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**EARLY GROWTH OF ROOTS AND SHOOTS OF MAIZE AS AFFECTED BY
TILLAGE-INDUCED CHANGES IN SOIL PHYSICAL PROPERTIES**

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SUMMARY

No-tillage systems (NT) are used increasingly to alleviate some of the negative effects of conventional tillage (CT) such as soil erosion, energy use, leaching and runoff of agricultural chemicals, and degradation of the soil structure. NT systems are very advantageous for a row crop such as maize because of the large distance between the rows and the initial slow growth of the plant in temperate climates. However, the long-term application of no-tillage systems in these climates leads to a cooler layer of surface soil early in the season, which is associated with increased mechanical impedance. This may lead to stress conditions for the growth of the shoot and root, particularly in the topsoil at the beginning of the growing season. Therefore, maize is subjected to a combination of soil physical stresses during establishment.

The objective of this study was to investigate the effects of the main tillage-induced changes in the physical properties of the soil on above- and below-ground parts of maize seedlings, in terms of growth and function:

- [1] Under field conditions, the lateral and vertical distribution as well as the morphology of the root system of maize at an early growth stage, as affected by tillage intensity, were characterized. Furthermore, attention was paid to the effect of the sidebanding of NP-fertilizer on the distribution and morphology of the roots.
- [2] Under controlled conditions, the physical conditions of the soil under conventional and no-tillage in the field were simulated, whereby combinations of vertically varied soil temperature and soil bulk density were applied.
 - [2a] First, the early growth and performance of the shoot and roots of maize was investigated.
 - [2b] Second, the morphology, distribution and functioning of the roots were studied with regard to shoot growth and the utilization efficiency of phosphorus and nitrogen fertilizer. Phosphorus was used as a model macroelement to determine whether the effects of soil properties on the roots lead to an inadequate supply of nutrients to the shoot.

The results were as follows:

- [1] In the field, the soil temperature decreased, and the bulk density and penetration resistance of the topsoil increased in the NT compared with the CT system. Shoot growth and development were slower in the NT system. The root length density (RLD) was higher and the mean root diameter smaller in the CT than in the NT system, while the vertical and horizontal distribution of the roots did not change. RLD increased in the fertilizer zone, independent of the tillage system, but the mean root diameter did not change. Higher influx rates of P per unit root length compensated for the reduced extension of the root system in the NT system.
- [2a] Under controlled conditions, the rate of leaf expansion was drastically reduced, and the roots were concentrated near the soil surface when the bulk density of the topsoil was higher. Thus, intensive use of water and N from the subsoil occurred only in the presence of a uniformly loose soil profile. The bulk density of the topsoil was negatively correlated and temperature of the topsoil was positively correlated with the photosynthetic activity. Both these soil properties acted independently on all the measured plant parameters. The bulk density of the soil was the major growth-limiting factor, both for the shoot and for the roots.
- [2b] In the second series of growth chamber experiments, the bulk density of the topsoil caused a linear decrease in the length and weight of the roots, an increase in the diameter of the roots both in the top- and in the subsoil, and a decrease in the root:shoot ratio. Shoot and root growth were equally reduced by the decreasing temperature of the topsoil. In general, root length, mean diameter, and vertical distribution were influenced positively by the level of P in the topsoil. Soil temperature and level of P may have had compensatory effects on root growth. Bulk density and temperature of the topsoil acted independently on all the parameters measured but showed some interactions with P.

It is concluded that the lower temperature of the topsoil in spring was the main limiting factor for the early growth of NT maize in temperate climates. However, good soil management, particularly the avoidance of soil compaction and an adequate supply of nutrients to the maize seedlings, through a local application of starter fertilizer, must be ensured.

RÉSUMÉ

Le semis direct est une technique largement utilisée pour pallier aux effets négatifs des méthodes conventionnelles de travail du sol tels que l'érosion, le lessivage et le ruissellement des produits chimiques ou la dégradation de la structure du sol. Le semis direct est particulièrement intéressant pour une culture comme le maïs qui offre une faible protection du sol en début de saison du fait d'un large interligne et d'une croissance juvénile ralentie en climat tempéré. Cependant, une application à long terme du semis direct peut se manifester par des couches superficielles du sol se réchauffant plus lentement et présentant une plus forte résistance à la pénétration des racines en comparaison avec des sols travaillés conventionnellement. Ceci peut donner lieu à un ensemble de conditions de croissance défavorables durant la période d'établissement du maïs.

Le but de cette étude était de mesurer les effets, en termes de croissance et de fonctionnement, des principales modifications de propriétés physiques du sol, induites par le semis direct, sur les parties aériennes et souterraines des jeunes plants de maïs:

- [1] en conditions de champ, les effets de l'intensité de travail du sol sur la distribution horizontale et verticale ainsi que sur la morphologie du système racinaire du maïs ont été caractérisés à un stade de croissance précoce. De plus, une attention particulière a été donnée à l'effet de l'engrais NP, placé en bande au moment du semis, sur la distribution et la morphologie des racines;
- [2] les propriétés physiques du sol caractéristiques des systèmes de travail du sol conventionnel et de semis direct ont été reproduites en conditions contrôlées. Différentes combinaisons de gradients verticaux de densité et de température du sol ont été appliquées:
 - [2a] dans une première série d'essais, la croissance et le fonctionnement des feuilles et des racines de maïs ont été analysés;
 - [2b] dans une deuxième série d'essais, la morphologie, la distribution et le fonctionnement des racines ont été analysés en tenant compte de la croissance des parties aériennes et de l'efficacité d'utilisation de l'azote et du phosphore. Le phosphore a été utilisé comme élément nutritif modèle

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pour tester l'effet des propriétés du sol sur le prélèvement d'éléments nutritifs par les racines.

Les résultats de ces essais étaient les suivants:

- [1] En champ, la température du sol à 5 cm était plus basse et la densité apparente ainsi que la résistance à la pénétration du sol étaient plus élevées en surface dans le cas du semis direct que dans le cas du labour. Là, les taux de croissance et de développement des plantes étaient plus bas qu'ici. De même, la densité de longueur de racines (RLD) était réduite et le diamètre moyen des racines plus grand, alors que la distribution horizontale et verticale du système racinaire demeurait inchangée, en valeurs relatives. RLD était significativement plus élevée à proximité de la bande d'engrais placée au semis, indépendamment du travail du sol. Le diamètre moyen des racines n'a pas été influencé par la présence de l'engrais. La taille réduite du système racinaire en semis direct a été partiellement compensée par des taux de prélèvement de P par unité de longueur de racine plus élevés.
- [2a] En conditions contrôlées, le taux d'expansion de la surface foliaire a été sévèrement réduit et les racines se sont concentrées en surface dans les traitements avec une couche superficielle compacte. En conséquence, un prélèvement important d'eau et d'azote des couches plus profondes n'a pu avoir lieu que dans les traitements avec un substrat meuble sur toute la profondeur. Le degré de compaction de la couche supérieure du substrat était corrélé négativement et la température de cette couche positivement avec l'activité photosynthétique des feuilles. Ces deux facteurs (densité et température du substrat) agissent de façon indépendante sur tous les paramètres mesurés. La densité du substrat a été le principal facteur limitant pour la croissance aussi bien des racines que des parties aériennes.
- [2b] Dans la deuxième série d'essais en phytotron, l'accroissement de densité de la couche supérieure du substrat provoqua une diminution linéaire de la longueur et de la masse racinaires, un accroissement du diamètre moyen des racines aussi bien dans la couche supérieure qu'en profondeur, ainsi qu'une baisse du rapport racine:partie aérienne. La croissance des racines et des parties aériennes a été réduite dans une égale mesure par la baisse de température du substrat à 5 cm. De manière générale, l'élongation des racines, leur diamètre moyen et la croissance

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en profondeur ont été influencés positivement par un apport de P dans la zone de semis. La croissance des racines dans le cas de températures basses du substrat a pu être partiellement compensée par un apport de P plus élevé, et vice versa. La densité et la température du substrat agissent indépendamment sur tous les paramètres mesurés. Il y a par contre eu certaines interactions avec le facteur P.

En conclusion, le réchauffement plus lent de la couche supérieure du sol au printemps semble être le principal facteur limitant la croissance juvénile du maïs dans le cas du semis direct en climat tempéré. Néanmoins, il est primordial de protéger le sol contre toute compaction et dégradation de la structure et d'assurer un approvisionnement adéquat des plantules en éléments nutritifs, par exemple au moyen d'un apport localisé d'engrais au moment du semis.

1 GENERAL INTRODUCTION

In the recent years the interest in agricultural sustainability has increased considerably. Sustainable agriculture should have as its goal the prevention of soil degradation, which is estimated to affect about 35% of the earth's soil surface (Mabbutt, 1984), the maintenance of the productive potential of the soil, and the reduction of environmental pollution (Unger and McCalla, 1980; Lal, 1989; Carter, 1994). No-tillage systems affect these aspects of agricultural sustainability (Lal, 1991; Ehlers and Claupein, 1994). They bring about a significant improvement in several important soil properties (erosion control, carbon sequestration, soil organic matter enhancement, water conservation) (Unger and McCalla, 1980; Lal, 1991; Ehlers and Claupein, 1994). Thus, no-tillage is a system approach to arable farming, whereby long-term sustainability and preservation of the environment and natural resources are given priority over short-term economic returns (Lal, 1989; Lal, 1991). This is very advantageous for a row crop such as maize (*Zea mays* L.), which is susceptible to soil degradation because of the wide row spacing and its slow initial growth. However, a minimum disturbance of the soil, combined with crop residues on the soil surface, results in changes in the physical and chemical properties of the soil after a continuous application of no-tillage systems (Blevins et al., 1983). The kind, extent, and timing of these changes are likely to depend on the soil type and on the climate (Khakural et al., 1992; Blevins and Frye, 1993).

1.1 LITERATURE REVIEW

1.1.1 Soil physical properties under no-tillage

1.1.1.1 Temperature

In the spring, a large quantity of crop residues on the soil surface and an increased soil water content of the topsoil are the two major causes of a slower warming of the soil in no-tillage systems compared with conventional tillage in temperate climates (Tollner et al., 1984; Khakural et al., 1992; Arshad and Azooz, 1996). Thus, temperatures that are lower by 1 to 2°C have been found near the surface of the soil during the first weeks

after planting spring barley or maize (Cox et al., 1990; Arshad and Azooz, 1996). Temperature differences between tillage systems disappear later in the season (Carefoot et al., 1990). In summer, the decrease in maximum soil temperature in no-tillage soils compared to conventionally tilled soils is proportional to the amount of surface area covered by mulch (van Doren and Allmaras, 1978).

1.1.1.2 Bulk density, porosity, and penetration resistance

Due to the lack of disturbance of the topsoil, the most obvious differences in the soil physical properties in no-tillage systems compared to conventionally tilled soils are a higher dry bulk density near the surface (0-15 cm depth) (Tollner et al., 1984; Kaspar et al., 1991) and larger aggregates (Ross and Hughes, 1985). The difference in bulk density is maximal at planting and may become nearly insignificant later in the season (Kitur et al., 1993). With no-tillage, the total pore volume in the topsoil decreases and the pore size distribution changes, with larger pores disappearing and finer pores predominating (Hill et al., 1985). However, the number of biopores and the pore continuity are greater under no-tillage than under conventional tillage due to a higher biotic activity, especially of earthworms (Edwards et al., 1988), and to undisturbed root channels created by preceding crops (Dexter, 1991).

As a consequence of the higher bulk density under no-tillage, the resistance of the soil to root penetration, as measured with penetrometer probes, increases in the topsoil (Unger and Jones, 1998). However, standard penetrometers do not usually detect the presence of biopores (Ehlers et al., 1983), hence leading to an overestimation of mechanical impedance to root growth. Furthermore, the generally higher soil water content in no-till topsoils (see below) can counteract the possible restrictive effect of increased bulk density on roots.

1.1.1.3 Water content and aeration

The water content at the soil surface is usually higher under no-tillage because of the slower rate of evaporation and an increased water storage capacity (Ehlers and Claupein, 1994). This is due to the combined effects of more residues on the soil surface, undisturbed soil, changes in pore size distribution, an increased organic matter content, and a more stable and homogeneous soil structure (Khakural et al., 1992; Arshad and Azooz, 1996). Thus, the capacity of the soil to retain available water

increases in the topsoil (Lal, 1995; Larney and Lindwall, 1995; Parent et al., 1995). The greatest differences in the total available soil water between no-till soils and ploughed land always occurs early in the growing season (Baeumer and Bakermans, 1973). However, the rates of water infiltration increase under no-tillage because of the higher stability, greater continuity, and higher number of biopores (Logsdon et al., 1990; Rosenberg, 1992).

The reduction in the number of large, mostly air-filled, pores and the increased water content could result in a reduced aeration of no-tilled soils. This was found to be critical only on medium to heavy soils in humid regions (Baeumer and Bakermans, 1973).

1.1.2 Effects of soil physical properties on the early growth of maize

The delays in seed germination, field emergence, and/or early plant growth that commonly occur after no-tillage planting of maize are often considered to be a direct effect of the lower temperature of the topsoil on the shoot meristem (Al Darby and Lowery, 1987; Hayhoe et al., 1996), because the shoot apex of maize remains below the soil surface until about the sixth leaf stage (Swan et al., 1996). However, responses of shoot growth to tillage depend to a large extent on root growth and activity. Root growth and activity, in relation to tillage, are influenced by a combination of physical factors that determine temperature regime, number, size distribution and continuity of pores, and soil moisture (Mackay and Barber, 1987; Lal, 1989; Voorhees, 1989).

1.1.2.1 Temperature

The lower root-zone temperature in the spring under no-tillage may affect not only the shoot, but also the roots, because early root elongation, branching, and nutrient uptake are highly temperature-dependent processes (Bourdu, 1984; Bowen, 1991; Kaspar and Bland, 1992). At low temperatures, the growth of the roots is reduced and less branching occurs (Cutforth et al., 1986). Root length is likely to be more sensitive to suboptimal temperatures than root dry weight (Kaspar and Bland, 1992). Reductions in the soil temperature near 15 °C as small as of 2 to 3°C adversely affected the root growth of maize seedlings (Richner et al., 1996). Low soil temperature also hinders the uptake of water and nutrients (Nielsen and Humphries, 1966; Nielsen, 1974; Engels and Marschner, 1988) and modifies the gravitropic response of maize roots (Fortin, 1990; Tardieu and Pellerin, 1990; Matthews and Zobel, 1995).

1.1.2.2 Penetration resistance

It is widely accepted that mechanical impedance to root growth causes a decrease in the root elongation rate, an increase in root diameter, and a change in the pattern and rate of lateral branching (Russell, 1977; Bennie, 1996; Misra and Gibbons, 1996). Hence, it is considered to be one of the main physical factors controlling root elongation and proliferation along a soil profile (Barley and Greacen, 1967; Bengough and Mullins, 1990; Barraclough et al., 1991). With gradients of mechanical impedance, as encountered in the field, compensatory growth (Kirkegaard et al., 1992) or, vice versa, residual effects of mechanical impedance on the growth of the roots (Bengough and Young, 1993) may occur in looser soil layers. However, in untilled soils, vertically oriented biopores gain in importance as preferential pathways of root growth compared with tilled soils (Jakobsen and Dexter, 1988; Logsdon and Allmaras, 1991).

1.1.2.3 Water content and aeration

The increased soil water content at the soil surface of no-till plots was responsible not only for the effect of increased mechanical impedance on root penetration, but also for changes in root distribution with depth (Dwyer et al., 1988; Kovar et al., 1992). Indeed, the water content of the soil can have a direct influence on the growth rate (Logsdon et al., 1987), branching (Rahman et al., 1994), distribution of roots (Barraclough et al., 1991; Gallardo et al., 1996), and direction of root growth (Nakamoto, 1993); the growth of roots can increase locally in soil layers with the most favorable moisture conditions (Reader et al., 1993; Gallardo et al., 1996).

A minimum number of air-filled pores for root elongation was found to be 10 to 12 % (Grable and Siemer, 1968). Impaired soil aeration reduces root extension (Logsdon et al., 1987) and root branching (Liang et al., 1996) of maize seedlings. Oxygen deficiency at the seminal roots of maize seedlings decreased the production of top dry matter to a greater extent than oxygen deficiency at the nodal roots (Ramirez and Rodriguez, 1987); the reduction in shoot growth was not due to a reduced uptake of water or inorganic nutrients (Atwell et al., 1985).

Zobel (1993) suggested that stress symptoms frequently develop when two or more stressful conditions act synergistically, thus, speaking for studies that include a combination of stress factors in contrast to numerous investigations based on a single factor.

1.1.3 Conclusions

Most of the changes in the soil physical properties induced by the long-term application of no-tillage in temperate climates may lead to conditions that are stressful for shoot and root growth, particularly in the topsoil early in the growing season. Therefore, maize is subjected to a combination of soil physical stresses during establishment (Fig.1.1). As a consequence, the final yield may be lower because crop stands must be established as soon as possible after planting, with roots colonizing the subsoil as early as possible (Tisdall, 1996) and leaf area expanding rapidly (Giauffret et al., 1995) if productivity is to be high.

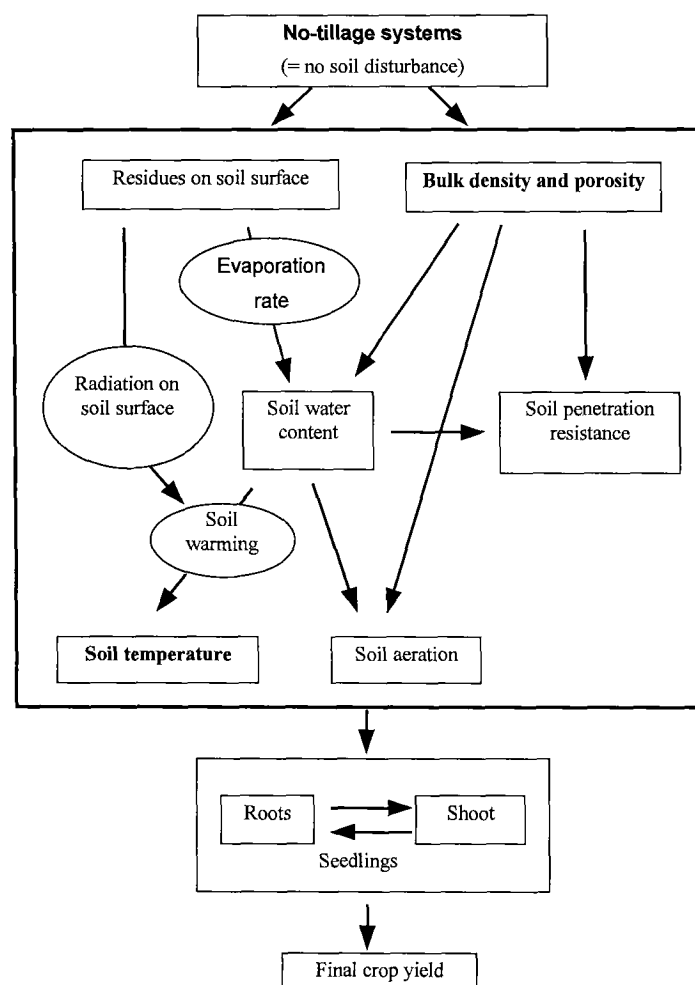


Fig. 1.1. Pathways for the effects of continuous application of no-tillage systems on the soil physical properties.

1.2 HYPOTHESES

According to the literature, the present study is based on the following hypotheses:

- i. A low root-zone temperature and a high bulk density of the topsoil are the most important changes in soil physical properties that are induced by the long-term application of no-tillage systems in term of effects on the early growth of maize.
- ii. Soil temperature and soil bulk density lead to poor early growth of maize in no-tillage systems, as compared with conventional tillage systems, by affecting the growth, morphology, distribution, and functioning of the root systems of the maize seedlings.
- iii. The combined effects and vertical variation of these two factors must be considered, which was generally not the case in studies published thus far.
- iv. It is very difficult to relate differences in root growth and activity to differences in soil physical parameters under field conditions (Kovar et al., 1992; Dwyer et al., 1996). Thus, these relationships should be reproduced and investigated in growth chamber studies, as suggested by Zobel (1995).

1.3 OBJECTIVE AND STRUCTURE OF THE STUDY

The objective of this study was to investigate the effects of the main tillage-induced changes in soil physical properties on above- and below-ground parts of maize seedlings in terms of growth and function.

The study was divided into two parts (Fig. 1.2):

I. Field conditions

The lateral and vertical distribution and the morphology of the root system of maize at an early growth stage as affected by tillage intensity were characterized. Furthermore, attention was paid to the effect of the sidebanding of NP-fertilizer on the distribution and morphology of roots (cf. Chapter 2).

II. Controlled conditions (growth chamber)

The objective of the controlled-environment study was the simulation of soil physical conditions as found in the field under conventional tillage and no-tillage, whereby combinations of vertically varied soil temperature and soil bulk density were applied.

- a. In a first step, the early growth and performance of the shoot and roots of maize were analyzed (cf. Chapter 3).
- b. In a second step, the focus was on the morphology, distribution, and functioning of the roots with regard to shoot growth and phosphorus fertilizer utilization efficiency. Phosphorus was used as a model macroelement to determine whether the effects of soil properties on the roots lead to an inadequate nutrient supply to the shoot, because the acquisition of P was found to be closely related to root growth (Mackay and Barber, 1984) and root morphology (Schenk and Barber, 1980) (cf. Chapter 4).

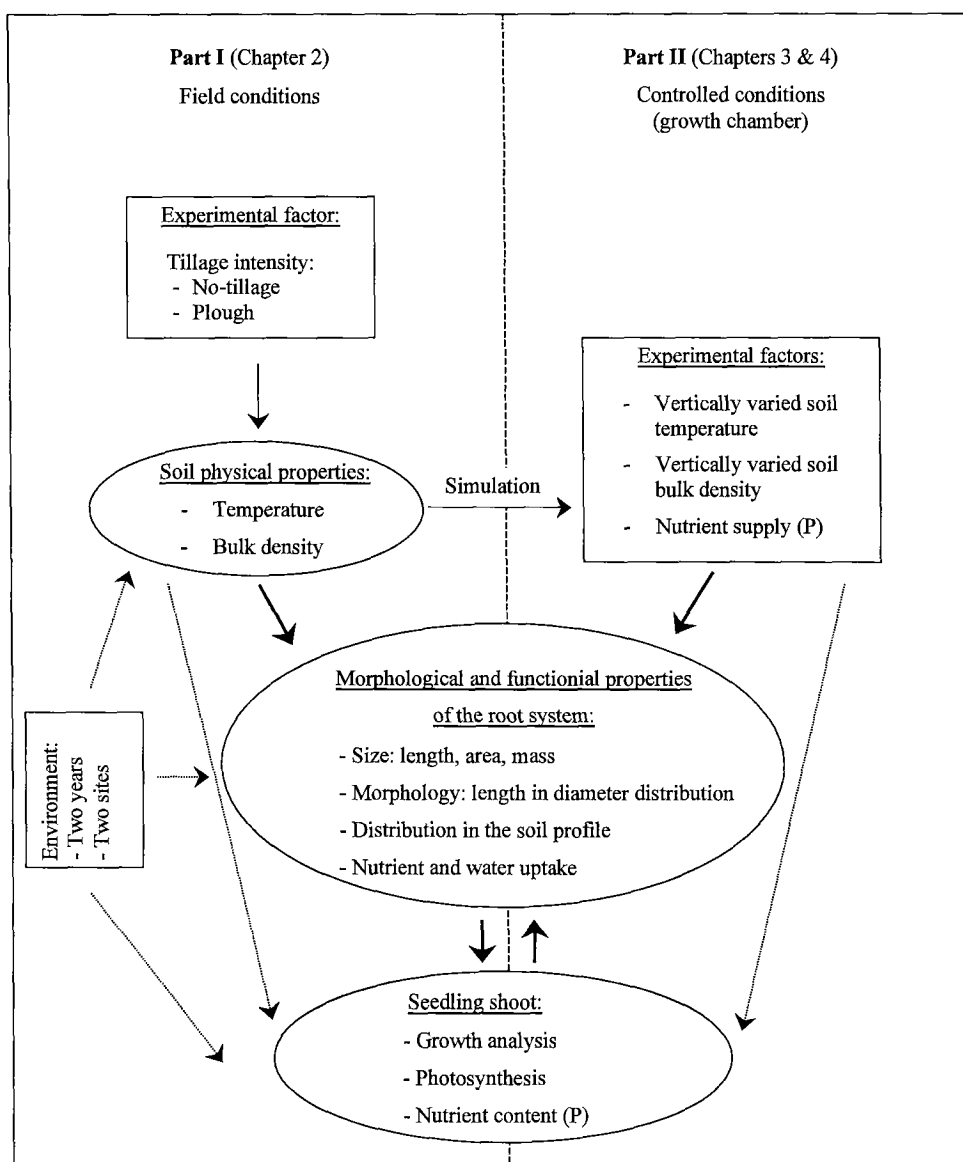


Fig. 1.2. Structure of the thesis.

2 ROOT DISTRIBUTION AND MORPHOLOGY OF MAIZE SEEDLINGS AS AFFECTED BY TILLAGE AND FERTILIZER PLACEMENT

Chassot, A., P. Stamp, and W. Richner. 2001. *Plant Soil* 231:123-135.

2.1 ABSTRACT

Suboptimal soil conditions are known to result in poor early growth of maize (*Zea mays* L.) in no-tillage (NT) systems in contrast with conventional tillage (CT) systems. However, most studies have generally focused on maize roots at later growth stages and/or do not give details on root morphology. In a two-year field study at two locations (silt loam and loam soils) in the Swiss midlands, we investigated the impacts of tillage intensity, NT vs. CT, and N-P-fertilizer sidebanding on the morphology, vertical and horizontal distribution, and nutrient uptake of maize roots at the V6 growth stage. The length density (RLD) and the length per diameter-class distribution (LDD) of the roots were determined from soil cores taken to a depth of 0.5 m and at distances of 0.05 and 0.15 m from both sides of the maize row. The temperature of the topsoil was lower, and the bulk density and penetration resistance were greater in the topsoil of NT compared with CT. The growth and the development of the shoot were slower in NT. RLD was greater and the mean root diameter smaller in CT than in NT, while the vertical and horizontal distribution of roots did not differ between CT and NT. RLD increased in the zone enriched by the sidebanded fertilizer, independent of the tillage system, but LDD did not change. The poorer growth of the roots and shoots of maize seedlings was presumably caused by the lower topsoil temperature in NT rather than by mechanical impedance. The placement of a starter fertilizer at planting under NT is emphasized.

2.2 INTRODUCTION

No-tillage (NT) systems are widely accepted as means of reducing some of the negative impacts (such as soil erosion, energy use, leaching and runoff of agricultural chemicals) associated with conventional tillage (CT) systems (Uri et al., 1998). NT systems are particularly beneficial for a row crop like maize (*Zea mays* L.), which is susceptible to the leaching of agrochemicals and to soil loss and degradation because of the large distance between the rows and its slow initial growth in cold wet climates. However, NT systems have disadvantages. Slower seed zone warming can occur in the spring during early maize growth because most of the residues of the previous crop are left on the soil surface (Azooz et al., 1995) and because of a higher thermal conductivity of untilled soils (Azooz and Arshad, 1995). In a review of the effects of conservation tillage systems on soil properties, Cannell et al. (1994) reported that the topsoil bulk density in NT systems usually is greater than in tilled soils; this greater soil density is often associated with increased penetration resistance but the soil water content is not usually affected or even increases.

The effects of tillage-induced changes in soil temperature and bulk density on plant growth are mediated through the growth and function of the roots. There is also a direct effect of soil temperature on the shoots of maize seedlings, because the shoot apex remains below the surface of the soil until about the V6 growth stage (Beauchamp and Lathwell, 1967; Ritchie et al., 1996). According to Richner et al. (1996), fluctuations in the topsoil temperature (as small as 2 to 3°C around 15°C) can adversely affect the growth of roots and shoots of maize seedlings. This can have long-term effects; at silking, maize root length density below the 0.30-m soil depth was correlated with the growing degree days for the two weeks following planting (Kuchenbuch and Barber, 1988). This may explain why the lower topsoil temperature is one of the main factors that hinders the emergence of maize and the growth and development of seedlings in NT systems (Al-Darby and Lowery, 1987). In contrast, there is no consensus about the effects of bulk density on the distribution and function of roots, because of the formation of vertically oriented biopores that are suitable for preferential root growth in NT systems (Ehlers et al., 1983; Martino and Shaykewich, 1994); these biopores may counteract the possible negative effect of increased bulk density on roots.

The combination of reduced soil temperature and increased soil strength may be responsible for the poor early growth of maize in NT systems, which may have an adverse affect on the final yield (Gavito and Miller, 1998; Janovicek et al., 1997). The exact causes of this early decrease in growth rate, however, have not yet been determined. Gavito and Miller (1998) and Miller et al. (1995) mentioned the possibility of an “unknown factor”, such as altered soil density, temperature, moisture, or their combined effects. Data on maize roots that were affected by tillage systems are often based on later sampling times around anthesis. They generally focus on vertical root length density gradients rather than on horizontal gradients. Root mass is usually assessed, but precise information about root morphology is rarely given. Furthermore, the effect of tillage on root proliferation differs from site to site owing to the wide range of potential effects of tillage on soil conditions (Dwyer et al., 1996).

The objectives of this study were to characterize the lateral and vertical distribution and the morphology of the root system of maize at an early growth stage as affected by tillage intensity and to determine whether differences in soil temperature and strength between the tillage systems affect the distribution, morphology, and function of maize roots and, ultimately, the growth of the shoots. Furthermore, Mallarino et al. (1999) reported that the sidebanding of NP fertilizer promotes the early growth of maize, this study therefore focused on the effect of the sidebanding of NP-fertilizer on the distribution and morphology of roots.

2.3 MATERIALS AND METHODS

2.3.1 Experimental sites

A field experiment was carried out in 1997 and 1998 at two sites in the Swiss midlands: in Schafisheim (47°23'N, 8°09'E, 429 m above sea level) on an Orthic Luvisol (FAO classification) and in Zollikofen (47°00'N, 7°28'E, 555 m above sea level) on a Gleyic Cambisol (FAO classification). Soil characteristics at Schafisheim were 15% clay, 35% silt, 50% sand, 3.3% organic matter, and pH 6.7 and at Zollikofen 14% clay, 51% silt, 36% sand, 2.7% organic matter, and pH 6.3. Precipitation and the daily mean air temperatures were measured at each site (Table 2.1). The 1998 growing season was characterized by a dry period without rain for the

Table 2.1. Monthly precipitation and mean air temperature in Schafisheim and Zollikofen in April, May, and June in 1997 and 1998.

Month	Precipitation (mm)		Mean air temperature (°C)	
	1997	1998	1997	1998
<i>Schafisheim</i>				
April	71	81	7.6	8.3
May	40	35	13.2	14.8
June	139	109	16.0	17.1
<i>Zollikofen</i>				
April	68	115	7.4	7.5
May	55	41	13.3	13.9
June	144	49	15.8	16.9

Table 2.2. Effect of tillage on soil contents of P and K, mineral nitrogen concentration in the soil solution within the row (N_{\min}), and gravimetric water content (θ_g) of the soil (0-30 cm) at the V6 stage of maize at two sites in the Swiss midlands in 1997 and 1998.

Year	Site	Tillage	P (mg kg ⁻¹)	K (mg kg ⁻¹)	N_{\min} (mg L ⁻¹)	θ_g (kg kg ⁻¹)
<i>0-15 cm</i>						
1997	Schafisheim	CT	15.5	70.8	20	0.20
		NT	14.9	102.9	30	0.21
	Zollikofen	CT	3.4	22.4	8	0.22
		NT	3.7	24.3	3	0.21
1998	Schafisheim	CT	16.0	65.8	37	0.25
		NT	16.3	82.7	19	0.28
	Zollikofen	CT	4.9	28.8	14	0.18
		NT	4.4	27.1	14	0.22
<i>15-30 cm</i>						
1997	Schafisheim	CT	9.9	46.8	10	0.22
		NT	8.9	61.1	10	0.19
	Zollikofen	CT	2.8	18.0	4	0.24
		NT	2.8	18.0	7	0.21
1998	Schafisheim	CT	12.1	43.7	8	0.25
		NT	9.9	45.4	14	0.23
	Zollikofen	CT	3.5	15.2	9	0.23
		NT	2.5	12.7	8	0.21

first three weeks after planting. The nutrient and water contents of the experimental plots at the V6 growth stage of maize are given in Table 2.2.

2.3.2 Experimental treatments

This study was conducted in 1997 and 1998 within the scope of a tillage experiment initiated in 1995 in Zollikofen and in 1996 in Schafisheim. The study was based on a four year rotation of winter wheat, oilseed rape, winter wheat, and maize; white mustard (*Brassica alba* L. cv. Martigena) was included as a cover crop between winter wheat and maize. The plots were arranged so that four rotation crops were grown each year. The tillage treatments described in this study were CT and NT. Throughout the crop rotation, all crop residues were left on the soil surface. The tillage of the individual plots was the same each year. The CT treatment was moldboard plowed to a depth of 0.25 m and rototilled at a depth of 0.10 m immediately prior to planting with a conventional planter with double-disk openers (Kuhn Nodet Planter II, Montereau, France). The NT plots were sown without any prior tillage using a no-till planter with a double-disk opener assembly following a ripple coulter (Kinze 2000, Kinze, Williamsburg, IO, USA). Maize (cv. Granat) was planted at 100000 plants ha⁻¹ in 0.75-m rows and at 105000 plants ha⁻¹ in 0.78-m rows in CT and NT, respectively. The planting dates were 3 May 1997 and 8 May 1998. A mixture of dry fertilizer (diammonium phosphate and NH₄NO₃, 30 and 17 kg ha⁻¹ of N and P, respectively) was banded on one side of each row, 0.05 m to the side and 0.05 m below the seeds at planting. The rates of N and P applied at planting were made up by a side-dressing application at the V4 growth stage and by a broadcast application before planting, respectively. The fertilizer rates applied with basal dressing and starter fertilization, which were based local recommendations, were the same for both tillage systems, whereas the N side-dressing at V4 was measured on a per-plot-basis according to a soil N_{min} test (Wehrmann and Scharpf, 1979). The basal dressing included 35 kg ha⁻¹ P, 133 kg ha⁻¹ K, and 18 kg ha⁻¹ Mg. Calculated side-dressing N rates did, on average, not differ among tillage systems; averaged across all years, sites, and tillage systems, 107 kg N ha⁻¹ were applied. Weeds were controlled by spraying 1.500 kg ha⁻¹ a.i. atrazine [6-chloro-N-ethyl-N'-(1-methylethyl)-1,3,5-triazine-2,4-diamine] and 1.920 kg ha⁻¹ a.i. metolachlor [(S)-2-chloro-N-(2-ethyl-6-methyl-phenyl)-N-(2-methoxy-1-methyl-ethyl)-acetamide]] premergence on all plots. Glyphosate (N-

[phosphonomethyl] glycine) and ammonium sulfate were applied (1.08 and 10 kg ha⁻¹ a.i., respectively) before planting in the NT plots.

2.3.3 Measurements

The temperature of the soil was measured hourly at a depth of 0.05 m with one in-row temperature probe in each plot and recorded with a data logger (Hobo H8 Temp Logger, Onset Computer Corporation). Daily growing degree days (GDD) were computed from hourly soil temperature using a base temperature of 8°C (Jones and Kiniry, 1986).

The bulk density (BD) of the soil was measured to a depth of 0.30 m in 0.05-m increments in all plots at the time of root sampling, using a steel sampler (0.109 m inner diameter and 0.05 m height). Three in-row-subsamples per plots were taken next to the locations of root sampling (see below). The soil cores were weighed and their moisture content determined after drying in an oven (105°C) to constant mass.

Penetration resistance (PR) was measured at the time of root sampling at ten random locations in each plot using a hand-held recording cone penetrometer (Anderson et al., 1980). The measurements were made in the row at intervals of 0.035 m to a depth of 0.49 m. The semi-angle of the cone was 15° and the diameter 0.013 m. The penetration rate was approximately 0.03 m s⁻¹. Measurements were made in Zollikofen because of the large number of stones in the soil in Schafisheim, which would have made interpretation difficult (Anderson et al., 1980).

Before sampling the roots, the shoots of the center plant, where root sampling was to occur, and of its two adjacent plants in the row were cut at ground level and their growth stages determined. The leaf area of the visible leaf blades and of the visible leaf blades of partially expanded leaves of the center plants was measured with a leaf area meter (LI-COR 3100, Lincoln, NE, USA). The plant material of all three plants was oven-dried for 48 h at 65°C and ground using a sample mill (Cyclotec 1093, Tecator AB, Höganäs, Sweden). The total N concentration of 50 mg of plant material was determined using an elemental analyzer (LECO CHN-1000, LECO Instrumente GmbH, Kirchheim bei München, Germany). The total P concentration of 50 mg of plant material was determined after dry ashing the samples at 550°C for 6 h and then dissolving the ash with 1 l HCl 20% kg⁻¹ dry matter. Phosphorus in the solution was measured by colorimetry.

Root sampling was done using the soil-core method (Böhm, 1979) when 50% of the plants in the CT plots had reached the V6 growth stage. This growth stage was reached 38 and 47 days after planting in 1997, and 32 and 41 days after planting in 1998 at Schafisheim and Zollikofen, respectively. The soil cores were taken to a depth of 0.5 m at three locations per plot using an auger (0.050 m inner diameter and 0.25 m length) attached to a hand-held, power-driven sampler. At each sampling location, cores were taken at distances of 0.05 and 0.15 m from a plant on each side of the row. In 1997 cores were taken additionally from mid-way between crop rows (0.375 m from the row). No roots were found (data not shown) and this position was omitted from the sampling in 1998. Only non-wheel track interrows were sampled, because wheel traffic affects the growth and distribution of roots (Kaspar et al., 1991). The soil cores were divided into 0.05 m sections down to 0.30 m and into 0.10 m sections down to 0.50 m. These segments were washed using a semiautomatic hydropneumatic elutriation system (Gillison's Variety Fabrication Inc., Benzonia, MI, USA) equipped with a 290- μm sieve (Smucker et al., 1982). Live (white) roots were separated from the rest of the organic matter and stained with fuchsin dye (Pararosaniline P-1528, Sigma Chemical Co., St. Louis, MO, USA) for at least 12h at 4°C. They were rinsed under running tap water, suspended in a thin layer of water, and uniformly distributed on a glass tray, which was placed on a scanner to obtain grayscale images (resolution 600 by 600 dpi). Because a root must be at least three pixels (dots) wide to be detected by the used image-analysis program (see below), the theoretical lower size limit of resolution was 127 μm , which is three times the pixel size of the scanner (42.33 μm at a resolution of 600 dpi). The root images were analyzed to determine the length and diameter of the roots using the computer program ROOT DETECTOR (Walter and Bürgi, 1996). The program is based on an algorithm for the segmentation and local description of elongated, symmetric line-like structures developed by Koller et al. (1995). The length and the mean diameter are computed separately for each measured root segment. Thus, the total measured root length can be sorted into user-defined diameter classes, which yields the length per diameter-class distribution (LDD) of the roots. In this study, we used the following diameter classes: 0 – 200, 200 – 400, 400 – 800, 800 – 1600, and 1600 – 3200 μm . Root length density (RLD) was calculated by dividing the root length by the volume of the core segment. The roots were dried in an oven for 48 h at 65°C and the dry weight determined.

2.3.4 Experimental design and statistics

The experiment was designed as a randomized complete block with three replicates. BD and PR were analyzed according to a split plot design with tillage as the main plot factor and soil depth as the subplot factor. RLD data were analyzed according to a split-split-split plot design with tillage as the main plot, NP-fertilizer banding as the subplot, horizontal distance from the plant as the sub-subplot, and depth as the sub-sub-subplot. To analyze the LDD, the median diameter and the percentage of total measured root length in the 0 to 200 10-6 m diameter class (pRL_{200}) were analyzed according to the above ANOVA model. The median root diameter was determined for each sample by taking the upper limit of the diameter class in which 50% of total measured root length was reached. Based on exploratory analysis, the 0 to 200 10-6 m diameter class was selected. In this class, most of the variability was due to the experimental treatments.

If subsamples were taken within plots, they were pooled before statistical analysis. The plot averages were subjected to ANOVA, and significant differences were separated by orthogonal contrasts or Fisher protected LSD tests when appropriate. Some data sets were transformed in order to meet assumptions for ANOVA. However, all the results are presented in their original scale of measurement. Significant differences were accepted at $P < 0.05$, unless otherwise stated.

2.4 RESULTS

2.4.1 Soil physical parameters

The temperature of the topsoil (at a depth of 0.05 m) was significantly lower in the NT treatment compared with CT during early maize growth (Table 2.3); across all environments, mean daily soil temperature (T), maximum daily soil temperature (T_{max}), and growing degree days (GDD) based on T ($T_b = 8^\circ\text{C}$) were reduced by 0.9, 1.6, and 13.1°C , respectively, under NT as compared with CT in the earlier period of measurement, but were similar thereafter, while the daily minimum soil temperature (T_{min}) was not affected. The interaction between the site and the measurement period was significant for T , T_{max} , and GDD. These values were lower at Zollikofen than at Schafisheim in the earlier measurement period, but about the same thereafter. Only in

1998 was the mean daily soil temperature lower in the first half of June as well (data not shown).

Table 2.3. Means of the daily mean (T), maximal (T_{\max}), and minimal (T_{\min}) daily soil temperature at a depth of 5 cm and cumulative growing degree days (GDD) in two periods of measurement as a function of tillage at two sites in the Swiss midlands; data averaged over 1997 and 1998.

Site	Period of measurement ^a	Tillage	Soil temperature variables (°C)			
			T	T_{\max}	T_{\min}	GDD ^b
Schafisheim	17-31 May	CT	18.3 a ^c	23.6 a	13.3 a	150 a
		NT	17.2 b	22.0 b	13.2 a	129 b
	1-15 June	CT	19.7 a	24.0 a	15.9 a	175 a
		NT	19.4 a	23.2 a	16.1 a	172 a
Zollikofen	17-31 May	CT	17.2 a	22.1 a	12.9 a	129 a
		NT	16.1 b	19.7 b	12.9 a	113 b
	1-15 June	CT	19.6 a	23.6 a	16.0 a	171 a
		NT	19.2 a	22.6 a	16.3 a	164 a

^a 17 May, 1 June, and 15 June correspond approximately to VE, V3, and V6 growth stages (Ritchie et al., 1996), respectively, in the CT treatment.

^b GDD were computed from hourly soil temperature using a base temperature of 8°C (Jones and Kiniry, 1986)

^c Means followed by the same letter in the same growth period do not differ significantly at $\alpha = 0.05$.

BD was significantly lower under CT than under NT ($P < 0.001$) from 0 m to a depth of 0.25 m (Fig. 2.1). From 0.30 to 0.50 m, there was no difference in BD between CT and NT (data not shown). The sum of squares for depth was partitioned into orthogonal polynomial contrasts. Bulk density increased linearly ($P < 0.001$) with depth in CT and NT, and the quadratic component was significant in CT only.

PR followed a pattern similar to that of BD. The interaction between tillage and depth was highly significant ($P < 0.001$). From 0 to 0.32 m, CT showed a significantly reduced penetration resistance compared with NT (Fig. 2.2). Below that depth there was no significant difference between CT and NT with little further change of PR values (data not shown).

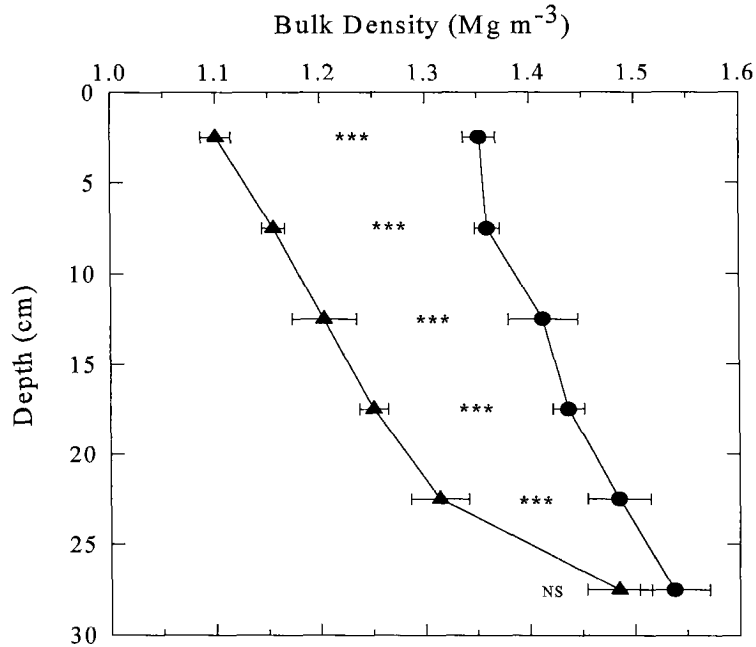


Fig. 2.1. Soil bulk density as a function of depth and tillage at the V6 stage of maize, averaged over two years and two sites.
 ▲ CT; ● NT; *** Significant at the $\alpha = 0.001$ level; NS is not significant. Horizontal bars are standard errors.

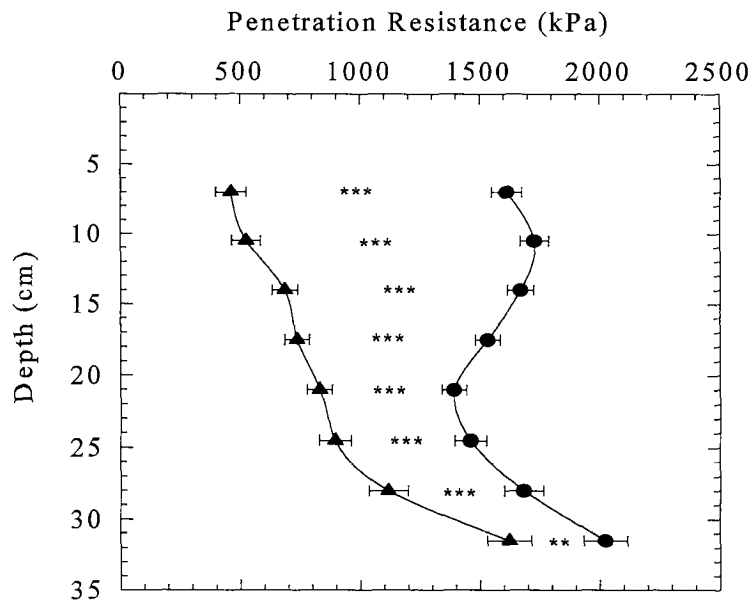


Fig. 2.2. Soil penetration resistance as a function of depth and tillage at the V6 stage of maize at Zollikofen, averaged over two years.
 ▲ CT; ● NT; **, *** Significant at the $\alpha = 0.01$ and 0.001 levels, respectively; NS is not significant. Horizontal bars are standard errors.

2.4.2 Shoot parameters

Tillage had a strong effect on SDW which was higher in 1997 than in 1998. Averaged across both sites, SDW under NT was reduced by 36% compared with CT in 1997 ($P < 0.01$) (Table 2.4). In 1998 a significant reduction (23%) in SDW in NT was observed in Schafisheim.

Plants under NT showed a significantly delayed development. The difference between the tillage treatments was larger in 1997 ($P < 0.001$) than in 1998 ($P < 0.01$), with fewer fully expanded leaves under NT in 1997 and 1998 (0.8 and 0.4, respectively).

Table 2.4. Means and analysis of variance for shoot dry weight (SDW) and number of fully expanded leaves (NLF) of maize at the V6 stage as a function of tillage at two sites in the Swiss midlands.

Year	Site	Tillage	Shoot variables	
			SDW (g)	NLF
1997	Schafisheim	CT	5.1 a ^a	5.4 a
		NT	3.4 b	4.7 b
	Zollikofen	CT	9.4 a	6.0 a
		NT	5.8 b	5.0 b
1998	Schafisheim	CT	11.2 a	5.4 a
		NT	8.6 b	4.9 b
	Zollikofen	CT	9.6 a	5.4 a
		NT	9.9 a	5.0 b

Source of variation	df		
Year (Y)	1	**	NS
Site (S)	1	NS	NS
Y x S	1	*	NS
Reps within Y x S	8		
Tillage (T)	1	***	***
T x Y	1	*	*
T x S	1	NS	NS
T x Y x S	1	NS	NS
Error	8		
Total	23		
R ²		0.87	0.83
CV (%)		11.1	2.1

^a Means followed by the same letter within a year x site combination do not differ significantly at $\alpha = 0.05$. *, **, *** Significant at the $\alpha = 0.05, 0.01, \text{ and } 0.001$ levels, respectively; NS is not significant.

2.4.3 Root parameters

2.4.3.1 Growth and distribution of roots

RLD was mainly affected by distance from the plant row and by depth. Averaged across all treatments, the highest RLD was found close to the young plant, i.e. between depths of 0.05 and 0.15 m at 0.05 m from the plant row (Table 2.5). RLD decreased strongly with increasing depth and horizontal distance from the plant row. There was a highly significant ($P < 0.001$) interaction among year, site, tillage, fertilizer banding, distance from the plant, and depth on RLD. Therefore, an individual ANOVA was performed for each year-site combination and for each distance from the plant row (Table 2.6).

Table 2.5. Percentage of total measured root length as a function of depth and distance from the row. Data are averaged over all treatments.

Depth (cm)	Distance (cm)		
	5	15	Total
	%		
0-5	17	2	19
5-15	53	7	60
15-30	13	5	18
30-50	1	2	3
Total	84	16	100

At Zollikofen, RLD decreased by 55 and 33% under NT compared with CT in the 0.05 to 0.15 m soil layer, in the position closest to the plant row, in 1997 and 1998, respectively (Figs. 2.3 and 2.4). The tillage effect on RLD did not depend on fertilization status. At Schafisheim there was no significant tillage effect on RLD in 1997. In 1998, the RLD of the topsoil was higher under NT than under CT on the fertilized side of the row and lower on the unfertilized side of the row. The effect of tillage was higher and more consistent at Zollikofen than at Schafisheim in both years. At Zollikofen, RLD under CT tended to be higher than under NT at nearly all depths and positions. No significant differences in RLD between the tillage treatments were found in soil layers below 0.20 m.

Table 2.6. Analysis of variance for root length density of maize at the V6 growth stage for two years at two sites in the Swiss midlands.

Source of variation	df	1997		1998	
		Schafisheim	Zollikofen	Schafisheim	Zollikofen
<i>5 cm from the plant row</i>					
Replication	2				
Tillage (T)	1	NS	NS	NS	*
Error a	2				
Fertilizer band (F)	1	**	**	***	NS
T x F	1	NS	NS	*	NS
Error b	4				
Depth (D)	7	***	***	***	***
T x D	7	NS	**	NS	**
F x D	7	*	***	***	***
T x F x D	7	NS	NS	**	NS
Experimental error	56				
Total	95				
R^2		0.65	0.64	0.77	0.67
CV (%)		114	123	105	126
<i>15 cm from the plant row</i>					
Replication	2				
Tillage (T)	1	NS	NS	NS	NS
Error a	2				
Fertilizer band (F)	1	NS	NS	NS	NS
T x F	1	NS	NS	NS	NS
Error b	4				
Depth (D)	7	*	***	***	***
T x D	7	NS	**	***	NS
F x D	7	NS	NS	*	NS
T x F x D	7	NS	NS	NS	NS
Experimental error	56				
Total	95				
R^2		0.59	0.68	0.56	0.47
CV (%)		177	119	142	143

*, **, *** Significant at the $\alpha = 0.05, 0.01, \text{ and } 0.001$ levels, respectively; NS is not significant.

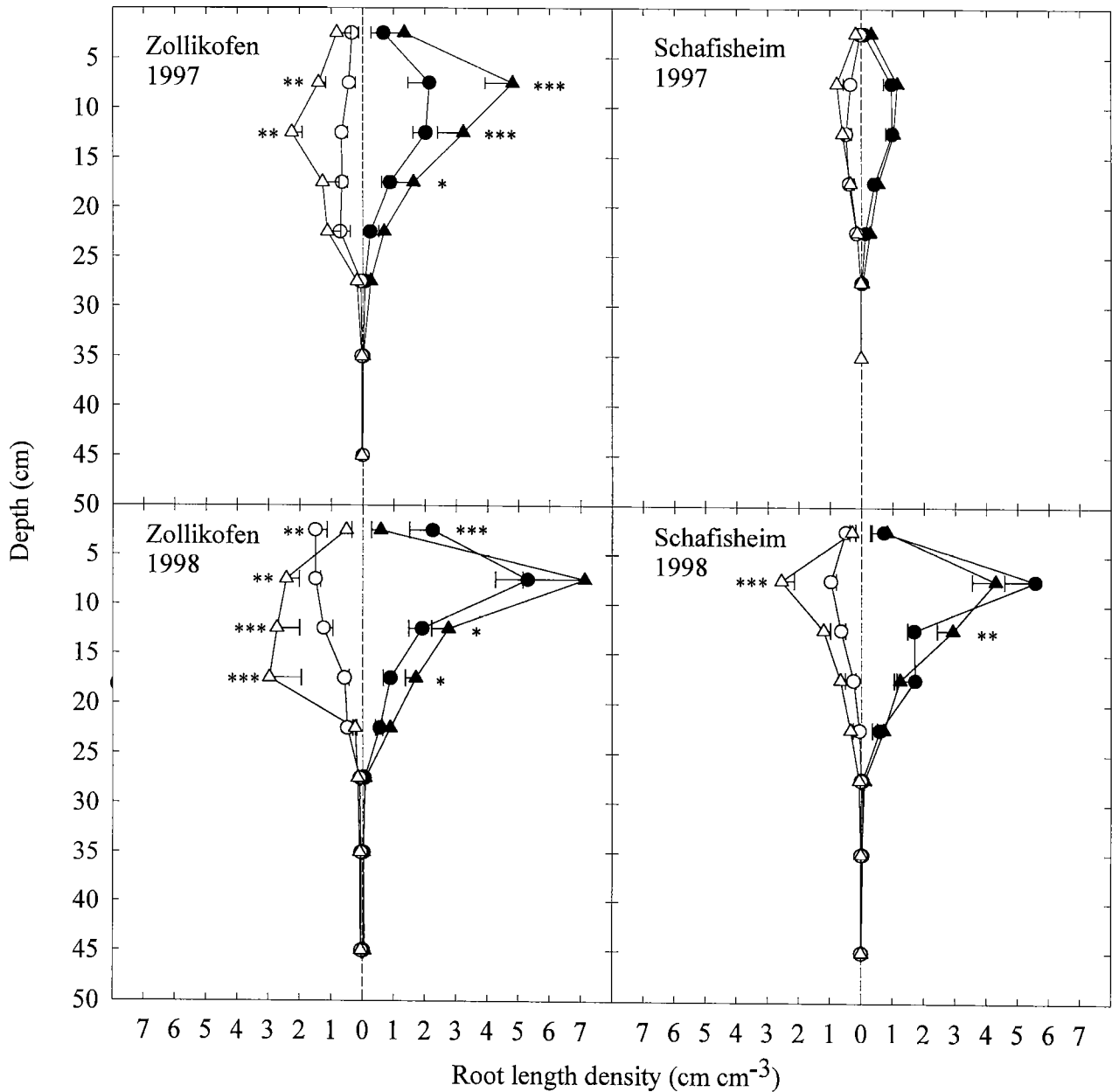


Fig. 2.3. Root length density at the V6 stage of maize as a function of depth, tillage, and NP-fertilizer placement at 5 cm from the plant row at Zollikofen and Schafisheim in 1997 and 1998.

▲ CT; ● NT; open symbols: unfertilized row side; filled symbols: fertilized row side; *, **, *** Significant at the $\alpha = 0.05, 0.01$ and 0.001 levels, respectively; blank is not significant. Horizontal bars are standard errors.

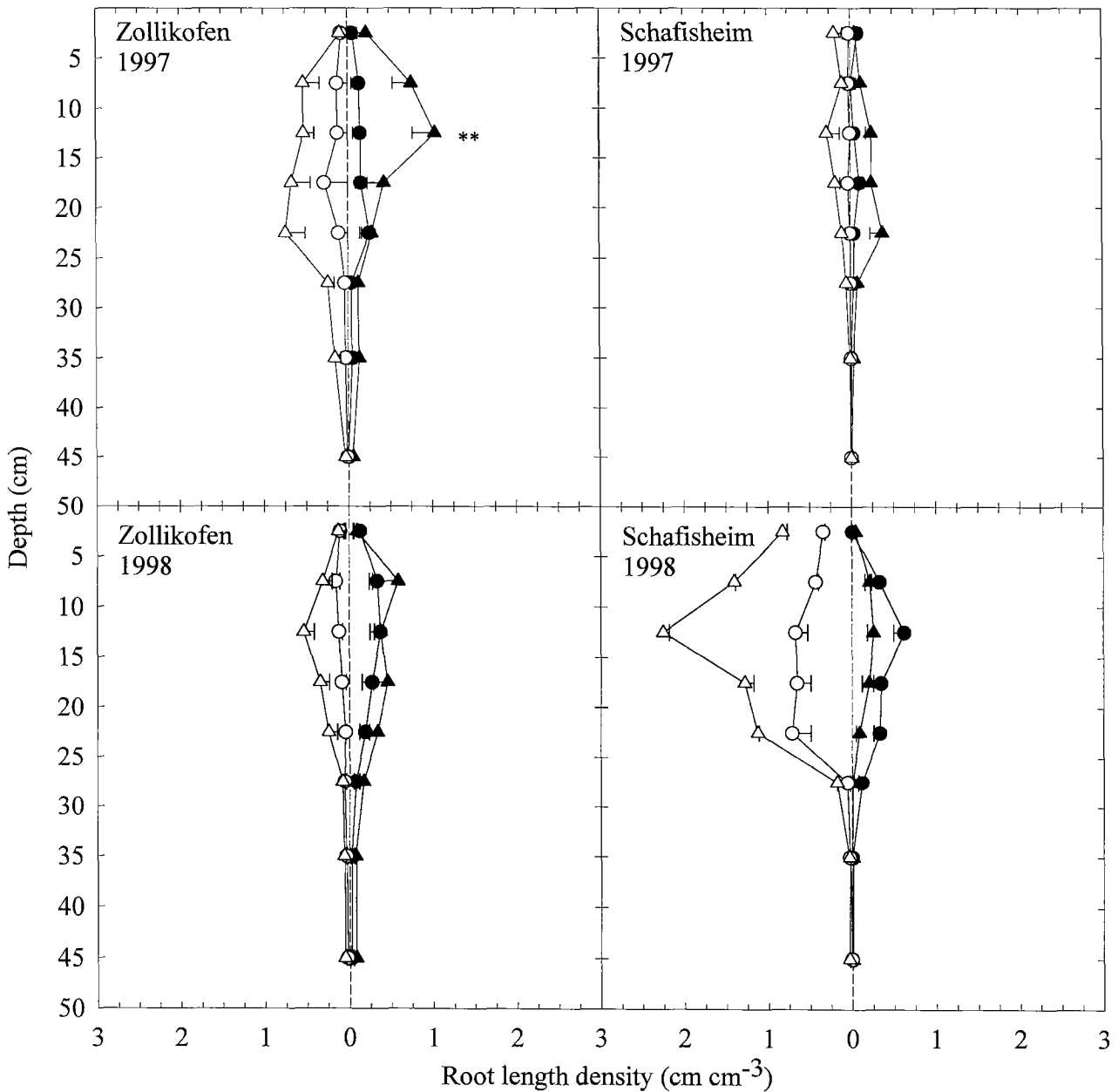


Fig. 2.4. Root length density at the V6 stage of maize as a function of depth, tillage, and NP-fertilizer placement at 15 cm from the plant row at Zollikofen and Schafisheim in 1997 and 1998.

▲ CT; ● NT; open symbols: unfertilized row side; filled symbols: fertilized row side; *, **, *** Significant at the $\alpha = 0.05, 0.01$ and 0.001 levels, respectively; blank is not significant. Horizontal bars are standard errors.

The effect of the NP starter fertilizer on RLD was significant only in soil layers from 0.05 to 0.15 m, at a distance of 0.05 m from the plant row (Figs. 2.3 and 2.4). The RLD was as much as three times higher on the fertilized side of the row compared to the unfertilized side of the row. At 0.15 m from the plant row, the RLD was generally the same on both sides of the row. The effect of fertilizer, as described above, was weaker at Schafisheim in 1997 compared with the other three environments. The relative distribution of RLD along the soil profile was drastically altered by the placement of the starter fertilizer, with a larger portion of roots in the 0.05 to 0.10 m soil layer on the fertilized side of the row than on the unfertilized side of the row.

2.4.3.2 Root morphology

The interaction between tillage and the distance from the plant had a significant effect on LDD. At 0.05 and 0.15 m from the row, the median root diameter was lower, and pRL_{200} was higher under CT than under NT (Table 2.7). The differences in the median diameter and pRL_{200} between the tillage systems were larger 0.15 m from the row than they were 0.05 m from the row. There was no significant effect of fertilizer banding on root morphology (data not shown). LDD was similar at all depths (Fig. 2.5).

Table 2.7. Root morphological characteristics of maize at the V6 growth stage in the 0 to 50 cm deep layer as a function of distance from the plant row and tillage. Data are averaged over two years and two sites in the Swiss midlands.

Distance from the row (cm)	Tillage	Root morphological characteristics	
		Median root diameter ^a (10 ⁻⁶ m)	pRL_{200} ^b (%)
5	CT	317 a ^c	36 a
	NT	348 b	31 b
15	CT	344 a	31 a
	NT	447 b	23 b

^a The median diameter is the upper limit of the diameter class in which 50% of total root length was reached

^b pRL_{200} is the length of roots thinner than 200 10⁻⁶ m, as a percentage of the total measured root length.

^c Means followed by different letters within a tillage system x distance combination differ significantly at $\alpha = 0.05$

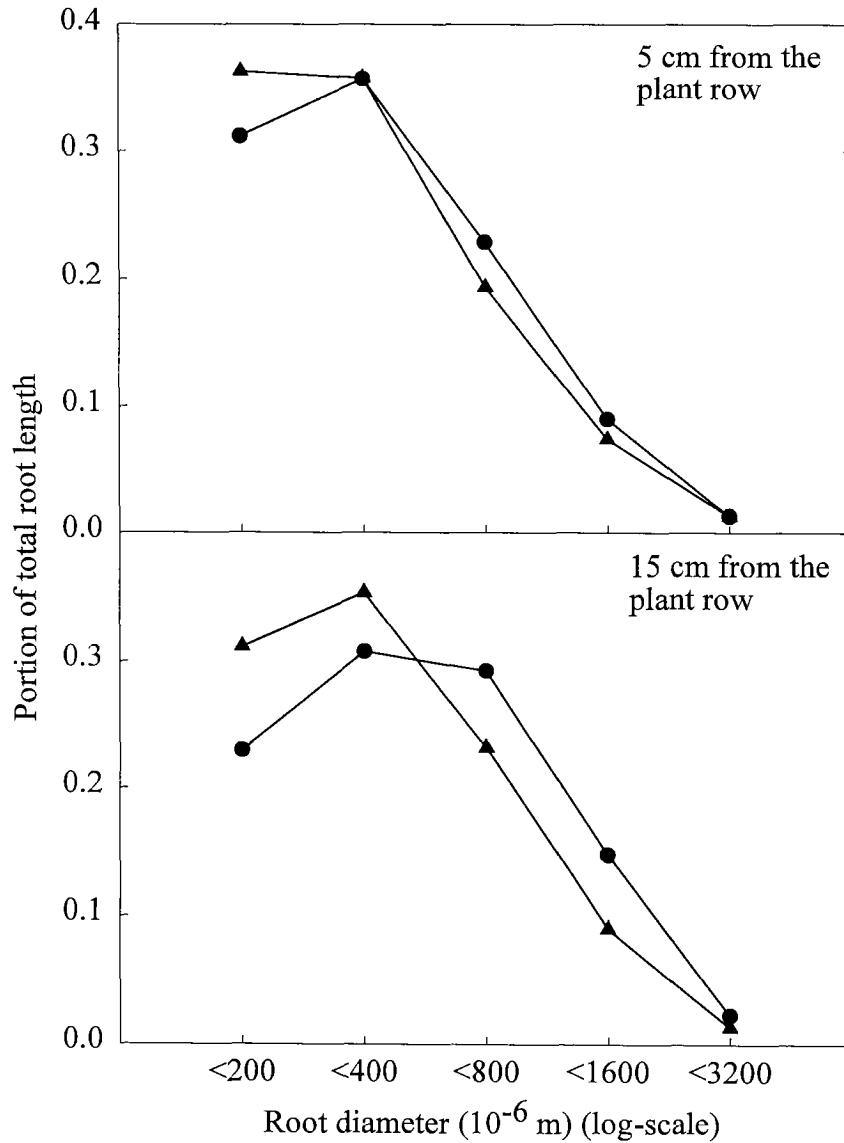


Fig. 2.5. Distribution of root length by diameter classes at the V6 stage of maize from 0 cm to the depth of 50 cm as a function of tillage and distance from the plant row, averaged over two years and two sites.

▲ CT; ● NT.

Table 2.8. Means and analysis of variance for N concentration of shoot dry matter (N_c), P concentration of shoot dry matter (P_c) of maize at the V6 stage as a function of tillage at two sites in the Swiss midlands.

Year	Site	Tillage	Nutrient concentration (g kg ⁻¹)	
			N_c	P_c
1997	Schafisheim	CT	35.6 a ^b	4.6 a
		NT	37.3 a	3.9 b
	Zollikofen	CT	35.4 a	4.1 a
		NT	37.7 a	4.0 a
1998	Schafisheim	CT	44.1 a	5.5 a
		NT	45.5 a	6.2 b
	Zollikofen	CT	42.8 a	4.4 a
		NT	39.1 a	4.7 b

Source of variation	df		
Year (Y)	1	***	***
Site (S)	1	NS	***
Y x S	1	NS	**
Reps within Y x S	8		
Tillage (T)	1	NS	NS
T x Y	1	NS	***
T x S	1	NS	NS
T x Y x S	1	NS	*
Error	8		
Total	23		
R^2		0.88	0.95
CV (%)		3.1	2.8

*, **, *** Significant at the $\alpha = 0.05$, 0.01, and 0.001 levels, respectively; NS is not significant.

^a Means followed by the same letter within an year x site combination do not differ significantly at $\alpha = 0.05$.

2.4.3.3 *Nutrient supply to the shoot*

The content of nitrogen in shoot dry matter (N_c) was not significantly affected by tillage, but it was significantly affected by year ($P < 0.001$). N_c was 3.6% in 1997 and 4.3% in 1998 across all treatments (Table 2.8). The content of phosphorus in shoot dry matter (P_c) responded to tillage dependent on the year. In 1997, P_c was lower under NT than under CT, the difference was significant ($P < 0.001$) at Schafisheim only. In 1998, the opposite occurred with a significantly higher P_c under NT than under CT at both sites. P_c was higher in 1998 than in 1997 and higher at Schafisheim than at Zollikofen.

2.5 DISCUSSION

Nearly all the root length (97%) was found in the A_p -horizon, as measured here; differences in root growth, distribution, or morphology between the tillage treatments can be explained by changes in the rooting environment as caused by tillage. Mengel and Barber (1974) observed, at a similar maize growth stage, that about 20% of the total measured root length was found in layers below 0.30 m. The discrepancy between those results and ours might be due to the fact that their sampling was done directly over the plant and, thus, included mainly the vertically growing seminal roots. There were large differences in BD and PR of the topsoil between the tillage treatments, whereas there were hardly any differences between sites and years. Nevertheless, the effect of tillage intensity on the roots varied greatly among the environments (site by year combinations), indicating that factors other than BD and PR were involved. The soil water content is known to modify the bulk density and penetration resistance. The resistance to penetration (RP) decreases with increasing WT independently of soil type (Busscher et al., 1997). The predominantly moist soil conditions and the generally higher topsoil water contents in NT compared with CT during our study could have alleviated the detrimental impacts of increased BD and PR in NT to some extent.

The reduction in the temperature of the topsoil in NT, as found in this and many other studies, can be related to the residues that covered the soil surface and perhaps to higher contents of water in the topsoil (Anderson, 1987; Khakural et al., 1992) which increases the thermal conductivity of the soil. The maize shoot apex remains below

the soil surface until about the V6 stage (Swan et al., 1996); thus, the lower soil temperature observed in all environments in NT was a major factor causing a delay in the development of the plant as well as a slower shoot growth. The soil temperature in the early part of the growing season has been considered to be one of the major factors affecting the emergence of maize and seedling growth and development (Al-Darby and Lowery, 1987; Hayhoe et al., 1996; Tardieu and Pellerin, 1991).

The reductions in RLD, especially at Zollikofen, and the greater root diameters observed under NT are probably typical responses of roots to a reduced soil temperature (Bowen, 1991) as well as to increased soil mechanical impedance (Bennie, 1996). The difference in the mean root diameter, which reflects the degree of root branching, between the tillage systems increased with distance from the plant row, indicating that it was associated with a delay in development and/or growth. This is probably also due to the reduced topsoil temperature. At Zollikofen, the effect of tillage on root growth and morphology was more consistent than at Schafisheim. In general, root length and weight were reduced in NT compared with CT at all sampling positions and depths. The soil at Zollikofen is finely textured (silt loam) and poorly drained, a soil that usually needs to be tilled (Cannell et al., 1994; Carter, 1994). Based on experiments conducted on a soil with a texture similar to that of the soil at Zollikofen, Hughes et al. (1992) concluded that NT might be unsuitable for such soils because it restricts the development of the roots. In addition, Zollikofen is a slightly cooler site than Schafisheim; thus, further reduction of the soil temperature in a system without tillage is more critical for the early growth of maize at this site. Despite this, the growth of maize shoots at Zollikofen was affected by the lack of tillage only in 1997. In 1998, a three week period without rain after the maize was planted led to a dry seedbed in the plowed treatment, whereas the water content in the topsoil under NT remained higher. This counterbalanced partly the benefits of moldboard tillage. A similar observation has been made by Azooz et al. (1995).

The relative distribution of roots with depth and distance from the row did not seem to be affected by tillage, contrary to several reports that roots accumulated in the topsoil of untilled soils (Ball-Coelho et al., 1998; Barber, 1971). The lack of differences in the relative distribution of the roots in both tillage systems indicates i) that mechanical impedance was not great enough to alter the principal patterns of root distribution and ii) that soil water patterns must have been similar in the two tillage treatments, as soil water was identified as a major factor in the early distribution of maize roots (Dwyer

et al., 1996; Kovar et al., 1992). Under NT, 41.8% more biopores were counted below the plow layer than under CT at Zollikofen in the second experimental year (Nakamoto, personal communication), thus, counterbalancing adverse effects of the higher soil strength on maize root growth. The greater number of biopores could be associated to the significantly higher abundance of vertically burrowing (anecic) earthworms under NT compared with CT (Maurer, personal communication). The difference in moisture content mentioned above was too brief to have an effect on root distribution.

Root distribution was drastically modified by the presence of an NP-fertilizer band. RLD increased severalfold in the immediate vicinity of the enriched zone, similar to previous studies (Duncan and Ohlrogge, 1958; Kaspar et al., 1991). The root response was as strong in the NT treatment as in the CT treatment, indicating the lack of restriction to root growth by increased penetration resistance under NT. The placement of starter fertilizer has been considered to be effective in improving the early growth of maize when the soil temperature and/or the nutrient status of the soil is low (Marschner, 1995). Contrary to previous results (Anderson, 1987; Kaspar et al., 1991), no effect of localized nutrient supply on LDD was observed in our study.

The relatively stronger reduction of root length compared with shoot dry weight under NT suggests that the shoot might require more nutrients per unit root length (Engels et al., 1992; Krannitz et al., 1991). Mackay and Barber (1984) found that low soil temperature inhibited root growth more than the uptake kinetics per unit root length, particularly in combination with soil compaction (Al-Ani and Hay, 1983). The reduced extension of the root system under NT at Zollikofen must have been partially compensated for by a greater uptake of nutrients per unit root length. Thus, despite reduced root growth, shoot growth was probably not limited by the negative effect of low temperature on P supply in the root zone. Furthermore, reductions in shoot dry matter occurred in the NT treatment in both years at Schafisheim, although root growth was hardly affected by the lack of tillage at this site. Based on these findings and because the content of P in the shoot was always in the sufficiency range of 4.0 to 8.0 g kg⁻¹ (Jones and Eck, 1973), it is concluded that reductions in shoot growth under NT were not due to a limited supply of P but to the low temperature in environment of the shoot apex. As mentioned above, the placement of fertilizer at planting contributed greatly to this result because there was an ample supply of N and P to the roots. A slow rate of growth of the shoots, due to a limited nutrient supply, is more

likely to occur in nutrient-poor soils (Engels and Marschner, 1990). Gavito and Miller (1998) and Miller et al. (1995) associated the lack of P deficiency in NT treatments to the contribution of the mycorrhizae. Both studies referred to an “unknown factor” that causes a reduced rate of shoot growth in NT systems.

2.5.1 Conclusions

The increased bulk density of the topsoil in the NT treatment probably restricted root growth only to a limited extent, more pronounced in the soil with the finer texture. This confirms that such soils must be tilled more intensively. The lower temperature of the topsoil under NT was probably the main cause of the reduction of the growth of roots and shoots of maize seedlings, mainly because of a direct effect of temperature on the meristems. An indirect temperature effect, caused by an insufficient supply of nutrients to the shoot due to a smaller root system, did not occur owing to the increased root growth in the zone enriched by the placement of a starter fertilizer. This emphasizes the importance of placing fertilizer in the root zone at planting under NT.

3 GROWTH OF SHOOTS AND ROOTS OF MAIZE SEEDLINGS AS AFFECTED BY A COMBINATION OF BULK DENSITY AND TEMPERATURE OF LAYERED SOIL

Chassot, A., J. Leipner, R.M. Hausherr, and W. Richner. 2001. (submitted).

3.1 ABSTRACT

A continuous application of no-tillage systems under temperate climates results in denser and, early in the season, cooler surface layers of the soil, as compared with conventional tillage. This leads to stressful conditions for the establishment of the maize crop. Early growth and functioning of the shoots and roots of maize seedlings were analyzed by simulating the field conditions in a controlled-environment system that allowed the maintenance of gradients in soil properties between the topsoil (0-10 cm) and the subsoil (10-50 cm). Vertically varied soil temperature (13.5 and 17.5°C daily mean temperatures, topsoil/subsoil) and soil bulk density (1.15 and 1.30 Mg m⁻³, topsoil/subsoil) were combined. Growth analysis, study of N uptake using ¹⁵N-labeling, and measurement of photosynthetic characteristics were performed on plants grown in 0.5-m high sand columns up to the 3-leaf growth stage. At the higher topsoil bulk density, the rate of leaf expansion was drastically reduced and the roots concentrated near the soil surface. Thus, intensive use of water and N from the subsoil occurred only in presence of a continuously loose soil profile. The topsoil bulk density was correlated negatively and topsoil temperature positively with the photosynthetic activity. These two soil properties acted independently on all measured parameters. Soil bulk density was the major growth-limiting factor. It is concluded that in no-tillage systems, early subsoil colonization by the roots and a rapid expansion of the leaf area, two conditions essential for a high productivity of maize, might not be satisfactory as a result of the stressful soil conditions.

3.2 INTRODUCTION

No-tillage systems, introduced to alleviate some of the negative impacts associated with conventional tillage, such as soil erosion and structure degradation, can also have some disadvantages. Continuous application of the no-tillage system results in cooler topsoil early in the season, combined with increased resistance to penetration (Blevins et al., 1983; Cannell et al., 1994). However, for high productivity, crop stands must be established soon after planting, with roots colonizing the subsoil as early as possible (Tisdall, 1996) and, for maize, the leaf area should expand rapidly (Giauffret et al., 1995).

It is well documented that low temperatures in the root zone reduce not only the growth of roots of maize, but also the growth of shoots, in particular the expansion of leaves (Watts, 1973; Engels and Marschner, 1990); roots grow more slowly as the soil strength increases (Bengough and Mullins, 1990). A possible interaction between soil temperature and soil mechanical impedance has been reported (Pearson et al., 1970; Abbas Al-Ani and Hay, 1983; Bengough et al., 1994). Furthermore, vertical gradients of soil temperature and mechanical impedance, as encountered in the field, play a major role in root distribution (Shierlaw and Alston, 1984; Lipiec et al., 1993) and the partitioning of assimilates (Sowinski et al., 1998). Compensatory growth in warmer (Russell, 1977) or looser (Kirkegaard et al., 1992) soil layers and residual effects of mechanical impedance on the growth of roots (Bengough and Young, 1993) and of leaves (Masle, 1998) may occur. Most studies on the effects of soil parameters on the growth of the shoot and roots were conducted under uniform conditions throughout the whole soil profile and/or with one factor only.

The aims of this work were to study the combined effects of vertically changing soil temperature and soil strength on the early growth of the shoot and roots of maize under controlled conditions and thus, to simulate the physical soil conditions as found in the field in conventional and no-tillage systems. Impacts on the performance of leaves, and on the functioning of roots were investigated as well.

3.3 MATERIAL AND METHODS

3.3.1 Experimental system

The experimental system that was used to control the root-zone temperature was located in a growth chamber (E15, Conviron, Winnipeg, Canada; air temperature 17.5°C/12.5°C (day/night), 16 h photo- and thermoperiod, 65% relative humidity, and 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD)). This system, modified according to Richner et al. (1992), consisted of three (i) root-temperature boxes each containing two separate water baths, one above the other, which enabled independent control of temperature of the upper (0-10 cm) and lower (10-50 cm) root zones, (ii) growth columns (24 aluminum tubes per root-temperature box, 6 cm in diameter and 50 cm long, in each box), and (iii) cooling/heating systems (Julabo Labortechnik GmbH, Seelbach, Germany; models HP and FP40 for the upper and lower water baths, respectively).

The growth columns were divided into two sections: an upper section, 10 cm long, was closed at the lower end by a steel grid with a mesh size of 3 mm, which ensured unrestricted root growth and a lower section, 40 cm long, sealed at the bottom by a PVC disc. Each section was filled with the growth substrate and subsequently assembled and sealed with silicon. Two millimeters between the sections were left free of soil to prevent an exchange of nutrient solution and to minimize heat transfer between the two sections. After sowing, the tops of the columns were capped to prevent evaporation from the soil surface and to minimize heat exchange with the air. The cap consisted of a watertight cylindrical container encasing a PVC tube to enable shoot growth, and four syringe needles (35 mm long) inserted downwards to ensure irrigation of the upper soil layer. The bottom of the container was insulated with Styrofoam covered by aluminum foil.

The growth substrate was quartz sand (particle size of 0.08 to 0.2 mm) mixed dry with 5% (w/w) vermiculite powder (particle size of 0.08 to 0.1 mm) (Vermex Pulver E, Vermica AG, Bözen, Switzerland). This substrate was chosen, because vermiculite holds a good water and nutrients, and sand can be reproducibly packed, which is essential in root studies. Furthermore, sand is not cohesive; thus, its resistance to penetration varies little over a wide range of water content in contrast to most soils in

which penetrometer resistance increases, often quite sharply, with decreasing soil water content (Tsegaye et al., 1995).

In order to obtain a uniform volumetric water content of 20%, independent of the dry bulk density, the gravimetric water content was adjusted with a modified Hoagland nutrient solution containing 7 mM $\text{Ca}(\text{NO}_3)_2$, 2.0 mM MgSO_4 , 1.0 mM H_3PO_4 , 1.5 mM K_2SO_4 , 0.16 mM FeNA-EDTA, 0.05 mM KCl, 18.0 μM MnSO_4 , 12.0 μM H_3BO_3 , 1.5 μM ZnSO_4 , 0.6 μM CuSO_4 , 4.2 μM MoO_3 , depending on the treatment (see below). In order to obtain a nearly neutral pH, 1 ml conc. H_2SO_4 per liter nutrient solution was added. N in the upper section (0-10 cm) was labeled with 10% ^{15}N -enriched $\text{Ca}(\text{NO}_3)_2$ (10.6 atom% ^{15}N) (Isotec Inc., Miamisburg, Ohio, USA), so that the contribution of nitrogen taken up from this section to the total nitrogen content of the plant tops could be determined.

3.3.2 Experimental treatments

There were three soil temperature treatments, consisting of either a warm soil layer (19°C/15°C, day/night) on top of a cooler one (13.5°C) or a cool layer (15°C/11°C, day/night) on top of a warmer one (17.5°C) and a homogeneous, warm treatment (19°C/15°C, day/night, in the upper and 17.5°C in the lower layer) as a control. Under field conditions, daily temperature fluctuations are much smaller at greater soil depths compared with the topsoil; thus, the temperature of the lower soil compartment was set to a constant level. The temperatures of the root zone were selected to coincide with average soil temperatures in the Swiss midlands from mid-April to early June. The difference in topsoil temperatures was slightly higher than the typical differences in the temperature of the topsoil in conventional and no-tillage systems.

To induce soil mechanical resistance to root penetration, moist substrate was packed into the two tube sections at two average bulk densities (1.30 and 1.45 Mg m^{-3}). By combining the upper and lower tube sections, bi-layered columns made of either a layer with low bulk density on top of a layer with high bulk density or the vice versa, and homogeneously packed columns with either two layers at low bulk density or two layers at high bulk density were obtained. Substrate was packed into the lower sections using a wooden pestle in 10-cm increments to achieve a homogeneous bulk density over the profile. After each addition of substrate, the surface was scratched before the next addition of substrate to prevent the formation of a smeared layer. The choice of bulk density and moisture content represented a compromise between

obtaining a range of penetration resistance sufficient to impede but not to completely halt root elongation, at a moisture content sufficient for rapid root elongation, and maintaining a large air-filled porosity, well in excess of the 10% aeration assumed to be acceptable for root growth and respiration (Grable and Siemer, 1968). The initial air-filled porosity was 20 and 27% in the high and low bulk density treatments, respectively.

To reduce variability between replicate seedlings, maize seeds (*Zea mays* L. cv. Granat) were selected according to shape and weight, so that only seeds with a shape typical for the cultivar and with a mass within one standard deviation of the mean (225 to 270 mg) were used. The seeds, treated with the system insecticide Gaucho[®] (Bayer AG, Zurich, Switzerland), were pregerminated on moist vermiculite in the dark at 15°C for two to three days. Seeds with a radicle 0.5 to 1 cm long were planted at a depth of 2 cm. The seed was covered with loose substrate, and the surface was covered with the plexiglas container.

Two harvests were made, the first at the 2-leaf growth stage, corresponding approximately to the transition from hetero- to autotrophic growth (Cooper and MacDonald, 1970), and the second at the 3-leaf growth stage when the first roots had reached the bottom of the cylinder. The harvest was made when 50% of the plants in a temperature treatment had reached the desired stage. Those plants that were not harvested before the 3-leaf growth stage were irrigated with 40 ml of deionized water at the 2-leaf growth stage.

The experimental design was a split-split-plot with three replications and one plant per treatment. Table 3.1 presents the structure of the experiment and the treatments. All results were subjected to analysis of variance and the means separated using the Fisher's protected LSD test. Unless otherwise specified, the level of significance was 0.05.

Table 3.1. Experimental design and treatments.

ANOVA design	Factors		Levels		
			<i>Code</i>	Topsoil	Subsoil
Main plot	Temp	Soil temperature ^a (°C)	<i>Control</i>	17.5	17.5
			<i>C_{top}</i>	13.5	17.5
			<i>C_{sub}</i>	17.5	13.5
Subplot	Stage	Stage of growth		2-leaf	
				3-leaf	
Sub-subplots	BD _{top}	Topsoil bulk density (Mg m ⁻³)		1.30	
				1.45	
	BD _{sub}	Subsoil bulk density (Mg m ⁻³)			1.30
					1.45

^a Daily mean temperatures

3.3.3 Measurements

3.3.3.1 Plant leaf area

A non-destructive measurement of leaf area was made by measuring the length of each leaf of each plant every two to three days from the 1-leaf to the 3-leaf growth stage. The length of the leaf was measured with a ruler after it emerged from the sheath, from the leaf tip to the ligule of the last fully developed leaf. In order to estimate the leaf area from the measurements of leaf length, linear regression models were derived from leaf measurements on one hundred other plants, grown under conditions as described above (soil bulk density 1.30 Mg m⁻³ in the whole profile; no control of soil temperature). Each leaf position was treated separately because of different length-area relationships.

Plant leaf area was calculated using the obtained regression parameters for each date on which leaf length was measured. The area of the fully expanded coleoptile (leaf 1), measured as described above, was added.

3.3.3.2 Leaf performance

The chlorophyll a fluorescence was measured with a pulse amplitude modulation fluorometer (PAM-2000, Walz, Effeltrich, Germany). A dark leaf clip was placed on

the leaf and closed to enable the leaf to adapt to the dark for 20 min before exposing it to a 0.8 s saturation flash (PPFD > 4000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) to determine the minimal fluorescence yield (F_o) and the maximum fluorescence in a dark-adapted leaf (F_m). The maximum quantum efficiency of photosystem II primary photochemistry (F_v/F_m) was calculated as follows:

$$F_v/F_m = \frac{(F_m - F_o)}{F_m}$$

Photosynthesis was measured on the third leaf by CO_2 fixation (LI-6200; LI-COR, Lincoln, NE, USA) at growth conditions.

To determine the chlorophyll concentration, leaf disks, 10 mm in diameter, were cut from the middle part of the third leaf, homogenized in liquid nitrogen, and extracted in 6000 mm^3 ice-cold acetone (80% [v/v]) for 0.5 h. The concentration of chlorophyll was determined photometrically (U-2000, Hitachi, Tokyo, Japan) according to Arnon (1949).

3.3.3.3 *Shoot and root dry weights*

The shoots were cut at ground level, and the fresh weight was determined. The leaf blades of the fully expanded leaves and the visible part of the leaf blade of partially expanded leaves were cut, the fresh weight was determined, and the area was measured with a leaf area meter (LI-COR 3100, Lincoln, NE, USA). The two fractions of shoot material were oven-dried for 48 h at 65°C for the determination of their dry weight.

The roots from the upper and lower sections of the tube were washed separately under pressurized tap water. The roots from the upper soil layer were then separated into three categories (seminal, mesocotyl, and adventitious roots) and the rest of the seed was removed carefully. All the fractions were dried at 65°C for 48 h, and the dry weights were determined separately.

3.3.3.4 *N and water uptake*

Dried shoot samples were ground sequentially in a sample mill (Cyclotec 1093, Tecator AB, Höganäs, Sweden) and in a ball mill (Type MM2, Retsch, Arlesheim, Switzerland) to a very fine powder. After redrying, the samples (5 mg) were weighed into tin caps (0.04 ml, Lüdi AG, Flawil, Switzerland) and analyzed for ^{15}N with a continuous flow mass spectrometer in the Stable Isotope Facility of the University of

California, Davis, USA. The relative contribution of N from the upper root zone to the total shoot N ($\%N_{top}$), a yield-independent parameter, was calculated as:

$$\%N_{top} = \frac{\text{atom}\% \text{ } ^{15}\text{N-excess in shoot material}}{\text{atom}\% \text{ } ^{15}\text{N-excess in the nutrient solution of the upper root zone}} \cdot 100$$

where atom% ^{15}N -excess is the atom% ^{15}N in excess of natural abundance (=0.3663%). The atom% ^{15}N -excess in the nutrient solution of the upper root zone was 1.0234%.

The amount of water taken up from the topsoil and the subsoil was determined gravimetrically. The corresponding tube sections were weighed before planting and at harvest, after removing the shoots and before root washing. Water uptake was calculated as the difference between the initial and the final tube-section weights, in consideration of the irrigation water and the weight of the roots at harvest.

3.3.4 Growth analysis

3.3.4.1 Leaf area

In a first step, a polynomial of second order was fitted to the growth curves of leaf area from the 1-leaf to the 3-leaf stage (data not shown). The coefficient of the quadratic term did not differ significantly from zero, indicating that the expansion of leaf area was linear during this period of growth. Thus, the linear regression model

$$Y = \alpha + \beta X + E$$

was fitted to each growth curve. α and β are the model parameters, which correspond to the leaf area at the 1-leaf stage and to the expansion rate of leaf area, respectively, Y is the total leaf area, X the number of days since the first measurement of leaf length, and E the residual error.

3.3.4.2 Elongation of individual leaves

Using the same data, the same method of growth analysis, as described above for the plant leaf area, was applied to the elongation of the leaves 2, 3, and 4.

3.3.4.3 Absolute growth rates for shoot and roots

The mean absolute growth rates (AGR) were calculated for the dry weights of shoot, topsoil roots and all roots by dividing the values obtained at the 3-leaf stage by the number of days after sowing (Hunt, 1982).

3.3.4.4 *Relative shoot growth rate and its components*

The mean relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) were computed according to Hunt (1982). The above parameters were highly variable due to their construction (simple ratios between two quantities or rates of change involving more than one variate measured on different plants), thus making it difficult to detect significant effects among treatments.

In one replication, the rate of appearance of the leaf tip was estimated by dividing the number of leaves (from leaf 2 to the last leaf) by the number of days from the appearance of the second leaf tip to the appearance of the last leaf tip. A leaf tip was considered to have emerged when it was visible above the whorl of older leaves, when observed from the side of the plant.

3.4 RESULTS

No significant interaction was found between soil temperature and soil bulk density for any of the variables measured. Therefore, the data are presented for a single factor, as averaged over the levels of the other.

3.4.1 Effect of soil bulk density

The bulk density of the topsoil was the main source of variation of all the parameters studied. At the three-leaf stage, the dry weights of the shoot and all roots were highly significantly ($P < 0.001$) reduced by 46% and 40%, respectively, at high bulk density of the topsoil compared with the lower bulk density (Fig. 3.1). The decrease in shoot dry weight was due primarily to the highly significant effect ($P < 0.001$) of the bulk density of the topsoil on the rate of leaf area expansion (Table 3.2), leading to a 45% smaller final leaf area (Fig. 3.2). When the topsoil was stronger, there was a tendency towards lower rates of leaf appearance and elongation of individual leaves, the latter increasing with leaf number (Table 3.2). The effect of topsoil bulk soil density was statistically significant for leaves 3 and 4 ($P < 0.01$ and $P < 0.001$, respectively).

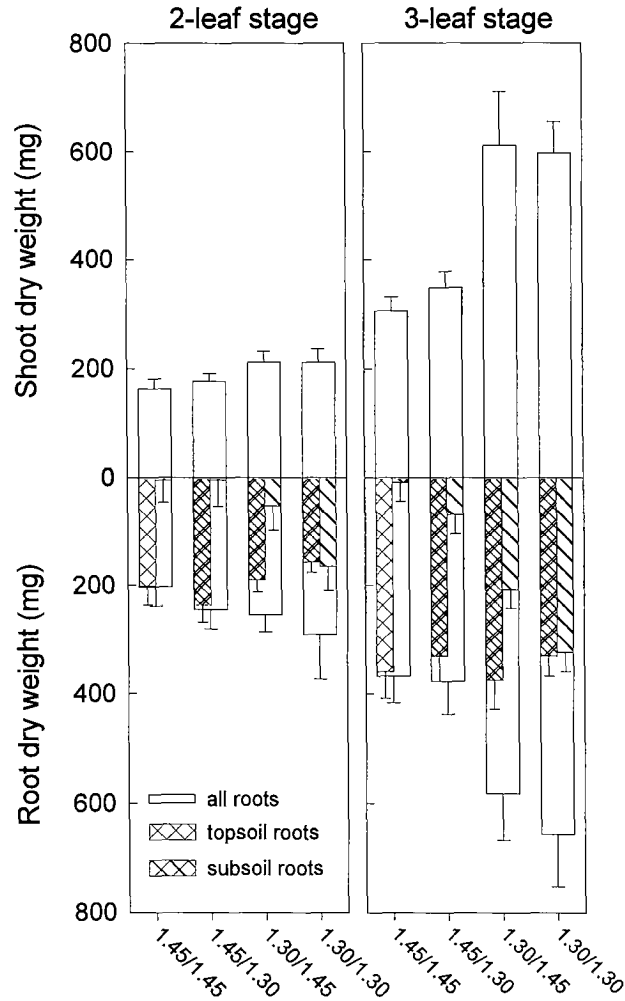


Fig. 3.1. Dry weight of the shoot, of all the roots, of the roots in the topsoil, and of the roots in the subsoil as a function of bulk density of the topsoil and of the subsoil at the 2- and the 3-leaf growth stages of maize. Vertical error bars are standard errors.

Root growth was directly affected by the bulk density of the surrounding soil. At the 2-leaf growth stage, a high bulk density in the topsoil significantly ($P < 0.05$) reduced the dry weight of topsoil roots by 21% compared with loose topsoil, whereas topsoil bulk density had no effect on this trait at the 3-leaf stage. The dry weight of the subsoil roots was affected indirectly by the strength of the topsoil, because only a small fraction of the roots penetrated the deeper layer, and directly by the strength of the subsoil. Independently of each other, high bulk densities in both the topsoil and the subsoil significantly decreased the dry weight of subsoil roots by 79% ($P < 0.01$) and 56% ($P < 0.01$), respectively, at the 2-leaf growth stage and by 76% ($P < 0.001$)

and 45% ($P < 0.05$), respectively, at the 3-leaf growth stage. As a consequence, the resources that were available in the subsoil, such as water and N, were exploited to a greater extent only in the absence of a compact soil layer, especially in the topsoil (Table 3.3). When the subsoil was looser than the topsoil, compensation of root growth occurred, causing a slight increase in shoot growth (Fig. 3.1). A higher NAR, which is an estimate of the carbon-assimilatory capacity of the leaves, and a higher rate of leaf area expansion, caused by the more rapid elongation of the younger leaves, were responsible for this compensation (Tables 2 and 4); however, it was not associated with a higher proportion of N and/or of water taken up from the subsoil (Table 3.3). At high bulk density of the topsoil, the proportion of adventitious roots in the dry matter of the root system decreased by 16% at the 2-leaf stage and by 11% at the 3-leaf stage compared with the looser topsoil. The plants in all the treatments had, on average, four elongated adventitious roots from the first phytomere at the 3-leaf stage (data not shown).

The dense topsoil caused a decrease in RGR of shoots, which was mainly due to reductions in NAR, the physiological component, but not in LAR, the morphological component (Table 3.4), which represents the ratio of photosynthesizing to respiring material in the plant. The photosynthetic activity was significantly ($P < 0.05$) reduced by a high bulk density of the subsoil (Fig. 3.3). This was not associated with a decrease in chlorophyll concentration and/or reduced maximum efficiency of photosystem II (F_v/F_m).

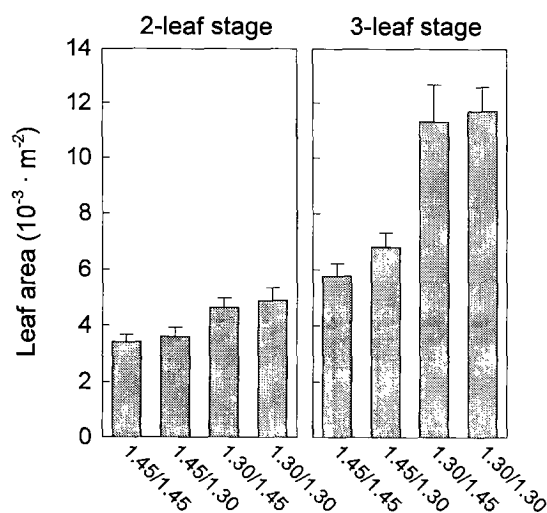


Fig. 3.2. Total leaf area as a function of bulk density of the topsoil and the subsoil at the 2- and the 3-leaf growth stages of maize. Vertical error bars are standard errors.

3.4.2 Effect of soil temperature

The absolute growth rates of the shoot and roots were lower when the temperature of the topsoil was lower, whereas the temperature of the subsoil had no effect on the growth rates (Table 3.5). However, there were no significant temperature effects on shoot growth due to the relatively small differences in temperature among the treatments, for the reasons mentioned above, and to the experimental design, which gives little power for testing the effect of soil temperature, the main plot factor. The maximum growth rate of roots in the topsoil occurred at a low temperature of the subsoil, indicating compensatory growth in the warmer topsoil. Interestingly, in the treatment with a cooler topsoil, the fraction of root dry weight in the upper layer at the 3-leaf stage was the largest, while the proportion of N that originated in the topsoil was the lowest (Table 3.3).

The parameters of leaf expansion were affected by soil temperature (Table 3.2), but statistically significantly ($P < 0.05$) only for the elongation rate of leaf 4. A reduced topsoil temperature (13.5/17.5°C, topsoil/subsoil) generally had a more adverse effect on parameters of leaf growth than a cool subsoil (17.5/13.5°C). Except for the elongation rate of leaf 2, which was not affected by a low topsoil temperature, the rank order of temperature treatments was 17.5/17.5°C > 17.5/13.5°C > 13.5/17.5°C for all parameters of leaf expansion. In contrast to the other parameters of leaf growth, the rate of leaf development was stronger affected by the soil temperature than by the soil bulk density treatments (Table 3.2).

Photosynthetic activity, chlorophyll concentration, and maximum quantum efficiency of primary photochemistry of photosystem II (F_v/F_m) were lower when the temperature of the topsoil was low, though this was not statistically significant (Fig. 3.3).

Table 3.2. Plant leaf area at the 1-leaf stage, expansion rate of plant area, elongation rate of individual leaves, and rate of appearance of leaf tips (RALT) from the 1- to the 3-leaf growth stage of maize as a function of temperature and bulk density of the topsoil and the subsoil. Values are means \pm SE.

Topsoil	Subsoil	Plant leaf area at the 1-leaf stage (cm ²)	Expansion rate ^a of plant leaf area (cm ² d ⁻¹)	Elongation rate ^a of individual leaves (cm d ⁻¹)			RALT ^b (lf. tip d ⁻¹)
				Leaf 2	Leaf 3	Leaf 4	
Soil temperature (°C)							
17.5	17.5	8.14 \pm 1.32	4.42 \pm 0.31	0.29	1.29	1.50 a ^c	0.19
13.5	17.5	3.72 \pm 1.59	3.31 \pm 0.44	0.29	0.98	1.17 b	0.12
17.5	13.5	9.40 \pm 1.07	3.85 \pm 0.23	0.22	1.00	1.29 b	0.17
Soil bulk density (Mg m ⁻³)							
1.45	1.45	7.85 \pm 1.64	2.77 \pm 0.28	0.29	0.99	1.09	0.16
1.45	1.30	8.29 \pm 1.84	3.26 \pm 0.23	0.28	1.03	1.20	0.15
Mean		8.07 \pm 1.20	3.01 \pm 0.19 b	0.28	1.01 b	1.15 b	0.15
1.30	1.45	5.84 \pm 1.61	4.71 \pm 0.43	0.28	1.21	1.45	0.17
1.30	1.30	6.36 \pm 1.92	4.70 \pm 0.22	0.22	1.13	1.53	0.17
Mean		6.10 \pm 1.22	4.70 \pm 0.24 a	0.25	1.17 a	1.49 a	0.17

^a Expansion rates of leaf area and elongation rates of individual leaves correspond to the slopes of the linear regression models fitted to the growth curves of these traits.

^b Measured only in one replication.

^c Means followed by the same letter within an experimental factor are not significantly different at $\alpha=0.05$.

Table 3.3. Proportions of N (%N_{top}) and water (%H₂O_{top}) taken up from the topsoil and fraction of root dry weight in the topsoil (%RDW_{top}) as a function of temperature and bulk density of the topsoil and the subsoil at two growth stages of maize. Values are means ±SE.

Topsoil	Subsoil	%N _{top} (%)	%H ₂ O _{top} (%)	%RDW _{top} (%)
<i>2-leaf stage</i>				
Soil temperature (°C)				
17.5	17.5	76 ±5	95 ±6	84 ±4
13.5	17.5	78 ±3	76 ±6	87 ±5
17.5	13.5	71 ±2	100 ±0	86 ±4
Soil bulk density (Mg m ⁻³)				
1.45	1.45	76 ±4.9	100 ±0 a ^a	99 ±0.5
1.45	1.30	79 ±3.9	74 ±12.3 b	98 ±1.6
Mean		77 ±3.0	87 ±7.2	99 ±0.8 a
1.30	1.45	76 ±3.6	91 ±1.0 a	75 ±3.3
1.30	1.30	70 ±4.5	63 ±11.9 b	66 ±7.8
Mean		73 ±3.0	77 ±6.2	70 ±4.5 b
<i>3-leaf stage</i>				
Soil temperature (°C)				
17.5	17.5	71 ±7	72 ±4 a	74 ±7
13.5	17.5	62 ±7	75 ±4 a	80 ±6
17.5	13.5	66 ±5	88 ±4 b	77 ±5
Soil bulk density (Mg m ⁻³)				
1.45	1.45	80 ±5.7	69 ±5.5 a	98 ±1.2 a
	1.30	79 ±7.0	69 ±4.8 a	91 ±3.3 b
Mean		79 ±4.0 a	69 ±4.0	94 ±1.9
1.45	1.45	58 ±4.8	65 ±6.8 a	67 ±4.1 c
	1.30	48 ±4.6	54 ±7.3 b	53 ±3.4 d
Mean		53 ±3.0 b	58 ±5.2	60 ±3.0

^a Means followed by the same letter within an experimental factor are not significantly different at $\alpha=0.05$.

Table 3.4. Relative growth rate (RGR) and net assimilation rate (NAR) from the 2- to the 3-leaf growth stage of maize and leaf area ratio (LAR) at the 3-leaf stage as a function of bulk density of the topsoil and the subsoil. Values are means \pm SE.

Soil bulk density (Mg m ⁻³)		RGR (d ⁻¹)	NAR (g m ⁻² d ⁻¹)	LAR (m ² g ⁻¹)
Topsoil	Subsoil			
1.45	1.45	0.058 \pm 0.02	2.75 \pm 0.71	0.019 \pm 0.071
1.45	1.30	0.065 \pm 0.01	3.20 \pm 0.56	0.020 \pm 0.078
Mean		0.061 \pm 0.01 a ^a	2.98 \pm 0.44 a	0.020 \pm 0.053
1.30	1.45	0.085 \pm 0.01	4.27 \pm 0.78	0.020 \pm 0.104
1.30	1.30	0.087 \pm 0.01	4.16 \pm 0.41	0.020 \pm 0.072
Mean		0.086 \pm 0.01 b	4.21 \pm 0.43 b	0.020 \pm 0.061

^a Means followed by the same letter are not significantly different at $\alpha=0.05$.

Table 3.5. Absolute growth rates (AGR) of the shoot, of the topsoil roots, and of the total roots from planting to the 3-leaf growth stage of maize as a function of soil temperature. Values are means \pm SE.

Soil temperature (°C)		AGR (mg dry matter d ⁻¹)		
Topsoil	Subsoil	Shoot	Topsoil roots	Roots total
17.5	17.5	15.2 \pm 1.7 a ^a	11.3 \pm 0.9 a	17.1 \pm 2.3 a
13.5	17.5	13.2 \pm 2.2 a	8.9 \pm 1.3 b	11.9 \pm 1.9 b
17.5	13.5	14.1 \pm 1.2 a	12.0 \pm 1.0 a	16.7 \pm 2.0 a

^a Means followed by the same letter are not significantly different at $\alpha=0.05$.

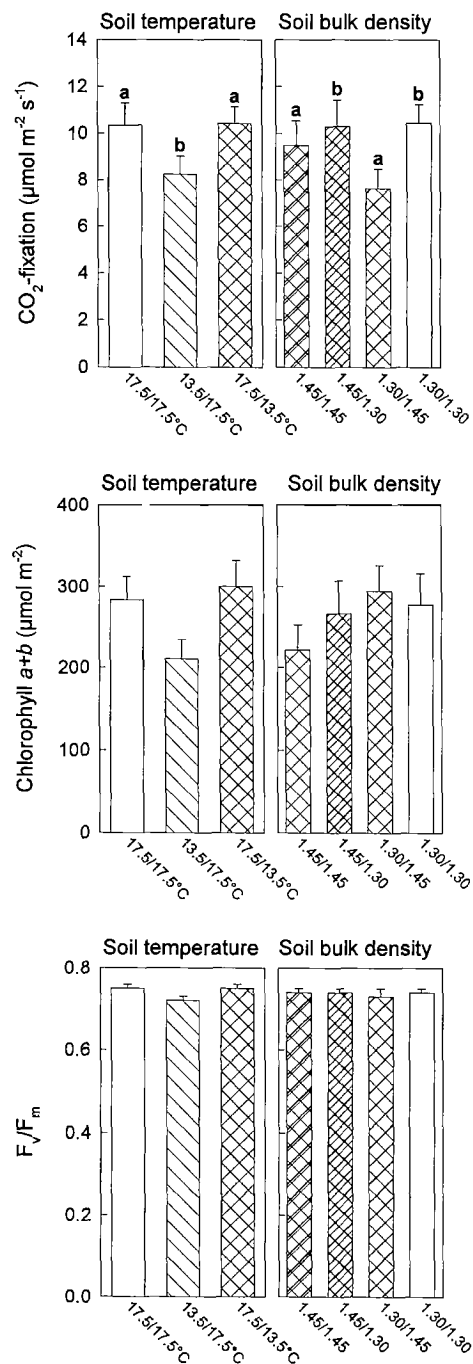


Fig. 3.3. Photosynthesis, leaf chlorophyll concentration, and maximum quantum efficiency of photosystem II primary photochemistry (F_v/F_m) as a function of temperature and bulk density of the topsoil and the subsoil at the 3-leaf growth stage of maize. Vertical error bars are standard errors. Means followed by the same letter within an experimental factor are not significantly different at $\alpha=0.05$.

3.5 DISCUSSION

The effects of soil temperature and soil bulk density did not depend on each other as far as the parameters measured in this study were concerned. This is in contradiction to previous reports, in which it was suggested that a higher temperature can compensate for the detrimental effects of soil resistance (Abbas Al-Ani and Hay, 1983) by influencing the maximum growth pressure of mechanically impeded roots (Bengough et al., 1994). The reasons for this lack of interaction are unclear; it might be due to the relatively narrow range of the tested soil temperatures, which were all set at suboptimal levels for the chilling-sensitive maize plant, simulating temperature ranges in the field.

The growth of the shoot and particularly the leaf expansion were dramatically reduced when the surface layer was dense. There are a number of possible reasons for the reduction in leaf expansion: (i) an indirect effect due to a reduced water and/or nutrient uptake (Busscher and Lipiec, 1993), (ii) an insufficient carbon supply due to a smaller and less active source (smaller leaf area and reduced leaf performance) and/or a higher sink demand (increased osmotic pressure in the roots and higher root:shoot dry weight ratio) (Atwell, 1993), (iii) a direct effect of soil resistance on leaf growth by means of chemical root signals (Masle and Passioura, 1987; Young et al., 1997).

In this study, the first hypothesis is improbable for the following reasons: the increase in shoot dry weight in the bulk density treatment 1.45/1.30 Mg m⁻³ (topsoil/subsoil) compared with 1.45/1.45 Mg m⁻³ was associated with an increase in root dry weight in the subsoil but not with a decrease in N and/or water uptake from the topsoil, i.e., an increase in the subsoil contribution. Similarly, the decrease in the uptake of N and water from the topsoil, i.e., the higher fraction of N and water from the subsoil, in the bulk density treatment 1.30/1.30 Mg m⁻³ (topsoil/subsoil) compared with 1.30/1.45 Mg m⁻³ did not lead to higher shoot dry weights.

The hypothesis of carbon limitation cannot be rejected because, in the treatments with a high bulk density of the topsoil, as well a reduction of the source activity as an increase in the sink demand probably occurred; the leaf area and its production efficiency, as indicated by the NAR, were reduced and the demand of the root system for assimilates increased, due to a slightly higher root:shoot dry weight ratio in the treatments with a dense topsoil compared with the other treatments (data not shown).

Furthermore, the consumption of assimilates is greater in compact soils due to increased root respiration and/or root exudation (Helal and Sauerbeck, 1986). The elongation rate of roots was found to be the first mechanism affected by a reduced carbon supply (Aguirrezabal et al., 1993). Thus, as mentioned in the first hypothesis, the supply of water and nutrients to the shoot might become limiting. However, the growth of maize seedlings is hardly affected by the leaf area prior to the 2-leaf stage due to heterotrophic growth and thereafter because the transition to autotrophic growth is gradual (Cooper and MacDonald, 1970). The third hypothesis, the involvement of phytohormones, was not tested in this study. Nevertheless, a direct effect of soil resistance on shoot growth might have occurred; the effect of strength of the subsoil on the rate of leaf elongation was observed mainly for the leaves 4 and higher, which grew after the first roots had reached the subsoil. These results contrast to those reported by Masle (1998) who suggested that the effects of root impedance on leaf expansion are generally determined before the emergence of the blade, during the period from the initiation of the primordium to the formation of the leaf intercalary meristem. Consequently, the impedance of the lower soil layer is probably of minor importance for leaf expansion in our study. There was also a tendency towards a higher mean RGR, associated with a higher NAR, from the two- to the three-leaf stage in looser subsoil, which might be due to higher photosynthetic activity.

In general, root growth was affected by the strength of the soil surrounding it. This is the assumption of models of root growth through structured soils (Jakobsen and Dexter, 1987), where the elongation rate of a root at a given time is considered to depend only on the resistance of the soil at that time. However, a residual effect of mechanical impedance on root growth, i.e., a delay before the rate of root elongation increases when the roots reach a zone of lesser mechanical impedance (Bengough et al., 1997), cannot be excluded. It is well established that the rate of root elongation decreases sharply when the mechanical impedance of the soil increases, whereas root dry weight is not necessarily affected (Barley, 1962; Goss, 1977; Logsdon et al., 1987). Accordingly, at the 3-leaf stage, there was no difference in the dry weight of roots in the topsoil between the bulk density treatments. Masle et al. (1990) reported that the accumulation of dry weight by the roots of wheat seedlings was initially considerably lower than that of the shoot; the reverse is increasingly true thereafter. Furthermore, when the lower soil layer was looser than the topsoil, the root system

compensated for growth in that layer, at least partially. This phenomenon was mentioned by Brouwer (1981) who reported that, when shoot growth is not affected by partial derooting or local inhibitory treatments in the root zone, the remaining root members compensate completely for the reduction elsewhere.

Water use from the subsoil was drastically reduced by a dense layer in the topsoil and/or in the subsoil. Thus, considerable amounts of water were taken up from the subsoil only in the bulk density treatment 1.30/1.30 Mg m⁻³ (topsoil/subsoil). Maize grown in this treatment had the lowest stomatal resistance (data not shown). It might be argued that water was a limiting factor in the treatments with a compacted layer as a consequence of the concentration of roots near the soil surface. This did not occur, however, because a significant difference in leaf area was not observed between plants having all of their roots concentrated in the topsoil and plants with roots that reached the subsoil (data not shown). Even when only a single root reached the subsoil, the plants could probably supply sufficient water to the shoot with regard to the low evaporative demand. Some investigators (Lipiec et al., 1988) attributed lower growth rates in lower bulk density treatments to lower unsaturated hydraulic conductivity of the soil and, thus, a smaller flow of water to the roots. This was not verified in this study. Were there differences between the bulk density treatments in the water supply to the roots in the top layer of soil that may have affected root growth in the bottom layer? This question was raised by Bengough and Young (1993) who concluded that this was not the case due to the counteraction of water availability and root-soil contact in a bulk density treatment.

Leaf growth and development, photosynthesis, and root growth decreased with decreasing temperature of the topsoil. Engels and Marschner (1990) reported that the shoot growth of maize seedlings at suboptimal temperature of the root zone was limited both by a reduced supply of nutrients through the roots and by a direct decrease in the temperature of the shoot meristem. Barlow et al. (1977) also attributed decreases in shoot growth to restricted water uptake, which lowered the plant water potential. He found that suboptimal soil temperatures affected the growth of corn seedlings primarily by decreasing leaf elongation. Root growth was more affected by low soil temperature than shoot growth. This was also observed by Engels (1994) and can, presumably, be attributed to the growth crisis of maize seedlings, as reported by (Derieux et al., 1989), which mainly affects root growth and which is related to the beginning of translocation of assimilates to the roots around the 2-leaf growth stage.

Barber et al. (1988) found that soil temperature is the primary factor affecting the distribution of maize roots during the first four to six weeks of growth. Furthermore, not only the growth rate of the root system seemed to be reduced at low soil temperature, but also the uptake capacity, as shown by the discrepancy between the fraction of root dry weight in the upper soil layer and the proportion of N taken up from this layer in the treatment with a cool topsoil. Similar results were reported by Abbas Al-Ani and Hay (1983) from a study of the root systems of different cereal seedlings.

3.5.1 Conclusions

For high productivity of maize, the colonization of the subsoil by the roots and a large interception of solar radiation by the leaf area need to be achieved as early as possible. In no-tillage systems, these two conditions might not be met, as suggested by the findings of this study in which the physical characteristics of the soil, as in the field under conventional and no-tillage systems, were simulated. It was found that the additive effects of soil strength and soil temperature lead to a delay in shoot development, a reduced rate of growth of the shoot and particularly of the leaves, a concentration of roots near the soil surface, and a decreased functioning of leaves and roots.

In this model study under controlled conditions, soil resistance was the major growth-limiting factor, overriding the effect of soil temperature. As a result of the biopore system in the field, the soil resistance encountered by the roots should be lower, making the negative effects of reduced soil temperature on growth increasingly important compared with soil density.

4 ROOT CHARACTERISTICS OF AND PHOSPHORUS SUPPLY TO MAIZE SEEDLINGS AS AFFECTED BY A COMBINATION OF BULK DENSITY AND TEMPERATURE OF LAYERED SOIL

Chassot, A. and W. Richner. 2001. (submitted).

4.1 ABSTRACT

Under temperate climates, no-tillage results in cooler and denser topsoils than conventional tillage, and in surface accumulation of immobile nutrients. Hence, early growth, morphology, and functioning of maize roots may be affected. The field conditions were simulated in a controlled-environment system allowing gradients in soil properties between topsoil (0-10 cm) and subsoil (10-50 cm). Combinations of vertically varied soil temperatures (13.5/15.5, 15.5/15.5, 17.5/15.5°C, topsoil/subsoil), bulk densities (BD) (1.15/1.30, 1.30/1.30, 1.45/1.30 Mg m⁻³, topsoil/subsoil), and P levels (0.031/0.031 and 0.310/0.031 g l⁻¹, topsoil/subsoil) were applied on maize seedlings grown in sand columns (0.5 m high) until the three-leaf growth stage. The length, length-per-diameter distribution, depth distribution, and functioning (P uptake) of the roots were investigated. BD and temperature of the topsoil acted independently on all parameters, but showed some interactions with P. An increase in topsoil BD caused a linear decrease in root length, root weight, and the root:shoot ratio, an increase in root diameters in both top- and subsoil, and a concentration of roots near the soil surface. This resulted in a greater contribution of the topsoil to the nutrient supply of the shoot, as shown for ¹⁵N-labeled N. In general, length, diameter, and topsoil fraction of roots were influenced positively by increasing topsoil P level, particularly at high BD. Shoot and root growth were reduced to the same extent by decreasing topsoil temperature. There was possibly a trade-off between the adverse effects of low soil temperature and the positive impacts of a high P supply on root growth. It is concluded that in strong soils, especially if combined with reduced temperatures, particular attention needs to be paid to the P supply.

4.2 INTRODUCTION

No-tillage systems (NT) are used increasingly to alleviate some of the negative effects of conventional tillage (CT), namely soil erosion and degradation of the soil structure. However, the absence of soil disturbance results in cooler surface layers early in the season, and this is associated with increased mechanical impedance (Cannell et al., 1994) and a pronounced accumulation of P and K in the upper 5 cm of the soil (Robbins and Voss, 1991). These characteristics may have an adverse effect on root parameters that are important for nutrient uptake and fertilizer utilization efficiency (e.g. root length, root radius, distribution of roots in the soil profile, and physiological characteristics of the roots) (Barber and Silberbush, 1984; Mackay and Barber, 1984; Masle and Passioura, 1987; Engels and Marschner, 1990; Schröder et al., 1996). Most studies on the effects of soil factors on root parameters were conducted under uniform conditions throughout the soil profile and/or with one tested factor only. Furthermore, in studies with a range of soil temperatures, large differences between the temperature levels were applied, contrary to the small differences measured between CT and NT topsoils.

The objectives of this work were to study the combined effects of vertically changing soil temperature, soil strength, and level of soil P on the early growth of maize under controlled conditions and, thus, to simulate soil physical conditions in the field under CT and NT. Emphasis was put on the growth, morphology, distribution and functioning of the roots with regard to shoot growth and fertilizer utilization efficiency. Phosphorus was used as a model macroelement to determine whether the effects of soil properties on roots lead to an inadequate supply of nutrients to the shoot, because the acquisition of P was found to be closely related to root growth (Mackay and Barber, 1984) and root morphology (Schenk and Barber, 1980).

4.3 MATERIAL AND METHODS

4.3.1 Experimental system

The experimental system that was used to control the root-zone temperature was located in a growth chamber (E15, Conviron, Winnipeg, Canada; air temperature 17.5°C/12.5°C (day/night), 16 h photo- and thermoperiod, 65% relative humidity, and

400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD)). This system, modified according to Richner et al. (1992), consisted of (i) root-temperature boxes containing two separate water baths, one above the other, which enabled independent control of temperature of the upper (0-10 cm) and lower (10-50 cm) root zones, (ii) growth columns (24 aluminum tubes, 6 cm in diameter and 50 cm long, in each box), and (iii) cooling/heating systems (Julabo Labortechnik GmbH, Seelbach, Germany; models HP and FP40 for the upper and lower water baths, respectively).

The growth columns were divided into two sections: an upper section, 10 cm long, was closed at the lower end by a steel grid with a mesh size of 3 mm, which ensured unrestricted root growth and a lower section, 40 cm long, sealed at the bottom by a PVC disc. Each section was filled with the growth substrate and subsequently assembled and sealed with silicon. Two millimeters between the sections were left free of soil to prevent an exchange of nutrient solution and to minimize heat transfer between the two sections. After sowing, the tops of the columns were capped to prevent evaporation from the soil surface and to minimize heat exchange with the air. The cap consisted of a watertight cylindrical container encasing a central PVC tube to enable shoot growth, and four syringe needles (35 mm long) inserted downwards to ensure irrigation of the upper soil layer. The bottom of the cap was insulated with Styrofoam covered by aluminum foil.

The growth substrate was quartz sand (particle size of 0.08 to 0.2 mm) mixed dry with 5% (w/w) vermiculite powder (particle size of 0.08 to 0.1 mm) (Vermex Pulver E, Vermica AG, Bözen, Switzerland). This substrate was chosen, because vermiculite holds a good water and nutrients, and sand can be reproducibly packed, which is essential in root studies. Furthermore, sand is not cohesive; thus, its resistance to penetration varies little over a wide range of water content in contrast to most soils in which penetrometer resistance increases, often quite sharply, with decreasing soil water content (Tsegaye et al., 1995). In order to obtain a uniform volumetric water content of 20%, independent of the dry bulk density, the gravimetric water content was adjusted with a modified Hoagland nutrient solution containing 7 mM $\text{Ca}(\text{NO}_3)_2$, 2.0 mM MgSO_4 , 1.0 or 10.0 mM H_3PO_4 , (depending on the P treatment; see below), 1.5 mM K_2SO_4 , 0.16 mM FeNA-EDTA, 0.05 mM KCl, 18.0 μM MnSO_4 , 12.0 μM H_3BO_3 , 1.5 μM ZnSO_4 , 0.6 μM CuSO_4 , 4.2 μM MoO_3 . In order to obtain a nearly neutral pH, 1 ml conc. H_2SO_4 per liter nutrient solution was added. N in the upper

section (0-10 cm) was labeled with 10% ^{15}N -enriched $\text{Ca}(\text{NO}_3)_2$ (10.6 atom% ^{15}N) (Isotec Inc., Miamisburg, Ohio, USA), so that the contribution of nitrogen taken up from this section to the total nitrogen content of the plant tops could be determined.

4.3.2 Experimental treatments

Three temperature levels (15/11°C, 17/13°C, and 19/15°C day/night) were applied to the topsoil, combined with a uniform temperature in the subsoil (15.5°C), thus, giving a warm layer of soil on a cooler layer, a cool layer on a warmer layer, and a homogeneous temperature treatment. Under field conditions, daily fluctuations in temperature are much smaller at greater soil depths compared with the topsoil; thus, the temperature of the lower soil compartment was kept constant. The temperatures of the root zone were selected to coincide with the average soil temperature from mid-April to early June in the Swiss midlands. The differences in the temperature of the topsoil were based on typical differences in the temperature of the topsoil between conventional and no-tillage systems.

To induce soil mechanical resistance to root penetration, moist substrate was packed in the upper section of the tubes at three average bulk densities (1.15, 1.30, and 1.45 Mg m^{-3}). The bulk density of the substrate in the lower section of the tube was 1.30 Mg m^{-3} . Thus, bi-layered columns consisting of either a layer with low bulk density on top of a layer with a higher bulk density, or vice versa, and homogeneously packed columns were obtained. Substrate in the bottom sections was packed using a wood pestle in 10-cm increments to achieve homogeneous bulk density over the whole depth. After each addition of substrate, the surface was scratched before more substrate was added to prevent the formation of a smeared layer. The choice of bulk density and moisture content represented a compromise between a range of penetration resistance sufficient to impede but not to halt root elongation, with sufficient moisture for rapid root elongation, whilst maintaining sufficient porosity, well in excess of the 10% aeration assumed to be acceptable for root growth and respiration (Grable and Siemer, 1968). The initial air-filled porosity was between 20 and 27%, depending on the bulk density treatments.

A fertilization treatment was included by applying two concentrations of P in the upper layer (0.031 and 0.310 g P l^{-1} nutrient solution). Thus, a P-enriched seed zone was created. The ratio between high and low concentrations of P was selected to match the ratio in the field between the zone enriched by a starter fertilizer and the

bulk soil (James and Hurst, 1995). In the bottom section, there was 0.031 g P per L nutrient solution.

To reduce variability between replicate seedlings, maize seeds (*Zea mays* L. cv. Granat) were selected by shape and weight; only seeds with a shape typical of the cultivar and with a mass within one standard deviation of the mean (225 to 270 mg) were used. The seeds, treated with the systemic insecticide Gaucho® (Bayer AG, Zurich, Switzerland), were pregerminated on moist vermiculite in the dark at 15°C for two to three days. Seeds with a radicle 0.5 to 1 cm long were placed in a 2-cm deep depression of 1 cm diameter, made in the center of the top soil layer, tapering for 1 cm at the bottom of the depression, where the radicle was placed. The seed was then covered with loose substrate and the surface of the columns was capped with the Plexiglas container described above.

Two harvests were made: the first one at the two-leaf growth stage (fully expanded leaves), corresponding approximately to the transition from hetero- to autotrophic growth (Cooper and MacDonald, 1970), and the second at the three-leaf stage, when the first roots reached the bottom of the cylinder. These growth stages correspond to the V2 and V3 stages of development, respectively, as defined by Ritchie et al. (1996). Within a temperature treatment, the harvest was made when 50% of the plants had reached the desired stage. The plants that grew until the V3 growth stage were irrigated with 40 ml of deionized water at the V2 growth stage.

4.3.3 Measurements

The shoots were cut at ground level, and the fresh weight was determined. The leaf blades of the fully expanded leaves and the visible part of the leaf blade of partially expanded leaves were cut, the fresh weight was determined, and the area was measured with a leaf area meter (LI-COR 3100, Lincoln, NE, USA).

The two fractions of shoot material, i.e., stem and leaves, were oven-dried at 65°C for 48 h, their dry weights determined and, after pooling, ground sequentially in a sample mill (Cyclotec 1093, Tecator AB, Höganäs, Sweden) and a ball mill (Type MM2, Retsch, Arlesheim, Switzerland) to a very fine powder. After redrying, 5 mg of plant material were put into tin caps (0.04 ml, Lüdi AG, Flawil, Switzerland) and analyzed for ¹⁵N by an Integra continuous flow mass spectrometer (Scientific Europa, Cambridge, UK) at the Stable Isotope Facility of the University of California, Davis, USA. The shoot P concentration was determined after dry ashing 50 mg of plant

material at 550°C for 6 h and then dissolving the ash in 1 l HCl 20% kg⁻¹ dry matter. Phosphorus in the solution was measured by colorimetry.

The roots of the upper and lower tube sections were washed separately under pressurized tap water and the seed was carefully removed. The roots were stained with fuchsin dye (Pararosaniline P-1528, Sigma Chemical Co., St Louis, MO, USA) for at least 12h at 4°C, rinsed under running tap water, suspended in a thin layer of water, and evenly distributed on a glass tray, which was placed on a scanner to obtain 8-bit grayscale images (resolution 600 by 600 dpi). Because a root must be at least three pixels (dots) wide to be detected by the used image-analysis program (see below), the theoretical lower size limit of resolution was 127 µm, which is three times the pixel size of the scanner (42.33 µm at a resolution of 600 dpi).

The scanned-root images were analyzed to determine the length and diameter of the root objects using the computer program ROOT DETECTOR (Walter and Bürgi, 1996). The program is based on an algorithm for the segmentation and local description of elongated, symmetric line-like structures developed by Koller et al. (1995). The length and the mean diameter are computed separately for each measured root segment. Thus, the total measured root length can be sorted into user-defined diameter classes, which yields the length per diameter-class distribution (LDD) of the roots. In this study, the following diameter classes were used: 0 – 200, 200 – 400, 400 – 800, 800 – 1600, and 1600 – 3200 µm. After scanning, all root fractions were dried at 65°C for 48 h and the dry weight of each fraction was determined.

4.3.4 Calculations and statistics

Mean absolute growth rates (AGR) for the dry weights of the shoot and the root, for leaf area and for root length were calculated by dividing the values obtained at harvest by the number of days after sowing (Hunt, 1982).

The relative contribution of N from the upper root zone to the total shoot N (%N_{top}), a yield-independent parameter, was calculated as:

$$\%N_{top} = \frac{\text{atom\% } ^{15}\text{N-excess in shoot material}}{\text{atom\% } ^{15}\text{N-excess in the nutrient solution of the upper root zone}} \cdot 100 \quad [1]$$

where atom% ¹⁵N-excess is the atom% ¹⁵N in excess of natural abundance (=0.3663%). The atom% ¹⁵N-excess in the nutrient solution of the upper root zone was 1.0234%.

The influx of P (or net translocation rate; Engels and Marschner, 1992) was calculated according to the following formula (Williams, 1948):

$$In = \frac{U_2 - U_1}{t_2 - t_1} \cdot \frac{\ln(RSA_2 / RSA_1)}{RSA_2 - RSA_1} \cdot 10^6 \quad [2]$$

where In = P influx ($\text{mg m}^{-2} \text{ d}^{-1}$), U = P content of the shoot (mg), RSA = root surface area (mm^2), t = time (d), and the indices 1 and 2 refer to the first (two-leaf stage) and second (three-leaf stage) harvests.

Shoot demand per unit root was computed according to Engels and Marschner (1992) using the same formula as for P influx (Eq. [2]), whereby U was replaced by the shoot fresh weight at sampling times (t) 2 and 1, respectively. Shoot demand per unit root is the amount of shoot growth (shoot weight increment per unit of time) that has to be supplied with nutrients by a unit of root.

The P fertilizer utilization efficiency (PFUE) ratio was calculated according to Finck (1982) as the difference in P uptake of the shoot between the two P treatments, divided by the difference in the application rate of P between the two P treatments.

The experimental design was a split-split-plot with three replications and one plant per treatment. The structure of the experiment and the treatments are given in Table 4.1. All results were subjected to an analysis of variance and the means separated using the Fisher's protected LSD test. Unless otherwise specified, the level of significance was $\alpha = 0.05$.

Table 4.1. Experimental design and treatments.

ANOVA design	Factors	Levels		
		Code	Topsoil	Subsoil
Main plot	Soil temperature ^a (°C)	13.5/15.5	13.5	15.5
		15.5/15.5	15.5	15.5
		17.5/15.5	17.5	15.5
Subplot	Stage of growth at harvest		2-leaf	
			3-leaf	
Sub-subplot	Soil bulk density (Mg m^{-3})	1.15/1.30	1.15	1.30
		1.30/1.30	1.30	1.30
		1.45/1.30	1.45	1.30
Sub-subplot	P concentration in soil solution (g l^{-1})	P_{low}/P_{low}	0.031	0.031
		P_{high}/P_{low}	0.310	0.031

^a Daily mean temperatures

4.4 RESULTS

Significant interactions were found only between the factors P on the one hand and bulk density or temperature on the other but not between temperature and bulk density for any of the variables measured. Therefore, the data are presented as two-way combinations of P with bulk density or temperature, averaged over the levels of the other factor.

4.4.1 Effect of soil bulk density

The shoot dry weight (SDW) and the leaf area (LA) were limited first by the bulk density of the topsoil and second by the level of P in the topsoil (Table 4.2 and Fig. 4.1). The effect of the former was highly significant at both harvests, whereas the effect of the latter was significant at the three-leaf stage only. Earlier, the seed reserves contributed to a large extent to the P supply of the seedlings, because the fraction of the total seed P used by the seedling increased from 75 to 90% on average from the two- to the three-leaf stage (data not shown). At the three-leaf stage, SDW and LA were equally high at the two lower bulk densities of the topsoil (1.15 and 1.30 Mg m^{-3}) but only with P-enriched seed zone. At low P, shoot growth tended to decrease linearly with increasing strength of the topsoil. At the highest bulk density (1.45 Mg m^{-3}), SDW and LA were very small, independent of the P treatment. This lower growth rate was associated with a significantly higher content of P in the shoot dry matter (Table 4.3), indicating that the reduced growth was probably due not only to a limited P supply. In general, the shoot P content was related to the level of P in the soil and to the growth stage but was hardly related to the bulk density of the topsoil.

Table 4.2. Dry weight of the shoot (SDW) and all roots (RDW), fraction of RDW (TopW) and of root length (TopL) in the topsoil, fraction of shoot N taken up from the topsoil (%N_{top}), and root area:leaf area ratio (RA:LA) as a function of bulk density (BD) and P content of the topsoil at the two- and the three-leaf stage of maize. Values are means ±SE.

Bulk density (Mg m ⁻³)		P		SDW (mg)	RDW (mg)	TopW (%)	TopL (%)	%N _{top} (%)	RA:LA (m ² m ⁻²)
Topsoil	Subsoil	Topsoil	Subsoil						
<i>2-leaf stage</i>									
1.15	1.30	P _{low} ^a	P _{low}	223.4 ±16.3	104.9 ±12.9	62	67	70 ±2.7	0.64 ±0.05
1.15	1.30	P _{high}	P _{low}	283.3 ±16.3	115.6 ±12.9	76	84	75 ±1.7	0.65 ±0.05
Mean				253.4 ±11.5 a ^b	110.3 ±9.1 a	69	76	73 ±1.6	0.65 ±0.04 a
1.30	1.30	P _{low}	P _{low}	226.5 ±17.7	108.4 ±14.1	70	67	71 ±2.7	0.54 ±0.06
1.30	1.30	P _{high}	P _{low}	287.0 ±16.3	127.3 ±14.1	78	76	74 ±3.1	0.56 ±0.05
Mean				256.8 ±12.0 a	117.9 ±9.9 a	74	72	73 ±1.6	0.55 ±0.04
1.45	1.30	P _{low}	P _{low}	190.7 ±16.3	79.8 ±12.9	95	96	71 ±1.7	0.30 ±0.06
1.30	1.30	P _{high}	P _{low}	203.1 ±16.3	95.0 ±12.9	100	100	73 ±2.1	0.35 ±0.05
Mean				196.9 ±11.5 b	87.4 ±9.1 b	98	98	72 ±1.6	0.33 ±0.04 c
<i>3-leaf stage</i>									
1.15	1.30	P _{low}	P _{low}	545.0 ±47.7 b	318.6 ±24.3 b	44	40	46 ±1.8 ab	1.25 ±0.13
1.30	1.30	P _{high}	P _{low}	708.4 ±44.4 c	364.9 ±22.6 b	51	45	46 ±2.4 ab	0.95 ±0.12
Mean				626.7 ±32.5	341.7 ±16.5	48	43	46 ±2.3	1.10 ±0.09 a
1.30	1.30	P _{low}	P _{low}	424.0 ±44.4 ab	198.2 ±22.6 a	54	38	52 ±3.7 b	0.79 ±0.12
1.30	1.30	P _{high}	P _{low}	713.2 ±44.4 c	314.5 ±25.9 b	47	30	38 ±2.7 a	0.81 ±0.12
Mean				568.6 ±31.4	256.3 ±17.3	50	34	46 ±2.3	0.80 ±0.09
1.45	1.30	P _{low}	P _{low}	369.7 ±40.8 a	185.5 ±20.8 a	85	88	73 ±3.4 c	0.29 ±0.11
1.30	1.30	P _{high}	P _{low}	406.7 ±40.8 a	190.3 ±20.8 a	93	81	77 ±1.9 c	0.42 ±0.11
Mean				388.2 ±28.9	187.9 ±14.7	89	85	75 ±2.1	0.36 ±0.08 c

ANOVA^c

<i>2-leaf stage</i>				
BD ^a		***	*	NS
P		**	†	NS
BD x P		NS	NS	NS
<i>3-leaf stage</i>				
BD		***	***	***
P		***	**	NS
BD x P		**	†	NS

^a As described in Table 4.1.^b Means followed by the same letter at a given stage of growth are not significantly different at α=0.05 according to the Fisher's protected LSD test.^c †, *, **, *** are significant at the α = 0.10, 0.05, 0.01, and 0.001 levels, respectively; NS is not significant.

Table 4.3. Phosphorus content (g kg^{-1} dry wt) in the shoot dry matter as a function of the P content, the bulk density (BD), and the temperature (Temp) of the topsoil at the two- and the three-leaf stage of maize. Values are means \pm SE.

P	Soil bulk density (topsoil/subsoil) (Mg m^{-3})			Soil temperature (topsoil/subsoil) ($^{\circ}\text{C}$)			
	1.15/1.30	1.30/1.30	1.45/1.30	13.5/15.5	15.5/15.5	17.5/15.5	Mean
	<u>2-leaf stage</u>						
P_{low}^a	1.45 \pm 0.14	1.51 \pm 0.16	1.75 \pm 0.13	1.27 \pm 0.09 c	1.50 \pm 0.17 a	1.70 \pm 0.16 a	1.57 \pm 0.06
P_{high}	3.88 \pm 0.13	3.75 \pm 0.13	4.12 \pm 0.13	3.31 \pm 0.18 d	3.86 \pm 0.21 b	4.37 \pm 0.13 e	3.21 \pm 0.06
Mean	2.66 \pm 0.09 a^b	2.63 \pm 0.10 a	2.94 \pm 0.09 b	2.28 \pm 0.09	2.82 \pm 0.11	3.12 \pm 0.10	
	<u>3-leaf stage</u>						
P_{low}	0.95 \pm 0.17 a	1.05 \pm 0.17 a	1.05 \pm 0.16 a	1.07 \pm 0.08	1.04 \pm 0.03	1.01 \pm 0.06	1.08 \pm 0.07
P_{high}	2.13 \pm 0.17 b	2.31 \pm 0.16 b	2.98 \pm 0.20 c	2.54 \pm 0.23	2.76 \pm 0.28	2.10 \pm 0.17	1.96 \pm 0.07
Mean	1.54 \pm 0.12	1.68 \pm 0.12	2.01 \pm 0.13	1.80 \pm 0.11	1.87 \pm 0.12	1.57 \pm 0.13	
ANOVA ^c	2-leaf stage	3-leaf stage					
Temp ^a	NS	NS					
BD	†	*					
P	***	***					
Temp x BD	NS	NS					
Temp x P	*	NS					
BD x P	NS	*					
Temp x BD x P	NS	NS					

^a As described in Table 4.1.

^b Means followed by the same letter at a given stage of growth are not significantly different at $\alpha=0.05$ according to the Fisher's protected LSD test.

^c †, *, **, *** Significant at the $\alpha = 0.10, 0.05, 0.01, \text{ and } 0.001$ levels, respectively; NS is not significant.

The total root length was strongly affected by the bulk density of the topsoil but not by the soil P status (Fig. 4.1). The relationship between root length and soil bulk density was nearly linear. The reduction of root growth occurred both in the topsoil and in the subsoil, being more pronounced in the latter, even though the bulk density of the subsoils was the same.

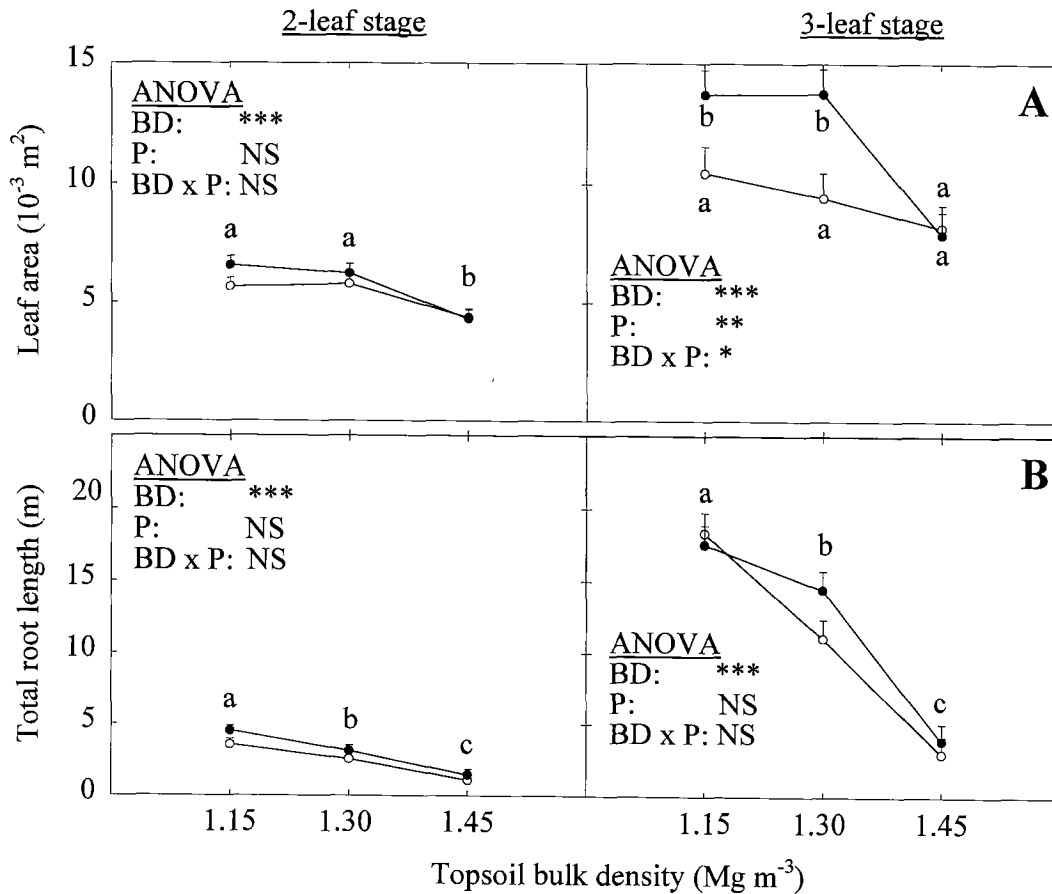


Fig. 4.1. Leaf area (A) and total root length (B) per plant as a function of bulk density and P content of the topsoil at the two- and the three-leaf stage of maize.

● high P; ○ low P. Treatments followed by the same letter are not significantly different at $\alpha = 0.05$. Vertical bars are standard errors. ANOVA: *, **, *** are significant at the $\alpha = 0.05, 0.01, \text{ and } 0.001$ levels, respectively; NS is not significant.

The root:shoot ratio was affected by soil strength. At the three-leaf stage, the root area:leaf area ratio, i.e., the ratio between the areas of nutrient and water absorption and carbon assimilation, decreased with increasing resistance of the upper soil layer. Hence, root growth was inhibited to a larger extent than shoot growth. The relative decrease in the root:shoot ratio was stronger at low P than at high P and more pronounced from 1.30 to 1.45 Mg m⁻³ than from 1.15 to 1.30 Mg m⁻³.

The vertical distribution of RDW was similar to that of root length at the two-leaf stage and differed slightly at the three-leaf stage, with a higher fraction of RDW than root length in the upper layer (Table 4.2) due to the increasing contribution of the first adventitious roots to the root system. The proportion of roots in the subsoil increased from the two- to the three-leaf stage. In the treatment with a topsoil bulk density of 1.45 Mg m⁻³, the roots did not reach the lower soil layer at the two-leaf stage, and at the three-leaf stage, root growth in the subsoil was still poor. A higher level of P in the topsoil generally resulted in longer roots and a higher RDW, both in the topsoil and in the subsoil. In stronger topsoils (1.30 and 1.45 Mg m⁻³), this led to a larger fraction of the root length in the subsoil, and, as a consequence, a significantly lower %N_{top} (at 1.30 Mg m⁻³), i.e., a greater contribution of the subsoil to the N supply of the shoot (Table 4.2). In the other treatments, P had no effect on %N_{top}. At the two-leaf stage, more than 70% of N came from the topsoil, independent of the bulk density of the topsoil, whereas at the three-leaf stage, there was a significant effect of bulk density. In a strong topsoil (1.45 Mg m⁻³), a larger fraction of N was taken up from the upper layer than in case of looser topsoils (75 and < 50%, respectively). %N_{top} was related to the portion of root length in the topsoil and not to the absolute root length in the topsoil.

There was a significant effect of the interaction between the bulk density of the topsoil and the P status on the P influx per unit root area (Fig. 4.2). At low P, the influx rate was uniformly low at all bulk densities, whereas, at high P, it increased sharply with increasing bulk density of the topsoil. The demand of the shoot per unit root showed an opposite tendency; it was independent of the bulk density at high P but not at low P, where it was markedly higher at 1.45 Mg m⁻³ compared with the lower topsoil densities.

Root diameters generally increased with bulk density (Fig. 4.3). At 1.45 Mg m⁻³, the fraction of root length in the topsoil was significantly lower in the diameter classes between 200 and 800 µm and higher in the diameter class from 1600 to 3200 µm at

the two-leaf stage. The LDD was similar at the two- and the three-leaf stage except for a shift towards finer roots at the three-leaf stage due to the increase in differentiation of the root system with plant age. A similar situation was found in the subsoil, although the bulk density of this layer was the same in all treatments. P had no effect on the root length per diameter distribution.

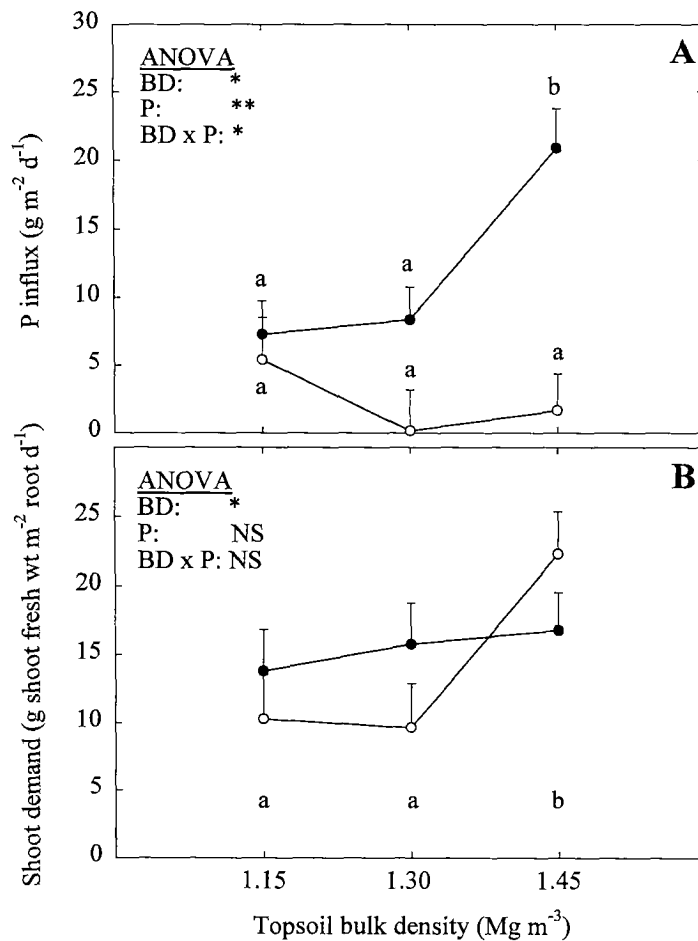


Fig. 4.2. Phosphorus influx (A) and shoot demand (B) per unit root surface area from the two- to the three-leaf stage of maize as a function of bulk density and P content of the topsoil. Phosphorus influx was calculated according to Williams (1948).

● high P; ○ low P. Treatments followed by the same letter are not significantly different at $\alpha = 0.05$. Vertical bars are standard errors. ANOVA: *, ** are significant at $\alpha = 0.05$ and 0.01, respectively; NS is not significant.

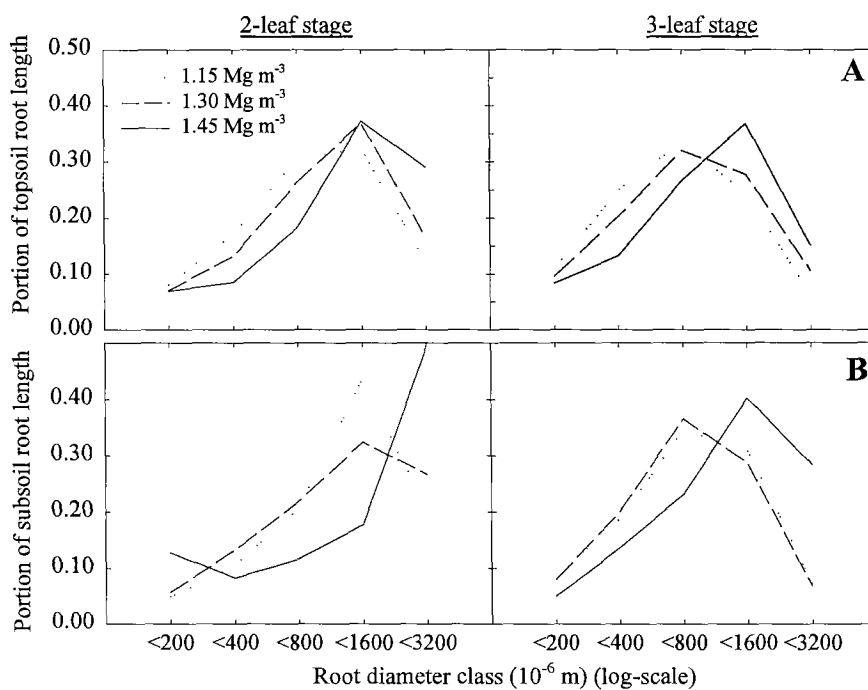


Fig. 4.3. Distribution of root length by diameter classes in the topsoil (0-10 cm) (A) and in the subsoil (10-50 cm) (B) as a function of bulk density of the topsoil at the two- and the three-leaf stage of maize, averaged over temperature and P treatments.

4.4.2 Effect of soil temperature

The absolute growth rates of LA and SDW increased significantly with increasing temperature and P in the topsoil (Table 4.4 and Fig. 4.4). Although the effects of these two factors were additive, the response to the temperature of the topsoil seemed to depend on P; at 13.5°C of the topsoil in the low P treatment, the growth rates were unexpectedly high. At a high level of P in the topsoil, the relationship between the growth rate of the two parameters and the topsoil temperature was linear. The P content in the shoot increased significantly with increasing topsoil P at both growth stages and with increasing topsoil temperature at the two-leaf but not at the three-leaf stage. There was a decrease in the shoot P content from the two- to the three-leaf stage (Table 4.3).

Table 4.4. Absolute growth rates (AGR) for the dry weights of the shoot and of the roots from planting to the three-leaf growth stage of maize as a function of temperature (Temp) and P content of the topsoil. Values are means \pm SE.

Temperature (°C)		P		AGR (mg d ⁻¹)	
Topsoil	Subsoil	Topsoil	Subsoil	Shoot	Roots
13.5	15.5	P _{low} ^a	P _{low}	11.7 \pm 1.2	5.9 \pm 0.6 a
13.5	15.5	P _{high}	P _{low}	14.6 \pm 1.3	5.8 \pm 0.7 a
Mean				13.2 \pm 0.9 a ^b	5.8 \pm 0.5
15.5	15.5	P _{low}	P _{low}	11.1 \pm 1.4	5.8 \pm 0.7 a
15.5	15.5	P _{high}	P _{low}	17.2 \pm 1.3	8.1 \pm 0.7 b
Mean				14.2 \pm 1.0 a	7.0 \pm 0.5
17.5	15.5	P _{low}	P _{low}	15.0 \pm 1.3	8.4 \pm 0.7 b
17.5	15.5	P _{high}	P _{low}	19.6 \pm 1.2	11.0 \pm 0.7 c
Mean				17.3 \pm 0.9 b	9.7 \pm 0.5
ANOVA ^c					
Temp				*	*
P				***	**
Temp x P				NS	†

^a As described in Table 4.1.

^b Means followed by the same letter at a given stage of growth are not significantly different at $\alpha=0.05$ according to the Fisher's protected LSD test.

^c †, *, **, *** are significant at the $\alpha = 0.10, 0.05, 0.01,$ and 0.001 levels, respectively; NS is not significant.

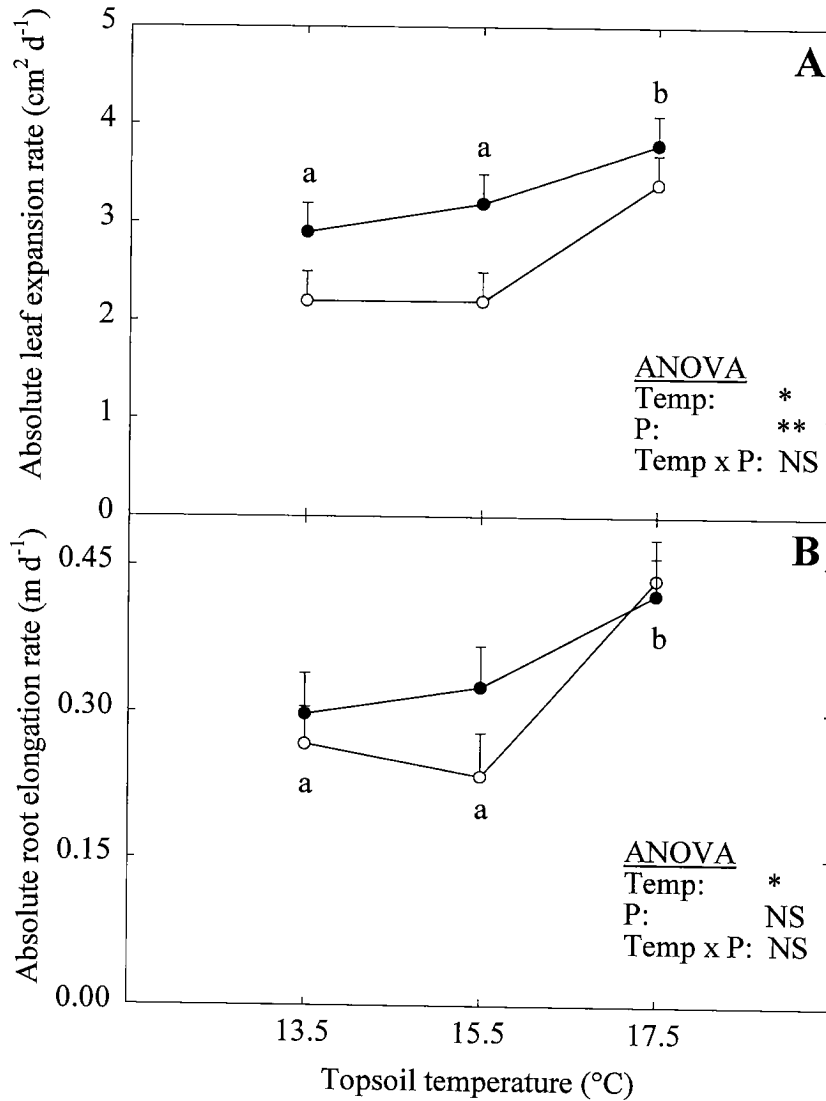


Fig. 4.4. Absolute rates of leaf expansion (A) and root elongation (B) from planting to the three-leaf stage of maize as a function of temperature and P content of the topsoil.

● high P; ○ low P. Treatments followed by the same letter are not significantly different at $\alpha = 0.05$. Vertical bars are standard errors. ANOVA: *, ** are significant at the $\alpha = 0.05$ and 0.01 levels, respectively; NS is not significant.

The effect of the temperature and the P status of the topsoil on the growth of the roots, in terms of length (Fig. 4.4) and mass (Table 4.4), was similar to that on the shoot, except that the difference among the P levels was smaller. Furthermore, the interaction ‘temperature x P’ on the root growth rate was weakly significant. The increase in the growth rate from 15.5 to 17.5°C was more pronounced at low P than at high P, and the relative difference in the growth rates between the two P levels was higher at 15.5°C than at 17.5°C. This interaction was found for the growth rate of the shoot as well. The temperature of the topsoil did not have a significant effect on the root area:leaf area ratio (Table 4.5) or on the P influx or shoot demand per unit root (Fig. 4.5).

Table 4.5. Fraction of root dry weight (TopW) and root length (TopL) in the topsoil (Top), fraction of shoot N taken up from the topsoil (%N_{top}), and root area:leaf area ratio (RA:LA) as a function of temperature and P content of the topsoil at the two- and the three-leaf stage of maize. Values are means ±SE.

Temperature (°C)		P		TopW (%)	TopL (%)	%N _{top} (%)	RA:LA (m ² m ⁻²)
Topsoil	Subsoil	Topsoil	Subsoil				
<u>2-leaf stage</u>							
13.5	15.5	P _{low} ^a	P _{low}	68	71	71 ±1.9	0.57 ±0.05
13.5	15.5	P _{high}	P _{low}	84	88	77 ±1.7	0.50 ±0.05
Mean				76	80	74 ±1.6	0.54 ±0.04
15.5	15.5	P _{low}	P _{low}	75	70	74 ±2.3	0.45 ±0.06
15.5	15.5	P _{high}	P _{low}	79	84	72 ±2.2	0.53 ±0.05
Mean				77	77	73 ±1.6	0.49 ±0.04
17.5	15.5	P _{low}	P _{low}	80	83	68 ±2.4	0.46 ±0.06
17.5	15.5	P _{high}	P _{low}	87	92	74 ±2.8	0.53 ±0.05
Mean				84	88	71 ±1.6	0.50 ±0.04
<u>3-leaf stage</u>							
13.5	15.5	P _{low}	P _{low}	53	60	53 ±5.3	0.80 ±0.11
13.5	15.5	P _{high}	P _{low}	65	54	58 ±6.2	0.63 ±0.12
Mean				59	57	55 ±2.2	0.71 ±0.08
15.5	15.5	P _{low}	P _{low}	62	63	64 ±5.6	0.76 ±0.13
15.5	15.5	P _{high}	P _{low}	64	63	56 ±6.9	0.76 ±0.12
Mean				63	63	59 ±2.3	0.76 ±0.09
17.5	15.5	P _{low}	P _{low}	59	56	59 ±5.1	0.77 ±0.12
17.5	15.5	P _{high}	P _{low}	51	45	50 ±6.5	0.79 ±0.11
Mean				54	51	54 ±2.2	0.78 ±0.08

^a As described in Table 4.1.

The vertical distribution of root length was hardly affected by the temperature of the topsoil (Table 4.5). At 17.5°C, the portion of the root length in the upper soil layer was highest at the two-leaf stage, and was lowest at the three-leaf stage. At the latter stage, more than 50 percent of the root length was found in the subsoil at high topsoil P and slightly less at low topsoil P. Although the effect of temperature on %N_{top} was not significant, the contribution of the subsoil to shoot N tended to increase at high temperature and high P status of the topsoil.

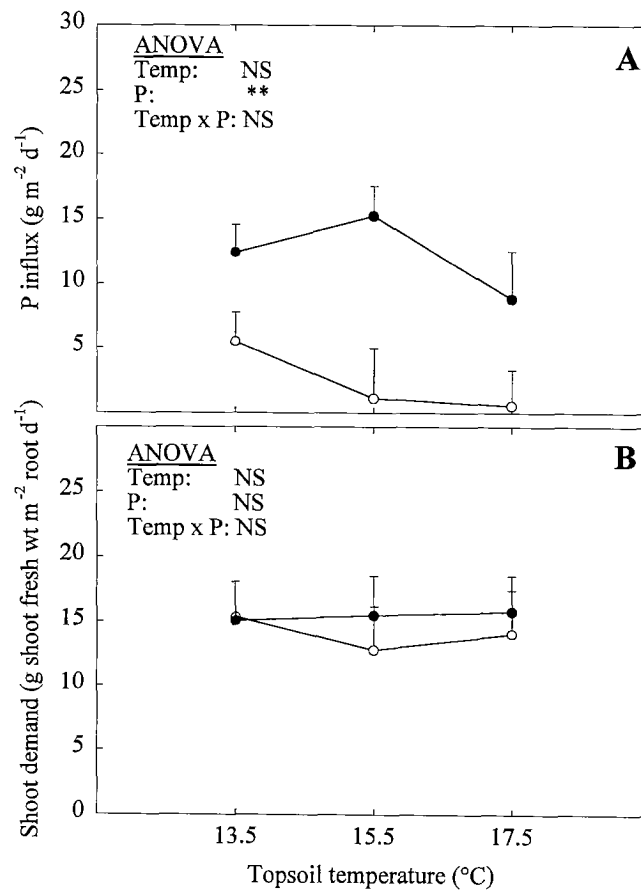


Fig. 4.5. Phosphorus influx (A) and shoot demand (B) per unit root surface area from the two- to the three-leaf stage of maize as a function of temperature and P content of the topsoil. Phosphorus influx was calculated according to Williams (1948).

● high P; ○ low P. Vertical bars are standard errors. ANOVA: *, **, *** are significant at $\alpha = 0.05, 0.01, \text{ and } 0.001$, respectively; NS is not significant.

The temperature of the topsoil did not have a significant effect on the distribution of root length by diameter classes, and there was no interaction with soil P (Fig. 4.6). The fraction of very fine roots (with a diameter below 200 μm) in the topsoil was approximately 10% at all soil temperatures and slightly lower in the subsoil except for the warm treatment (17.5 $^{\circ}\text{C}$ topsoil temperature). In general, there was a tendency towards finer roots in the upper and lower soil layers with increasing topsoil temperature.

The temperature of the topsoil did not appear to affect the influx of P or the shoot demand per unit root area (Fig. 4.5). This is in agreement with the stability of the root:shoot ratio as related to soil temperature (Table 4.5).

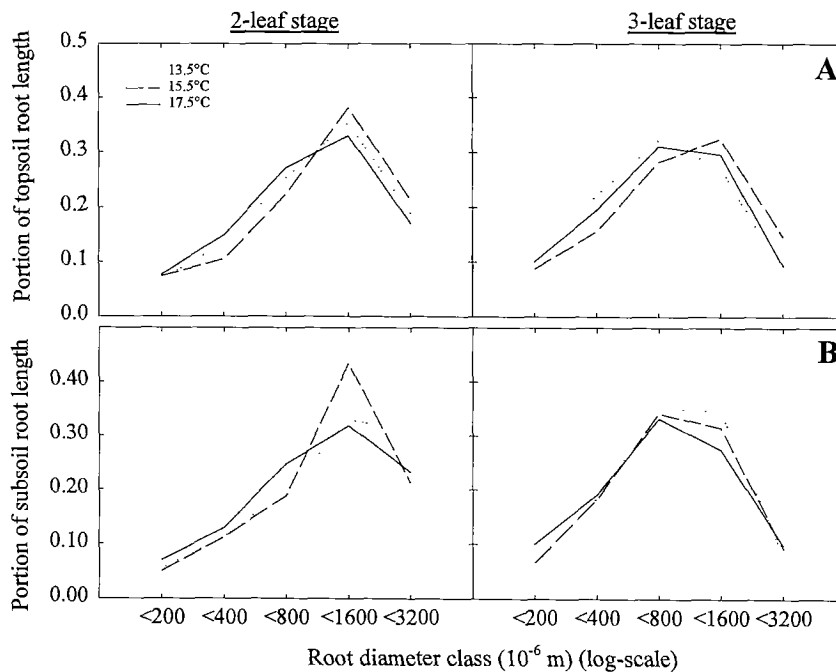


Fig. 4.6. Distribution of root length by diameter classes in the topsoil (0-10 cm) (A) and in the subsoil (10-50 cm) (B) as a function of temperature of the topsoil at the two- and the three-leaf stage of maize, averaged over temperature and bulk density treatments.

4.5 DISCUSSION

The lack of interaction between topsoil temperature and bulk density on the parameters measured here contrasts with the findings of other investigators (Abbas Al-Ani and Hay, 1983; Bengough et al., 1994). However, Engels and Marschner (1992) found similar patterns of shoot and root growth of plants grown in nutrient solution and in soil of different temperature in the root zone, indicating an effect of soil temperature that is independent of mechanical impedance to root growth.

The bulk density of the topsoil was the main limiting factor for shoot and root growth. The roots were shorter and the root diameter greater with increasing bulk density of the topsoil, as reported by most investigators (Bennie, 1996). Total root length and total root dry weight decreased linearly with increasing topsoil bulk density and root distribution with depth changed dramatically. The presence of a strong surface layer (1.45 Mg m^{-3}) resulted in a concentration of roots near the soil surface; only a small fraction of the roots reached lower layers. Thus, the plants were able to extract water and nutrients from a limited soil volume, as shown by the high fraction of N taken up from the topsoil (75% at the three-leaf stage) and by a decrease in P fertilizer utilization efficiency (PFUE) with increasing compaction of the topsoil (data not shown). However, a limited nutrient and/or water supply was not solely responsible for the sharp decrease in shoot growth at high topsoil strength (1.45 Mg m^{-3}) at high P, because this growth depression was associated with a significantly higher P content in the shoot dry matter. Furthermore, it has been established that a small portion of the root system can be responsible for a large part of the total water uptake by the plant (Stone et al., 1976). Hence, factors other than P and/or water uptake limited shoot growth, too. Several authors have mentioned an effect of soil resistance on shoot growth via root-derived hormonal signals (Masle and Passioura, 1987; Tardieu and Jensen, 1994).

Root length and root dry weight in the subsoil were affected by the strength of the topsoil as well. This might be partly due to a persistent effect of the mechanical impedance of the upper soil layer on root growth in the lower layer, as described by Bengough et al. (1997). However, the main cause was probably an hindered vertical extension of the roots into the subsoil due to compaction of the topsoil at the early seedling stage.

The diameter of the roots in the subsoil varied with the bulk density of the topsoil, although the bulk density of the subsoil was the same in all treatments. This means that not only was the mechanical impedance of the surrounding soil decisive for the root diameter, but also that of the previously encountered soil layer. In an experiment with peas in a layered soil of different penetration resistance, Bengough and Young (1993) found that the root diameter in the bottom section containing loose soil was the same in all treatments. This difference might be due to the different root systems of maize and peas. The higher average root diameter at high strength of the topsoil might be due to a lower degree of root branching and/or to thicker individual roots. The exact cause was not determined here, and conflicting results are presented in the literature (Logsdon et al., 1987; Seiffert et al., 1995). At a given root length density, plants with thicker roots are at a disadvantage as far as acquisition of water and nutrients is concerned compared with plants with thinner roots, because the ratio of the volumes of the rhizosphere and of the roots is lower in thicker than in thinner roots. This is especially important in relatively dry soil and for immobile nutrients such as P.

In this experiment, P was also a limiting factor for shoot growth, but to a lesser degree than bulk density. Thus, only in treatments with a looser topsoil (1.15 and 1.30 Mg m⁻³) were plants able to take advantage of the P-enriched seed zone, as shown by the marked increase in shoot dry weight and leaf area at high P. In general, the length, diameter, and vertical distribution of roots were influenced positively but to a limited extent by the level of P in the topsoil. Interestingly, not only root growth in the upper one, but also in the lower soil layer was stimulated at high levels of P in the topsoil, especially with strong surface layers.

The surface area of the roots per unit of leaf area, corresponding to the ratio between water and nutrient absorption and carbon assimilation area, decreased with higher bulk density of the topsoil, especially at low P, resulting in a high shoot demand per unit root surface area. On the other hand, the P supply from the soil at low P was so limiting that an effect of bulk density on the P influx was not found, contrary to the high P treatment, where the P influx was significantly higher, probably because of a better contact between soil and roots (Veen et al., 1992). Therefore, a disproportion of shoot demand per unit root and P translocation rate from the root to the shoot (P influx) occurred at low P, leading to the most severe decrease (40%) in shoot P concentration from the two- to the three-leaf stage.

The highly significant differences in shoot P concentrations between the two levels of soil P, already at the two-leaf stage, suggest that the growth substrate rather than the seed was the major source of P for the shoots. Translocation of soil-derived P to the shoot was, therefore, already important before the two-leaf stage in this study. This is in contradiction to previous results (Barry and Miller, 1989) but can be explained by the low P content of the seeds in this study (on average 2 mg g⁻¹ seed dry weight) (O'Dell et al., 1972). Moreover, the low P concentrations in plants grown at low P in the topsoil suggest that nutrient availability limited plant growth in this case.

In agreement with published results (Walker, 1969; Barlow et al., 1976), both shoot and root growth were reduced by decreasing temperature of the topsoil, despite uniform air temperatures. The tendency for roots to be thinner as temperature increased also agrees with previous studies (Stamp, 1983; Cutforth et al., 1986). However, contrary to the literature (Engels and Marschner, 1990), no change in the shoot:root ratio was observed, probably as a result of the narrow range of tested soil temperatures (Walker, 1969).

In general, shoot growth at suboptimal root temperature can be limited both by a direct temperature effect on the shoot meristem and by a reduced nutrient supply through the roots (Engels and Marschner, 1990). According to Walker (1969) who reported statistically different dry weights of roots and shoots of maize seedlings when soil temperatures differed by 1 or 2°C, a direct effect of temperature most certainly occurred here.

A temperature-induced reduction in the nutrient supply through the roots can be due to: (i) effects on the uptake efficiency per unit root length (Bravo and Uribe, 1981; Mackay and Barber, 1984), (ii) effects on the growth, morphology, and/or distribution of the roots (Engels and Marschner, 1992), and (iii) effects on the supply of nutrients by the soil (Marschner, 1995). The latter was probably not the case at the temperatures tested here and, thus, will not be discussed. As far as (i) is concerned, temperature did not seem to affect the P influx in this study. Moreover, temperature did not appear to affect the demand of the shoot per unit root, indicating that the shoot and the roots were similarly influenced by the temperature of the topsoil. This was also shown by the fact that the shoot:root ratio did not change with soil temperature. Engels and Marschner (1992) reported a disproportion of shoot demand per unit root and P influx in treatments where a low root-zone temperature was combined with a high shoot-base temperature but not in the treatments in which the temperature of the

root zone and shoot base was uniform as in our study. The positive effect of higher topsoil temperature on root growth (see (ii) above) resulted in a higher PFUE (data not shown) and higher P contents in the shoot dry matter at the two-leaf stage. This was probably also due to the tendency of the roots to explore the subsoil more intensively and/or to thinner roots with increasing soil temperatures. At the three-leaf stage, however, there was a tendency towards lower shoot P concentration in the warmer treatments. This is an additional confirmation that low soil temperature in a range simulating conditions in the spring does not necessarily limit growth by reducing P uptake, as concluded by Walker (1969). Engels (1993) also found a slight decrease in P concentration with increasing root temperature in 3-week-old maize, but others found the reverse (Grobbelaar, 1963) or no effect (Patterson et al., 1972). The reasons for this inconsistency are not yet clear but may be related to the different varieties of maize, rooting media, climatic conditions, and the soil temperature treatments in these studies. Furthermore, higher soil temperatures may compensate for a lower level of soil P, and vice versa, as shown by the interaction between temperature of the topsoil and the level of P in the topsoil on root growth and as suggested by Mackay and Barber (1984).

4.5.1 Conclusions

The controlled-environment system applied in our study allowed to realistically simulate vertical gradients in soil temperature, bulk density and P supply, and to study their impacts on growth and P uptake of maize seedlings. The early growth of maize seedlings was affected by the additive effects of decreased temperature and increased bulk density of the topsoil, which are typical of NT conditions. Both factors limited shoot growth by direct effects: in the case of temperature, on the activity of the shoot meristem and, in the case of bulk density, possibly via root-derived signals translocated to the shoot. Furthermore, in strong soils, a lower root:shoot ratio as well as changes in root distribution and morphology put a greater stress on the capacity of the root to absorb nutrients per unit of root. Therefore, an indirect effect of soil strength as a result of hampered nutrient supply by the roots might occur, particularly in nutrient-poor soils. However, the situation might be different in the field under NT due to biopores that enable the roots to bypass zones of high mechanical impedance (Ehlers et al., 1983). Shoot growth in NT as compared with CT is not likely to be reduced by an indirect temperature effect (i.e., by reduced nutrient supply),

particularly in rich soils, because the small differences in soil temperature between the CT and NT treatments do not lead to significant changes in the nutrient supply through the roots. These conclusions are in agreement with those of McGonigle et al. (1999) who reported that a limited supply of P was not the cause of the smaller shoot dry mass in NT. However, our study clearly demonstrates the importance of P supply through the roots for the growth of maize seedlings, already at early stages. P concentration in the shoot tissue was mainly determined by P availability in the growth substrate and P dilution by growth.

5 GENERAL DISCUSSION AND CONCLUSIONS

In the field, the temperature of the topsoil was lower and the bulk density higher in no-tillage plots compared to conventional tillage plots. At the same time, the growth rate of the shoots and roots of maize seedlings was lower under no-tillage. These results generally agree with published results (cf. Chapter 1). To meet the objectives of the present study and to test our hypotheses, the following questions had to be answered:

- i. Are changes in the physical properties of the topsoil mainly responsible for the observed plant responses to tillage intensity?
- ii. Does the response of the shoot to tillage-induced stress depend on indirect effects (via the root system) or/and on direct effects on the shoot meristem ?
- iii. Do the temperature and bulk density of the topsoil act synergistically or independently on plant growth?
- iv. Does the enrichment of the topsoil with nutrients such as P compensate for unfavorable conditions in untilled soil?
- v. Was the simulation of the physical properties of untilled soil under controlled conditions adequate?

The slow development of plants in the field (0.5 to 1 phyllochron under NT compared to CT) was attributed mainly to the direct effect of the lower temperature of the topsoil on the shoot meristem (cf. Chapter 2). This was confirmed in a growth chamber study (cf. Chapter 3) in which the rate of leaf development was found to be mainly related to the temperature of the topsoil. It was suggested that the difference in the development of the seedlings between NT and CT was mainly responsible for the difference in the growth of shoots and roots between the two tillage treatments. Thus, the strong increase in the bulk density and penetrometer resistance of the topsoil under NT could not have affected the growth of the plants in the field. This might indicate that bulk density and penetrometer resistance are poor predictors of early crop growth under NT (Cannell et al., 1994). Growth chamber studies, however, showed that the bulk density of the topsoil has a strong effect on plant growth. This discrepancy between the results of studies in the field and under controlled conditions , also

reported by Tinker (1981), was presumably due mainly to the composition of the substrate used in the growth chamber studies, in particular the lack of aggregation and biopores. Thus, the contrasting findings may indicate the importance of biopores for root growth in soils with a high bulk density. Nevertheless, the method applied in the model study under controlled conditions produced results that help in interpreting and extrapolating the field data as well as offering many experimental advantages. Chapter 4 reports that root length decreases linearly with increasing bulk density of the soil. The vertical distribution of the roots was hardly affected by an increase in the bulk density of the topsoil (1.15-1.30 Mg m⁻³), but was strongly affected by a further increase from 1.30 to 1.45 Mg m⁻³, which resulted in a concentration of the roots near the surface. Shoot growth responded similarly to high P with very little change from 1.15 to 1.30 Mg m⁻³ but a sharp decrease sharply at higher bulk density; at low P, however, shoot growth decreased linearly with increasing bulk density. This may indicate that a “mild” stress, induced by mechanical impedance to root growth, does not necessarily lead to a change in the distribution of the roots or to a decrease in shoot growth, at least in nutrient-rich soil. These results may explain some of the similarity in the vertical distribution of roots in the field in the NT and CT treatments, despite the large difference in the bulk density of the topsoil in the two tillage systems. Another explanation (Chapter 2) may be the role played by the biopores. Nevertheless, some of the reduction in root growth under NT may be due not only to the direct effect of a lower temperature of the topsoil, but also to the higher bulk density of the soil, owing to the greater sensitivity of root elongation to this soil parameter. Furthermore, the benefits of a nutrient-rich root zone for early maize growth, as suggested by the evaluation of the field data, was confirmed by the results obtained under controlled conditions. This is crucial for immobile nutrients such as P, even more pronounced in relatively dry soils, because both a lower temperature and higher bulk density of the soil lead to a smaller root system with a higher mean root diameter and, possibly, to a lower root:shoot ratio. Hence, the shoot demand per unit of volume of rooted soil will increase and, thus, a greater strain will be put on the capacity of the roots to supply nutrients and water. This strain is put on the root system under no-till conditions; it could be lessened by an increased influx of nutrients per unit root as a result of a better root-soil contact in denser soils. However, a prerequisite is a nutrient-rich root zone, which can be achieved in the field by sidebanding fertilizer at planting.

The soil temperature plays a major role in shoot growth through a direct effect on the shoot meristem on the one hand and through an indirect effect, as a result of a reduced supply of nutrients through the roots and/or the interaction of soil temperature and bulk density, on the other. Neither of these effects could be clearly demonstrated in the growth chamber experiments. This was probably due to the small differences between the soil temperature treatments. The different soil temperatures were selected to reflect conditions in the field under CT and NT. Therefore, the results of experiments under controlled conditions can be extrapolated to the field with regard to effect of temperature on the early growth of maize. Interactions between the impact of soil temperature and soil bulk density as well as indirect effects of soil temperature on shoot growth via a reduced nutrient uptake are more likely to be detected if a wide range of soil temperatures is applied (from suboptimal to supraoptimal). This was, however, beyond the scope of this study.

It can be argued that another soil physical parameter, in addition to temperature and bulk density, may have had an effect on the early growth of maize in the NT treatment in the field. As mentioned in Chapter 1, hypoxia may occur under certain conditions. The effects on roots are similar to those caused by high bulk density (Voorhees et al., 1975). Although it was not investigated in this study, the occurrence of hypoxia was improbable due to the considerable air-filled porosity of the soil in the field and of the substrate in the growth-chamber experiment (above 20%, data not shown). This is well above the 10% aeration, generally assumed to be sufficient for root growth and respiration (Grable and Siemer, 1968).

It is concluded that the lower temperature of the topsoil in spring was the main limiting factor for the early growth of maize under NT in temperate climates. However, good soil management, particularly the avoidance of soil compaction, and a sufficient supply of nutrients to maize seedlings, obtained by a local application of starter fertilization, must be ensured. Furthermore, it is necessary to develop and evaluate maize genotypes that are better adapted to unfavorable conditions in non-tilled soils.

6 REFERENCES

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