Fertilizer requirements of irrigated grain and oilseed crops. Alberta Agriculture and Forestory. http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/agdex149 (accessed May 9 2017).

Meisinger, J., Bandel, V., Stanford, G., and Legg, J. 1985. Nitrogen utilization of corn under minimal tillage and moldboard plow tillage. I. Four-year results using labeled N fertilizer on an Atlantic coastal plain soil. Agronomy Journal 77:602-611.

Miflin, B., and Lea, P. 1977. Amino acid metabolism. Annual Review of Plant Physiology 28:299-329.

Miflin, B. J., and Habash, D. Z. 2002. The role of glutamine synthetase and glutamate dehydrogenase in nitrogen assimilation and possibilities for improvement in the nitrogen utilization of crops. Journal of Experimental Botany 53:979-987.

Mohammadi, R., B. Sadeghzadeh, H. Ahmadi, N. Bahrami and A. Amri. 2015. Field evaluation of durum wheat landraces for prevailing abiotic and biotic stresses in highland rainfed regions of Iran. The Crop Journal 3: 423-433.

Moll, R., Kamprath, E., and Jackson, W. 1982. Analysis and interpretation of factors which contribute to efficiency of nitrogen utilization. Agronomy Journal 74:562-564.

Morgan, J.A. and W.J. Parton. 1989. Characteristics of ammonia volatilization from spring wheat. Crop Science 29: 726-731.

Munier-Jolain, N.G., and C. Salon. 2005. Are the carbon costs of seed production related to the quantitative and qualitative performance? An appraisal for legumes and other crops. Plant, Cell and Environment 28: 1388-1395.

Murphy, K.M., K.G. Campbell, S.R. Lyon and S.S. Jones. 2007. Evidence of varietal adaptation to organic farming systems. Field Crops Research 102: 172-177.

Muruganandam, S., Israel, D. W., and Robarge, W. P. 2009. Activities of nitrogen-mineralization enzymes associated with soil aggregate size fractions of three tillage systems. Soil Science Society of America Journal 73:751-759.

Muruganandam, S., Israel, D. W., and Robarge, W. P. 2010. Nitrogen transformations and microbial communities in soil aggregates from three tillage systems. Soil Science Society of America Journal 74:120-129.

Musyoka, M.W., N. Adamtey, A.W. Muriuki and G. Cadisch. 2017. Effect of organic and conventional farming systems on nitrogen use efficiency of potato, maize and vegetables in the Central highlands of Kenya. European Journal of Agronomy 86: 24-36.

Muurinen, S., Kleemola, J., and Peltonen-Sainio, P. 2007. Accumulation and translocation of nitrogen in spring cereal cultivars differing in nitrogen use efficiency. Agronomy Journal 99:441-449.

Muurinen, S., Slafer, G. A., and Peltonen-Sainio, P. 2006. Breeding effects on nitrogen use efficiency of spring cereals under northern conditions. Crop Science 46:561-568.

Nacry, P., Bouguyon, E., and Gojon, A. 2013. Nitrogen acquisition by roots: Physiological and developmental mechanisms ensuring plant adaptation to a fluctuating resource. Plant and Soil 370:1-29.

Namai, S., Toriyama, K., and Fukuta, Y. 2009. Genetic variations in dry matter production and physiological nitrogen use efficiency in rice (*Oryza sativa* L.) varieties. Breeding Science 59:269-276.

Nass, H. G., Reisser, B. 1975. Grain filling period and grain yield relationships in spring wheat. Canadian Journal of Plant Science 55:673–678.

Nass, H. G., Ivany, J. A., MacLeod, J. A. 2003. Agronomic performance and quality of spring wheat and soybean cultivars under organic culture. American Journal of Alternative Agriculture, 18, pp 164170.

Nelson, A., S. Quideau, B. Frick, D. Niziol, J. Clapperton and D. Spaner. 2011. Spring wheat genotypes differentially alter soil microbial communities and wheat breadmaking quality in organic and conventional systems. Canadian Journal of Plant Science 91: 485-495.

Nielsen, R. N loss mechanisms and nitrogen use efficiency. Purdue Nitrogen Management Workshops, 2006. 1-5.

O'donovan, J. T., Grant, C. A., Blackshaw, R. E., Harker, K. N., Johnson, E., Gan, Y., Lafond, G. P., May, W. E., Turkington, T. K., and Lupwayi, N. Z. 2014. Rotational effects of legumes and non-legumes on hybrid canola and malting barley. Agronomy Journal 106:1921-1932.

Obara, M., Ishimaru, T., Abiko, T., Fujita, D., Kobayashi, N., Yanagihara, S., and Fukuta, Y. 2014. Identification and characterization of quantitative trait loci for root elongation by using introgression lines with genetic background of indica-type rice variety IR64. Plant Biotechnology Reports 8:267-277.

Obara, M., Kajiura, M., Fukuta, Y., Yano, M., Hayashi, M., Yamaya, T., and Sato, T. 2001. Mapping of QTLs associated with cytosolic glutamine synthetase and NADH-glutamate synthase in rice (*Oryza sativa* L.). Journal of Experimental Botany 52:1209-1217.

Okon, Y., and Labandera-Gonzalez, C. A. 1994. Agronomic applications of azospirillum: An evaluation of 20 years worldwide field inoculation. Soil Biology and Biochemistry 26:1591-1601.

Ondersteijn, C., Beldman, A., Daatselaar, C., Giesen, G., and Huirne, R. 2002. The Dutch mineral accounting system and the European nitrate directive: Implications for N and P management and farm performance. Agriculture, Ecosystems and Environment 92:283-296.

Orsel, M., Filleur, S., Fraisier, V., and Daniel-Vedele, F. 2002. Nitrate transport in plants: Which gene and which control? Journal of Experimental Botany 53:825-833.

Ortiz-Monasterio, R., Sayre, K., Rajaram, S., and Mcmahon, M. 1997. Genetic progress in wheat yield and nitrogen use efficiency under four nitrogen rates. Crop Science 37:898-904.

Osman, A., C. Almekinders, P. Struik and E.L. van Bueren. 2016. Adapting spring wheat breeding to the needs of the organic sector. NJAS-Wageningen Journal of Life Sciences 76: 55-63.

Pacheco, Á.V., Mateo; Alvarado, Gregorio; Rodríguez, Francisco; Crossa, José; Burgueño, Juan,. 2015. GEA-R (Genotype x Environment Analysis with R for Windows) Version 4.0. International Maize and Wheat Imrovement Center.

Palta, J., and I. Fillery. 1995. N application enhances remobilization and reduces losses of pre-anthesis N in wheat grown on a duplex soil. Crop and Pasture Science 46: 519-531.

Palta, J.A., X. Chen, S.P. Milroy, G.J. Rebetzke, M.F. Dreccer and M. Watt. 2011. Large root systems: are they useful in adapting wheat to dry environments? Functional Plant Biology 38: 347-354.

Pang, J., S.P. Milroy, G.J. Rebetzke and J.A. Palta. 2015. The influence of shoot and root size on nitrogen uptake in wheat is affected by nitrate affinity in the roots during early growth. Functional Plant Biology 42: 1179-1189.

Pathak, R., Lochab, S., and Raghuram, N. 2011. Plant systems| improving plant nitrogen-use efficiency. In: Moo-Young, M. (ed.) Comprehensive biotechnology, 2nd edn. Elsevier, Amsterdam. p.209-218.

Pathak, R. R., Ahmad, A., Lochab, S., and Raghuram, N. 2008. Molecular physiology of plant nitrogen use efficiency and biotechnological options for its enhancement. Current Science 94:1394.

Paull, J., Hennig, B. 2011. A world map of organic agriculture. European Journal of Social Science 24:360-369.

Paulsen, H., U. Volkgenannt and E. Schnug. 2002. Contribution of organic farming to marine environmental protection. LANDBAUFORSCHUNG VOLKENRODE 52: 211-218.

Peoples, M.B., E.W. Boyer, K.W. Goulding, P. Heffer, V.A. Ochwoh, B. Vanlauwe, et al. 2012. Pathways of nitrogen loss and their impacts on human health and the environment.

Peterson, C. J., Graybosch, R. A., Baenziger, P. S., and Grombacher, A. W. 1992 Genotype and environment effects on quality characteristics of hard red winter wheat. Crop Science 38:98-103.

Pimentel, D., Hepperly, P., Hanson, J., Douds, D., and Seidel, R. 2005. Environmental, energetic, and economic comparisons of organic and conventional farming systems. BioScience 55:573-582.

Plett, D., Toubia, J., Garnett, T., Tester, M., Kaiser, B. N., and Baumann, U. 2010. Dichotomy in the nrt gene families of dicots and grass species. PloS One 5:e15289.

Poorter, H., and Nagel, O. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: A quantitative review. Functional Plant Biology 27:1191-1191.

Porter, L. K., Follett, R. F., and Halvorson, A. D. 1996. Fertilizer nitrogen recovery in a no-till wheat-sorghum-fallow-wheat sequence. Agronomy Journal 88:750-757.

Poutala, R. T., Korva, J., Varis, E. 1993. Spring wheat cultivar performance in ecological and conventional cropping systems. Journal of Sustainable Agriculture 3:63–83.

Presterl, T., Groh, S., Landbeck, M., Seitz, G., Schmidt, W., and Geiger, H. 2002. Nitrogen uptake and utilization efficiency of European maize hybrids developed under conditions of low and high nitrogen input. Plant Breeding 121:480-486.

Przystalski, M., Osman, A., Thiemt, E. M., Rolland, B., Ericson, L., Østergârd, H., Levy, L., Wolfe, M., Büchse, A., Piepho, H. P., and Krajewski, P. 2008. Comparing the performance of cereal varieties in organic and nonorganic cropping systems in different European countries. Euphytica 163:417–433. doi:10.1007/s10681-008-9715-4.

Pswarayi, H., H. Kubota, H. Estrada and D. Spaner. 2014. Evaluation of wheat cultivars to test indirect selection or organic conditions. Agronomy Journal 106: 441-451.

Quilleré, I., Dufossé, C., Roux, Y., Foyer, C. H. F., Caboche, M., and Morot-Gaudry, J.-F. 1994. The effects of deregulation of NR gene expression on growth and nitrogen metabolism of nicotiana plumbaginifolia plants. Journal of Experimental Botany 45:1205-1211.

Raun, W. R., and Johnson, G. V. 1999. Improving nitrogen use efficiency for cereal production. Agronomy Journal 91:357-363.

Ray, D.K., N.D. Mueller, P.C. West and J.A. Foley. 2013. Yield trends are insufficient to double global crop production by 2050. PloS one 8: e66428.

Regehr, A., Oelbermann, M., Videla, C., and Echarte, L. 2015. Gross nitrogen mineralization and immobilization in temperate maize-soybean intercrops. Plant and Soil 391: 353-365.

Reid, T.A., R.-C. Yang, D.F. Salmon, A. Navabi and D. Spaner. 2011. Realized gains from selection for spring wheat grain yield are different in conventional and organically managed systems. Euphytica 177: 253-266.

Reid, T. A., Yang, R.-C., Salmon, D. F., and Spaner, D. 2009. Should spring wheat breeding for organically managed systems be conducted on organically managed land? Euphytica 169:239-252.

Reilly, K., Cullen, E., Lola-Luz, T., Stone, D., Valverde, J., Gaffney, M., Brunton, N., Grant, J., and Griffiths, B. S. 2013. Effect of organic, conventional and mixed cultivation practices on soil microbial community structure and nematode abundance in a cultivated onion crop. Journal of the Science of Food and Agriculture 93:3700-3709.

Richie, S. W., Hanway, J.J., and Benson, G.O. 1986. How a corn plant develops. Iowa: Iowa State University of Science and Technology. https://s10.lite.msu.edu/res/msu/botonl/b_online/library/maize/www.ag.iastate.edu/departments/agronomy/corngrows.html (accessed October 12 2015).

Robertson, G. P. 1997. Nitrogen use efficiency in row-crop agriculture: Crop nitrogen use and soil nitrogen loss. In: Jackson, L. E. (ed.) Ecology in agriculture. Academic press, New York. Academic Press, New York. p.347-365.

Robinson, D. 2001. Root proliferation, nitrate inflow and their carbon costs during nitrogen capture by competing plants in patchy soil. Plant and Soil 232:41-50.

Rodrigues, O., J.C.B. Lhamby, A.D. Didonet and J.A. Marchese. 2007. Fifty years of wheat breeding in Southern Brazil: yield improvement and associated changes. Pesquisa Agropecuária Brasileira 42: 817-825.

Romagosa, I., Fox, P. N. 1993. Genotype × environment interaction and adaptation. Plant breeding series, Plant breeding. pp:373-390.

Ruidisch, M., Bartsch, S., Kettering, J., Huwe, B., and Frei, S. 2013. The effect of fertilizer best management practices on nitrate leaching in a plastic mulched ridge cultivation system. Agriculture, Ecosystems and Environment 169:21-32.

Ryan, M., Derrick, J., and Dann, P. 2004. Grain mineral concentrations and yield of wheat grown under organic and conventional management. Journal of the Science of Food and Agriculture 84:207–216.

Sainju, U. M., Caesar-Tonthat, T., Lenssen, A. W., Evans, R. G., and Kolberg, R. 2009. Tillage and cropping sequence impacts on nitrogen cycling in dryland farming in eastern Montana, USA. Soil and Tillage Research 103:332-341.

Sanford, D., and C. MacKown. 1986. Variation in nitrogen use efficiency among soft red winter wheat genotypes. Theoretical and Applied Genetics 72: 158-163.

San Francisco, S., Urrutia, O., Martin, V., Peristeropoulos, A., and Garcia-Mina, J. M. 2011. Efficiency of urease and nitrification inhibitors in reducing ammonia volatilization from diverse nitrogen fertilizers applied to different soil types and wheat straw mulching. Journal of the Science of Food and Agriculture 91:1569-1575.

Sandhu, K., Arora, V., Chand, R., Sandhu, B., and Khera, K. 2000. Optimizing time distribution of water supply and fertilizer nitrogen rates in relation to targeted wheat yields. Experimental Agriculture 36:115-125.

Sayre, K., S. Rajaram and R. Fischer. 1997. Yield potential progress in short bread wheats in northwest Mexico. Crop Science 37: 36-42.

Scharf, P. C., Kitchen, N. R., Sudduth, K. A., Davis, J. G., Hubbard, V. C., and Lory, J. A. 2005. Field-scale variability in optimal nitrogen fertilizer rate for corn. Agronomy Journal 97:452-461.

Schenk, M. 1996. Regulation of nitrogen uptake on the whole plant level. Plant and Soil 181:131-137.

Scow, K., O. Somasco, N. Gunapala, S. Lau, R. Venette, H. Ferris, et al. 1994. Transition from conventional to low-input agriculture changes soil fertility and biology. California Agriculture 48: 20-26.

Seufert, V., N. Ramankutty and J.A. Foley. 2012. Comparing the yields of organic and conventional agriculture. Nature 485: 229-232.

Shanahan, J., Kitchen, N., Raun, W., and Schepers, J. S. 2008. Responsive in-season nitrogen management for cereals. Computers and Electronics in Agriculture 61:51-62.

Sheehy, J., Dionora, M., Mitchell, P., Peng, S., Cassman, K., Lemaire, G., and Williams, R. 1998. Critical nitrogen concentrations: Implications for high-yielding rice (*Oryza sativa* L.) cultivars in the tropics. Field Crops Research 59:31-41.

Shen, J., Li, C., Mi, G., Li, L., Yuan, L., Jiang, R., and Zhang, F. 2013. Maximizing root/rhizosphere efficiency to improve crop productivity and nutrient use efficiency in intensive agriculture of China. Journal of Experimental Botany 64:1181-1192.

Sherrard, J., Lambert, R., Below, F., Dunand, R., Messmer, M., Willman, M., Winkels, C., and Hageman, R. 1986. Use of physiological traits, especially those of nitrogen metabolism for selection in maize. Biochemical Basis of Plant Breeding 2:109-130.

Shindo, H. and T. Nishio. 2005. Immobilization and remineralization of N following addition of wheat straw into soil: determination of gross N transformation rates by ^{15}N-ammonium isotope dilution technique. Soil Biology and Biochemistry 37: 425-432.

Sial, M. A., Arian, M. A., and Ahmed, M. 2000. Genotype × environment interaction on bread wheat grown over multiple sites and years in Pakistan. Pakistan Journal of Botany 32:85-91.

Siddique, K., R. Belford and D. Tennant. 1990. Root: shoot ratios of old and modern, tall and semi-dwarf wheats in a Mediterranean environment. Plant Soil 121: 89-98.

Simmonds, N.W. 1995. The relation between yield and protein in cereal grain. Journal of Science of Food and Agriculture 67: 309-315.

Simpson, R. J., Lambers, H., and Dalling, M. J. 1982. Translocation of nitrogen in a vegetative wheat plant (*Triticum aestivum*). Physiologia Plantarum 56:11-17.

Sinebo, W., Gretzmacher, R., and Edelbauer, A. 2004. Genotypic variation for nitrogen use efficiency in Ethiopian barley. Field Crops Research 85:43-60.

Singh, V., and A. Arora. 2001. Intraspecific variation in nitrogen uptake and nitrogen utilization efficiency in wheat (*Triticum aestivum* L.). Journal of Agronomy and Crop Science 186: 239-244.

Slafer, G.A., F.H. Andrade and S.E. Feingold. 1990. Genetic improvement of bread wheat (*Triticum aestivum* L.) in Argentina: relationships between nitrogen and dry matter. Euphytica 50: 63-71.

Smith, J., R. Papendick, D. Bezdicek and J. Lynch. 1993. Soil organic matter dynamics and crop residue management. Soil Microbial Ecology, Marcel Dekker, New York: 65-95.

Snyder, C., and Spaner, D. 2010. The sustainability of organic grain production on the Canadian prairies-a review. Sustainability 2:1016-1034.

Sowers, K. E., Pan, W. L., Miller, B. C., and Smith, J. L. 1994. Nitrogen use efficiency of split nitrogen applications in soft white winter wheat. Agronomy Journal 86:942-948.

Spargo, J. T., Alley, M. M., Follett, R. F., and Wallace, J. V. 2008. Soil nitrogen conservation with continuous no-till management. Nutrient Cycling in Agroecosystems 82:283-297.

Spiertz, J., and De Vos, N. 1983. Agronomical and physiological aspects of the role of nitrogen in yield formation of cereals. Plant and Soil 75:379-391.

Spiess, D. 2015. Soil group map of Alberta. Alberta Agriculture and Forestry. Available www1.agric.gov.ab.ca/soils/soils.nsf/soilgroupmap (Accessed Nov. 28, 2017)

Stopes, C., Lord, E., Philipps, L., and Woodward, L. 2002. Nitrate leaching from organic farms and conventional farms following best practice. Soil Use and Management 18:256-263.

Starling, W., and Richards, M. C. 1993. Quality of commercial samples of organically-grown wheat. Aspects of Applied Biology 36:205–209.

Struik, P., and Yin, X. 2009. QTL× E× M: Combining crop physiology and genetics. In: Østergård, H., Lammerts Van Bueren, E., and Bouwman-Smiths, L. (eds.) Proceedings of the bioexploit/eucarpia workshop on the role of marker assisted selection in breeding varieties for organic agriculture. BioExploit, Wageningen, The Netherlands. p.18-21.

Sun, Y., Ma, J., Sun, Y., Xu, H., Yang, Z., Liu, S., Jia, X., and Zheng, H. 2012. The effects of different water and nitrogen managements on yield and nitrogen use efficiency in hybrid rice of china. Field Crops Research 127:85-98.

Statistics Canada. 2011. Field crop reporting series. http://www.statcan.gc.ca/pub/22-002-x/2012006/tablesectlist-listetableauxsect-eng.htm. (accessed April 8 2013).

Swain, E. Y., Rempelos, L., Orr, C. H., Hall, G., Chapman, R., Almadni, M., Stockdale, E. A., Kidd, J., Leifert, C., and Cooper, J. M. 2014. Optimizing nitrogen use efficiency in wheat and potatoes: Interactions between genotypes and agronomic practices. Euphytica 199:119-136.

Sylvester-Bradley, R., and Kindred, D. R. 2009. Analysing nitrogen responses of cereals to prioritize routes to the improvement of nitrogen use efficiency. Journal of Experimental Botany 60:1939-1951.

Syswerda, S., Basso, B., Hamilton, S., Tausig, J., and Robertson, G. 2012. Long-term nitrate loss along an agricultural intensity gradient in the upper Midwest USA. Agriculture, Ecosystems and Environment 149:10-19.

Tabuchi, M., Sugiyama, K., Ishiyama, K., Inoue, E., Sato, T., Takahashi, H., and Yamaya, T. 2005. Severe reduction in growth rate and grain filling of rice mutants lacking *OSGS1*; 1, a cytosolic glutamine synthetase1; 1. The Plant Journal 42:641-651.

Tanji, K., Broadbent, F., Mehran, M., and Fried, M. 1979. An extended version of a conceptual model for evaluating annual nitrogen leaching losses from croplands. Journal of Environmental Quality 8:114-120.

Tilman, D., K.G. Cassman, P.A. Matson, R. Naylor and S. Polasky. 2002. Agricultural sustainability and intensive production practices. Nature 418: 671.

Tinker, P. B., and Nye, P. H. 2000. Solute movement in the rhizosphere, Oxford University Press, New York.

Tkachuk, R. 1969. Nitrogen-to-protein conversion factors for cereals and oil-seed meals. Cereal Chemistry.

Tonitto, C., David, M., and Drinkwater, L. 2006. Replacing bare fallows with cover crops in fertilizer-intensive cropping systems: A meta-analysis of crop yield and n dynamics. Agriculture, Ecosystems and Environment 112:58-72.

Trachsel, S., Kaeppler, S., Brown, K., and Lynch, J. 2013. Maize root growth angles become steeper under low n conditions. Field Crops Research 140:18-31.

UN (United Nations), Department of Economic and Social Affaires, Population Division. 2015. World Population Prospects: The 2015 Revision, Key Findings and Advance Tables. Working Paper, No. ESA/P/WP. 241.

Unger, P.W. 1991. Organic matter, nutrient, and pH distribution in no-and conventional-tillage semiarid soils. Agronomy Journal 83: 186-189.

USDA (United States Department of Agriculture). Economics, Statistics and Market Information System. 2017. Wheat outlook. http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1293 (accessed April 2 2017).

Van Bueren, E. L., Backes, G., De Vriend, H., and Østergård, H. 2010. The role of molecular markers and marker assisted selection in breeding for organic agriculture. Euphytica 175:51-64.

Van Der Heijden, M. G., Bardgett, R. D., and Van Straalen, N. M. 2008. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters 11:296-310.

Van Sanford, D., and Mackown, C. 1986. Variation in nitrogen use efficiency among soft red winter wheat genotypes. Theoretical and Applied Genetics 72:158-163.

Van Vuuren, M., Robinson, D., and Griffiths, B. 1996. Nutrient inflow and root proliferation during the exploitation of a temporally and spatially discrete source of nitrogen in soil. Plant and Soil 178:185-192.

Vance, C. P. 2001. Symbiotic nitrogen fixation and phosphorus acquisition. Plant nutrition in a world of declining renewable resources. Plant Physiology 127:390-397.

Veresoglou, S. D., Chen, B., and Rillig, M. C. 2012. Arbuscular mycorrhiza and soil nitrogen cycling. Soil Biology and Biochemistry 46:53-62.

Vidmar, J. J., Zhuo, D., Siddiqi, M. Y., Schjoerring, J. K., Touraine, B., and Glass, A. D. 2000. Regulation of high-affinity nitrate transporter genes and high-affinity nitrate influx by nitrogen pools in roots of barley. Plant Physiology 123:307-318.

Vigil, M. and D. Kissel. 1991. Equations for estimating the amount of nitrogen mineralized from crop residues. Soil Science Society of America Journal 55: 757-761.

Waddington, S.R., J. Ransom, M. Osmanzai and D.A. Saunders. 1986. Improvement in the yield potential of bread wheat adapted to northwest Mexico. Crop Science 26: 698-703.

Walch-Liu, P., Ivanov, I. I., Filleur, S., Gan, Y., Remans, T., and Forde, B. G. 2006a. Nitrogen regulation of root branching. Annals of Botany 97:875-881.

Walch-Liu, P., Liu, L.-H., Remans, T., Tester, M., and Forde, B. G. 2006b. Evidence that l-glutamate can act as an exogenous signal to modulate root growth and branching in *arabidopsis thaliana*. Plant and Cell Physiology 47:1045-1057.

Wang, H., T. McCaig, R. DePauw, F. Clarke and J. Clarke. 2003. Physiological characteristics of recent Canada Western Red Spring wheat cultivars: Components of grain nitrogen yield. Canadian Journal of Plant Science 83: 699-707.

Wang, X., and Below, F. E. 1992. Root growth, nitrogen uptake, and tillering of wheat induced by mixed-nitrogen source. Crop Science 32:997-1002.

Wang, R. X., Hai, L., Zhang, X. Y. et al. 2009. QTL mapping for grain filling rate and yield-related traits in RILs of the Chinese winter wheat population Heshangmai × Yu8679. Theoretical and Applied Genetics 118:313–325.

Wang, X., Wei, Y., Shi, L., Ma, X., and Theg, S. M. 2015. New isoforms and assembly of glutamine synthetase in the leaf of wheat (*Triticum aestivum* L.). Journal of Experimental Botany 66:6827-6834.

Watkins, N., and Barraclough, D. 1996. Gross rates of n mineralization associated with the decomposition of plant residues. Soil Biology and Biochemistry 28:169-175.

Weber, A., Gutser, R., Michel, H., Wozniak, H., Chen, G., Xu, H., and Niclas, H. Dicyandiamide and 1h-1, 2, 4-triazole–a new effective nitrification inhibitor for reducing nitrous oxide emissions from cultivated land. In: Weiske, A., ed. Greenhouse Gas Emissions from Agriculture–Mitigation Options and Strategies 2004 Leipzig, Germany. 273-275.

Wiebe, L. 2015. Examining the growth and nitrogen economy of organically selected spring wheat cultivars (Master of science thesis: University of Manitoba).

Wiebe, L., Fox, S. L., and Entz, M. H. 2016. Organic selection may improve yield efficiency in spring wheat: a preliminary analysis. Canadian Journal of Plant Science. 97: 298-307.

Wiesler, F., and Horst, W. 1994. Root growth and nitrate utilization of maize cultivars under field conditions. Plant and Soil 163:267-277.

Wojciechowski, T., M. Gooding, L. Ramsay and P. Gregory. 2009. The effects of dwarfing genes on seedling root growth of wheat. Journal of Experimental Botany. doi.10.1093/jxb/erp107.

Wolfe, M. S., Baresel, J.P., Desclaux, D., Goldringer, I., Hoad, S., Kovacs, G., Löschenberger, F., Miedaner, T., Østergârd, H., Lammerts van Bueren, E. T. 2008. Developments in breeding cereals for organic agriculture. Euphytica 163:323-346.

Wu, J., Bernardo, D., Mapp, H., Geleta, S., Teague, M., Watkins, K., Sabbagh, G., Elliott, R., and Stone, J. 1997. An evaluation of nitrogen runoff and leaching potential in the high plains. Journal of Soil and Water Conservation 52:73-80.

Xu, G., X. Fan and A.J. Miller. 2012. Plant nitrogen assimilation and use efficiency. Annual Review of Plant Biology 63: 153-182.

Yadav, R., Singh, V., Dwivedi, B., and Shukla, A. K. 2003. Wheat productivity and n use-efficiency as influenced by inclusion of cowpea as a grain legume in a rice–wheat system. The Journal of Agricultural Science 141:213-220.

Yanai, J., Kosaki, T., Nakano, A., and Kyuma, K. 1997. Application effects of controlled-availability fertilizer on dynamics of soil solution composition. Soil Science Society of America Journal 61:1781-1786.

Yan, L., Helguera, M., Kato. K., Fukuyama, S., Sherman, J., and Dubcovsky, J. 2004. Allelic variation at the *VRN*-1 Promoter region in polyploidy wheat. Theoretical and Applied and Genetics 109:1677-1686.

Yang, W., Xiang, Z., Ren, W., and Wang, X. 2005. Effect of S-3307 on nitrogen metabolism and grain protein content in rice. Chinese Journal of Rice Science 19:63-67.

Yang, J. C., Zhang, J. H. 2006. Grain filling of cereals under soil drying. New Phytolgist 169:223–236.

Yienger, J., and Levy, H. 1995. Empirical model of global soil-biogenic noχ emissions. Journal of Geophysical Research 100:11447-11464.

Zebarth, B., Drury, C., Tremblay, N., and Cambouris, A. 2009. Opportunities for improved fertilizer nitrogen management in production of arable crops in eastern Canada: A review. Canadian Journal of Soil Science 89:113-132.

Zhao, G., Hörmann, G., Fohrer, N., Li, H., Gao, J., and Tian, K. 2011. Development and application of a nitrogen simulation model in a data scarce catchment in south China. Agricultural Water Management 98:619-631.

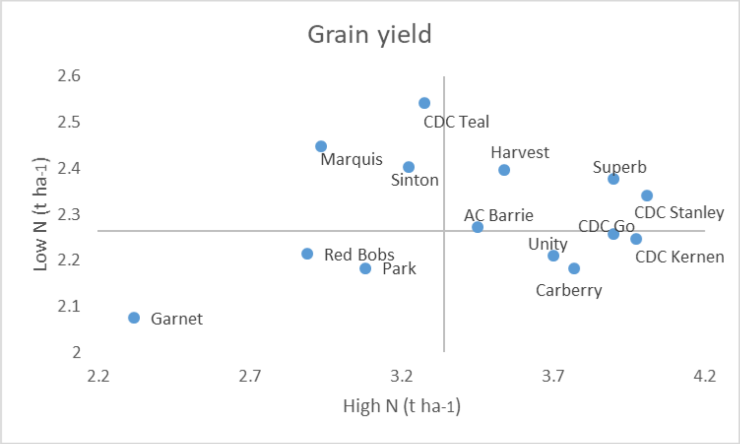
Zhou, C., Cai, Z., Guo, Y., and Gan, S. 2009. An arabidopsis mitogen-activated protein kinase cascade, MKK9-MPK6, plays a role in leaf senescence. Plant Physiology 150:167-177.

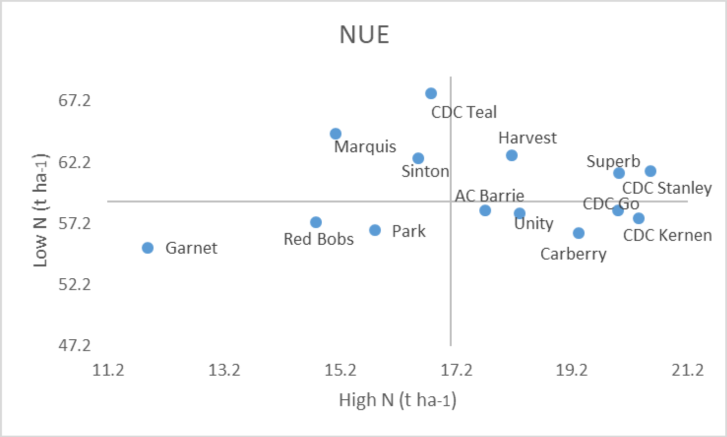
Ziadi, N., Bélanger, G., Claessens, A., Lefebvre, L., Cambouris, A. N., Tremblay, N., Nolin, M. C., and Parent, L.-É. 2010. Determination of a critical nitrogen dilution curve for spring wheat. Agronomy Journal 102:241-250.

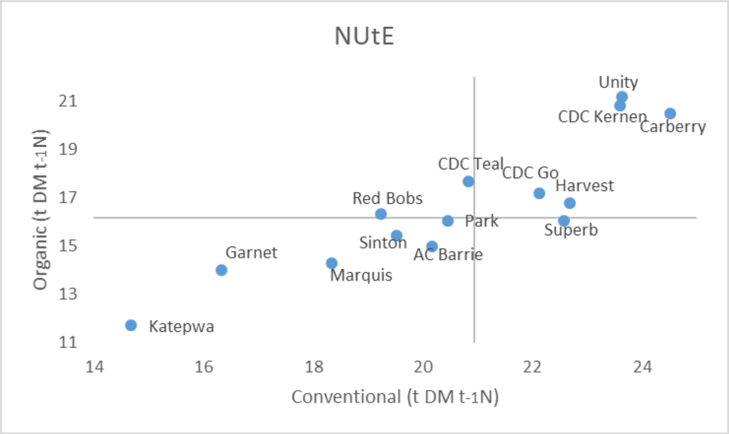
Zorb, C., Niehaus, K., Barsch, A. 2009. Levels of compounds and metabolites in wheat ears and grains in organic and conventional agriculture. Journal of Agricultural and Food Chemistry 57:9555–9562.

Appendices

Apendix 3-1. Genotype by environment interaction of Canada Western Red Spring wheat cultivars for grain yield, NUE, and NUtE in high and low N treatments under conventional management system.

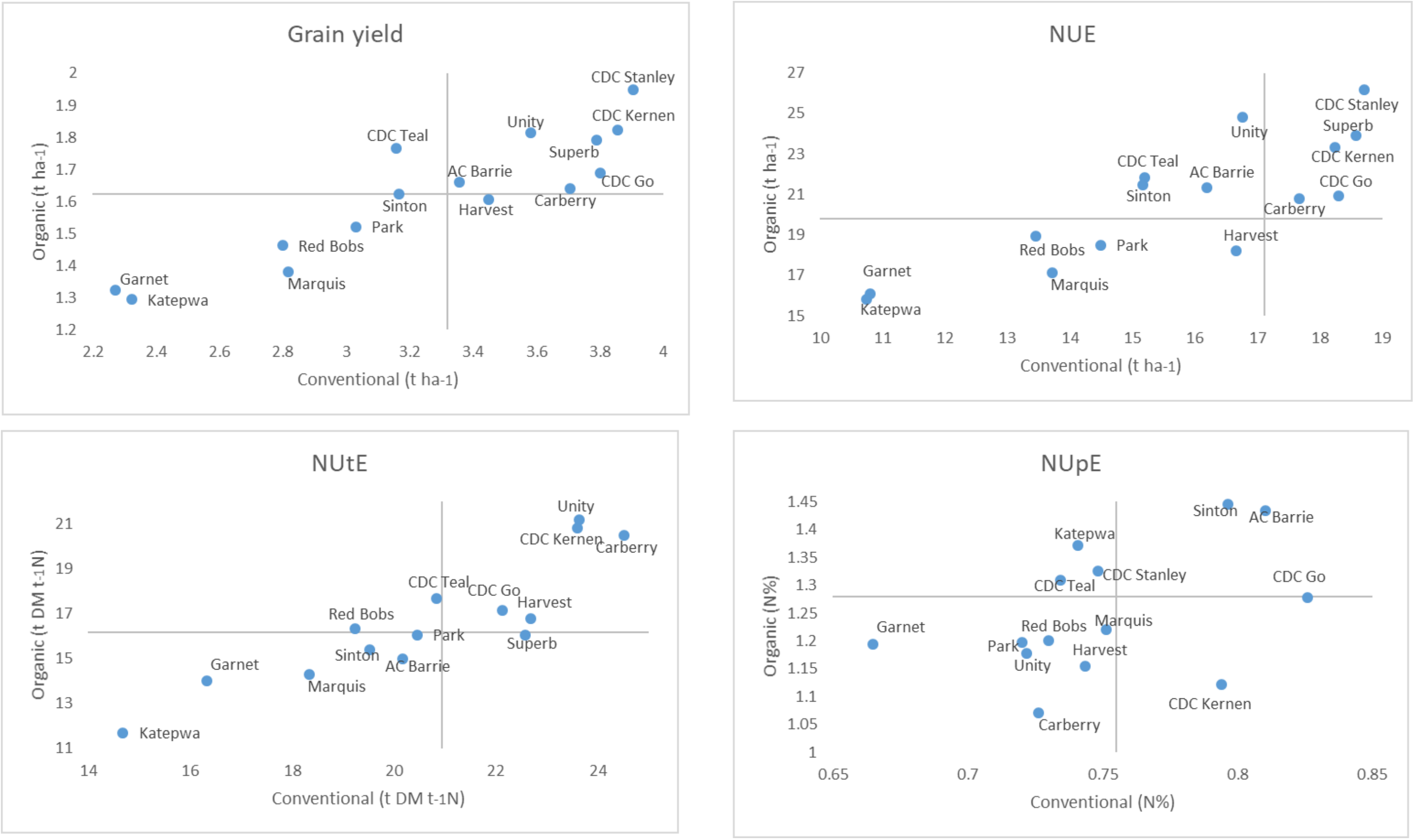






Lines in figures indicate mean values.

Apendix 4-1. Genotype by environment interaction of Canada Western Red Spring wheat cultivars for grain yield, NUE, NUtE, and NUpE under conventional and organic management systems.



Lines in figures indicate mean values.