

**CHANGES IN THE SOIL VOLUME EXPLOITED BY ROOTS AS  
INFLUENCED BY DIFFERENTIAL P TREATMENTS**

by  
**Maarten Kamper**

**Dissertation submitted in partial fulfillment of the requirements for the degree  
MAGISTER SCIENTIA in Soil Science  
in the  
Department of Plant Production and Soil Science  
Faculty of Natural and Agricultural Sciences  
University of Pretoria  
Pretoria**

**February 2004**

**Supervisor: Professor A.S. Claassens**



**REVELATION 5:5:** “Then one of the elders said to me: Stop weeping! See, the Lion of the tribe of Judah, the *Root* of David has won! He can open the scroll and open its seven seals!”

## ABSTRACT

Due to the fact that the mechanism of acquisition of phosphorus (P) by roots, is mainly by interception, sufficient P uptake is only ensured by maximal root development (“exploitation”). Pot and field trials were conducted to determine the percentage exploitation of the soil volume by roots. The influence of P on root growth of *Zea Mays* was also studied. Previously, roots were described in terms of root density ( $\text{cm cm}^{-2}$ ,  $\text{cm cm}^{-3}$ ,  $\text{gram cm}^{-2}$  and  $\text{gram cm}^{-3}$ ). In this study roots are described in terms of exploitation which combines length, mass and the rhizosphere. The Gompertz function was used to model exploitation by roots as influenced by P application.

P along with nitrogen and potassium, had a highly significant ( $P < 0.001$ ) effect on root growth in the pot experiments. The root systems’ function changed after 14 days from nutrient acquisition to shoot supportive.

P had no significant effect on root growth in the field trial. Growth was governed by soil moisture, as dryer positions exhibited higher growth. The high P plot had much less root growth in the subsoil than the low P plot. Gompertz functions revealed subtle differences between different treatments.

During the first two weeks (when most P uptake occur) roots exploited at the most 1% of the top soil volume. This implies that any soil analysis (Bray-1 value), should be divided by  $\approx 100$  to render the “exploitable” P. When considering the total P uptake of a maize crop ( $5 \text{ kg P ton}^{-1}$ ), this means that the crop acquires only  $\approx 6\%$  of its P from the “plant available” pool (that is represented by the Bray-1 value). This suggests that roots are indeed able to extract the P from “plant unavailable” pools. Therefore, the term “plant available” is misleading and not descriptive concerning P uptake, and its use should be discontinued.



**Declaration:**

I, the undersigned, hereby declare that the work contained in this thesis is entirely my own original research, except where acknowledged, and that it has not at any time, either partly or fully, been submitted to any other university for the purposes of obtaining a degree.

Signed: *Mkayen*.....

Date: *2004/04/23*.....

## CONTENTS

<b>ABSTRACT .....</b>	<b>iii</b>
<b>LIST OF TABLES .....</b>	<b>x</b>
<b>LIST OF FIGURES .....</b>	<b>viii</b>
<b>INTRODUCTION.....</b>	<b>1</b>
<b>CHAPTER 1: INTRODUCTION.....</b>	<b>1</b>
1.1 THE DEVELOPMENT OF MAIZE ROOTS .....	1
1.1.1 Root growth .....	1
1.1.2 Uptake rate of P over time .....	2
1.1.3 Root morphology .....	2
1.1.4 Genetic factors influencing root growth.....	3
1.2 FACTORS INFLUENCING ROOT GROWTH .....	3
1.2.1 Soil physical factors .....	3
1.2.1.1 Effect of soil moisture on root growth and resultant P uptake.....	3
1.2.1.2 Effect of soil temperature on root growth and resultant P uptake.....	4
1.2.1.3 Effect of soil strength on root growth and resultant P uptake .....	5
1.2.2. Soil chemical factors .....	5
1.2.2.1 Effect of P concentration (placement) .....	5
1.2.2.2 Effect of pH on root growth and subsequent P uptake .....	6
1.2.2.3 Relation between P uptake and root growth .....	6
1.2.3. Soil microbiology .....	8
1.3 HISTORICAL METHODOLOGY IN THE STUDY OF ROOTS .....	8
1.3.1. The measurement of root length .....	8
1.3.2. Surface and volume of the root .....	9
1.3.3. Root density .....	10
1.4. MODELLING OF ROOT GROWTH .....	11
1.5 EXPLOITATION/UTILISATION OF SOIL VOLUME .....	13
1.6 THE MAIN OBJECTIVES OF THIS STUDY WERE TO: .....	13

<b>CHAPTER 2: MATERIALS AND METHODS..</b>	<b>14</b>
2.1 LAYOUT OF THE POT AND FIELD TRIALS.....	15
2.2 DETERMINATION OF VOLUME AND EXPLOITATION.....	16
2.3 MODELLING OF ROOT GROWTH .....	17
2.4 STATISTICAL ANALYSIS .....	18
<b>CHAPTER 3: RESULTS AND DISCUSSION .....</b>	<b>19</b>
<b>3.1. FIRST POT TRIAL .....</b>	<b>19</b>
3.1.1. Root growth and distribution in pots .....	19
3.1.2. Comparison between length and mass .....	20
3.1.3. Exploitation of soil volume .....	25
<b>3.2 Second pot trial .....</b>	<b>29</b>
3.2.1. General growth .....	29
3.2.1.1 Shoot mass and P content of the different treatments .....	29
3.2.1.2 Root development in the different areas of the pot.....	30
3.2.2. Comparison between length and mass.....	32
3.2.2.1 Root: shoot ratio.....	33
3.2.2.2 Length: mass ratio.....	34
3.2.2.3 Root radii .....	36
3.2.3. Exploitation of soil volume .....	37
3.2.3.1 Modelling of root exploitation .....	39
3.2.4 General conclusions on the results of the second pot trial.....	40
<b>3.3 FIELD TRIAL .....</b>	<b>42</b>
3.3.1 Root growth over a 16 week period after planting .....	42
3.3.1.1 Climatic conditions .....	42
3.3.1.2 Root growth in the high and low P treated plots over a 16 week period .....	43
3.3.2 Length to mass ratio .....	47
3.3.3 Exploitation of the soil volume under field conditions .....	50
3.3.3.1 Modelling of the exploitation volume .....	52
3.3.4 Conclusion .....	54
<b>CHAPTER 4: CONCLUSIONS .....</b>	<b>55</b>



**REFERENCES** ..... 57

**ACKNOWLEDGEMENTS** ..... 65

**APPENDIX** ..... 66

## LIST OF FIGURES

Figure 1. Sample positions for the first pot trial (one plant).....	14
Figure 2. Sample positions for the second pot trial.....	15
Figure 3. Sampling positions for the field trial .....	15
Figure 4. Root growth and distribution in the pot, for the 40 mg kg <sup>-1</sup> treatment .....	19
Figure 5. Influence of P application on root length and mass for the respective areas in the pot.....	21
Figure 6. Root length to mass ratios for the different treatments and areas in pots ...	22
Figure 7. Root radii of the OS and OK areas .....	24
Figure 8. Influence of P treatments on the volume of soil exploited by roots of the different areas in the pot (OS and 7S) .....	25
Figure 9. Predicted exploitation (%) of soil by roots by the Gompertz equation in the central areas (OS and 7S) .....	27
Figure 10. Representation of the four different areas and when the major growth occurred.....	28
Figure 11. Increase in shoot dry mass over four weeks for the different P treatments .	29
Figure 12. Changes in P-content of the shoots.....	30
Figure 13. Root mass and length in the different areas as influenced by different P levels over time.....	31
Figure 14. The relative growth between different areas.....	32
Figure 15. The root: shoot (mass) ratios of the different treatments.....	33
Figure 16. Influence of P level on length and mass ratios in different areas.....	35
Figure 17. Radii of the central (KP) and side (K) areas of the different treatments....	36
Figure 18. Percentage soil exploited by roots in different areas.....	38
Figure 19. Changes in the predicted (line) and measured (dot) exploitation volume by roots as influenced by P application and time.....	40
Figure 20. The minimum and maximum temperatures as well as rainfall (vertical bars) at the experimental farm during the course of the field trial.....	42
Figure 21. Root growth in the high and low P plots in the top (0-10cm) soil.....	43
Figure 22. Root growth in the high and low P plots between the 30 to 40cm depths..	44
Figure 23. Root growth of the high and low P plots between the 60 to 70cm depths..	45
Figure 24. Root growth of the high and low P plots between the 80 to 90cm depths..	46
Figure 25. Length to mass ratios of the different position sand plots in the 0-10cm depth.....	47





Figure 26. Length to mass ratios of the different position sand plots in the 30-40cm depth..... 48

Figure 27. Length to mass ratios of the different position sand plots in the 60-70cm depth..... 48

Figure 28. Length to mass ratios of the different position sand plots in the 80-90cm depth..... 49

Figure 29. The exploitation of roots at different depths and positions..... 51

Figure 30. Changes in the predicted (line) and measured (dot) root exploitation as influenced by P over time..... 53



## LIST OF TABLES

Table 1. Characteristics of the soils used.....	14
Table 2. Mean values and significant differences at $LSD_{TUKEY}$ 0.05 of level of fertilisation .....	46
Table 3. Mean values and significant differences at $LSD_{TUKEY}$ 0.05 of level of fertilisation.....	49

## CHAPTER 1: INTRODUCTION

Little attention has been given to the root development of agricultural crops in soil, and as a result even less is known about the relationship between phosphorus (P) uptake and the size of the developed root system. In literature no information exists on the relation between the root's exploited soil volume, resultant P uptake and its relation to P extraction methods (for instance the Bray-1).

This study follows the work of Ochwoh (2002) and De Jager (2002), who studied the phenomenon of P desorption and its relation to the so-called "plant available" and "fixed" P. It aims to interpret their results *via* a study of the root system, therefore incorporating a so called "root factor" in the study of soil P, especially with regards to the effective "exploitation/utilisation" of the soil volume by root systems (percentage of soil used by roots).

### HISTORICAL BACKGROUND

Nobbe (1862) was the first to suggest that nutrient levels in soil influence root development. Through subsequent studies, it became clear that the study of roots is remarkably complex, since it is influenced by numerous chemical, physical and microbiological factors. It also involves laborious sampling and root-soil separation techniques, making it difficult to obtain sufficient repetitions as well as the implementation of standard statistical procedures.

#### 1.1 THE DEVELOPMENT OF MAIZE ROOTS

##### 1.1.1 Root growth

Before looking at the different factors influence on root development, it is necessary to be acquainted with the growth of maize roots in general.

The general growth of maize roots occurs (in phases), in close relation to the top growth. In older cultivars, the growth is rapid for approximately 80 days, during this time the highest root development occurs in the top 0-15cm soil layer, thereafter no major root development occurs (Foth, 1962; Mengel & Barber, 1974a). In modern

cultivars, the rapid growth phase is much shorter, in the region of 50 days. Therefore, for *Zea mays*, most root development happens in the first half of the life cycle of the plant.

Growth in terms of the eventual size of the root system, Oikeh *et al.* (1999) found that size alone does not always relate well to the yield, but also the efficiency of nutrient use. Larger root systems seem to lead to higher drought resistance.

### 1.1.2 Uptake rate of P over time

The uptake rate of P by maize roots is similar to that of potassium, calcium, magnesium, boron, copper, manganese, zinc and iron. Since root deterioration occurs after 80 days after planting (D.A.P.) and only roots younger than 20 days are actively involved in nutrient uptake, it follows that most P uptake ( $\approx 80\%$ ) takes place within 20 D.A.P. The effect of P on relative growth rate can already be observed from 10 to 15 D.A.P. (Mengel & Barber; 1974b; Hajabbasi & Schumacher; 1994).

Barber (1958) found that a stronger relationship exists between shoot P content and yield, than between soil P content and yield. A shoot P concentration of  $5\text{mg kg}^{-1}$  at 30 D.A.P. is deemed necessary for maximal yield (Barry & Miller, 1989).

From these findings it can be seen that most P uptake occurs very early in the life cycle of the plant. Adequate P nutrition early in the plant's development is therefore vital for optimal growth.

### 1.1.3 Root morphology

Cahn *et al.* (1989) found that a relationship exists between elongation rate and root diameter of *Zea mays* in a rhizotron. The relationship is, however, of little use in the field, where numerous other factors can influence the roots' morphology.

In an investigation of root diameters, Pallant *et al.* (1993) found that more than 56% of the total root length of maize is made up of roots whose diameters are less than

0.175mm. More than 35% of the total root length had a diameter smaller than 0.125mm. It is suggested that maize roots develop within a narrow range of diameters. Plant age and different environments seem to have very little effect on the diameter of the roots, suggesting strong genetic influence of root length and distribution (see 1.1.4).

In a study done on morphological changes of maize roots as affected by a P deficiency, it was found that the elongation rate of axial roots remained constant, while the emergence of new axial roots and the elongation of first-order laterals were drastically reduced (Mollier & Pellerin, 1999). These morphological responses are similar to what is observed when root growth is limited by the availability of carbohydrates. The authors suggest that a P deficiency affects root morphology through its effect on the plant's carbohydrate "budget", and that P deficiency has no direct effect on the root morphogenesis.

#### **1.1.4 Genetic factors influencing root growth**

"The growth of maize is cultivar dependent". This statement is also valid for P uptake and utilisation efficiency. Cultivars with larger root systems seem to have higher yields (Fox, 1978; Eghball & Maranville, 1993). From this it seems that genetic factors do influence P uptake, but indirectly. Therefore, the genetic factor can be equally ranked along with the physical, chemical and microbiological factors that govern root growth and P uptake.

### **1.2 FACTORS INFLUENCING ROOT GROWTH**

Root growth is influenced by physical, chemical and microbiological factors.

#### **1.2.1 Soil physical factors**

##### *1.2.1.1 Effect of soil moisture on root growth and resultant P uptake*

Soil moisture's influence on P uptake by onion (*Allium cepa*) was investigated by Dunham and Nye (1973). The results showed that total P uptake was 1.7 nanomoles in the "dry" state, compared to 43 nanomoles in the "wet" state.

For *Zea mays* roots, it was found that optimal growth and P uptake occurs at a matric potential of between  $-20$  kPa and  $-33$  kPa (Olsen *et al.*, 1961; Bar-Yosef & Lambert, 1981; Mackay & Barber, 1985a).

From their results, Mackay and Barber (1985a) also suggested that even diffusion of P is enhanced by an increase in soil moisture, which is supported by the data of Heslep and Black (1954). In a follow up study (Mackay & Barber, 1985b), the influence of soil moisture and P level on root hair development was determined. P uptake was compared at different levels of added P moisture levels. Root hair growth was affected more by soil moisture than by soil P, and as soil moisture increased, there was a decrease in the density of root hairs. Other important findings were:

- root hair length varied from 0.288-0.416mm
- the amount of root hair on the primary roots was the same as that on secondary roots, suggesting that primary roots are just as involved in nutrient uptake as secondary roots.

Other studies showed that P uptake and root distribution correlated well with plant available water (Rex *et al.*, 1985; Aina & Fapohunda, 1986; Eghball & Maranville, 1993).

#### 1.2.1.2 *Effect of soil temperature on root growth and resultant P uptake*

In different studies it was found that optimal dry mass production as well as optimal P uptake occurred at a temperature of approximately  $25$  °C. At other temperatures (especially lower temperatures), P deficiencies are likely to occur (Knol *et al.*, 1964; Mackay & Barber, 1984).

#### 1.2.1.3 *Effect of soil strength on root growth and resultant P uptake*

Greacen and Oh (1972) used principles from statics to describe root growth as influenced by soil strength, wall pressure and hydrostatic pressure. When these forces are in equilibrium, no growth occurs, and when a certain threshold value is exceeded (wall pressure), growth occurs. A relationship was also found to exist between internal pressure and root growth.

Concerning the effect of soil strength on root development, it was found that optimal root growth occurs at soil strengths ranging from 500 to 1000 kPa. At pressures exceeding 2000 kPa, root growth is terminated (Bar-Yosef & Lambert, 1981; Ehlers *et al.*, 1983; Vogel, 1995).

Dwyer *et al.* (1995) investigated whether tillage practices had a notable influence on root growth of maize. The main conclusion was that tillage has no direct influence on root growth, but rather that it influences soil temperature, soil moisture and soil density, which in turn influence root growth.

Concerning soil density, studies showed that it strongly determines diffusion of especially oxygen and P, where increased soil density decreases diffusion (Heslep & Black, 1954).

## **1.2.2 Soil chemical factors**

### *1.2.2.1 Effects of P concentration (placement)*

Since band placement is a common practice for application of P, many attempts have been made to determine and model its effect on root growth. Root growth in fertilised and unfertilised soil is then compared, and a determination of the most efficient placement of P done (De Wit, 1953; Anghinoni & Barber, 1980a; Anghinoni & Barber, 1980b; Zhang & Barber, 1992). These models were developed in pot trials. They performed well under greenhouse conditions at optimal moisture and temperature conditions, but application to field conditions is limited.

Barber and Woodruff (1962) found that band placement of P alone is insufficient for the maize plant to achieve maximum yield if the rows are far apart.

Roots in P band placed rows tend to be more numerous, finer, silkier and more extensively developed in terms of higher order laterals than their counterparts in unfertilised areas. P content of plants was also higher for those plants where P was placed near the seed (Duncan & Ohlrogge, 1958; Garg & Welch, 1967).

Baker and Woodruff (1962) investigated the effect of change in soil volume on P uptake. At a constant P concentration, if the soil volume was increased 32 fold, P uptake increased by  $\approx 75\%$ . This illustrates the importance of interception, because more interceptable P (higher soil volume) resulted in higher P uptake.

The combined effects of wheel traffic, tillage and placement of nitrogen, phosphorus and potassium (NPK) fertiliser, on maize root distribution was studied by Kaspar *et al.* (1991). Increased NPK application increased the length:weight ratio, but had no effect on total root length. Wheel traffic decreased root growth by a factor of two, and it is assumed that compaction caused by uncontrolled trafficking can result in restricted P uptake.

#### 1.2.2.2 *Effect of pH on root growth and subsequent P uptake*

In a study on soybeans, Riley and Barber (1971) found that in a lowering of the soil pH value, the length of roots increased. When fertiliser N was applied as ammonia ( $\text{NH}_4^+$ -N, acidifying), root length was longer and the shoot P content was higher than plants fertilised with nitrate ( $\text{NO}_3^-$ -N, neutralising).

Marschner *et al.* (1986) comments that the rhizosphere pH might differ by as much as 2 pH units less from that of the bulk soil. Iron and manganese deficiencies seem to induce  $\text{H}^+$  excretion by roots to enhance Fe availability, and as a consequence, P availability.

It seems that at a low pH (such as in the rhizosphere) there is a marked increase in P availability.

#### 1.2.2.3 *Relation between P uptake and root growth*

In a study on mostly clay loam soils, Fried *et al.* (1957) compared the rate of P release to the soil solution with the P uptake rate by barley roots. The rate of P release in solution, was found to be from  $14.6 - 16.85 \text{ kg ha}^{-1} \text{ hour}^{-1}$ ; which is nearly 250 times the uptake rate of roots.



It can be stated that the rate of P diffusion ( $D_e = 1 \times 10^{-10} \text{ cm}^2 \text{ s}^{-1}$ ; Barber, 1984) from the desorption surface to the absorbing root is the limiting factor that governs eventual P uptake.

Newman and Andrews (1973) reported (for wheat): as root length increased, so did P uptake. An interesting observation was made in terms of the contrasting behaviour of P and K: at increased root density, K uptake decreased while P uptake increased. This illustrates again that K uptake occurs by diffusion/mass flow and P uptake by interception, since roots compete for K, but not for P.

The influence of root hair on P uptake was found to be measurable only at low levels of P, and root hair density increased as the level of soil-P was decreased (Schenk & Barber; 1979, 1980).

In the 1980s the following facts were known with regards to P uptake:

- root length determines P uptake
- genotypes with a higher root length per gram of shoot have higher opportunity for P uptake
- influx kinetics of P are heritable: genotypes with finer root systems (higher root surface) have a higher P uptake
- predicted P uptake (sensitivity analysis), is influenced more by the extent of the root system than by changes in P concentration in the soil solution (Barber, 1984, Steffens, 1984).

Rex *et al.* (1985) found that P content in plants correlated well with rooting density. P content of soil (EUF-P) had little influence on P content of plants.

In contrast, for N, Wiesler and Horst (1994) showed that N uptake was not related to rooting density and that very low root densities are sufficient to utilise soil N effectively. This finding illustrated the contrasting behaviour of N and P in relation to their uptake by roots. N uptake occurs by mass flow and diffusion while P uptake occurs by means of interception.

### 1.2.3. Soil microbiology

Marschner *et al.* (1986) reported for wheat (*Triticum aestivum* L.) that inoculation with diazotroph bacteria *Azospirillum* increased root length and enhanced formation of lateral roots and root hairs, similarly as was found with the application of auxin. Kabir (1999) investigated the extent of the vertical distribution of arbuscular mycorrhizae, extraradical hyphae and glomolean spores under maize cultivation, it was found that its distribution imitates that of the maize roots. Root colonisation, total hyphae density and spore density were the highest in the topsoil (0-15cm depth), and that tillage reduced total hyphae density and spore density at 0 to 5cm depth. Roots and its growth are therefore strongly dependant upon microbiological factors.

In studies of the relationship between vesicular arbuscular mycorrhizal (VAM) fungi and soil P, it was found that as soil P was increased, VAM colonisation decreased. The Barber-Cushman uptake model had a good correlation between predicted and observed uptake at high soil P, while it under-predicted P uptake at low soil P, implying that VAM is more involved in P uptake at low levels of P (Lu *et al.*, 1994; Lu & Miller, 1994). Quantitatively, it was found that nearly 40% of the total P uptake is attributed to VAM, which decreases as soil P is increased (Lambert *et al.*, 1979).

## 1.3 HISTORICAL METHODOLOGY IN THE STUDY OF ROOTS

### 1.3.1 The measurement of root length

Newman (1966) and Tennant (1975) introduced methods which, due to their simplicity, low cost and reasonable accuracy; remain in use to the present day. In these methods roots are placed on a grid, the number of root-grid intersections is counted and by means of a formula the root length is determined. Drawbacks include the fact that it assumes random distribution of the roots; and when anisotropic distribution and overlapping occur, underestimation results. Visual counting may also be subjective. During the 1980s, two methods were introduced for the measurement of root length: video camera and optical scanner. These methods are deemed more accurate, less time-consuming and more objective than the older methods. They have however, some serious drawbacks:

- the devices and accompanying root analysis software are expensive
- fine roots are often underestimated because they are not successfully detected, due to small diameter and near transparency.

Mass measurements are popular due to the availability and accuracy of the analytical balance. Length measurements are more difficult to obtain and not as trustworthy as a gravimetric analysis. A useful approach is to use a mass measurement and to relate it to a length. Costa *et al.* (2000) presented a relationship where root mass is related to length:

$$y = -1.1156 + 0.1789x \quad (r^2 = 0.98)$$

x: dry weight (gram)  
y: length (km)

Although this relationship is probably strongly cultivar-dependent, it is nonetheless useful when determining root length by means of mass measurement.

### 1.3.2 Surface and volume of the root

To determine root surface area, chemical methods have been introduced, which comprises the measuring of an amount of adsorbent by the root system (Carley & Watson, 1966). The subsequent use of these methods was very limited despite their simplicity.

To determine the volume of the root, the following steps can be followed: using root mass and length and assuming a density of 1 gram cm<sup>-3</sup> (Hackett, 1969), the formula of a cylinder can be used to calculate root volume (Schenk & Barber, 1979).

To determine the size and volume of the rhizosphere has always been a challenge. A simple method is to gently shake the roots a certain number of times: the soil adhering to the roots is assumed to be rhizosphere soil. Average rhizosphere thickness was found to be  $\approx 0.51$ mm for pot grown *Sorghum bicolor*. Root plus rhizosphere volume was found to be  $\approx 14\%$  of the total soil volume in the pot. The method is acceptable because of its usefulness for physically large samples and for a large number of samples (Ortas, 1997).

### 1.3.3 Root density

To determine root density in soil, techniques can be divided into destructive and non-destructive (Brown & Scott, 1984):

- Destructive: necessitate removal of soil cores or the excavation of trenches or pits to sample roots. Drawbacks include the fact that continuous monitoring of the roots through the season is impossible and the soil profile is destroyed.
- Non-destructive: allows continuous visual observation of the roots. This includes the use of rhizotrons, medical duodenoscope, periscope-like devices (endoscopes) and video recording systems.

Time constraints usually determine which technique is to be used. The following comparison by (Brown & Scott, 1984) illustrates the differences in time needed for the different techniques:

Technique	Time per sample
Mini rhizotron	40 minutes
Framed monolith	26 hours
Pin board	26 hours
Core-sampling	9.5 hours
Scope method	1 hour

In pot and field studies, the “core break” method is also popular since it is less time consuming than the direct assessment of core roots: a core is extracted, split open and exposed roots are counted. By using the Lang and Melhuish (1970) relationship, root density can be determined:

$$L = 2N_r$$

$L$  : root length  
 $N_r$  : number of roots per unit surface (for eg. cm<sup>2</sup>)  
 2 : factor assuming random orientation of the roots

Escamilla *et al.* (1991) found that the factor of 2 actually varies between 1.3 (preferential horizontal orientation) to 7.6 (preferential vertical orientation). This also indicates that roots are very seldom randomly orientated in natural conditions,

therefore extensive calibration is necessary to establish a unique factor for every particular soil. This highlights a disadvantage of the method, because the fact that not all the roots are directly assessed, but only those exposed on the central surface.

Perriet *et al.* (1999) used X-ray computed tomography to study roots *in situ*. Soil cores were extracted and scanned by a medical X-ray device. Disadvantages include high cost, a lack of sensitivity towards very fine roots and limited usefulness when the number of samples is large.

#### 1.4 MODELLING OF ROOT GROWTH

Of the numerous ways to describe plant growth, the Richards family of equations is well known, of which the logistic curve and the Gompertz curve are variations:

Logistic:  $y = \frac{a}{1 + bc^x}$

Gompertz:  $\log y = \log a + c^x \log b$

$a$ : total biomass (gram)

$b$ : proportionality constant with respect to  $a$

$c$ : growth rate (gram/day)

$x$ : time after planting

It is assumed that root growth can also be described by using the above-mentioned functions (Steyn, *et al.* 1984).

To describe distribution, models like that of Newman and Andrews (1973), which produced a mathematical expression for soil exploitation of roots, and that of Page and Gerwitz (1974), which used Fick's law to describe root growth. Rose (1983) and Pagès *et al.* (1989) produced models where the root system is depicted as a sum of its individual constituents. Each constituent (primary roots, secondary roots, angles and emission times) has each its own particular equation, which is combined with that of the other constituents to form the eventual model for the entire root system. Due to size and complexity, these models are usually computer based. In the model produced by Benjamin *et al.* (1996) growth is divided into horizontal and vertical directions, and the root system is expressed as a combination of the two. Transpiration, soil moisture, soil density and elemental uptake are also incorporated.

Many attempts were made to link a crop growth model to a root growth model. The main advantage to this is that it may circumvent tedious root sampling. Factors that should be considered are: varying root:shoot ratio due to dependence on soil fertility, soil moisture, cultivar, and temperature (Asseng *et al.*, 1997; Kage *et al.*, 2000).

Grant and Robertson (1997), linked P transformations in soil with a root growth model. The model also considers the following:

- feedback mechanisms for C, P and N ratios
- inorganic P transport
- organic P transformations
- mycorrhizal dynamics
- root-shoot transfer of C (carbohydrate dynamics).

Due to the large number of input variables (52 input variables and 19 equations), and its complexity, this model has very limited applications in field conditions.

Klepper and Rickman (1990) identified problems commonly experienced with root models. They report that, for instance, the Gerwitz and Page (1974) model, although simple, does not work in conditions of intermittent rainfall. Models seem to work well in controlled conditions (glasshouse), but not in field situations. They list a number of requirements that an ideal root growth model should have:

- it should be related to a canopy growth model, and to also take account of carbohydrate fluxes required to grow root systems
- it must state the number and origin of specific axes
- it must account for frequency of occurrence of primary, secondary and higher order branches
- it must consider age of root segments
- it must consider variation of uptake properties of a root segment over time
- it must have the ability to interact with spatial descriptions of soil properties, as for example pockets of P and N, aeration, moisture and branching rate.
- it should take into account calcium deficiency, aluminium toxicity, soil texture, density, water content and root death ( $\approx 1\%/day$ ).

## 1.5 EXPLOITATION/UTILISATION OF SOIL BY ROOTS

In the literature, models as well as all other published research concerning roots, it was customary to express roots as density. This was done in one of the following ways: unit length per unit surface ( $\text{cm cm}^{-2}$ ); unit length per unit volume ( $\text{cm cm}^{-3}$ ); unit mass per unit surface ( $\text{g cm}^{-2}$ ); and unit mass per unit volume ( $\text{g cm}^{-3}$ ). The main drawback of the above-mentioned means of expression is that the rhizosphere is neglected. The amount of soil exploited/utilised by roots is unknown. Wiersum (1961) presented percentage of soil utilised by roots. The percentage of the soil utilised varied from 0.1 to 33%. This data is one of the only examples in literature, using the concept “utilisation”, to express the behaviour of roots. Barber (1984) reports a value of 0.4% exploitation/utilisation in his 1974 field experiment, but no mention is made of how that value was determined. It is thus unknown how “root relevant” a soil analysis value is: does a root have access to the whole amount of a particular element as determined by chemical analysis?

## 1.6 THE MAIN OBJECTIVES OF THIS STUDY WERE TO:

- 1) investigate P's influence on root growth in greenhouse and field conditions
- 2) introduce a more comprehensive and descriptive way to describe roots, namely “exploitation” percentage, an expression that incorporates root length, root mass and the rhizosphere, in order to determine what percentage of the soil volume is used by the root system
- 3) model exploitation over time using the Gompertz function
- 4) relate exploitation to soil analysis value to arrive at a “factor of utilisation” by roots

## CHAPTER 2: MATERIALS AND METHODS

### 2.1 LAYOUT OF THE POT AND FIELD TRIALS

Pot and field experiments were conducted with *Zea mays* (PANNAR 6479) using a sandy clay loam (SCL), taken from an Acrosol and a loamy, mesic, thermic Kandiudalf respectively, characteristics of which are presented in table 1.

**Table 1:** Characteristics of the soils used.

Trial	Soil	pH <sub>(H<sub>2</sub>O)</sub>	Sand (%)	Silt (%)	Clay (%)	P (Bray-1)	
pot	Acrosol	4.9	76	1.5	23.6	1.9 mg/kg	
Field	Kandiudalf	5.3	63	14	23	7mg/kg*	70mg/kg**

\* low P plot

\*\* high P plot

For the pot trials, using 4 litre pots, four levels of P (0, 20, 40 and 80mg P/kg soil) were applied as Ca(HPO<sub>4</sub>)<sub>2</sub>. Soil moisture was maintained at 17% (v/v) at density of 1.1 g cm<sup>-1</sup>. For the first pot experiment three seeds were sown, thinned to one plant per pot after one week. The remaining plant was in the centre of the pot. Two replications were used for a total of 56 pots.

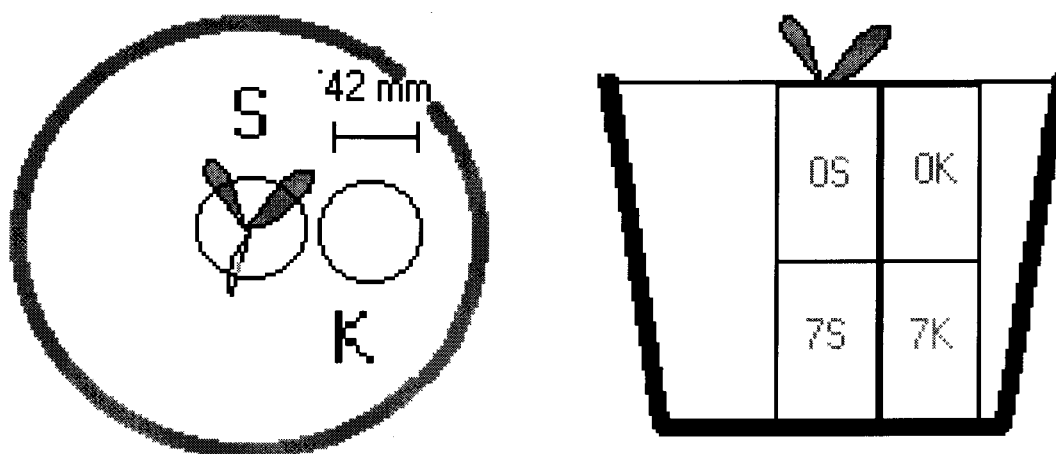


Figure 1. Sample positions for the first pot trial (one plant). S = centre, K = side of the pot, 0 = 0-7cm depth and 7 = 7-14cm in the pot.



For the second pot experiment five seeds were sown, thinned to three plants per pot after one week. Additional N (as  $(\text{NH}_4)_2\text{SO}_4$ ) and K (as KCl) were applied at a rate of 100 and 75 kg/ha respectively. Shoots were harvested, weighed and analysed for P by the vanadomolybdate method.

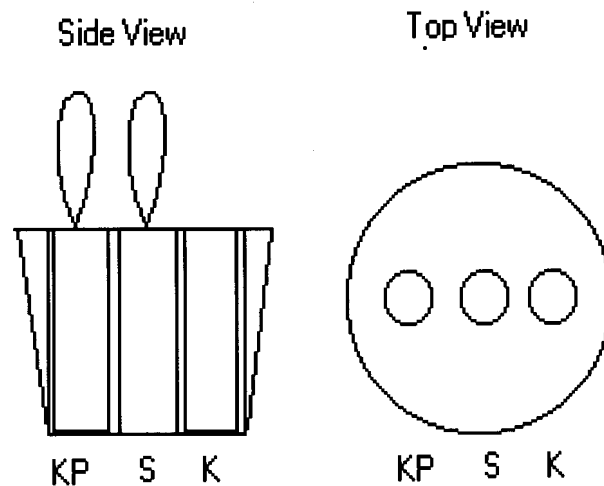


Figure 2. Sample positions for the second pot trial. KP = side with plant, S = centre with plant and K = side without plant

For the field trial a high P (Bray-1: 70 mg/kg) and a low P (7 mg/kg) plot from a  $2^5$  factorial long term fertiliser trial, established in 1939, were selected. P application ceased in 1993 for the high P plot due to P toxicity (Nel et al. 1996). The field trial's plants were planted on November 25, 2001, at a density of 50 000 plants/ha with rows 0.9m apart.

Two sampling positions were selected: between rows (BR) and in the rows (R). For both sampling positions, samples were taken 10 cm from the stem at depths of 0-10cm, 30-40cm, 60-70cm and 80-90cm respectively.

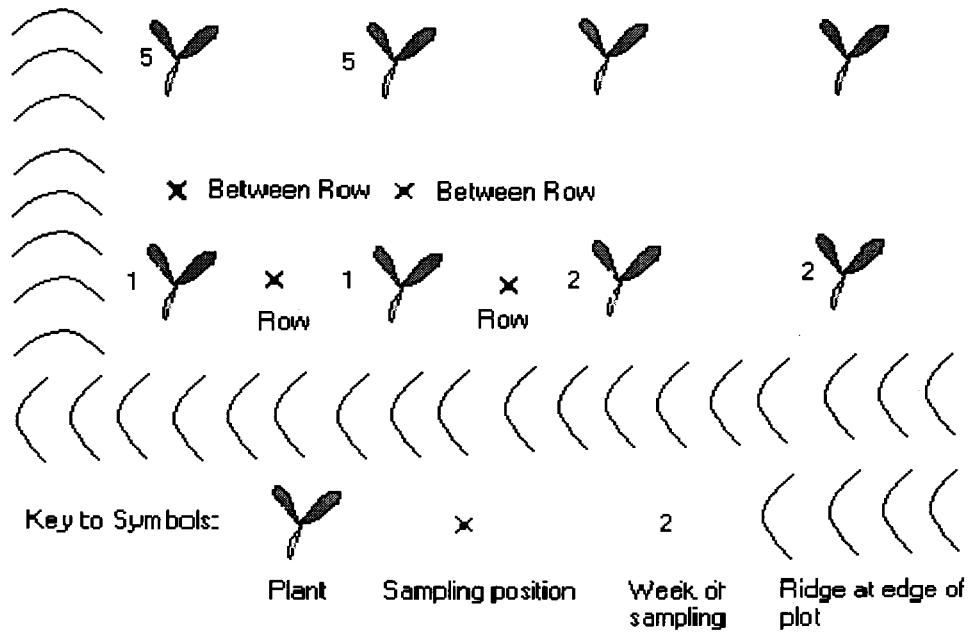


Figure 3. Sampling positions for the field trial.

For the pot experiments enough pots were used to take samples twice a week for four weeks. Soil cores (250 cm<sup>3</sup>) were sampled at the centre of the pot and at the side of the pot (Figure 1 and 2). The field trial's soil cores (60 cm<sup>3</sup>) were sampled in the rows (R) and between the rows (BR) to a depth of 80cm for 16 weeks (Figure 3).

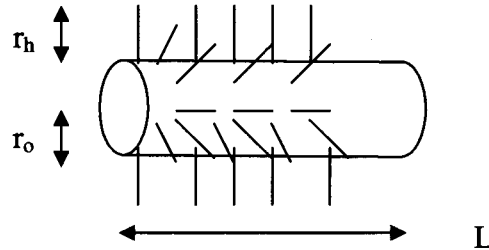
## 2.2 DETERMINATION OF VOLUME AND EXPLOITATION

Soil cores (from the pots and field) were placed on 1 mm sieves, and shaken under water for 10 minutes to separate roots from soil. Root fresh mass and length were determined. Length determination was performed using a Geotron WLM1 device using the methodology of Tennant (1975). Shoots were also harvested with roots (second pot experiment) and the fresh mass, dry mass (24h@70°C) and P content were determined. To determine the root radius, the formula of Schenk and Barber (1979) was used:

$$r_o = \sqrt{(Fw / L_R) \times \pi}$$

$r_o$  : root radius (cm)  
 $Fw$ : fresh mass (gram)  
 $L_R$ : root length (cm)

Assuming a density of  $1 \text{ g cm}^{-3}$  for roots (Hackett, 1969), the volume of roots is equal to fresh mass. The term “exploitation” is defined as: the volume of the root plus the volume of the rhizosphere. The size of the rhizosphere is assumed to be the length of root hair. Mackay and Barber (1985b) found that the root hair length to vary between 0.21mm and 0.46 mm. For this study, root hair length was assumed to be 0.3 mm, which was added to the radius of the root to determine total volume of the root and rhizosphere:



$$V_r = \pi (r_o + r_h)^2 \times L_R \quad r_h: \text{root hair length (cm)}$$

$r_o$ : root radius (cm)

$L_R$ : root length (cm)

$V_r$ : exploited volume by the fresh root ( $\text{cm}^3$ )

Percentage exploitation volume of roots expressed as a percentage of the total soil volume that is exploited by the root:

$$V_e = \frac{V_r}{V_c} \times 100$$

$$V_e = \left( \frac{\pi \left[ \left( \sqrt{\frac{F_w}{L_R} \times \pi} \right) + 0.03 \right]^2 \times L_R}{V_c} \right) \times 100$$

$V_e$ : exploited volume (%)

$V_c$ : soil core volume ( $\text{cm}^3$ )

$F_w$ : root fresh mass (gram)

$L_R$ : root length (cm)

## 2.3 MODELLING OF ROOT GROWTH

The Gompertz function (Steyn *et al.* 1984) was used to express root growth in relation to P:

$$y = ab^{c^x} \quad a > 0, b > 0 \text{ and } 0 \leq c \leq 1$$

$$\log y = \log a + c^x \log b$$

$$y' = a' + b'c^x$$

$$y' = a'(1-b^*c^x), \quad b^* = -b'/a'$$

$y'$ : percentage exploitation

$a'$ : total root biomass (gram)

$b'$ : constant of proportionality with respect to  $a$

$c'$ : growth rate (gram day<sup>-1</sup>)

$x'$ : time (day)

## 2.4 STATISTICAL ANALYSIS

Brown and Scott (1984) state that root data is usually not normally distributed, and that transformations may be necessary. Therefore tests for normal distribution were done, and afterwards, standard analysis of variance using SAS package (version 8.2, 2001). Data sets were treated as randomised block design (RBD), treating every sampling time as a block, using the F test and Tukey's studentised range test (Honest Significant Difference (HSD)) at the 5% level of significance.

## CHAPTER 3: RESULTS AND DISCUSSION

### 3.1 FIRST POT TRIAL

#### 3.1.1 Root growth and distribution in pots

The roots extracted from soil samples taken at different areas in the pot were weighed and represented in Figure 4. The pots that received  $40 \text{ mg kg}^{-1} \text{ P}$  were selected since it represents the results of all the treatments, since the tendency was the same for all the P treatments ( $0, 20, 40$  and  $80 \text{ mg kg}^{-1} \text{ P}$ ).

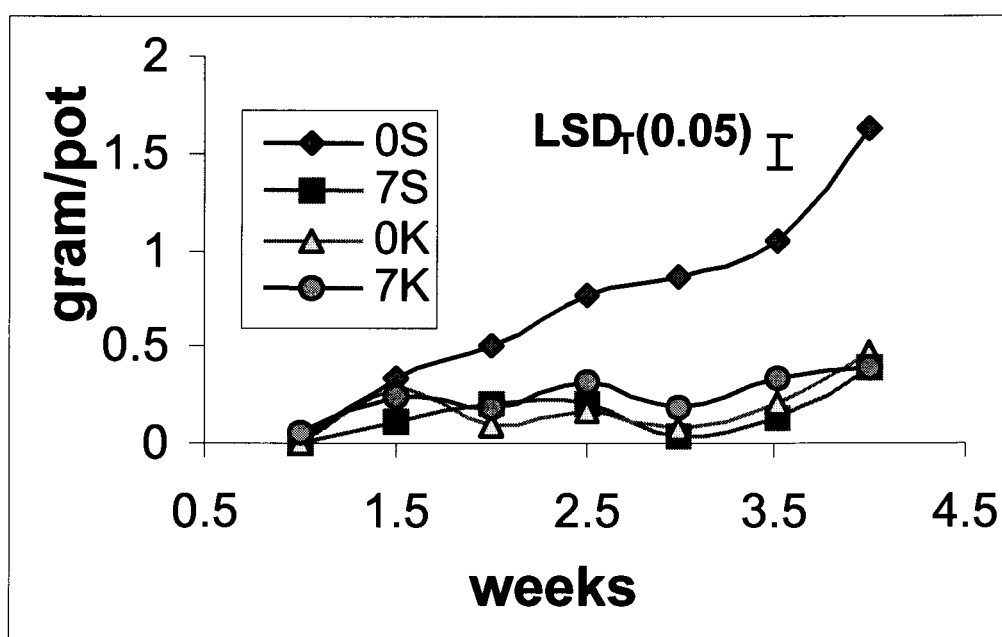


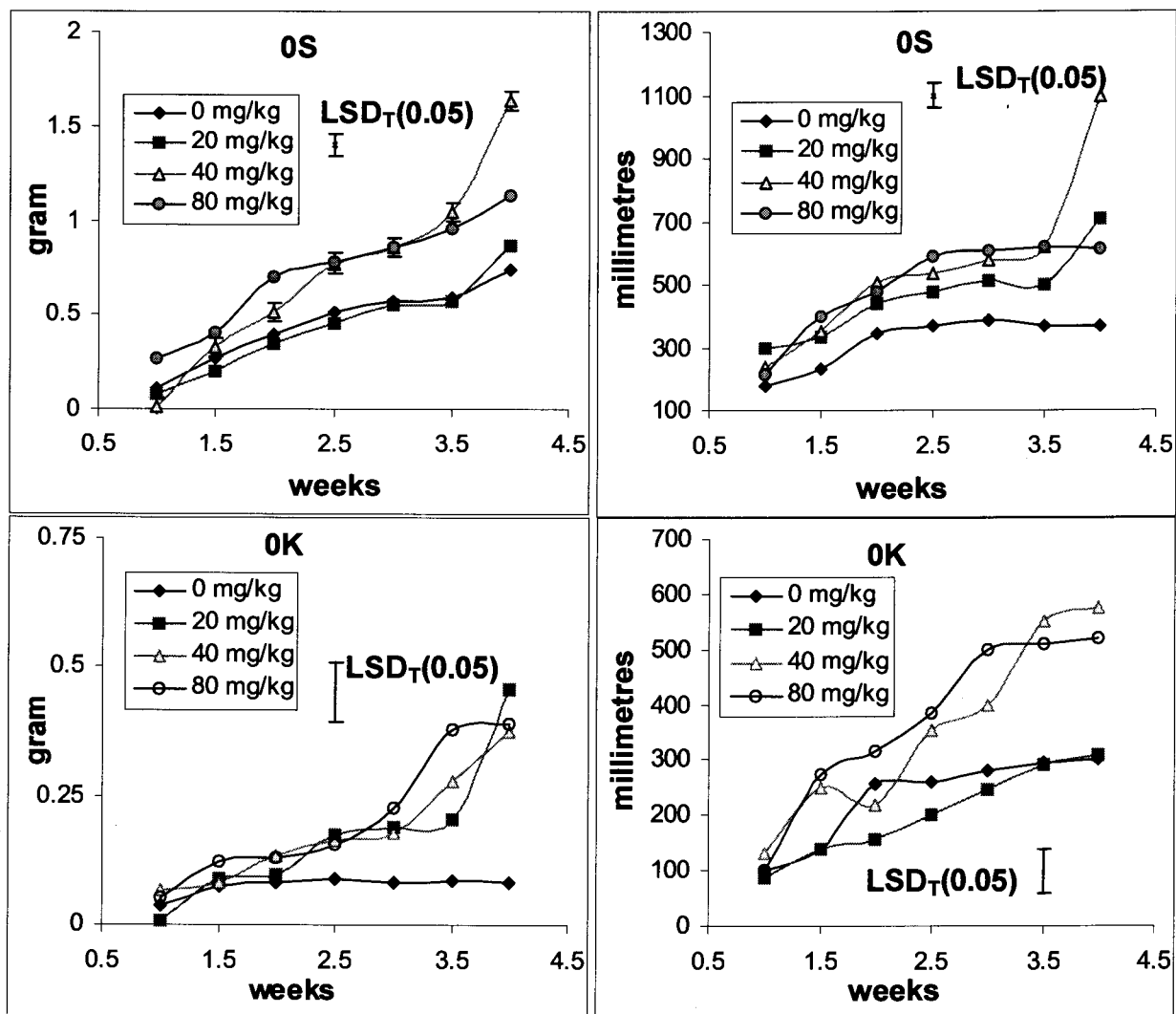
Figure 4. Root growth and distribution in the pot, for the  $40 \text{ mg kg}^{-1} \text{ P}$  treatment ( $\text{LSD}_{\text{Tukey}0.05} = 0.088 \text{ g}$ ).

According to Figure 4, most growth occurred at the centre of the pot, in the topsoil (0 to 7 cm), while the growth that occurred in the other three areas was similar. Similar patterns occurred for all the other treatments ( $0, 20$  and  $80 \text{ mg kg}^{-1}$ ). A possible explanation for the poor growth in the subsoil is that poor aeration occurred in the 7S and 7K areas, and that normal drainage did not occur at the bottom of the pots.

Since most root development occurs only at the centre of the pot (S), it is assumed that the plant did not have to “search” for nutrients but started to form brace roots instead in the central area (OS).

### 3.1.2 Comparison between length and mass

The influence of P treatments on root mass and length is illustrated in Figure 5, which serves to compare mass and length measurements of all the respective areas in the pot.



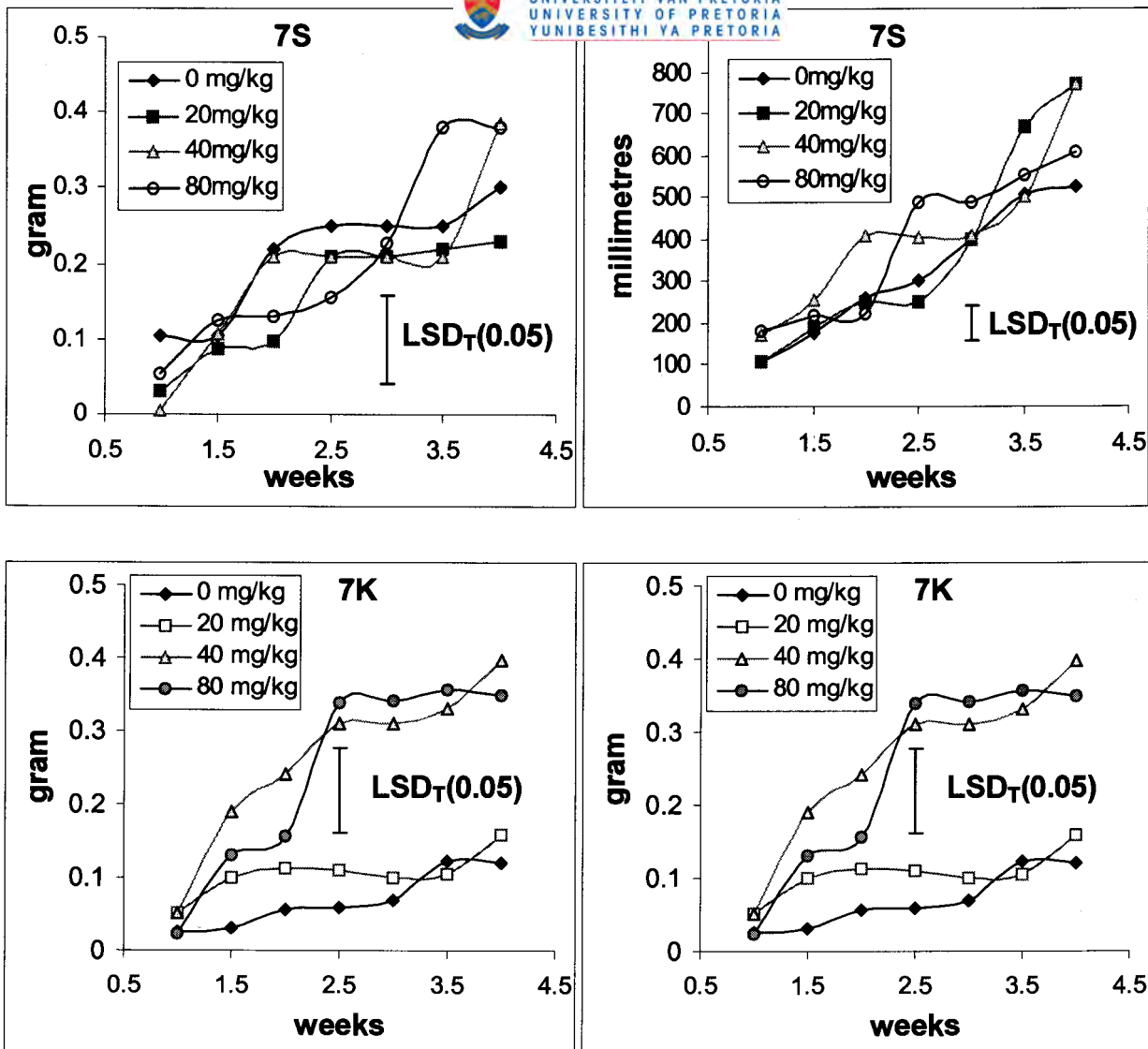


Figure 5. Influence of P application on root length and mass for all the respective areas in the pot.

The root length in the OS area increased steadily for the first 2.5 weeks whereafter root length remained nearly constant. A sudden increase occurred for the 20 and 40 mg kg<sup>-1</sup> treatments again after week 3.5. The root mass showed a constant steady increase, indicating a constant thickening of the roots for all treatments after 2.5 weeks. In the 40 and 80 mg kg<sup>-1</sup> treatments, there were a sudden increase in both root length and mass after 3.5 weeks. From this data it can be concluded that an increase in P application increase root length and mass up to 40 mg kg<sup>-1</sup> P, where after length and mass decreased. The side area at the surface (OK), showed steady increase in growth. Root mass did not respond to P additions beyond 20 mg kg<sup>-1</sup>, while the root length did respond.

In the 7S area, no significant differences in either root mass or length was observed. Increased levels of P decreased mass and increased length. In the side area (7K) there was a steady increase in root length for all treatments except the zero P after approximately two weeks. The root mass of the 40 and 80 mg kg<sup>-1</sup> P treatments increased much, indicating thicker roots. The root mass in the 0 and 20 mg kg<sup>-1</sup> P treatments did not alter much. Increased P application caused root length to decrease for the first 1.5 weeks, and to eventually increase length after 3.5 weeks.

Statistically, only the 0S area showed significant differences between P treatments. In the 0K areas, differences between treatments became significant only after week 2.5. The mass measurement of the 7K area shows that P application beyond 20 mg kg<sup>-1</sup> resulted in significant differences.

To illustrate the morphological change in root development, the root length: mass ratios for the 0S and 0K areas are presented in figure 6.

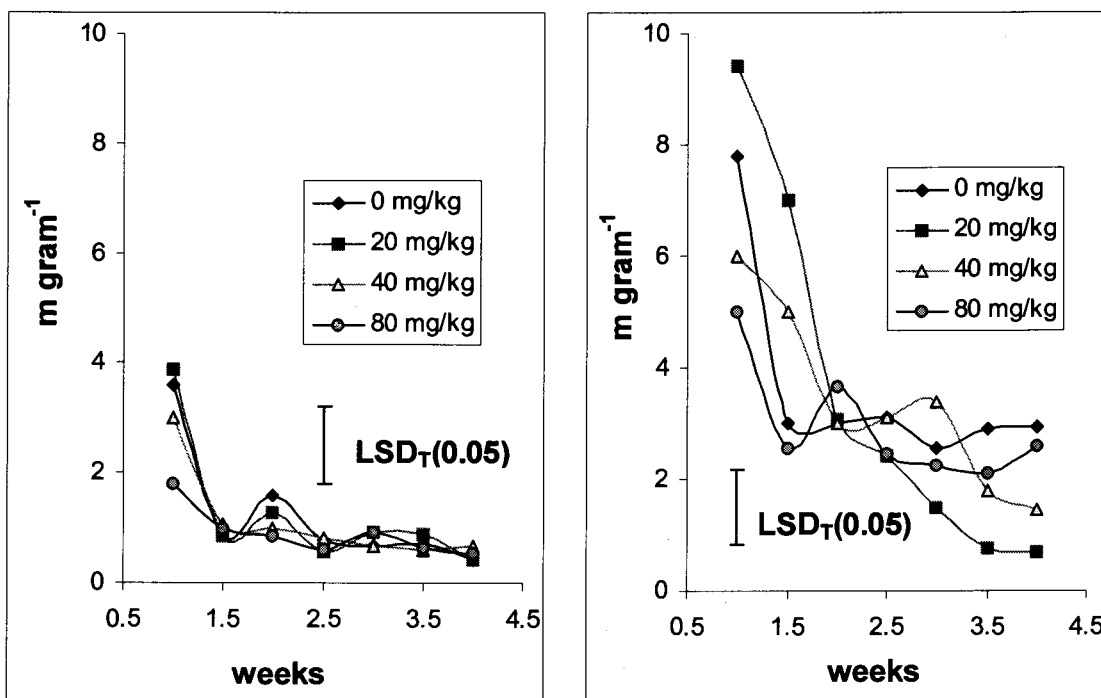


Figure 6. Root length to mass ratios for the different P treatments and areas in the pot.

The reason for the selection of the surface areas (0S and 0K) was to study the behaviour of roots in the central area and those of the side area. In the deeper areas (7S and 7K) intermingling of brace and fibrous roots may occur. As can be seen from



Figure 6, increased P levels lead to decreased length to mass ratios, implying shorter root length for every unit mass. Of significance is the observation that in the first week, the roots are highly fibrous (high length: mass ratio), followed by an increase in mass (decreasing length: mass ratio). When assuming that fibrous roots are more involved in nutrient uptake, the observation suggests that nutrient uptake is the primary function of all the roots during the first week; thereafter the function of the roots seems to change from nutrient acquisition to shoot supporting (brace). This observation is similar to that of Mengel and Barber (1974a), which indicates that most P uptake occurs during the first week.

The pattern observed for the length: mass ratio in the first week is as follows:

$20 \text{ mg kg}^{-1} \text{ P} > 0 \text{ mg kg}^{-1} > 40 \text{ mg kg}^{-1} \text{ P} > 80 \text{ mg kg}^{-1} \text{ P}$ , which indicates that at lower soil P levels, root length is enhanced relative to root mass. The  $20 \text{ mg kg}^{-1} \text{ P}$  application seems to lead to the “optimum” growth condition, a fact supported by the evidence from the second pot experiment.

Another observation is that the roots of the OK (thin and fibrous roots) area are much longer than those of the central area (OS), which shows that the thick (brace) roots occur in the centre, while the more fibrous roots occur farther away from the centre of the plant. This can be seen from figure 7, where root radii of the OK and OS areas are presented.

Figure 7 shows that increased soil P had a tendency to increase root radii in the first week in the OS area, whereafter no significant differences in root radius occurred. In the OK area no notable differences occurred in the radii between the treatments

Due to the steady increase in root radii in the OS area, it indicated that brace roots developed, since there was a gradual increase in radii, especially that of the  $0 \text{ mg kg}^{-1} \text{ P}$  treatment. That trend was not observed in the OK area, since radii of all treatments remained relatively constant over the 4 week period.

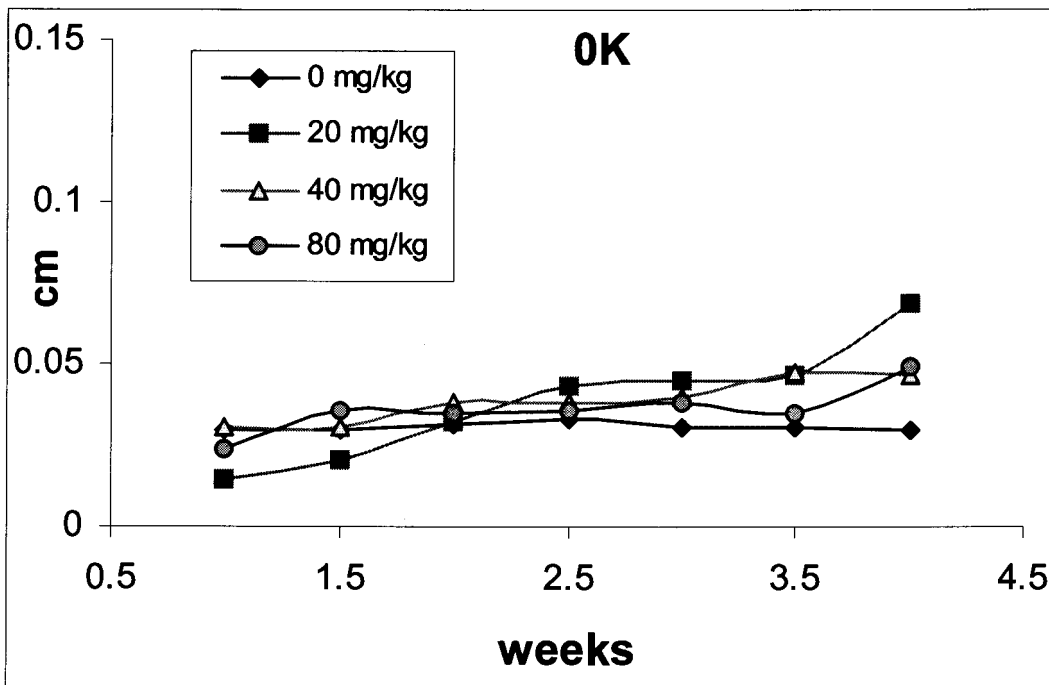
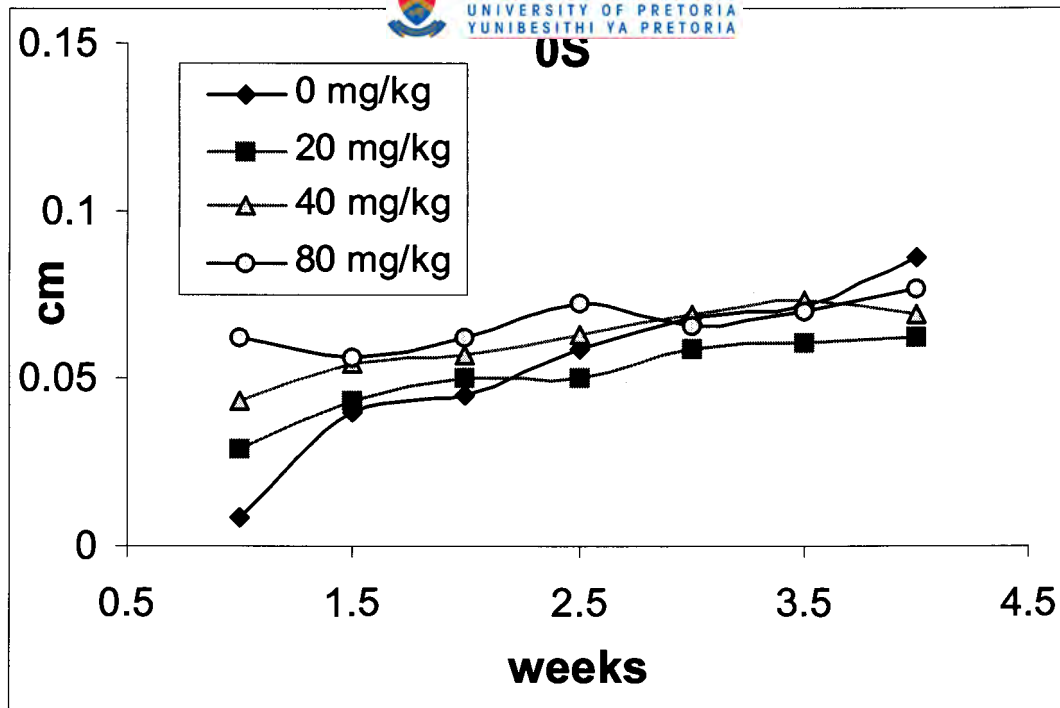


Figure 7. Root radii in the OS and OK areas.

To summarize, length and mass determinations, when used together, are effective in revealing the response of the root system to different levels of P application. Roots tend to be heavier and shorter at increased concentrations of soil P. The root system's function also changes within the first week, presumably from nutrient acquisition to shoot supporting.

### 3.1.3. Exploitation of soil volume

In the previous discussion, it was shown that root length and mass determinations can give very different answers regarding root behaviour. When considering root exploitation, it combines the mass and length determinations to give a comprehensive expression of root growth. From these morphological changes in response to P treatments can be studied more holistically.

Figure 8 shows that the side area (OK) is more responsive to changes in P level than the central area (OS), since the differences between treatments are more pronounced. The OK area also had a more positive slope than the OS area, suggesting that new root development is sustained longer. This can be attributed to the different functioning of the particular roots: the side area roots are more involved in nutrient uptake than its central area counterparts. Those two particular areas were selected to show the difference in behaviour of the central (brace) and the side area (thin and fibrous) roots, as mentioned earlier in 3.1.2.

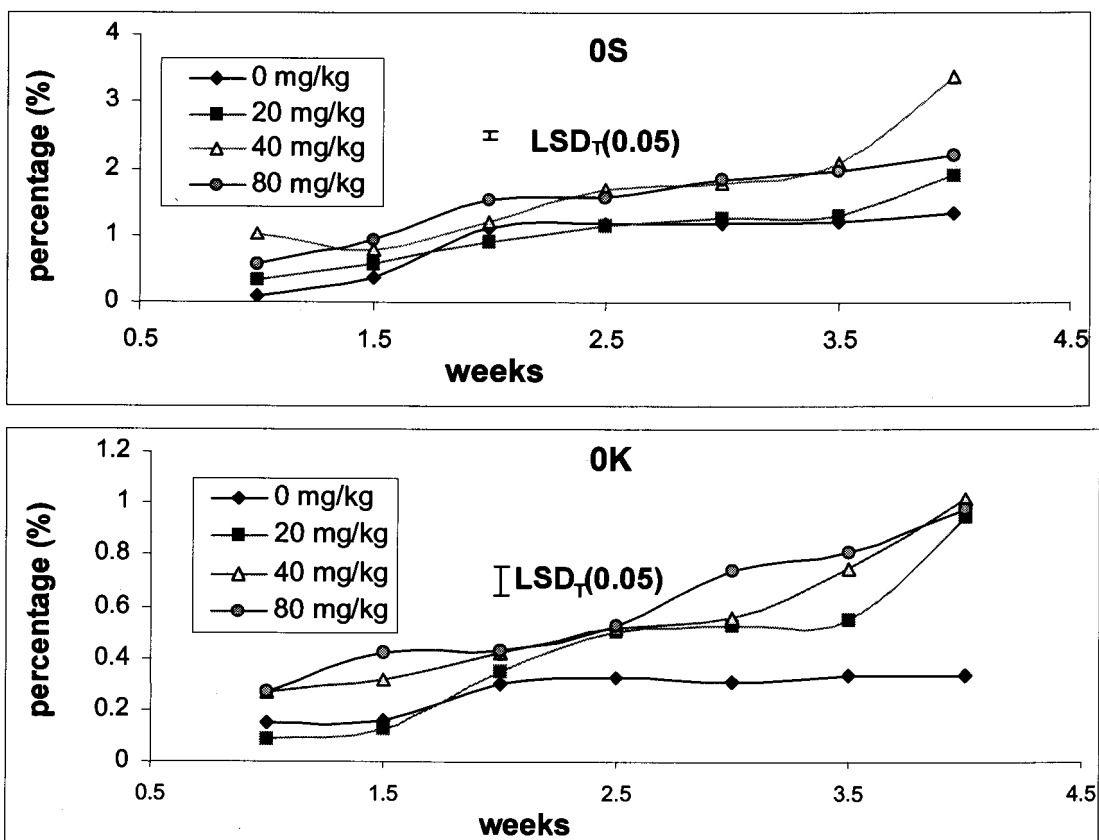


Figure 8. Influence of P treatments on the volume of soil exploited by the roots of the different areas of the pot.

The general trend was that increased levels of P application led to higher percentages of soil volume exploitation. This is because increased P increased the root length and mass. The exploitation in the side area (OK) was much lower than that of the central area (OS). Most of the acquired P must have come from the central area. There was a tendency that the exploitation of the soil volume started to increase after 3.5 weeks, indicating that exploitation of soil volume will increase later on, especially in the side areas.

Statistically, it can be seen that more significant changes in percentage exploitation occurred in the central area, in response to P fertilisation.

To compare the soil exploitation of the first pot experiment with that of the second pot experiment's KP graph (figure 20), the OS and 7S areas were combined. When the exploitation of roots in the OS+7S area is analysed with the Gompertz equation, it can be seen that the increased application of P and its effect on root growth can be predicted:

$$y = a(1 - bc^t)$$

where y: percentage exploitation

a: total biomass (gram)

b: potential growth relative to a

c: growth rate, where an increase in c means a lower growth rate

t: duration after emergence

According to the predicted root development by the model, it was found that soil P strongly influenced the values of the constants:

- As P was increased, so did the “a” constant (value of saturation). This means that an increase in P increased the eventual size of the exploited volume, since it increased the final amount of biomass
- As P was increased, the “b” constant decreased. This is an indication of the growth relative to the saturation value (a). This shows that the 0 mg kg<sup>-1</sup> treatment had much higher relative growth during its life cycle than the higher P treatments

- The growth rate “c” decreased with increasing levels of P, therefore, in a P deficient environment roots have a higher root growth rate than is the case for adequately fertilised environments.

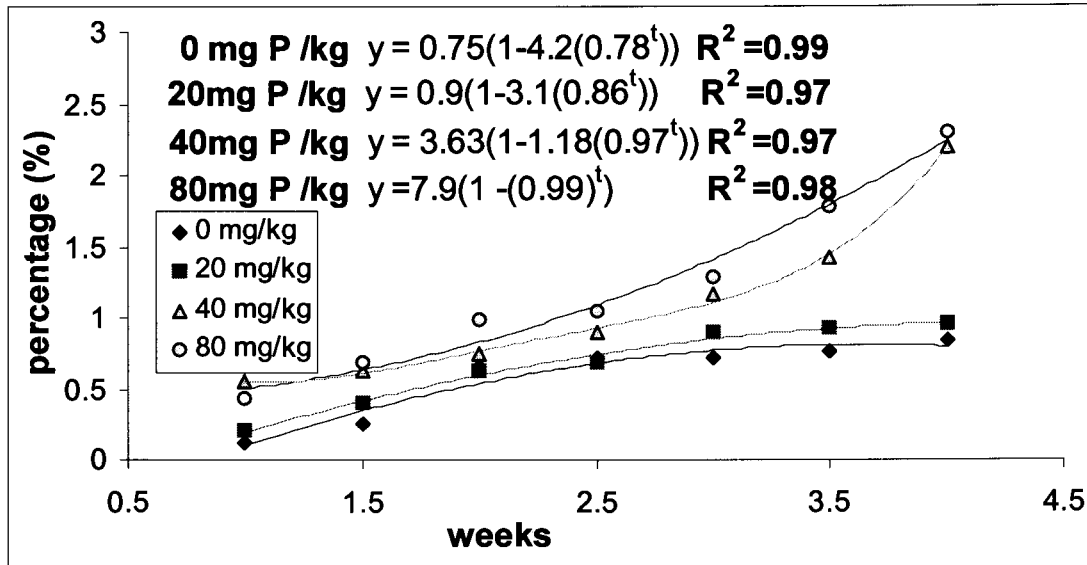


Figure 9. Predicted exploitation (%) of soil by roots by the Gompertz equation, in the central areas (0S and 7S).

From the discussion it can be seen that this simple equations can accurately describe the behaviour of roots under varying concentrations of P.

The following conclusions can be made:

- P fertilisation had a highly significant ( $P < 0.0001$ ) effect on root growth
- significant differences ( $LSD_T 0.05$ ) in root growth did occur as a result of varying P levels and various regions in the pot
- uniform growth in the whole pot did not occur; growth occurred differently in the respective areas. Figure 10 is a graphical representation of growth in the different areas during the duration of the experiment

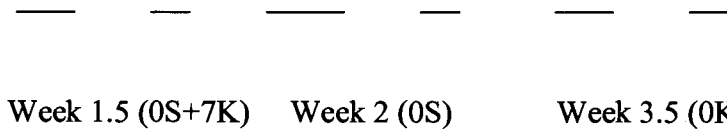


Figure 10. Representation of the four different areas and when the major growth occurred.

- only the OS area had a highly significant interaction with P level and duration, which shows that a very small portion of the pot responded to the P level (Table A2)

### 3.2 SECOND POT TRIAL

In the first pot trial, roots were studied under simple conditions: only one plant per pot, and studying only P's effect on it, whilst ignoring shoots. In the second pot trial three plants per pot were used, additional N and K were applied, shoot P content and shoot growth were determined in relation to root growth. This ensured that root behaviour could be studied under more factors of influence, and in relation to the rest of the plant.

#### 3.2.1 General growth

##### 3.2.1.1 Shoot mass and P content of the different treatments

In Figure 11 it is shown that application of P beyond 20 mg kg<sup>-1</sup> did not cause an increase in shoot growth. This suggests that the lack of other essential nutrients may have prevented further increases in shoot growth as application of P was increased beyond 20 mg kg<sup>-1</sup> P.

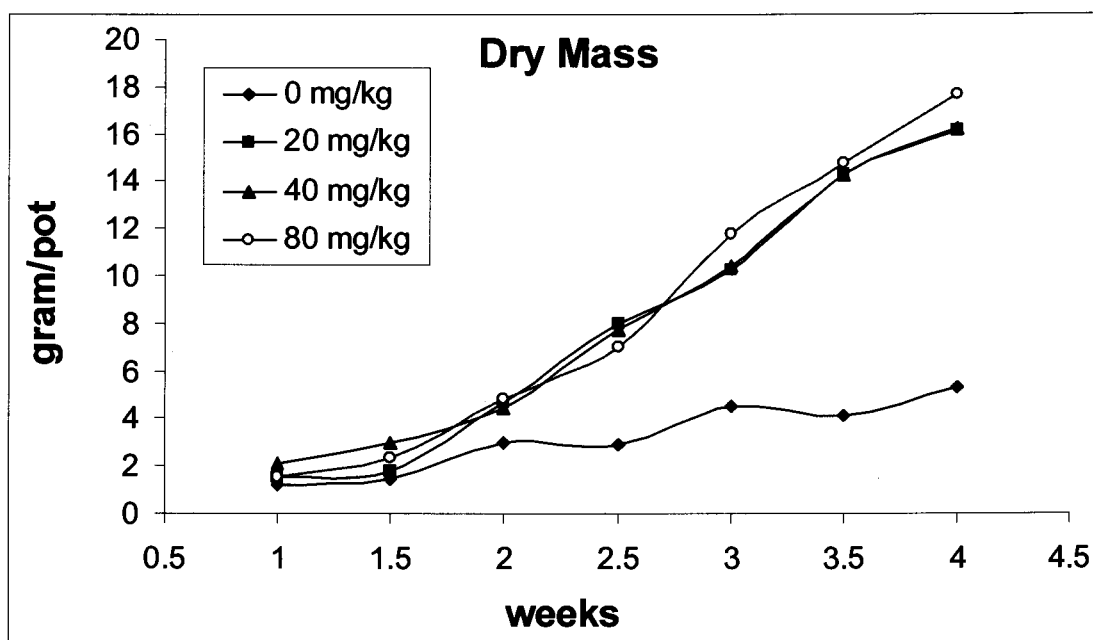


Figure 11. Increase in shoot dry mass over four weeks under different P treatments.

Increased levels of P increased shoot P content during the early growth stages as shown by Figure 12. Over time however, differences in shoot P content became less so after 4 weeks no differences occurred.

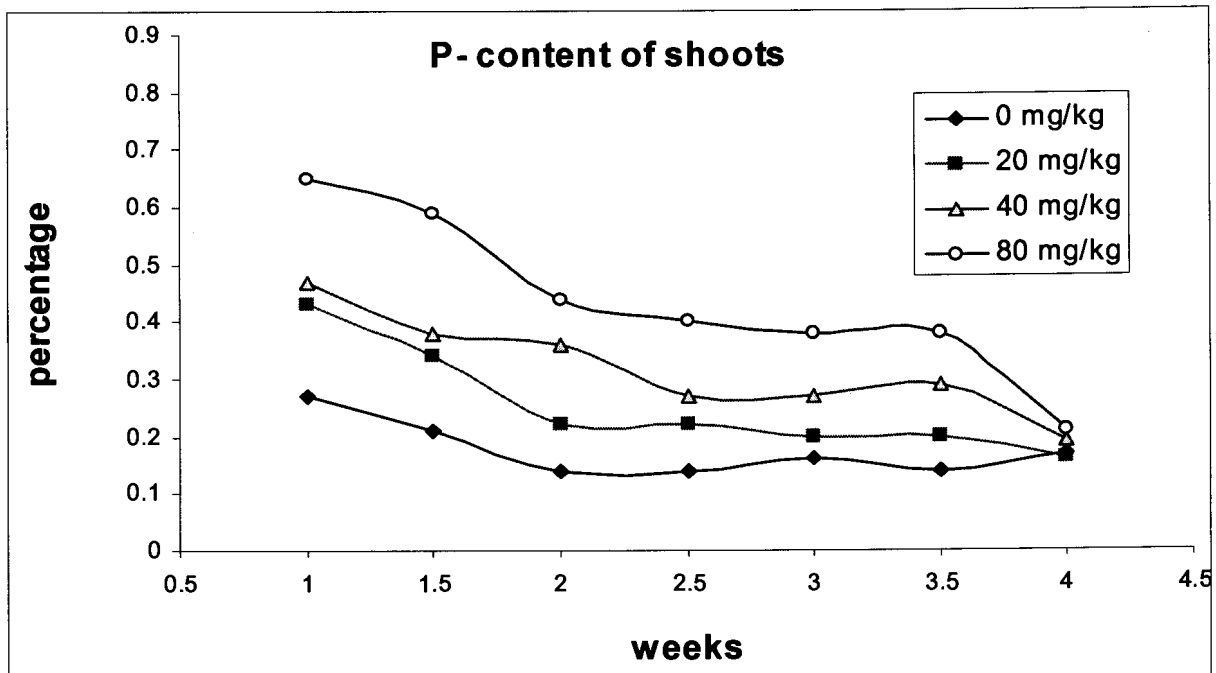


Figure 12. Changes in P-content of the shoots.

### 3.2.1.2 Root development in the different areas of the pot

In figure 13, growth in the different areas is shown. In all areas, root growth continued throughout the growth period similar to the top growth. The growth rate tends to level off towards the end as was also found in pot trial 1. In this trial the amount of root growth increased significantly more with P application compared with the first pot trial, while the amounts of P application were similar. This is due to additional N and K as well as more plants per pot. Application of P resulted in significant differences in root development between treatments only after week 2.5, as shown by the  $LSD_T 0.05$  values.

The side area under a plant (KP) is the area which had by far the most growth. An explanation is that since the plant is situated at the side of the pot, roots that grow against the side “turn” and grow in backwards toward the centre of the pot. This results in more roots being sampled. In the other areas, the increase in roots seemed to have leveled off after 2.5 weeks.

As mentioned in the Materials and Methods (chapter 2), additional N and K were applied. This probably caused roots not to respond to P beyond  $20 \text{ mg kg}^{-1}$ .



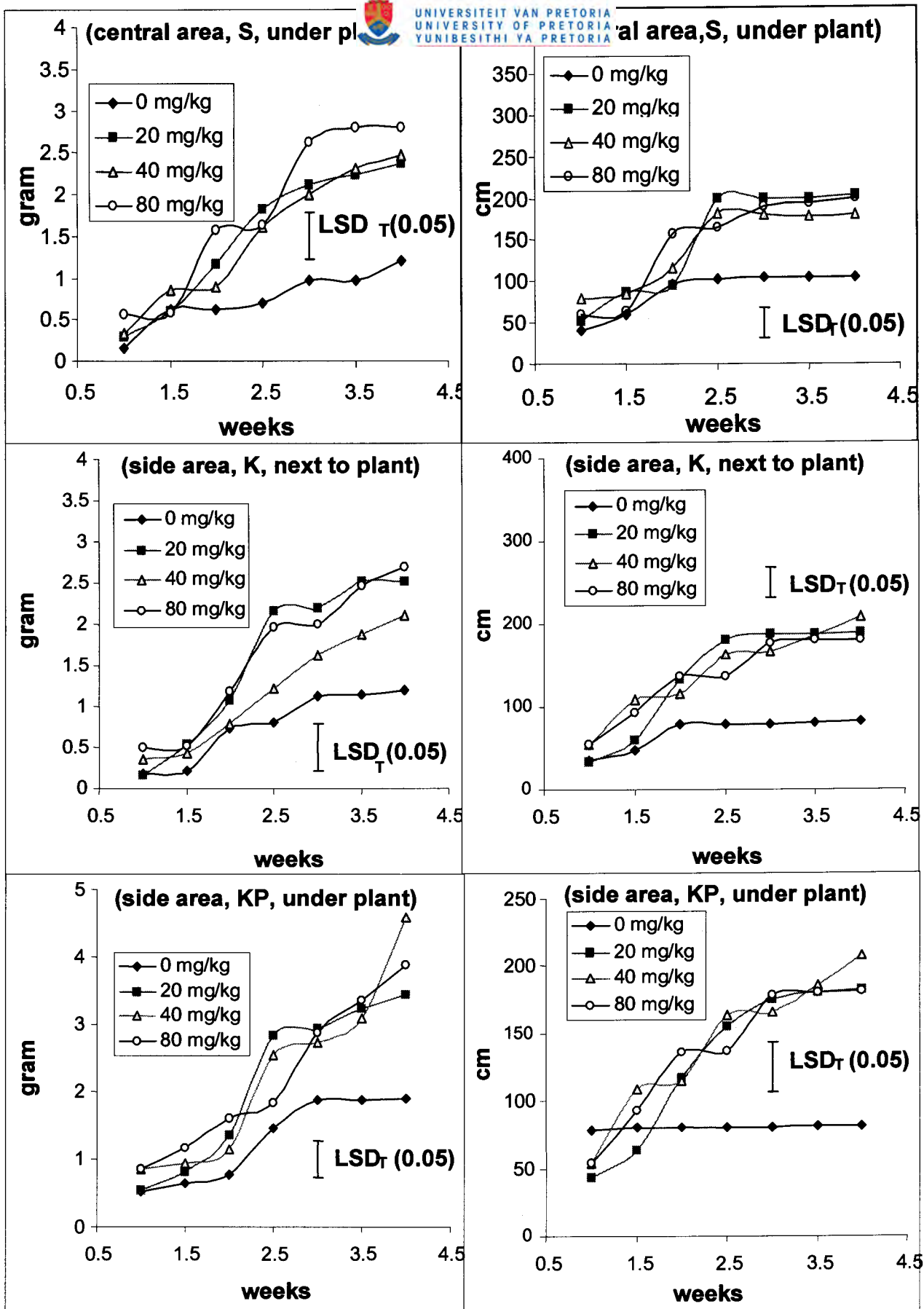


Figure 13. Root mass and length in the different areas as influenced by different P levels over time.

To demonstrate the relative root growth in different areas in the pots, ratios between root mass in different areas are calculated and illustrated in Figure 14. Concerning growth in the different areas relative to one another, Figure 14 shows what the first pot trial also showed, which is that most growth occurred during the first two weeks in the central (S and KP) areas, rather than in the outer area (K). This is illustrated by the s/k ([central area with plant]/[side area without plant]) curve. After the second week, the ratio's of the growth rate were constant, indicating that growth in the different areas were similar. This shows again the dynamic nature of the root system prior to the second week after emergence.

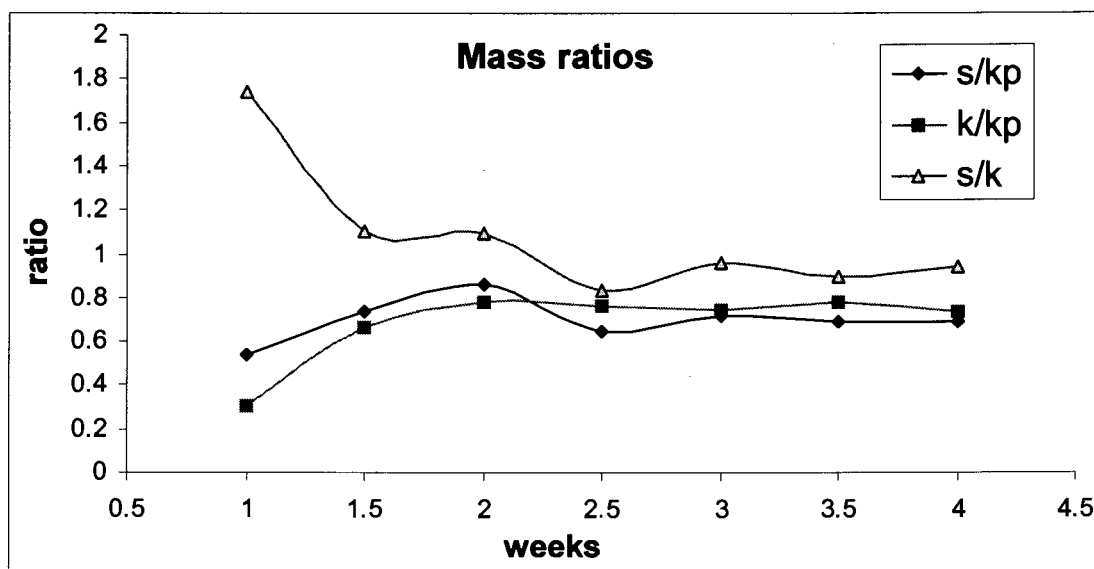


Figure 14. The relative growth between the different areas.

### 3.2.2 Comparison between root length and mass

As shown in figure 13, in both the length and mass measurements, P application did not increase root growth significantly beyond 20 mg kg<sup>-1</sup> (similar to the top growth). This is contrary to the results of the first pot trial where increased P addition led to increased root growth. Significant differences between the treatments only started to occur from week 2.5 onwards. The data given in Figure 13 indicated that root length of the OP treatment, in the KP (side, under plant) area, developed in the first week, where after root length stayed constant. The fact that root mass increased indicated that roots only thickened. As already mentioned, P application beyond 20 mg kg<sup>-1</sup> did not result in any significant increase, showing that it is indeed the optimum

concentration. Root length of the OP treatment developed for 2 weeks in the K and S areas, where after growth stopped, although roots continued to thicken.

The result of the side area (K) can also be interpreted as follows: increased P application increased mass whilst having no effect on the length of the fine roots. This is contrary to the finding of the 1<sup>st</sup> pot trial where P application increased root growth in the central areas and very little in the side area. The fact that N and K were applied in this trial was probably responsible for these differences.

### 3.2.2.1 Root: shoot ratio

The root: shoot ratios of the different treatments are presented in Figure 15. The regression equations with their respective regression coefficients are as follows:

$$0 \text{ mg kg}^{-1}: y = -0.0061x + 0.0683 \quad R^2 = 0.41$$

$$20 \text{ mg kg}^{-1}: y = -0.0073x + 0.0612 \quad R^2 = 0.45$$

$$40 \text{ mg kg}^{-1}: y = -0.0045x + 0.0496 \quad R^2 = 0.64$$

$$80 \text{ mg kg}^{-1}: y = -0.0138x + 0.0815 \quad R^2 = 0.96$$

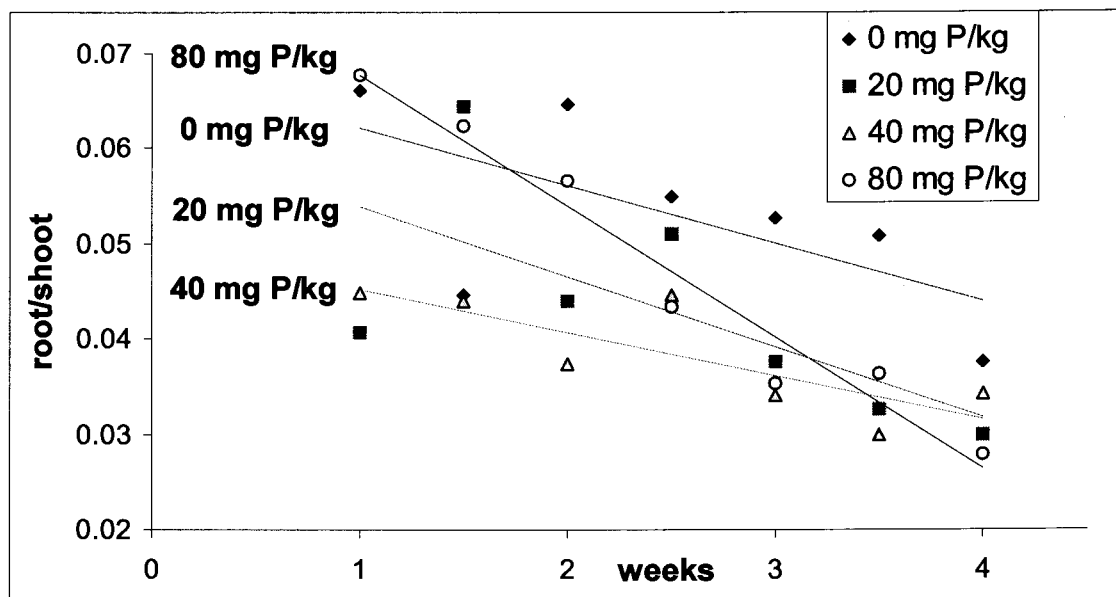


Figure 15. The root: shoot (mass) ratios of the different treatments.

From Figure 15 and the regression equations the following can be deduced:

- The root: shoot ratio constantly decreases as the plants age. Since maximal root development occurs in the beginning of the growth cycle and becomes progressively less. The uptake of P and other immobile elements (Fe, Zn, Cu, etc)

therefore is at a maximum very early in the life cycle

- The  $R^2$  values increase with increasing P fertilisation. This was also previously observed that higher variation exists at a low level of P application.
- All regression lines have negative slopes. This shows that the biomass production of the top growth became more than the roots over the growth cycle. Relative root development is at a maximum just after planting and decreased over time.
- As the levels of P application were increased, the more negative the slopes of the trend lines became. This indicates that at lower levels of P fertilisation, the development of the root system kept on for a longer period of time relative to the shoots. At high levels of soil P, higher amounts of shoot are formed relative to the roots.
- The trend of the different lines resembles that of the P content graph (Figure 12). This confirms findings in literature (Barber, 1984) that P uptake is strongly associated with root development.

When the length and the mass measurements are compared (Figure 13), it can be seen that the mass determination of the roots is definitely more sensitive than the length determination. This is because with for fibrous roots, root-measuring devices are simply not sensitive enough to detect small differences in length.

#### 3.2.2.2. *Length: mass ratio*

In Figure 17 it is shown that for a certain mass, longer roots are produced with no P fertilisation for the areas with plants (KP and S). As P application was increased, root length per unit mass (gram) decreased. This is similar to the findings of first pot trial (Figure 6) where it was found that higher levels of P application resulted in increased root mass but no increase in root length. In the area without a plant (K), the pattern was reversed: increased P levels lead to higher length per unit mass.

P additions beyond  $20 \text{ mg kg}^{-1}$  did not significantly affect root growth as shown by the length: mass ratio (similar for the 20, 40 and  $80 \text{ mg kg}^{-1}$  treatments). In general, it can be seen that roots in the side area (K) are longer per unit mass than those of the central area (KP). At low levels of P addition, higher length to mass ratios were induced, meaning that root morphology is changed by varying the concentration of P.

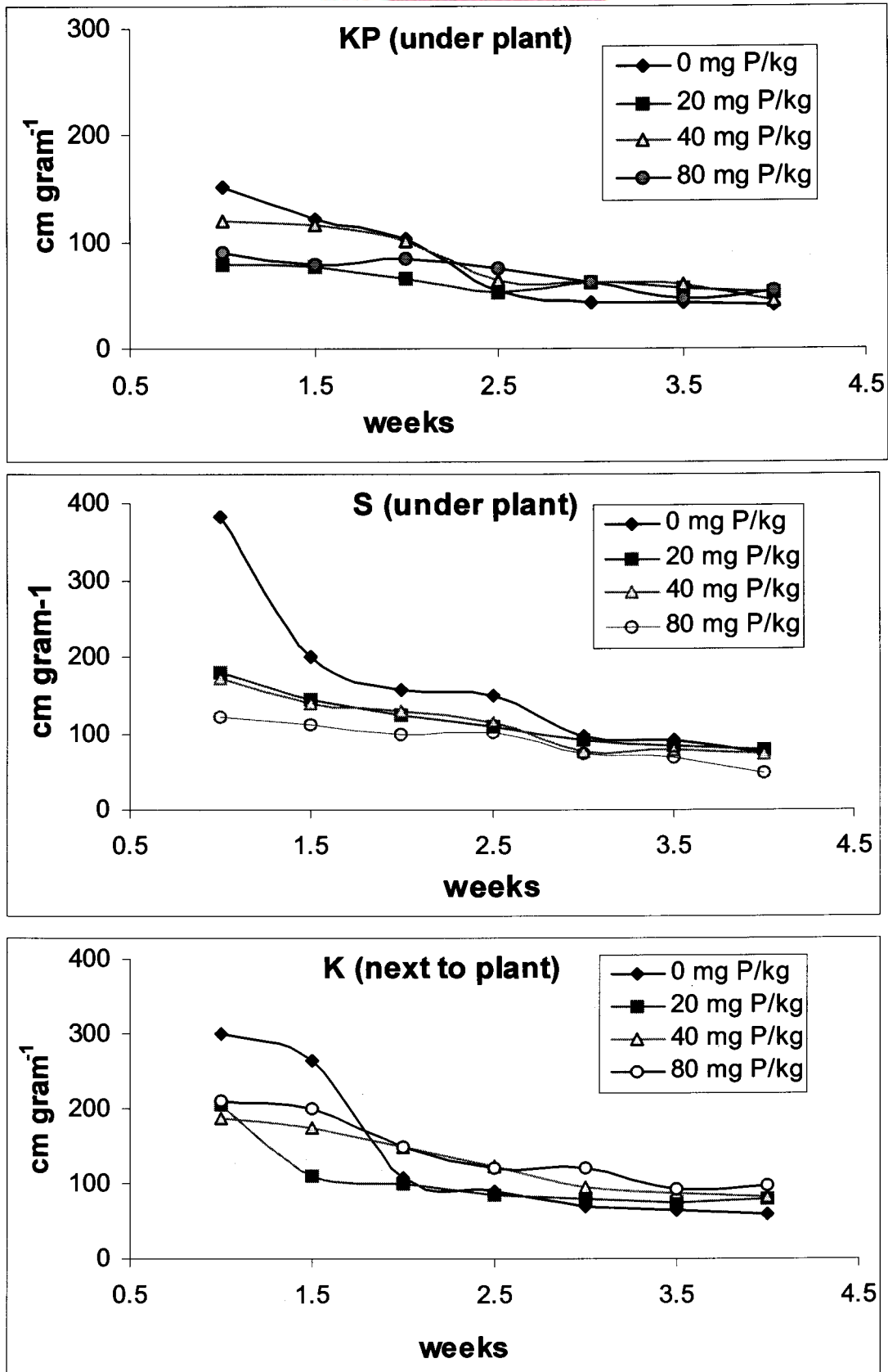


Figure 16. Influence of P level on length and mass ratios in different areas.

The larger length: mass ratio for the 0 mg kg<sup>-1</sup> treatment occurred only for the first 1.5 weeks, where after no difference between the different treatments could be noticed. This behaviour suggests that a P deficiency in soil enhances root growth, but only for the first ≈ 15 days after emergence. This shows that the first 10 to 15 days after planting are critical for P uptake. This finding is similar to that of Hajabashi and Schumacher (1994).

### 3.2. 2. 3. Root radii

It can be seen in Figure 18 that P level clearly influences root morphology. The two areas were selected on the assumption that they will represent behaviour of the fine roots (K) and thick roots (KP).

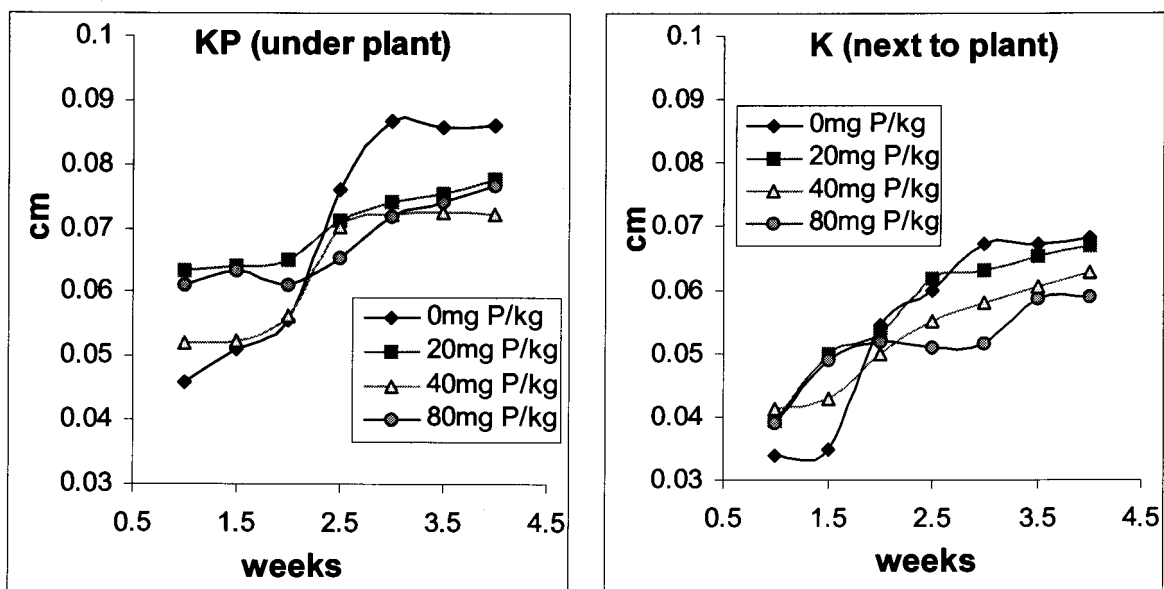


Figure 17. Radii of the central (KP) and side (K) areas of the different treatments.

The KP graph shows that beneath the plant, the application of P results in a gradual increase in radius over time. With no P application, the roots produce thin fibrous roots up to 14 days after emergence (D.A.E.) and then a sudden increase in radii. Adequate P results in a gradual transition from thin fibrous to thicker roots over time. The lines of the different treatments cross at 2 weeks, indicating a transition occurred in root morphology of both the K and KP areas.

To conclude the discussion on root radii, it can be stated firstly that the morphological change in response to P application 15 D.A.E. is opposite to that in the first two

weeks after emergence. As previously mentioned, since most P uptake occurs during the first two weeks, the root system's function changes: from nutrient acquisition to support of the plant. This is most apparent in the 0 mg kg<sup>-1</sup> P treatment.

In conclusion, it can be stated that root-measuring devices still have difficulty in detecting very fine fibrous roots, which represents the majority of maize roots. Another problem encountered is the fact that fine roots are often intertwined, making accurate length determinations difficult. Root mass determinations can be used as a standard to assess the accuracy of root length measuring devices. In terms of radius, the results of the 1<sup>st</sup> pot trial were different from those of the 2<sup>nd</sup> pot trial. Increased application of P had no effect on the radii of the 1<sup>st</sup> pot trial, whilst decreasing the radii of the 2<sup>nd</sup> pot trial. The different findings can be attributed to N and K's effect on root growth, rather than P. This finding is therefore similar to that of Duncan & Ohlrogge (1958), who found that application of N decreased radii. The fact that more plants per pot were planted, may also have influenced the radii.

### 3.2.3 Exploitation of soil volume

As one of the objectives of this study was to determine the volume of soil exploited by the root system. In Figure 19 the exploitation of roots in the KP and K areas is represented. Three plants per pot were used in contrast to one plant per pot for the first pot trial. When the values are divided by three and compared to that of the first pot trial, the average percentage of exploitation per plant of the second pot trial is higher than that of the first pot trial. This observation can be interpreted as showing that N and K also influence root growth, since that is the only difference in the soil fertility between the first and the second pot trials.

Although significant differences occurred between P treatments of the K and S areas, while no significant differences occurred beyond 20 mg P kg<sup>-1</sup> in the KP area. In contrast to the earlier presentation of root growth in terms of length and mass (Figure 13) with exploited volume, significant differences between treatments could be observed very early in the growth cycle. Differences were statistically significant from the first week after planting, instead of 2.5 weeks. Another observation is that with length and mass measurements (Figure 13) no significant differences occurred

beyond 20 mg P kg<sup>-1</sup>, while significant differences occurred when roots were expressed as exploitation.

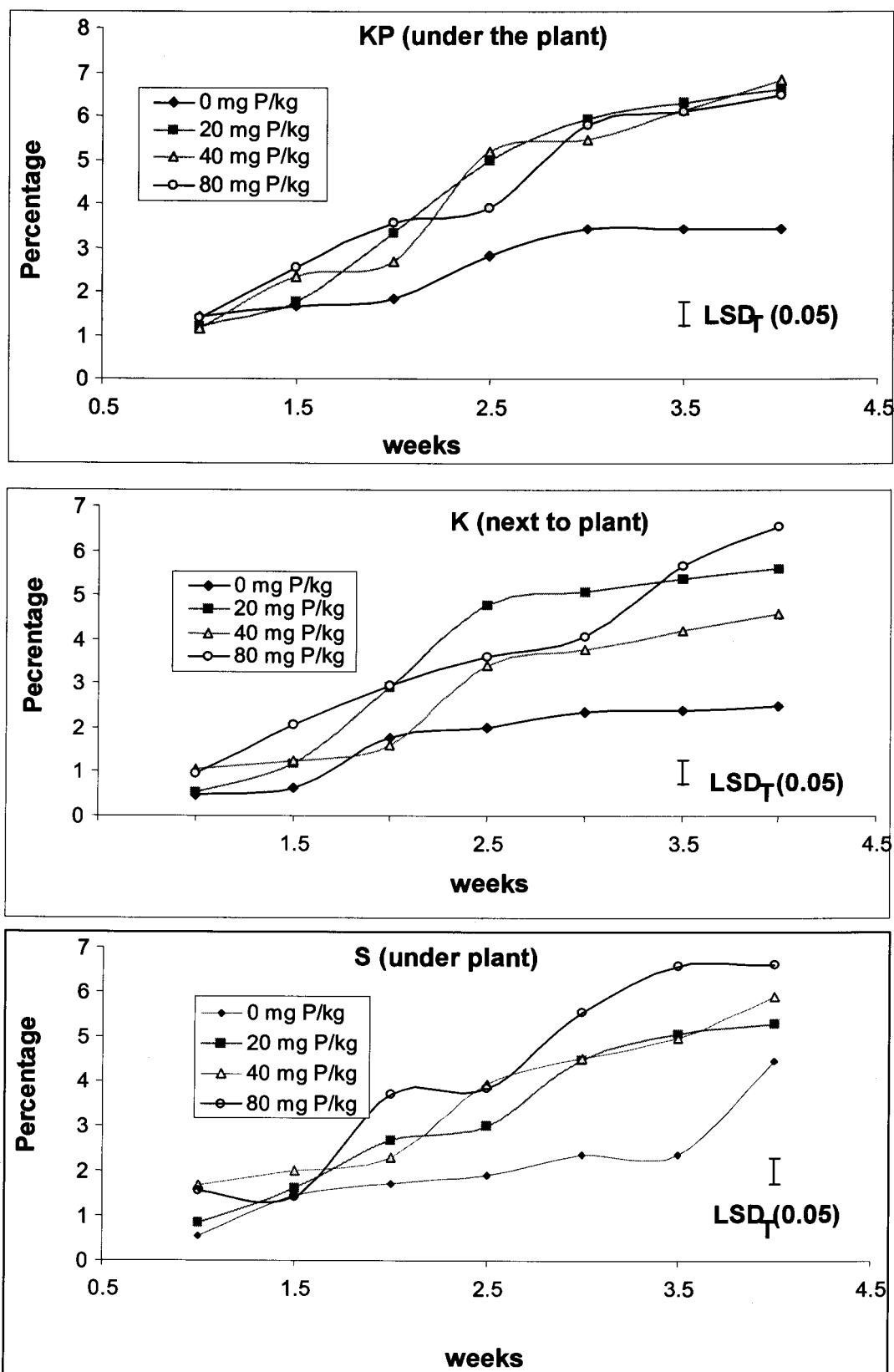


Figure 18. Percentage soil exploited by roots in different areas



At the fourth week, the central (KP) and side (K) areas had nearly similar percentages of exploitation ( $\approx 6\%$ ), which is contrary to the first pot trial where the exploitation percentage in the side area (OK) was nearly three times lower than that of the central area (OS). An explanation is that since three plants were used, roots from the central area had simply grown into the side area. From Figure 18 it can be seen that:

- at four weeks, percentage exploitation is roughly 2% per plant
- P application strongly influenced exploitation in the side area (K) and the central area with plant (S).
- The  $0 \text{ mg kg}^{-1}$  P treatment was significantly lower than the P treated plants in all areas.
- In the K and S areas, exploitation was proportional to the amount of P application. Variation was also higher in these two areas compared with the KP area.

### 3.2.3.1 Modelling of root exploitation

When the exploitation of roots in the central area (KP) is analysed with the Gompertz equation, the increased application of P and its effect on root growth a reliable prediction can be made.

$$y = a(1 - bc^t) \quad \text{where } y: \text{percentage exploitation}$$

The models for the 2<sup>nd</sup> pot trial are presented in figure 20. As with the 1<sup>st</sup> pot trial, with increased P application, the “a” values (total biomass) increased, the “b” values (relative growth from planting to harvesting) decreased and the “c” values (growth rate) increased. As mentioned earlier, a significant difference exists between P treated plants and the  $0 \text{ mg kg}^{-1}$  P treatment. No significant differences occurred between P treatments, which indicates that the  $20 \text{ mg kg}^{-1}$  P treatment was adequate for optimal root development.

Concerning the  $R^2$  values, it is a similar observation to the root:shoot ratios (Figure 15): variation decreases with an increase in P application.

A comparison between the first and the second pot trials' exploitation showed the following:

- the first pot trial had a maximal exploitation of  $\approx 1.5\%$  per plant

- the second pot trial had a maximal exploitation of  $6/2 = 2\%$  per plant
- The “a” values of the second pot trial’s equations are between 3 to 6 times higher than those of the first pot trial. To be able to compare trial 1 and 2, division by three gives equal amounts for the 0 and 20 mg kg<sup>-1</sup> treatments and nearly double the amounts for the higher treatments. This shows the influence of elements deficient in the 1<sup>st</sup> trial (N and K), on root growth.

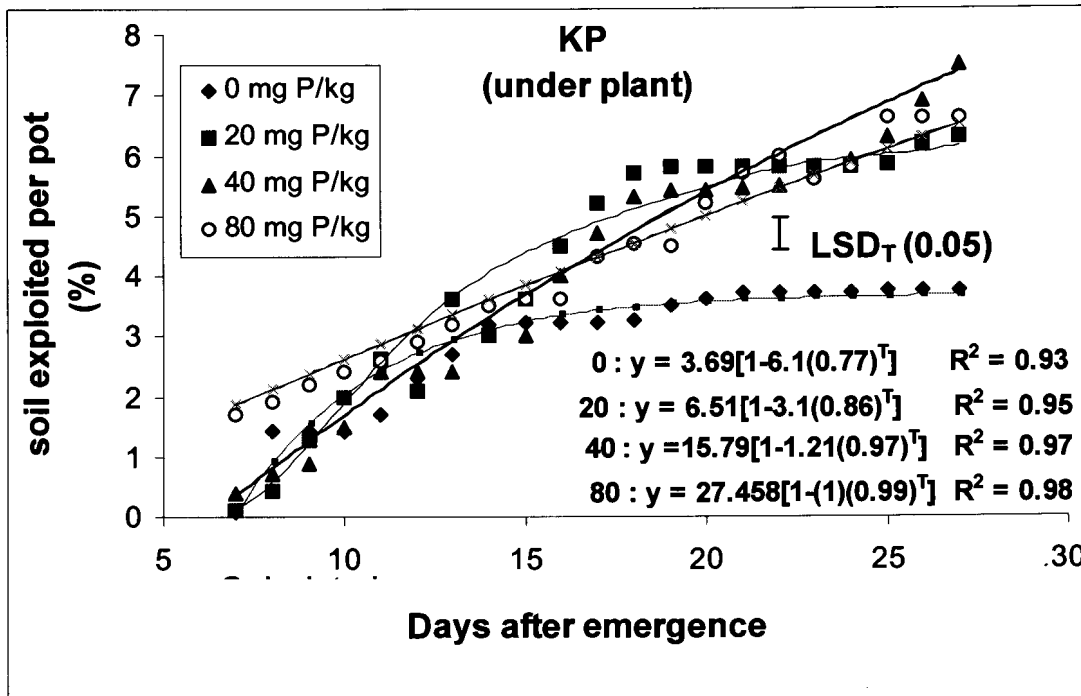


Figure 19. Changes in the predicted (line) and measured (dot) exploitation volume by roots as influenced by P application and time.

The KP area was selected since it is the same as the 0S + 7S areas of the 1<sup>st</sup> pot trial. These two areas were selected due to the fact that most root development occurred in the particular areas.

### 3.2.4. General conclusions of the results of the second pot trial

- The pattern of the shoot growth is directly proportional to the growth in the central (KP) area.
- In the 2<sup>nd</sup> trial, the growth in the different areas were similar after 2 weeks. Growth occurred mainly in the central areas beneath the plant for the first two weeks in the 1<sup>st</sup> trial. Roots started to grow in the side areas only after the second week. It is

interesting that for the whole growth cycle, by far the most growth occurred in the central area; since its amount of biomass is nearly double that of the side areas.

- The P content of the shoots over the growth period follows the growth pattern of the central (KP) area. This means that the uptake of P occurs mainly in the central area, if it is assumed that P uptake is related to root growth.
- For the first ten days after emergence, root growth is described appropriately by the statement: “the lower the P concentration, the longer the roots”. After ten days, P’s influence on root development seems less pronounced. This indicates once again that the first ten to fifteen days after emergence are crucial in the total uptake of P.
- No significant increase is observed in root mass and in shoot development for P applications beyond  $20 \text{ mg kg}^{-1}$ .
- N and K also influenced root growth, this can be seen in the different behaviour of root radii and biomass between the 1<sup>st</sup> and 2<sup>nd</sup> pot trials.
- P had a highly significant ( $P < 0.0001$ ) effect on root mass: increased P increased root mass
- Highly significant interactions ( $P < 0.0001$ ) occurred for both pot trials (duration, area and P level) from early in the growth period till harvesting
- P’s effect on root exploitation can easily be modelled using the established Richards family of growth equations (Steyn *et al.* 1984). The developed model succeeded in not only showing P’s effect on exploitation, but also in detecting subtle differences.

The following facts were demonstrated by the model:

- increased P application increased total percentage exploitation (“a” value)
- the zero P treatment showed the greatest proportional growth during the growth period, as demonstrated by the behaviour of the “b” value
- the growth rate (c) decreased with increasing P, meaning that in a P deficient soil, roots will have a higher growth rate.

### 3.3 FIELD TRIAL

For this study, use was made of two P treatment plots of a long term (started in 1939) NPK trial at the experimental farm of the U.P.

#### 3.3.1 Root growth over a 16 week period

##### 3.3.1.1 Climatic conditions

As it was expected that temperature and rainfall influence the growth of maize plants. The minimum and maximum temperatures as well as the rainfall for the particular growth period are shown in Figure 20.

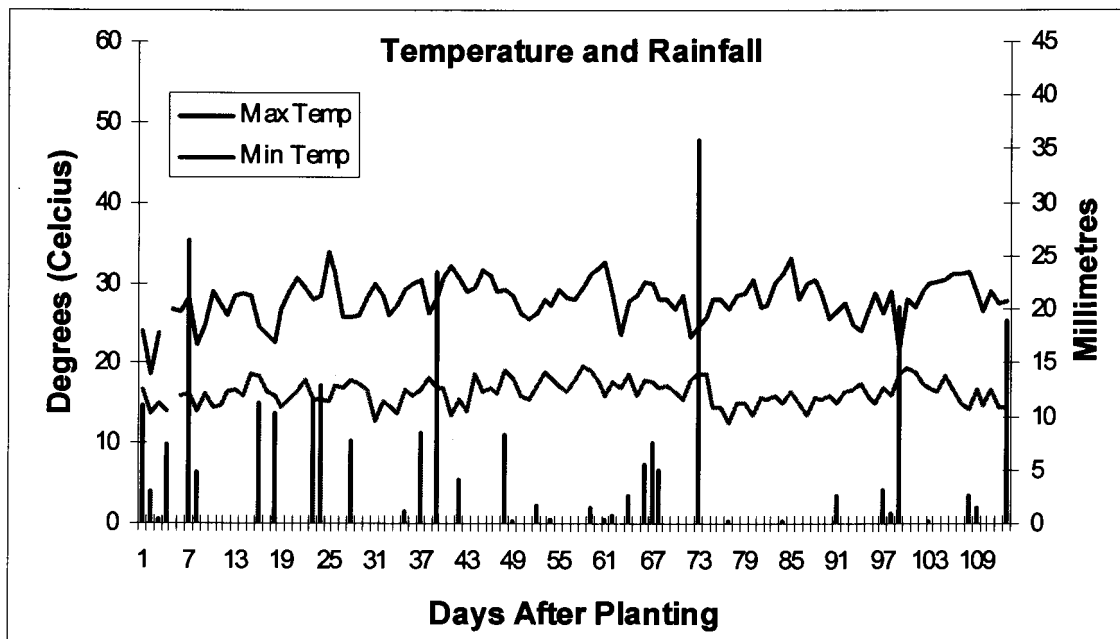


Figure 20. The minimum and maximum temperatures, as well as rainfall (vertical bars) at the experimental farm during the course of the field trial (Data courtesy of the South African Weather Service).

When the minimum and maximum temperatures are studied during the course of the experiment, it can be seen that no major fluctuations in ambient temperature occurred during the course of the trial. Therefore soil temperature as a growth factor remained relatively constant. In contrast, rainfall was irregular and it is assumed that rainfall, therefore soil moisture, had a larger effect on root development than soil temperature. Rainfall is incorporated in the subsequent presentation and discussion on root development for the field trial.

### 3.3.1.2. Root growth in the high and low P treated plots over a 16 week period

The method of sampling for the field trial is set out in figure 3. The procedure was unaltered for the entire 16 weeks. The root growth (gram per 60 cm<sup>3</sup> core) in the 0 to 10cm layer is presented in Figure 21.

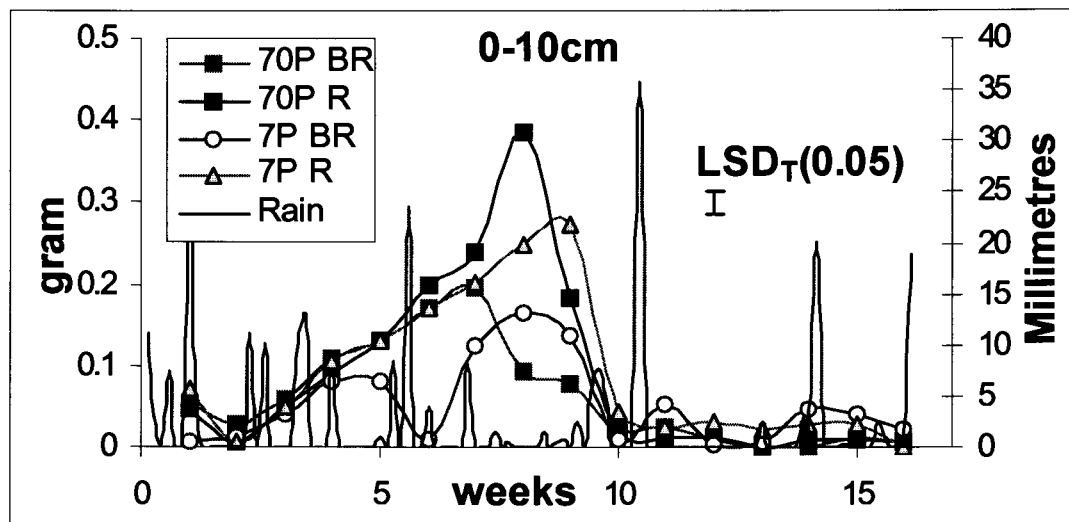


Figure 21. Root growth in high and low P plots in the top (0-10cm) soil.

There was a steady increase in root growth for the first 7 weeks. Little differences in root growth between the high-P and low-P plot were observed. As can be seen from Figure 22, the root growth at week 7 was in the following order:

**70 P Row (R) > 7 P Row (R) > 7 P Between Row (BR) > 70 P Between Row (BR).**

The highest amount of growth occurred in the rows. An interesting observation is that the 70 P plot had both the highest and the lowest amount of root growth. This indicates that normal root growth was possible in the rows, and that little root growth occurred or was stimulated between the rows. P was not applied in the rows, since P application ceased in 1993 it can be assumed that the distribution of P is random. It can be seen that after the rapid root development for 7 weeks, much less roots were harvested subsequently. Rainfall did not seem to have a definite influence on root development in the top soil.

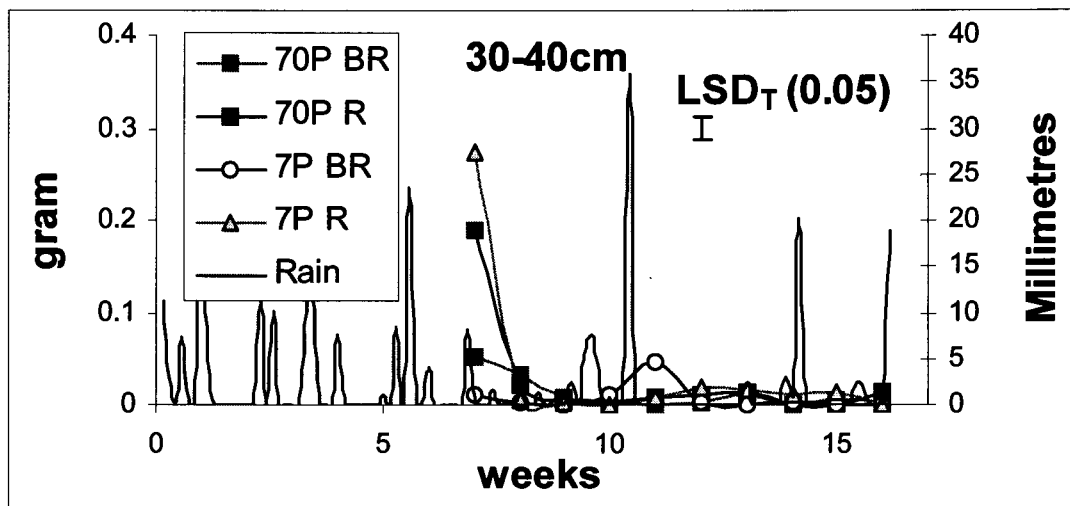


Figure 22. Root growth in high and low P plots between the 30 to 40cm depths.

In the 30-40 cm soil depth root development was different to that of the 0-10cm depth as illustrated by Figure 22. It shows that root growth in general was in the following order:

$$7P \text{ Row (R)} > 70P \text{ Row (R)} > 70P \text{ (BR)} > 7 P \text{ (BR)}$$

At this depth, the growth maximum occurred earlier than in the 0 to 10cm depth i.e. before 7 weeks (30-40cm) compared to approximately 8 weeks (0-10cm). Similar to the 0-10cm depth, the higher growth occurred in the rows.

In terms of P concentration, the observed pattern of the 0-10cm depth is reversed: the low P plot had higher growth at week 7, which shows that low soil P cause greater growth in the subsoil. Here again after 7-10 weeks, root mass in the sampled area declined and was variable, since no significant differences between the treatments could be observed. The reason for this decline in root mass may be due to the fact that roots, once a certain area is exploited, will keep on developing in new unexploited areas. It can be expected that many of the thin fibrous roots may die and not be evaluated later during the observation period.

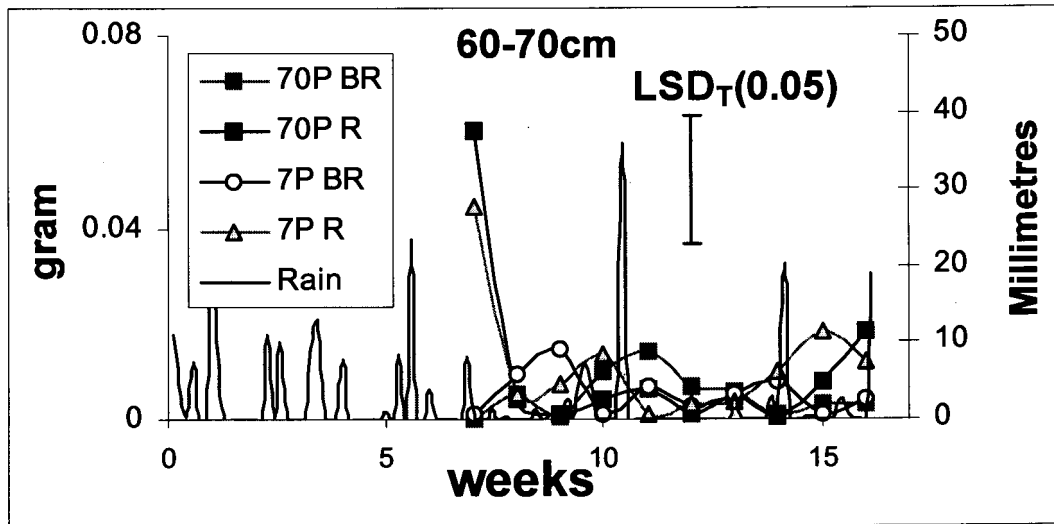


Figure 23. Root growth in high and low P plots between the 60 to 70cm depths.

The pattern of root growth was quite similar to that observed in the 40-60 cm depth.

In Figure 23 it can be seen that root growth was in the following order:

$$70 \text{ P Row (R)} > 7 \text{ P Row (R)} > 7 \text{ P (BR)} > 70 \text{ P (BR)}.$$

The observed pattern of the previous depths is again observed for the 60-70cm depth: the higher growth occurred in the rows at week 7. After week 8 though, the roots had alternating behaviour in terms of higher growth that occurred in: either the low or the high P plots, which changed on a weekly basis. However more root growth was observed at this depth after 8 weeks.

Of all the depths, roots in this depth (60 to 70cm) showed the greatest response to rainfall. Rain that fell in week 10 seems to have stopped root development in the 70 P (R), 7 P (BR) and 70 P (BR).

The growth of the roots after week 14 was very intriguing. At week 14 rainfall of 20 mm was recorded, which induced root growth in the rows (R) of both the low P and high P plots and simultaneously terminated growth in the between row (BR) positions. This observation can probably be explained as follows: the canopy of the mature maize plant deflects raindrops away from the rows (R) toward the between the rows (BR) positions. This result in the drying of the subsoil in the rows, and this

seemed to force the plants to enhance root growth in the row (R) positions. It therefore seemed that soil moisture had influenced root growth at this depth.

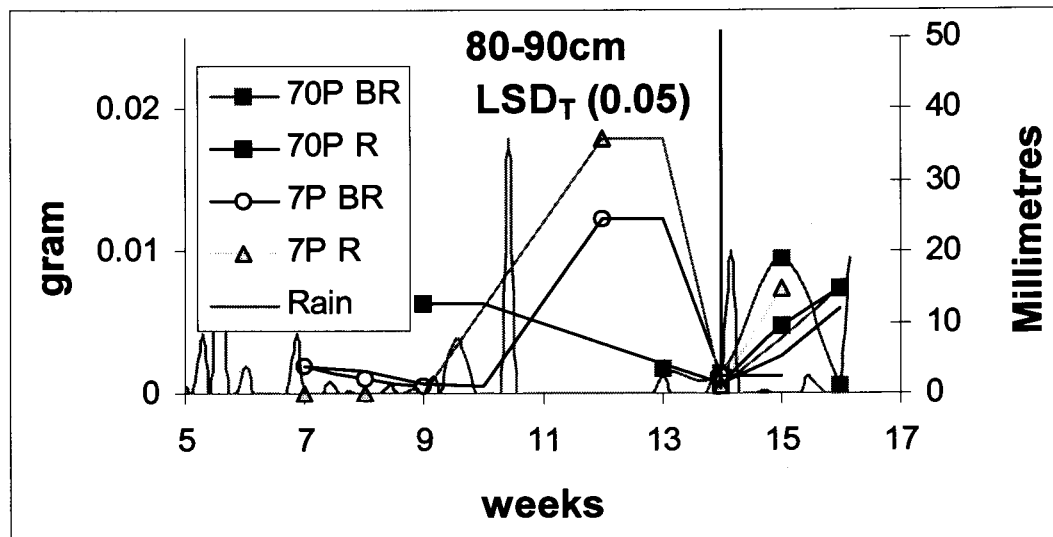


Figure 24. Root growth in high and low P plots between 80 to 90cm depths.

Root development at this depth was much later and according to Figure 24 it can be seen that root growth was in the following order:

**7 P Row (R) > 7 P Between Row (BR) > 70 Between Row (BR), 70 P Row (R).**

In contrast to the observed patterns of the other depths, maximum growth occurred in week 12. Due to the presence of the saprolite layer, roots were either absent or sampling was not possible to the specific depth. Therefore, due to the small amount of data, an assessment of root growth in this depth should be interpreted carefully. Root development was most prominent in the low-P plot and virtually absent in the high-P plot. This shows that P does not stimulate root development in field conditions, which is also shown in table 10.

**Table 2.** Mean values and significant differences at  $LSD_{TUKEY} = 0.05$  of level of fertilisation.

P level (Bray-1)	Mean value ( $g/cm^3$ )	$LSD_{TUKEY}$
7P	0.0299 *, c	0.0134
70P	0.0287 c	
* Means with the same letter are not significantly different at $\alpha = 0.05$		



Statistically the 0-10 cm and the 30-40 cm depths showed significant differences between level of P and sampling position, especially at week 7. No statistical significant differences were observed for the deeper depths.

### 3.3.2. Length to mass ratio

The length to mass ratios were determined using the length and the mass measurements. This was done in order to study the morphological changes induced by different levels of P at the different depths.

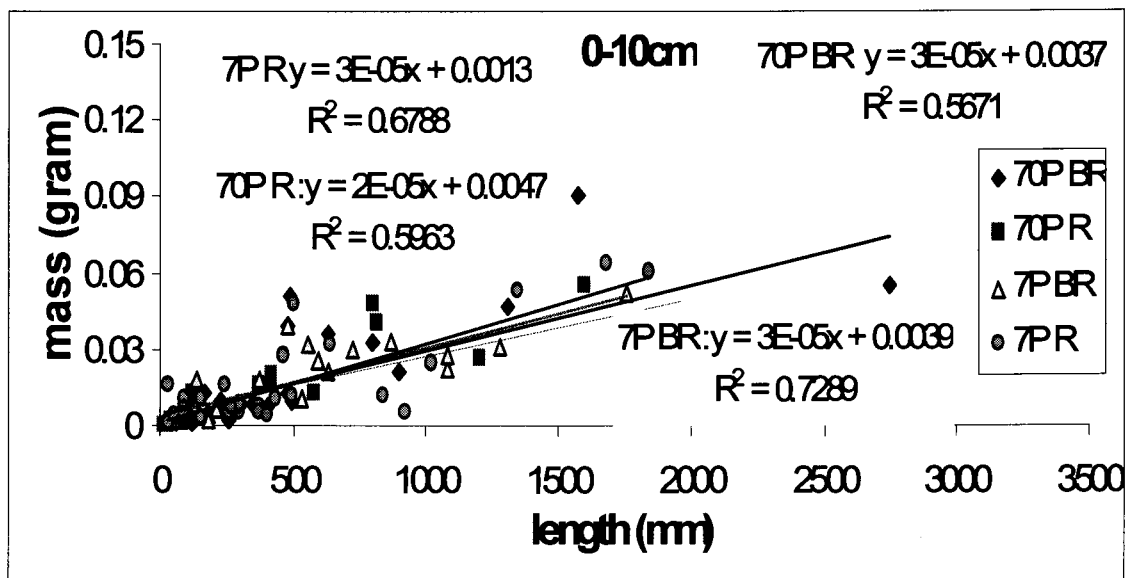


Figure 25. Length to mass ratios of the different positions and plots in the 0-10cm depth.

According to Figure 25 it can be seen that the ratios were nearly identical between the different plots and positions. When looking at the regression coefficients, it can be seen that the high P plots had higher variation, which is contrary to the findings of the pot experiments.

In Figure 26 the length to mass ratios is presented for the 30 to 40cm depth. The lengths to mass ratios for the row (R) positions are similar to those of the between the row (BR) positions, as illustrated by the trendline equations. The row (R) position of the high P plot shows excessive growth in comparison to the other positions. Its appearance is however influenced by the presence of an outlier (1050, 0.07). The

average slope of the row (R) positions is higher than that of the between row (BR) positions. This means that thicker roots are formed in the row (R).

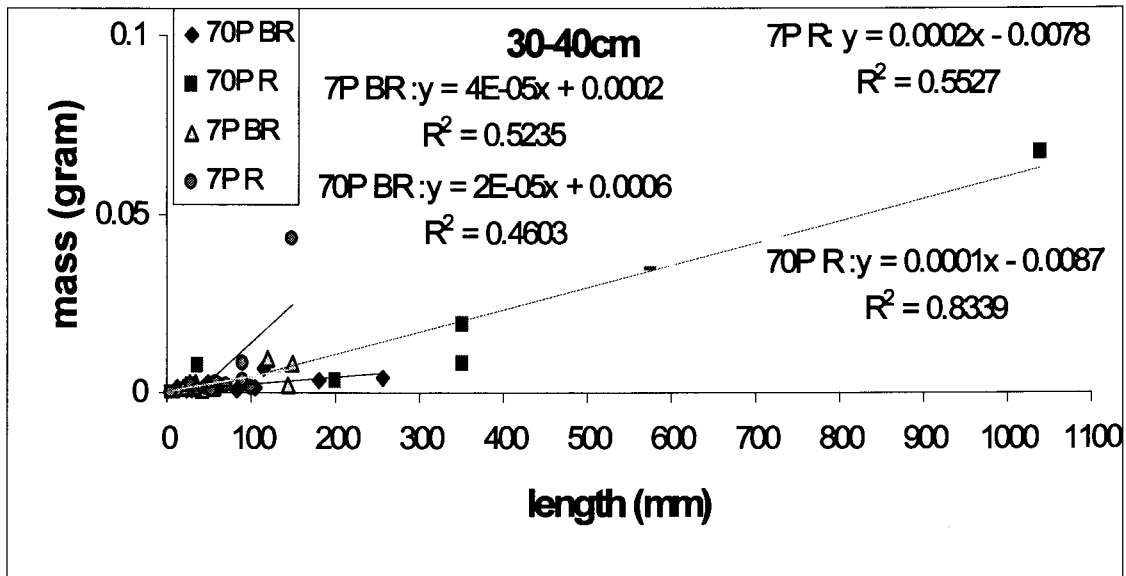


Figure 26. Length to mass ratios of the different positions and plots at the 30 to 40cm depth.

In Figure 27 the length to mass ratios are presented for the 60-70 cm depth. An interesting observation is that for the high P plot, the length to mass ratio in the row (R) is identical to that of the between the row (BR) positions. For the low P plot, the observation is different: the roots were much heavier in the row (R) position than in the between row (BR) positions.

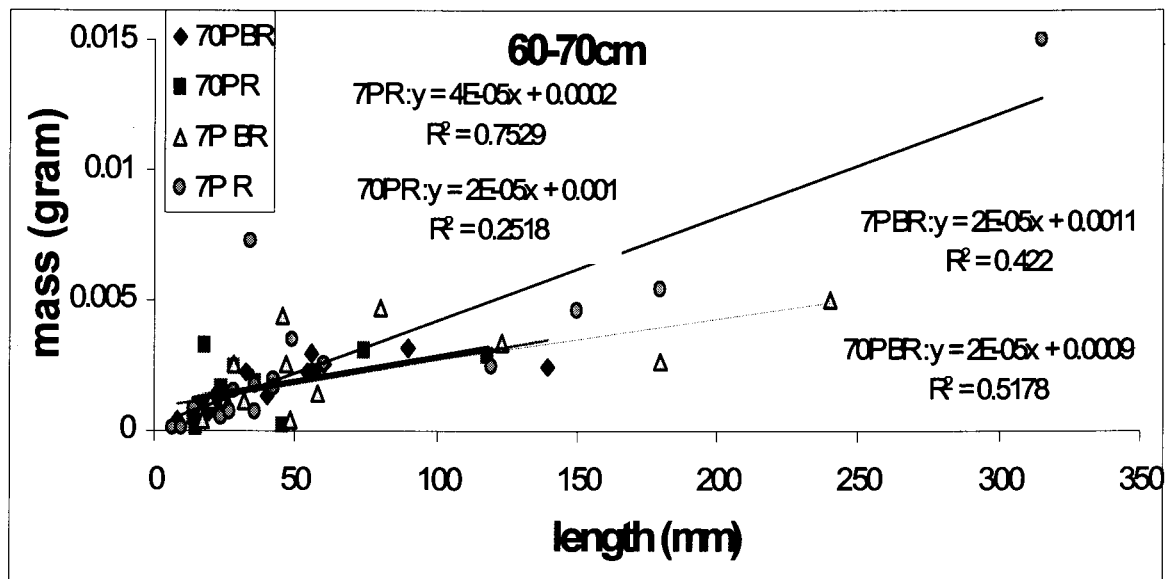


Figure 27. Length to mass ratios of the different positions and plots at the 60 to 70cm depth.

In contrast to other depths, the amount of biomass produced by the low P plot is much higher than that of the high P plot. Roots were also much longer and more fibrous for the low P plot than for the high P plot. This observation has serious implications regarding the drought resistance of plants: highly fertilised plants have a low drought resistance because little root development occurs in the wetter subsoil.

In Figure 28 the length to mass ratios of the 80 to 90cm depth are presented. As with all the other depths, the row position produced higher biomass than the between row position. As mentioned earlier, the small amount of data at this depth does not allow an accurate assessment of the growth of roots at this depth.

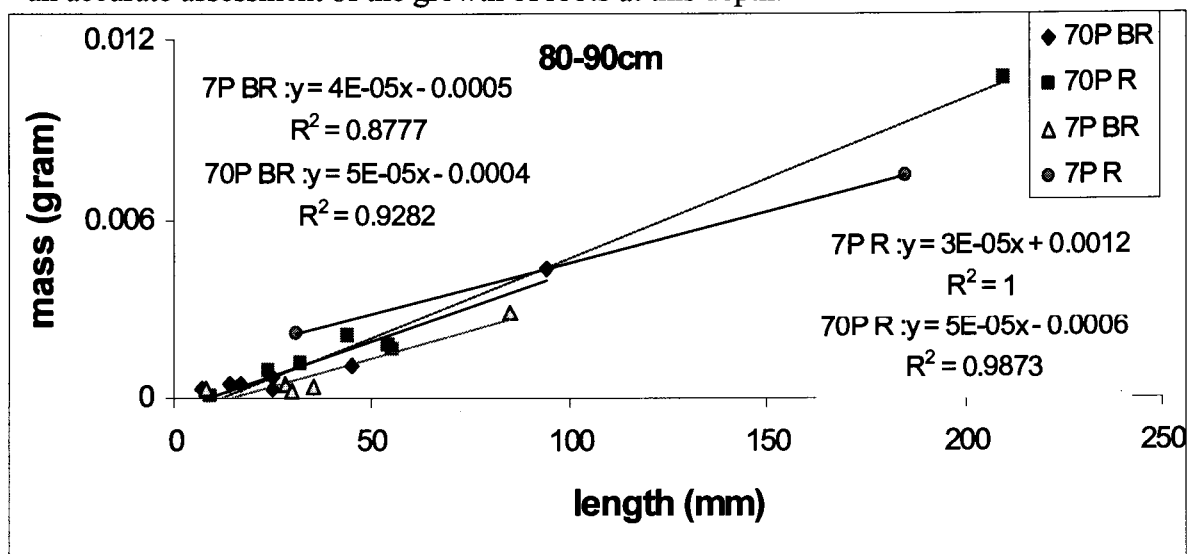


Figure 28. Length to mass ratios of the different positions and plots at the 80 to 90cm depth.

In general, the slopes of the length to mass ratios showed no major change for the different depths. At all the depths, the row positions had much higher biomass, the reason being the probably drier subsoil caused increased root development. This is shown by Table 3:

Table 3. Mean values and significant differences at  $LSD_{TUKEY} = 0.05$  of fertilisation.

Position	Mean value ( $g/60cm^{-3}$ )	$LSD_{TUKEY}$
Between rows	0.018 *, b	0.0018
Row	0.034 ab	
*Means of the same letter are not significantly different at $\alpha = 0.05$		

With respect to P's influence on root growth in field conditions, the most important observation is that of the behaviour of the roots at the 60-70cm depth: roots in the low P plot had much higher mass, longer length and were more fibrous than those of the high P plot. These have implications for the ability of maize plants to withstand drought, as already explained. At the other depths there was no major effect of P on the length to mass ratio.

### **3.3.3. Exploitation of the soil volume under field conditions**

The exploitation of roots as a percentage of the soil volume is presented in Figure 29. In general, the shapes of the root growth curves that are expressed as percentage exploitation resemble the previously presented growth curves based on mass measurement. The behaviour of the exploitation curves is also similar in terms of response to rainfall and sampling position.

The percentage exploitation of the roots in the 0 to 10cm-depth layer is nearly 10 times that of the other depths. Noteworthy is the observation that the average exploitation after week 10 decreased to approximately 0.2%. This indicates that some of the finer roots must have died and that root development took place in other areas that were not sampled.

In conclusion, it can be seen that the maximum percentage exploitation/utilisation is in the order of 4 %, and is achieved in the 0-10cm layer nearly 8 weeks after emergence. From literature it is known that most uptake of P occurs in the first 2 weeks (Mengel & Barber , 1974b; Hajabashi & Schumacher, 1994). At that stage the exploitation is in the order of 0.5-1%. It can be seen that the percentage of exploitation/utilisation of soil by maize plants in field conditions is extremely small.

Although roots may have developed into other areas, it is unlikely that they would have achieved higher percentages of exploitation.

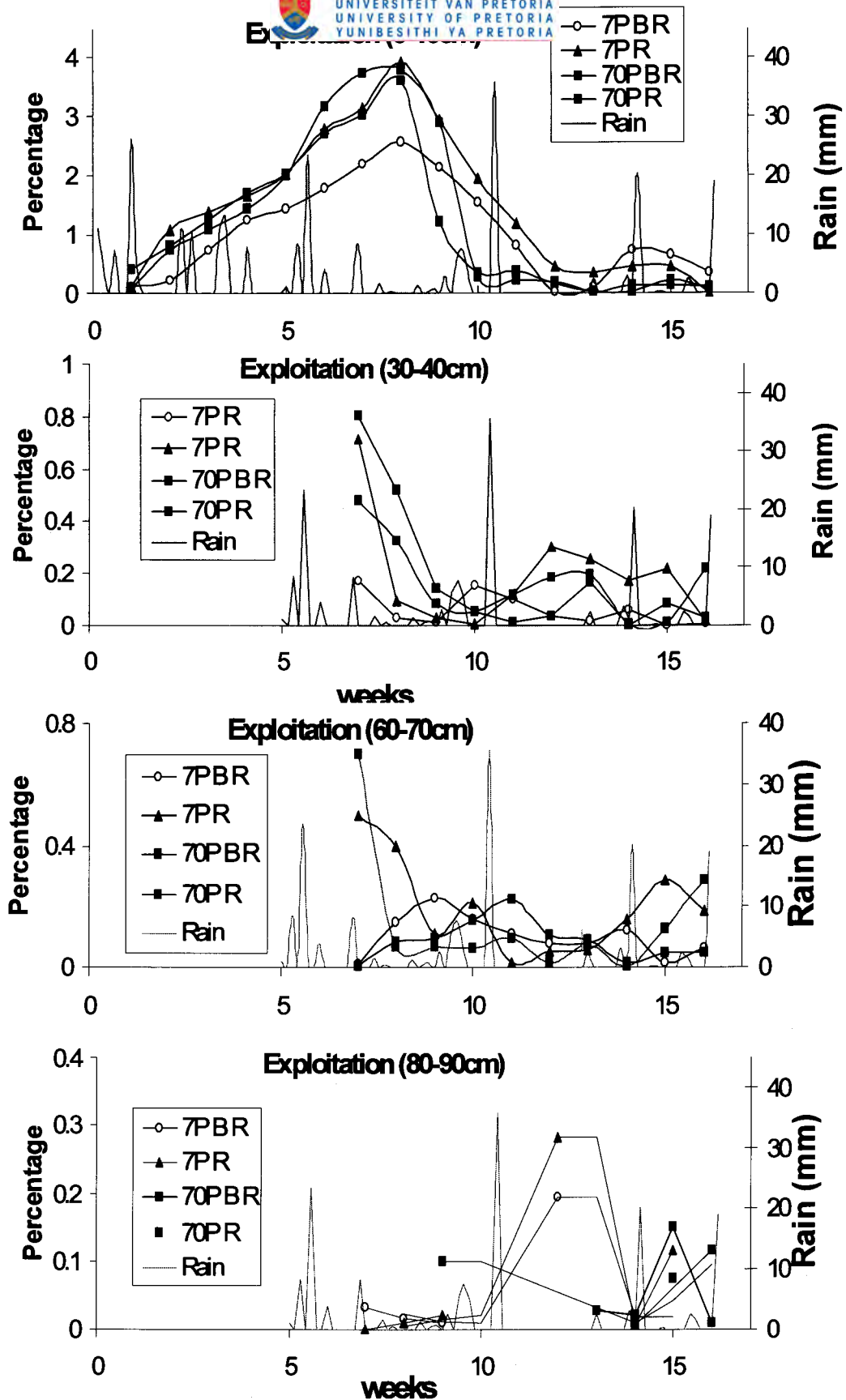


Figure 29. The exploitation of roots at different depths and positions.

To illustrate the low amount of exploitation, the following example is given: a soil has a Bray-1 value of  $10 \text{ mg kg}^{-1}$  (representing the “labile” P pool). A hectare of soil with a depth of 30cm contains 4 500 000 kg of soil (at  $\rho = 1500 \text{ kg m}^{-3}$ ). This means 45 000 000 mg of P is potentially available to the plants. At an exploitation of  $\approx 1\%$  (first two weeks), this means that 450 000 mg of P or 1% of the available P is “exploitable” or potentially available to the plant. A Bray-1 value must then be divided by approximately 100 to arrive at a value that gives the “exploitable” P. Therefore, a Bray-1 value of  $10 \text{ mg kg}^{-1}$  divided by 100 gives an “exploitable P” value of approximately  $0.01 \text{ mg kg}^{-1}$ .

Approximately 3-4 kg of P are removed per hectare by every ton of maize (FSSA, 2003). A Bray -1 value of  $10 \text{ mg kg}^{-1}$  represents 45 kg P per hectare with a depth of 30cm, but only 0.45 kg is exploitable/utilisable by the crop at a certain time. This means that the Bray-1 value accounts for only 6.4 % of the P that is used by the plants, and that 93.6% must come from other sources such as diffusion and more plant “unavailable” pools of P. Barber (1984) claims that diffusion accounts for 92% of the total acquired P, but simultaneously cites a diffusion coefficient of  $9.5 \times 10^{-9} \text{ cm}^2/\text{s}$ , 1000 times less than that of N. Diffusion as a major contributor of P can be ruled out.

Mass flow is also an unlikely contributor, since the solubility of common P compounds is low and therefore the plant will acquire very small amounts of its P requirements from the soil solution. It can be stated that a plant must acquire most of its P from the “plant unavailable” pool! This is probably true for all the immobile elements such as calcium, zink, copper, iron, etc.

#### 3.3.3.1. *Modelling of the exploitation volume*

As mentioned previously in the discussions of the exploitation in the pot trials, the Gompertz growth function was used. For the field trial, only the 0-10cm depth and the first seven weeks were considered. This is because the maximum growth occurred in this depth, during that time as well as the fact that it has the most data.

In Figure 31 the prediction of exploitation for the first eight weeks is presented. As with the pot experiments, an increase in the application of P resulted in an increase in

biomass (“a” constant). The relative growth from emergence till week 16 (“b” constant) was on average slightly lower for the high P plot, a pattern that was similarly observed in the pot trials. In the pot trials, an increase in P application resulted in a lowering of the growth rate (“c”). This is not observed in the field trial, where the high soil P plot had slightly higher “c” values than the low P plot. Despite a tenfold higher amount of soil P, exploitation in the high P plot was only slightly higher than that of the low P plot.

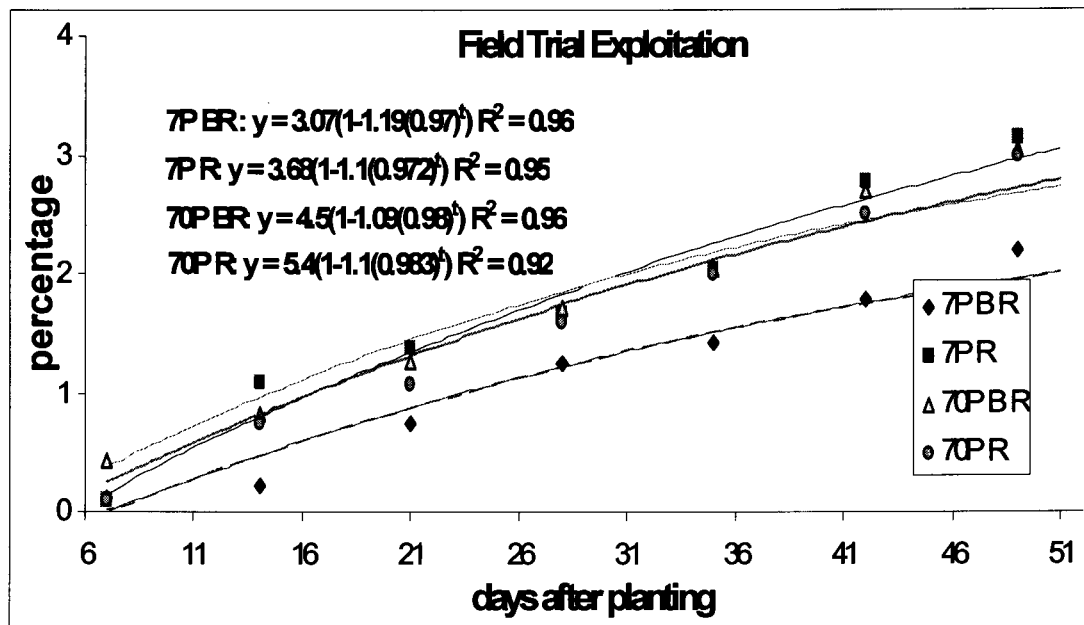


Figure 30. Changes in the predicted (line) and measured (dot) root exploitation as influenced by P over time.

According to figure 30, it was demonstrated that the Gompertz equation was able to predict the exploitation of roots in the field trial. From figure 30 it can be observed that the predicted and measured exploitation were similar. Exploitation in the row (R) was much higher than the exploitation between the rows (BR). It appears that the model used was able to model the exploitation of the roots and it can be used to predict the percentage exploitation (or growth) of roots in terms of sampling position and fertilisation.

### 3.3.5. Conclusion

It can be stated that root growth and the resulting exploitation volume are governed by the position: beneath the plant, row (R), and between the rows (BR). At all depths the

root development showed a maximum at 8-9 weeks, where after root mass did not increase. Rainfall influenced development in the deeper layers, especially in the 60-70cm depth. Evidence from this depth (60-70cm) indicates that the size of the canopy may have influenced root growth and probably stimulated root development in the rows. Verification of this argument must however come from actual determination of soil moisture in the two positions (row and between rows) for the different depths. A plant physiological explanation can also not be ruled out.

The model showed that position and P level affect eventual size of the root system.

The exploited percentages obtained are very low, especially for the first two weeks when most P uptake occurs. As already mentioned, this fact has implications for any soil analysis, since “exploitable” P is approximately 1% that of the analysed value.

Statistically, no significant differences occurred between the low P and the high P plot. This is in direct contrast to the findings of the pot experiments. It seems that at the optimal soil moisture level, the influence of P on root development is different from field conditions where soil moisture is mostly sub optimal. Significant differences occurred in the 0-10 cm and 30-40 cm depths between the different sampling positions and P level

The uptake of P and percentage exploitation in field conditions is therefore a function of numerous factors, of which P concentration is but one.



## CHAPTER 4. CONCLUSION

From the three trials it is clear that the measurement of roots is still problematic, especially length measurements. Mass measurements are by far the most accurate way to measure roots.

The addition of P strongly affects root morphology. Roots right beneath the stem increased in mass, while roots at the sides of the pots became more fibrous with increased P application. The application of P strongly increased the growth in the central area, whilst having a minor effect on roots in the side areas. P uptake and shoot growth is almost directly proportional to root growth in the central area (OS and KP). The second pot trial showed that N and K also stimulated root growth.

Root systems are very dynamic in the first two weeks after planting, as reflected in the length to mass and root to shoot ratios. This is also when most of the P uptake occurs.

P had a highly significant ( $P < 0.0001$ ) effect on root growth in the pot trials, but no significant effect in the field trial, where the average growth in the high and low P plots were similar. In the subsoil, the low P plot had the most root development.

Root growth can be modelled easily by means of the Gompertz function. The model enables prediction of the influence of P application on root growth.

Exploitation is a more comprehensive way in expressing root systems, in comparison with the traditional ways of expression, since it combines length and mass measurements as well as rhizosphere. It shows how much soil is “used” by the root system. Roots exploit at the most 3-4% of the top soil volume at full maturity. During the first two weeks when most P uptake occurs, the value is close to 1%. This implies that any soil analysis value (such as a Bray-1 value) should be divided by  $\approx 100$  to yield the “exploitable” P.

When considering the fact that a maize crop removes 3-4 kg P  $\text{ton}^{-1}$ , and assuming immobility in soil, this means that the crop acquires only  $\approx 6\%$  of its P from the “plant available” pool, as represented by the Bray-1 value. This suggests that roots are able

to extract the P from so called “unlabile” (plant unavailable) P pools . Therefore, the term “plant available” as are measured by different extraction methods do not really describe plant available P because much more P (than that extracted) is obtained by the plant from other sources. This shows that the Bray-1 extractant is not accurately simulating P removal from soil by roots.

The scenario for P could probably also apply for all other immobile elements such as calcium, iron, manganese and molybdenum. Scope for a future study is to determine how reliable currently used extractants simulate the elemental uptake of the root.

## REFERENCES

- AINA, P.O. & FAPOHUNDA, H.O., 1986. Root distribution and water uptake patterns of maize cultivars field grown under differential irrigation. *Plant and Soil* 94, 257-265.
- ANGHINONI, I. & BARBER S.A., 1980a. Predicting the most efficient phosphorus placement for corn. *Soil Science Society of America Journal* 44, 1016-1020.
- ANGHINONI, I. & BARBER S.A., 1980b. Phosphorus application rate and distribution in the soil and phosphorus uptake by corn. *Soil Science Society of America Journal* 44, 1041-1044.
- ASSENG, S, RICHTER, C. & WESSOLEK, G., 1997. Modelling root growth of wheat as the linkage between crop and soil. *Plant and Soil* 190, 267-277.
- BAKER, D.E. & WOODRUFF, C.M., 1962. Influence of volume of soil per plant upon growth and uptake of phosphorus by corn from soils treated with different amounts of phosphorus. *Soil Science* 94, 409-412.
- BARBER, S.A., 1958. Relation of fertilizer placement to nutrient uptake and crop yield I. Interaction of row phosphorus and the soil level of phosphorus. *Agronomy Journal* 50, 535-538.
- BARBER, S.A. 1984. *Soil Bionutrient Availability: a Mechanistic Approach*. John Wiley and Sons, Inc., New York.
- BARRY, D.A.J. & MILLER, M.H., 1989. Phosphorus nutritional requirement of maize seedlings for maximum yield. *Agronomy Journal* 81, 95-99.
- BAR-YOSEF, A. B. & LAMBERT, J.R. 1981. Corn and cotton root growth in response to soil impedance and water potential. *Soil Science Society of America Journal* 45, 930-935.

- BENJAMIN, J.G., AHUJA, L.R. & ALLMARAS, R.R., 1996. Modelling corn rooting patterns and their effects on water uptake and nitrate leaching. *Plant and Soil* 179, 223-232.
- BOHN, H.L., MCNEAL, B.L. & O'CONNOR, G.A., 1985. Soil Chemistry. John Wiley and Sons, Inc. New York.
- BROWN, S. & SCOTT, G., 1984. Roots , nutrient and water influx, and plant growth. ASA Special Publication Number 19. Published by SSSA, CSSA and ASA. Madison.
- CAHN, M. D., ZOBEL, R.W. & BOULDIN, D.R., 1989. Relationship between root elongation rate and diameter and duration of growth of lateral roots of maize. *Plant and Soil* 119, 271-279.
- CARLY , H.E. & WATSON, R.D., 1966. A new gravimetric method for estimating root-surface areas. *Soil Science* 102 (5), 289-291.
- COSTA, C., DWYER, L.M., HAMILTON, R.I., HAMEL, C., NANTAIS, L., & SMITH, D.L., 2000. A sampling method for measurement of large root systems with scanner-based image analysis. *Agronomy Journal* 92, 621-627.
- DE JAGER, P.C., 2002. A P sorption and desorption study on an acid sandy clay soil. M.Sc. Thesis, University of Pretoria.
- DE WIT, C.T., 1953. A physical theory on the placement of fertilisers. *Verslag landbouwkundig onderzoek* 59, 1-82.
- DUNCAN, W.G. & OHLROGGE, A.J., 1958. Principles of nutrient uptake from fertilizer bands II. Root development in the band. *Agronomy Journal* 50, 605-608.
- DUNHAM, R.J. & NYE, P.H., 1976. The influence of soil water content on the uptake of ions by roots. *Journal of Applied Ecology* 12, 967-984.

DWYER, L.M., MA, B.L., STEWART, D.W., HAYHOE, H.N., BALCHIN, D., CULLEY, J.L.B. & MCGOVERN, M., 1995. Root mass distribution under conventional and conservation tillage. *Canadian Journal of Soil Science* 76, 23-28.

EGHBALL, B & MARANVILLE, J.W., 1993. Root development and nitrogen influx of corn genotypes grown under combined drought and nitrogen stress. *Agronomy Journal* 85, 147-152.

EHLERS, W., KÖPKE, U., HESSE, F. & BÖHM, W., 1983. Penetration resistance and root growth in tilled and untilled loess soil. *Soil Tillage Research* 3, 261-275.

ESCAMILLA, J.A., COMERFORD, N.B. & NEARY, D. G. 1991. Soil core break method to estimate pine root distribution. *Soil Science Society of America Journal* 55, 1722-1726.

FOTH, H.D., 1962. Root and top growth of corn. *Agronomy Journal* 54, 49-52.

FOX, R.H., 1978. Selection for phosphorus efficiency in corn. *Communications in Soil Science and Plant Analysis* 9 (1), 13-37.

FRIED, M., HAGEN, C.E., SAIZ DEL RIO, J.F. & LEGGET, J.E., 1957. Kinetics of phosphate uptake in the soil-plant system. *Soil Science* 84 (6), 427-437.

FSSA (FERTILISER SOCIETY OF SOUTH AFRICA). Fertiliser Guidelines. 6<sup>th</sup> edition.

GARG, K.P. & WELCH, L.F., 1967. Growth and phosphorus uptake by corn as influenced by phosphorus placement. *Agronomy Journal* 59, 152-154.

GERWITZ, A, & PAGE, E. R., 1974. An empirical model to describe plant root systems. *Journal of Applied Ecology* 11, 773-783.

GRANT, R.F. & ROBERTSON, J.A., 1997. Phosphorus uptake by root systems: mathematical modelling in *ecosys. Plant and Soil* 188, 279-297.

GREACEN, E.L. & OH, J.S., 1972. Physics of root growth. *Nature New Biology* 235, 24-25.

HACKETT, C., 1969. A study of the root system of barley II. Relationships between root dimensions and nutrient uptake. *New Phytologist* 68, 1023-1030.

HAJABBASI, M.A. & SCHUMACHER, T.E., 1994. Phosphorus effects on root growth and development in two maize genotypes. *Plant and Soil* 158, 39-46.

HESLEP, J.M. & BLACK, C.A., 1954. Diffusion of fertilizer phosphorus in soils. *Soil Science* 78, 389-401.

KABIR, Z., O'HALLORAN, I.P., WIDDEN, P. & HAMEL, C., 1998. Vertical distribution of arbuscular mycorrhizal fungi under corn (*Zea mays* L.) in no-till and conventional tillage systems. *Mycorrhiza* 8, 53-55.

KAGE, H. , KOCHLER, M. & STÜTZEL, H., 2000. Root growth of cauliflower (*Brassica oleracea* L. *botrytis*) under unstressed conditions: Measurement and modelling. *Plant and Soil* 223, 131-145.

KASPAR, T.C., BROWN, H.J. & KASSMEYER, E.M., 1991. Corn root distribution as affected by tillage, wheel traffic, and fertilizer placement. *Soil Science Society of America Journal* 55, 1390-1394.

KLEPPER, B. & RICKMAN, R.W., 1990. Modelling crop root growth and function. *Advances in Agronomy* 44, 113- 129.

KNOLL, H.A., LATHWELL, D.J. & BRADY, N.C., 1964. The influence of root zone temperature on the growth and contents of phosphorus and anthocyanin of corn. *Soil Science Society of America Proceedings* 28, 400-403.

LAMBERT, D. H., BAKER, D. E., & COLE, H., 1979. The role of mycorrhizae in the interactions of phosphorus with zinc, copper and the other elements. *Soil Science Society of America Journal* 43, 976-980.

LANG, A. R. G. & MELHUIISH, F. M., 1970. Lengths and diameters of plant roots in non random populations by analysis of plane surfaces. *Biometrics* 26, 421-431.

LONGSDON, S. D. & ALLMARAS, R. R., 1991. Maize and soybean root clustering as indicated by root mapping. *Plant and Soil* 131, 169-176.

LU, S., BRAUNBERGER, P.G., & MILLER, M.H., 1994. Response of vesicular-arbuscular mycorrhizas of maize to various rates of P addition to different rooting zones. *Plant and Soil* 158, 119-128.

LU, S. & MILLER, M.H., 1993. Determination of the most efficient phosphorus placement for field-grown maize (*Zea mays* L.) in early growth stages. *Canadian Journal of Soil Science* 73, 349-358.

LU, S. & MILLER, M.H., 1993. Prediction of phosphorus uptake by field-grown maize with the Barber-Cushman model. *Soil Science Society of America Journal* 58, 852-857.

MACKAY, A.D., & BARBER, S.A., 1984. Soil temperature effects on root growth and phosphorus uptake by corn. *Soil Science Society of America Journal* 48, 818-823.

MACKAY, A.D., & BARBER, S.A., 1985a. Soil moisture effects on root growth and phosphorus uptake by corn. *Agronomy Journal* 77, 519-523.

MACKAY, A.D., & BARBER, S.A., 1985b. Effects of soil moisture and phosphate level on root hair growth of corn roots. *Plant and Soil* 86, 321-331.

MARSCHNER, H., RÖMHELD, V., HORST, W. J., & MARTIN, P., 1986. Root-induced changes in the rhizosphere: importance for the mineral nutrition of plants. *Zeitschrift für Pflanzenernährung und Bodenkunde* 149, 441-456.

MENGEL, D. B., & BARBER, S.A., 1974a. Development and distribution of the corn root system under fields conditions. *Agronomy Journal* 66, 341-344.

MENGEL, D.B., & BARBER, S.A., 1974b. Rate of nutrient uptake per unit of corn root under field conditions. *Agronomy Journal* 66, 399-402.

MOLLIER, A., & PELLERIN, S., 1999. Maize root system growth and development as influenced by phosphorus deficiency. *Journal of Experimental Botany* 50, 487-497.

NEL, P.C., BARNARD, R.O., STEYNBERG, R.E., DE BEER, J.M. & GROENEVELD, H.T., 1996. Trends in maize grain yields in a long-term fertilizer trial. *Field Crops Research* 47, 53-64.

NEWMAN, 1966. A method of estimating root length in a sample. *Journal of Applied Ecology* 3, 139-145.

NEWMAN, E.I. & ANDREWS, R.E., 1973. Uptake of phosphorus and potassium in relation to root growth and root density. *Plant and Soil* 38, 49-69.

NOBBE, F., 1862. Über die feinere Verastelung der Pflanzenwurzeln. *Landw. Versuchs-Stat.* 4: 212-224.

OCHWOH, V.A., 2002. Studies on P desorption and fractionation characteristics Rustenburg and Loskop reddish-brown soils. PHD Thesis, University of Pretoria.

OIKEH, S.O., KLING, J.G., HORST, W.J., CHUDE, V.O. & CARSKY, R.J., 1999. *Field Crops Research* 62, 1-13.

OLSEN, S.R., WATANABE, F.S., DANIELSON, R.E., 1961. Phosphorus absorption by corn roots as affected by moisture and phosphorus concentration. *Soil Science Society Proceedings* , 289-294.

ORTAS, I., 1997. Determination of the extent of rhizosphere soil. *Communications in Soil Science and Plant Analysis* 28, 1767-1776.



PAGE, E.R. & GERWITZ, A., 1974. Mathematical models, based on diffusion equations, to describe root systems of isolated plants, row crops and swards. *Plant and Soil* 41, 243-249

PAGÈS, L., JORDAN, M.O., & PICARD, D., 1989. A simulation model of the three-dimensional architecture of the maize root system. *Plant and Soil* 119, 147-154.

PALLANT, E., HOLMGREN R.A., SCHULER, G.E., McCracken, K.L., & DRBAL, B., 1993. Using a fine root extraction device to quantify small diameter corn roots ( $\geq 0.025\text{mm}$ ) in field soils. *Plant and Soil* 153, 273-279.

PERRIET, A., CAPOWIEZ, Y., MORAN, C.J., KRETZSCHMAR, A., 1999. X-ray computed tomography to quantify tree rooting spatial distributions. *Geoderma* 90, 307-326.

REX, M., HARRACH, T., & NÉMETH, K., 1985. The influence of rooting density in the soil on P removal by cereals on soils with different yield potential. *Plant and Soil* 83, 127-132.

RILEY, D. & BARBER, S.A., 1971. Effect of ammonium and nitrate fertilization on the phosphorus uptake as related to root-induced pH changes at the root-soil interface. *Soil Science Society of America Proceedings* 35, 301-306.

ROSE, D.A., 1983. The description of the growth of root systems. *Plant and Soil* 75, 405-415.

SCHENK, M.K. & BARBER, S.A., 1979. Root characteristics of corn genotypes as related to P uptake. *Agronomy Journal* 71, 921-924.

SCHENK, M.K. & BARBER, S.A., 1980. Potassium and phosphorus uptake by corn genotypes grown in the field as influenced by root characteristics. *Plant and Soil* 54, 65-76.

STEYN, A.G.W., SMIT, C.F., & DU TOIT, S.H.C., 1984. Moderne statistiek vir die praktyk. Van Schaik.

STEFFENS, D., 1984. Wurzelstudien und phosphat-aufnahme von weidelgras und rotklee unter feldbedingungen. *Zeitschrift für Pflanzenernaehrung und Bodenkunde* 147, 85-97.

TENNANT, D., 1975. A test of modified line intersect method of estimating root length. *Journal of Ecology* 63, 995-1001.

VOGEL, H., 1995. Maize root profiles in gleyic sandy soils as influenced by ridging ploughing in Zimbabwe. *Tropical Agriculture* 72, 120-125.

WIERSUM, L.K., 1961. Utilization of soil by the plant root system. *Plant and Soil* 15, 189-191.

WIESLER, F. & HORST, W.J., 1994. Root growth and nitrate utilization of maize cultivars under field conditions. *Plant and Soil* 163, 267-277.

ZHANG, J. & BARBER, S.A., 1992. Maize root distribution between phosphorus-fertilized and unfertilized soil. *Soil Science Society of America Journal* 56, 819-822.

## ACKNOWLEDGEMENTS

I wish to thank the following persons:

- Our Heavenly Father for His Grace through all the years of study
- Professor A. S. Claassens for his grace, and for sharing his vast knowledge with his students
- My wife Ursula, for all her support and encouragement
- My parents for all their “inputs”
- The personnel of our department, particularly messrs. Charl Hertzog and Burger Cillié who assisted with the execution of the respective trials and P Analyses as well as invaluable advice
- Dr. Thomas Fyfield and the Institute for Soil, Climate and Water who gave kind permission and advise on the use of the Geotron WLM1 root length measuring device
- Ms. Wendy Nkuna of the South African Weather Service for supplying the weather data
- Mr. Piet Fourie, manager of SOILLAB, for his interest and allowing opportunity for the completion and printing of the manuscripts
- The late professor D. G. Haylett, for being instrumental in the establishment of the long term fertiliser trial in 1939, and all those involved in the maintenance of the trail for the past 65 years. May this extremely precious facility be preserved for future generations of agricultural scientists, and may the University management not succumb to monetary pressure by selling this unique piece of earth to capitalists...

## **APPENDIX-Statistical analysis**

### A.1.1. FIRST POT EXPERIMENT (0S area):

#### **ANALYSIS OF VARIANCE**

Variable v1: root mass gram

<b>Source</b>	<b>DF</b>	<b>Sum of squares</b>	<b>Mean square</b>	<b>F value</b>	<b>P<sub>R</sub> &gt; F</b>
<b>Model</b>	27	11.24	0.41	10.68	< 0.0001
<b>Error</b>	28	1.09	0.039		
<b>Corr. Total</b>	55	12.34			

$$R^2 = 0.911 \quad CV = 30.19 \quad \sqrt{MSE} = 0.197 \quad V1 \text{ mean} = 0.654$$

### A.1.2. FIRST POT EXPERIMENT (0K area):

#### **ANALYSIS OF VARIANCE**

Variable v1: root mass gram

<b>Source</b>	<b>DF</b>	<b>Sum of squares</b>	<b>Mean square</b>	<b>F value</b>	<b>P<sub>R</sub> &gt; F</b>
<b>Model</b>	27	1.14	0.042	2.58	0.0075
<b>Error</b>	28	0.45	0.016		
<b>Corr. Total</b>	55	1.60			

$$R^2 = 0.711 \quad CV = 73.73 \quad \sqrt{MSE} = 0.128 \quad V1 \text{ mean} = 0.17$$

### A.1.3 FIRST POT EXPERIMENT (all areas combined):

Test for normality:

<b>Test</b>	<b>D</b>	<b>P<sub>R</sub> &lt; D</b>
Kolmogorov-Smirnov	0.21*	< 0.01

\* values between 0 and 1 indicates normal distribution.

**Table A1.** Kolmogorov-Smirnov test for normality for the first pot experiment

Normality data:

N: 224	Variance: 0.11	Kurtosis: 10.95
Mean: 0.27	STD deviation: 0.33	Skewness: 2.81

## ANALYSIS OF VARIANCE

Variable v1: root mass gram

Source	DF	Sum of squares	Mean square	F value	$P_R > F$
Model	27	1.14	0.042	2.58	0.0075
Error	28	0.45	0.016		
Corr. Total	55	1.60			

$$R^2 = 0.711 \quad CV = 73.73 \quad \sqrt{MSE} = 0.128 \quad V1 \text{ mean} = 0.17$$

<u>Interaction</u>	<u>Growth Time</u>	<u>Area in pot</u>	<u>P level</u>
Time × P level	Week 1.5 to 4		0 to 80 p.p.m.
P level × Area		0S, 7S, 0K and 7K	0 to 80 p.p.m.
Time × Area	Week 1.5 to 4	0S and 7K	
	Week 2 to 4	7S	
	Week 3.5 to 4	0K	
Time × P level × Area	Week 1.5 to 4	0S	20 p.p.m.
	Week 1.5 to 4	0S	40 p.p.m.
	Week 2 to 4	0S	0 to 80 p.p.m.

**Table A2.** Summary of all highly significant interactions ( $P < 0.0001$ ) between growth time, area in the pot and level of phosphate fertilisation on root mass.

P level (p.p.m.)	Mean (gram)
0	0.187 <sup>c*</sup>
20	0.257 <sup>b</sup>
40	0.347 <sup>a</sup>
80	0.303 <sup>ab</sup>
<b>n = 224</b>	<b>LSD<sub>0.05</sub> = 0.058</b>

\*Means of the same letter are not significantly different at  $\alpha = 0.05$  according to Tukey's studentized range test (HSD).

**Table A3.** Tukey's test for significant difference for phosphate level's influence on root growth.

## A.2 SECOND POT EXPERIMENT:

Test for normality:

Test	D	$P_R < D$
Kolmogorov-Smirnov	0.127	< 0.01

\* values between 0 and 1 indicates normal distribution.

**Table A3.** Kolmogorov-Smirnov test for normality for the second pot experiment

### Normality data:

N: 251                      Variance: 1.116                      Kurtosis: 0.076

Mean: 1.51                      STD deviation: 1.05                      Skewness: 0.77

### A.2.1 ANALYSIS OF VARIANCE

Variable v1: root mass gram

Source	DF	Sum of squares	Mean square	F value	$P_R > F$
<b>Model</b>	83	248.66	2.99	19.27	< 0.0001
<b>Error</b>	168	26.11	0.155		
<b>Corr. Total</b>	251	274.77			

$R^2 = 0.904$        $CV = 26.36$        $\sqrt{MSE} = 0.394$       **V1 mean = 1.49**

### Interactions:

Source	DF	Type III SS*	MS**	F value	$P_R > F$
<b>Time (T)</b>	6	129.56	21.59	138.91	< 0.0001
<b>Fertilisation (F)</b>	3	40.48	13.49	86.82	< 0.0001
<b>T × F</b>	18	23.97	1.33	8.57	< 0.0001
<b>Sector (area) (S)</b>	2	32.92	16.46	105.9	< 0.0001
<b>T × S</b>	12	6.9	0.57	3.7	< 0.0001
<b>F × S</b>	6	2.33	0.38	2.5	0.024
<b>T × F × S</b>	36	12.47	0.34	2.23	0.0003

\*Sum of squares \*\*Mean square

<b><u>Interaction</u></b>	<b><u>Growth Time</u></b>	<b><u>Area</u></b>	<b><u>P level</u></b>
<b>Time × P level</b>	Week 1.5 to 4		0 to 80 p.p.m.
<b>P level × Area</b>		S, K and KP	0 to 80 p.p.m.
<b>Time × Area</b>	Week 2 to 4	S, K and KP	
<b>Time × P level × Area</b>	Week 2.5 to 4	S, K and KP	0 to 80 p.p.m.

**Table A4.** Summary of all highly significant interactions ( $P < 0.0001$ ) between growth time, area in the pot and level of phosphate fertilisation on root mass.

Phosphate level:

<b>P level</b>	<b>Mean value</b>	<b>Standard error</b>	<b>LSD</b>
<b>0 p.p.m.</b>	0.81 <sup>*,c</sup>	0.049	0.139
<b>20 p.p.m.</b>	1.71 <sup>ab</sup>	* Means with the same letter are not significantly different at $\alpha = 0.05$	
<b>40 p.p.m.</b>	1.62 <sup>b</sup>		
<b>80 p.p.m.</b>	1.82 <sup>a</sup>		

**Table 9.** Mean values and significant differences at  $\alpha = 0.05$  of level of fertilisation.

### A3. FIELD TRIAL

Test for normal distribution

Parameter	Test	D value	Pr > D
Root mass	Kolmogorov-Smirnoff	0.33	< 0.01

**Table A5.** Kolmogorov –Smirnoff test for normal distribution.

**Normality data:**

N: 298                      Variance: 0.004                      Kurtosis: 38  
Mean: 0.029                      STD deviation: 0.067                      Skewness: 5.16

#### A.3.1 ANALYSIS OF VARIANCE

Variable v1: root mass gram

Source	DF	Sum of squares	Mean square	F value	Pr > F
<b>Model</b>	18	0.54	0.030	10.23	< 0.0001
<b>Error</b>	279	0.82	0.0029		
<b>Corr. Total</b>	297	1.36			

$R^2 = 0.39$      $CV = 184.9$      $\sqrt{MSE} = 0.05$     **V1 mean = 0.029**

Interactions:

Source	DF	Type III SS*	MS**	F value	Pr > F
<b>Time (T)</b>	12	0.31	0.026	8.9	< 0.0001
<b>Fertilisation (F)</b>	1	0.002	0.002	0.84	0.359
<b>Row (R)</b>	1	0.018	0.018	6.33	0.0125
<b>F × R</b>	1	0.0005	0.0005	0.20	0.6525
<b>Depth</b>	3	0.14	0.048	16.58	< 0.0001

\*Sum of squares \*\*Mean square

Position	Mean value	Standard error	LSD
<b>Between rows</b>	0.018 * <sup>a</sup> b	0.0055	0.0018
<b>Row</b>	0.034 <sup>ab</sup>		
*Means of the same letter are not significantly different at $\alpha = 0.05$			

**Table A6.** Mean values and significant differences at  $\alpha = 0.05$  of area.