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Introductory Paper at the Faculty of Landscape Planning, Horticulture and Agricultural Science 2009:1
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ISSN 1654-3580

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Summary
The main emphasis of the introductory paper is to highlight the importance of nutrients, their uptake, transport, translocation and use efficiency in cereal crop production. Among the cereals, mainly wheat and barley are discussed in details. Among the nutrients, nitrogen, as one of the most important nutrients, is most deeply described in this paper. Quantitative and qualitative aspects of proteins in wheat and barley are also described in relation to nutrient availability. Nitrogen mineralization and leaching is discussed for cereal cultivation.

Preface
Cereals are edible seeds or grains of the grass family, *Gramineae*. They are used as food, feed and fiber in many parts of the world. Nutrients play a very crucial role in crop production. Nitrogen (N) supply is the main factor controlling crop growth and yield of winter and spring cereals. This introductory paper elucidates the journey of nutrients e.g. nitrogen in cereals like wheat and barley up to their final destination, matured grain. This review also gives a background to an ongoing PhD-study focusing on role and function of nutrients, specifically nitrogen in cereal crop production. Furthermore effect of certain genetic, environmental and agronomic factors on the nitrogen cycle and qualitative aspects of cereals are also discussed.

Contents

Introduction

Cereals

The word *cereal* derives from *ceres*, the name of the pre-Roman goddess of harvest and agriculture. Cereals can be defined as grains or edible seeds of the grass family, *Gramineae* (Bender and Bender, 1999; McKevith, 2004). Wheat, maize, rice, barley, rye, oat, triticale, millet and sorghum are cereal crops most commonly grown in different parts of the world (Shewry, 2007). Cereals are staple foods for human nutrition and their incorporation into a wide range of products is of great economic importance (Saulnier et al., 2007). The cereal grain group contains important amounts of major nutrients and thereby forms an essential part of a balanced diet (Truswell, 2002). Cereals are a major source of dietary proteins for humans. Cereal dietary fiber also has a major impact on the nutritional quality of cereal foods (Fincher and Stone, 1986). The components in cereals like proteins, starch, lipids etc, have major effects on the end use of the cereal grain for milling, baking and animal feed.

Nutrient uptake, transport and translocation in cereals are important due to a number of reasons. First of all many quality aspects of products e.g. bread, pasta, noodles produced by cereal plants are related to the protein composition. Plant protein composition is determined by nutrient availability for the plant during growth until plant harvest. In addition, the nutrient use efficiency is important in order to hinder nutrient leakage in seas and lakes and due to the decreased cost of fertilizer for the farmer.

Wheat

Wheat was originated in Southwest Asia, Tigris and Euphrates river valley, in the area known as the Fertile Crescent (Smith and Wayne, 1995). Sowing of grains from wild grasses, cultivation and repeated harvesting led to domestication of wheat. Selection of mutant forms with tough ears which remained intact during harvesting, larger grains, and a tendency for the spikelets to stay on the stalk until harvested was the set-off of modern agriculture (Dubcovsky et al., 1997).

Bread wheat (*Triticum aestivum*) produces one-seeded fruits, which are called grains or kernels (Hoseney, 1994). The pleasant flavor, long shelf-life and unique gluten-forming characteristics of wheat products like pasta, noodles, bread, chapatti etc make them very attractive among other cereals (Nelson, 1985).

The group *Triticeae* has five genera i.e. *Aegilops*, *Elymus*, *Hordeum*, *Secale* and *Triticum* in it. The basic number of chromosomes in *Triticum* and related species are x=7. The wild species are diploids (2n = 2x = 14), e.g. with genome designation AA (*Triticum monococcum*), DD (T. tauschii) and SS (*T. speltoides*), or tetraploids (2n = 4x = 28), e.g. with the genomes AABB (e.g. *T. turgidum*) or AAGG (*T. timopheevi*) (Waines and Barnhart, 1992). Nowadays the hexaploid wheat which is mostly being cultivated in the world is *Triticum aestivum*, AABBDD, (2n=6x=42) (Zohary and Hopf, 1993).

Bread-making quality

The art of bread-making was learned by humans more than forty centuries ago. Bread has been a popular staple food for ages, although not in the same pattern we know today. Baking of yeast-leavened and sour dough breads are one of the oldest biotechnological processes (Barrett, 1975). Up till today wheat is considered as the preferable crop for bread and other flour products because of its supreme baking performance as compared to other cereals like barley and rye (Dewettinck et al., 2008). Flour from wheat consists mainly of starch (70–75%), water (14%) and proteins (10–12%). In addition, non-starch polysaccharides (2–3%), in particular arabinoxylans (AX) and lipids (2%) are important minor flour constituents relevant for bread production and quality (Goesaert et al., 2005). Quantity, composition (quality), type and viscoelastic properties of wheat gluten proteins are important for bread-making (Finney and Barmore, 1948; Shewry and Halford, 2002). Dough mixing requirement, rheological properties of optimally mixed dough and gas retention property of fermenting dough are determined by gluten proteins (Fig 1). Gas retention properties in turn determine loaf volume and crumb structure of the resulting bread (Gan et al., 1995). Gluten proteins determining bread-making quality are influenced by a number of environmental and genetic factors (MacDonald, 1992; MacRitchie, 1999; Johansson et al., 2001)

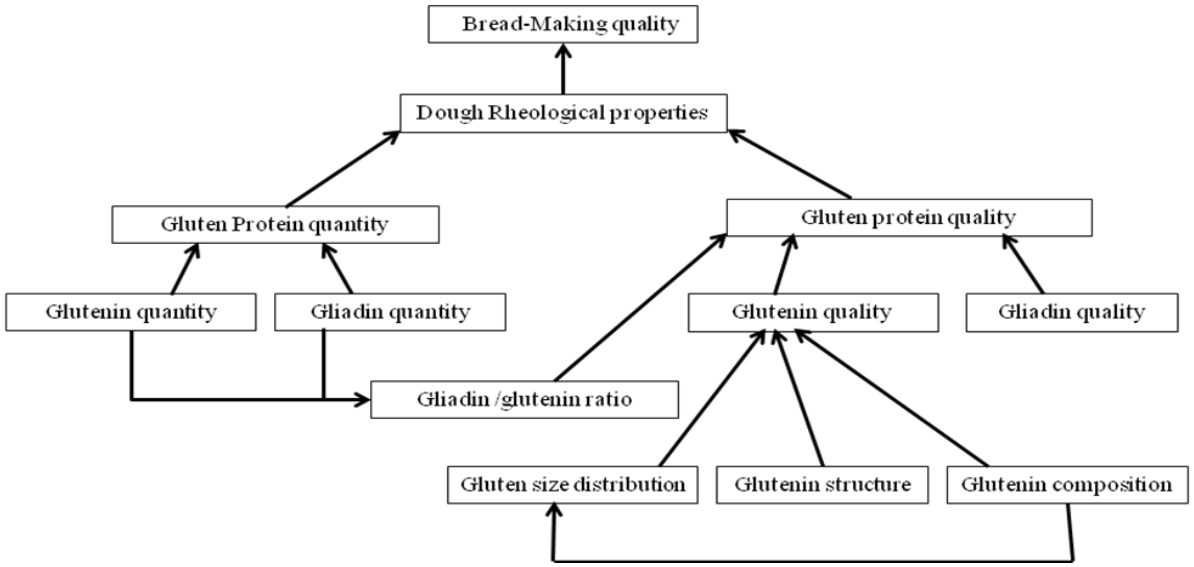

Figure 1. Factors affecting rheology and bread-making characteristics of wheat adapted from Veraverbeke and Delcour (2002).

In wheat bread-making a number of ingredients i.e. flour, water, salt, yeast or other micro-organisms, fat and sugar are mixed into visco-elastic dough, which is fermented and baked. During all steps of bread-making, complex chemical, biochemical and physical transformations occur, which affect and are affected by the various flour constituents. For bread-making process the proper ratio and interaction of different components like proteins, lipids, carbohydrates, water etc, which constitute the flour, are of crucial importance (Kuktaite, 2004).

Components of wheat flour

Starch

Starch is the most important reserve polysaccharide of many cereals (Parker and Ring, 2001). In wheat, starch is the most abundant component present in the grain endosperm (Lineback and Rasper, 1988). It consists of the glucose polymers, amylose and amylopectin. Amylose is essentially linear, consisting of (1→4)-α-linked d-glucopyranosyl units with molecular weight (MW) in the range of 10^5–10^6 and a degree of polymerization (DP) of 500–6000 glucose residues (Lineback and Rasper, 1988). Carbohydrates can be divided into two main types: available and unavailable. Available carbohydrates are those digested and absorbed by humans, which include (non-resistant) starch and soluble sugars. In contrast, unavailable carbohydrates (dietary fiber) are not digested by the endogenous secretion of the human digestive tract (Southgate, 1991). Dietary fiber is mainly composed of resistant starch (RS), cellulose and other complex polysaccharides, such as arabinoxylans, β-glucans, pectins and arabinogalactans, together with lignin (Muralikrishna and Rao, 2007).

Lipids

In wheat grain, lipids are present in small amounts (2%). Essential fatty acids (palmitic and linoleic acids), fat-soluble vitamins and phytosterols are important components of wheat grain lipids (Ruibal-Mendieta et al., 2004). Based on solubility under specific extraction conditions lipids are classified as starch lipids, both free and bound, and non-starch lipids (NSL). Approximately 2/3–3/4 of the total wheat flour lipids is comprised by NSL that are predominantly triglycerides and other non-polar (NP) lipids such as digalactosyl diglycerides (DGDG). NP lipids are mainly present in the free NSL fraction, while glyco- and phospholipids are mainly associated with proteins and present in the bound NSL fraction. The fatty acid pattern of the flour lipids is dominated by linoleic acid (C18:2) with lower amounts of palmitic (C16:0) and oleic acids (C18:1) (Eliasson and Larsson, 1993; Hoseney, 1994).

Flour lipids have a positive effect on formation of dough and loaf volume during the process of bread-making. Loaf volume is negatively affected by the free fatty acids in NP lipids while glycolipids in polar lipids have positive impact on the loaf volume (MacRitchie, 1983). Furthermore, loaf volume is affected positively and negatively by polar and NP lipids respectively (McCormack et al., 1991). The volume and softness of steamed bread and morphology of short-dough biscuits is also influenced by lipids (Pomeranz et al., 1991; Papantoniou et al., 2004).

Wheat proteins

The word *protein* means *primary substance*, according to Mulder and Berzelius who proposed the name in 1838 (Tracey, 1967). The scientific study of wheat grain proteins extends back for over 250 years, with the isolation of wheat gluten first being described in 1745 (Beccari, 1745). Osborne classified wheat protein according to the basis of solubility and functionality in 1908. Proteins were divided into three major types: simple, conjugated and derived. Osborne concluded that the proteins present in plant tissues were “simple” and comprised of four major types: albumins (soluble in water and dilute buffers), globulins (soluble in salt solutions), prolamins (soluble in 70 - 90% ethanol) and

glutelins (soluble in dilute acid or alkali) (Table 1). The gluten proteins of wheat classically fall into two of these groups, with the alcohol-soluble gliadins and the alcohol-insoluble glutenins. Glutenins are known being the biggest polymers in nature (Shewry and Halford, 2002). In 1970 the glutelin fraction was divided into two fractions according to solubility in dilute acetic acid. The fraction which was insoluble in dilute acetic acid corresponded to the fifth fraction according to the Osborne fractions (Chen and Bushuk, 1970).

Grain proteins of wheat can also be divided into structural/metabolic (non-gluten) and storage proteins (gluten) (Shewry, 2003). Structural/metabolic proteins consist of albumin, globulin and amphiphilic proteins. Non-membrane amphiphilic proteins have been reported to have large effects on grain hardness and dough rheological properties (Dubreil et al., 1998).

Wheat storage proteins are collectively known as prolamins because of their high content of the amino acids, proline and glutamine. Another system of classification divided prolamins into three groups: sulphur-rich, sulphur-poor and high molecular weight glutenin subunits (HMW-GS). Sulphur rich prolamins include β-, γ-gliadins, B- and C-low molecular weight glutenins (LMW-GS). Sulphur poor prolamins contain ω-gliadins and D- LMW-GS (Shewry and Halford, 2002).

The individual polypeptides of wheat storage proteins are synthesized on ribosomes on the rough endoplasmic reticulum (RER) and pass via the usual translocation machinery into the lumen, with the loss of an N-terminal signal peptide (Levanony et al., 1992). Once within the lumen it is probable that protein folding and disulphide bond formation occurs with no further post-translational modifications taking place (i.e. no glycosylation or proteolysis) (Shewry, 2003).

The genes which are responsible for encoding gliadins and glutenin subunits are located to several complex loci on the homologous chromosomes 1 and 6. Each of these homologous chromosomes consists of several tightly linked genes. Genes responsible for coding HMW-GS occur on the long arm of chromosomes 1A, 1B and 1D, while the genes responsible for coding LMW-GS, ω- and γ- gliadins are located on the short arm of chromosomes 6A, 6B and 6D (Payne, 1987).

Table 1. Classification of proteins according to Osborne, modified from Goesaert et al., (2005).

Osborne fraction	Solubility behaviour	Composition	Biological role	Functional role
Albumin	Water and dilute buffers	Non-gluten proteins (mainly monomeric)	Metabolic and structural proteins	Protection from pathogens
Globulin	Dilute salt	Non-gluten proteins (mainly monomeric)	Metabolic and structural proteins	Providing food reserve to embryo
Gliadin	Aqueous alcohols	Gluten proteins (mainly monomeric gliadins and low molecular weight glutenin polymers)	Prolamins-type seed storage proteins	Dough viscosity/plasticity
Glutenin	Dilute acetic acid	Gluten proteins (mainly HMW glutenin polymers)	Prolamins-type seed storage proteins	Dough viscosity/plasticity
Residue	Unextractable in water and dilute buffers but extractable with Urea+ DTT+SDS SDS+ Phosphate buffers+ sonication etc	Gluten proteins (high molecular weight polymers) and polymeric non-gluten proteins (triticins)	Prolamins-type (gluten) and globulin-type (triticin) seed storage proteins	

Albumins and globulins

The non-prolamin proteins; albumins and globulins of wheat, comprises 15-20% of total wheat flour proteins. Albumins are soluble in water and globulins are soluble in salts (Pence et al., 1954; Singh and Skerritt, 2001). The molecular weights (MW) of albumins and globulins are mostly lower than 25,000, although a significant proportion of the proteins has MW between 60,000 and 70,000 (Veraverbeke and Delcour, 2002). Albumins and globulins are considered to have nutritionally better amino acid compositions because of their higher lysine and methionine contents as compared to the rest of the proteins in the wheat grain (Lasztity, 1984). Alpha- amylase/trypsin, serpins and purothionins are predominant albumins and globulins. These predominant albumins and globulins serve as nutrient reserves for the germinating embryo. Secondly they also help in protecting embryo from insects and pathogens before germination (Dupont and Altenbach, 2003).

Gluten

The rubbery mass that is left when wheat flour is washed with water to remove starch, non-starchy polysaccharides, and water-soluble constituents, is called gluten. Gluten is comprised of 80–85% protein and 5% lipids; most of the remainder is starch and non-starch carbohydrates (Wall, 1979; Wieser, 2007). Wheat storage proteins play a crucial role in forming the strong, cohesive dough that will retain gas and produce light baked products. These properties make wheat alone suitable for the preparation of a great diversity of food products- breads, noodles, pasta, cookies, cakes, pastries and many other foods (Day et al., 2006).

Gluten proteins are present in the mature wheat grain endosperm where they form a continuous matrix around the starch granules. Gluten contains hundreds of protein

components which are present either as monomers or, linked by inter- and intra- chain disulphide bonds (cysteine oxidized form), as oligo- polymers (Wrigley and Bietz, 1988). The properties of the various types of gluten proteins are summarized in Table 2 (D' Ovidio and Masci, 2004).
In the amino acid composition of gluten, cysteine residues are in minor amount≈(2%), although this little amount is very crucial for the structure and functionality of gluten. Cysteine (oxidized form) normally form inter-chain disulphide bonds within and between proteins (Wieser, 2003).

Table 2. Classification and properties of wheat gluten proteins, adopted from D'Ovidio and Masci, (2004).

Group	Subunit structure	Total fraction %	Molecular weight, Da	Amino acid composition, mol %
HMW subunits of glutenins	Polymeric	6-10	65 - 90000	30 - 35 Gln 10 - 16 Pro 15 - 20 Gly 0.5 - 1.5 Cys 0.7 - 1.4Lys
LMW Subunits of glutenins	Polymeric	70-80	30 - 45000	30 - 40 Gln 15 - 20 pro 2 - 3 Cys <1.0 Lys
α-Gliadins β-Gliadins γ -Gliadins	Monomeric Monomeric Monomeric	70-80	30 - 45000	30 - 40 Gln 15 - 20 pro 2 - 3 Cys <1.0 Lys
ω - Gliadins	Monomeric	10-20	40 - 75000	40 - 50 Gln 20 - 30 Pro 8 - 9 Phe 0 Cys 0 - 0.5 Lys

Gliadins
Gliadins are monomeric proteins that consist of single chain polypeptides and constitute from 30 to 40% of total flour protein content. Gliadins are polymorphic mixture of proteins soluble in 70% alcohol (Anderson and Greene, 1997). The bonds which are formed in the gliadins are intra-chain cysteine disulphide bridges resulting in less or more globular monomeric nature of gliadins (Shewry et al., 2003). Gliadins are rich in proline and glutamine and have a low level of charged amino acids (Shewry, 2003). The molecular weights of gliadins is 30–80 kDa and they are classified into four groups of α, β, γ and ω on the basis of molecular mobility at low pH in acid polyacrylamide gel electrophoresis (Shewry et al., 1986). Wieser grouped gliadins into four different classes ω5-, ω1 and 2-, α/β- and γ-gliadins (Wieser, 2007). This division was based on sequences and composition of amino acids, and molecular weights of different classes of gliadins. α, β and γ gliadins contain inter-chain disulfide bonds, while ω-gliadins lack cysteine

residues and do not form disulphide bonds (MacRitchie, 1987; Wieser, 2007). The α/β- and γ- gliadins are the major components, whereas the ω-gliadins occur in much lower proportions of wheat varieties (Wieser and Kieffer, 2001).
Hydrated gliadins have little elasticity and are less cohesive than glutenins; they contribute mainly to the viscosity and extensibility of dough system (Wieser, 2007). Gliadins may associate with one another or the glutenins through hydrophobic interactions and hydrogen bonds (Veraverbeke and Delcour, 2002).

Glutenins

Glutenins are the polymeric proteins of wheat gluten and they are extractable in dilute acetic acid (Field et al., 1983). Glutenins and gliadins have very similar amino acid composition, thus glutenin have high levels of glutamine and proline and low levels of charged amino acids (Goesaert et al., 2005). In wheat flour dough, baking performance strongly depend on the molecular weight distribution of glutenins. Glutenins appear to be largely responsible for gluten elasticity (MacRitchie, 1992; Wieser, 2007). In addition, glutenins have the ability to form the largest and most complex protein polymers in nature with MWs of more than 10 millions, making wheat glutenins outstanding proteins in the plant kingdom (Wrigley, 1996; Wieser, 2007).
Two classes of glutenin subunits, HMW-GS and LMW-GS are present in wheat and they are released at the reduction of disulphide bonds with reducing agents and determined when analyzed by electrophoresis. The glutenin subunits released has also been further classified into four subgroups (A, B, C and D) on the basis of electrophoretic mobility on SDS-PAGE. The subgroup A is determined to be HMW-GS and subgroups B, C and D are referred to as LMW-GS (Shewry and Tatham, 1990; Wrigley, 1996; Gianibelli et al., 2001; Wang et al., 2006). It was also observed that high-molecular-weight gliadins, once reduced and separated by SDS-PAGE, had mobilities similar to those of B and C subunits of LMW-GS (Payne and Corfield, 1979).
HMW-GS constitute no more than 10% of total flour protein; although they may be the most important determinants of bread-making quality because of their importance in forming the glutenin polymer (Shewry et al., 1992). LMW-GS were first identified by gel filtration of extracts of wheat flour as high-molecular-weight gliadins linked by disulphide bonds, distinguishing them from monomeric gliadins (Beckwith et al., 1966). Six HMW-GS genes are present in hexaploid wheat and because of gene silencing only three of these genes are always expressed in all cultivars.
After running wheat protein samples on 2D gel electrophoresis at least fifteen to twenty different LMW-GS proteins are found in wheat (hexaploid) (Lew et al., 1992; Gianibelli et al., 2001). HMW-GS have molecular weights between 65 and 90 kDa, based on derived amino acid sequence, and 80–130 kDa on SDS-PAGE. They are encoded at complex loci on the long arms of chromosomes 1A, 1B and 1D of hexaploid wheat, the *Glu-A1*, *Glu-B1* and *Glu-D1* loci, respectively (Payne et al., 1984; Gianibelli et al., 2001). Molecular analyses have shown that each locus consists of two genes encoding subunits designated x-type, (higher molecular weight) and y-type (lower molecular weight). Similar to HMW-GS subunits, LMW-GS subunits are linked together through inter and intra chain disulphide bridges (Veraverbeke and Delcour, 2002). B and C subgroups contain about 60% of total LMW-GS. The subgroups B and C of LMW-GS have molecular weights 42–51 kDa and 30–40 kDa respectively. The amino acid sequences of

LMW-GS in C subgroup are similar to amino acid sequence of γ- and α-gliadins. Highly acidic LMW-GS, having molecular weight 58 kDa, are present in subgroup D. These LMW-GS are derived from modified ω-gliadins (Gianibelli et al., 2001). The LMW-GS have also been classified into LMW-m subunits which have methionine as the first amino acid in the sequence, and LMW-s subunits which have serine as the first amino acid in the sequence (Lew et al., 1992). The set of genes at *Glu-A3*, *Glu-B3* and *Glu-D3* loci on chromosomes 1AS, 1BS and 1DS help in encoding some of the C group LMW-GS and many of the B group LMW-GS (Jackson et al., 1983; Masci et al., 2002).

All cultivars contain 1Bx, 1Dx and 1Dy subunits, while other cultivars also contain a 1By and/or 1Ax and 1Ay subunit (Payne and Lawrence, 1983). The silencing of some of the genes could be caused by the presence of a transposon-like insertion in the coding region (Harberd et al., 1986). The full amino acid sequences of a number of subunits have been determined, including x-type and y-type proteins encoded by all three genomes, by sequencing of genomic DNA (Shewry et al., 1992). Allelic variation in the subunits encoded by active genes results in proteins subunits with different mobility on gel electrophoresis (Figure 2),

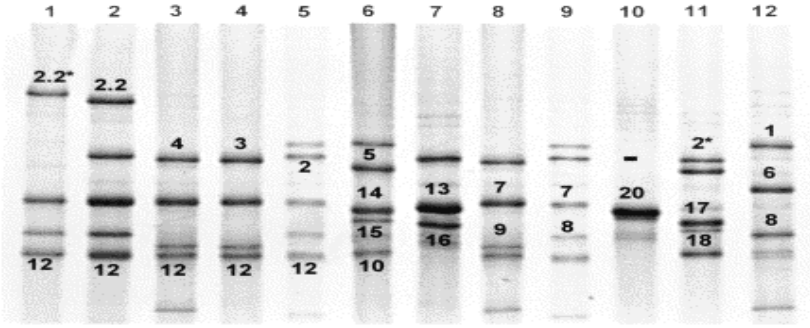

Figure 2 *SDS–PAGE of major allelic forms of HMW subunits present in different wheat cultivars and lines. Alleles at the Glu-D1 locus are shown in lanes 1–6, at the Glu-B1 from 6 to 12, at the Glu-A1 from 11 to 12 (Payne and Lawrence, 1983; Shewry et al., 2000)*

Glutenin polymer

It is nearly impossible to extract the intact glutenin polymer from wheat flour. It is also difficult to obtain a true estimate of the amount and size of the glutenin polymer. Nonetheless, the amount of unextractable protein, mainly glutenin polymer, the amount of polymer extracted by sonication, and the variations in types and amounts of HMW-GS and LMW-GS contained within the glutenin polymers have all been reported to correlate with bread-making quality (Field et al., 1983; Gupta et al., 1992; Bean et al., 1998).

Several approaches have been combined to give details of the secondary structure of HMW-GS. The β-turns formed by the repetitive domains of the HMW subunits were organized to form a regular structure and a model based on the β-spiral formed by a repetitive polypentapeptide sequence present in elastin, an elastomeric connective tissue of mammals was proposed (Tatham et al., 1985) (Figure 3).

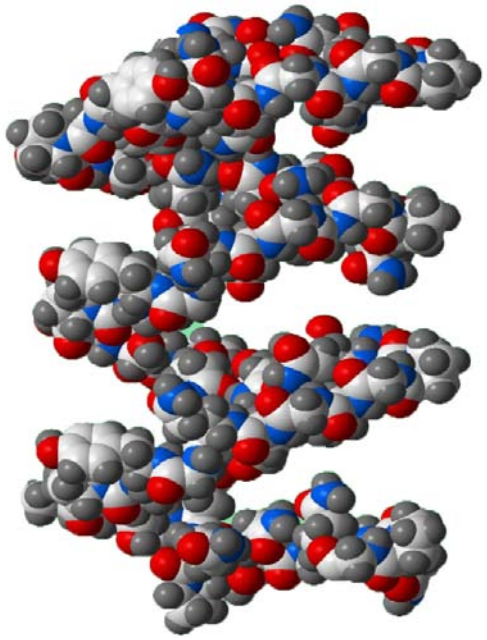

Figure 3 *A β-spiral model of the consensus repeat peptides present in the HMW subunits of glutenin (Parchment et al., 2001). Atoms are shown in white (carbon), blue (nitrogen), red (oxygen) and grey (hydrogen) (Shewry et al., unpublished results*).

HMW-GS play a key role in affecting gluten viscoelastic properties through their major effect on determining the size distribution of glutenin (MacRitchie and Lafiandra, 1997). The glutenin polymers consist of LMW-GS of about 40 kDa. These subunits are joined together by inter-chain disulphide bonds to high molecular weight glutenin subunits (HMW-GS) of about 90 kDa (Gupta et al., 1992; Dupont and Altenbach, 2003).
Beside the above mentioned model for the glutenin polymer several additional hypothetical models have been proposed (Ewart, 1979; Graveland. et al., 1985; Kasarda, 1999). Kasarda (1999) suggested that glutenin polymer is formed of different subunits, randomly linked through disulphide bonds in a linear fashion, and that polymer size is modulated by the incorporation of chain extender or chain terminator subunits, the former having two or more cysteine residue available for intermolecular disulphide bonds and the latter a single residue. Based on biochemical and microscopy results, two models were proposed by Lindsay in 1999 in which HMW-GS and LMW-GS participate as a backbone of the polymer. In the first model, the backbone of the polymer is composed of HMW and LMW subunits oligomers. In the second model, the backbone of the polymer is composed of HMW subunit oligomers only (Lindsay and Skerritt, 1999).
The number and position of cysteine residues available for intermolecular bonds have been suggested to be responsible, to a certain extent, for qualitative differences of different allelic subunits through their effect on the amount of large-sized glutenin polymer (Bietz, 1987; Weegels et al., 1996).

Effect of genetic background on proteins

In wheat, bread-making character of dough is strongly influenced by genetic background, determining protein concentration and composition (MacDonald, 1992; Weegels et al., 1996; Johansson and Svensson, 1998). Presence or absences of specific allelic variants of HMW-GS are correlated with bread-making quality (Wieser and Zimmermann, 2000). HMW-GS 5+10 at the Glu-D1 locus is related to better bread-making quality as compared to HMW-GS 2+12 (Payne, 1987). The reason for better quality of wheat cultivars having HMW subunit pair 5+10 is related to the extra cysteine group on 1Dx5 compared to 1Dx2, which enables formation of additional disulphide link and increased polymer size (Shewry et al., 1992; Johansson and Svensson, 1999). Furthermore, it has been observed that cultivars and landraces having an over expression of Glu1Bx7 ($Bx7^{OE}$) have improved dough strength (Butow et al., 2002; Marchylo et al., 1992).

Variation in amount and size distribution of polymeric proteins according to cultivar might be due to the differences in structure, number of cysteine residues and hydrophobicity between different protein subunits (Lindsay and Skerritt, 1998; Shewry et al., 1992).

Effect of environment on proteins

Environment generally has a significant influence on flour quality by its effects on relative quantity of specific proteins, protein subunits and protein groups, proportions of composition, concentration, polymerization and amount and size distribution of polymeric proteins. Temperature, water access and fertilizer are the most crucial environmental conditions (Johansson et al., 2001, 2002; Dupont and Altenbach, 2003). Environmental interactions during grain filling alter the time course for grain development and influence final grain weight, protein and starch contents (Altenbach et al., 2003). The protein quality in the grain is also affected by the entanglements of the glutenin subunits into protein macromolecules which are influenced by the environment in which the wheat plant is cultivated (Jia et al., 1996).

Flour protein content is significantly increased under water deficit mainly due to higher rates of accumulation of grain nitrogen (N) and lower rates of accumulation of carbohydrates. Irrigation, on the other hand, may decrease flour protein content by dilution of nitrogen with carbohydrates (A.Ozturk and Aydin, 2004). Irrigation also influenced the protein accumulation during grain filling (Altenbach et al., 2003). Moisture content of the wheat grain relates negatively to the polymerization of grain storage proteins (Johansson et al., 2008).

Temperature during grain filling period is of utmost importance for the protein concentration for spring wheats (Johansson and Svensson, 1998). In another investigation seasonal variation, differences in fertilizer application and cultivar variation were found to be very important for determining the protein concentration (Johansson and Svensson, 1999). The proportion of gliadins to glutenins accelerates at high temperature and the proportion of large polymer in flour decreases at high temperature in controlled environment of different wheat cultivars. Genotypes having alleles for the HMW-GS 1Dx5, 1Dy10 generally showed less variability in storage protein composition in response to high temperature than genotypes with alleles for the HMW-GS 1Dx2, 1Dy12 (Blumenthal, 1995; Panozzo and Eagles, 2000; Irmak et al., 2008).

When wheat plants do not receive high levels of fertilizer, protein content may be increased by heat because of differential effects of temperature on protein and starch deposition, and this may or may not lead to differences in flour protein composition and quality (Finney and Fryer, 1958; Daniel and Triboi, 2000). Percentage of unextractable polymeric proteins in total polymeric proteins is significantly correlated with temperature and different timings of nitrogen fertilizer during grain filling (Johansson et al., 2003, 2004).

Prior to anthesis, yield and grain protein content are influenced by genetics, environment, nitrogen (N) fertilization and other aspects of crop management by effects on such factors as stand density, root growth, number of tillers and number of florets per head (Bahrman et al., 2004). After anthesis, kernel growth is directly impacted by soil and air temperature, water and N, as well as source–sink relations with leaves and stems. Adding post-anthesis N may directly increase grain protein content without reducing yield, whereas post-anthesis heat or drought may increase grain protein content but reduce yield because of heating effects on starch production (Fowler, 2003).

Variation in N application not only influences protein components i.e. glutenin and gliadins but also influences gluten strength among different cultivars (Johansson et al., 2001). Increase in protein content and gliadins to glutenin subunits ratios were found with the increase in the amount of N fertilizer (Gupta et al., 1992; Johansson et al., 2001). Increased N availability favors the production of storage proteins such as gliadins and glutenins, where gliadins most closely correlated with total protein increase in the grain (Dupont et al., 2006a). Gliadins increase preferentially over glutenins as N accumulation increases in the grain (Triboi et al., 2000; Wieser and Seilmeier, 1998).

As a result, the ratio of gliadins to glutenins was positively correlated with grain N content, even when both gliadins and glutenins increased (Wieser and Seilmeier, 1998). Some investigation showed that the proportions of ω-gliadins and HMW-GS glutenins in flour protein increased and proportions of LMW-GS and γ-gliadins decreased with N fertilization (Wieser and Seilmeier, 1998).

On the other hand the proportions of ω-gliadins increased with added N and increased temperature. Proportions of α-gliadins decreased with N and increased with temperature, while γ-gliadins increased with N and decreased with temperature (Daniel and Triboi, 2000). No significant change was observed in ratio of HMW-GS to LMW-GS in response to added N. Temperature and N fertilization altered the ratio of HMW-GS to LMW-GS, the amount of HMW-GS per grain, and the proportion of HMW-GS per unit of flour protein. Raising the growing temperature increased the rate and shortened the duration of accumulation of HMW-GS (Dupont et al., 2007). Supplying N after anthesis increased the rate of accumulation of HMW-GS, increased HMW-GS amount per grain, and increased HMW-GS relative amount compared to sulfur-rich gluten proteins such as LMW-GS (Dupont et al., 2006b; Wieser and Seilmeier, 1998). Positive effect of increased protein content on loaf volume resulting from increased nitrogen fertilization has been associated with increased ratio between monomeric and polymeric proteins (Gupta et al., 1992).

Barley

Barley (*Hordeum vulgare* L.) is an ancient important cereal grain crop widely grown for human and animal feed and for brewing (Hughes and Baxter, 2001). This cereal ranks fifth among all crops like wheat, maize, rice, sugarcane, soybean and potato in dry matter production in the world today (FAO, 2007).

Barley was one of the first agricultural domesticates together with wheat, pea (*Pisum sativum*) and lentil (*Lens culinaris)* dating from about 10,000 years ago in the Fertile Crescent of the Middle East (Smith, 1998). Historically, barley has been an important food source in many parts of the world, including the Middle East, North Africa and Northern and Eastern Europe (Iran, Morocco, Ethiopia, Finland, England, Denmark, Russia and Poland), and in Asia (Japan, India, Tibet and Korea) (Chatterjee and Abrol, 1977; Newman and Newman, 2006; Baik and Ullrich, 2008).

Barley belongs to the grass family and is a diploid and self pollinated crop (Zohary and Hopf, 2000). Barley is comprised of two main subspecies i.e., *vulgare* and *spontaneum* (C. Koch). Barley is a diploid species with 14 chromosomes (2n=2x=14) (Bothmer et al., 1995). There are different types of barley like two rowed and six rowed barley, hulled and naked barley (hulless).

Barley grain contains starch (65-68%), free lipids (2-3%), minerals (1.5-2.5%), and β-glucan (4-9%) (Quinde et al., 2004; Baik and Ullrich, 2008). The soluble dietary fiber in the barley grain is 3-20% and total dietary fiber comprised 11-34 % (Fastnaught, 2001). In barley starch the amylose content varies from 0% in zero amylose waxy to 5% in waxy, 20–30% in normal and up to 45% in high-amylose barley (Merritt, 1967; Bhatty and Rossnagel, 1997; Baik and Ullrich, 2008).

The cell wall (CW) components which are predominant in barley endosperm are β-glucan and arabinoxylans (~25% w/w), cellulose (~2% w/w), glucomannans (~2% w/w) and arabinogalactan-peptides represent minor constituents (Celus et al., 2006; Wilson et al., 2006; Lazaridou et al., 2008).

The usefulness of barley β-glucans in barley food products is known for lowering blood cholesterol (Cavallero et al., 2002; Behall et al., 2004) and glycemic index (Pins and Kaur, 2006; Baik and Ullrich, 2008). In barley most of the free phenolics are flavanols and tocopherols, whereas the bound phenolics are mainly phenolic acids (ferulic acid and *p*-coumaric acid) (Holtekjolen et al., 2006). Barley is a rich source of tocols, including tocopherols and tocotrienols, which are known to reduce serum LDL cholesterol through their antioxidant action (Qureshi et al., 1986, 1991).

Barley proteins

The protein content in barley grains represents, approximately, 8–15% of its total mass. Proteins in barley grain can be classified into albumins, globulins, prolamins (hordeins) as described by Osborne, 1924 together with some other proteins (chaperons), enzymes and unknown fractions (Fox et al., 2002; Osman et al., 2002; Boren et al., 2004; Østergaard et al., 2004).

Beer proteins

The majority of beer proteins are mainly albumins and lies in the 10–40 kDa size range. The main function of the beer proteins is their contribution to mouth feel, flavor, texture, body, color and nutritional value (Osman et al., 2002; Leiper et al., 2003). Protein Z,

LTP, hordein, glutelin fragments and other proteins present in beer have been associated to foam formation and/or stabilization (Evans and Sheehan, 2002; Ferreira et al., 2005; Perrocheau et al., 2005; Cizkova et al., 2006).

Hordein

The hordein fraction, extracted with alcoholic media in the presence of a reducing agent, comprises 35–55% of the total barley grain proteins and is the main barley storage protein (Rahman et al., 1982; Osman et al., 2002). Hordeins exist both in monomeric and aggregated forms.

Barley hordeins are divided into B, C, D and γ groups on the basis of their electrophoretic mobilities and amino acid compositions. Hordein fraction comprises of B and C hordeins (70–80% and 10–20% respectively) and the D and γ hordeins (less than 5% of the total hordein fraction) (Tatham and Shewry, 1995). The proteins previously classified as A hordeins are the smallest polypeptides, average (MW) 15 k Da, and they might be alcohol-soluble albumins or globulins or breakdown products of larger hordeins rather than true hordeins (Baxter, 1981). The B hordeins can be subdivided into B1, B2 and B3 subtypes (Skerritt and Janes, 1992). Furthermore, a distinction is made between the sulfur-rich (B and γ hordeins), the sulfur-poor (C hordeins) and the high molecular weight (HMW) prolamins (D hordeins). C type hordeins, as well as some B type hordeins, appear as monomers, while most B and D hordeins are linked by inter-chain disulfide bridges. Most γ hordeins are monomers with intra-chain disulfide bonds, but polymeric types may also occur (Shewry and Tatham, 1990; Shewry et al., 1994; Tatham and Shewry, 1995; Sheehan and Skerritt, 1997).

The four groups (B, C, D and γ hordeins) are encoded by the genes: *Hor2* (B-fraction), *Hor1* (C-fraction), *Hor3* (D-fraction) and *Hor5* (γ-fraction), located on barley chromosome 5 (1H) (Kreis and Shewry, 1992). N-terminal sequences of the hordeins contain repeats and motifs rich in glutamine and proline (Shewry, 1993)

In barley, HMW subunits form a backbone, which binds LMW subunits through disulfide bridges to form a gel-like aggregate (Moonen et al., 1987). Barley gel protein is a polymer containing HMW and LMW subunits, the D and B hordeins, respectively (Smith and Lister, 1983). Hordein extraction with increasing concentration of sulphydryl reducing agents revealed that D hordeins are extracted only at the highest 2-mercaptoethanol concentration, suggesting that they form the gel protein ‘backbone’ (Skerritt and Janes, 1992).

β-glucan

β-glucan comprises about 75% of the total cell wall non-starch polysaccharides. It is the major component of the cell walls of the barley endosperm cells (Fincher, 1975). The content of β-glucan ranges between 4-9% in barley (Oscarsson et al., 1996; Andersson et al., 1999). In cereals, β-glucans are normally considered as unbranched, linear polysaccharides of β-d-glucopyranose (Woodward et al., 1983). β-glucan contains approximately 30% (1→3)-linkages and 70% (1→4)-linkages. The molecule of β-glucan is relatively flexible with an irregular shape caused by the two different bonds in the polymer (Izydorczyk et al., 1998). β-glucans are linear homopolymers of d-glucopyranosyl (Glcp) residues (Izydorczyk and Dexter, 2008).

Arabinoxylans

Arabinoxylans (AX) are also non starch polysaccharides present in barley (Oscarsson et al., 1996; Andersson et al., 1999). AX constitutes 4–8% of the barley kernel (Lethonen & Aikasalo, 1987). They represent approximately 25 and 70% of the cell wall polysaccharides of endosperm and aleurone layer, respectively (Fincher and Stone, 1986). They consist of a backbone of (1–4)-linked β-D –xylopyranosyl residues. Some of these residues are substituted at O-2, O-3 or at both O-2 and O-3 with α-l-arabinofuranosyl residues (Oscarsson et al., 1996).

They are either water unextractable (WU) or extractable (WE). Some AX are solubilized from the cell walls but are not extensively degraded by endogenous enzymes during malting. Solubilized AX is, therefore, responsible for high viscosity of malt water-extract, which possibly leads to problems such as a diminished rate of wort or beer filtration (Fincher and Stone, 1986).

***Beta*-amylase**

Beta-amylase synthesized and accumulated during grain development consisting of approximately 1–2% of total *N* in the mature grain (Kreis et al., 1987), is one of the proteins found in the starchy endosperm (Hejgaard and Boisen, 1980). *Beta*-amylase is composed of monomeric proteins with molecular weights in the range of 53–64 kDa. *Beta*-amylase, which releases maltose from the non-reducing chain ends of gelatinized starch and related substrates, is considered as the most important enzyme responsible for diastatic power (Arends et al., 1995).

Barley bread-making quality

Poor baking quality along with taste and appearance factors are the key reasons which limits the use of barley in human foods. However, recent research interest has suggested use of barley in wide range of food products due to its nutritional importance (Bilgi and Celik, 2004).

WU Arabinoxylans has negative impact and WE Arabinoxylans has positive impact on barley bread characteristics. β-glucan of barley has detrimental effects on bread-making properties (Gill et al., 2002). Due to high percentage of dietary fiber, β-glucans binds tightly appreciable amounts of water in dough. This results in suppressing the water availability for the gluten network development thus reducing gas holding capacity. Decreased dough extensibility, loaf height and volume reductions and alterations to crumb structures of barley breads are the effects of incorporation of β-glucan (Gill et al. 2002). The use of hull less barley (15%) as a replacement of wheat flour during bread-making enhanced the contents of total and soluble dietary of baked products (Gill et al. 2002). Bread-making quality of barley is also strongly affected by the baking process (Jacobs et al., 2008).

Malting

Barley is the most important raw material for beer production. Malted barley is the barley with a husk that protects the embryo during the handling of the grain and is an important aid during the wort filtration. The aim of the malting process is the production and activation of enzymes. These enzymes and molecules also contribute to the hydrolysis of

β-glucans and hordeins (water insoluble proteins), which would otherwise restrict access of enzymes to the starch granules (Hughes and Baxter, 2001).
There are three main parts of malting:
1) Steeping
2) Germination
3) Kilning
Barley grain is soaked until germination begins (steeping), is then held under moist and warm conditions for several days (germination) and finally is dried in a stream of air whose temperature is slowly raised (kilning) (Jones, 2005). The grain imbibes water during controlled cycles of water spraying, or water immersion, followed by aeration, until the water content of the grain reaches 42–48%. Barley grain germination is initiated by the uptake of water. Water enters the grain via the embryo, and after approximately 24 h, the first visible sign of germination is the appearance of the root, as a white 'chit'. Germination is typically allowed to proceed over a period of around 5 days to obtain green malt, which is then stopped during the dewatering and kilning phase by forced flow of hot air (Silva et al., 2008).
Malting conditions can be varied, depending on the malt characteristics needed. Barley grain that is germinated on filter paper or some other medium and air-dried or freeze–dried is not malt, but is simply germinated barley. The 'biological' germination of barley begins during the steeping process and is already well established when what malters call 'germination' begins (Jones et al., 2000; Jones, 2005).
The process of malting, involves a series of enzyme degradations of the materials which are tightly packed in the kernel endosperm, as a result of incomplete natural germination process. Endosperm cell walls are degraded, and starch granules are released from the matrix of the endosperm in which they are embedded. This leads to physical weakening of the endosperm. These structural changes and biochemical degradations of the endosperm components are referred to as endosperm modification (Gunkel et al., 2002; Gamlath et al., 2008).
The malt is stable for storage and has a friable texture suitable for the milling process, which precedes brewing (Silva et al., 2008). In brewing, after malt mashing and separation of the wort, brewers' spent grain (BSG) is obtained as the barley malt residue. The composition of BSG changes with variation in barley variety, time of harvest, adjuncts added and brewing technology (Santos et al., 2003). BSG has been mainly used as an animal feed (Mussatto et al., 2006).

Brewing of barley

Brewing is the process in which alcoholic beverages and alcoholic fuels are produced with the help of fermentation. In this process normally four steps are involved as described:

1. Malting (based on germination of barley)
2. Wort production (mashing i.e. extraction and hydrolysis of the components of malt and possibly other cereals, followed by separation of non-soluble components and boiling with hops or hop extracts)
3. Fermentation (primary and secondary fermentation)
4. Downstream process (filtration, stabilization and bottling etc) (Linko et al., 1998).

Effect of proteins on malting

Although protein is only one of several traits related with malting quality, it is the most important requirement of the malting industry, ranging between 8.5 and 12.5% (Gali and Brown, 2000). It is often hard to keep concentration of grain protein concentration (GPC) below this limit as GPC is largely influenced by environmental conditions such as fertilizer i.e. nitrogen (Weston et al., 1993; Eagles et al., 1995), drought and temperature (Morgan and Riggs, 1981; Savin and Nicolas, 1996). High availability of nitrogen is associated with increase in protein level above the limit in malting barley (Eagles et al., 1995). High protein contents also decrease available carbohydrates, with a negative influence on the brewing process (Fox et al., 2002; Silva et al., 2008).

Due to the diversity in protein types the influence of barley proteins on malt and beer quality characteristics is rather complex. The proteins in barley have different range of functions in the processes of malting and brewing (Shewry and Darlington, 2002).

Proteins in barley grains, which are determinants of beer quality, are modified during the process of malting (Jegou et al., 2000). A range of proteolytic enzymes degrade proteins into amino acids and small peptides. These amino acids and peptides provide sufficient nutrients for brewing yeasts to grow rapidly and metabolize sugars into alcohol (Baxter, 1981; Jones, 2005).

Hordeins play a crucial role in determining the malting quality (Howard et al., 1996). Normally less than half of the amounts of hordeins are present in the well-modified malt as compared to original barley (Baxter, 1981). The relative proportion of B fraction of hordein was associated with malting quality due to its effect on diastatic power, the total activity of starch-degrading enzymes in barley malt (Delcour and Verschaeve, 1987; Peltonen et al., 1994). A significant negative correlation with malt extracts across environment, varieties and different treatments was found due to levels of D hordein fraction (Howard et al., 1996). However, in later studies no relationship was found between D hordeins and malting quality. This was found by using pairs of near-isogenic barley lines with and without D Hordeins (Brennan et al., 1998). A negative correlation was found for grain nitrogen content and D: B hordein ratio, in relation to the malting quality (Peltonen et al., 1994). A higher B to C hordein ratio was correlated to superior malting quality whereas C-hordeins increased under conditions of high fertility (Molina-Cano et al., 1995; Shewry et al., 1983). A negative relationship was also found between the ratios of B: C hordeins and grain nitrogen percentage (Shewry et al., 1983; Molina-Cano et al., 2001).

BSG, the main by-product of the brewing industry, is rich in proteins and dietary fiber (Mussatto et al., 2006). BSG solids have been extracted with alkaline / SDS solutions followed by protein precipitation to yield a highly purified protein solid. The low solubility of the nitrogenous constituents in conventional protein solvents may be due to associations between cellulosic material and protein. During mashing, a complex is formed between residual gel protein in the malt and the glutelins. As a result, an impenetrable layer is formed on the BSG through disulfide bridges between hordeins which can be formed causing mash separation difficulties. The oxidation of free protein thiol groups to disulfide bridges during mashing appears to be a good indicator of the formation of a gel protein aggregate (Pöyri et al., 2002; Celus et al., 2006).

Effect of nitrogen on malting

In malting barley, adequate nitrogen management is essential because high nitrogen availability is required for high yields but if in excess it could be detrimental to quality (Giese and Hejgaard, 1984). When environmental conditions favored high nitrogen uptake efficiency, a larger proportion of D-hordein was synthesized, thus decreasing malting quality. N supply had a marked effect on the accumulation of β-amylase and D-hordein (Giese and Hejgaard, 1984).

The proportions of the hordein fraction were significantly affected by N treatment and cultivar as well as the interaction between these two parameters. However grain protein content was significantly affected by both N treatment and cultivar, but there was no significant interaction between N treatment and cultivar (Molina-Cano et al., 2001; Qi et al., 2006).

Synthesis of β-amylase during barley grain development was regulated by nitrogen nutrition (Giese and Hopp, 1984) and high levels of β-amylase were generally correlated with increased grain protein content (Swanston, 1980). β-amylase activity was significantly influenced by N treatment, cultivar and N treatment - cultivar interaction between the two, with N treatment being the most important factor regulating β-amylase activity. A significant positive correlation was found between the protein content and beta-amylase activity (Yin et al., 2002; Qi et al., 2006). This correlation implies a potential risk of causing the protein content to be above the upper limit for malting, while β-amylase activity can be improved by means of genetics and agronomy (Wang et al., 2003).

Nitrogen

Background

Nitrogen is the most frequently deficient nutrient in crop production. Therefore, most non legume cropping systems require nitrogen inputs. Many nitrogen sources are available for use in supplying nitrogen to crops. Nitrogen is quantitatively the most important mineral nutrient taken up from the soil by plants. Nitrogen shortage is one of the main constraints limiting the productivity of major crops such as wheat and other cereals (Glass, 2003). The increase in use of nitrogen (N) fertilizers for enhancing the agricultural production has been under consideration for the last fifty years (Hirel et al., 2007).

For environmental and economic reasons, nitrogen fertilizers should be utilized as efficiently as possible in agriculture. The diversity and functioning of the non-agricultural neighboring bacterial, animal, and plant ecosystems is deteriorated due to the intensive use of nitrogenous fertilizers (Hirel et al., 2007). Despite the detrimental effects on the biosphere, the use of fertilizers (N in particular) in agriculture, together with an improvement in cropping systems, mainly in developed countries, has helped in providing food, feed and fiber (Cassman, 1999).

Nitrogen use efficiency

Cereals require large amounts of nitrogen (N) fertilizers for maximum yield, while nitrogen use efficiency (NUE) is around 33-78 % (Raun and Johnson, 1999). The improvement of NUE, particularly in cereals, is a major goal of crop improvement (Hirel et al., 2007). NUE is defined as the amount of nitrogen (N) removed by crop minus the amount of N coming from soil plus the amount of N deposited in rain divided by the amount of fertilizer applied to crop (Raun and Johnson, 1999; Glass, 2003)

The NUE can be divided into two processes: uptake efficiency, the ability of the plant to remove N from the soil normally present as nitrate or $NH4^+$ ions, and the utilization efficiency, the ability of the plant to transfer the N to the grain, predominantly present as protein (Moll et al., 1982, 1987; Lea and Azevedo, 2006). Improvement of NUE is very crucial regarding two concerns.

1. Cost of nitrogenous fertilizers in crops such as corn and wheat generally accounts for up to 40% of production costs (Bock, 1984)
2. Excessive nitrogenous based fertilizer leaching into lakes and rivers is responsible for environmental constraints especially problem with the terrestrial ecosystem as these ecosystem become N saturated (Matson et al., 2002; Good et al., 2007).

Nitrogen uptake and remobilization

Nutrient uptake is the movement of nutrient to the plants. It also refers to amount of solute which is removed from the external medium. Nutrients are mostly available in the form of ions. They may be anions or cations. For ions to be absorbed by plant roots they must come in contact with the root surface. There are generally three ways and two processes in which nutrient ions may reach the root surface. These three ways are:

- Root interception
- Mass flow on ions in solution
- Diffusion of ions in the soil solution

The contribution of the diffusion was estimated by the difference between total nutrition needs and the amount supplied by interception and mass flow.
The processes involved in the movement of nutrients ions from the soil to roots are:

- Active ion uptake
- Passive ion uptake

Plants are able to take up N in the form of nitrate, $NH4^+$ ions and amino acids (Lea and Azevedo, 2006) or obtain it through the symbiotic action of nitrogen-fixing bacteria (Bogino et al., 2006; Andrews et al., 2007). Both NO_3^- (nitrate ions) and NH_4^+ (ammonium ions) usually serve as a source of nitrogen for plant growth.
Plants are able to accumulate nitrate to high concentrations, the majority of which is concentrated in the vacuole by an NO_3^-/H^+ exchanger (De Angeli et al., 2006). Other than accumulation of nitrate on large scale plants have the ability to grow successfully in a wide range of available nitrate applications. Due to these two specific properties of plants the uptake of nitrate by plant roots is not a simple process, and is operated by four different transport systems:
(1) Constitutive high-affinity (cHATS)
(2) Nitrate-inducible high-affinity (iHATS)
(3) Constitutive low-affinity (cLATS)
(4) Nitrate-inducible low-affinity (iLATS) (Glass, 2003; Lea and Azevedo, 2006; Okamoto et al., 2006).
Nitrate transporters *NRT1* and *NRT2* are identified as the two gene encoding nitrate transporters families in plants (Williams and Miller, 2001). When nitrate from soil enters into the plant cell it is reduced into nitrite by the action of nitrate reductase (NR). Nitrite further goes on under reduction into $NH4^+$ by nitrite reductase when it is transported to plastid. $NH4^+$ is incorporated into carbon skeleton through the glutamine synthetase (GS)-glutamate-oxoglutarate amino transferase (GOGAT) pathway (Miflin and Habash, 2002). The amino group of glutamate can be transferred to different amino acids by a suite of aminotransferase (Lam et al., 1996).
Plants normally do not tend to accumulate higher amounts of $NH4^+$ ions as compared to nitrate ions. With exception of some crops such as rice, toxicity symptoms frequently occur if crop plants are grown in $NH4^+$ in the absence of nitrate (Britto and Kronzucker, 2002).
The N requirement for protein synthesis in the developing kernel is met by the mobilization of previously assimilated N present in vegetative tissues and by direct uptake and assimilation of N during grain filling. Mobilization of previously assimilated N has been suggested as the major source of N for the kernel (Austin et al., 1977). The plant life cycle with regard to the management of N can be roughly divided into two main phases occurring successively in some species or overlapping in others. During the first phase, i.e. the vegetative phase, young developing roots and leaves behave as sink organs for the assimilation of inorganic N and the synthesis of amino acids originating from the N taken up before flowering and then reduced via the nitrate assimilatory pathway (Hirel and Lea, 2001). These amino acids are further used for the synthesis of enzymes and proteins mainly involved in building up plant architecture and the different components of the photosynthetic machinery.
In the second phase at a certain stage of plant development which generally starting after flowering, the remobilization of the N accumulated by the plant takes place. At this stage,

shoots and/or roots start to behave as sources of N by providing amino acids released from protein hydrolysis that are subsequently exported to reproductive and storage organs represented, for example, by seeds, bulbs, or trunks. In most plants N is accumulated in the vegetative organs in the form of proteins. During grain filling, the nitrogen accumulated in the vegetative organs is remobilized to the ear (Triboi and Triboi-Blondel, 2002). Sixty to 95% of grain N comes from the remobilization of N stored in roots and shoots before anthesis (Palta and Fillery, 1995). After flowering, both the size and the N content of the grain can be significantly reduced under N deficient conditions (Dupont and Altenbach, 2003).
Nitrogen is the most susceptible nutrient to different transformations which affect availability of nitrogen to plants. Mineralization, immobilization, nitrification and denitrification, leaching and NH_4^+ ammonium volatilization are different types of transformations from which nitrogen undergoes (Petersen et al., 1998).

Mineralization
Simply mineralization refers to the process where a substance is converted from an organic substance to an inorganic substance, thereby becoming mineralized. In nitrogen mineralization, organic nitrogen from decaying plant and animal residues (proteins, nucleic acids, amino sugars and urea) is converted to ammonia (NH_3^-) and ammonium (NH_4^+) ions. This process is also called ammonification. The resultant ammonia can be converted back to organic N (immobilization) where it is taken up by microbes and plants (assimilated), or nitrified to nitrate (NO_3^-). Besides inorganic N applied to the soil, organic soil N mineralized during the growth period also contributes to crop nutrition (Appel and Mengel, 1992).
In contrast to the mineral N content available from fertilizers which is immediately available to plants and may be easily quantified, the release from organic forms is dependent on the mineralization process (Beauchamp, 1986). Nitrogen mineralization is affected by many factors including the composition or quality of the organic material, agricultural practices (e.g. cultivation), temperature, humidity, soil pH, aeration and soil structure and texture (Jarvis et al., 1996).
Furthermore, mineralization of soil N also depends on C/N-ratio, cellulose content, N content, water soluble N and litter. The light organic matter fractions of the soil, microbial respiration, ATP content, microbial biomass are also included. The diversity of factors correlated with N mineralization reflects the variation in substrates and microbial communities being used and temporal changes in substrate quality (Bengtsson et al., 2003).

Immobilization
In nitrogen immobilization, ammonia and nitrate are taken up by microbes and is largely immobilized, or made unavailable to plants depending on C : N ratios. When N is abundant, both microbes and plants assimilate ammonia and nitrate. Proteins, nucleic acids, and other organic N constituents of microbial cells and cell walls are formed with the help of incorporated N. When a plant completes its life cycle and dies, different microbes decomposes and decays the biomass of the plant. As a result, some of the plant biomass nitrogen, in the form of NH_4^+, is released back into the soil with the process of mineralization. The rest of the nitrogen into the plant biomass is converted in soil organic

matter in the form of stable organic nitrogenous compounds. Plants cannot use these stable nitrogenous compounds easily and readily. Therefore, the net result of immobilization-mineralization is a decrease in the availability of the N added to soil as fertilizer, and also the partial conversion of this N to a form NH_4^+ that is not subject to loss from most soils (Mulvaney et al., 1993).

Return of organic materials, such as crop residues, catch crops and green manures, has a marked influence on carbon (C) and nitrogen (N) turnover in agricultural soils. The synchronization of N supply with plant demand is important for environmental and agronomic reasons (Kumar and Goh, 2000).

The amount of carbon and nitrogen present in the soil depicts the C : N ratio (C : N ratio of humus is 10 : 1) and this is very critical for the decomposition process. Optimum levels of C: N ratio (80 : 1- 12 : 1) is ideal for maximum decomposition since a favorable soil environment is created to bring about an equilibrium between mineralization and immobilization process which will be upset if C : N ratio is less than the optimum (Bengtsson et al., 2003). C : N ratios less than 20 mean that excess N is present and nitrification proceeds (with a net gain of N). With ratios between 20 and 30, nitrification and immobilization rates are in equilibrium and there is no net gain or loss of N. With a ratio greater than 30, N is limited and net immobilization occurs with uptake (or loss) of N from the active N cycle. When N is limited at high C : N ratios, nitrogen-fixation by free-living nitrogen fixers are stimulated.

In the presence of a simple substrate such as glucose, mineral N is quickly consumed and disappears within a few days. With complex substrates, such as cellulose from plant residues, the process is slower, and the supply of mineral N is never completely exhausted (Mulvaney et al., 1993).

Leaching process of nitrogen

Drained agricultural land has been identified as a major source of pollution to both surface and ground waters (Randall and Mulla, 2001). In Asia, Europe and Northern America intensive agricultural practices have led to both higher production costs and a greater risk from environmental hazards such as ground and surface water pollution by nitrate leaching (Randall and Mulla, 2001). From several decades great emphasis is given on efficient use of nutrients within agricultural production systems.

A major contributing reason for this is the negative effects on surface water and groundwater quality, which to a large extent are attributed to agricultural nonpoint-source pollution of nutrients, which have been observed in many countries. Especially in cold and humid regions this problem is recognized, where large amounts of water percolate through soil during periods without a crop (Morecroft et al., 2000). NO_3^- (nitrate) leaching losses from agricultural soil have to be reduced in order to improve the use of fertilizers and to avoid NO_3^- from accumulating in surface and ground waters (Gustafson, 1987).

The most crucial effects of leaching of nitrogenous fertilizers applied to the agricultural fields are the eutrophication of freshwater (Beman et al., 2005) and marine ecosystems (Giles, 2005). Nitrogen as nitrate is soluble and mobile and susceptible to transport to groundwater, which has become increasingly degraded by nitrate (Spalding and Exner, 1993).

In Sweden, about 45% of the anthropogenic nitrogen loads reaching the seas come from arable land (SNV, 1997). Continuous use of organic and inorganic fertilizers, aiming for maximum crop production can increase the risk of N contaminating surface waters and groundwater, stimulating eutrophication (Carpenter et al., 1998). Serious coastal eutrophication problems have been identified in the coastal areas of southern Sweden (which are prone to N leaching (SJV, 2007) due to transport of nitrogen in lowland rivers (Stålnacke et al., 1999). This ongoing eutrophication has led to widespread hypoxia and large permanently reducing bottom areas in marine costal ecosystems in southern Sweden (Vahtera et al., 2007; Salazar et al., 2009).

Acknowledgments
Firstly I would like to thank Almighty Allah and His Prophet Mohammad (P.B.U.H) for completion of this paper. I am sincerely thankful to my supervisors Dr. Eva Johansson, Dr. Ramune Kuktaite and Dr. Allan Andersson for their valuable and critical comments which helped me a lot in improving this paper. I am also thankful to Dr. Peter Shewry for giving me kind permission to use his research images in my introductory paper. Lastly I really appreciate the positive criticism and guidance from my all colleagues regarding completion of this introductory paper.

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