Nitrogen Redistribution in Spring Wheat

Root Contribution, Spike Translocations and Protein Quality

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Abstract

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This thesis summarises solution culture experiments studying pre- and postanthesis nitrogen translocation and distribution in spring wheat (*Triticum aestivum* L.) Partitioning of biomass and harvest index (HI) were dependent on phenological development rate. Nitrogen concentration in plant parts during growth was more dependent on development rate than on N supply. The remaining nitrogen concentration in the plant parts at maturity was dependent on nitrogen concentration during growth.

The roots were the last vegetative part to senesce and were competitors with the grain during late grain filling in respect of nitrogen. The capability to take up, distribute and redistribute nitrogen was maintained after complete yellowness. A considerable amount of nitrogen was redistributed from the roots to the grain during grain filling. At maturity, the roots contained 10-20% of all plant nitrogen. Genetic variation was found for root nitrogen concentration. Root weight was negatively correlated with grain nitrogen concentration, nitrogen harvest index (NHI) and total nitrogen harvest index based on the entire plant (NHI_{tot}).

Nitrogen concentration in grain in different spikelet positions reached end concentration 14 days before grain filling was completed. During late grain filling, nitrogen accumulation in the spikelets ceased from top to base in the spike. Differences in protein composition and polymerisation of protein between spikelets were observed in one of two cultivars. The last nitrogen taken up was incorporated into all types of protein within a spikelet.

Response to temperature differed between cultivars. An appropriate response to temperature was important in achieving high HI, high nitrogen redistribution to the grain and high NHI.

Two different ways to achieve high nitrogen concentration in the grain were distinguished. High grain nitrogen concentration in a cultivar was due to either high rate of nitrogen redistribution from vegetative parts to the grain or low root weight and low shoot weight.

The results presented in this thesis provide new knowledge about nitrogen redistribution in the plant, nitrogen accumulation and protein polymers within the spike.

Key words: abortion, carbohydrates, grain quality, labelled nitrogen, nitrogen partitioning, nitrogen remobilisation, nitrogen retranslocation, nitrogen uptake, root mortality.

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Contents

Appendix

Papers I-V

This thesis is based on the following papers, which will be referred to by their Roman numerals.

I. Andersson, A., Oscarson, P. & Johansson, E. Variations in development rate, vegetative characters, yield and grain nitrogen concentration in two spring wheat cultivars grown in solution culture (Manuscript).

II. Andersson, A., Johansson, E. & Oscarson, P. Post-anthesis nitrogen accumulation and distribution among grains in spring wheat spikes. The Journal of Agricultural Sciences (in press).

III. Andersson, A., Johansson, E. & Oscarson, P. Nitrogen redistribution from the roots in post-anthesis plants of spring wheat. Plant and Soil (in press.)

IV. Andersson, A. & Johansson, E. Temperature influence on nitrogen partitioning in entire plants of different spring wheat cultivars. (Submitted)

V. Andersson, A., Oscarson, P., Prieto-Linde, M.L. & Johansson, E. Differences in polymeric proteins among grains in spring wheat spikes. (Submitted).

Objectives

In crop production, nitrogen fertilisation is a common practice to improve yield and quality. In cereal production in general, nitrogen fertilisation takes place early in the crop season, but often extra nitrogen applications are given before anthesis in order to increase protein concentration in the crop. The major proportion of the nitrogen amount found in the grain at maturity can be found in the aboveground plant parts at flowering (Austin *et al.*, 1977; Heitholt *et al.*, 1990; Palta *et al.*, 1994; Fangmeier *et al.*, 1999). High nitrogen use efficiency is desired for nitrogen applications in agriculture. Higher nitrogen use efficiency is generally found when nitrogen is applied late (at flowering) compared to when it is applied early (Wuest & Cassman, 1992; Raun & Johnson 1999; Cassman, Doberman & Walters, 2002). However, late applied nitrogen might alter protein composition and nitrogen accumulation in the spike (Johansson, Prieto-Linde & Svensson, 2004).

The objectives of the present thesis were to study:
Nitrogen redistribution in the entire wheat plant from vegetative parts including roots to the grain and influences on grain nitrogen concentration and grain quality;
Influences of nitrogen taken up late on nitrogen concentration and protein polymer composition within the spike;
Influences of temperature and genetic background on nitrogen redistribution.

Background

Nitrogen fertilisation

Nitrogen is one of the most limiting elements in natural ecosystems (Vitousek *et al*., 2002) and limits yields in non-fertilised agriculture. Nitrogen fertilisers are applied in order to increase yield and improve crop quality.

Ambitions when nitrogen fertilisers are used in agriculture include: a) high nitrogen use efficiency (NUE) of the fertiliser; b) low cost to the farmer; and c) low pollutant effect on the environment. Several strategies exist to fulfil these ambitions. In brief, most strategies are based on analyses of nitrogen in the soil and in the crop during crop development and thereafter application of nitrogen according to the needs of the plants in order to obtain a desired yield and quality (Börjesson & Gustafsson, 2002; Cassman, Doberman & Walters, 2002; Raun *et al*., 2002; Mullen *et al*., 2003).

Desired grain protein concentration and quality differ according to the intended end-use of the wheat. In production of wheat, the strategy for nitrogen supply is therefore dependent on the desired yield and nitrogen concentration in the grain. In production of bread wheat, for example, a late nitrogen application is often recommended in order to increase the protein concentration up to certain limits

determined by the baking and milling industry (Fajersson, 1961; Lütke Entrup & Oemichen, 2000; Fogelfors, 2001; Woolfolk *et al*., 2002).

Nitrogen in the soil

Nitrogen is present mainly in organic matter in the soil, in amounts of about 4-12 tonnes ha^{-1} (Hansen *et al*., 2000; Knudsen, Östergaard & Schultz, 2000). Plants do not take up nitrogen from the organic pool. Mineralised nitrogen in the form of ammonium ions and nitrate ions is available to plants.

Annually, 1-2% of the soil organic nitrogen is mineralised to ammonia and ammonium ions and further to nitrate through microbes. In Sweden this gives a nitrogen supply of 20-120 kg ha^{-1} $year^{-1}$ (Kirchmann, Johnston & Bergström, 2002). Mineralisation rate increases with increasing temperature, soil humidity and soil air content (Knudsen, Östergaard & Schultz, 2000).

New organic matter such as crop residues is mineralised faster than old organic matter, and the amount of nitrogen mineralised in the autumn depends to a high degree on mineralisation of crop residues (Kirchmann, Johnston & Bergström, 2002). The ratio C/N in the organic matter determines the microbiological processes that nitrogen will undergo. If the organic matter has a C/N ratio below 20 mineralisation of nitrogen begins, while if the C/N ratio is above 20 nitrogen is immobilised in the soil (Knudsen, Östergaard & Schultz, 2000).

A common method for analysing mineralised nitrogen in the soil is analysis of frozen, thawed samples (including roots) extracted with 2 M KCl (Lindén, 1981; P-O Persson, pers. comm.).

Nitrogen leaching

Nitrate ions are dissolved in the soil water and follow water movements in the soil. They can thus be leached to drainage water or groundwater, while ammonium ions can be bound to particles in the soil. In northern Europe, crops take up nitrate during the crop growing period and the concentration of nitrate in soil is low during this period. The crops also take up water, resulting in general in no downwards movement of water in the soil profile during the growing period. Due to the absence of downward water movements and low nitrate concentration in the soil, nitrate leaching normally does not occur during the growing season. In the arable soils of northern Europe, nitrate leaching occurs in the autumn after harvest, when the nitrate concentration in the soil increases due to nitrogen mineralisation and downward movement of water in the soil profile. Nitrate leaching continues during winter if the soil is not frozen (Knudsen, Östergaard & Schultz, 2000; Kirchmann, Johnston & Bergström, 2002).

The leaching from an unfertilised crop is only slightly lower than that from an optimally inorganic nitrogen-fertilised crop (Knudsen, Östergaard & Schultz, 2000; Kirchmann, Johnston & Bergström, 2002) and nitrogen leaching is therefore not dependent on the amount of nitrogen applied as long as it is below the

optimum level and fertilisation is managed in an appropriate manner (Knudsen, Östergaard & Schultz, 2000; Kirchmann, Johnston & Bergström, 2002).

Nitrogen leaching is greater from manured soils than from inorganic nitrogen-fertilised soils (Knudsen, Östergaard & Schultz, 2000; Kirchmann, Johnston & Bergström, 2002). In computer simulations, no differences in nitrogen leaching per hectare were found between conventional and organic crop production (Berntsen *et al*., 2004). Organic farming leaches more nitrogen per unit produced in comparison to when inorganic nitrogen fertilisers are used (Kirchmann, Johnston & Bergström, 2002).

Root zone nitrogen leaching is the amount of nitrogen in the soil which cannot be reached and caught by the roots and is therefore leached to groundwater or drainage water. Using the simulation model SOIL-N (Johnsson *et al*., 1987; Eckersten, Jansson & Johnsson, 1998), the root zone nitrogen leaching has been estimated to be on average 24 kg nitrogen ha^{-1} in Sweden (range 15-40 kg nitrogen ha^{-1}) and is the same as 150 years ago in spite of large changes in agriculture (Albertsson, Kvist & Löfgren, 1999). In Denmark, the root zone nitrogen leaching has been estimated to be on average 71 kg ha^{-1} using the empirical model N-LES (Simmelsgaard *et al.*, 2000). The differences between regions and countries are mainly due to soil conditions, climate, different types of crops and animal intensity (livestock units ha^{-1}).

On the way to the sea the amount of nitrogen in water streams is reduced mainly by denitrification and the amount reaching the sea is considerably lower than the amount leaching from the root zone (Albertsson, Kvist & Löfgren, 1999).

Nitrogen in crops

Nitrogen uptake by wheat

Nitrogen uptake, measured as nitrogen amount in aboveground plant parts, has been thoroughly studied by scientists. Nitrogen is mostly taken up during the vegetative phase of phenological development and about 80% of the nitrogen found in aboveground plant parts at maturity is already present in the aboveground plant parts at anthesis (Austin *et al.*, 1977; Heitholt *et al.*, 1990; Palta *et al.*, 1994; Fangmeier *et al.*, 1999). Nitrogen applied early in the season stimulates tillering and vegetative plant growth, while nitrogen applied late in the season has a greater influence on nitrogen concentration in the grain (Fajersson, 1961; Lütke Entrup & Oemichen, 2000; Fogelfors, 2001).

Through soil measurements, wheat cultivars at different nitrogen fertilisation levels were found to absorb all soluble nitrogen in the soil (Bertholdsson & Stoy, 1995). The residual nitrogen in the soil after harvest was slightly higher for high protein cultivars and thus these cultivars are not advantageous in soil nitrogen uptake. Through experiments in solution culture, Oscarson *et al*. (1995b) have shown that wheat cultivars have an overcapacity to take up nitrogen in comparison to the nitrogen demand.

Nitrogen redistribution in wheat

The behaviour and fate of nitrogen in aboveground plant parts has been extensively studied and is well known. Nitrogen is rapidly cycled, recycled and transported in wheat plants (Simpson, Lambers & Dalling, 1982; Cooper *et al.*, 1986) and in other plant species (*e.g*. Ourry *et al.*, 1989). Redistribution of nitrogen from aboveground plant parts to grain has been broadly studied (*e.g*. Austin *et al.*, 1977; Van Sanford & MacKown, 1987; Feller & Fischer, 1994; Fangmeier *et al.*, 1999; Masclaux *et al.*, 2001). The redistribution of nitrogen occurs during senescence as a saving to offspring. Senescence is a highly organised and well-regulated process (Hörtensteiner & Feller, 2002). The nitrogen flow and the amount of nitrogen redistributed vary due to the source-sink ratio, which is regulated by the weather (*e.g*. temperature, drought) and by intrinsic properties of the organs (Dalling, Boland & Wilson, 1976).

Nitrogen redistribution from the roots has only been superficially studied. Previous investigations have shown that generally in plant species, the roots tend to reallocate <30% of their nitrogen content (Peoples & Dalling, 1988; Culvenor, Davidson & Simpson, 1989; Culvenor & Simpson, 1991; Volenec, Ourry & Joern, 1996). The roots are the last organs to senesce (Peoples & Dalling, 1988), and are still active during grain filling. Remobilisation of nitrogen from the roots to the grain may therefore play a role for the nitrogen economics of the whole plant (Dalling, Boland & Wilson, 1976; Simpson, Lambers & Dalling, 1983). The roots may play a major role in crop stands in both assimilating nitrogen when the crop is suffering nitrogen deficiency (Vouillet & Devienne-Barret, 1999) and in remobilising nitrogen to the grain during grain filling.

Wheat root systems show differences in biomass between years and stands (Barraclough & Leigh, 1984), which is another possible cause of variation in nitrogen redistribution to grain.

Nitrogen recovery in crops

Important challenges in nitrogen fertilisation include keeping input costs low and minimising pollution of the environment (Raun & Johnson, 1999; Cassman, Doberman & Walters, 2002; Delgado, 2002). There are several ways to measure the efficiency of nitrogen fertilisation (Schindler & Knighton, 1999) (Table 1) but the parameters are not always measured similarly, which makes comparisons difficult (see footnotes to Table 1). World nitrogen use efficiency (NUE) is estimated to be 33% and NUE is generally higher in developed countries than in developing countries (Raun & Johnson, 1999) (Table 1).

Pollution by nitrogen compounds from nitrogen fertilisation is caused by denitrification, volatilisation and/or leaching, which may be prevented by better nitrogen management and fertilisation strategies.

In many countries, there are monitoring programmes to control nitrogen pollution to the environment. The Swedish Board of Agriculture has a programme in which plant nutrient balances are calculated at farm level in order to increase NUE.

Table 1. *Nitrogen recovery (%) in some crops in different parts of the world*

Source	Nitrogen recovery %
1. World-wide cereal NUE	33
1. Developed country world-wide cereal NUE	42
1. Developing countries world-wide cereal NUE	29
2. Maize, north-central USA	37
3. Summer barley	80
3. Summer wheat	73
3. Winter barley	71
3. Winter wheat	71
3. Feed winter wheat	75
3. Summer malt barley	85
4. Winter wheat	80
5. Winter wheat	97
6. Winter wheat in Sweden	82 – 92

1. NUE =100 [(Total cereal grain nitrogen removed) – (nitrogen coming from the soil + nitrogen deposited in the rainfall)] (fertiliser nitrogen applied to cereals)$^{-1}$] (Raun & Johnson, 1999).

2. 100[(Nitrogen amount in fertilised total crop - nitrogen amount in unfertilised total crop) (fertilizer nitrogen applied)$^{-1}$]. (Cassman, Doberman & Walters, 2002).

3. Comparison (normal) value for nitrogen efficiency 100[(grain nitrogen amount) (fertilizer nitrogen applied+ nitrogen in seed)$^{-1}$]. (The Swedish Board of Agriculture, 2003 STANK).

4. Nitrogen efficiency 100 [(grain nitrogen amount) (fertilizer nitrogen applied)$^{-1}$], (Albertsson & Lundström, 2002).

5. Nitrogen efficiency of the nitrogen fertiliser 100[(Nitrogen amount in fertilised total crop - Nitrogen amount in unfertilised total crop) (fertiliser nitrogen applied)$^{-1}$], (Albertsson & Lundström, 2002).

6. Nitrogen recovery [(nitrogen amount in grains) (optimal supply of nitrogen)$^{-1}$] depending on soil, (Mattson, 2003).

NUE can be increased by better crop rotations, plant breeding for better harvest index (HI), plant protection, soil management, and well adapted fertiliser applications in the field, irrigation and precision agriculture (Raun & Johnson, 1999; Cassman, Doberman, Walters, 2002).

The later the time of application, the better is in general the NUE (Wuest & Cassman, 1992; Raun & Johnson, 1999; Cassman, Doberman & Walters, 2002). Nitrogen applied in late season can be adjusted to the existing nitrogen status in the plant stand and thus increase NUE in comparison to pre-plant application or early season application. However, there is indication that late versus early nitrogen uptake in the plant might influence grain protein concentration and composition, and baking quality (Johansson, Prieto-Linde & Svensson, 2004).

Precision agriculture provides the potential to improve NUE. Site-specific fertilisation provides an opportunity to vary the nitrogen supply according to site. The existing N status in the stand at a specific site can be detected using optical sensors and fertilisation adjusted accordingly, thus increasing NUE (Raun *et al*., 2002; Cassman, Doberman, Walters, 2002; Mullen *et al*., 2003).

Fig. 1. Young wheat plant developing tillers, nodal roots, and seminal roots.

The wheat crop

Plant morphology

At maturity, the wheat plant consists of a main shoot and a variable number of tillers, the latter mainly determined by environmental variations. A tiller is a branch coming from the base of a plant or the axils of the lower leaves (Figure 1). In field growing of cereals, a high number of tillers plant^{-1} are developed and successively aborted (Darwinkel, 1978; Simons, 1982; Whaley *et al*., 2000; Berry *et al.*, 2003). During the abortion and senescence of tillers, nitrogen is withdrawn from the aborted tiller to surviving parts of the plant (Peoples & Dalling, 1988).

Grass species have two types of roots, seminal and nodal. The seminal roots are developed from primordia in the seed, while the nodal roots are developed from the basal nodes of a tiller (Mac Key, 1973) When a tiller has 3 leaves, the nodal roots begin to form in order to supply that tiller with water and plant nutrients (Klepper, Belford & Rickman, 1984). The number of nodal roots formed in a plant is correlated to the number of tillers in the plant (Mac Key, 1979; Mac Key, Jordan & Zobel, 1980; Wang & Below, 1992).

The spike consists of 10-25 spikelets. Every spikelet is able to produce 7-12 floret primordia, but later the least-developed floret primordia abort, resulting in 0-6 florets per spikelet (Langer & Hanif, 1973; Hay and Kirby, 1991) (Figure 2). The spikelets are initiated after the double ridge stage of the spike primordium. The low mid spikelets in the spike are formed first and are favoured in growth and nitrogen accumulation (Langer & Hanif, 1973; Kirby, 1974; Simmons & Moss,

Fig. 2. Spikelet with 3 fertile florets

1978). Such a priority has also been observed within the spikelet, with lowest priority given to the distal florets and the highest priority to the second floret from the base (Simmons & Moss, 1978).

The average grain weight within a cultivar does not vary much despite different growing conditions, except for special conditions that reduce the grain filling period (Hay & Walker, 1989).

Plant phenological development

The number of primordia to tillers, spikelets and florets is normally far in excess of the number of adult organs that can be supported by the plant. Tillers, spikelets and florets that cannot be supported by the plant are successively aborted. In the intra-plant competition, the last primordium or organ to be developed is aborted first, *e.g.* the last tiller in the plant aborts first, as does the last spikelet in the spike and the last floret (grain) in the spikelet (Hay & Walker, 1989; Tashiro & Wardlaw, 1990; Hay & Kirby, 1991; Wheeler *et al.*, 1996). The phase of organ mortality is therefore of least importance as the formation phase for the final numbers of tillers, fertile spikelets and fertile florets (Hay & Kirby, 1991). In field cropping, inter-plant competition caused by the plant density (plants m^{-2}) also influences the development of plant organs and the grain yield of a plant.

The growing conditions affect the possibilities for the plant organs to grow. A slow development gives a long growing period and a good opportunity for the plant organs to develop and survive with high number of tillers $plant^{-1}$, high number of spikelets $spike^{-1}$ and a great number of grains $spike^{-1}$ (Hay & Kirby 1991). Although the mortality of tillers, spikelets or grains or of the primordia to

such organs is important for grain yield, it is not well understood and needs to be studied further.

Nitrogen in the grain

Grain nitrogen concentration is influenced both by accumulation of starch and by accumulation of nitrogen. These accumulation processes are regarded as independent and are controlled by separate mechanisms (Jenner, Ugalde & Aspinal, 1991).

Grain nitrogen amount and grain nitrogen concentration are influenced by spikelet position in the spike and grain position in the spikelet (Levi & Anderson, 1950; Simmons & Moss, 1978; Stoddard, 1999). Grains in acropetal spikelets have a lower nitrogen concentration than grains in basal spikelets. Acropetal grains in the spikelet have a lower nitrogen concentration than the two basal grains in the spikelet (Levi & Anderson, 1950; Simmons & Moss, 1978; Stoddard, 1999; Bramble *et al.*, 2002).

Baking quality

The main quality factor in producing and marketing wheat is protein concentration, often measured as nitrogen concentration and multiplied by a conversion factor to get the protein concentration (Jenner, Ugalde, & Aspinal, 1991).

Baking quality is dependent not only on grain protein concentration, but also on grain protein composition and amount and size distribution of polymeric proteins (Payne *et al*. 1987; Johansson, Prieto-Linde & Jönsson, 2001; Johansson *et al*., 2003). Baking quality is determined by the genetic background (Payne *et al*., 1987; Johansson *et al*., 1993, Johansson, Prieto-Linde & Jönsson, 2001) and by the environment during growing and grain filling (Fajersson, 1961; Peterson *et al*., 1992; Johansson & Svensson 1998, 1999; Johansson *et al.,* 2002, 2003).

The weather during the grain filling period is of great importance for bread-making quality. Poor bread-making quality is obtained when grain filling occurs in cold and wet weather (Johansson & Svensson, 1998, 1999; Johansson, 2002). During grain filling, high temperature of above 20 ^{o}C result in small grains with high protein concentrations (Sofield, Evans & Wardlaw, 1974; Altenbach *et al.*, 2003; Gooding *et al.*, 2003). During grain filling, the weather influences the protein polymerisation that affects the baking quality (Johansson *et al.*, 2003).

Wheat genetics

Genetic development of wheat

Wheat belongs to the tribe Triticeae in Poaceae, the grass family. In the tribe Triticeae, hybridisations between species in the same genus or related genus have occurred. The cultivated wheat, *Triticum aestivum*, is a hexaploid with genomes AABBDD coming from three progenitors (wild einkorn *Triticum boeoticum*, wild emmer T. *dicoccoides* and *Aegilops tausschii* Coss)(Salamini *et al.*, 2002).

The cultivation of wheat started in the Fertile Crescent about 8000 B.C. The first cultivated wheats were einkorn, diploid *Triticum moncoccum* and emmer, tetraploid *Triticum dicoccoides.* The progenitor to einkorn is wild einkorn and the progenitor to emmer is wild emmer. In the area of the Fertile Crescent, wild relatives to the cultivated wheats frequently appeared and cultivated emmer hybridised with *Aegilops tausschii* Coss and formed the hexaploid *Triticum aestivum* (Salamini *et al.*, 2002).

Wild plant species are favoured by diaspore dispersal over the ripening time. In the wild wheat progenitors of the cultivated bread wheat T. *aestivum*, the spike axis (rachis) disarticulates into diaspores each consisting of a spikelet and a corresponding section of the rachis (Bor & Guest, 1968; Kerber & Rowland, 1974; van Slageren, 1994; Salamini *et al.*, 2002). In the wild wheat progenitors, the grains cannot easily be separated from the other parts of the spikelet.

Harvest index and nitrogen harvest index

Over the past two centuries, plant breeding has improved yield and quality. Alteration of the partitioning of dry matter in the plant is the main reason for the increase in grain yield. Harvest index (HI) is a factor denoting the harvested share of the plant. For grain crops, HI is calculated as (dry weight grain yield) (dry weight for above ground plant parts)$^{-1}$. To improve yields, plant breeding has successively increased HI and now the HI for new wheat cultivars is about 0.45 compared to 0.25 for old growing materials (Corbellini & Borghi, 1985; Feil & Geisler, 1988; Brancourt-Hulmel *et al.*, 2003).

Nitrogen harvest index (NHI) is an index for nitrogen recovery in the harvested product. For grain crops, NHI is calculated as (nitrogen amount in grain yield) (nitrogen amount in aboveground plant parts)$^{-1}$. NHI in bread wheat is in general 0.70-0.80 (Corbellini & Borghi, 1985; Bertholdsson & Stoy, 1995; Calderini, Torres-León & Slafer, 1995; Brancourt-Hulmel *et al.*, 2003). Reported extreme values are 0.51-0.91 (Van Sanford & MacKown, 1987).

Correlations between plant parameters are often investigated. Positive correlations have been found for HI to NHI, and HI to grain yield. Negative correlations have been found for HI to straw weight; and grain yield to grain nitrogen concentration (Heitholt *et al.*, 1990; Bertholdsson & Stoy, 1995; Calderini, Torres-León & Slafer, 1995; Ehdaie & Waines, 2001).

The cultivation technique used in this thesis enables calculation of HI and NHI based on the entire plant including the roots, HI_{tot} and NHI_{tot} respectively. HI_{tot} is calculated as (dry weight grain yield) (dry weight for the entire plant)$^{-1}$, and NHI_{tot} is calculated as (nitrogen amount in grain yield) (nitrogen amount in entire plant)$^{-1}$.

Materials and methods

To represent a wide genetic variation in nitrogen behaviour, the experiments were carried out with cultivars with different genetic backgrounds, origins, release ages and nitrogen concentrations in the grain. The cultivars are described in more detail in the individual papers.

The plants in the experiments were grown in aerated solution culture to full maturity in growing chambers with controlled environments (Ingestad, 1982; Mattson *et al.*, 1992; Oscarson *et al.*, 1995a). The nitrogen supply was controlled by daily doses and the nitrogen amount (NA) was set to follow the equation:

$$NA_t = NA_{t-1}\, e^{RA}$$

where NA_t is the NA of the plant at Day t and NA_{t-1} the NA one day before Day t. The daily nitrogen doses were calculated from NA_t-NA_{t-1}. RA is the relative addition rate of nitrogen, the rate at which nitrogen is given to the plants (NA added x plant NA^{-1} day^{-1}). RA was altered during the phenological development. When the relative addition rate of nitrogen is kept at a growth-limiting level, the nitrogen added daily is taken up within 24 h and is equal to the relative increase in plant nitrogen amount (Mattson *et al.*, 1992; Oscarson *et al.*, 1995a, b; Oscarson, 1996).

To trace the fate of nitrogen supplied at specific times the daily doses were transformed to contain an ^{15}N-enriched nitrogen source. ^{15}N was given three days before each sampling time in the rapid development trial and four days before each sampling time in the slow development trial in Paper I. The use of labelled nitrogen is common in nitrogen uptake, transport and remobilisation studies (*e.g.* Recous, Machet & Mary, 1988; Palta & Fillery, 1993; Reining, Merbach, & Knopf, 1995).

With the method used here, the N supply could be varied in any desired way. We used a supply mimicking N uptake in field-grown wheat. All nitrogen was recovered and there were no losses to the surrounding environment.

The plant parts were dried, weighed, ground and analysed for nitrogen and ^{15}N. Nitrogen and ^{15}N were measured in a mass spectrograph in combination with a Carlo Erba nitrogen analyser using the Dumas method through volatilisation of nitrogen.

Polymeric and monomeric proteins were extracted in dilute sodium dodecyl sulphate (SDS) (Gupta, Khan & MacRitchie, 1993). Amount and size distribution of polymeric proteins were measured by percentage unextractable polymeric protein in the total polymeric protein (UPP) and analysed according to Johansson, Prieto-Linde & Jönsson, (2001) using size exclusion-high performance liquid chromatography (SE-HPLC).

After extraction, polymeric, monomeric proteins and protein classes (albumins, globulins, gliadins and glutenins) were analysed for nitrogen and ^{15}N.

Results and Discussion

Dry matter partitioning and development rate

In plant breeding and crop production, plant dry matter partitioning is often discussed. In Paper I, the plant dry matter partitioning in two experiments with different phenological development rates is described. The main conclusion is that the partitioning of biomass is dependent on phenological development rate and that the development rate for a cultivar is dependent on the sensitivity to the environment. Thus the response to the environment might not be linear between cultivars (Table 2).

Temperature has in general a great effect on phenological development rate. The influence of temperature alone or in combination with nitrogen supply; CO_2 concentration in the air; photoperiod; and/or vernalisation on the development rate has been studied (*e.g*. Frank & Bauer, 1982, 1996; Batts *et al.*, 1996; van Oijen *et al.*, 1998).

In Paper IV, we investigated the effect of temperature and genetic background on the nitrogen partitioning and the N-redistribution. Six cultivars with different genetic background were investigated. An increase in temperature of 5 ^{o}C lowered the grain filling period for the main spikes on average for the six cultivars from 55.5 days to 35.5 days. Temperature generally has a strong influence on the duration of grain filling (Sofield, Evans & Wardlaw, 1974; Gibson & Paulsen, 1999; Altenbach *et al.*, 2003; Gooding *et al.*, 2003).

The result is consistent with previous findings that increased temperature in the range 18-24 ^{o}C shortens the grain filling period and reduces yield (Housley & Ohm, 1992; Wheeler *et al.*, 1996; Moot *et al.*, 1996).

Root weight was positively correlated to root nitrogen amount; to grain total weight; and to shoot weight (excl. grain), and negatively correlated to root nitrogen concentration; to grain nitrogen concentration; to NHI; and to NHI_{tot}. Root properties are seldom investigated and no other results were available for comparison. For the cultivars used (Paper IV), correlations with the aboveground parameters were in accordance with previous findings (Heitholt *et al*., 1990; Bertholdsson & Stoy, 1995; Calderini, Torres-León, & Slafer, 1995; Ehdaie & Waines, 2001).

Table 2. *Harvest index (HI), harvest index for the entire plant (HI_{tot}), and total grain yield dry weight g plant^{-1} for two cultivars in a slow development trial (ST) and a rapid development trial (RT). Data recalculated from Paper I*

	Sport			WL		
	HI	HI_{tot}	Grain yield	HI	HI_{tot}	Grain yield
ST	0.343	0.272	2.24	0.441	0.330	2.93
RT	0.535	0.489	1.36	0.583	0.522	2.13

Nitrogen uptake

With the method used, the daily nitrogen supply was taken up within 24 hours. All nitrogen supplied was taken up and was recovered at the sampling times (Papers III and IV). The roots maintained their capability to absorb nitrogen through the whole senescence period (Papers II and III), in agreement with findings by Oscarson *et al.* (1995b) and Oscarson (1996). Interestingly the capability to take up and distribute nitrogen was maintained even after complete yellowness of the aboveground plant parts. During the growing period, the root system has been found to have a great overcapacity with respect to the demand of the shoot (Oscarson *et al.*, 1995b).

Nitrogen concentration in plants

In the experiments with the same daily nitrogen supply regime but different plant phenological development rates, the nitrogen concentration in all plant parts was more dependent on development rate than on nitrogen supply (Paper I). A fast phenological development rate gave higher nitrogen concentration in the plant and in the grain than a slow development rate, despite the same daily nitrogen supply.

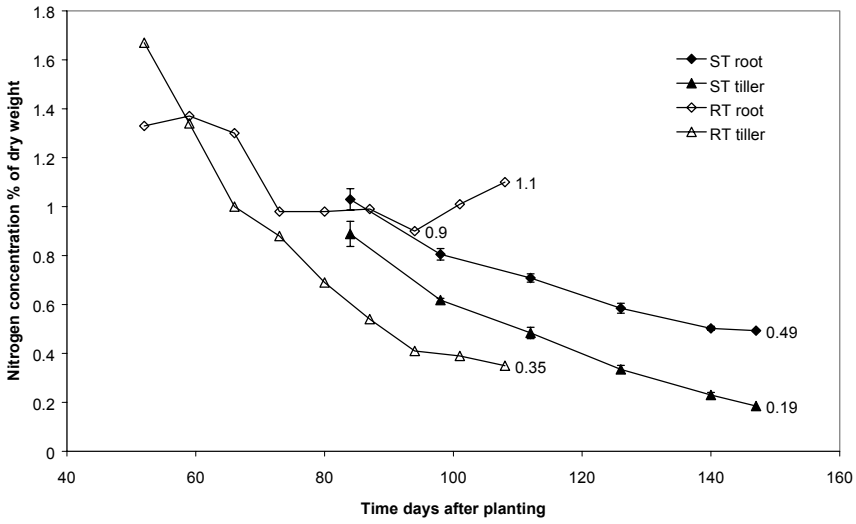

Fig. 3. Nitrogen concentration in roots and tillers in a rapid development trial (RT) and a slow development trial (ST) for cv WL.

The remaining nitrogen concentration at maturity was higher in the experiment with high nitrogen concentration (rapid development trial) than in the experiment with low nitrogen concentration (slow development trial) (Paper I). The remaining nitrogen concentration in vegetative parts at maturity is thus dependent on the nitrogen concentration in the plant during growth (Figure 3).

During grain filling, the nitrogen concentration declined in the aboveground vegetative parts of the plants (Papers I, III), in agreement with earlier findings (Siman, 1974; Austin *et al.*, 1977; Heitholt *et al.*, 1990; Palta *et al.*, 1994; Fangmeier *et al.*, 1999). The roots exhibited the same pattern as the aboveground parts but the end concentration was higher in the roots than in the aboveground plant parts (Paper III).

Fourteen days before the grain filling period was finished, the N concentration in the grain was already at the end level for each spikelet (Paper II), which indicates that the duration of the grain filling period *per se* does not influence the nitrogen concentration in the grain (Figure 4). The nitrogen concentration might instead be dependent on a ratio of two rates, the rate of nitrogen flow to the grain /carbohydrate flow to the grain. This supports the conclusion of Panozzo & Eagles (1999) that higher rate of nitrogen accumulation and lower rate of carbohydrate accumulation rather than differences in duration of accumulation are the reason for high grain nitrogen concentration during stresses such as high temperature and drought.

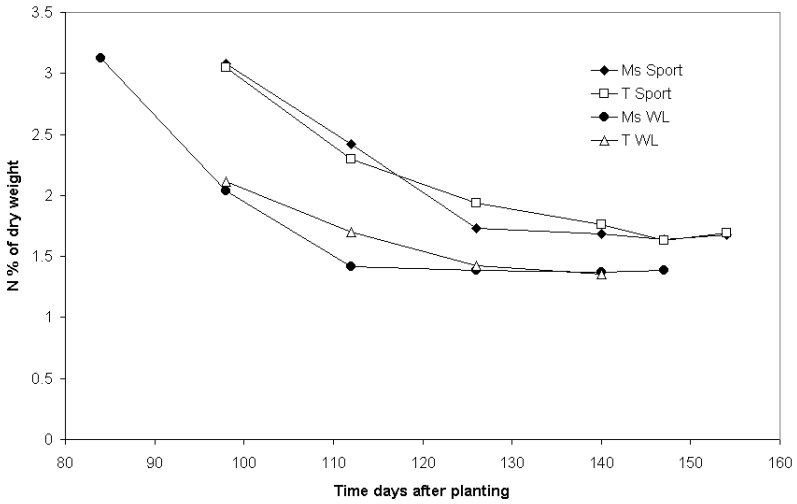

Fig. 4. Grain nitrogen concentration (% of dry weight) in main shot spikes (Ms) and tiller spikes (T) in two spring wheat cultivars during grain filling period. Standard error for Ms spikes = 0.03 and standard error for T spikes = 0.06 based on pooled standard deviation for values 112 – 140 days after planting (degrees of freedom = 6)

A suggestion is that the speed of senescence determines the rate of nitrogen flow to the grain and the duration of grain filling (Rao & Croy, 1972; Harms & Nowak, 1990). During development of the wheat plant there is an abortion system with unknown processes ensuring an appropriate grain size for mature grain by regulating the number of grains spike^{-1}. The existence of such a system was indicated by a lower number of grains spike^{-1} when the temperature was high after anthesis (Paper IV). The importance of appropriate grain size was shown by the mean grain weight being almost the same in the experiments in Paper I, despite differences in number of grains spike^{-1} and grain filling period. The abortion system might have an impact on the nitrogen concentration in the grain.

Nitrogen distribution

Within plant

At anthesis, the nitrogen present in the plant was located in the roots, main shoots and tillers. After grain development, the grain became the major nitrogen sink in the plant and nitrogen was redistributed from vegetative parts to the grain. The grain contained the greatest proportion of plant nitrogen amount at maturity, but the vegetative parts still contained a considerable amount of nitrogen. The highest amounts in the vegetative parts were present in the roots, which had 10-20% of the total nitrogen amount (Papers III, IV). The importance for agriculture of the nitrogen amount in the roots is discussed further in the general discussion.

The roots were the last vegetative part to senesce in the present experiments, in accordance with findings by Peoples & Dalling (1988). Thus the roots play a major part in the redistribution of nitrogen in the plant. Redistribution of nitrogen from the root contributed to a high degree to the nitrogen amount in grain at maturity for the six cultivars investigated (Paper IV). High protein cultivars exhibited a faster decline in root N amount than low protein cultivars and thus the difference between cultivars in redistribution rates of nitrogen from the roots (Papers III, IV) is similar to that found in aboveground plant parts (Rao & Croy, 1972; Harms & Nowak, 1990).

The correlations found between NHI and NHI_{tot} versus other plant parameters demonstrate that the roots play a major part in nitrogen partitioning in the plant. The roots compete with the grain in demand for nitrogen, as is apparent from the fact that the roots are the last plant part to senesce.

Within spike

The formation of grains in the spike is unequal. This might lead to differences in nitrogen accumulation within the spike and therefore nitrogen accumulation within the spike was investigated in Paper II.

The accumulation of both redistributed nitrogen and nitrogen recently taken up by roots in spikelets within the spike was uniform in the grain initiation stage. However during grain maturation, a priority in accumulation of nitrogen to the lowermost spikelets in the spike became apparent (Figure 5).

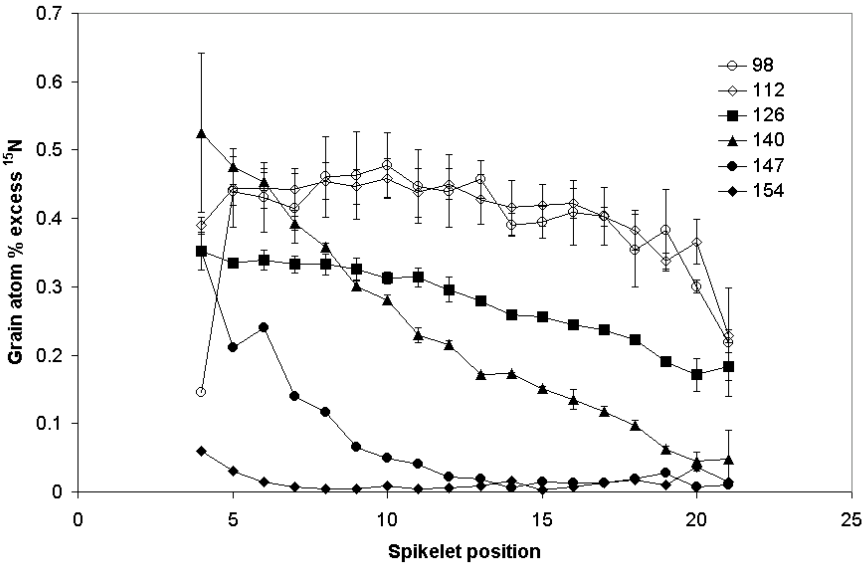

Fig. 5. Atom % excess ^{15}N in grains spikelet^{-1} in cv. Sport at different sampling times. Value reduced to one comparable supply of ^{15}N (0.563% excess ^{15}N) at all sampling times. Spikelet positions numbered from the base of the spike. Symbols and text refer to days after planting. Vertical bars represent ± SE.

Table 3. *Pearson correlation coefficient (corr coeff) for correlations in the spike at the end of the grain filling period in two cultivars (WL and Sport) grown in two types of experiment, RT with high grain nitrogen concentration and ST with low nitrogen concentration. Spikelet positions numbered from base to top in the spike*

Experiment and cultivar	Correlation	Corr coeff	P
RT Sport	Grain ^{15}N atom % excess with spikelet position	-0.884	0.001
	Chaff ^{15}N atom % excess with spikelet position	-0.860	0.001
	Grain ^{15}N atom % excess with chaff ^{15}N atom % excess	0.965	0.000
RT WL	Grain ^{15}N atom % excess with spikelet position	-0.906	0.000
	Chaff ^{15}N atom % excess with spikelet position	-0.694	0.026
	Grain ^{15}N atom % excess with chaff ^{15}N atom % excess	0.758	0.011
ST Sport	Grain ^{15}N atom % excess with spikelet position	-0.992	0.000
ST WL	Grain ^{15}N atom % excess with spikelet position	-0.991	0.000

RT Sport 73 days after planting in spikelet region 3-12
RT WL 80 days after planting in spikelet region 3-12
ST Sport 140 days after planting in spikelet region 5-10
ST WL 140 days after planting in spikelet region 5-10

At the end of the grain filling period, there was a negative correlation between recently taken up nitrogen (as grain ^{15}N atom % excess and as chaff ^{15}N atom % excess) and spikelet position numbered from the bottom of the spike and thus there were differences in cessation of influx duration for nitrogen in the different spikelets. The negative correlation was found in both the rapid development trial and in the slow development trial and is thus independent of nitrogen supply and nitrogen concentration in the plant (Table 3).

The target for the last root flux was only the basal spikelets with heavy grain weight and not the apical spikelets with low grain weight. Thus, nutrients are likely to reach light and heavy grains differently during the grain filling period. This might be an explanation for the different nutrient concentrations in light and heavy grains in the spike (*e.g*. Calderini & Ortiz-Monasterio, 2003).

In contrast to their wild progenitor, cultivated wheats have a tough rachis that enables all spikelets to be harvested (Kerber & Rowland, 1974; Salamini *et al.*, 2002). A conclusion from the present experiments was that in spite of the tough rachis, the order of maturation of spikelets from top to base inherited from the wild progenitor has not changed.

Protein polymers within the spike

The uneven cessation time observed for nitrogen accumulation within the spike raised questions regarding whether this leads to variation in baking quality due to spikelet position and whether the components determining baking quality are built unevenly over time. Investigating these questions was the main purpose of Paper V.

From 98 days after planting up to maturity, polymerisation of proteins, *i.e*. the percentage of total and large UPP, increased in all spikelets. Increased polymerisation of proteins in pooled grains from the entire wheat spike has been found in previous studies (Panozzo, Eagles & Wootton, 2001; Daniel & Triboi, 2002; Johansson *et al.,* 2004).

Uniform nitrogen concentration and uniform protein composition and polymerisation between spikelets seem to be desirable properties in achieving uniform baking quality among grains in the spike. Unfortunately these properties were not combined in the cultivars investigated. Differences in protein composition and polymerisation between spikelet positions were found for cultivar WL, which had uniform nitrogen concentration between spikelets (Paper II). Cv. Sport, with different nitrogen concentration between spikelet positions, had smaller variations in protein composition and polymerisation than cv. WL (Paper V).

At 140 days after planting, the nitrogen concentration in both SDS-extractable and unextractable proteins increased in spikelets from base to top of the spike. This indicates that the solubility and extractability of grain compounds vary with spikelet position. The reasons for this and its importance were not investigated in the present study but need to be further investigated.

The last nitrogen taken up was incorporated into all protein classes (albumins, globulins, gliadins and glutenins) within the spikelets (Paper V). However, this nitrogen was incorporated to a higher extent in the protein classes (albumins, globulins, gliadins and glutenins) in the lower spikelets in cv. WL but in the SDS-extractable and unextractable proteins in cv. Sport (Paper V). This variation might be due to differences in maturation time (Daniel & Triboi, 2002; Altenbach *et al.*, 2003), between the cultivars or to cultivar differences in protein build-up pattern.

Cultivar properties

Cultivars

The cultivars used in this thesis were chosen to represent wide genetic differences in respect of grain yield and grain nitrogen concentration. More details are given in Paper IV.

Response to environment

The response to temperature was not uniform for the six cultivars. The cultivars shortened the grain filling period for the main spike by 16 to 25 days when the temperature was increased by 5 ^{o}C during grain filling (Figure 6).

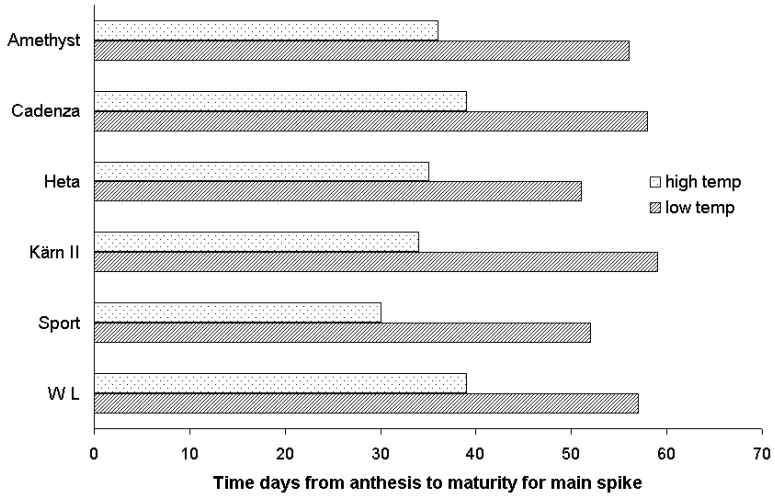

Fig. 6. Time in days from anthesis to maturity for six cultivars grown in 18 ^{o}C day temperature and 12 ^{o}C dark temperature (low temp) and 23 ^{o}C day temperature and 17 ^{o}C dark temperature (high temp)

HI is often increased when the grain filling period is prolonged (Spierz, 1977; Gibson & Paulsen, 1999; Gooding *et al.*, 2003), and this was also the case in the present experiments, although not for all cultivars. One of the cultivars in particular exhibited a slow senescence in the low temperature regime and a low HI together with a low NHI and NHI_{tot}. The vegetative parts of this cultivar remained green for a long time and the nitrogen concentration was maintained at a high level in the vegetative parts, especially in the roots during the grain filling period. Thus straw and roots became competing sinks with the grain. Despite the long grain filling period in the low temperature regimes, this did not result in a rise in HI in comparison to the high temperature regime.

Slow senescence and low HI have been reported in irrigated wheat production in China (Zhang *et al.*, 1998; Yang *et al.*, 2000). Drought during the grain filling period, leading to a shortened grain filling period, may then improve the HI (Zhang *et al.*, 1998; Yang *et al.*, 2000; Altenbach *et al.*, 2003) and lead to more complete nitrogen remobilisation (Palta *et al.*, 1994).

A conclusion is that appropriate senescence is important for grain filling, *i.e*. the cultivars need to react to the prevailing temperature in a normal way.

High grain nitrogen concentration

Two different ways to obtain high nitrogen concentration in the grain could be distinguished from the cultivars in the experiments. One was by having high HI and NHI with low straw and root weight, due to a short period in the vegetative stage and thus a small remaining nitrogen amount in the vegetative parts. The other way was by having a long period in the vegetative stage but a short grain filling period, resulting in small grain with a high nitrogen concentration. This type had a high nitrogen redistribution rate from vegetative parts to the grain (Rao & Croy, 1972; Harms & Nowak, 1990).

General discussion

Root development

In field growing of cereals there is simultaneous root biomass production and root mortality. This makes instant field investigations for estimation of root production and root contribution to the nitrogen amount difficult. Total root production (Sauerbeck & Johnen, 1976; Hansson & Steen 1984; Hansson, 1987; Steingrobe *et al*., 2001) and nitrogen amount in the roots may be underestimated due to root mortality. In unfertilised barley, considerable root mortality was found already 3-4 weeks after sowing, but in well nitrogen-fertilised barley, root mortality did not start until after anthesis (Hansson, 1987). A large proportion of the root system produced normally dies during the growing period. For example, at harvest of

winter wheat the root system may be only 25% to 50% of the total root system produced (Steingrobe *et al*., 2001).

In solution culture experiments in this thesis, all roots were sampled together. The plant dry weight partitioning in samples from the solution-cultured wheat resembled the dry weight partitioning (total biomass production including dead roots) found by Steingrobe *et al*. (2001).

Root properties such as root depth and root penetration are of great importance for successful crop production in agriculture. The negative correlation between root weight and NHI found in the present experiments indicates that there could be a risk of important agronomic root properties being lost if NHI is used as a selection criterion in plant breeding.

Root nitrogen

The amount of nutrient redistribution from dying roots preceding root mortality is not known. It is likely that nitrogen is withdrawn from the dying roots and distributed to actively growing parts of the plant, similarly to the way nitrogen is withdrawn and redistributed from the shoots. However, some amounts of nitrogen remain in the dead roots, of at least a similar concentration as in the present experiments (5 mg g^{-1} root dry weight). In studies with labelled nitrogen in spring wheat (Rroco & Mengel, 2000), 12% of the nitrogen in the plants was later found in the soil during the growing period. With the technique used in this thesis, all nitrogen was recovered in the plant. This discrepancy between results might be due to root mortality (Hansson & Steen 1984; Hansson, 1987; Steingrobe *et al*., 2001). Another explanation might be that nitrogen released from the roots was taken up again in this solution culture cultivation.

Another question concerns the fate of nitrogen in dead roots in the soil (Hansson & Steen, 1984), which form part of the soil organic material and are later mineralised. Existing knowledge about the rate of mineralisation of dead root nitrogen is limited. Roots have a low C/N ratio and are therefore mineralised faster than other crop residues. The possibility exists that the roots might be mineralised later in the same growing period in which they die (Kätterer & Andrén, 1996).

Root nitrogen and nitrogen fertilisation

The roots may play a major role in crop stands in both assimilating nitrogen when the crop is suffering nitrogen deficiency (Vouillet & Devienne-Barret, 1999) and, as found in the present experiments, in redistributing nitrogen to the grain during grain filling. Wheat root systems show differences in biomass between years, stands (Barraclough & Leigh, 1984) and cultivars as shown in these experiments. Root mortality also differs between fertilisation regimes and years (Hansson, 1987; Steingrobe *et al*., 2001). During field cultivation, it is therefore likely that root mortality, nitrogen mineralisation in the soil from roots that died earlier in the growing season and root nitrogen redistribution from the root system will show variations between cultivars, years and stands. The capacity for nitrogen

redistribution from the root system is hard to measure in plant stands. Thus, the nitrogen behaviour in the root system may act as a source of error when nitrogen in aboveground parts only is measured by plant analysis or canopy reflectance in order to determine the need for nitrogen fertilisation in crops. A variation between years in redistribution of nitrogen from the roots may to some extent cause variation in grain protein amount, protein concentration and composition, and thus wheat quality.

Recovery of nitrogen

High nitrogen use efficiency is a challenge for plant breeding and crop production. Recovery of fertiliser nitrogen in the grain is low world-wide (Raun & Johnson, 1999; Cassman, Doberman & Walters, 2002; Delgado, 2002). Processes in the soil and inappropriate spreading of fertiliser are the main causes of this low value.

NHI measures the efficiency of nitrogen translocation in the aboveground plant to the grain. In field cultivation of wheat, NHI is in the range 0.70-0.80. In this investigation, NHI was somewhat higher (0.79-0.84). Based on the entire plant (including roots), NHI_{tot} demonstrates the efficiency in the entire plant of nitrogen translocation to grain. In the present study NHI_{tot} was 0.69-0.77, which seems to be the biological maximum recovery of plant nitrogen in the grain, regardless of processes in the soil. This value is considerably higher than the world-wide NUE, and about the same as comparison values from nutrient balance calculations (Table 1).

Nitrogen mineralisation from organic materials and immobilisation to organic material are ongoing processes in the soil. The dead roots will also undergo these processes sooner or later. Assuming that the plants in the study in Paper III represented field growing at a density of 250 plants m^{-1} and assuming 60% mortality (Steingrobe *et al*., 2001), the dead roots would contain 16.5-18 kg nitrogen ha^{-1}, corresponding to 11-12% of nitrogen supplied. This is similar to the N loss figures from the root system to the soil found by Rroco and Mengel (2000).

Nitrogen harvest index

NHI has been proposed as a criterion in selection of plants with high nitrogen use efficiency. In the study in paper IV, NHI was positively correlated to HI and negatively correlated to shoot weight and root weight, indicating that the common process of selection for high HI also implies high NHI. Selection directly for high NHI also implies selection for low shoot weight and root weight. However, low root weight often seems to be a disadvantage in crop production. NHI_{tot} was negatively correlated with root nitrogen concentration. Instead of breeding directly for high NHI, breeding for low straw nitrogen concentration (Cassman *et al.*, 1992; Przulj & Momcilovic, 2001) and low root nitrogen concentration might be a better solution.

Protein quality

Good quality is essential for some specific end-uses of the wheat harvest, *e.g*. for milling and baking. Uniform quality is another important character (Johansson, Prieto-Linde & Jönsson, 2001). Baking quality is both genetically and environmentally influenced (Payne *et al*., 1987; Johansson, Prieto-Linde & Jönsson, 2001). Environmental variation in baking quality is caused by differences in protein polymer composition (Johansson *et al.*, 2002). Differences in amount and size distribution of polymeric proteins according to spikelet position were found in one of two cultivars investigated in the study in paper V. The protein composition variation according to spikelet position described in Paper V is likely to cause a non-desired quality variation in the wheat produced.

Polymerisation of proteins increased during grain development, similarly to previous investigations (Panozzo, Eagles & Wootton, 2001; Daniel & Triboi, 2002; Johansson *et al*., 2004). Differences in amount and size distribution of polymeric proteins due to environment arose early during the grain filling period and remained throughout this period. The influence of temperature on the duration of the grain filling period and variation in N supply has been shown to alter the amount and size distribution of polymeric proteins in the total spike (Johansson *et al*., 2004). The later part of the grain filling period is important for variation in amount and size distribution of polymeric proteins (Johansson *et al*., 2004). Variation in cessation time of nitrogen influx in different spikelets in the spike might thereby also cause variation in the amount and size distribution of polymeric proteins.

Conclusions

The influx period of root nitrogen flow finishes at different times for the spikelets in a spike. The cessation order is basipetal, *i.e*. from top to base. Apical spikelets contain small grains and have the shortest influx period. As the influx period varies for different spikelets in the spike, this is the explanation for the observed variation in protein polymer composition, which in turn most likely influences quality stability in wheat.

The roots may be a great sink and store for nitrogen in the plant during its development and are a major sink for nitrogen newly taken up post-anthesis in plants. The nitrogen in the roots may be a source of nitrogen remobilisation to the grain, but the degree of remobilisation from the roots is dependent on the prevailing nitrogen sink/source relationship in the plant. Even after remobilisation from the roots, a large proportion of the nitrogen amount in the plant remains in the roots. Therefore nitrogen use efficiency in the whole plant is affected to a great extent by the nitrogen amount in the roots.

Temperature affects harvest index and to a lesser extent nitrogen harvest index. Low temperature during grain filling leads in general to higher harvest index. If

senescence is delayed, active plant parts such as the straw and especially the roots become competing sinks to the grain in respect of carbohydrates and nitrogen compounds. Low root nitrogen concentration might be a breeding trait, since there is a negative correlation between root nitrogen concentration and grain yield and NHI_{tot}, *i.e*. low root nitrogen concentration gives a higher yield and higher NHI_{tot}.

Future research

The root system may play a great role in nitrogen partitioning in crops. In situations with deficiencies, the root system acts as a sink, while in situations of surplus in the senescing plant, it acts as a source for nitrogen distributed to the grain. In precision agriculture, the nitrogen in the root system in combination with root mortality and root nitrogen mineralisation might be the main reasons for deviations from the expected results. The ability of the roots to redistribute nitrogen to the grain needs to be investigated under field conditions.

Root mortality and mineralisation of roots may act as a source of nitrogen leaching during the vegetative period and after harvest. The role of the senescing root system in nitrogen leaching from fields needs further investigation.

Breeding for nitrogen-efficient cultivars is best achieved by breeding for low nitrogen concentration in waste products such as straw and roots. In future studies on HI and NHI root biomass, root nitrogen amount and nitrogen mineralisation from the soil need to be taken into consideration.

In agriculture, the nitrogen translocation rate in the plant determines the time for the latest possible fertiliser application. In precision agriculture, late application to satisfy the yield and quality demand of nitrogen to the crop is the best alternative. In addition to soil and weather conditions, timing of fertilisation is dependent on the translocation rate in the plant. The latest possible fertiliser application time that does not decrease the protein composition or polymer composition needs to be investigated.

Uniform quality in wheat between deliveries to millers and bakers is important for good baking results. The reasons for differences in protein polymers between spikelets in the spike and the importance for uniform baking results need to be studied.

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Personal coomunication

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