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Associations among early-season root and shoot traits, nutrient use efficiency and grain yield of spring wheat

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Cover: Nine spring wheat cultivars used in this thesis
(photo: H. Liu)

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Abstract

Nutrient-efficient and high-yielding spring wheat is needed in high-latitude regions. The aims of this thesis were: (1) to evaluate the effects of soil compaction and differential weather conditions on plant growth and grain yield, (2) to identify critical nutrient elements limiting plant growth and grain yield, and (3) to identify root and shoot traits at an early growth stage (early vigor) influencing nutrient use efficiency and grain yield of spring wheat. This thesis is based on a two-year field trial and a three-week greenhouse experiment. Nine spring wheat genotypes were field-grown on compacted and non-compacted soils during two cropping seasons with contrasting weather conditions. In addition, the same genotypes were greenhouse-grown for three weeks in rhizoboxes to further explore the genotype-specific associations between early vigor and nutrient accumulation. Soil compaction increased plant biomass in the drier year but decreased it in the wetter year, compared to the non-compacted treatment. In addition to nitrogen, magnesium-to-phosphorus ratio co-limited total plant biomass and grain yield. Depending on the nutrient of interest, different root system traits were identified as relevant for their accumulations. Furthermore, a potential trade-off was found between nitrogen uptake efficiency and grain-specific nitrogen efficiency (i.e., grain yield per nitrogen accumulation), and it might be partly triggered by some trade-offs seen between root system traits already at an early growth stage. I emphasize that weather conditions significantly influence the interactions between compacted soil and plant growth. I suggest that the potential of early vigor to improve nutrient use efficiency and grain yield should be further investigated, together with the spatial and temporal dynamics of soil resources.

Keywords: early vigor, nutrient use efficiency, roots, soil compaction, spring wheat

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Samband mellan rot- och skottegenskaper, växtnäringseffektivitet och kärnavkastning hos vårvete

Sammanfattning

Näringseffektiva och högavkastande vårvetesorter behövs i regioner på nordliga breddgrader. Syftet med denna avhandling var att utvärdera effekterna av markkompaktering och olika väderförhållanden på tillväxt och kärnavkastning; att identifiera kritiska näringsämnen som begränsar tillväxt och kärnavkastning; och att identifiera rot- och skottegenskaper i ett tidigt tillväxtstadium (tidig växtkraft) som påverkar växtnäringseffektivitet och kärnavkastning. Avhandlingen är baserad på ett tvåårigt fältförsök och ett tre veckors växthusförsök. Nio genotyper av vårvete odlades på kompakterade och icke-kompakterade jordar under två odlingssäsonger med kontrasterande väderförhållanden. Dessutom odlades samma genotyper i växthus i tre veckor i speciella odlingslådor för rotobservation för att ytterligare undersöka de genotypspecifika kopplingarna mellan tidig växtkraft och växtnäringsupptag. Markkompaktering ökade tillväxten under det torrare året men minskade den under det blötare året jämfört med den icke-kompakterade behandlingen. Förutom kväve visade sig det att magnesium-fosforkvoten begränsade biomassatillväxt och kärnavkastning. Beroende på näringsämnet av intresse är olika rotsystemegenskaper relevanta för deras upptag. Ett negativt samband mellan kväveupptagningseffektivitet och kväveomvandlingseffektivitet (dvs. kärnavkastning per kvävemängd i växten) kan delvis förklaras av negativa samband som jag fann mellan olika rotegenskaper. Jag vill gärna lyfta fram att väderförhållandena väsentligt påverkar samspelet mellan kompakterad jord och biomassatillväxt respektive kärnavkastning. Jag föreslår att potentialen för tidig växtkraft för att förbättra växtnäringseffektivitet och kärnavkastning bör undersökas ytterligare tillsammans med markens resursers rumsliga och tidsmässiga dynamik.

Nyckelord: markkompaktering, rotsystemets egenskaper, tidig växtkraft, vårvete, växtnäringseffektivitet

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Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. **H. Liu**, T. Colombi, O. Jäck, T. Keller, M. Weih. Differential effects of soil compaction on grain yield of wheat: Weather conditions influence the interactions between compacted soil and crop growth and yield (accepted manuscript by the Science of the Total Environment).

II. **H. Liu**, F. Fiorani, O. Jäck, T. Colombi, K.A. Nagel, M. Weih (2021). Shoot and root traits underlying genotypic variation in early vigor and nutrient accumulation in spring wheat grown in high-latitude light conditions. Plants 10: 174.

III. M. Weih, **H. Liu**, T. Colombi, T. Keller, O. Jäck, P. Vallenback, A. Westerbergh (2021). Evidence for magnesium-phosphorus synergism and co-limitation of grain yield in wheat agriculture. Scientific Reports 11: 9012.

IV. **H. Liu**, O. Jäck, T. Colombi, A. Westerbergh, M. Weih. Evidence for a link between root system traits and a commonly observed trade-off between nitrogen use efficiency traits in spring wheat (manuscript).

Papers II and III are reproduced with the permission of the publishers.

The contribution of Hui Liu to the papers included in this thesis was as follows:

I. Main author. Planned the study in collaboration with the co-authors; conducted the experimental work with TC and OJ; and analyzed the data and wrote most of the manuscript with help from TC and MW.

II. Main author. Participated in the planning of the sampling methodology; conducted the experimental work with help from OJ; and analyzed the data and wrote most of the manuscript with help from MW.

III. Co-author. Conducted the experimental work; and contributed to the writing of the manuscript, which was led by MW.

IV. Main author. Planned the study in collaboration with the co-authors; conducted the experimental work with help from OJ; and analyzed the data and wrote most of the manuscript with help from MW.

Abbreviations

LAP	leaf area productivity
LAR	leaf area ratio
Mg	magnesium
N	nitrogen
P	phosphorus
PNC	plant nitrogen concentration
PNP	plant nitrogen productivity
RGR	relative growth rate

1. Introduction

1.1 Nutrient-efficient spring wheat

Wheat is one of the most common arable crops in many high-latitude regions and contributes carbohydrates and protein to human and livestock diets. Spring wheat generally has lower grain yield compared to winter wheat when grown in high-latitude regions, which are referred to the regions north of 55° N, e.g., Sweden, Norway, Denmark and Canada. For example, the mean grain yield for spring wheat in Sweden was 4.7 Mg ha^{-1} between 2013 and 2017, whilst that of winter wheat was 7.0 Mg ha^{-1} (Swedish Board of Agriculture & Statistics Sweden 2018). Improving the grain yield of spring wheat has been an important aim of wheat breeders in these regions (Chawade et al., 2018). However, the cool climate with short cropping seasons makes it challengeable to increase the yield of spring wheat.

Proper plant growth requires at least 16 nutrient elements, of which nitrogen (N) is considered quantitatively most important (Reich et al., 2014). Mineral fertilization is widely used to enhance wheat yield. However, the production of mineral fertilizers consumes large amounts of energy, their application is a key cost factor in farm economy and often associated with environmental issues (Lopez et al., 2014; Xu et al., 2012). The efficiency of nutrient use should therefore be improved for both economic and environmental reasons.

It is important to define the term nutrient use efficiency before considering the assessment and improvement of it. A discussion of different methodologies for assessing nutrient use efficiency is found elsewhere (Weih et al., 2018). In this thesis I used the nutrient accumulation efficiency concept (Weih et al., 2011; Weih et al., 2018), which divides the overall nutrient accumulation efficiency (the ratio between the final nutrient yield and the nutrient amount in the initial seed) into nutrient uptake efficiency (the ratio between the mean nutrient amount in plant during the entire growth period and the nutrient amount in the initial seed), grain-specific nutrient efficiency (the ratio between the grain yield and the mean plant nutrient amount during the entire growth period) and grain nutrient concentration. In wheat breeding, the efforts to improve nutrient use efficiency have so far mainly focused on N, whilst other nutrients were poorly considered (Cormier et al., 2016; Lopez et al., 2017). Recent investigations in wheat field-grown in Sweden showed that the accumulations of several nutrient elements were positively correlated with N (Hamner et al., 2017; Asplund et al., 2016). Thus, N appears to be an appropriate prioritized target in wheat breeding. However, plant growth at some developmental stages and in some environments may be co-limited by more than a single nutrient (Reich et al., 2014; Weih et al., 2018), and it is possible that the strong focus on N alone has jeopardized greater progress in breeding towards improved nutrient use efficiency. Therefore, in this thesis, I study the N use efficiency with consideration of other nutrient elements.

1.2 Abiotic environment affecting nutrient use efficiency and grain yield

The use of heavy farm machinery in intensive agriculture has resulted in widespread soil compaction in many regions of the world (Batey, 2009; Hamza and Anderson, 2005). Compacted soil typically shows a degraded structure with low porosity, and low pore continuity and connectivity (Horn et al., 1995). The effects of compaction on soil water availability to plants depend on the frequency and intensity of precipitation. Compaction reduces water infiltration rate and therefore limits soil water availability to plants when precipitation occurs above a certain intensity; furthermore, compaction reduces soil water evaporation and consequently increases water availability to plants under dry conditions (Lipiec and Hatano, 2003). The availabilities of soil nutrients to plants are also affected by soil properties. For example, the mineralization of soil N is associated with soil moisture and soil temperature (Sathya et al., 2009).

Compaction increases soil penetration resistance through lowering soil porosity (Batey, 2009; Hamza and Anderson, 2005). Moreover, compaction decreases air and water transport capability of soil due to its negative effects on soil pore continuity and connectivity, which in turn may lead to soil hypoxia (Horn and Smucker, 2005; Kuncoro et al., 2014). Both high soil penetration resistance and poor soil aeration can reduce root elongation rate, delay the initiation of lateral roots, and result in shallow root systems (Barraclough and Weir, 1988; Blackwell and Wells, 1983; Colombi et al., 2018; Dresbøll et al., 2013), which limit the access of plants to soil water and nutrients. Soil penetration resistance and aeration are strongly affected by soil moisture. Soil penetration resistance increases upon soil drying, whilst soil aeration decreases when soil moisture increases (Bengough et al., 2011; Tracy et al., 2011). Therefore, weather conditions in a given year might have a strong influence on the interactions between soil compaction, root growth, and ultimately shoot growth and grain yield.

1.3 Plant traits influencing nutrient use efficiency and grain yield

Early vigor, which usually refers to rapid shoot and root growth early in the cropping season, is critical for spring wheat grown under the short cropping seasons in high-latitude regions (Bertholdsson and Kolodinska Brantestam, 2009; Chawade et al., 2018). Compared to wheat genotypes with lower early vigor, genotypes with higher early vigor have earlier and faster root extension and proliferation (Palta and Watt, 2009), which improves the access to water and nutrients in subsoil layers. In addition, genotypes with higher early vigor have larger leaf canopies, and therefore enhance light interception to maximize plant growth rate early in the growing season (Regan et al., 1992).

The growth of a wheat root system begins with the seminal roots that arise from primordia in the embryo, and continues with the nodal roots originating from basal nodes of the main shoot and tillers (Figure 1). The growth of both seminal and nodal roots usually continues to the flowering period. The seminal roots are very important for the early establishment of wheat plants, and this thesis therefore focuses on the traits of seminal roots. Root-based mechanisms of enhancing nutrient uptake include: (1) increasing the exploitation of soil volume by altering root traits; (2) exuding a variety of inorganic and organic substances to convert poorly plant-available nutrient forms into more easily accessible forms for plants; and (3) changing the capacity or affinity of nutrient transporters to carry more nutrients to across the plasma membrane (Rengel and Marschner, 2005). This thesis tackles the first aspect. Root architectural traits, which largely determine the spatial and temporal distribution of root foraging, have important roles in soil resource capture particularly in strongly resource-limiting environments. A deep root system (indicated by steep main root angle or few main roots) is beneficial for accessing mobile nutrients (e.g., N) that quickly move through the soil profiles and are generally more available at greater depth. Shallow-angled roots are ideal for accessing immobile nutrients (e.g., P and K), which often concentrate in topsoil. Root anatomical traits such as cortical aerenchyma formation (Klein et al., 2020; Saengwilai et al., 2014a), large cortical cell size (Chimungu et al., 2014a; Colombi et al., 2019) and few cortical cell files (Chimungu et al., 2014b) can reduce the metabolic costs of root construction and maintenance, and enhance nutrient acquisition and shoot biomass accumulation (Lynch, 2019). The above root architectural and anatomical traits assessed at an early growth stage are therefore expected to improve nutrient use efficiency and grain yield of spring wheat grown in high-latitude regions.

Relative growth rate (RGR, the increase in plant biomass per unit of initial biomass and time) and the separation of different components driving RGR mechanistically link plant growth to growth-limiting resources such as light and nutrients. When light is expected to be a key factor for growth, RGR is separated into the components leaf area ratio (LAR, leaf area per unit of whole plant biomass) and leaf area productivity (LAP, whole plant biomass production per unit of leaf area and time; Lambers et al., 1990; Weih, 2001). When N is expected to be a key factor for growth, RGR is separated into the components mean plant N concentration and N productivity (whole plant biomass production per unit of plant N pool and time; Lambers et al., 1990; Weih, 2001). Different drivers for the variation in RGR may be found in different species and growth conditions (Weih, 2001; Poorter and Remkes, 1990). For example, the relative importance of LAP and LAR in determining RGR appears to depend on the light environment, and LAP was identified as the best general driver of variation in RGR of herbaceous species grown under high-light conditions (Shipley, 2002; Shipley 2006). In this context, it is interesting that long-day treatments of about 16 h, typical for high-latitude environments, have been shown to promote leaf area and biomass growth in many grass species; and that light supply at a low irradiance over a longer period can be more efficient than a high irradiance short-day treatment (Adams and Langton, 2005). It is therefore possible that the relatively high importance of LAP for variation in RGR previously observed under high-light conditions (Shipley, 2002; Shipley 2006) is also seen in spring wheat grown under the long diurnal photoperiods in high-latitude regions.

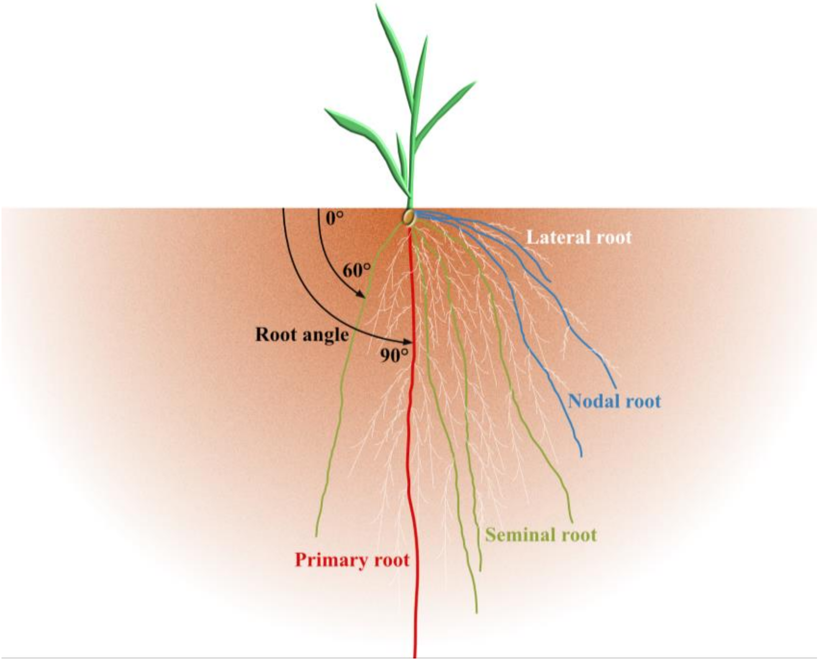

Figure 1. Root angle and various root classes of a wheat plant (illustration: H. Liu).

1.4 Co-limitation of grain yield by nutrients other than nitrogen and phosphorus

As N and phosphorus (P) often limit plant growth, modern crop production systems are typically characterized by high N and P application rates. Theoretical considerations suggest that the accumulation of all essential nutrient elements for plant growth should scale in proportion to each other (Sterner, 2002). Deviations from proportionality could indicate that those nutrients that are accumulated less than proportional become growth limiting. It is therefore possible that the high N and P application rates result in co-limitation of plant growth and yield by other nutrients. When many nutrient elements are involved, the proportional accumulation of nutrients in relation to each other can be evaluated using products of element concentrations (i.e., stoichiometric niche volumes) and the calculation of scaling exponents. This allows to explore, for example, if the concentrations of other nutrients increase faster or slower than the combined concentration of N and P (Ågren and Weih, 2020). A faster increase of the other nutrients in relation to N and P is reflected by a scaling exponent > 1, whilst a slower increase of the other nutrients in relation to N and P is reflected by a scaling exponent < 1.

2. Aims and hypotheses

With spring wheat as a model plant, the main aims of this thesis were: (1) to evaluate the effects of soil compaction under differential weather conditions on plant growth and grain yield, (2) to identify critical nutrient elements limiting plant growth and grain yield, and (3) to identify root and shoot traits at an early growth stage influencing nutrient use efficiency and grain yield.

The following overall hypotheses were tested:
(H1) Soil compaction reduces plant growth and grain yield (Paper I).
(H2) Under long-photoperiod conditions, leaf area productivity and nitrogen productivity are reliable predictors for variation in the relative growth rate of total plant biomass at early growth stages (Paper II).
(H3) Nutrient elements other than nitrogen can co-limit plant growth and grain yield (Papers II & III).
(H4) A higher nitrogen accumulation is associated with a deeper root system, greater root cortical aerenchyma area, larger cortical cell size and fewer cortical cell files at an early growth stage (Papers II & IV).

3. Materials and methods

3.1 Plant materials (Papers I to IV)

Nine spring wheat genotypes were grown in a field trial and a greenhouse experiment: ‘KWS Alderon’ (‘Alderon’, Germany, KWS W185), ‘Bjarne’ (Sweden, NK 97520), ‘Boett’ (Sweden, SW 71034), ‘Dacke’ (Sweden, W 26267), ‘Diskett’ (Sweden, SW 45456), ‘Happy’ (Sweden, SW 91003), ‘Quarna’ (Switzerland, CH 21112283), ‘Rohan’ (Sweden, SW 01198), and a landrace originating in Dalecarlia (‘Dala’, Sweden). These genotypes represent the commonly grown spring wheat cultivars in northern Europe. They considerably vary in establishment time, leaf size, height, disease resistance, grain yield and protein content (information from the Swedish wheat breeder Lantmännen).

3.2 Field trial (Papers I, III & IV)

3.2.1 Site description and experimental design

A field trial was carried out during the 2018 and 2019 cropping seasons in Uppsala, Sweden (59° 45’ N, 17° 42’ E), a region that is characterized by a boreal-temperate climate. The months May, June and July (i.e., from the emergency to the grain-filling of spring wheat) in 2018 were warmer and drier than the corresponding long-term means; whilst May, June and July in 2019 were cooler and wetter than in 2018 (Figure 1 in Paper III).

The field experiment had a split-plot design with four blocks, where each block contained soil compaction and non-compaction treatments. The soil compaction treatment was carried out by double track-by-track passing using a front loader in April 2018. In 2019, the same experimental site was used, the soil was re-compacted using the same method, and the positions of the genotypes were re-randomized. The effects of soil compaction on soil bulk density were similar in the two years (Figure 2 in paper I). The nine spring wheat genotypes presented above were grown in individual plots (2 m x 12 m) under each treatment. Wheat seeds were sown on 10th May 2018 and 23rd April 2019. Seed rates were 550 seeds m^{-2} as is common in the region. At sowing, 140 kg ha^{-1} of N, 24 kg ha^{-1} of P and 46 kg ha^{-1} of K were applied.

3.2.2 Measurement of soil moisture and penetration resistance

Soil volumetric water content was continuously recorded using time-domain reflectometry sensors (5TM, Decagon Devices, Pullman, USA) at 0.1 and 0.3 soil depths from crop emergence until maturity. Soil cylinders were sampled at the same depths at crop flowering, and oven-dried at 105 °C for 72 h to determine soil bulk density. Temporal dynamics of soil penetration resistance were quantified with soil volumetric water content and soil bulk density as described in Paper I.

3.2.3 Quantification of root and shoot traits

I used the BBCH-scale (Lancashire et al., 1991) for defining developmental stages of wheat plants. Root crowns were sampled at the beginning of stem elongation (BBCH 30) to quantify various architectural and anatomical traits. Four representative plants were selected from 0.5 m x 0.5 m areas at both ends of each plot. All the four representative root crowns were included for architectural measurements and two representative root crowns were selected for anatomical analyses. The numbers of seminal roots were counted, and the angles between the outermost seminal roots and the soil surface were measured along an arc with a 50 mm radius (Colombi and Walter, 2016). To assess the anatomical traits, 3 cm-long seminal root samples were taken 3 cm from the root bases. Root cross-sections of around 150 µm thickness were manually cut from each individual root sample. The cross-sectional areas of the root, the aerenchyma, the metaxylem vessels, as well as the radial diameter of cortical cell were assessed as described in Paper IV.

To assess the aboveground plant biomass at different developmental phases, shoots within 0.5 m x 0.5 m areas in each plot were sampled at the beginning of stem elongation (BBCH 30), flowering (BBCH 65) and maturity (BBCH

89). The shoots were harvested with scissors at approximately 15 mm above the soil surface, oven-dried at 65 °C for 72 h and weighted. The relative growth rate (RGR; d^{-1}) of shoot biomass from sowing to the beginning of stem elongation, and from the beginning of stem elongation to flowering were calculated according to the following equation:

$$RGR = \frac{\ln w2 - \ln w1}{t2 - t1} \qquad \text{(Eq. 1)}$$

where w1 and w2 are the shoot biomass values at times (t) 1 and 2, respectively. To assess grain yield, the central plot area (2 m x 6 m) was harvested with a combine harvester on 17th August 2018 (i.e., 99 days after sowing) and 23rd August 2019 (i.e., 122 days after sowing), respectively.

3.3 Greenhouse experiment (Paper II)

The experiment was carried out in an automated GrowScreen-Rhizo 1 phenotyping platform (Nagel et al., 2012) in November 2017. The experimental layout was a randomized complete block design with eight blocks and the same nine wheat genotypes as were used in the field experiment. The rhizoboxes were filled with sieved peat substrate characterized by low nutrient concentration. All plants were irrigated twice per day with 100 mL of deionized water and supplied three times per week with 200 mL of 100 % modified Hoagland solution (Hoagland and Arnon, 1950). Day light was set to 16 h to represent typical photoperiods for the time of spring wheat sowing in high-latitude regions.

Visible root system depths were quantified non-destructively using the automated GrowScreen-Rhizo 1 phenotyping system (Figure 2) and the image-based software tool GROWSCREEN-Root (Nagel et al., 2012). When the deepest root had reached the bottom of the rhizobox (i.e., at the beginning of tillering), all plants were separately harvested and divided into above and below ground parts. The total leaf area was determined using a leaf area meter (LI-3100C, Licor, Lincoln, USA). The roots were carefully washed and the numbers of seminal roots were counted for each plant. The length of main roots and lateral roots was measured with a scanner as described in Paper II. Seminal root samples (3 cm long) were taken 3 cm from the root bases of every individual plant for anatomical measurements. The cross-sectional areas of the root, the aerenchyma, the metaxylem vessels, as well as the radial diameters of cortical cells were measured as described in Paper II. The roots and shoots were oven dried at 65 °C for 48 h to determine the root and shoot dry weights. The RGR of the entire plant biomass from sowing to harvest was calculated according to Eq. 1. Differences in RGR among genotypes were related to differences in leaf area ratio (LAR, leaf area per unit of whole plant biomass), leaf area productivity (LAP, whole plant biomass production per unit of leaf area and time), plant N concentration (PNC), and plant N productivity (PNP, whole plant biomass production per unit of plant N amount and time) based on the following functional relationships (Lambers et al., 1990; Hunt, 1982):

$$\mathrm{RGR} = \mathrm{LAR} \times \mathrm{LAP} \qquad \text{(Eq. 2)}$$

$$\mathrm{RGR} = \mathrm{PNC} \times \mathrm{PNP} \qquad \text{(Eq. 3)}$$

3.4 Nutrient assessments

Dried plant samples were ground in a stainless steel grinder to pass a 1-mm mesh before nutrient element analysis. The N concentration was analyzed on a LECO CNS/2000 analyzer using a standard method (SS-ISO13878). The contents of P, potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S) were extracted using 32.5 % nitric acid on a heat block and concentrations were determined using ICP-AES technique (Spectro Blue FMS 26, Spectro Analytical Instruments, Kleve, Germany) by applying internal standardization protocols (SS028311).

Two stoichiometric niche volumes were calculated: V_{NP} as the product of the plant N and P concentrations, and V_{oth} as the product of the concentrations of the other macro-nutrients (i.e., Ca, K, Mg and S). The scaling relation between V_{NP} and V_{oth} was analyzed with reduced major axes regression, and the scaling exponent (α) was calculated according to the following equation (Ågren and Weih, 2020; Niklas, 2006):

$$V_{oth} = \beta\, V_{NP}^{\alpha} \qquad \text{(Eq. 4)}$$

The overall N accumulation efficiency (NAE; g N per g N, eq. 7) and its components N uptake efficiency (U; g N per g N, eq. 5), grain-specific N efficiency (E; g N per g N, eq. 6) and grain N concentration (C; g N per g grain biomass) were calculated according to the following equations (Weih et al., 2018):

U = mean N amount during the entire growth period ⁄ N amount in initial seed (Eq. 5)
E = grain yield ⁄ mean N amount during the entire growth period (Eq. 6)
NAE = U × E × C (Eq. 7)

where the mean N amount during the entire growth period was calculated with the shoot N amounts at the beginning of stem elongation, flowering and maturity.

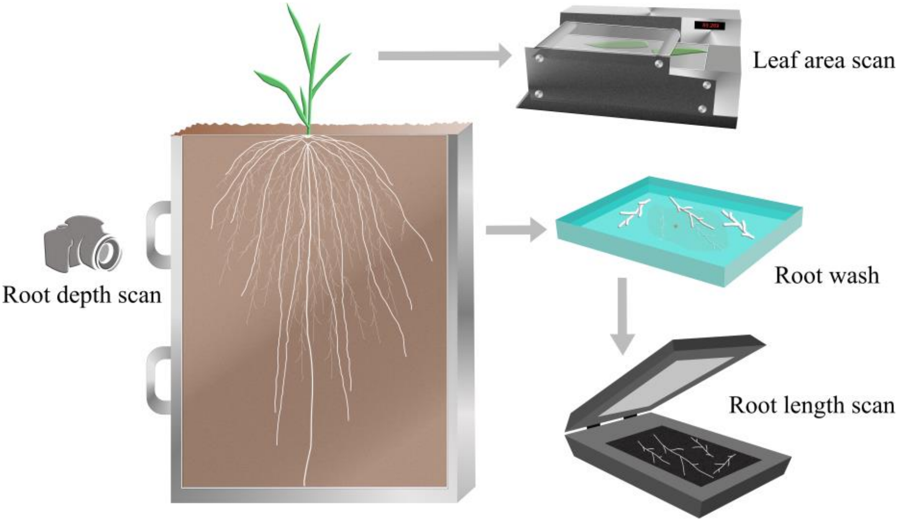

Figure 2. A wheat plant grown in the rhizobox, and the measurements of root system depth, root length and leaf area in the greenhouse experiment of this thesis (illustration: H. Liu).

4. Results

4.1 Temporal dynamics of soil physical conditions

The contrasting weather conditions in the two years affected the soil water contents at 0.1 m depth differently under the compacted and non-compacted treatments. Compared to the non-compacted treatment, the compacted treatment had higher soil water content at 0.1 m depth in the dry year 2018, whilst it resulted in lower soil water content at 0.1 m depth in the relatively wet year 2019 (Figure 3). Although the compacted treatment significantly increased soil bulk density (Figure 2 in Paper I), it did not always result in higher soil penetration resistance due to the interplay between soil water content and penetration resistance. Soil penetration resistance at 0.1 m depth under the compacted treatment was lower than the non-compacted treatment in 2018, whilst the pattern was reversed in 2019 (Figure 3).

In 2018, soil water content was high in the beginning of the cropping season due to a wet winter season. However, soil water contents were rapidly decreasing and consequently, penetration resistances were increasing from crop emergence to the end of the season (Figure 3), indicating that the plants were exposed to progressively deteriorating soil physical conditions throughout the cropping season in 2018. In 2019, soil water content and penetration resistance at 0.1 m depth were fluctuating throughout the cropping season. In spite of the fluctuations, the mean water content was higher and the mean penetration resistance was lower from crop emergence to stem elongation compared to those from stem elongation to maturity (Table 1 in Paper I), indicating that the soil physical conditions were better at the early plant growth phase than at the major plant growth phase and post-anthesis in 2019.

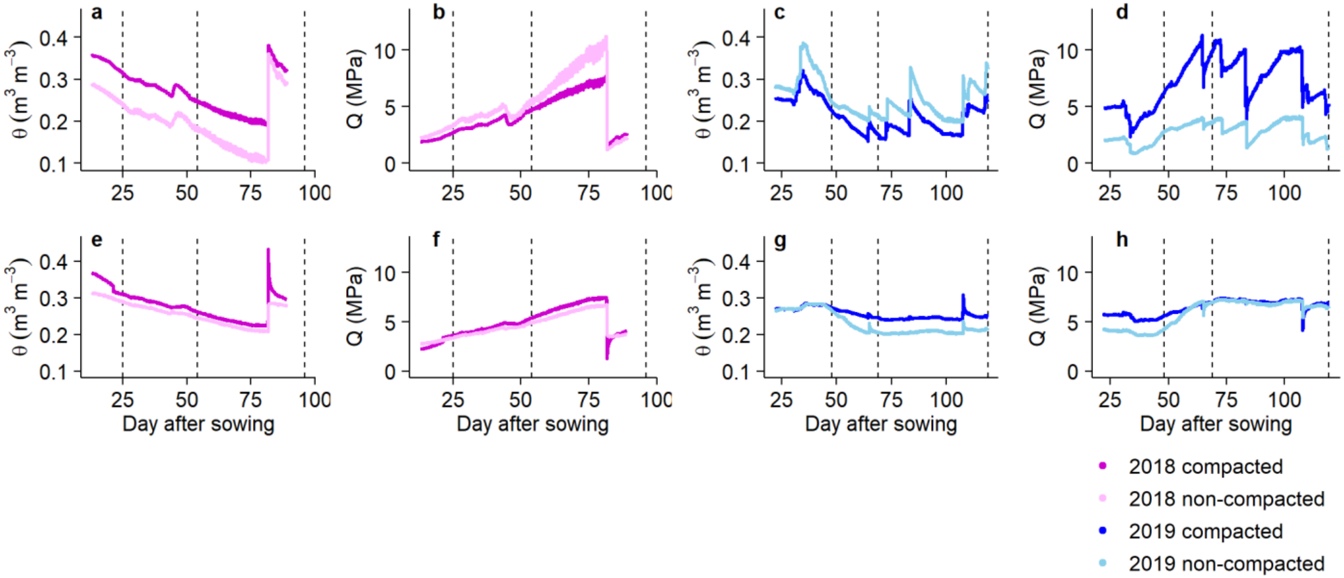

Figure 3. Dynamics of soil volumetric water content (Θ) and penetration resistance (Q) at 0.1 m (a – d) and 0.3 m (e – h) depth under two soil compaction treatments of the field trial carried out in the years 2018 and 2019. Dash lines indicate the beginning of spring wheat stem elongation, flowering and maturity. Figures are from Paper I (Liu et al., 2021a manuscript)

4.2 Effects of genotype and environment on early vigor, nutrient use efficiency and grain yield

Significant differences among genotypes (Figure 4) were found for most of the early vigor-related traits assessed in the greenhouse and in the field, including leaf area (Paper I), shoot biomass and the RGR of shoot biomass (Papers I & II), root length and biomass (Paper II), root system depth (Paper II), root angle and number (as indicators of root system depth; Papers II & IV). In the field, N uptake efficiency, grain-specific N efficiency, grain N concentration, and the accumulations of all the six macro-nutrients were significantly different among the genotypes (Papers III & IV). Grain number and yield also varied significantly among the genotypes (Paper III).

Figure 4. The nine spring wheat genotypes used in this thesis, and examples of the genotype differences in (a) root architectural traits in the greenhouse experiment, and (b) ear morphology in the field trial (photos: H. Liu).

Most of the plant traits assessed in the field significantly varied between years (Figure 5). Root angles were steeper and root numbers were fewer in the dry year 2018 than the relatively wet year 2019 (Table 1). Root metaxylem vessels were wider and fewer in 2018 than 2019 (Table 1). Nitrogen uptake efficiency, grain N concentration and grain yield were lower, whilst Mg-to-P ratio and grain-specific N efficiency were higher in 2018 than 2019 (Table 1). Nitrogen uptake efficiency, grain-specific N efficiency, grain N concentration and grain yield were also significantly affected by the interaction between year and genotype.

Figure 5. Impressions of year-to-year differences in root anatomical traits and shoot biomass of the spring wheat genotype ‘Bjarne’ grown under the non-compacted treatment of the field trial carried out in the dry year 2018 and the relatively wet year 2019 (photos: H. Liu).

Effects of soil compaction treatment on shoot traits were different between the two years. Compared to the non-compacted treatment, soil compaction increased the RGR of shoot biomass from sowing to stem elongation, and from stem elongation to flowering in the drier year 2018, but decreased the same traits in the wetter year 2019 (Table 1). Soil compaction tended to increase N uptake efficiency and grain yield in 2018, but had no significant effect on the same traits in 2019 (Table 1).

Table 1. Effects of year, soil compaction treatment, genotype and their interactions on various plant traits of nine spring wheat genotypes grown in a field trial in Central Sweden for two years; and the average values of the nine wheat genotypes for each treatment (compacted and non-compacted) and year (2018 and 2019). ***, ** and * denote significant effects at $p < 0.001$, $p < 0.01$ and $p < 0.05$, respectively, n.s. denotes non-significant effects ($n = 4$). This table is adapted from Paper I & IV (Liu et al., 2021a manuscript; Liu et al., 2021b manuscript).

	ANOVA							Treatment mean			
Trait (unit)	Genotype (G)	Year (Y)	Treatment (T)	Y × T	G × Y	G × T	G × Y × T	2018 compacted	2018 non-compacted	2019 compacted	2019 non-compacted
Seminal root angle (°)	***	***	n.s.	n.s.	n.s.	n.s.	n.s.	31.92	34.53	23.72	26.35
Seminal root number (-)	***	**	n.s.	n.s.	n.s.	n.s.	n.s.	4.89	4.63	5.52	5.13
Cortical cell diameter (μm)	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	31.45	26.78	28.04	24.48
Cortical cell number (-)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	3.58	3.43	3.47	3.42
Aerenchyma area (1000 μm^2)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	2.86	1.02	1.39	1.80
Metaxylem diameter (μm)	***	*	n.s.	n.s.	n.s.	n.s.	n.s.	46.73	44.15	42.22	40.87
Metaxylem number (-)	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	1.26	1.35	1.50	1.75
Relative growth rate of shoot biomass from sowing to stem elongation (d^{-1})	***	***	n.s.	***	**	n.s.	n.s.	0.015	0.011	0.035	0.038
Relative growth rate of shoot biomass from stem elongation to flowering (d^{-1})	***	***	n.s.	***	n.s.	n.s.	n.s.	0.078	0.073	0.052	0.056
Nitrogen uptake efficiency (g g^{-1})	***	***	n.s.	***	***	n.s.	n.s.	10.89	6.77	11.88	12.30
Grain-specific nitrogen efficiency (g g^{-1})	***	**	n.s.	n.s.	**	n.s.	n.s.	56.34	57.10	47.17	46.24
Grain nitrogen concentration (g g^{-1})	***	***	n.s.	n.s.	***	n.s.	n.s.	0.025	0.025	0.031	0.031
Magnesium-to-phosphorus ratio	***	**	n.s.	n.s.	n.s.	n.s.	n.s.	0.95	1.04	0.68	0.71
Grain yield (Mg ha^{-1})	***	*	n.s.	***	***	n.s.	n.s.	2.17	1.91	2.52	2.57

4.3 Relative growth rate of plant biomass and its determinants

Regarding light use, leaf area productivity instead of leaf area ratio determined the variation in RGR (Figure 6). In terms of plant N use, increased RGR was more related to higher plant N productivity than N concentration (Figure 6). Total leaf area was positively correlated with both RGR (Pearson r = 0.71, p = 0.031) and leaf area productivity (Pearson r = 0.93, p < 0.001).

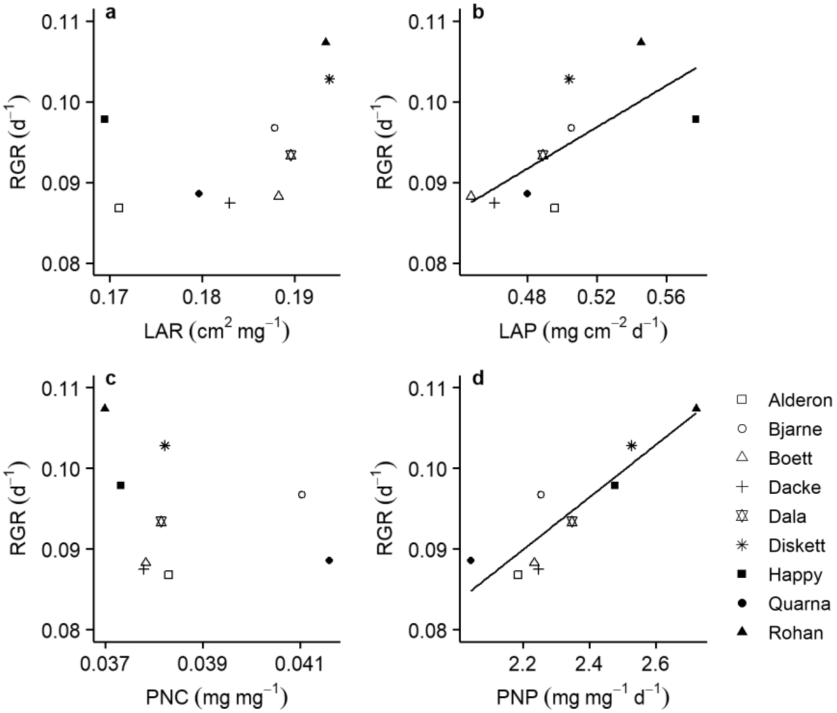

Figure 6. Relationships between relative growth rate (RGR) of whole plant biomass, leaf area ratio (LAR), leaf area productivity (LAP), plant N concentration (PNC) and plant N productivity (PNP) of nine spring wheat genotypes grown for three weeks in a greenhouse. Individual dots are the average values of eight replicates for each genotype at the end of the experiment. Statistics: (b) $r^2 = 0.416$, $p = 0.036$; (d) $r^2 = 0.797$, $p < 0.001$. Figures are from Paper II (Liu et al., 2021).

4.4 Critical nutrient elements limiting plant growth and grain yield

Nitrogen accumulation was strongly associated with total plant biomass in the greenhouse and grain yield in the field (Figure 7), suggesting that N limits plant growth and yield. The Mg-to-P ratio in the growing plant affected total plant biomass in the greenhouse, and grain yield and grain-specific N efficiency in the field (Figure 8). In addition, the Mg-to-P ratio was highly correlated with the scaling exponent. Depending on the nutrient of interest, different root system traits were identified as relevant for their accumulations (Paper II). Lateral root length was positively correlated with N accumulation; whilst main root length was positively correlated with the accumulations of P and Mg in the greenhouse (Figure 9).

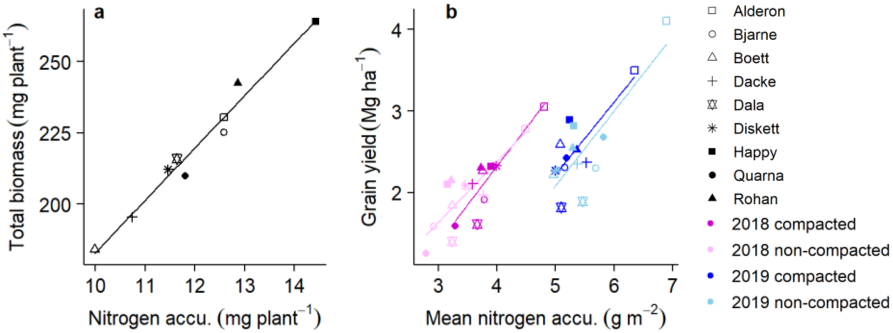

Figure 7. Total plant biomass and grain yield as functions of nitrogen accumulation for nine spring wheat genotypes grown in (a) the greenhouse and (b) the field experiment in Central Sweden under two soil compaction treatments during two years. Individual dots in (a) are the average values of eight replicates for each genotype grown after three weeks in the greenhouse. Mean nitrogen accumulation in (b) is calculated with the shoot N accumulation at the beginning of stem elongation, flowering and maturity in the field. Individual dots in (b) are the average values of four replicates for each genotype grown under each soil compaction treatment in each year. Statistics: (a) $r^2 = 0.97$, $p < 0.001$; (b) 2018 compacted: $r^2 = 0.79$, $p = 0.001$; 2018 non-compacted: $r^2 = 0.68$, $p = 0.006$; 2019 compacted: $r^2 = 0.62$, $p = 0.011$; 2019 non-compacted: $r^2 = 0.70$, $p = 0.015$.

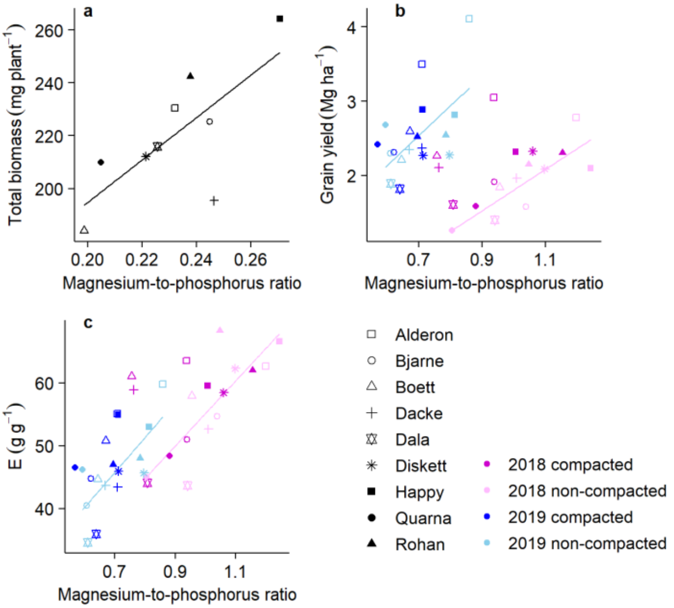

Figure 8. Total plant biomass, grain yield and grain-specific nitrogen efficiency (E) as functions of magnesium-to-phosphorus nutrient ratio for nine spring wheat genotypes grown in (a) the greenhouse and (b, c) the field experiment in Central Sweden under two soil compaction treatments during two years. Individual dots in (a) are the average values of eight replicates for each genotype grown after three weeks in the greenhouse. Individual dots in (b) and (c) are the average values of four replicates for each genotype grown in the field under each soil compaction treatment in each year. Statistics: (a) $r^2 = 0.54$, $p = 0.024$; (b) 2018 non-compacted: $r^2 = 0.60$, $p < 0.001$; 2019 non-compacted: $r^2 = 0.42$, $p = 0.048$; (c) 2018 non-compacted: $r^2 = 0.62$, $p = 0.012$; 2019 non-compacted: $r^2 = 0.65$, $p = 0.009$.

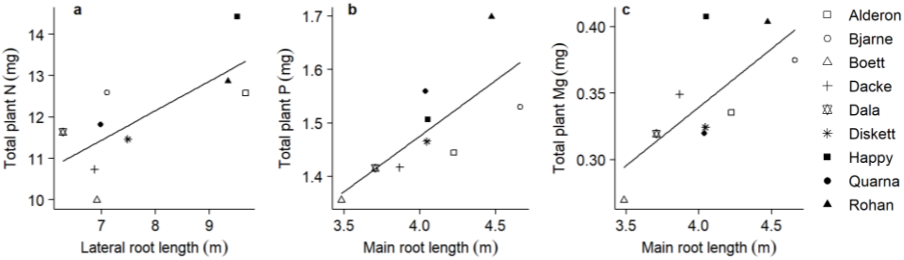

Figure 9. Relationships between root length and nutrient accumulations in whole plants of nine spring wheat genotypes grown for three weeks in a greenhouse. Individual dots are the average values of eight replicates for each genotype at the end of the experiment. Statistics: (a) $r^2 = 0.532$, $p = 0.026$; (b) $r^2 = 0.558$, $p = 0.021$; (c) $r^2 = 0.516$, $p = 0.029$. Figures are from Paper II (Liu et al., 2021).

4.5 Correlations between early vigor, nitrogen use efficiency and grain yield

Nitrogen uptake efficiency and grain N concentration increased with shallower root angle, higher root number and smaller root diameter; whilst grain-specific N efficiency showed the opposite pattern (Figure 1 in Paper IV). Nitrogen uptake efficiency and grain N concentration increased with higher metaxylem number and smaller metaxylem diameter; whilst grain-specific N efficiency showed the opposite pattern (Figure 2 in Paper IV). However, N uptake efficiency was not correlated with any of the above root traits assessed in the greenhouse. There were negative and significant relationships between root number and diameter, root number and root angle, metaxylem number and diameter, as well as N uptake efficiency and grain-specific N efficiency (Figure 10).

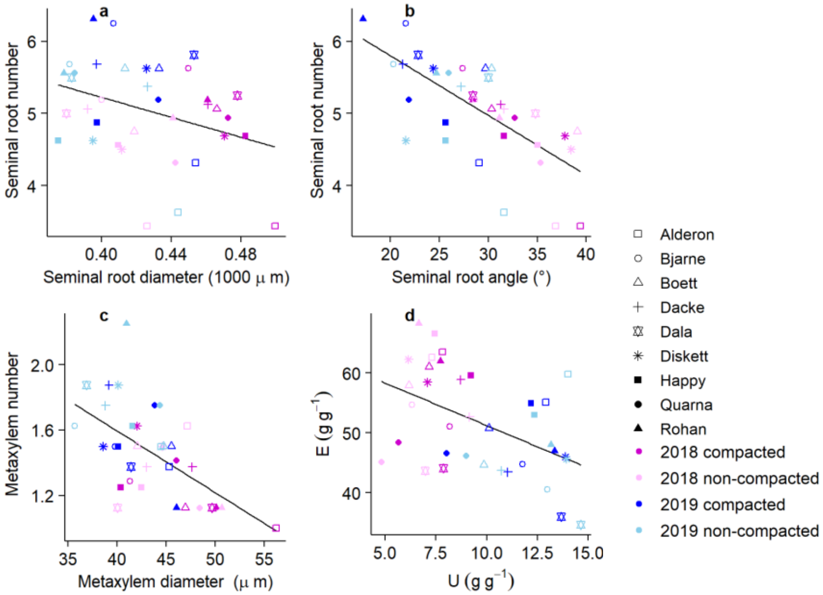

Figure 10. Relationships between root traits at the beginning of stem elongation, nitrogen uptake efficiency (U) and grain-specific nitrogen efficiency (E) of nine spring wheat genotypes field-grown in Central Sweden under two soil compaction treatments during the years 2018 and 2019. Individual dots are the mean values of four blocks for each genotype under each soil compaction treatment in each year. Statistics: (a) $r^2 = 0.12$, $p = 0.037$; (b) $r^2 = 0.48$, $p < 0.001$; (c) $r^2 = 0.35$, $p < 0.001$; (d) $r^2 = 0.23$, $p = 0.003$. Figures are from Paper IV (Liu et al., 2021b manuscript).

Higher seminal root number and faster RGR of shoot biomass from sowing to the beginning of stem elongation (i.e., higher early vigor) resulted in lower grain yield (Figure 11). Based on the data from the field and greenhouse, root aerenchyma, cortical cell diameter and cell file number were not correlated with plant biomass, grain yield or N use efficiency traits.

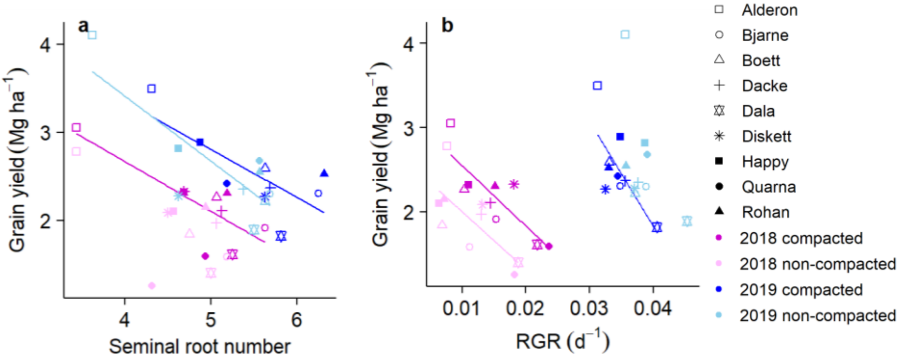

Figure 11. Relationships between root number at the beginning of stem elongation, relative growth rate (RGR) of shoot biomass from sowing to the beginning of stem elongation and grain yield of nine spring wheat genotypes field-grown in Central Sweden under two soil compaction treatments during the years 2018 and 2019. Individual dots are the average values of four blocks for each genotype under each soil compaction treatment in each year. Statistics: (a) 2018 compacted: $r^2 = 0.62$, $p = 0.012$; 2019 compacted: $r^2 = 0.56$, $p = 0.020$; 2019 non-compacted: $r^2 = 0.66$, $p = 0.008$; (b) 2018 compacted: $r^2 = 0.70$, $p = 0.005$; 2018 non-compacted: $r^2 = 0.52$, $p = 0.029$; 2019 compacted: $r^2 = 0.51$, $p = 0.030$. Figure (b) is from Paper I (Liu et al., 2021a manuscript).

5. Discussion

5.1 Weather conditions affect the interactions between compacted soil and plant growth

In the drier year 2018, the non-compacted treatment decreased shoot growth and grain yield when compared to the compacted treatment (Table 1), which has rarely been reported by others. In the relatively wet year 2019, the compacted treatment decreased shoot growth compared to the non-compacted treatment (Table 1), which is consistent with previous studies (Andersen et al., 2013; Colombi and Walter, 2017; Whalley et al., 2008). In my field experiment, the air-filled porosity was higher than 10 % during most time of the cropping season (Supplementary Figure S4 in Paper I), indicating a sufficient oxygen status for plant growth (Lipiec and Hatano, 2003). Soil penetration resistance is the main soil property that determines plant accessibility to water and nutrients, because high soil penetration resistance can result in reduced root elongation rate and delayed initiation of lateral roots (Bengough et al., 2011; Colombi et al., 2018). Therefore, the reduced shoot growth under the compacted treatment in 2018 and the non-compacted treatment in 2019 (Paper I) could have been caused partly by the reduced water and nutrient accessibility due to high soil penetration resistance; and partly by decreased water availability, which was indicated by a decreased soil water content (Figure 3). In my study (Paper I), soil compaction had contrasting effects on shoot growth and grain yield in the two years due to the reverse patterns of soil water content, as well as penetration resistance, under the two soil compaction treatments observed in the two years. Thus, the interactive effects of soil compaction and weather conditions on soil physical conditions should be considered when evaluating the impacts of soil compaction on plant growth and grain yield.

5.2 Leaf area productivity and nitrogen productivity drive the variation in relative growth rate of plant biomass

The relative importance of leaf area productivity (LAP) and leaf area ratio (LAR) in determining the relative growth rate (RGR) of plant biomass has been considered to depend on light conditions, with the importance of LAP increasing with irradiance (Shipley, 2006). As proposed in my second hypothesis (H2), LAP was identified to be a better predictor of variation in RGR compared to LAR under the 16 h photoperiods used in the greenhouse study of this thesis (Paper II). In contrast, in a study on 24 herbaceous species grown under slightly higher irradiance but shorter days (day length of 14 h and average quantum flux density of 315 µmol m^{-2} s^{-1}) than the plants in Paper II experienced (day length of 16 h and average quantum flux density of 144 µmol m^{-2} s^{-1}), RGR was associated with LAR but not LAP (Poorter and Remkes, 1990). It has been previously shown that a low irradiance treatment given over a longer period can be more efficient in supporting plant growth than a high irradiance short-day treatment (Adams and Langton, 2005); and that biomass production of a high-latitude grass species increased linearly with photoperiod between 10 and 16 h (Heide, 1982). The results of Paper II therefore indicate that the importance of LAP for variation in RGR previously observed under high-light conditions, is also relevant in spring wheat grown under the relatively long photoperiod in high-latitude regions. The photoperiod, instead of irradiance, could thus be an equally important factor for switching the relative importance of LAP and LAR in determining RGR. Because I found a strong and significant relationship between total leaf area and LAP, these results also indicate that greater partitioning to leaf area growth (rather than leaf thickening) resulted in enhanced light interception leading to greater LAP in these juvenile plants (Paper II).

Because leaves are the most important sinks for plant N, the enhanced light interception with greater leaf area observed here is probably also the reason for the significant relationship found between RGR and plant N productivity. Thus, RGR was driven more by the allocation of N to leaf area, which determines the productivity per unit N, than the mass-based concentration of N in the plant (Lambers, 1990). Nitrogen was however possibly not the only growth-limiting nutrient element in my study, because a strong correlation between Mg-to-P ratio and plant biomass was observed (Figure 8).

5.3 Magnesium-to-phosphorus ratio affect nitrogen use efficiency and grain yield

Higher grain yield has often been reported to result mainly from enhanced number of kernels (Maeoka et al., 2020), which in turn is determined already at the induction of flowering. In my study, the scaling exponent and particularly the Mg-to-P ratio were good predictors of the kernel numbers (Figure 4 in Paper III), which provides a mechanistic explanation linking the vegetative tissue nutrient concentrations to grain yield. Both Mg and P are heavily involved in various photosynthetic processes, and low Mg concentration has been reported to reduce grain-specific N efficiency (also called N conversion efficiency; Hauer-Jakli and Traenkner, 2019; Cakmak and Yazici, 2010). The observation of increasing grain-specific N efficiency with Mg-to-P ratio (Figure 8) could therefore indicate a synergistic mechanism of Mg and P in supporting photosynthetic N use and ultimately grain yield, which supports the fourth hypothesis (H4) of this thesis. Nevertheless, soil Mg and P availabilities are expected to influence the results. When nutrient availabilities differ from the ones in my study, co-limitation of growth by nutrients other than Mg and P might occur. The calculation of scaling exponents followed by an evaluation of specific element ratios can be a useful tool to identify the critical nutrient elements limiting plant growth and yield.

5.4 Influence of root architectural and anatomical traits on nitrogen use efficiency

It has been documented that steep main root angle and few main roots, which can be used as indicators for deep root systems, are beneficial for accessing N in deep soil layers and associated with high N accumulation particularly under N-limiting conditions (Gao and Lynch, 2016; Lynch, 2019; Schneider et al., 2021). In contrast to the third hypothesis (H3) of this thesis and the above studies, shallower root angle and more numerous roots (i.e., shallower root systems) resulted in greater N uptake efficiency in the field (Paper IV); and root system depth, root angle and root number were not associated with

N accumulation in the greenhouse (Paper II). The discrepancy in results could be due to the N fertilization having been applied. In the field (Paper IV), N fertilization was applied at sowing and concentrated at topsoil early in the cropping season, which could have facilitated large N uptake by a great number of shallow-angled roots early in the growing season. In the greenhouse experiment (Paper II), N fertilization was applied frequently and sufficiently, root architectural traits therefore had no significant influence on N acquisition. I suggest that the potential for breeding of root architectural traits (i.e., root system depth, root angle and number) to improve N uptake efficiency should be further investigated, together with the application of fertilizer and the spatial distribution of N in soil.

It is known that the capacity for axial transport of water and nutrients through a root system is largely determined by the size and number of xylem vessels; and decreased, constant or increased size and number of xylem vessels in response to drought have been observed in wheat, barley, rice and maize (Kadam et al., 2015; Klein et al., 2020; Oyiga et al., 2020). In the field experiment of this thesis, the decreasing soil moisture (Figure 3) indicates that the availabilities of water and N to plants were decreasing from the beginning towards the ends of each cropping season. Under such conditions, thinner and more metaxylem vessels are expected to be formed, which likely improved the N uptake efficiency of the plants in this study (Figure 2 in Paper IV) by restricting net N uptake early in the cropping season and thereby increasing N uptake during later growth. Similarly, thinner and more metaxylem vessels have been reported previously to improve water use efficiency under terminal drought (Feng et al., 2016; Zaman-Allah et al., 2011). Therefore, the potential of reduced diameter along with enhanced quantity of metaxylem vessels to improve N uptake efficiency in wheat breeding should be investigated in the context of the temporal dynamics of soil N availability.

Root cortical aerenchyma formation has often been found to be increased by edaphic stress, including hypoxia, drought and suboptimal availability of N (Jackson et al., 1985; Klein et al., 2020; Saengwilai et al., 2014a). However, aerenchyma formation was not responsive to soil compaction or drought in my study (Paper IV), probably because the effects of soil compaction and drought on soil properties were still relatively mild at the beginning of the cropping season. More intense aerenchyma formation, larger cortical cell sizes and fewer cortical cell file numbers have been regarded as promising breeding targets in maize, because they could reduce the metabolic costs of soil exploration by decreasing root respiration, and improve water and N capture under drought and N stress (Lynch et al., 2021). In contrast to Lynch et al. (2021), root aerenchyma, cortical cell sizes and cell file numbers were not associated with any of the N use efficiency traits or grain yield in my study (Paper II & IV) using spring wheat, which does not support my third hypothesis (H3). The potential of these root traits to be used as candidate traits in wheat breeding therefore is questionable and needs to be further investigated.

5.5 Are trade-offs between root traits linked to trade-offs between nitrogen use efficiency traits?

A trade-off is defined as a negative association between two or more traits, which is due to resource limitation of growth processes and cost-benefit considerations (Stearns, 1989). For example, and similar to the observations in my study, trade-offs occur between thick and numerous roots, and between wide and numerous xylem vessels (Bowsher et al., 2016; Kadam et al., 2015; Klein et al., 2020; Wen et al., 2019). Interestingly, also a negative relationship (possibly indicating a trade-off) between N uptake efficiency and grain-specific N efficiency (also called N conversion efficiency) has often been found (Lambers and Oliveira, 2008; Maire et al., 2009; Weih et al., 2018), whilst the mechanistic basis behind it is unclear. With increasing N uptake by roots, leaf N concentration increases but the photosynthetic rate per unit N decreases (Lambers and Oliveira, 2008). Moreover, with increasing N availability, plant growth and productivity are often increasingly co-limited by nutrient elements other than N (Weih et al., 2021). In my study, the inverse relationship between N uptake efficiency and grain-specific N efficiency closely reflected the negative relationships between some of the root system traits investigated (Figure 10). It is therefore possible that the negative association between N uptake efficiency and grain-specific N efficiency is partly caused by the trade-offs between root traits (i.e., root number and diameter, metaxylem number and diameter) already at an early growth stage. If the negative association between N uptake efficiency and grain-specific N efficiency is mechanistically linked to the physiological trade-offs between the above root traits, it is unlikely to be overcome by breeding, because physiological trade-offs cannot be eliminated by modern plant breeding technology (Weih, 2003).

5.6 High early vigor does not always predispose high yield

It has been frequently reported that higher early vigor was associated with higher grain yield of wheat (Botwright et al., 2002; Regan et al., 1992; Turner and Nicolas, 1998; Whan et al., 1991), because early vigor improved water use efficiency by shading the soil surface to reduce water loss from evaporation (López-Castañeda and Richards, 1994) and by increasing the ability of the crop to compete with weeds (Coleman et al., 2001; Dingkuhn et al., 1999; Mwendwa et al., 2020). In contrast to these studies, I observed that higher early vigor reduced grain yield (Figure 11). The maintenance of early vigorous root systems may demand additional carbon investment in roots (Atwell, 1990; Xiong et al., 2006). In addition, higher early vigor is associated with larger leaf area (Paper II), which could increase plant water loss by transpiration. Compared to the genotypes with lower early vigor, the genotypes with higher early vigor (e.g., 'Dala', 'Quarna' and 'Bjarne') presumably lost more plant water through transpiration due to the high air temperatures (Figure 1 in Paper I), especially during the later growth phases. Furthermore, the decreasing soil water content and increasing soil penetration resistance (Figure 3) indicate that the availability and accessibility of soil water was limited to replenish the plant water loss during the later growth phases. In my study, the genotypes with higher early vigor therefore could have suffered relatively more from the progressively deteriorating soil physical conditions than the ones with lower early vigor. Early vigor has been regarded as a promising trait in wheat breeding towards improved water and nutrient use efficiencies and grain yield (Botwright et al., 2002; Liao et al., 2006; Pang et al., 2014; Richards et al., 2002). However, the results from my thesis suggest that the potential of high early vigor to increase grain yield needs to be further investigated, especially along with the temporal dynamics of soil physical conditions, before being generally applied in wheat breeding.

6. Conclusions

Based on the experiments presented in this thesis, the following conclusions can be drawn:

- Soil compaction had contrasting effects on shoot growth and grain yield under contrasting weather conditions in this study, suggesting that the impacts of soil compaction on plant growth and yield should be evaluated in the context of the interactive effects of soil physical and weather conditions.
- Under the long-photoperiod conditions typical in high-latitude regions, and in contrast to the findings from other regions highlighting leaf area ratio as main driver of growth, wheat growth at an early stage is driven by leaf area productivity and nitrogen productivity.
- The assessment of nutrient scaling exponents and specific element ratios can be a useful tool to identify critical nutrient elements limiting wheat growth and yield. Magnesium-phosphorus synergism and co-limitation of growth and grain yield in spring wheat were observed in this study.
- Seminal root angle and number, metaxylem size and number deserve attention in breeding research. Their potential to improve nitrogen uptake efficiency should be further investigated in the context of the spatial and temporal dynamics of soil nitrogen availability.
- A potential trade-off between nitrogen uptake efficiency and grain-specific nitrogen efficiency (i.e., grain yield per nitrogen accumulation) could be partly triggered by some trade-offs seen between root system traits already at an early growth stage.
- Higher early vigor reduced grain yield under progressively drying and hardening soil conditions during entire cropping seasons. The results from this thesis therefore emphasize that the potential of early vigor to increase grain yield is strongly influenced by the temporal dynamics of the soil physical conditions.

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Popular science summary

Spring wheat is frequently cultivated in Sweden to produce flour for bread-making. To increase the grain yield and quality (e.g., protein content), with maintained or decreased fertilizer supply, we need to improve the nutrient use efficiency of spring wheat.

Soil compaction due to the use of heavy farm machinery is expected to reduce nutrient uptake, nutrient use efficiency, and grain yield. However, the influence of weather conditions on the interaction between compacted soil and crop growth with respect to grain yield is unclear. One of the aims of this thesis was to investigate the combined effects of soil compaction and contrasting weather conditions on spring wheat growth and grain yield. Modern crop production systems are typically characterized by high nitrogen fertilizer application, and commercial mineral fertilizers often contain substantial amounts of nitrogen but low amounts of other nutrients. Theoretical considerations suggest that the plant uptake of all essential nutrient elements for crop growth should scale in proportion to each other. It is therefore possible that a high nitrogen application results in co-limitation of crop growth and grain yield by other nutrients. Another aim of this thesis was therefore to identify critical nutrient elements co-limiting grain yield. The improvement of nutrient use efficiency can be achieved by means of breeding research targeting the specific phenotypic traits that are linked with nutrient use efficiency. Cultivars combining some of the desired traits can be used as genetic resources for breeding programs towards the development of more nutrient-efficient cultivars. This thesis therefore aimed to identify some phenotypic traits that are associated with nutrient use efficiency, in order to provide the relevant information on suitable breeding targets to spring wheat breeders.

Nine spring wheat cultivars were field-grown on compacted and non-compacted soils during two cropping seasons with contrasting weather conditions in central Sweden. Soil compaction increased crop growth in the drier year but decreased it in the wetter year, suggesting that soil compaction caused by heavy farm machinery can occasionally favor crop production at least in the short term of a single growing season. Crop growth and grain yield were co-limited by the magnesium-to-phosphorus ratio in the growing crop, in addition to the limitation by nitrogen. The critical concentrations of single nutrient elements, which are often applied in agronomy to assess possible limiting factors for grain yield, therefore should be replaced by nutrient ratios. Root angle and number, root xylem size and number, and shoot biomass at early growth stage are interesting traits for further breeding research towards improved nutrient use efficiency and grain yield of spring wheat grown in Sweden.

Populärvetenskaplig sammanfattning

Vårvete odlas ofta i Sverige för att producera mjöl till brödtillverkning. För att öka kärnavkastning och kärnkvalitet (t.ex. proteininnehåll) vid bibehållen eller minskad användning av konstgödsel måste vi förbättra vårvetets näringseffektivitet.

Markkompaktering på grund av användning av tunga jordbruksmaskiner förväntas minska näringsupptag, näringseffektivitet och kärnavkastning. Emellertid är väderförhållandenas inflytande på samspelet mellan kompakterad jord och biomassatillväxt respektive kärnavkastning oklart. Ett av syftena med denna avhandling var att undersöka de kombinerade effekterna av markkompaktering och kontrasterande väderförhållanden på vårvetes tillväxt och kärnavkastning. Moderna växtodlingssystem kännetecknas vanligtvis av tillämpningen av stora mängder kvävegödselmedel, och kommersiellt mineralgödsel innehåller ofta betydande mängder kväve men bara få andra näringsämnen. Teoretiska överväganden tyder på att växtupptaget av alla viktiga näringsämnen för grödans tillväxt ska skala i proportion till varandra. Det är därför möjligt att en hög kvävetillförsel resulterar i sambegränsning av tillväxt och kärnavkastning av andra näringsämnen. Ett annat syfte med denna avhandling var därför att identifiera kritiska näringsämnen som begränsar kärnavkastning. Förbättringen av växtnäringseffektivitet kan uppnås med hjälp av växtförädlingsforskning som riktar sig mot de specifika fenotypiska egenskaperna som är kopplade till näringseffektivitet. Vetesorter som kombinerar några av de önskade egenskaperna kan användas som genetiska resurser för växtförädlingsprogram för utveckling av mer näringseffektiva sorter. Denna avhandling syftade därför till att identifiera några fenotypiska drag som är förknippade med näringseffektivitet, för att ge relevant information om lämpliga växtförädlingsmål till växtförädlare av vårvete.

Nio vårvetesorter odlades i fält på kompakterade och icke- kompakterade jordar under två odlingssäsonger med kontrasterande väderförhållanden i mellersta Sverige. Markkompaktering ökade grödans tillväxt under det torrare året men minskade den under det blötare året, vilket tyder på att markkompaktering orsakad av tunga jordbruksmaskiner ibland kan gynna växtodlingen åtminstone på kort sikt (dvs. en växtsäsong). Grödans tillväxt och kärnavkastning begränsades av magnesium-till-fosforkvoten i den växande grödan, förutom begränsningen av kväve. Kritiska koncentrationer av enskilda växtnäringsämnen, som ofta används i jordbruksforskningen för att bedöma möjliga begränsande faktorer för kärnavkastning, bör därför ersättas med näringskvoter. Rötters vinkel och antal, rotxylemets storlek och antal, och skottbiomassan i ett tidigt tillväxtstadium är intressanta drag för ytterligare forskning mot förbättrad näringseffektivitet och kärnavkastning av vårvete som odlas i Sverige.

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(Photo: Hui Liu)

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Nutrient-efficient and high-yielding spring wheat is needed to maintain and enhance future crop production. This thesis evaluated the effects of soil compaction under differential weather conditions on grain yield, identified critical nutrient elements limiting grain yield, and investigated early-season root and shoot traits influencing nutrient use efficiency and grain yield of spring wheat. Results of this thesis have implications on the management and pre-breeding of spring wheat.

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