Phosphorus Uptake in Six Selected Scandinavian Wheat and Barley Cultivars at Low Soil Phosphorus Availability as Related to Root Hair Length

Fosforopptak i seks utvalgte skandinaviske hvete- og byggsorter ved låg fosfortilgjengelighet i jorda i forhold til rothårslengde

MSc-thesis in Agroecology

by

Jon Magne Holten

Department of Soil and Water Sciences
Agricultural University of Norway
Ås

Spring 2002

Summary

Lower soil phosphorus (P) levels are to be expected if more sustainable agriculture practices (organic farming, low-input farming) are adopted. Crop plants can be adapted to lower soil P levels by selecting and breeding for higher P efficiency. Longer root hairs are found to enhance the P efficiency of cereals by increasing the P uptake.

In this study, three pairs of Swedish and Norwegian cereal cultivars (wheat cvs. NK0058 and Diamant; 6-row barley cvs. NK94682 and Herse; 2-row barley cvs. Tyra and Herta), with respectively short and long root hairs within each pair as measured in solution culture were grown. The cultivars were grown at four soil P levels (Po: 35 mg P-AL kg-' soil; P16:49 mg; P32: 87 mg; P48: 130 mg) in a long-term PK fertilisation field trial. The choice of cultivars was based on root hair lengths measured in a previous solution culture experiment. The aim of this study was to investigate the effect of cultivar and soil P level on P concentration (P utilisation efficiency), P uptake efficiency, grain chemical composition, root hair length, dry matter production, grain yield, root growth, 1000-grain weight, hectolitre-weight and phenological development.

The results showed higher dry matter production and grain yield at low soil P levels in Diamant, Herse and Herta than in NK0058, NK94682 and Tyra, respectively, indicating a higher P efficiency in these cultivars. Total P uptake at low soil P levels was also higher, and the P concentration (mg P g^{-1} shoot dry matter, P utilisation efficiency) tended to be lower, suggesting higher P uptake and P utilisation efficiencies in these three cultivars. Probably the P uptake efficiency accounted for most of the variation between the cultivars, whereas variation in the P utilisation efficiency was of less importance. Dry matter production, grain yield and P uptake generally increased with increasing soil P level. However for most cultivars, except for the modern cultivar Tyra, dry matter and grain yield decreased at the highest soil P level. As soil P level increased, the differences in yield and P uptake within the three pairs of cultivars diminished, suggesting that the factors increasing the P uptake at low soil P are less important at high soil P level.

Recordings of phenological development and grain moisture content confirmed that increasing soil P level increases the rate of development in cereals. 1000-litre weight and hectolitre-weight were generally found to increase with increasing soil P level.

Root growth in the topsoil was found to increase as the soil P level increased. The root hairs grew longer in field soil than in the previous solution culture experiment. The ranking of cultivars with regard to root hair was only in part similar to that found in solution culture, and the differences in root hair length was much smaller or insignificant in this study as compared to the solution culture experiment. Hence, ranking of cultivars in terms of root hair length might prove difficult. A previous study reported longer root hairs in barley as a response to lower soil P level. In contrast, these results suggested the opposite.

The higher P uptake in Diamant, Herse and Herta might be due to longer root hairs. However, it is suggested that variations in other factors such as root exudation of organic acids and phosphatase and lowering of rhizosphere pH were as important factors for the higher P uptake.

Grain concentrations of N, P, K, Ca and Mg were consistent with former findings. There were no effects of cultivar or P level on the grain concentrations of N, Ca and Mg in this study.

In conclusion, this study suggested that there is great variation in P efficiency between cereal genotypes. This may only in part be explained by different root hair lengths. Adapting crops to lower soil P levels, by selection and breeding, is thus a possible means of increasing the sustainability of the agroecosystem.

Sammendrag

Lågere fosfor (P)-nivå i jorda forventes hvis mer bærekraftige jordbruksmetoder (økologisk landbruk, låg-input landbruk) kommer i bruk. Jordbruksvekster kan tilpasses lågere P-nivå i jorda ved utvelging og avl for høgere P-effektivitet. Lange rothår kan øke P-effektiviteten til korn ved å øke P-opptaket.

I dette studiet ble det brukt tre par av svenske og norske kornsorter (hvete: NK0058 og Diamant; seksrads-bygg: NK94682 og Herse; torads-bygg: Tyra og Herta) med henholdsvis korte og lange rothår målt i næringsløsning innen hvert par. Sortene ble dyrket ved fire ulike P-nivå (P0: 35 mg P-AL kg-' jord; P16: 49 mg; P32: 87 mg; P48: 130 mg) i et langvarig PK-gjødslingsforsøk i felt. Valget av sorter var basert på rothårsmålinger i et tidligere forsøk i næringsløsning. Målet med dette studiet var å undersøke effekten av kornsort og P-nivå på: P-konsentrasjon (P-utnyttingseffektivitet), P-opptakseffektivitet, kjemisk innhold i kornet, rothårslengde, tørrstoffproduksjon, kornavling, rotvekst, 1000-kornvekt, hektolitervekt samt fenologisk utvikling.

Resultatene viste en høgere tørrstoffproduksjon og kornavling ved lågt P-nivå i Diamant, Herse og Herta, noe som tyder på en høgere P-effektivitet i disse sortene. Det totale P-opptaket ved lågt P-nivå var også høgere, og P-konsentrasjonen (mg Pg^{-1} tørrstoff i skudd, P-utnyttingseffektiviteten) tenderte til å være lågere. Dette tyder på en høgere effektivitet i P-opptak og P-utnytting i disse tre sortene. Sannsynligvis så betydde P-opptakseffektiviteten mest for variasjonen mellom sortene, mens derimot var variasjonen i P-utnyttingeffektiviteten mindre viktig. Generelt så steg tørrstoffproduksjonen, kornavlinga og P-opptaket med økende P-nivå. På det høgste P-nivået avtok både tørrstoffproduksjonen og kornavlinga for alle sortene unntatt Tyra. Ved økende P-nivå avtok forskjellene i tørrstoffproduksjon og kornavling innen de tre sortsparene, noe som tyder på at de faktorene som øker P-opptaket ved låge P-nivå er mindre viktige ved høge P-nivå.

Registreringer av fenologisk utvikling og vassprosent i kornet bekrefta at økende P-nivå øker utviklingshastigheten i korn. Generelt så økte 1000-kornvekta og hektolitervekta med økende P-nivå.

Rotveksten i matjordlaget økte med økende P-nivå. Rothårene var lengre i feltjorda enn i det tidligere næringsløsningsforsøket. Rangeringa av kornsorter i forhold til rothårslengda i dette studiet var bare delvis lik den som ble funnet i næringsløsning og dessuten var forskjellene i rothårslengde ikke signifikante eller mye mindre i dette studiet sammenligna med i næringsløsningsforsøket. Derfor kan rangering av kornsorter for rothårslengde vise seg å være vanskelig. En tidligere studie viste at økt P-nivå i jorda ga lengre rothår i bygg, mens derimot disse resultatene tydet på det motsatte.

Lengre rothår i Diamant, Herse og Herta kan være årsaken til det høgere P-opptaket i disse tre sortene. Imidlertid tydet resultatene på at også variasjon i andre faktorer som eksudasjon fra rota av organiske syrer og fosfatase og lågere pH i rhizosfzren var like viktige faktorer for det høgere P-opptaket.

Konsentrasjonen av N, P, K, Ca og Mg i kornet var i samsvar med tidligere resultat. I dette studiet var det ingen effekt av kornsort eller P-nivi p i konsentrasjonen av N, Ca og Mg i kornet.

Som konklusjon har dette studiet vist at det er stor variasjon i P-effektivitet mellom kornsorter. Dette kan bare delvis kan forklares med ulik rothirslengde. En mulig måte å øke bærekraften i agroøkosystemet på, er derfor ved seleksjon og avl for P-effektive jordbruksvekster for å tilpasse de til lågere P-nivå.

Preface

My starting point for this MSc-thesis in agroecology is a personal commitment in the development of organic farming, and in general, sustainable food systems. Phosphorus (P) uptake in cereals in low-P soil and the influence of root hairs is a tiny subsystem of the agroecosystem. However tiny, this work might contribute to more sustainable agroecosystem, as it demonstrates possible advances in the P uptake efficiency of cereal cultivars.

This thesis-work has been closely linked with the work of Anne-Kristin Løes who is doing a PhD-study on the same topic as me. Her PhD-study, as well this thesis, are parts of the Strategic Institute Research Programme (SIP): *"Nutrient supply in organic farming systems with small amounts of animal manure* (Næringsforsyning i økologiske dyrkingssystemer med lite husdyrgjødsel)".

Thanks are first and foremost due to my supervisors Anne-Kristin Løes and Tore Krogstad for discussions and very helpful comments during the progress of this thesis-work. Thanks are also due to Øyvind Vartdal, Torill Tredal, Ivan Digernes and many others at the Department of Soil and Water Sciences for help in the field and in the laboratory. I am also thankful to my Mum and Dad for listening to me when the motivation was low, and to my sisters Rannei and Kari just for being there. And special thanks to Rannei, you were a great help when I was sampling and washing the root cores in June last summer!

Ås, 30 May 2002

Jon Magne Holten

Contents

1. Introduction

1.1 Sustainability in agroecosystems

This thesis comprises a study on a specific topic focusing on a relatively low organisational level of the agroecosystem, namely P uptake in cereals and the effect of root hairs.

The organisational level of an agroecosystem, being at the field level, the farm level or even higher in the food system, determines in large part the research methodology applied. When narrowing down to soil-plant interactions, the appropriate methodology at this level of resolution is of necessity a reductionistic approach, which also has been the traditional approach in the agricultural sciences for several decades. P uptake in cereals and the effect of root hairs is a subsystem of the agroecosystem (suprasystem).

My aim is to contribute to the development of more sustainable agroecosystems. The research questions asked and the conclusions drawn are therefore within the context of enhanced sustainability of the agroecosystem. Since P is a nutrient that often is in scarce for plant growth, and root hairs have been shown to increase the P uptake of plants, I have chosen to study this topic.

1.2 Phosphorus in soil

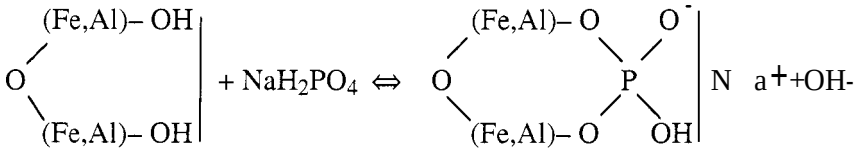
Soil phosphorus (P) is often a limiting nutrient for plant growth. Total P content in mineral soils of a temperate climate is in the range of 0.02 to 0.08%. The P concentration in the soil solution is typically very low, because P is strongly adsorbed (Mengel and Kirkby, 1987). In general, Norwegian soils are slightly acidic and under such circumstances, P is mainly adsorbed to aluminium (A1)- and iron (Fe)-oxides as shown in the example below.

> "Compared to the other major nutrients, P is by far the least mobile and available to plants in most soil conditions. The poor mobility of soil inorganic P is due to the large reactivity of phosphate ions relative to numerous soil constituents and to the consequent strong retention of most of soil P onto those (Hinsinger, 2001)".

Because of its low mobility in soil, the distance of phosphate diffusion is very small. A substantial amount is associated with the soil organic matter, and the organic P fraction may constitute 25-65% of total P (Schachtschabel *et* al., 1998). A P-AL level of about 7 mg P per 100 g soil (bottom range of the high soil P class) is regarded as optimal with regard to both

yield level and a sufficiently low risk of stimulating algae-growth by erosion to water bodies (Krogstad and Løvstad, 1987).

Ion sorption of phosphate to AI- and Fe(II1)-oxides is exemplified by the formation of an inner-sphere complex:



In conventional agriculture the plant P requirement is fulfilled by application of easily soluble mineral P fertilisers. Contrary to conventional agriculture, it is a main aim in organic farming systems that the farm is self-sufficient with P as well as other nutrients (IFOAM, 2002). Reduced input of external P is also desired due to sustainability reasons, because (i) mineral P is a limited non-renewable resource, and (ii) surplus application of P may cause eutrophication of surface waters.

In studies of five Norwegian dairy farms, decreasing concentrations of plant available P were found after long-term organic management (Løes and Øgaard, 2001). With lower soil P concentrations and low P inputs, plants may suffer from P deficiency. However, crop plants are able to adapt to low P conditions by increased nutrient efficiency, for instance by increased root growth, root exudation and increased utilisation efficiency (Marschner, 1995). Several authors have suggested selection and breeding as means of increasing the P efficiency of cultivars of crop species (e.g. Caradus, 1994; Batten, 1992; Föhse et al., 1991; Clark and Duncan, 1991; Gerloff and Gabelmann, 1983).

1.3 Phosphorus efficiency

From an agronomic point of view genotypical differences in the nutrient efficiency of crop plants is usually defined by differences in the growth or in the yield when the nutrient supply is suboptimal (Marschner, 1995). Phosphorus efficiency has two components: (i) the efficiency of absorbing P from the soil (P uptake efficiency), and (ii) the efficiency with which

P in the plant is utilised to produce yield (P utilisation efficiency) (Sattelmacher *et al.*, 1994). As a rule in nutrient efficiency, the uptake of nutrients by the roots plays the most important role (Marschner, 1995). Factors that contribute to increased P efficiency among genotypes have been reviewed by Ahmad *et al.* (2001):

P uptake efficiency

When soil P availability is low, factors such as root morphology (root radius, specific root length and root surface per unit of shoot weight) and root physiology (the affinity of the uptake system for the nutrient, K, (mmol/L), and, external nutrient concentration where net uptake is zero (influx=efflux) C_{min}, (µmol/L)), rhizosphere pH, root exudates and mycorrhiza are important in P uptake.

P utilisation efficiency

Under P stress, some genotypes may have better use of stored P, either within a certain tissue or by higher rates of translocation between shoot organs. In P-efficient crop genotypes, lower proportions of total P are retained in roots and stems and higher proportions translocated to leaves compared to inefficient genotypes.

Breeding and selection for P efficiency

In Danish trials, Schjørring and Nielsen (1987) showed there were great differences in P uptake and grain yield of barley cultivars grown in soil of moderate P deficiency, and there were similar results for corn in USA (Nielsen and Barber, 1978). Romer and Schenk (1998) in a screening of spring barley cultivars also showed the influence of cultivar on P uptake efficiency and P utilisation efficiency. Hence, it should be possible to adapt cereal cultivars to a lower soil P level. Gahoonia *et al.* (1997) suggested longer root hairs as a breeding criterion for more P efficient cereal cultivars.

1.4 Root hairs

1.4.1 Form

Root hairs are tubular outgrowths from epidermal root cells (trichoblasts) that considerably increase the total root surface. Root hairs emerge just behind the zone of root elongation. The cell walls of the root hair may remain visible for a long time, however the functional life span of a root hair is just a few days (Jungk, 2001; Hofer, 1996). The growth of the root and the

"movement" of the root hair zone through the soil appear to be the mechanism that continuously provides access to undepleted soil, i.e. it makes the soil nutrients spatially available (Jungk, 2001).

Root hair length, density, and coverage are important characteristics of the root hairs in a certain root system. Whereas root hair length is the most important characteristic of the single root hair, density and coverage characterise the root hair stand of a certain root system. Depending on species and cultivar, average length of root hairs varies from 0.1 to 1.5 mm for a diameter of 5-20 μm (Hofer, 1996),i.e. the root hair diameter is 20-30 times smaller than the diameter of the root cylinder. Root hair length and density vary considerably between species (Itoh and Barber, 1983).

Root hair growth varies with several environmental factors such as aeration, presence and numbers of soil microorganisms, soil moisture, soil nutrient status and soil physical properties (Barber, 1995). Wide variation in root hair formation exists among barley and wheat cultivars (Gahoonia *et* al., 1997; Løes, 2002), showing that root hair growth is under genetic control. Ranlung of barley and wheat cultivars with regard to root hair length were found to be similar in solution culture and in field conditions (Gahoonia et al., 1999). When screening cultivars for root hair lengths, solution culture is preferred to field experiments because it is less laborious.

A reduction in soil P level was found to increase root hair length in barley (Gahoonia et al., 1999). Longer root hairs as a response to low-P availability have also been reported in Arabidopsis thaliana (Bates and Lynch, 1996) and in rape, spinach and tomato (Fohse and Jungk, 1983). The latter authors conclude that it is the P content of the plant and not the P concentration of the growing media directly that decides the root hair formation.

1.4.2 Function

Root hairs increase 1. the nutrient absorptive capacity by increasing the root surface area, and 2. expand the nutrient depletion zone around the root. This is especially important for the uptake of water and less mobile nutrients (such as P). Root hairs also play a role in anchorage of the plant, but this is probably most significant at a root tip scale (Bailey et al., 2002).

Transport of nutrients from soil to the root proceeds by mass flow and diffusion (Barber, 1995). In most cases, diffusion is the mechanism that dominates ion transport from soil to roots. The driving force of net diffusion is a concentration gradient. In a given soil, a root surface that could create a higher concentration gradient would cause a higher flux from soil. Root hairs are assumed to have an influx (uptake rate per unit surface area) similar to that of the root cylinder (Tinker and Nye, 2000). Root hairs may, nevertheless, exceed the root cylinder in its ability to create a steep concentration gradient. The volume of soil that delivers a nutrient to a unit of sink surface depends on the radius of the sink. Therefore, per unit surface area, root hairs have a larger volume of soil to feed on than a bold root cylinder. As a consequence, when the sink has a smaller radius, the concentration gradient to drive a certain flux is attained at a lower concentration of the nutrient in the bulk soil. Once within the root, P is rapidly translocated in the plant (Marschner, 1995). In conclusion, due to their small diameter, root hairs are more efficient than the root cylinder in drawing advantage from the laws of diffusion (Jungk, 2001). The nutrients in the root hair cylinder (i.e. the soil volume around the root cylinder with root hairs) are largely depleted within a few days, and longevity more than a few days probably hardly contribute to the nutrient acquisition.

Jungk (2001) concluded that the less mobile nutrients (such as P) are spatially available only in the root hair cylinder, whereas the more mobile nutrients, such as nitrate and chloride, move to a larger extent from further distant soil. In case of phosphate, the length of root hairs is, therefore, important for the volume of soil feeding a unit of root.

Cost/benefit analysis of carbon respired for P acquisition (Bates and Lynch, 2000b) supports the view that extension of the root surface area through root hairs is an efficient strategy for improving P uptake, when P availability is low. In a study with Arabidopsis thaliana, Bates and Lynch (2001) conclude that root hairs confer a competitive advantage to plants in low P environments. Direct evidence on the participation of root hairs in P uptake of plants was given by use of radioisotope phosphorus tracer P32 (Gahoonia and Nielsen, 1998).

1.5 Other factors

Besides root hairs, other factors such as mycorrhiza, root exudation and lowering of the pH in the rhizosphere, also influence the P uptake efficiency. These mechanisms are partly also under genetic control, as will be shown below.

1.5.1 Mycorrhiza

The radius of mycorrhizal hyphae is even smaller than that of root hairs, and hence the P uptake efficiency of mycorrhiza is greater than root hairs. Most crop species and all cereal species (Gramineae) are mycorrhizal, whereas species belonging to Brassicaceae (e.g. rape and Arabidopsis) are non-mycorrhizal. However, the importance of mycorrhiza in P acquisition in annual crops like cereals is probably minor compared to root hairs (Gahoonia et al., 1999), because significant mycorrhizal development only occurs after 3-6 weeks (Baon et al., 1994; Jakobsen et al., 1992) and almost whole the P uptake by cereals occurs in the first 10 weeks. Furthermore, in studies of 10 barley cultivars (Jakobsen and Nielsen, 1983) and 27 wheat lines (Kapulnik and Kushnir, 1991), no significant variations in mycorrhizal infection were found. For this reason, mycorrhiza was not studied in the present study.

1.5.2 Root exudation

There is genotypic difference in the ability of cereal cultivars to release organic acids, acid phosphatase and to lower the rhizosphere pH. A barley cultivar took up more P from strongly adsorbed soil P, which was attributed to its ability to release more organic acids, especially citric acid, from its roots (Gahoonia et al., 2000). Similar results were found for wheat (Zhu et al., 2001). As a rule, organic acids mobilise P from Fe- and/or Al-phosphates by a combination of desorption by anion (ligand) exchange and chelation of Fe and A1 (Marschner, 1995). Efficiency of P acquisition is also influenced by root-induced pH change (Gahoonia and Nielsen, 1992), and variation in the ability to change rhizosphere pH has been observed among wheat and barley cultivars (Gollany and Schumacher, 1993).

Barley cultivars have been shown to differ in their rhizosphere phosphatase activity, which may increase mobilisation and depletion of P from the soil organic P fraction (Asmar et al., 1995; Römer and Schenk, 1998). In rhizosphere studies, barley cv. Pallas absorbed nearly two times more P than a root hairless mutant discovered among a population of wild type Pallas

producing normal root hairs. The acid phosphatase activity near Pallas roots was higher and Pallas mobilised more organic P in the rhizosphere than the mutant. This suggests a link between root hair formation and rhizosphere phosphatase activity (Gahoonia *et* al., 2001).

1.6 Aims

The aim of this study was to investigate

- whether wheat and barley cultivars with long root hairs measured in solution culture had a higher P uptake efficiency and/or P utilisation efficiency by low soil P conditions,
- how wheat and barley cultivars differed in root hair length in field conditions as compared to solution culture,
- if root hair length in wheat and barley is decreased with increasing soil P level, and
- how soil P level affected root growth, grain quality (1000-grain weight and hectolitre-weight) and phenological development.

2. Materials and methods

2.1 Experimental design

The field plot experiment was carried out May-September 2001 in a long-term PK fertilisation field trial established in 1966. The field trial is situated at Ås in the county of Akershus, southeastern Norway (59°39'43''N, 10°45'49"E, 65 meter above sea level). The field trial has an experimental design with four phosphorus (P) levels and four potassium (K) levels, and with two replicates. For this experiment the K_{50} level and all four P levels were chosen, namely P_0K_{50}, $P_{16}K_{50}$, $P_{32}K_{50}$ and $P_{48}K_{50}$ (see below). Altogether 8 fertilisation plots. These fertilisation plots (7.5 x 3.6 m) were divided into three plots of equal size (7.5 x 0.6 m = 4.5 m^2), allowing three cultivars to be grown at each fertilisation plot. The six cultivars of this experiment were divided between the two replicates at each P level. Three of the cultivars (NK0058, Diamant and Tyra) were grown in one of the two P replicates; the three other cultivars (NK94682, Herse and Herta) were grown in the other P replicate. In total the six cultivars grown at four P levels make 24 plots. There was only one replicate for each cultivar and P level. To avoid edge effects, all sampling was performed 50 cm inside of the borderline of the fertilisation plot. See Figure 2.1 for details.

The crop rotation of the field trial has mostly consisted of spring cereals, but grass, potatoes and swedes have also been grown.

2.2 Soil and field treatments

100 kg nitrogen (N) ha^{-1} $year^{-1}$ is applied to the entire trial. The P and K fertilisation has been as follows since the trial started:

	P_0	P_{16}	P_{32}	P_{48}	K_0	K_{50}	K_{100}	K_{150}
kg P ha^{-1} $year^{-1}$	0	16	32	48				
kg K ha^{-1} $year^{-1}$					0	50	100	150

Under Norwegian conditions, the P32 level is the typical amount of P added. Fertilisers used are: $Ca(NO_3)_2$ (15.5% N), superphosphate P8 (8% P) and KC1 (49% K). In 2001, the N, P and K fertilisers were applied 2 weeks before sowing. The soil of the trial is a clay loam. Further soil characteristics are presented in Table 2.1.

$P_{16}K_{50}$ NK0058 Diamant Tyra	P_0K_{100}	$P_{32}K_0$	$P_{32}K_{100}$	$P_{48}K_{150}$	P_0K_0	$P_{16}K_{150}$	$P_{48}K_{50}$ **NK94682** Herse Herta
$P_{32}K_0$	$P_{16}K_{50}$ **NK94682** Herse Herta	$P_{48}K_{150}$	$P_{16}K_{150}$	P_0K_{100}	$P_{48}K_{50}$ NK0058 Diamant Tyra	P_0K_0	$P_{32}K_{100}$
$P_{48}K_{100}$	$P_{48}K_0$	$P_{16}K_{100}$	P_0K_{50} NK94682 Herse Herta	$P_{16}K_0$	$P_{32}K_{150}$	$P_{32}K_{50}$ NK94682 Herse Herta	P_0K_{150}
P_0K_{150}	$P_{32}K_{150}$	P_0K_{50} NK0058 Diamant Tyra	$P_{48}K_0$	$P_{32}K_{50}$ NK0058 Diamant Tyra	$P_{16}K_{100}$	$P_{48}K_{100}$	$P_{16}K_0$

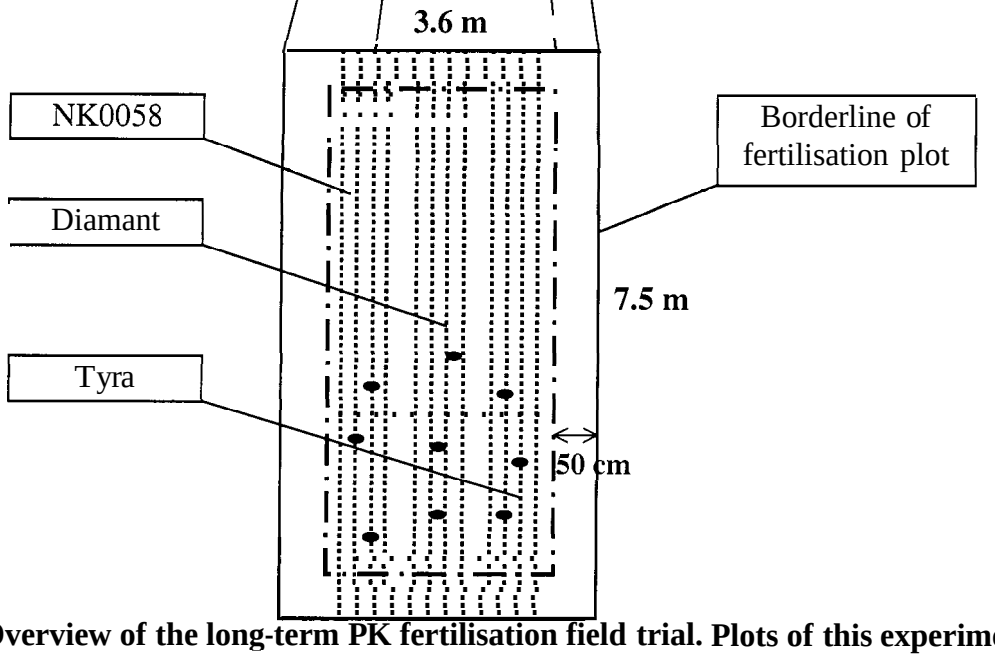


Figure 2.1. Overview of the long-term PK fertilisation field trial. Plots of this experiment are marked with grey. P_0K_{50} … $P_{48}K_{50}$ denote the soil P level. The enlarged plot is an example of how the sowing rows were arranged in each plot. Dots show where root samples approximately were taken.

In Norway, P-AL levels between 2.6 and 6.5 mg P per 100 g soil are classified as medium, and between 6.6 and 15.0 mg as high (Krogstad, 1992).

Table 2.1. Soil characteristics (depth 0-20 cm) of the fertilisation plots used in the present experiment. The values are means of the two P replicates.

P level	Clay	Silt	Sand	Org. C	pH	P-AL	Total P	Inorg. P	Org. P
	%					mg 100 g^{-1}			
P_0K_{50}	27	40	33	3.6	5.6	3.5	130	63	67
$P_{16}K_{50}$	24	43	33	3.2	5.7	4.9	126	70	56
$P_{32}K_{50}$	26	39	35	3.5	5.7	8.7	151	84	67
$P_{48}K_{50}$	21	37	42	2.9	5.6	13.0	124	80	44

Table adapted from Øgaard (1995).

2.2.1 Sowing and field treatment

Harrowed on 8 May 2001. Date of sowing: 22 May. Sowing amounts: Wheat: 24 g m^{-2}, barley: 19 g m^{-2}. Using an Øyjord experimental sowing machine, each cultivar was sown in four rows with row spacing of 15 cm. Between the cultivars there was a row spacing of 30 cm. Sprayed with herbicide (Starane and Express) against common thistle *(Cirsium awense* L.) on 12 June 2001.

2.3 Genotypes

Two spring wheat *(Triticum aestivum* L.), two 6-row and two 2-row barley *(Hordeum vulgare* L.) cultivars were chosen for this study because they had respectively long and short root hairs in a previous low-P solution culture experiment with Scandinavian wheat and barley cultivars (Løes, 2002) as shown in Table 2.2.

Table 2.2. Overview of the Scandinavian cereal cultivars studied in this field experiment and their years of approval, ancestors and mean root hair lengths measured in low-P circulating nutrient solution.

Cultivar	Species	Year of approval	Ancestors	Mean root hair length, mm
NK0058 [a]	Spring wheat	-	Brakar/T1022	0.43
Diamant	Springwheat	1938	DiamantII = Diamant x Ekstra Kolben, Svalov 1938	0.82
NK94682	6-row barley	Under approval	Arve//HS72-8/MØ75-278/3/PH107	0.34
Herse	6-row barley	1939	Maskin x Asplund	0.56
Tyra	2-row barley	1988	Sold/Sv71164	0.34
Herta	2-row barley	1949	Kenia x Isaria	0.55

[a] NK0058 is a dwarf line used in breeding.

2.4 Field sampling of roots

On 18 June nylon bags (in-growth technique) were placed in the soil in the two middle sowing rows of each plot with three replicates to produce fresh root samples. The nylon bags were put to a depth of approximately 20 cm using a metal cylinder with diameter 5 cm. Surrounding topsoil was put into the nylon bag and compacted by hand and a stick to obtain approximately similar soil density in the nylon bags. The nylon bags were removed on 17 July by cutting around them with a long knife, put in plastic bags and stored at 4ºC. The soil was washed out from the root samples the three following days. Prior to washing, the samples were soaked in water overnight. The roots were carefully washed with a shower using a sieve (mesh diameter 2 mm) and 1-3 baths. As it was not attempted to keep all of the roots, some fine roots were washed away. The roots were stored in a 50% ethanol solution in small glasses at 4ºC for 6 months until root hair lengths were measured.

2.4.1 Root hair analysis

From each root sample 5 representative images were taken. In each image, 20 root hairs were measured. As there were 3 replicates, 15 images were taken and 300 root hairs were measured for every plot. Because many root hairs were curled and entangled, only root hairs, on which you could see the beginning and the end, were measured. However, there were enough such root hairs to provide a representative measurement of the average root hair length. The samples were coded so it was not known from which P level and cultivar the sample came. Only root hairs from fertiliser levels P_0 and P_{32} were measured.

Analysis of root hair lengths was performed using a digital camera DC100 (Leica) fitted to a light microscope (Leica MZ6) and the image processing software (UTHSCSA *ImageTool* programme) at 10x magnification.

2.4.2 Root length

After root hair measurements, the root samples obtained from the nylon bags (in-growth technique) were dried at 105ºC for 20 hours and weighed for determination of dry matter.

2.5 Phenological development

Phenological development as described by Zadoks *et* al. (1974) was recorded weekly from germination until ripening. During grain formation (Zadoks 70-90), Zadoks values were sometimes hard to estimate due to lack of reference material. Fungi infestation was recorded on 13 August (Zadoks 74 - 89). Photographs of the 8 fertilisation plots (Pictures 1-16) were taken on 15 and 30 August.

2.5.1 Grain moisture content

The grain moisture content of the barley and the wheat was registered by harvest. 15 randomly chosen heads were picked, threshed and dried. For the barley, the grain moisture content in the stand was also registered on 14 August (2 weeks before harvest), however then 10 representative heads were picked. Barley: drying temperature 130°C for 17 hours, wheat: 105°C for 47 hours.

2.6 Chemical and physical plant analyses

2.6.1 Sampling of plant material during growth season

Fresh plant material (shoot) was harvested three times during the growing season (21 June, Zadoks 14-30 – tillering/stem elongation; 16 July, Zadoks 56-64 – ear emergence/anthesis; 9 August, Zadoks 73-86 – soft dough/hard dough) for determination of dry matter weight and P content. Shoots from 100 cm of sowing row (4 rows 6 25 cm x 15 cm = 0.15 m^2) were cut at the base, though dirty plant material was avoided. Due to the restricted size of the plots, by each sampling, the cutting started from where the last sampling ended. The shoots were put in paper bags and dried at 60°C. On 20 June, there was still poor germination in one sowing row in some plots; hence the DM (dry matter) yield was calculated on the basis of three sowing rows. Yield values for NK94682 P_{16} on 20 June and P values for Diamant P_{48} on 20 June are missing.

2.6.2 Harvest and threshing of crop

At final harvest (barley: 29 August, Zadoks 87-91 – grain hard; wheat: 5 September, Zadoks 87-91 – grain hard), the stands were cut with a garden scissor at the base, put in paper bags (3-5 bags for each of the 24 plots) and then dried at 60 °C for minimum 4 days. The area of the

plots that were harvested ranged between 2.9 and 3.15 m^2. The fourth sowing row of NK0058 P_{32} had only 50% yield compared to the other three sowing rows. Therefore, the total yield of this plot was adjusted by multiplying total yield with 8/7.

Immediately after drying, total yield (grain and straw) was recorded. The crop samples were stored at room temperature for 8-22 days before threshing. A representative portion of the straw of each sample was kept back for chemical analysis. When the threshing was completed, the grain was weighed. The straw yield was calculated as the difference between total yield and grain yield. After cleansing of the grain samples, 1000-grain weight and hl-weight was measured. For determination of 1000-grain weight, 200 grains were counted twice. The average figure was then multiplied with 5.

2.6.3 Plant chemical analyses

Dried shoots, grain and straw samples were finely ground using a plant mill (Falling Number 3100). These samples were again dried at 60°C overnight to ascertain complete dryness. All samples were shaken thoroughly to mix before digestion.

All plant samples, including grain and straw from the final harvest, were analysed for P. N was analysed in the grain only. For analyses of P and total N, the samples were digested using a modified Kjeldahl method. 150-200 mg sample was put into a test tube. 0.8 g Na_2SO_4, some Se and 3 ml H_2SO_4 (95-97%) were added. The samples were gradually heated to 380 "C using a digester (Tecator, Digestion System 40, 1016 Digester) and were let to stand for 1 hour after having become transparent. The samples were then diluted to 75 ml in the test tube with distilled water. P and N were determined colorimetrically (NSF, 1984; NSF, 1975).

Ca, Mg and K were determined in the grain only. 2 g of sample was put into a 25 ml beaker and heated at 500 "C overnight. Following cooling, the samples were wetted with distilled water. Some drops of HN03 (65%) were added and the samples were heated to dryness. Subsequently they were heated at 400 ºC for 1 hour. Then some drops of HCI (37%) were added. After dryness, they were heated for 1 hour. 10 ml 1 N HCI was added and the samples were filtrated into 100 ml flasks. The elements were measured using atom absorption (Perkin-Elmer, 2380 Atomic Absorption Spectrophotometer).

Every fifth sample had a replicate to measure the accuracy of the analysis. For P, K, Ca and Mg also standard reference material with known element composition was analysed.

P uptake was calculated as the P concentration multiplied with the DM production.

2.7 Statistical analyses

Statistical analyses were performed using Minitab (statistical software) and Excel as found appropriate. Root hair lengths of cultivars were compared using groupwise comparisons with Tukey's test *(P=0.05)*.The effect of P level on root hair lengths within the groups of genotypes were compared with one-way ANOVA.

3. Results

3.1 P uptake, P concentration and dry matter yields – a comparison of cultivars

This experiment was carried out in a long-term PK fertilisation trial, which has been designed to compare the effects of different soil P (and K) concentrations on crop plant nutrient composition. By start of this long-term PK trial in 1966, the initial P-AL level was 5.0 mg P per 100 g (Uhlen and Rød, 1983). Still after more than 30 years, the P_0 level, which has received no P fertiliser and from which the crops has been removed every year, had a P-AL concentration of 3.5 mg P per 100 g soil. This is classified as medium soil P, however in the bottom range of the medium soil P class. The reason for the relative high P-AL concentration is probably the relatively high clay content of this soil.

Apart from a few exceptions between mid and end of June (approx. 15-22 days after emergence; Zadoks 12-30 – second leaf unfolded to start of stem elongation) at P_0 in Herta and in particular Tyra, there were no visible symptoms of P deficiency in the cereal crops in this experiment. There were some signs of potassium deficiency (yellowish leaf tip of lower leaf) in mid June in Tyra at all P levels, and in Diamant, Herse and Herta at P_{48}.

Based on how the six cultivars initially were selected from the low-P solution culture experiment by Løes (2002) they were grouped together into three pairs of genotypes (spring wheat, 6-row barley, 2-row barley), one cultivar having short and one long root hairs within each pair (see Table 2.2). In the following sections, at first in general, and then for each pair of genotypes, P uptake, P concentration and dry matter production of the cultivars are presented. As the experiment had no replicates, the results must be interpreted with care.

Fungi infestation as recorded on 13 August (Zadoks 74-89 – soft dough/hard dough) showed some infestation in all cultivars, except from Herta which was little infested with fungi. There was no trend with regard to soil P level. The fungi infestation probably had a minor importance for the comparison of DM production and P uptake between the cultivars of this study, and is therefore not considered further.

3.1.1 General

P uptake

P uptake and dry matter (DM) production at the four P levels are shown in Figures 3.1, 3.2 and 3.3. The P uptake generally increased in all six cultivars as the P level increased, however the effect of increasing soil P concentration on plant P uptake levelled out at the two highest soil P levels. The final P uptake was highest in P_{48} for the barley, whereas for wheat, the final P uptake was highest in P_{16} (Diamant) and P_{32} (NK0058). For all genotypes, the final P uptake in P_0 was approximately 60% of the largest final P uptake. This shows that the P supply was not severely restricted in the experimental soil at P_0 (no P fertiliser added).

DM production

The lowest total DM production (grain and straw) by final harvest was attained in P_0 in all cultivars. In P_0, total DM production ranged between 5.5 t ha^{-1} (NK0058) and 7.6 t ha-' (Diamant) and between 2.3 t ha^{-1} (NK94682) and 3.7 t ha^{-1} (Herta) for the grain yield. Total DM production was 19-50 % higher (1.4-3.0 t ha^{-1}) in P_{32} compared to P_0 (lowest increase in Diamant and highest in NK94682). The grain yield increments were generally somewhat higher, however in NK94682 it was as much as 139% higher, which is a substantial increase. In P_{32}, total DM production ranged between 7.8 t ha^{-1} (Tyra) and 9.7 t ha^{-1} (Herta) and between 4.1 t ha^{-1} (NK0058) and 5.6 t ha^{-1} (NK94682) for the grain yield.

By final harvest, the DM production generally attained the highest values in P_{32} in all cultivars except for Tyra, which had the highest DM production in P_{48}, and Diamant, which had the highest DM production in P_{16}. The effect of increasing soil P level on total DM production (and grain yield) generally levelled out at the two highest P levels. Moreover, DM production and grain yield decreased in fact from P_{32} to P_{48} in all cultivars, except for in Tyra. This showed that even if the P uptake was considerable also from the P_0 soil, P fertilisation had a very significant effect on the yield level.

At low soil P levels, Herta and Diamant had a higher total DM production than Tyra and NK0058, respectively. The difference in DM production in these two pairs of cultivars decreased as the P level increased. Similar trends as described for total DM production, could also be seen in the P uptake for these two pairs. Longer root hairs, as found in solution culture

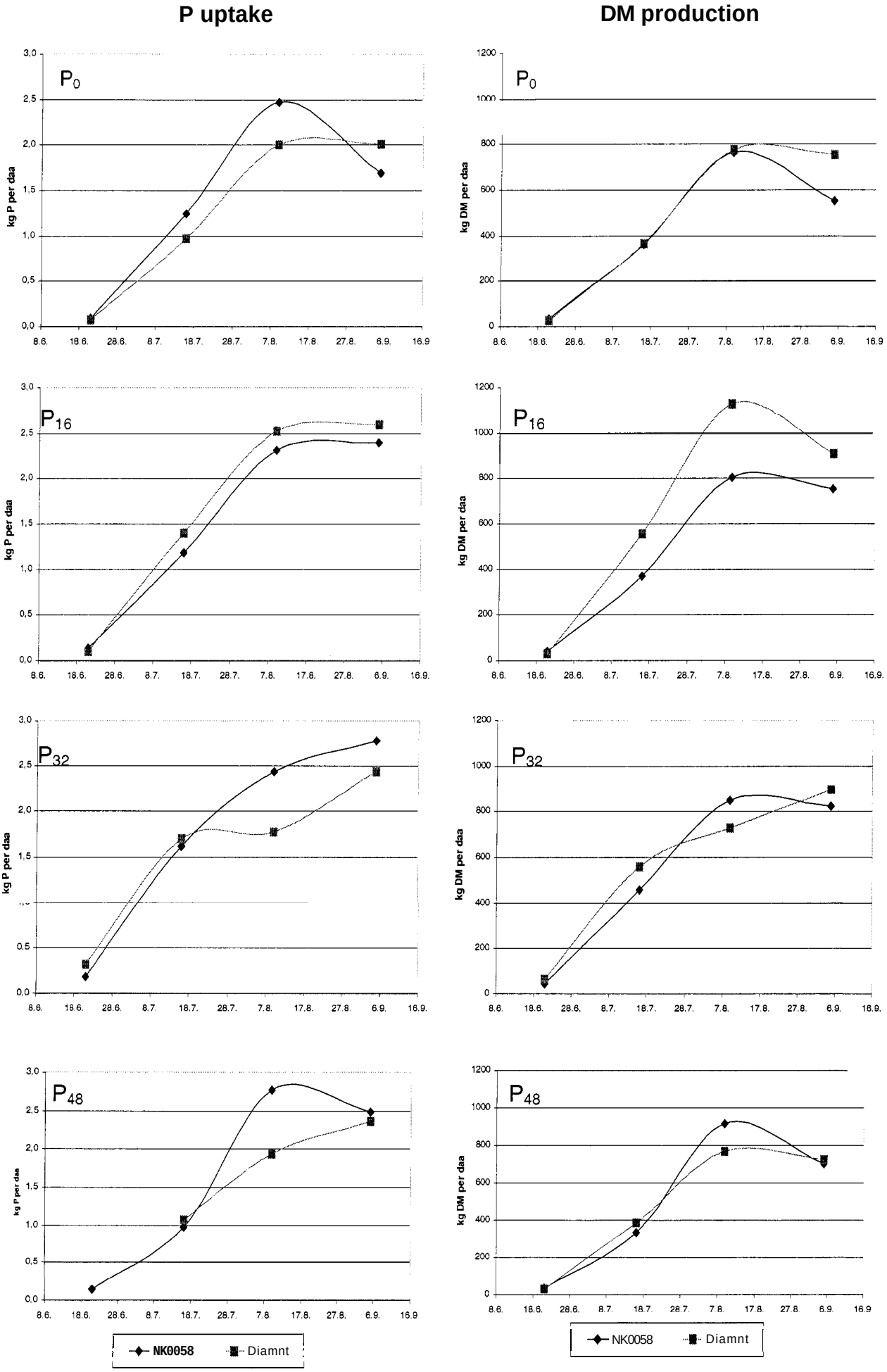


Figure 3.1. P uptake and DM production of NK0058 and Diamant at the four P levels during the growing season.

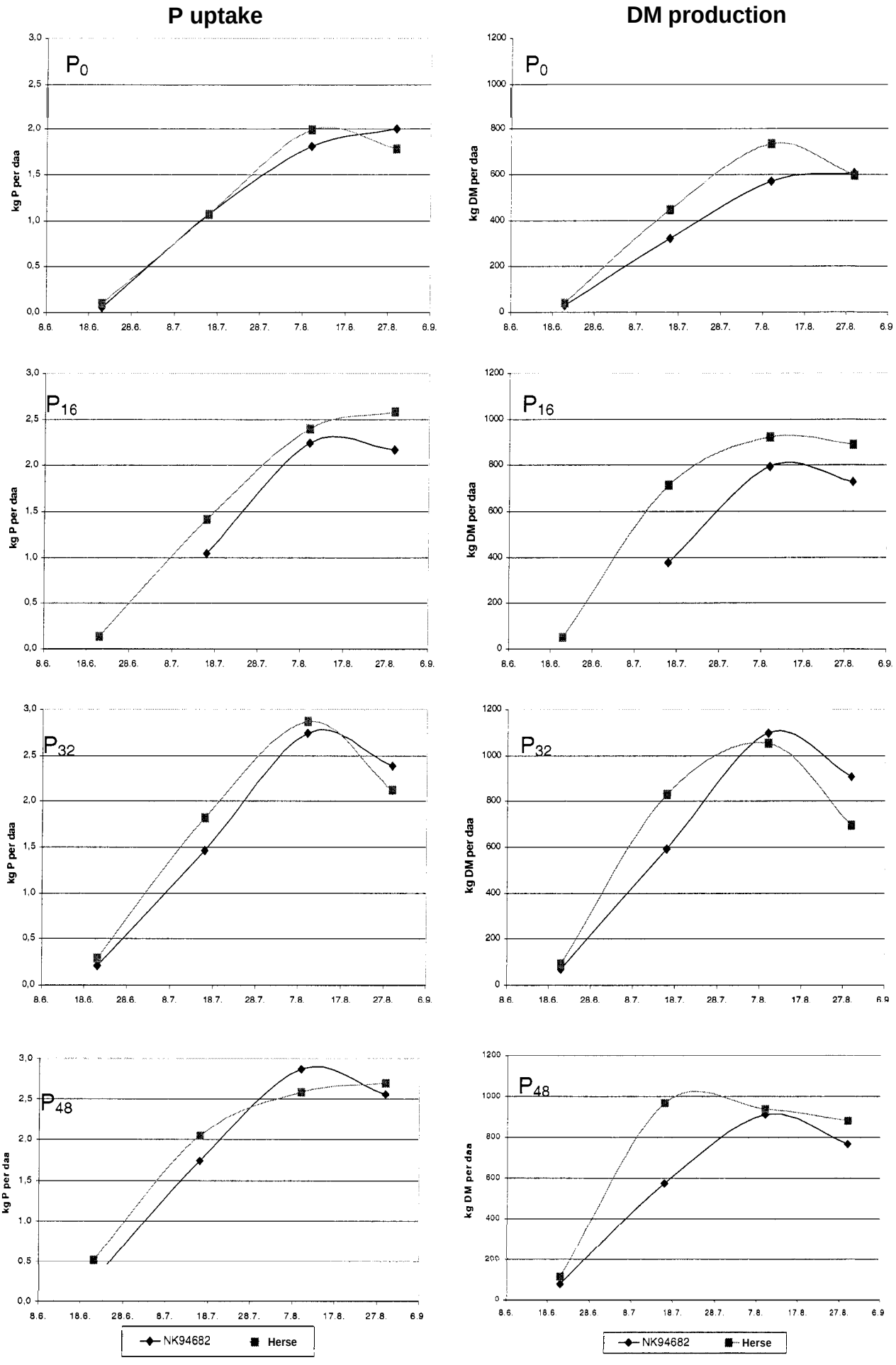


Figure 3.2. P uptake and DM production of NK94682 and Herse at the four P levels during the growing season.

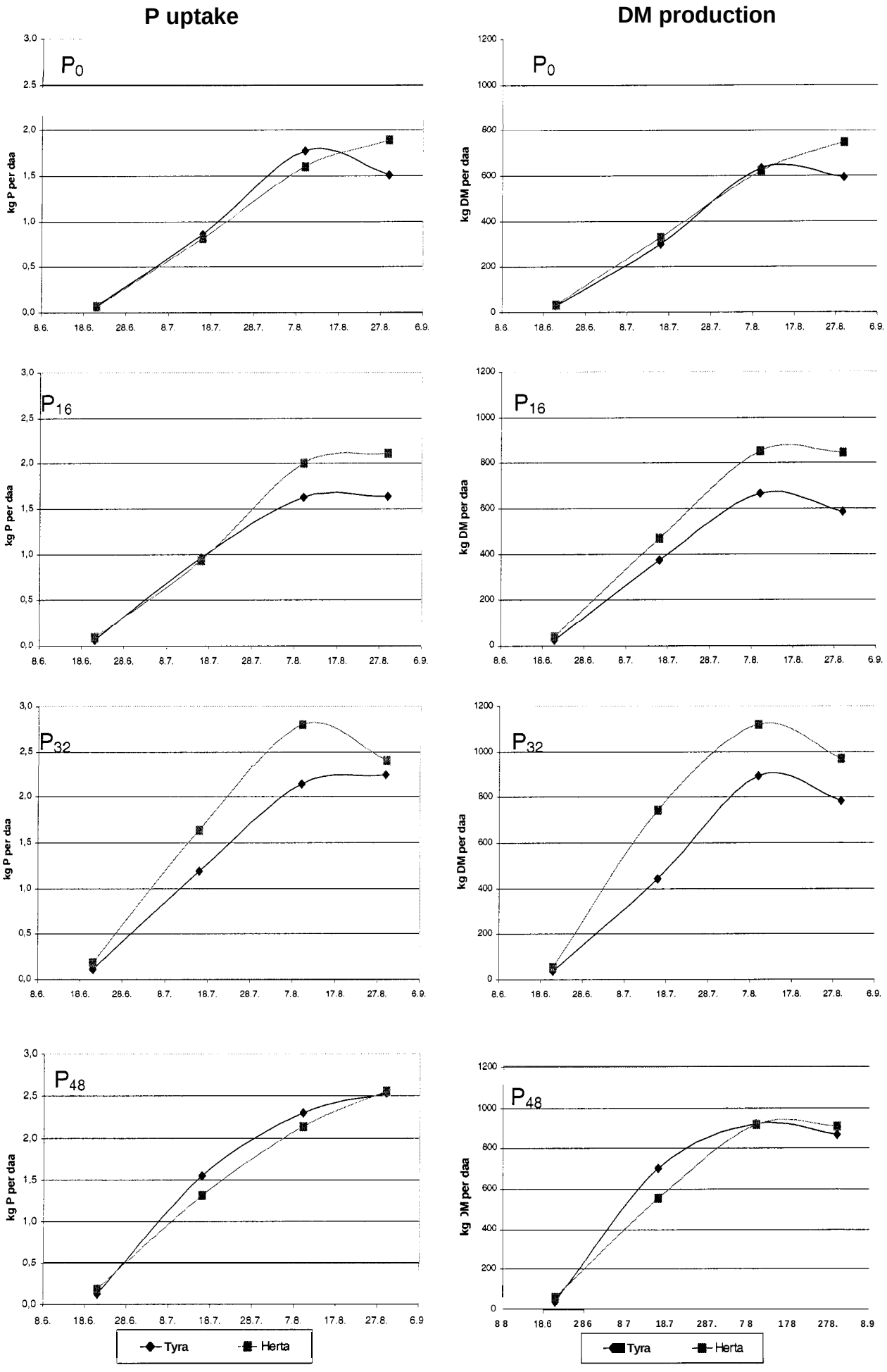


Figure 3.3. P uptake and DM production of Tyra and Herta at the four P levels during the growing season.

might be a logical explanation for this. Regarding NK94682 and Herse, the results were less conclusive in terms of DM production and P uptake.

Raw data for shoot, grain and straw dry matter, as well as harvest index, is provided at Appendix A.

Table 3.1. Phosphorus concentration at soil P levels P_0 and P_{32} in dry matter (DM) in shoots harvested at three times during the growing season and in grain and straw at final harvest. P harvest index is the proportion of the P taken up found in the grains. Zadoks values in parentheses [a].

Soil P level	21 June	16 July	9 August	Grain	Straw	P harvest index
	g P kg^{-1} DM					
P_0	(Z14-30)	(Z56-64)	(Z73-83)			
Wheat						
NKOO58	2.94	3.43	3.23	4.76	1.38	0.77
Diamant	2.65	2.65	2.58	4.73	0.73	0.86
6-row barley						
NK94682	1.70	3.34	3.19	5.15	2.15	0.60
Herse	2.32	2.40	2.70	4.50	1.11	0.83
2-row barley						
Tyra	2.47	2.86	2.80	3.71	0.93	0.85
Herta	1.76	2.46	2.57	3.86	1.19	0.76
P_{32}	(Z22-30)	(Z58-68)	(Z73-84)			
Wheat						
NKOO58	4.15	3.54	2.86	5.10	1.61	0.76
Diamant	4.82	3.05	2.44	4.74	0.91	0.82
6-row barley						
NK94682	2.90	2.47	2.50	3.69	0.96	0.86
Herse	3.18	2.19	2.73	4.48	0.66	0.92
2-row barley						
Tyra	3.02	2.70	2.39	4.09	0.96	0.87
Herta	3.33	2.20	2.50	3.84	0.86	0.84

[a] Z14 - fourth leaf unfolds; 2211222 - main shoot + one/two tillers; 230 - stem elongation; 240 - booting; Z50 - ear emergence; 260 - flowering; 270 / Z80 - milk / dough development.

P concentration

The two *P* levels P_0 and P_{32}, respectively with medium and high soil P concentration, were chosen to show the effect of cultivar and time in the season on the shoot P concentration (Table 3.1). Generally, the most pronounced difference between P_0 and P_{32} was the P concentration early in the season (21 June, Zadoks 14-30 – tillering/start of stem elongation),

which was 1.4-1.9 times higher in P_{32} as compared to P_0. A one-way ANOVA, using the six cultivars as replicates, showed that only on 21 June the shoot P concentrations differed between P_0 and P_{32} ($P=0.007$), whereas the P concentration later on in the season (16 July and 9 August) did not significantly differ. Mean P concentration on 21 June in P_0 and P_{32} was 2.31 and 3.57 g P kg^{-1} DM, respectively. According to Mengel and Kirkby (1987), cereals adequately supplied with phosphate have P concentration of 3-4 g P kg^{-1} in the dry matter during the vegetative period, whereas P deficient plants have a P concentration below 1. Thus, in P_0, particularly early on in the season, the P supply was sub-optimal, however not in the deficient range.

The P harvest index was higher in Diamant, Herse and Tyra than in NK0058, NK94682 and Herta, respectively (Table 3.1), indicating a higher P utilisation efficiency in these cultivars. Similar trends were obtained in soil P levels P_{16} and P_{48} (data not shown). Among the three pairs of cultivars, Tyra was the only modern cultivar having a high P harvest index.

In P_0 the shoot P concentration in all barley cultivars were lower on 21 June than later on in the season, whereas in the wheat, the P concentration remained almost the same (Table 3.1). Quite contrary to P_0, the P concentration in all cultivars in P_{32} decreased between 21 June and 16 July. Hence, it seems that increased soil P concentration mostly influenced the shoot P concentration early on in the season and to a lesser degree later.

Due to translocation of P (and most other nutrients) from the shoot into the grain kernel during ripening, the grain P concentration generally was 1.5-2 times higher than that of the shoot on 16 July. The grain P concentration generally was higher in the wheat cultivars than in the barley cultivars, which was particularly evident at P_{32}. However, barley cv. NK94682 made an exception. The high grain P concentration in NK94682 at P_0 was probably due to the low grain yield at this P level.

Generally, when grain P concentration was high, straw P concentration also was high. In barley, the straw P concentration can be attributed to the earliness of the cultivars (see section 3.4) due to translocation of P. The earliest cultivar will have the lowest straw P concentration by harvest. This held true for the earliest 6-row barley cv. Herse at P_0 and P_{32}, and for the earliest 2-row barley cv. Tyra at P_0 (but not in P_{32}).

3.1.2 NK0058 - Diamant (spring wheat)

P *uptake and P concentration*

The material indicated that Diamant (long root hairs in solution culture) had a higher P uptake than NK0058 (short root hairs) at the two lower P levels, P_0 and P_{16} (Figure 3.1) with medium soil P concentration. At the two higher P levels, with high soil P concentration, it seemed that NK0058 had the highest P uptake. In P_0 and P_{16}, Diamant had the highest P uptake at final harvest, though in the three first harvests in P_0 NK0058 was doing better than Diamant.

Among the four P levels, Diamant had the highest P uptake by final harvest in P_{16}, whereas NK0058 had the highest P uptake in P_{32} and P_{48}. This indicated that Diamant has a somewhat lower external P demand than NK0058 (Figure 3.1).

Generally, NK0058 had a higher P concentration in both P_0 and P_{32} in the shoot as well as in the grain and the straw (Table 3.1). The only exception from this pattern was on 21 June in P_{32} and P_{16} (data not shown for P_{16}). It was also evident from P levels P_0, P_{16}, P_{32} and P_{48} (data not shown for P_{16} and P_{48}) that much more of the P was retained in the straw in NK0058 than in Diamant at final harvest. Because NK0058 was earlier maturing than Diamant, the reason could not be delayed translocation of P. It is possible that NK0058 has a lower internal P use efficiency (dry matter production per unit P in the dry matter) than Diamant. The lower P harvest index in NK0058 pointed to this too.

DM production

Diamant had a higher total DM production by final harvest than NK0058 in P_0, P_{16} and P_{32}. The grain yield was higher in Diamant than NK0058 in P_0 and P_{16}. However, the difference decreased with increasing P level, and the DM production and grain yield were almost similar in P_{48} (Figure 3.1). Total DM production in Diamant and NK0058 was 7.6 and 5.5 t ha^{-1} in P_0, respectively, and 9.1 and 8.2 t ha^{-1} in P_{32}. Harvest indexes for both cultivars were approximately 50%. Diamant attained the highest total DM production and grain yield in P_{16}, whereas NK0058 attained the highest total DM production and grain yield in P_{32}.

Summed up, the results indicated that Diamant had higher a P uptake, DM production and grain yield at lower soil P concentrations than NK0058. The shoot P concentration and P harvest index indicated a higher P utilisation efficiency in Diamant than NK0058.

3.1.3 NK94682 - Herse (6-row barley)

P *uptake and P concentration*

The results did not indicate very clearly as to which cultivar of Herse (long root hairs in solution culture) and NK94682 (short root hairs) had the highest P uptake. However, Herse had a higher P uptake than NK94682 in three out of four P levels early in the growing season, and was clearly higher by final harvest in P_{16} (Figure 3.2). The P uptake in Herse P_{32} by final harvest will not be considered here because of an unexpectedly low registered DM production. At the lowest P level, NK94682 had a slightly higher P uptake by final harvest than Herse, but at P_{16}, Herse had a significantly higher P uptake during the entire growing season. At P_{48}, the P uptake by final harvest was very similar in NK94682 and Herse.

Regarding the shoot P concentrations (Table 3.1), Herse had higher P concentrations on 21 June at all four P levels (data not shown for P_{16} and P_{48}). A possible explanation for this may be a better P uptake capacity in Herse, maybe due to longer root hairs as found in solution culture. At P_0, the P concentration later on in the season was lower in Herse than in NK94682, particularly by the final harvest. Partly this could be due to higher P utilisation efficiency in Herse than in NK94682. The P harvest index also indicated a higher P utilisation efficiency in Herse. At P_{32}, the P concentrations differed just slightly, except from in the grain. The fact that NK94682 at P_{32} showed the lower grain P concentration might be due to a dilution effect due to the high grain yield in NK94682 at P_{32}. The most probable reason that NK94682 showed a high straw P concentration at P_0 was that NK94682 was later maturing than Herse.

DM production

Herse attained a higher total DM production than NK94682 by final harvest in P_{16} and P_{48}, and a higher grain yield in P_0, P_{16} and P_{48}. Having a grain yield of 2.3 t ha^{-1}, and a very low harvest index of 38%, NK94682 definitely had the lowest grain yield among the six cultivars at P_0. Furthermore, at P_{16}, Herse attained a grain yield of 5.6 t ha^{-1}, which was equivalent to the grain yield NK94682 attained at the higher soil P level P_{32}. However, at P_0 the DM productions were similar in the two cultivars. Between 21 June and 9 August, Herse had a higher DM production compared to NK94682 at all four P levels (except from on 9 August in P_{32}). However, on 9 August the difference decreased as the P level increased.

Summed up, there were no more than weak indications that Herse performed better than NK94682 at lower soil P concentrations. Higher DM production and grain yields in Herse in P_{16} and P_{48}, as well as a higher grain yield in P_0, pointed to this. Furthermore, higher P concentration on 21 June in Herse, as well as indications of higher P utilisation efficiency, suggested the same. However, due to much divergence between the P levels, the P uptake curves gave no good indications of which cultivar had the highest P uptake.

3.1.4 Tyra - Herta (2-row barley)

P *uptake and P concentration*

Herta (long root hairs in solution culture) had a higher P uptake than Tyra (short root hairs) by final harvest in P_0, P_{16} and P_{32} (Figure 3.3). In P_{16} and P_{32} the P uptake was higher also earlier on in the season. The results show clearly that the difference in P uptake by final harvest between the two cultivars was greatest at the two lower P levels (medium soil P concentration) and that the difference in P uptake diminished at the two higher P levels (high soil P concentration). For instance, by final harvest, Herta had taken up more P at P_0 than did Tyra at P_{16}, and nearly as much at P_{16} as did Tyra at P_{32}. However, there was virtually no difference in P uptake between Tyra and Herta during the entire season at P_{48}. This shows that the higher P uptake capacity in Herta was most pronounced at lower P levels and decreased as the soil P level increased.

In a limited period between mid June and end of June (tillering/beginning stem elongation) both Tyra and Herta showed visible signs of P deficiency (purple coloration of the sheath due to accumulation of anthocyanins) in P_0 and P_{16}. At P_0, the P concentration on 21 June was lower in Herta than in Tyra, however at P_{32} Herta had the higher P concentration (Table 3.1), whereas at P_{16} the P concentration in Tyra and Herta was similar (data not shown). This pattern was not expected, but should be interpreted with care due to the lack of replicates. Lower P concentrations in P_0 and P_{16} on 16 July and 9 August and in P_{32} on 16 July may suggest a higher P utilisation efficiency in Herta (data not shown for P_{16}). However, Tyra had higher P harvest index at all P levels as compared to Herta.

The higher P concentration in the straw in Herta P_0 was most likely because Herta is later maturing than Tyra. Thus, the translocation of nutrients was not fully completed by final harvest.

DM production

Herta attained a higher total DM production by final harvest than Tyra at all four P levels, as well as a higher grain yield in P_0, P_{16} and P_{32}. However, at P_{48} the DM production was almost similar. For instance, Herta attained as good DM production at P_0 as Tyra did at P_{32}. Between 21 June and 9 August Herta also had a higher DM production than Tyra In P_{16} and P_{32}. Furthermore, Tyra was the only cultivar among the six, which, in terms of DM production and grain yield, responded to the highest P level, whereas all the five other cultivars had a varying decrease in P_{48}.

Summed up, the results clearly indicated that Herta, in terms of P uptake, DM production and grain yield, performed better than Tyra at lower soil P concentrations.

3.2 Protein, magnesium, calcium and potassium concentration

The protein content of the barley cultivars decreased by increasing grain yield (Figure 3.4), demonstrating a dilution effect. For wheat, the protein content was not as clearly related to the grain yield level, and in general it was much higher than in barley. The average grain protein concentration in these four barley cultivars was 10.8 % and 14.1 % in the wheat.

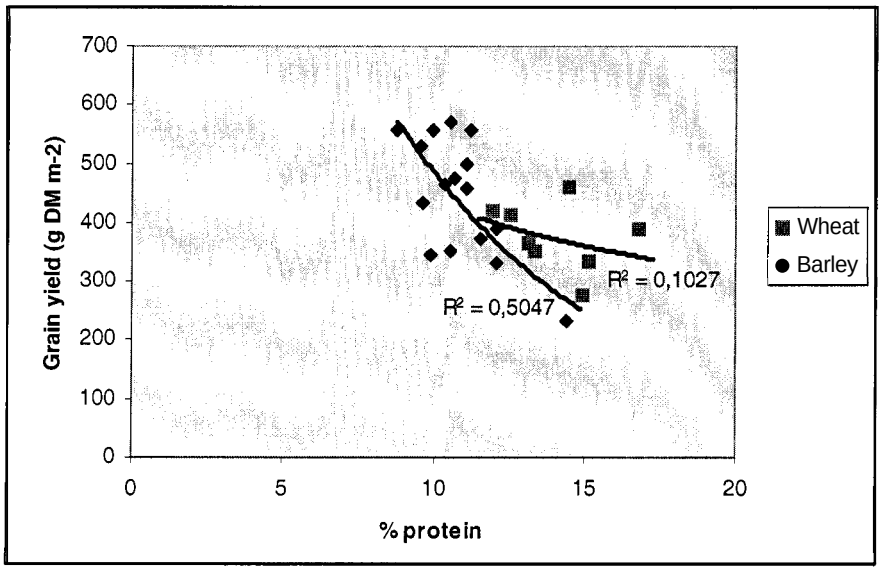


Figure 3.4. Crude protein concentration (g NH_4-N 100 g^{-1} DM x 6.25) plotted against grain yield for the 4 P levels and 6 wheat and barley cultivars. R^2 denotes the correlation coefficient.

The magnesium and calcium concentration did not show any trends with regard to cultivar or soil P level. Average grain concentrations were 1.23 mg Mg g^{-1} DM and 0.46 mg Ca g^{-1} DM.

For the barley, the grain potassium concentration declined with increasing soil P level. For the wheat the trend was opposite; high soil P level gave high potassium values (Table 3.2). Furthermore, using all four P levels as replicates, the average grain potassium concentration was higher in NK0058 than in Diamant (P=0.002), with respectively 5.56 and 4.31 mg K g^{-1} DM. Average grain concentration of all cultivars and P levels was 5.14 mg K g^{-1} DM.

Table 3.2. Average potassium concentration in the grain of the wheat and barley as affected by soil P level.

Soil **P** level	Wheat (N=2)	Barley (N=4)
	mg K g^{-1} DM	
P_0	4.61	5.81
P_{16}	4.70	5.28
P_{32}	5.23	5.01
P_{48}	5.20	4.86

Raw data for shoot P concentration and grain P, N, K, Ca and Mg concentrations is provided at Appendix B.

3.3 1000-grain weight and hectolitre-weight

In the barley cultivars there was generally a slightly increasing 1000-grain weight and hectolitre-weight as the soil P level increased (Figure 3.5). Average hectolitre-weight and 1000-grain weight for the barley was 70.5 kg and 42.8 g, respectively. However, the 2-row barley cultivars had higher hectolitre and 1000-grain weights than the 6-row cultivars. The Norwegian hectolitre-weight norm for barley is 64 kg and 79 kg for wheat. A 1000-grain weight below 30 g is regarded as poor (Uhlen, 2001). Wheat cv. Diamant had higher 1000-grain weight and hectolitre-weight than cv. NK0058. Average hectolitre-weights for NK0058 and Diamant were 71.3 kg and 81.3 kg, respectively, and average 1000-grain weights were 26.0 g and 36.5 g, respectively. The two wheat cultivars obtained the highest values in P_{32}. For all P levels and cultivars, it appeared that the hectolitre-weight and 1000-grain weight were well correlated for both barley (R^2=0.64) and wheat (R^2=0.95) in this study. Furthermore, a regression analysis within each cultivar, using the four soil P levels as

replicates, gave a good correlation between grain yield and 1000-grain weight for barley (R^2=0.77-0.94) and wheat (R^2=0.85 and 0.94).

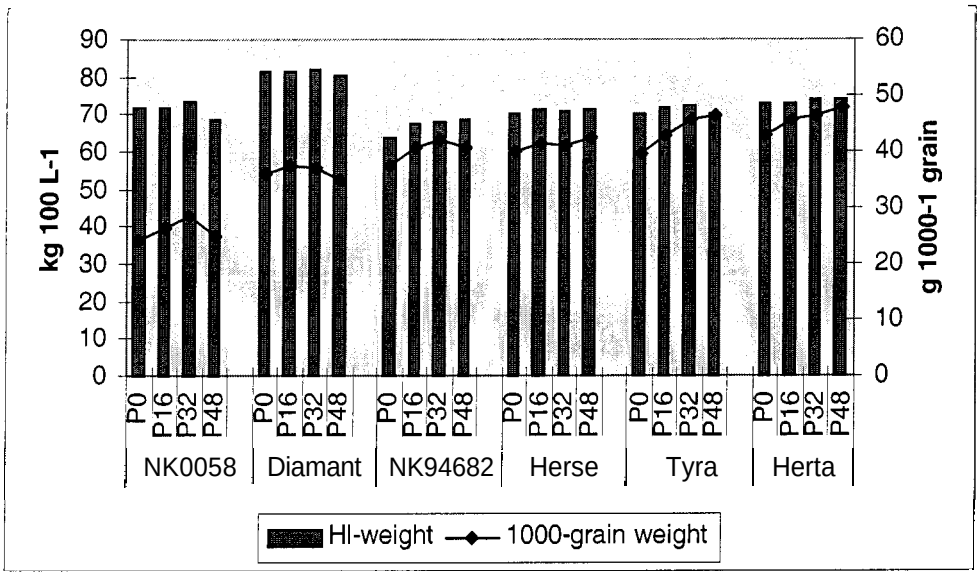


Figure 3.5. 1000-grain weight and hectolitre-weight.

3.4 Grain moisture content / phenological development

Among the barley cultivars, the 6-row cvs. NK94682 and Herse were earlier ripening than the 2-row cvs. Tyra and Herta as seen in the grain moisture content. Herse was earlier than NK94682 and Tyra was earlier than Herta (Figures 3.6 and 3.7). Among the wheat cultivars, NK0058 was earlier ripening than Diamant. By final harvest, the differences among the six cultivars were most pronounced at the lowest soil P level, however this tendency was not so clear in the wheat as in the barley.

Grain moisture content by final harvest gives a good indication of the development stage. Figures 3.6 and 3.7 show that increasing soil P level reduced the grain moisture content in all cultivars, except for NK0058. In other words, low soil P concentration delayed phenological development in the barley and the wheat. This tendency was further supported by the weekly recordings of phenological development and plant height (see Appendices C and D, and also Table 3.3 and Pictures 1-16), which showed a delayed phenological development from the tillering stage as the soil P level decreased. For most of the cultivars, there was a relatively greater difference in grain moisture content between the lowest and the three upper soil P

levels, than within the three upper soil P levels, suggesting a diminishing effect of soil P level on phenological development as the soil P level increases.

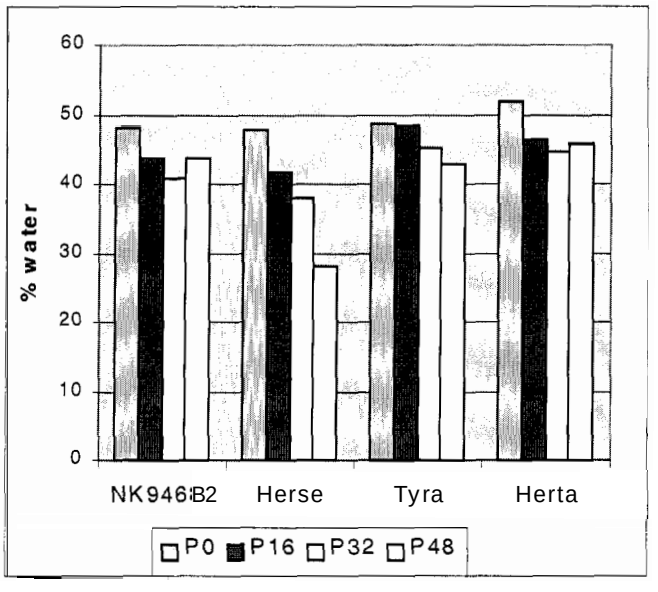


Figure 3.6. Grain moisture content of the barley cultivars at four different P levels on 15 August (Zadoks 81-89 – dough hard), 2 weeks before harvest.

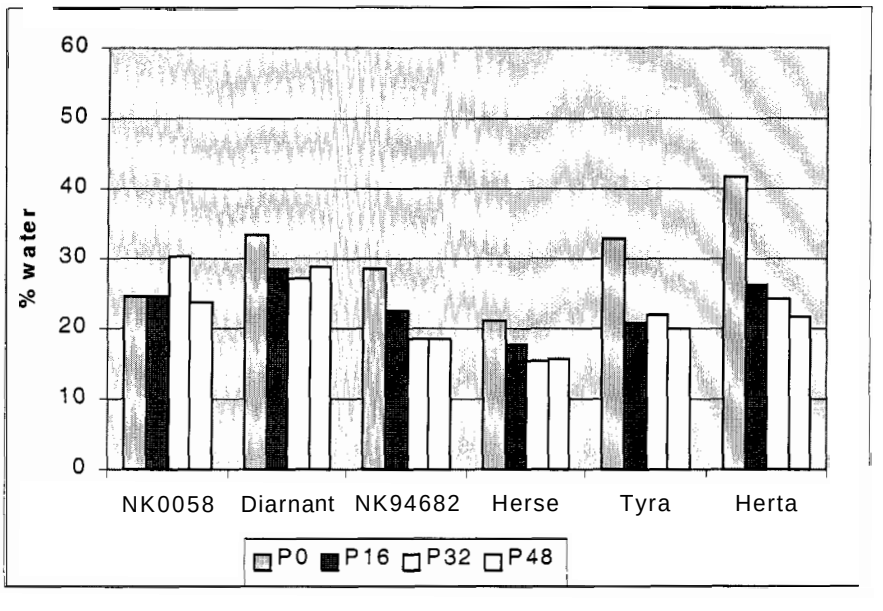
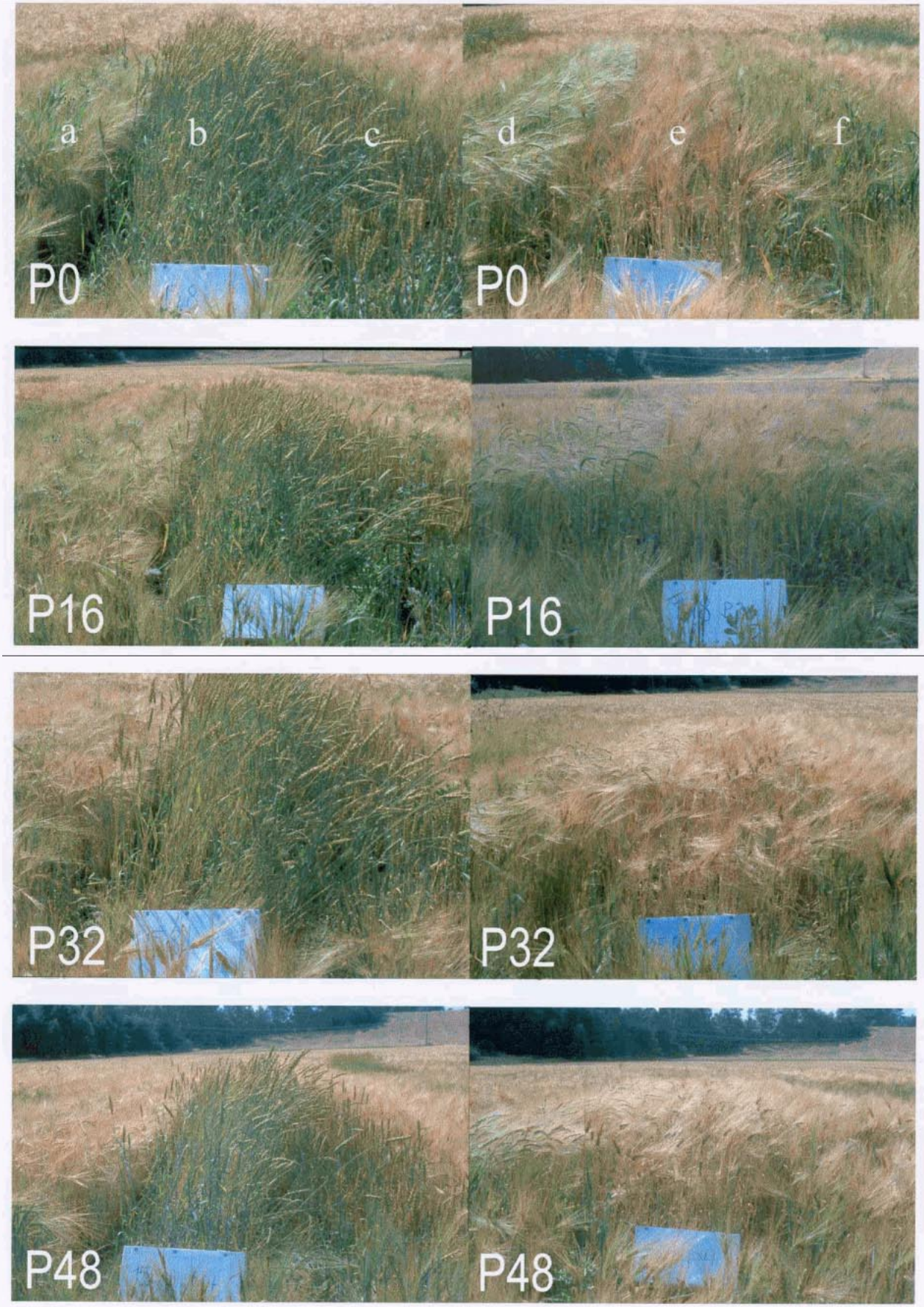
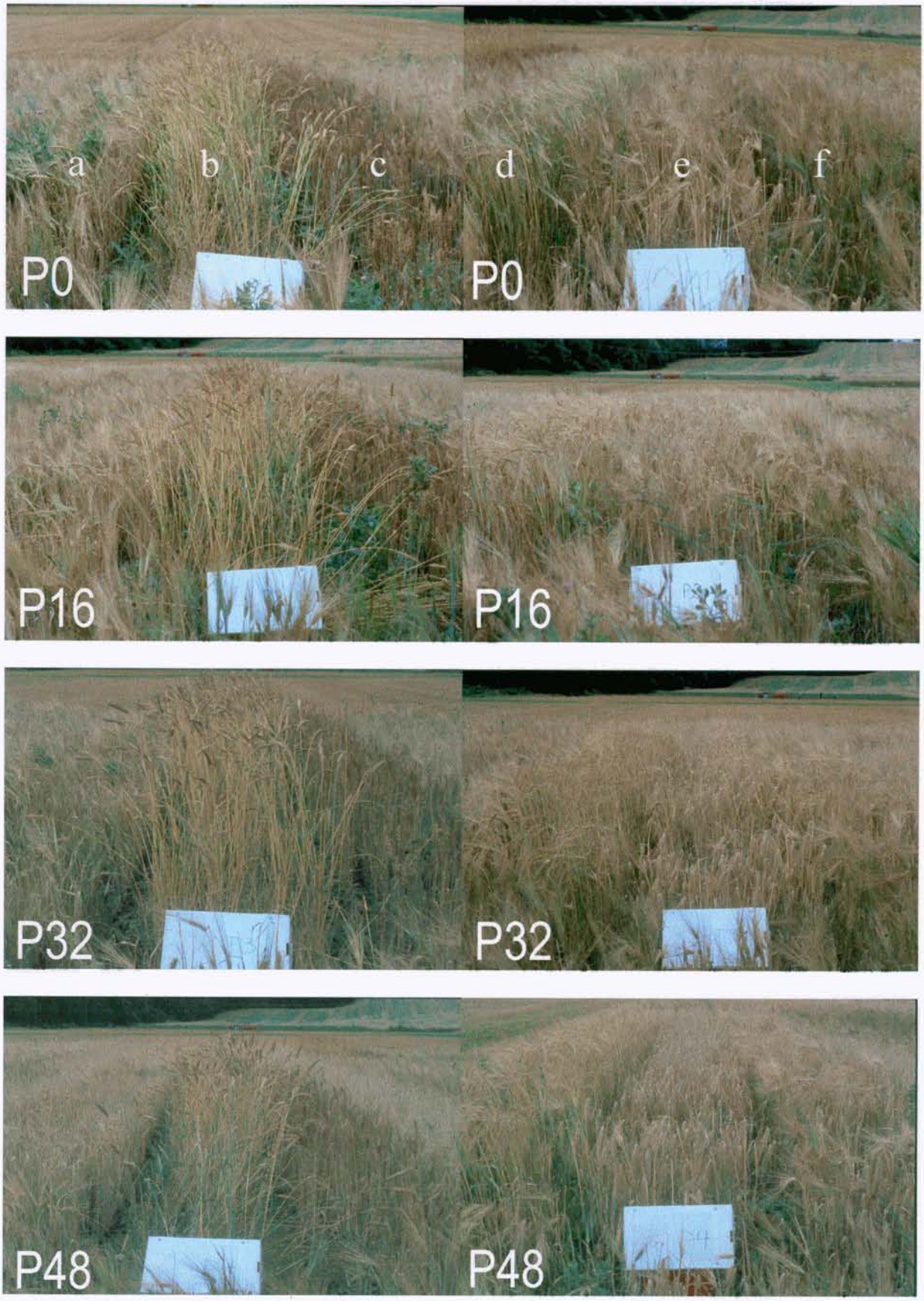


Figure 3.7. Grain moisture content of the wheat and barley cultivars at final harvest at four different P levels. The barley was harvested on 29 August and the wheat on 5 September.

Pictures 1-8 show the six cultivars at the four different soil P levels on 15 August 2001 (NK0058, Diamant and Tyra in one of two P fertiliser replicates, and NK94682, Herse and Herta in the other). The effect of the soil P level is demonstrated, as the cereal crops are more mature with increasing P level (P_0 through to P_{48}). The same trend is seen in Pictures 9-16,



Pictures 1-8. Photos taken on 15 August 2001 of the six cultivars nt the four P levels. a=Tyra, b=Diamant, c=NK0058, d=Herta, e=Herse, f=NK94682. The order of the cultivar is similar at all four P levels.



Pictures 9-16. Photos taken on 29 August 2001 of the six cultivars at the four P levels. a=Tyra, b=Diamant, c=NK0058, d=Herta, e=Herse, f=NK94682. The order of the cultivars is similar at all four P levels.

however the crops are more mature as this is 14 days later in the season. Zadoks values at the two dates are shown in Table 3.3.

Table 3.3. Zadoks values of the wheat and barley in P_0 and P_{48} on 15 and 30 August. Zadoks values refer to Pictures 1-16.

		15 August	30 August
		Zadoks values [a]	
Wheat	P_0	74	83
	P_{48}	76	87-89
Barley	P_0	81-86	86-90
	P_{48}	83-89	88-91

[a] Z70 - milk development; Z80 - dough development; Z90 - seed ripening.

3.5 Root in-growth

During four weeks, between 18 June (Zadoks 30 – tillering/stem elongation) and 17 July (Zadoks 56-64 – ear emergencelanthesis), the root length in the in-growth bags increased in all cultivars as the soil P level increased (Figure 3.8). However, the increase from one P level to the higher P level was not consistent in all cultivars due to great variation at some of the P levels in some cultivars. The two wheat cultivars, NK94682 and Tyra showed the best correlation to increasing soil P concentration. In Herta and Herse the correlation was less clear, however there were marked differences in root in-growth between the highest and the lowest soil P concentrations in these cultivars. However, the barley cultivars had markedly higher root in-growth than the wheat cultivars, and particularly so at the higher P levels.

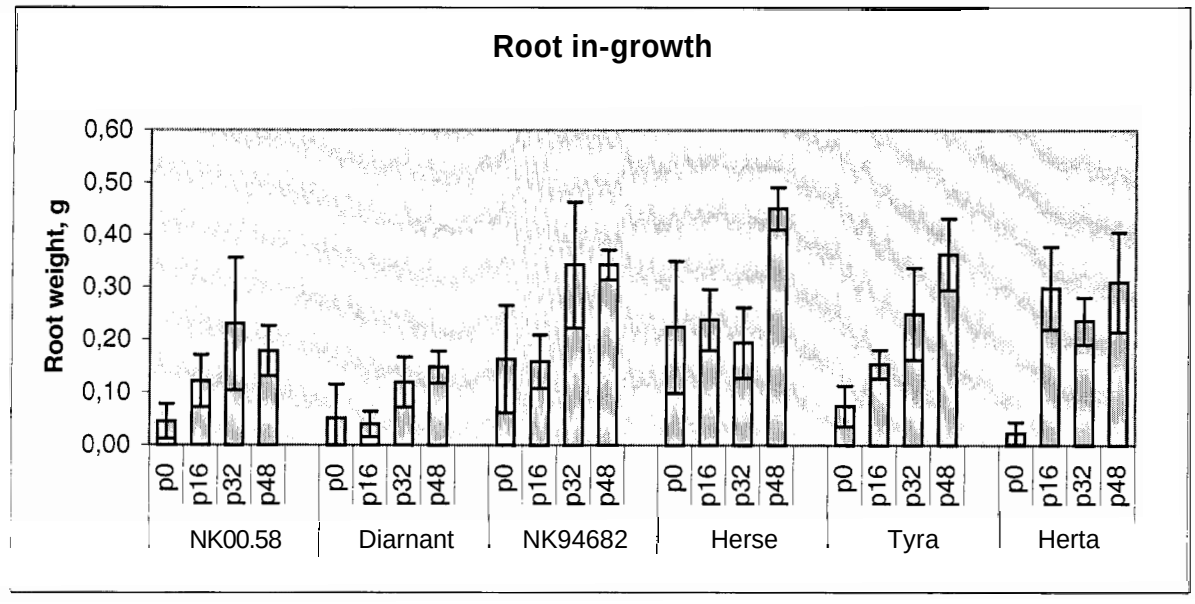


Figure 3.8. Root in-growth into nylon bags (05 cm) placed at 0-20 cm depth at four P levels between 18 June and 17 July. Bars denote standard deviation. N=3.

Table 3.4. The effect of soil P level on the relative rootlshoot ratio **(R/S** ratio) in the wheat and barley in mid July. The **FUS** ratio was calculated as mean root dry matter weight (root in-growth, g x 1000) divided with shoot dry matter weight (g m^{-2}). Roots were sampled on 17 July and shoots on 16 July.

Soil P level	Wheat (N=2)	Barley (N=4)
	R/S ratio	
P_0	0.13	0.33
P_{16}	0.20	0.45
P_{32}	0.36	0.42
P_{48}	0.46	0.53

The rootlshoot ratio in mid July increased with increasing soil P level (Table 3.4). The barley cultivars generally had a higher root/shoot ratio than the wheat. The cultivars with short root hairs measured in the solution culture (NK0058, NK94682 and Tyra) tended to have higher rootlshoot ratios as compared to the cultivars with short root hairs in the solution culture (Diamant, Herse and Herta) (Table 3.5). This was mainly due to higher shoot dry matter production on 16 July in Diamant, Herse and Herta, as there seemed to be no significant difference between the cultivars in root in-growth on 17 July (Figure 3.8).

Table 3.5. The effect of cultivar on the relative root/shoot ratio **(R/S** ratio) in mid July. **R/S** ratio is calculated as explained in Table 3.4. Values are means of the four P levels.

	R/S ratio
Wheat	
NK0058	0.37
Diamant	0.20
6-row barley	
NK94682	0.53
Herse	0.38
2-row barley	
Tyra	0.44
Herta	0.40

3.6 Root hairs

The root hair lengths of the six cereal cultivars of this study are presented in Table 3.6. The cultivars are arranged as pairs according to how the cultivars initially were selected from the previous solution culture experiment, with cultivars with short and long root hairs within each pair. Out of the four soil P levels, results from soil P levels P_0 and P_{32} were recorded. In this field experiment, the mean root hair lengths ranged from 0.74 to 0.98 mm. However, the variation in root hair length was very large within each cultivar and P level, as shown by the

large coefficients of variance *(33%* to *39%).* These coefficients were not notably changed by increasing the number of root hair counts, and seemed to be due to a large variability in the character root hair length. As shown for wheat cv. Diamant at P_0 (Figure *3.9),* there was no root hair length that dominated in the total population of root hairs, and hence a large CV is to be expected.

Table 3.6. Mean root hair lengths ± standard deviation (SD) for the six cereal cultivars at soil P levels P_0 and P_{32}. Root hairs measured on 4-week-old roots. Mean, SD and CV (coefficient of variance) are provided for each group of genotypes (wheat and barley). Cultivars with different letters within each group of genotype and P level have significantly different mean root hair lengths (Tukey's test, ***P=0.05).*** 300 root hair counts for each cultivar and P level.

	Root hair length (mm)	
	P_0	p_{32}
Wheat		
NK0058	*0.85 ± 0.31 b*	*0.79 ± 0.32 x*
Diamant	*0.74 ± 0.31 a*	*0.86 ± 0.31 y*
Mean – wheat	*0.80*	0.83
SD	*0.31*	0.31
CV	*39%*	38%
6-row barley		
NK94682	*0.79 ± 0.25 a*	*0.87 ± 0.29 x*
Herse	*0.86 ± 0.29 b*	*0.97 ± 0.30 y*
2-row barley		
Tyra	*0.85 ± 0.27 ab*	*0.90 ± 0.34 x*
Herta	*0.80 ± 0.28 ab*	*0.98 ± 0.32 y*
Mean – barley	*0.83*	0.93
SD	*0.27*	0.31
CV	33%	33%

Significance levels of root hair lengths of P_0 and P_{32} compared	
Wheat	*P=0.094*
Barley	*P<0.0001*
Wheat and barley	*P<0.0001*

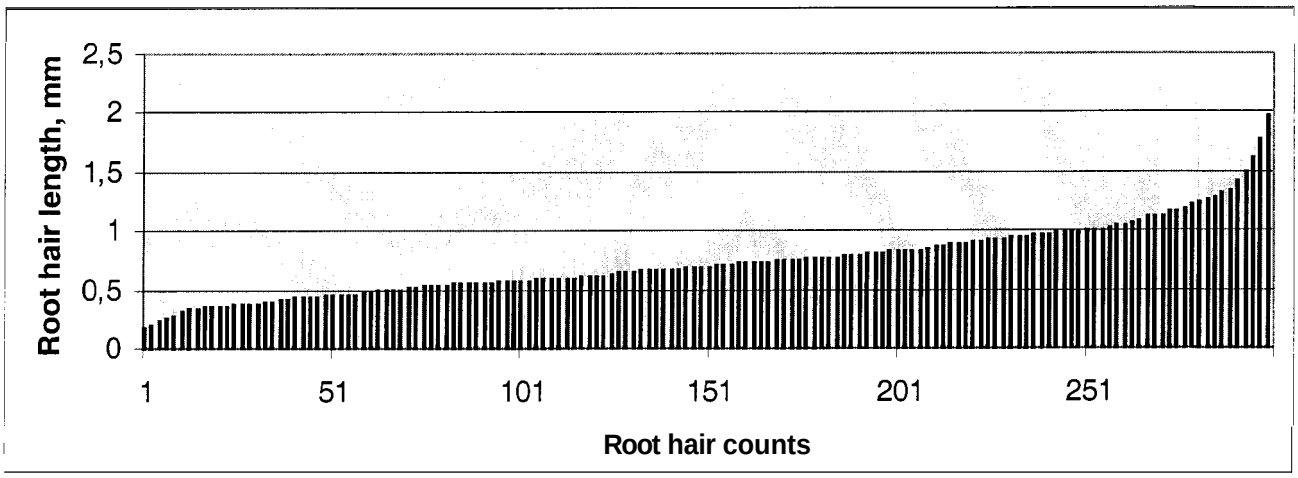


Figure 3.9.300 measurements of root hair lengths, arranged by increasing values, of wheat CV. Diamant at **P_0.**

Figure 3.10 demonstrates the great variability in root hair lengths, as exemplified by two selected images from two different replicates of Diamant at P_0.

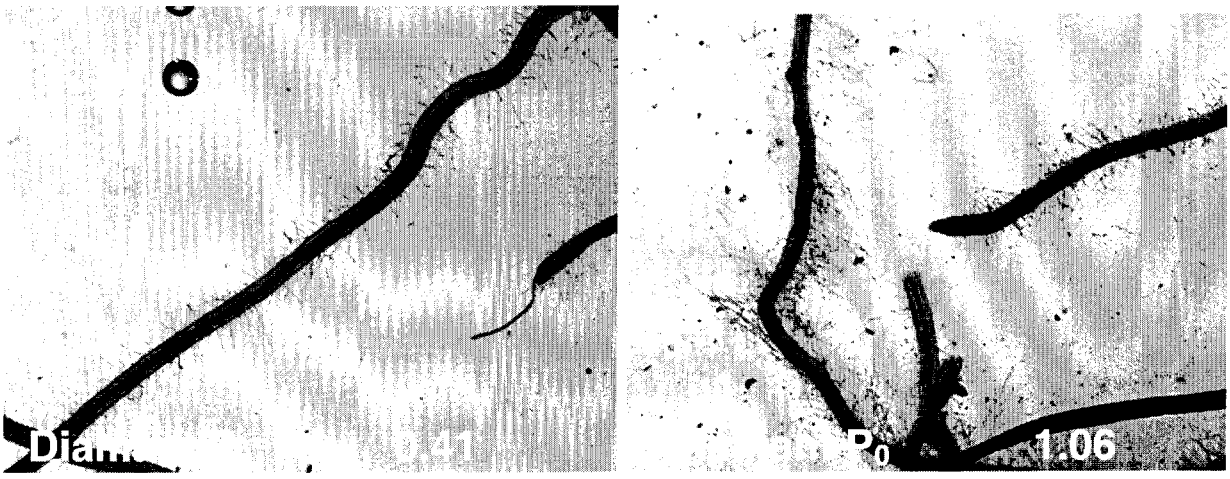


Figure 3.10. Two selected images of root hairs of Diamant at soil P level **P_0,** showing the great difference between two different replicates. The numbers show average root hair lengths (mm) in each image. 20 root hair counts for each image. The scales of the images are not necessarily exactly the same.

3.6.1 Effect of cultivar

Between the two pairs of barley cultivars, Herse had significantly longer root hairs than NK94682 at both soil P levels, whereas Herta only had longer root hairs than Tyra in P_{32}. In P_0 there was actually a tendency of longer root hairs in Tyra. In the cases Herse and Herta did have the longer root hairs, the root hairs were 0.07-0.10 mm longer. The two wheat cultivars differed significantly in root hair lengths at both soil P levels, however, at P_0 NK0058 had the

longer root hairs, whereas at P_{32}, Diarnant had the longer root hairs. Due to the rather divergent results for the wheat at the two P levels, one cannot say whether one or the other wheat cultivar in this study had the longer root hair length.

Figure **3.11.** Some selected images of root hairs of **NK94682** and Herse at soil P levels $\mathbf{P_0}$ and $\mathbf{P_{32}}$**.** The number shows average root hair length (mm) for each image. 20 root hair counts in each image. The scales of the images are not necessarily exactly the same.

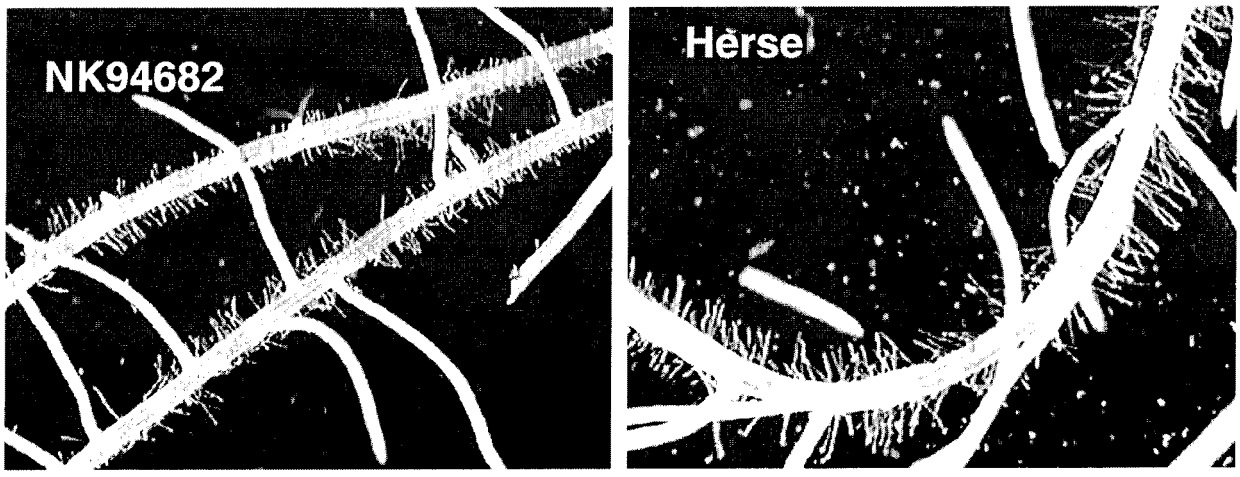


Figure **3.12.** Root hairs of **NK94682** and Herse grown in solution culture. It is clearly seen that Herse had longer root hairs than **NK94682** in the solution culture.

The root hairs covered just a proportion of the root in the solution culture as exemplified by barley cvs. NK94682 and Herse (Figure 3.12). It is also clearly seen that Herse had much longer root hairs than NK94682 when grown in the solution culture. In field soil the root hair coverage was close to 100 % (Figures 3.10 and 3.11). When grown in field the root hairs were also more curled as compared to the straighter root hairs from the solution culture.

3.6.2 Effect of soil P level and growth medium

The root hair lengths of all cultivars, except NK0058, were shorter at P_0, medium soil P concentration (35 mg P-AL kg^{-1} soil), than at P_{32}, high soil P concentration (87 mg P-AL kg^{-1} soil) (Table 3.6). The increase in root hair length from P_0 to P_{32} was very significant for barley ($P<0.0001$), however for wheat there was only a trend ($P=0.094$). Figure 3.11 shows images of NK946582 and Herse at soil P levels P_0 and P_{32}.

4. Discussion

4.1 P uptake, P concentration and dry matter yields

4.1.1 General comments

Within each of the three pairs of cultivars, there were indications of differences in P concentration, P uptake, grain yields and dry matter production. This was clearly shown in the spring wheat cvs. NK0058 and Diamant and the 2-row barley cvs. Tyra and Herta, however less so for the 6-row barley cvs. NK94682 and Herse. At low soil P level, the three cultivars (Diamant, Herse and Herta) with long root hairs in the previous solution culture experiment (Løes, 2002), performed best. These genotypes are also older as compared to the modern genotypes (see Table 2.2.). Variation in P uptake and dry matter production at low soil P level (i.e. P efficiency) among barley and wheat cultivars has been shown earlier (Schjørring and Nielsen, 1987; Gahoonia and Nielsen, 1996; Römer and Schenk, 1998). However, these authors did not relate the variation between cultivars to the age of the cultivars. Egle et al. (1999) showed that three new wheat genotypes from CIMMYT performed better than an older Mexican variety in terms of P uptake and grain yield at low P level, demonstrating that P efficiency not necessarily is linked to the age of the genotype.

The variation within the pairs of cultivars in P uptake, grain yield and dry matter production was greatest at low soil P level and decreased as the soil P level increased. This is consistent with other results (Schjørring and Nielsen, 1987; Gahoonia et al., 1999; Bates and Lynch, 2000a). This suggests that the effect of root hairs on the P uptake, or any other factor affecting the P uptake (e.g. rhizosphere exudation of organic acids, phosphatases etc), is greatest when access to P is limited. It also indicates that when soil P availability is high, root hairs (or other factors enhancing P uptake) are less important in the P acquisition. P transport in soil occurs by diffusion, and on soils low in available P, the effective diffusion coefficient D, ($cm^2 s^{-1}$) is usually smaller than on soils with higher available P levels. Hence root hairs should have a minimal influence on P uptake at high soil P level (Barber, 1995).

4.1.2 P concentration and dry matter yields

The results showed that the soil P level mostly influenced the shoot P concentration early in the season and to a lesser degree later. On 21 June there was a significantly lower shoot P concentration in the P_0 than the P_{32} treatment. However, there was no significant difference between the P treatments later on in the season. In an experiment with Arabidopsis, the maximum P concentration in the plants occurred at a later stage at the lowest P level as compared to the higher P levels (Bates and Lynch, 2000a). Similarly, it might be that the wheat and barley at P_0 reached maximum P concentration after the time of harvest of the shoots on 21 June, and therefore was not recorded. The reason for the lower P concentration in P_0 early in the season may also be a poorly developed root system. Lower root densities as soil P level decreased as shown in the root in-growth study, might have affected shoot P concentration most when the soil P level was low and thus access to P was limited.

Generally, decreasing shoot P concentration was recorded as the wheat and barley plants grew older (in P_{16}, P_{32} and P_{48}). This typical trend in cereals is discussed by Mengel and Kirkby (1987): Vigorous growth after tillering causes a dramatic reduction in the mineral concentration of the plant by dilution. Once the ears are fully developed, there is little change in the concentration of N, P and K expressed in terms of the whole plant. Within the plant itself, however, considerable changes occur between tissues, for during the ripening period high quantities of N and P are translocated from the leaves and stems to the grain.

In this field trial, the variation in grain yield and dry matter production between the cultivars was probably affected by other factors (internal and external) in addition to P efficiency and soil P level. Internal factors (genotypic) such as growth period and resistance to fungi infestation may account for part of the variation in grain yield and dry matter production among the cultivars. External factors (e.g. soil texture, soil moisture content, soil nutrient status etc) were probably negligible as the P plots were situated in a very homogenous field plot experiment. However, as this experiment had no replicates, there is no measurement of the possible variation between the P plots. As the calculations of P uptake are based on the dry matter production, sources of errors would affect the P uptake values as well as the dry matter values. Overall, the values are considered to be representative as the sampling area by final harvest was fairly large ($-3\ m^2$). The sampling area by the harvests of the shoots was

much smaller (0.15 m^2), however, fairly representative when comparing the cultivars and P levels within each date of harvest.

Generally, the dry matter production and grain yield increased with increasing soil P level. At P_0 the grain yield ranged from 2.3 to 3.7 t ha^{-1}, whereas at P_{32} it ranged from 4.1 to 5.6 t ha^{-1}. In terms of dry matter production and grain yield, most of the cultivars, and in particular the old wheat cultivar Diamant, responded negatively at the highest soil P level (P_{48}). At P_{48} the cultivars also had a higher grain P concentration, though never in the toxic range. However, the modem barley cultivar Tyra responded positively in terms of dry matter and grain yield at the highest soil P level, and grain P concentration was not increased. In a solution culture experiment, Loneragan and Asher (1966) reported that high P levels in the root medium depressed growth in some plant species. This effect may be dependent on P retarding the uptake and translocation of some micronutrients such as Zn, Fe and Cu (Mengel and Kirkby, 1987).

4.1.3 Grain P concentration

The higher P concentration in the grain of wheat compared to barley is consistent with findings of Uhlen and Tveitnes (1995) in a 12-year crop rotation trial with normal P applications (3.5 kg P ha-' year-'). This is because wheat is awnless when threshed, compared to barley, and therefore has a higher P content.

4.2 P uptake efficiency and P utilisation efficiency

In P efficiency, a distinction is made between P uptake efficiency (total P content in grain and straw) and P utilisation efficiency (g DM per mg P in shoots). Romer and Schenck (1998) found only a weak correlation between them, which suggests that these are two different traits. Therefore they suggested, in breeding of low P demand cultivars, a combination of high P uptake efficiency and high P utilisation efficiency may be possible.

Diamant, Herta and to some extent Herse, had a higher total P uptake (P in grain and straw) at the lower P levels compared to NK0058, Tyra and NK94682, respectively, indicating a higher P uptake efficiency in these cultivars. Higher shoot P concentration early in the season in Herse and Diamant as compared to NK94682 and NK0058, respectively, may indicate a

higher P uptake rate in these cultivars. However, the shoot P concentrations among the three pairs of cultivars later on in the season were opposite that of the shoot P concentrations early in the season. In P_0 Diamant, Herse and Herta had the lower shoot P concentrations by anthesis and grain formation, indicating a higher P utilisation efficiency (g DM per mg P in shoots) in these cultivars. For Tyra the relative high P harvest index indicated a high P utilisation efficiency. Nevertheless, the poor yield of Tyra at low soil P levels is probably due to a low P uptake efficiency. The higher total dry matter and grain yield in Diamant, Herta and partly Herse at the lower P levels (i.e. higher P efficiency), is therefore probably due to a combination of higher total P uptake and P utilisation efficiencies. The results could not tell to which extent the six different cultivars had a combination of, for instance, medium P uptake efficiency and high P utilisation efficiency, or vice versa. However, according to Marschner (1995), a higher P efficiency is usually attributed to the uptake of P by roots.

In five out of the six cultivars, the dry matter and grain yield was reduced at the highest P level (P_{48}) as compared to P_{32}. In an experiment with barley cultivars, high P availability reduced plant Zn uptake (Zhu *et* al., 2002). Unfortunately, Zn was not recorded in the plant tissue in this study. In conclusion, Zhu et al. suggested that high P uptake efficiency might potentially reduce Zn accumulation in plant tissues, which need be taken into account when selecting and breeding for P-efficient cultivars. This may be a possible explanation for the negative yield response in the P-efficient cultivar Diamant at high soil P level, and the positive yield response in the P-inefficient Tyra.

4.3 Protein, magnesium, calcium and potassium concentration

The average contents for N, Mg, Ca and K in the grain are in good agreement with the results of a 12-year crop rotation trial by Uhlen and Tveitnes (1995). The small deviations from the reported average grain chemical composition were small and show that most probably the access to all of these nutrients was sufficient during the experiment.

4.4 1000-grain weight and hectolitre-weight

In the barley cultivars both hectolitre and 1000-grain weights increased with increasing soil P level. However, in the wheat cultivars the highest values were obtained at the second highest P level, P_{32}, which also had the highest wheat grain yields. Grain weight is an imporrtant yield

component. As 1000-grain weight and grain yield were well correlated for both the barley and the wheat, this indicated that 1000-grain weight had a marked influence on the grain yield in this study. Dann (1969) found 1000-grain weight in wheat to increase with increasing P fertilisation, and suggested 1000-grain weight as a sensitive indicator of fertiliser effects. Higher P level was reported to increase 1000-grain weight also in barley (MacLeod, 1969). In the literature, nothing was found on the relationship between hectolitre-weight and P level, however, as found in this study, hectolitre-weight and 1000-grain weight were well correlated.

4.5 Grain moisture content / phenological development

The grain moisture content, as well as the recording of phenological development, clearly indicated that increasing soil P concentration increased the rate of development in the barley and the wheat from the tillering stage. In other words, low soil P concentration delayed phenological development. Other authors have reported similar results. Rodriguez et al. (1998) showed that P deficiency both delayed the emergence of leaves on the main stem and on the tiller, and delayed the time from emergence to anthesis in wheat. Elliot et al. (1997) reported that in acutely P deficient plants development was noticeably delayed from the early seedling stage. In severely deficient plants, and to a lesser extent in moderately stressed plants, anthesis was delayed and these plants ripened later than P-adequate plants. P fertiliser application increased the rate of crop development in barley from emergence to floral initiation and advanced anthesis (Shepherd et al., 1987).

There were no replicates of the soil P levels in this experiment. Nevertheless, the soil P level clearly had an effect on the phenological development, showing that the experiment was successful.

4.6 Root in-growth

There was generally an increased root weight in the in-growth bags as the P level increased. It is likely that cereal plants grow most roots where P is easily available. Increased root growth has also been found in corn as the soil P level increased (Mackay and Barber, 1985). Furthermore, the root/shoot ratio decreased with decreasing P level. This may be controversial, as many authors (e.g. Fohse et al., 1988) have found an increased root/shoot ratio in low-P soil, because more photosynthates are allocated to root growth. A likely

explanation for this discrepancy is that the soil P level of the lowest P level in this study was not extremely low; it was still in the medium P-AL class.

Furthermore, there was a marked difference in root in-growth between the two cereal species; the barley grew more roots in the topsoil than the wheat. Using the in-growth method no differences among the cultivars were found. However, the result suggested that the cultivars with short root hairs in the solution culture (NK0058, NK94682 and Tyra) had a higher root/shoot ratio as compared to the cultivars with long root hairs in the solution culture. This might be a mechanism compensating for the factors that enhanced the P uptake in the P-efficient cultivars (Diamant, Herse and Herta).

Average specific root lengths of 17 wheat and 35 barley cultivars were measured in a pot trial and found to be: 189 m root g-' root DM (wheat) and 223 m root g^{-1} root DM (barley) (Løes, pers. comm.'). The higher specific root length of barley as compared to wheat, suggested finer roots in barley.

4.7 Root hair length

4.7.1 Effect of cultivar

The root hair lengths of the six cultivars of this study only partly confirmed what was found in the previous low-P solution culture experiment (Løes, 2002). The three pairs of cultivars of this study were selected among the cultivars with the longest and shortest root hairs in the solution culture experiment. The results showed that Herse had longer root hairs than NK94682 in either P levels, and Herta had longer root hairs than Tyra in P_{32}. However, the results were inconclusive as to which of the two wheat cultivar had the longer root hairs, and in P_0, Tyra tended to have longer root hairs than Herta. These two results were unexpected, however they are difficult to explain. A systematic difference in average root hair length values due to operator is not likely, as parallel measurements of five samples gave quite comparable results. Average values measured by Jon Magne Holten/Anne-Kristin Løes were 0.41/0.44, 0.46/0.47, 0.49/0.48, 0.66/0.63 and 0.75/0.84, respectively. Furthermore, the root hair lengths were measured on 4-week-old roots, which were somewhat more deteriorated

[1] Anne Kristin Løes, NORSØK (Norwegian Centre for Ecological Agriculture), N-6630 Tingvoll, Norway

than younger roots. However, this error was systematic in all root samples, and would probably not affect the relative difference in root hair length between the cultivars and P levels.

Even though the number of root hair counts were increased from 60 to 300, the coefficient of variance (CV%) for root hair length remained high, which demonstrates that root hairs grown in soil exhibit a large variation in length.

In this study, the old cultivars Herse and Herta generally had the longest root hairs. However, old cultivars do not necessarily have long root hairs, as an old barley cultivar had the shortest root hair length in the previous solution culture experiment (Løes, 2002). Conversely, even though dwarf wheat NK0058 had short root hairs in the solution culture experiment, an other dwarf cultivar was reported to have long root hairs.

Compared to previously published results on root hair length in wheat and barley, the differences between the cultivars with longest and shortest root hairs of this study were much smaller. Gahoonia *et* al. (1999) presented two cultivars of wheat grown in field with approximately 1.3 and 0.6 mm long root hairs. Corresponding values for two pairs of barley cultivars were 1.1 and 0.6 mm. In the cases where the cultivars of this study did have significantly different root hair lengths, the difference between the cultivars with the longest and shortest root hairs were just 0.07-0.11 mm as compared to a difference of 0.5-0.6 mm in the study of Gahoonia *et* al. (1999). However, in the previous solution culture experiment, the difference in root hair length was 0.39 mm between Diamant (longest) and NK0058 (shortest) and 0.18-0.19 mm for Herse/Herta (longest) and NK94682/Tyra (shortest) (see Table 2.2). It was evident that under the field conditions of this study the differences in root hair lengths among the pairs of cultivars were much smaller than in the solution culture experiment.

From the results of this study it is difficult to suggest cultivars suited for breeding for particularly long root hairs, because of the small difference in average root hair length under field conditions.

4.7.2 Effect of growth medium (soil vs. solution culture)

The growing media clearly had a major impact on root hair length. As shown by the results, the root hair length was considerably longer by field conditions than in the solution culture. Therefore, it seems that the root hair length was more affected by the growing media (environment) than by the cultivar. Previously, similar root hair lengths of barley and wheat cultivars grown in low-P soil and low-P solution culture have been reported (Gahoonia et al., 1999).

Furthermore, the present results indicated that the ranking of the cultivars varied between the two different growing media. This makes it hard to tell whether a cultivar belongs to a group of cultivars with long or short root hairs.

The influence of the environment on root hair formation is well known. A number of environmental factors affect root hair formation: pH and concentration of Ca (Ewens and Leigh, 1985), nitrate concentration (Ewens and Leigh, 1985), phosphate concentration (Fohse and Jungk, 1983; Bates and Lynch, 1996), aeration (Jeschke and Stelter, 1976), soil moisture (Mackay and Barber, 1984), soil density (Michael, 2001) and soil texture (Greenland, 1979) etc. The solution culture generally produced shorter root hairs (see Table 2.2), than in the field conditions of this study. Longer root hairs in soil as compared to solution culture have also been found in maize (Zea mays L.) (Mackay and Barber, 1984) and barley (Gahoonia and Nielsen, 1997). Michael (2001) put forward a hypothesis that ethylene is the central regulatory mechanism governing root hair formation. Reduced gas exchange, causing a higher level of ethylene, would in this way increase root hair length. The soil of this study was dense clay and the growing season was fairly wet, which may have retarded the diffusion of ethylene in the soil, as compared to the circulating nutrient solution, which probably had a better gas exchange. The higher ethylene level might thus explain the longer root hairs in the field soil.

Gahoonia et al. (1999) suggested that ranking of cereal cultivars for root hair length could be performed in less laborious solution culture with reasonable accuracy. However, the results from the field conditions of this study indicated that ranking might not so easily be replaced by solution culture experiments. Due to this discrepancy, more research on root hair growth under different growth conditions is needed to clarify to which extent there is any interaction

between different cereal cultivars and environments. Furthermore, because the environmental factors may have more influence on the root hair length than the genotype (Løes, 2002), screening of cereal cultivars for root hair length should be performed under strictly defined growth conditions (texture, density, moisture, pH, nutrient concentration etc).

4.7.3 Effect of soil P level

The results of this field study showed that in five out of the six cereal cultivars, the root hair length was slightly, but significantly shorter at medium soil P concentration (P_0) than at high soil P concentration (P_{32}). This contrasts with former findings on the relation between root hair length and P level in the growing media. Increased root hair length by low P levels was found in barley grown in the field (Gahoonia et al., 1999), in maize grown in soil (Mackay and Barber, 1984), in rape (Bhat and Nye, 1973), in rape, tomato and spinach grown in solution culture (Fohse and Jungk, 1983) and in the model plant Arabidopsis thaliana (Bates and Lynch, 1996).

The apparent discrepancy on the relationship between P level and root hair length in this study compared to former studies may have several reasons. Except for the one study of barley grown in field, the former studies have been carried out in laboratory experiments, and, except for the two studies of barley and maize, only non-cereal species were used. This undermines the hypothesis of longer root hairs in cereals as a response to decreasing P level. Differing soil moisture content is an unlikely reason as the P plots of this study were situated in the same field plot experiment. As the P plots differed only very slightly in soil texture, this is also an unlikely reason. However, different soil density (not recorded) in the plots might be an alternative explanation for the different root hair lengths at the two soil P levels. When the in-growth tubes were placed in the soil and filled, the compaction of the soil might not have been similar in the in-growth tubes. According to the hypothesis of Michael (2001), higher levels of ethylene, due to reduced gas exchange, might have increased the root hair length in the most compacted in-growth tubes.

In the work of Gahoonia et al. (1999), the included pictures showed that the root hairs of barley almost disappeared at moderate P fertilisation (20 kg P ha-' yr^{-1}). Their results in barley could not be confirmed in this study, however for wheat Gahoonia et al. (1999) found no consistent relationship between soil P level and root hair length. No relationship between soil

P level and root hair length was also reported from another study in wheat (Ewens and Leigh, 1985) as well as for maize (Mackay and Barber, 1985) and for grass and legume species (Caradus, 1980). It is reasonable to believe that cereal species such as barley and wheat respond similarly to changing P level in their root hair growth.

The results of this study suggested that root hair length of wheat and barley did not decrease with increasing soil P level. Rather on the contrary, the results indicated that root hair length is increased with increasing P level. It is logical that the roots were affected by soil P level, as the root in-growth evidently was higher at high soil P levels (see Section 4.6).

4.8 Root hairs and P uptake efficiency

The results indicated that the three cultivars with long root hairs in the previous solution culture experiment were more P efficient as seen by the higher yield and higher total P uptake at low soil P level. The differences between the cultivars were probably due to higher P uptake efficiency, and to a lesser extent higher P utilisation efficiency. This has been demonstrated by other authors. In a field trial with wheat genotypes varying in P efficiency, Egle *et* al. (1999) showed only 10% variation in the P utilisation efficiency, whereas the variation in the P uptake efficiency was approximately 30%. However, the differences in root hair lengths as well as root growth within the pairs of cultivars were small or insignificant in this study. Due to the small variations in root hair length and root growth between the cultivars, the higher P uptake efficiency in these three cultivars was probably mostly attributed to other factors enhancing the P uptake. This suggests that variations between the cultivars in release of organic acids and acid phosphatase played an important role in the P uptake efficiency.

There is substantial evidence that root hairs are important for P acquisition (e.g. Misra *et* al., 1988; Gahoonia and Nielsen, 1998; Bates and Lynch 2000b). However, this study can only suggest a link between root hair length and P uptake efficiency. A root hairless barley mutant found in a population of wild type (Pallas, a barley cultivar) producing normal, 0.8 mm long root hairs can be taken as an example showing the importance of root hairs in P uptake (Gahoonia *et* al., 2001). Pallas depleted nearly two times more P from organic and inorganic fractions than the mutant. Pallas also induced higher activity of acid phosphatase in the rhizosphere than the mutant, suggesting a link between root hair formation and acid phosphatase activity.

5. Conclusion

The wheat and barley cultivars with long root hairs in the previous solution culture experiment were more P-efficient *(i.e.* higher yield and higher total P uptake at low soil P availability) compared to the cultivars with short root hairs. Compared to the previous solution culture experiment, the root hairs were longer in this field study, however the differences between the cultivars in root hair length were much smaller, and in a few cases insignificant. The variation in P efficiency between the cultivars might be due to different root hair lengths, however it is suggested that variations in other factors such as root growth, exudation of organic acids, acid phosphatase, and lowering of rhizosphere pH played an important role in this study.

Contrary to a previous study, this study suggested that root hair length of barley did not decrease with increasing soil P level. The results rather indicated longer root hairs in wheat and barley as a response to high P level.

As the soil P level increased, the variation between cultivars in terms of yield and total P uptake diminished, suggesting that the factors which were important for P uptake at low soil P availability, were less important at high soil P availability.

Increasing soil P level also advanced the rate of phenological development from the tillering stage, demonstrating this experiment was successful. Increasing soil P level increased 1000-grain and hectolitre-weight as well.

In conclusion, this study suggested that there is great variation in P efficiency between cereal genotypes, which in part may be explained by different root hair lengths. Adapting crops to lower soil P levels by selection and breeding for more P-efficient genotypes is thus a possible means of increasing the sustainability of agroecosystems.

6. References

Ahmad Z, Gill MA and Qureshi RH (2001). Genotypic variations of phosphorus utilization efficiency of crops. Journal of Plant Nutrition 24, 1149-1171.

Asmar F, Gahoonia TS and Nielsen NE (1995). Barley genotypes differ in extra-cellular phosphatase activity and depletion of organic phosphorus from rhizosphere soil. Plant and Soil 172, 117-122.

Baon JB, Smith SE and Alston AM (1994). Growth response and phosphorus uptake of rye with long and short root hairs: Interaction with mycorrhizal infections. Plant and Soil 167, 247-253.

Bailey PHJ, Currey JD and Fitter AH (2002). The role of root system architecture and root hairs in promoting anchorage against uprooting forces in *Allium cepa* and root mutants of *Arabidopsis thaliana*. Journal of Experimental Botany 53, 333-340.

Barber SA (1995). Soil Nutrient Bioavailability – A Mechanistic Approach. 2nded. John Wiley & Sons, New York, 414 p.

Bates TR and Lynch JP (2001). Root hairs confer a competitive advantage under low phosphorus availability. Plant and Soil 236,243-250.

Bates TR and Lynch JP (2000a). Plant growth and phosphorus accumulation of wild type and two root hair mutants of *Arabidopsis thaliana* (Brassicaceae). American Journal of Botany 87, 958-963.

Bates TR and Lynch JP (2000b). The efficiency of *Arabidopsis thaliana* (Brassicaceae) root hairs in phosphorus acquisition. American Journal of Botany 87,964-970.

Bates TR and Lynch JP (1996). Stimulation of root hair elongation in *Arabidopsis thaliana* by low phosphorus availability. Plant Cell Environment 19, 529-538.

Batten GD (1992). A review of phosphorus efficiency in wheat. Plant and Soil 146, 163-168.

Bhat KKS and Nye PH (1973). Diffusion of phosphate to plant roots in soil. I. Quantitative autoradiography of the depletion zone. Plant and Soil 38, 161-175.

Caradus JR (1994). Selection for improved adaptation of white clover to low phosphorus and acid soils. Euphytica 77, 243-250.

Caradus JR (1980). Distinguishing between grass and legume species for efficiency of phosphorus use. New Zealand Journal of Agricultural Research 24, 353-358.

Clark RB and Duncan RR (1991). Improvement of plant mineral nutrition through breeding. Field Crop Research 27, 219-240.

Dann PR (1969). Response by wheat to phosphorus and nitrogen with particular reference to "haying-off'. Australian Journal of Experimental Agriculture and Animal Husbandry 9, 625-629.

Egle K, Manske G, Romer W and Vlek PLG (1999). Improved phosphorus efficiency of three new wheat genotypes from CIMMYT in comparison with an older Mexican variety. Journal of Plant Nutrition and Soil Science 162, 353-358.

Elliot DE, Reuter DJ, Reddy GD and Abbott RJ (1997). Phosphorus nutrition of spring wheat (Triticum aestivum L.) 1. Effects of phosphorus supply on plant symptoms, yield, components of yield, and plant phosphorus uptake. Australian Journal of Agricultural Research 48, 855-867.

Ewens M and Leigh RA (1985). The effect of nutrient solution composition on the length of root hairs of wheat (Triticum aestivum L.). Journal of Experimental Botany 36, 713-724.

Fohse D, and Jungk, A (1983). Influence of phosphate and nitrate supply on the root hair formation of rape, spinach and tomato plants. Plant and Soil 74, 359-368.

Fohse D, Claassen N and Jungk A (1988). Phosphorus efficiency of plants. I. External and internal P requirement and P uptake efficiency of different plants species. Plant and Soil 110, 101-109.

Fohse D, Claassen N and Jungk A (1991). Phosphorus efficiency of plants. II. Significance of root radius, root hairs and cation-anion balance for phosphorus influx in seven plant species. Plant and Soil 132, 261-272.

Gahoonia TS and Nielsen NE (1992). The root-induced pH change on the depletion of inorganic and organic phosphorus in the rhizosphere. Plant and Soil 143, 183-189.

Gahoonia TS and Nielsen NE (1996). Variation in acquisition of soil phosphorus among wheat and barley cultivars. Plant and Soil 178,223-230.

Gahoonia TS, Care D and Nielsen NE (1997). Root hairs and acquisition of phosphorus by wheat and barley cultivars. Plant and Soil 191, 181-188.

Gahoonia TS and Nielsen NE (1998). Direct evidence on participation of root hairs in phosphorus (32P)uptake from soil. Plant and Soil 198, 147-152.

Gahoonia TS, Nielsen NE and Lyshede OB (1999). Phosphorus (P) acquisition of cereal cultivars in the field at three levels of P fertilization. Plant and Soil 211, 269-281.

Gahoonia TS, Asmar F, Giese H, Gissel-Nielsen G and Nielsen NE (2000). Root-released organic acids and phosphorus uptake of two barley cultivars in laboratory and field experiments. European Journal of Agronomy 12, 281-289.

Gahoonia TS, Nielsen NE, Priyavadan AJ and Jahoor A (2001). A root hairless barley mutant for elucidating genetic of root hairs and phosphorus uptake. Plant and Soil 235,211-219.

Gerloff GC and Gabelmann WH (1983). Genetic basis of inorganic plant nutrition. In: Encyclopaedia of Plant Physiology. A Lauchli and RL Bieleski (eds.), New series Vol. 15b, Springer Verlag, New York, pp. 453-480.

Greenland DJ (1979). The physics and chemistry of the soil-root interface: some comments. In: The Soil-Root Interface. JL Harley and RS Russel (eds.), Academic Press, London, pp. 83-98.

Gollany HT and Schumacher TE (1993). Combined use of calorimetric and microelectrode methods for evaluating rhizosphere pH. Plant and Soil 154, 151-159.

Hinsinger, P (2001). Bioavailability of soil organic P in the rhizosphere as affected by root-induced chemical change: a review. Plant and Soil 237, 173-195.

Hofer, R (1996). Root hairs. In: Plant roots – The hidden half. Y Waisel, A Eshel, and U Kafkafi (eds.), 2nded,. Marcel Dekker, New York, pp. 111-133

IFOAM (2002). International Federation of Organic Agricultural Movements. http://www.ifoam.org

Itoh S and Barber SA (1983). Phosphorus uptake by six plant species as related to root hairs. Agronomy Journal 75,457-461.

Jakobsen I and Nielsen NE (1983). Vesicular Arbuscular Mycorrhiza in field-grown crops. I. Mycorrhizal infection in cereals and peas at various time and soil depths. New Phytologist 93, 401-413.

Jakobsen I, Abbott LK and Robson AD (1992). External hyphae of vesicular-arbuscular mycorrhizal fungi associated with *Trifolium subterraneum* L. I. Spread of hyphae and phosphorus inflow into roots. New Phytologist 120,371-380.

Jeschke WD and Stelter W (1976). Measurement of longitudinal ion profiles in single roots of Hordeum and Atriplex by use of flameless atomic absorption spectroscopy. Planta 128, 107-112.

Jungk, A (2001). Root hairs and the acquisition of plant nutrients from soil. Journal of Plant Nutrition and Soil Science 164, 121-129.

Kapulnik Y and Kushnir U (1991). Growth dependency of wild, primitive and modern cultivated wheat lines on vesicular-arbuscular mycorrhiza fungi. Euphytica 56, 27-36.

Krogstad T and Løvstad Ø (1987). Fosfor i jord og vann. Jord og Myr 6, 189-208.

Krogstad, T (1992). Metoder for jordanalyser. Institutt for jordfag, Agricultural University of Norway. Rapport 6/92, 32 p.

Loneragan JF and Asher CJ (1966). Response of plants to phosphate concentration in solution culture: 11. Rate of phosphate absorption and its relation to growth. Soil Science 103, 311-318.

Løes, AK (2002). Rothår på bygg og hvete. Form og funksjon, i næringsløsning og i jord. In: Jord- og plantekultur 2002. The Norwegian Crop Research Institute (Planteforsk), pp. 214-219.

Løes, AK and Øgaard, AF (2001). Long-term changes in extractable soil phosphorus (P) in organic dairy farming systems. Plant and Soil 237, 321-332.

MacLeod LB (1969). Effects of N, P and K and their interactions on the yield and kernel weight of barley in hydroponic culture. Agronomy Journal 61, 26-29.

Mackay AD and Barber SA (1984). Comparison of root and root hair growth in solution and soil culture. Journal of Plant Nutrition 7, 1745-1757.

Mackay AD and Barber SA (1985). Effect of soil moisture and phosphate level on root hair growth of corn roots. Plant and Soil 86, 321-331.

Marschner H (1995). Mineral Nutrition of Higher Plants. 2nd ed. Academic Press, London. 889 p.

Mengel K and Kirkby EA (1987). Principles of Plant Nutrition. 4th ed. International Potash Institute, Worblaufen-Bern, Switzerland. 687 p.

Michael G (2001). The control of root hair formation: suggested mechanisms. Journal of Plant Nutrition and Soil Science 164, 111-119.

Misra RK, Alston AM and Dexter AR (1988). Role of root hairs in phosphorus depletion from macrostructure soil. Plant and Soil 107, 11-18.

Nielsen NE and Barber SA (1978). Differences among genotypes of corn in the kinetics of P uptake. Agronomy Journal 70, 695-698.

Nielsen NE and Schjørring JK (1983). Efficiency and kinetics of phosphorus uptake from soil by various barley genotypes. Plant and Soil 72,225-230.

NSF (Norges standardiseringsforbund) (1984). Bestemmelse av ortofosfat. NS 4725. 3rd edition.

NSF (Norges standardiseringsforbund) (1975). Vannundersøkelse. Bestemmelse av ammonium-nitrogen, NS 4746. 1st edition. 7 p.

Rodriguez, D, Pomar MC and Goudrian J (1998). Leaf primordia initiation, leaf emergence and tailoring in wheat (Triticum aestivum L.) grown under low-phosphorus conditions. Plant and Soil 202, 149-157.

Romer W and Schenk H (1998). Influence of genotype on phosphate uptake and utilization efficiencies in spring barley. European Journal of Agronomy 8, 215-224.

Sattelmacher B, Horst WJ and Becker HC (1994). Factors that contribute to genetic variation for nutrient efficiency of crop plants. Zeitschrift für Pflanzenernahrung und Bodenkunde 157, 215-224.

Schjørring JK and Nielsen NE (1987). Root length and phosphorus uptake by four barley cultivars grown under moderate deficiency of phosphorus in field experiments. Journal of Plant Nutrition 10, 1289-1295.

Schachtscabel, P, Blume, H-P, Briimmer G, Hartge, KH and Schwertmann U (1998). Lehrbuch der Bodenkunde. F Enke Verlag, Stuttgart, Germany. 494 p.

Shepherd KD, Cooper PJM, Allan AY, Drennan DSH and Keatinge JDH (1987). Growth, water use and yield of barley in Mediterranean-type environments. Journal of Agricultural Science 108, 365-378.

Tinker PB and Nye PH (2000). Solute Movement in the Rhizosphere. Oxford University Press, New York.

Uhlen AK (2001). Korn del III - Forelesningsnotat i PK210: Jordbruksvekster til frømodning. Landbruksbokhandelen, NLH-Ås, Norway. ISBN 82-557-0424-8. 97 p.

Uhlen G and RødD (1983). Frame experiments in comparison with pot- and field experiments for measuring phosphorus and potassium fertilizer responses. Meldinger fra Norges landbrukshøgskole 62 (23), 14 p.

Uhlen G and Tveitnes S (1995). Effects of long-term crop rotations, fertilizer, farm manure and straw on soil productivity. II. Mineral composition of plants, nutrient balances and effects on soil. Norwegian Journal of Agricultural Sciences 9, 143-161.

Zadoks, JC, Zhang, TT and Konzak, CF (1974). A decimal code for the growth stages of cereals. Weed Research 14,415-421.

Zhu YG, Smith FA and Smith SE (2002). Phosphorus efficiencies and their effects on Zn, Cu and Mn nutrition of different barley (Hordeum vulgare) cultivars grown in sand culture. Australian Journal of Agricultural Research 53, 211-216.

Zhu YG, Smith SE and Smith FA (2001). Plant growth and cation composition of two cultivars of spring wheat (Triticum aestivum L.) differing in P uptake efficiency. Journal of Experimental Botany 52, 1277-1282.

Øgaard, AF (1995). Phosphorus fertilization and plant-available phosphorus in relation to risk of eutrophication. Agricultural University of Norway. Doctor Scientiarum Thesis, 1995:l0

Appendix A

		Grain moisture content, %		Dry matter production, kg per daa					Harvest index	1000-grain weight,g	Hecto-litre-weight
	P level	15 Aug	30 Aug	21 June	16 July	9 Aug	Grain	Straw			
NK0058	P_0		24,6	32	362	766	275	279	49,6	24,2	71,9
	P_{16}		24,5	41	370	806	390	365	51,7	26,3	71,6
	P_{32}		30,3	45	459	849	414	408	50,4	28,5	73,2
	P_{48}		23,8	34	333	914	334	368	47,6	24,9	68,4
Diamant	PO		33,5	27	366	776	366	390	48,4	36,1	81,6
	P_{16}		28,4	29	555	1127	460	450	50,5	37,7	81,7
	P_{32}		27,2	66	559	727	421	475	47,O	37,3	81,7
	P_{48}		29,O	32	387	770	351	373	48,5	34,9	80,4
NK94682	P_0	48,0	28,5	31	321	569	233	373	38,4	37,4	63,9
	P_{16}	43,8	22,5		376	793	388	341	53,2	40,6	67,7
	P_{32}	40,9	18,6	71	593	1099	556	352	61,2	42,2	68,1
	P_{48}	43,7	18,5	77	576	912	465	303	60,5	40,7	68,5
Herse	P_0	47,7	21,1	42	445	737	330	267	55,3	40,0	70,1
	P_{16}	41,6	17,7	51	715	921	556	334	62,5	41,6	71,0
	P_{32}	37,9	15,6	91	829	1053	435	259	62,7	41,3	70,6
	P_{48}	28,2	15,6	116	967	941	570	312	64,6	42,6	71,2
Tyra	P_0	48,6	32,8	31	301	632	345	246	58,4	39,5	69,9
	P_{16}	48,5	20,8	27	373	665	353	232	60,3	43,O	71,7
	P_{32}	45,3	21,9	37	441	893	476	306	60,9	45,8	72,2
	P_{48}	43,O	20,O	37	703	919	558	308	64,4	46,4	70,4
Herta	P_0	51,8	41,6	34	331	622	373	374	49,9	42,8	72,6
	P_{16}	46,5	26,3	41	469	853	457	389	54,O	45,8	72,8
	P_{32}	44,6	24,3	54	741	119	530	438	54,8	46,5	74,1
	P_{48}	45,8	21,6	57	555	915	500	406	55,2	48,O	74,1

Appendix B

Cultivar	P level	Harvest	P	NH4-N	K	Ca	Mg
			g kg^{-1} DM				
B223			4,33				
B223		Reference value	4,27 ± 0,29				
B227			0,52				
B227		Reference value	0,508 ± 0,117				
Standard hay			2,78				
Standard høy			2,67				
Standard hay		Reference value	2,68 ± 0,05				
Standard bygg			3,70	17,0	4,47	0,378	1,09
Standard bygg			3,69	15,0	4,55	0,378	1,18
Standard bygg		Reference value	3,60 ± 0,19		4,53 ± 0,13	0,391 ± 0,017	1,17 ± 0,02
Diamant	PO	Grain 5 Sept	4,71	20,6	3,73	0,423	1,29
Diamant	PO	Grain 5 Sept	4,74	19,8	4,10	0,473	1,26
Diamant	P16	Grain 5 Sept	5,11	22,3	4,20	0,484	1,17
Diamant	P32	Grain 5 Sept	4,74	18,3	4,55	0,482	1,13
Diamant	P48	Grain 5 Sept	5,49	20,7	4,56	0,456	1,15
Herse	PO	Grain 29 Aug	4,50	18,6	5,00	0,485	1,20
Herse	P16	Grain 29 Aug	4,35	17,2	4,78	0,436	1,18
Herse	P32	Grain 29 Aug	4,48	14,7	4,95	0,515	1,34
Herse	P48	Grain 29 Aug	4,31	16,0	4,53	0,463	1,26
Herse	P48	Grain 29 Aug	4,51	16,2	4,52	0,420	1,08
Herta	PO	Grain 29 Aug	3,86	17,6	5,85	0,472	1,41
Herta	PO	Grain 29 Aug	3,87	17,8	5,90	0,507	1,31
Herta	P16	Grain 29 Aug	3,95	16,9	5,27	0,535	1,47
Herta	P32	Grain 29 Aug	3,84	14,6	5,00	0,487	0,97
Herta	P48	Grain 29 Aug	4,25	16,9	5,43	0,464	1,43
NK0058	PO	Grain 5 Sept	4,76	23,1	5,31	0,395	1,18
NK0058	P16	Grain 5 Sept	4,89	26,0	5,21	0,457	1,27
NK0058	P32	Grain 5 Sept	5,10	19,3	5,90	0,434	1,11
NK0058	P48	Grain 5 Sept	5,18	24,9	5,84	0,457	1,22
NK0058	P48	Grain 5 Sept	5,24	22,0	5,84	0,447	1,22
NK94682	PO	Grain 29 Aug	5,15	22,2	6,12	0,416	1,08
NK94682	P16	Grain 29 Aug	4,50	18,5	5,13	0,455	1,22
NK94682	P32	Grain 29 Aug	3,69	13,3	4,62	0,484	1,20
NK94682	P48	Grain 29 Aug	4,47	15,7	4,73	0,466	1,26
Tyra	PO	Grain 29 Aug	3,71	15,0	6,23	0,518	1,15
Tyra	P16	Grain 29 Aug	4,05	16,1	5,94	0,417	1,31
Tyra	P32	Grain 29 Aug	4,09	16,3	5,48	0,464	1,30
Tyra	P48	Grain 29 Aug	4,00	15,1	4,77	0,502	1,15
Diamant	PO	Straw	0,73				
Diamant	P16	Straw	0,56				
Diamant	P32	Straw	0,91				
Diamant	P48	Straw	1,22				
Diamant	P48	Straw	1,19				
Herse	PO	Straw	1,11				
Herse	P16	Straw	0,47				
Herse	P32	Straw	0,66				
Herse	P48	Straw	0,58				
Herta	PO	Straw	1,19				

Cultivar	Plevel	Harvest	P
			g kg" DM
Herta	P16	Straw	0,76
Herta	P32	Straw	0,86
Herta	P48	Straw	1,05
Herta	P48	Straw	1,07
NK0058	PO	Straw	1,38
NK0058	P16	Straw	1,42
NK0058	P16	Straw	1,35
NK0058	P32	Straw	1,61
NK0058	P48	Straw	2,02
NK94682	PO	Straw	2,15
NK94682	P16	Straw	1,24
NK94682	P32	Straw	0,99
NK94682	P32	Straw	0,92
NK94682	P48	Straw	1,58
Tyra	PO	Straw	0,93
Tyra	PO	Straw	0,93
Tyra	P16	Straw	0,90
Tyra	P32	Straw	0,96
Tyra	P48	Straw	0,99
Diamant	PO	O9.aug	2,58
Diamant	P16	O9.aug	2,24
Diamant	P32	O9.aug	2,44
Diamant	P48	O9.aug	2,52
Herse	PO	O9.aug	2,70
Herse	P16	O9.aug	2,61
Herse	P32	O9.aug	2,73
Herse	P48	O9.aug	2,75
Herta	PO	O9.aug	2,57
Herta	P16	O9.aug	2,39
Herta	P16	O9.aug	2,31
Herta	P32	O9.aug	2,50
Herta	P48	O9.aug	2,33
NK0058	PO	O9.aug	3,17
NK0058	PO	O9.aug	3,28
NK0058	P16	O9.aug	2,87
NK0058	P32	O9.aug	2,86
NK0058	P48	O9.aug	3,03
NK94682	PO	O9.aug	3,19
NK94682	P16	O9.aug	2,82
NK94682	P32	O9.aug	2,50
NK94682	P48	O9.aug	3,13
NK94682	P48	O9.aug	3,17
Tyra	PO	O9.aug	2,80
Tyra	P16	O9.aug	2,45
Tyra	P32	O9.aug	2,44
Tyra	P32	O9.aug	2,35
Tyra	P48	O9.aug	2,51
Diamant	PO	16 July	2,65
Diamant	P16	16 July	2,53
Diamant	P32	16 July	3,02
Diamant	P32	16 July	3,08
Diamant	P48	16 July	2,78

Cultivar	P level	Harvest	P
			g kg-' DM
Herse	PO	16 July	2,40
Herse	P16	16 July	2,01
Herse	P16	16 July	1,96
Herse	P32	16 July	2,19
Herse	P48	16 July	2,12
Herta	PO	16 July	2,46
Herta	P16	16 July	1,98
Herta	P32	16 July	2,25
Herta	P32	16 July	2,16
Herta	P48	16 July	2,38
NK0058	PO	16 July	3,43
NK0058	P16	16 July	3,20
NK0058	P32	16 July	3,54
NK0058	P48	16 July	2,94
NK94682	PO	16 July	3,34
NK94682	P16	16 July	2,78
NK94682	P32	16 July	2,47
NK94682	P48	16 July	3,03
Tyra	PO	16 July	2,86
Tyra	P16	16 July	2,58
Tyra	P32	16 July	2,70
Tyra	P48	16 July	2,20
Diamant	PO	21 June	2,65
Diamant	P16	21 June	3,56
Diamant	P16	21 June	3,61
Diamant	P32	21 June	4,82
Herse	PO	21 June	2,32
Herse	P16	21 June	2,69
Herse	P32	21 June	3,24
Herse	P32	21 June	3,12
Herse	P48	21 June	4,49
Herta	PO	21 June	1,76
Herta	P16	21 June	2,33
Herta	P32	21 June	3,33
Herta	P48	21 June	3,22
NK0058	PO	21 June	2,94
NK0058	P16	21 June	3,33
NK0058	P32	21 June	4,17
NK0058	P32	21 June	4,13
NK0058	P48	21 June	4,06
NK94682	PO	21 June	1,70
NK94682	P16	21 June	2,02
NK94682	P16	21 June	2,08
NK94682	P32	21 June	2,90
NK94682	P48	21 June	3,49
Tyra	PO	21 June	2,47
Tyra	P16	21 June	2,23
Tyra	P32	21 June	3,02
Tyra	P48	21 June	3,45
Tyra	P48	21 June	3,37

Appendix C

Date		O6.jun	13.jun	20.jun	27.jun	04.jul	1▮.jul	18.jul	25.jul	01.aug	O9.aug	15.aug	22.aug	29.aug
Days after emergence		8	15	22	29	36	43	50	57	64	72	78	86	93
	P level	Zadoks values												
NK0058	P0	12	13	14, 30	30	39	52	64	71	73	73	74	81	83
	P16	12	13 (21)	21, 30	31	39	56	64	71	-	73	76	77	87
	P32	12	13, 21	22, 30	31	45	54	64	71	73	73	75	79	88
	P48	12	13, 21	22, 30	31	45	56	64	73	73	75	76	81	89
Diamant	PO	12	12	14, 30	31	39	56	64	71	71	73	74	81	83
	P16	12	13 (21)	21, 30	31	39	56	64	71	-	75	75	79	85
	P32	12	13, 21	22, 30	31	43	56	68	71	71	73	75	80	88
	P48	12	13	21, 30	31	45	56	68	71	73	73	76	82	87
NK94682	P0	12	12	14, 30	30	39	50	58	75	83	83	85	87	
	P16	12	13, 21	21, 30	30	50	52	58	71	77	83	85	88	
	P32	12	13, 22	23, 30	32	50	56	58	75	83	84	85	89	
	P48	12	13, 22	23, 30	32	50	56	60	75	-	83	84	89	
Herse	PO	12	12	14, 30	30	39	50	60	75	83	83	86	89	
	P16	12	13, 21	21, 30	31	50	58	60	75	83	84	86	89	
	P32	12	13, 21	22, 30	32	50	58	60	75	83	84	88	90	
	P48	12	13, 23	22, 30	32	52	58	60	83	85	86	89	90	
Tyra	PO	12	12	21, 30	31	39	52	56	71	73	80	82	85	
	P16	12	13, 21	21, 30	31	45	52	58	71	-	77	80	85	
	P32	12	13, 21	23, 30	31	50	56	58	77	83	84	85	86	
	P48	12	13, 22	23, 30	32	50	56	60	75	83	84	86	89	
Herta	PO	12	12	13, 30	30	37	50	56	71	75	78	81	85	
	P16	12	13, 21	21, 30	32	45	52	58	75	75	77	83	85	
	P32	12	13, 22	22, 30	32	50	56	60	77	-		84	87	
	P48	12	13, 22	22, 30	31	45	56	58	75	-		83	88	

Appendix D

Date		13.jun	20.jun	27.jun	04.jul	11.jul	18.jul	25.jul	01.aug	09.aug
Days after emergence		15	22	29	36	43	50	57	64	72
	P level	Plant heigth, cm								
NK0058	P0	14	15	28	44	50	58	64	67	67
	P16	15	22	36	48	60	65	70	74	74
	P32	19	23	37	50	55	64	69	69	69
	P48	17	23	40	58	56	64	70	70	70
Diamant	P0	14	19	34	56	68	98	109	111	111
	P16	16	28	40	64	78	103	109	113	113
	P32	18	30	47	72	82	111	114	120	120
	P48	16	29	45	83	70	103	115	115	115
NK94682	P0	13	16	25	43	57	68	73	80	80
	P16	16	30	37	60	64	74	83	86	86
	P32	19	35	49	73	78	92	92	92	92
	P48	19	33	50	67	76	85	86	86	86
Herse	P0	14	17	30	45	60	83	91	98	98
	P16	19	32	45	72	80	95	98	98	98
	P32	20	33	44	70	90	102	107	107	107
	P48	21	41	57	78	90	96	96	96	96
Tyra	P0	14	16	27	43	53	68	74	80	80
	P16	14	24	30	42	58	66	80	80	80
	P32	17	30	40	52	70	74	77	79	79
	P48	16	28	38	55	67	77	79	79	79
Herta	P0	13	14	26	38	55	80	98	102	102
	P16	14	27	35	52	75	95	105	105	105
	P32	16	32	42	62	80	97	98	98	98
	P48	17	30	45	59	88	97	100	100	100