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Temporal and spatial root development of cauliflower (*Brassica oleracea* L. var. *botrytis* L.)

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Abstract

Row crops are often inefficient in utilizing soil resources. One reason for this appears to be inefficient rooting of the available soil volume. Five experiments were performed to study the temporal and spatial root development of cauliflower (cv. 'Plana'). The crop was grown with 60 cm between rows, and root development was followed in minirhizotrons placed under the crop rows, 15 cm, and 30 cm from the crop rows. Soil was sampled and analyzed for nitrate content at the final harvest and once during growth. In two of the experiments N fertilizer rate was varied and in two of the other experiments two cultivars were compared (cv. 'Plana' and 'Siria').

The rooting depth of cauliflower was found to be linearly related to temperature sum, with a growth rate of 1.02 mm day⁻¹ °C⁻¹. Depending on duration of growth this leads to rooting depths at harvest of 85–115 cm. Soil analysis showed that the cauliflower was able to utilize soil nitrogen down to at least 100 cm.

With Plana differences in root growth between row and interrow soil were only observed during early growth, but with Siria this difference was maintained until harvest. However, at harvest both cultivars had depleted row and interrow soil nitrate equally efficient. Nitrogen fertilizer did not affect overall root development significantly.

The branching frequency of actively branching roots was increased in all soil layers from about 6 to 10 branches cm⁻¹ by increasing N fertilizer additions from 130 to 290 kg N ha⁻¹. Increasing N supply increased the number of actively branching roots in the topsoil and reduced it in the subsoil.

The average growth rate of the roots was always highest in the newly rooted soil layers, but fell during time. At 74 days after planting very few roots were growing in the upper 60 cm of the soil whereas 70% of the root tips observed in the 80–100 cm soil layer were actively growing. Within each soil layer there was a large variation in growth rate of individual root tips.

Introduction

Row crops are often inefficient in utilizing soil resources, for example leaving unused nitrate nitrogen in the soil after harvest (Everaats et al., 1996; Greenwood et al., 1996). Several approaches to improve this have been tested. Changes have been made in the timing or placement of fertilizer (Everaats et al., 1996; Steingrobe and Schenk, 1994) and drip irriga-

tion has been used to ensure that the applied resources are available when and where they can be taken up by the crop. Different methods for predicting the need for water and nitrogen have also been tested, such as the placement of tensiometers in the soil to monitor soil water availability, soil sampling to analyze soil mineral nitrogen availability (Sørensen, 1993) and modelling (Greenwood et al., 1996).

All of these approaches are hampered by the lack of knowledge of the actual root development of the crop. It is important to know both the rooting depth and the horizontal distribution of the root system at

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any time to be able to predict how much of the soil resources are available to the crop. Knowledge of root distribution is also important to determine where and to which depth to place tensiometers or take soil samples to obtain meaningful results. When trying to model the crop needs and crop access to soil resources, the lack of knowledge of actual root development rates becomes a critical problem (Aguirrezabal et al., 1993; Klepper and Rickman, 1990).

It has been found that root growth varies strongly among crop species (e.g. Greenwood et al., 1982; Materechera et al., 1993; Thorup-Kristensen, 1993), and a more detailed description of the root development of many crops is needed. But also within the same crop species the actual root development depends on a number of factors such as soil compaction (Materechera et al., 1993), soil borne pests and diseases (Haverkort et al., 1994; Larkin et al., 1996), soil water content (Engels et al., 1994; Tsegaye et al., 1995), soil nutrient availability (Drew, 1975; Throup-Kristensen, 1993), and choice of cultivar (Kujira et al., 1994; Thorup-Kristensen, 1998; Wiesler and Horst, 1994).

The objective of this work was to measure horizontal and vertical growth rates of cauliflower roots to make estimates of the root distribution which can be used in crop modelling. We attempted to measure to what extent the uneven distribution of cauliflower roots within the soil volume is reflected in uneven utilization of soil mineral nitrogen. Finally we tested whether root growth rates are sensitive to fertilizer level or to choice of cultivar.

Materials and methods

Root growth of cauliflower (*Brassica oleracea* L. var. *botrytis* L.) was measured in two spring planted crops (planted around 20 April in 1993 and 1994) and three summer planted crops (planted around 20 June in 1993, 1994 and 1995). The transplants were grown in peat blocks (4×4×4 cm cubes) and planted in the field with a row distance of 60 cm and a planting distance within the rows of 50 cm.

In all experiments a randomized complete block design with three replicates was used. Each plot consisted of 12 rows with 10 plants. Two rows/plants were used as border plants, thus the area used for measurements consisted of 8 rows with 6 plants each. Two plants within each row were used for the root mea-

surements, the remaining four plants in each row were used for plant sampling or as internal border plants.

The crop was fertilized twice, at planting and again at the time when roots were observed in minirhizotrons 30 cm from the crop row, i.e. at the furthest distance from the plants. Twelve plants per plot were sampled and analyzed for dry matter production and nitrogen uptake (by combustion method, Hansen, 1989) at planting, at the time of the second fertilization, and again at the harvest of the cauliflower crop. At the same dates soil samples were taken and analyzed for ammonium-N and nitrate-N after extraction for 1 h in a 1 M KCl solution. Except for the soil sampling at planting, soil samples were taken both directly under the plants and at the maximum distance from the plants within the crop (30 cm from the rows, 25 cm from the plants within the row). The soil samples were taken in four soil layers of 25 cm down to one metre, with 9 samples combined into one bulk sample for analysis for each position in each plot.

The experiment was located at Research Centre Aarslev (10°27' E, 55°18' N), on a Typic Agrudalf soil. The upper 40 cm contains 2% organic matter, 11% clay, 14% silt, and 73% sand. The 40–100 cm layer contains 0.2% organic matter, 19% clay, 13% silt, and 67% sand. Weather data were obtained from a station sited at the research centre. Average daily air temperature at 2 m height (average of measurements made every 10 min) was used to calculate temperature sums. Temperature sums were calculated as the sum of the daily average temperatures minus a base temperature. As the best fit was obtained using a base temperature of 0 °C, this base temperature was used for all the calculations shown.

Fertilizer experiment

In the two spring plantings (April 1993 and 1994) the cultivar Plana was grown at three nitrogen fertilizer rates. The total N fertilization rate in 1993 was 130 kg N ha⁻¹ (N1), 210 kg N ha⁻¹ (N2), and 290 kg N ha⁻¹ (N3). As even the highest N fertilization in 1993 did not lead to significant N residues in the soil after harvest, the rates were increased in the next experiment, so that the levels in 1994 were 130 kg N ha⁻¹ (N1), 250 kg N ha⁻¹ (N2), and 370 kg N ha⁻¹ (N3). The fertilizer additions were split in two, at planting and immediately after the mid season soil sampling, so that the fertilization at planting was always 30 kg N ha⁻¹ higher than the amount added at mid season.

Cultivar experiment

In two of the summer plantings (June 1994 and June 1995) the cultivars Plana and Siria were compared. They were fertilized with nitrogen as the N2 treatment in the fertilizer experiment of 1994. The cultivars were chosen so that they differed in duration of growth and in leaf production, where Plana has a longer growth period and higher leaf production than Siria.

In a fifth planting (June 1993) only one treatment, Plana fertilized with 210 kg N/ha (as N2 in 1993) were grown in three replicates.

General root growth rates

One treatment (Plana grown at the N2 fertilizer level, i.e. 210 kg N ha⁻¹ in the 1993 experiments and 250 kg N ha⁻¹ in the 1994 and 1995 experiments) was included in all five experiments. The data from this treatment from all five experiments were used to make estimates of general root growth rates and effects on nitrogen depletion of the soil.

Root measurements

Directly before planting, minirhizotron glass tubes (7 cm in outer diameter and 150 cm long) were inserted into the soil (Thorup-Kristensen, 1993). The tubes were installed at six different positions relative to the cauliflower plants. There were tubes placed under the crop row, 15 cm from the crop row and in the middle of the interrow space, 30 cm from the crop rows. For each of these three positions tubes were placed either 10 cm or 25 cm behind plants in the row. The tubes were placed in the plots so that the minimum distance between two tubes was 75 cm, and there was only one tube for each crop row. The differences in position relative to the plants within the row did not show systematic effects and the results were thus combined before further calculations.

The holes for the minirhizotrons were made by drilling twice, first with a spiral auger with a diameter of 6.0 cm to remove most of the soil, and subsequently with a piston auger with a diameter of 7.4 cm. The use of a piston auger with a slightly higher diameter than the minirhizotrons was necessary to make insertion possible, as the holes shrank after drilling in the moist soil. The minirhizotrons were installed at an angle of 30° from vertical, reaching a depth of approximately 110 cm in the soil (Figure 1).

Two counting grids of 4×128 counting fields were painted on the 'upper' surface of each minirhizotron,

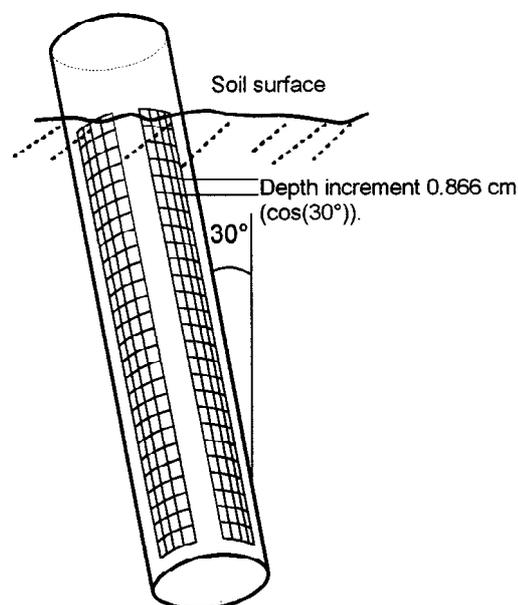


Figure 1. Minirhizotron with two counting grids. The rhizotrons are 150 cm long and have an outer diameter of 7 cm. Each grid net consists of 4×128 square counting fields of 1 cm². The distance between the two grids are 2 cm.

so that each grid sampled roots growing downwards on the respective side of the minirhizotron (Figure 1). There were two cm between the two grids. Each counting field was painted as a square with a field size of one cm². Due to the angle of 30° from vertical, each counting field extending one cm along the minirhizotron surface, represented a soil layer of only 0.866 cm (cos(30°)). The observations were made using a mini-video camera to record the roots on the minirhizotron surface on videotapes. The videotapes were subsequently analyzed by counting the number of grid fields showing roots.

Root intensities were calculated as simple averages of observations within each soil layer (fraction of counting fields where roots were observed) for each observation date. Rooting depth was measured on each counting grid as the depth of the deepest root observation.

Only one figure from each plot for rooting depth, and for root intensity within each soil layer, was used for further calculations from each of the three positions relative to the crop row. This was obtained as the average of the four observations of rooting depth or root intensity (two counting grids on each of two minirhizotrons placed either 10 or 25 cm behind the nearest plant, but at the same distance from the crop

row). Data were analysed with the GLM procedure of the SAS statistical package (SAS, 1990).

Detailed root growth analysis

In the first fertilizer experiment (April 1993) more detailed studies were made on root growth. At three dates during the growth period, roots were recorded twice with a 24-h interval. Growth rates of individual root tips and the fraction of root tips actually growing were measured by comparing videotapes recorded with this 24-h interval. Based on root diameter, the observed roots were divided into two different root classes. Where a branching main root (a thick root showing frequent branching with thinner roots) could be observed along the tube surface, the branching frequency was recorded as the number of observable laterals per cm main root.

Results

Root depth development

The general estimates of root development are based on results from all five experiments but using only the results obtained with the cultivar Plana grown at the N2 fertilizer level. The calculations are based only on results obtained during the first 1000 day °C after planting, as some of the crops were harvested after approximately 1000 day °C. Further, after this time the roots had reached the bottom of many of the minirhizotrons (approx. 100 cm), and continued rooting depth development after this time could thus not be measured. Growth and nitrogen uptake by the cauliflower is shown in Table 1 (for further details, see Van den Boogaard and Thorup-Kristensen 1998).

The observed rooting depth was found to be linearly related to temperature sum with a base temperature of 0 °C (Figure 2, Equation (1)). The regression equation for rooting depth development beneath the crop rows was

$$\text{Rooting depth (mm)} = -115 \text{ mm} + 1.02 \text{ mm day}^{-1} \text{ }^{\circ}\text{C}^{-1} \times \text{Tsum (day }^{\circ}\text{C)} \quad (1)$$

with intercepts of -144 and -209 mm, respectively, at 15 and 30 cm from the crop rows. This linear model for rooting depth, which included tube position and temperature sum (Tsum, day °C) showed a r^2 value of 0.91 whereas the r^2 was only 0.74 when the model

included chronological time (days after planting) instead of Tsum. Using a base temperature of 0 °C for calculation of Tsum was chosen as this gave a better fit to observed rooting depths than using other base temperatures.

The rate of downward penetration was not significantly different among tube positions relative to the crop row. From the time of planting there was a lag phase until the linear phase of rooting depth development started. Roots were first observed beneath the crop rows, and later also at 15 and 30 cm from the rows. According to Equation (1), a rooting depth of 10 cm was obtained after 211 day °C beneath the crop row, 238 day °C at 15 cm from the crop row and after 303 day °C at maximum distance 30 cm from the crop row.

At the beginning there were clear differences in root intensity and rooting depth among the positions, but during growth these differences became less clear. The two cultivars Plana and Siria showed quite different patterns of root development. Beneath the crop rows Siria was found to have a slightly faster rooting depth development than Plana, whereas at 15 cm and 30 cm from the crop rows Plana had a significantly faster rooting depth development than Siria (Table 2). Unlike Plana, Siria maintained significant differences between row and interrow soil in both rooting depth and root intensity until harvest.

As the various crops grew for approximately 950–1250 day °C, the rooting depth beneath the crop row at harvest should thus be between 85 cm and 115 cm. Observation of rooting depths of more than 100 cm was prevented by the length of the minirhizotrons, but at harvest the measured rooting depth was very close to 100 cm (Table 2) and roots were observed down to the bottom of many of the minirhizotrons. At harvest the measured rooting depth at 30 cm from the crop row was 83 cm, and roots were observed in 16% of the squares in the counting grid in the 80–100 cm soil layer (Table 2). At the positions of 0 and 15 cm from the crop rows, roots were observed in almost 25% of the counting squares in the 80–100 cm soil layer at that time.

Based on the estimates for 0 and 30 cm from the crop row, the horizontal root growth rate can be estimated to be 3.3 mm day⁻¹ °C⁻¹, which is more than three times as fast as the estimated rate of vertical root development. There were some indications in the results that high N fertilization reduced the rooting depth of cauliflower, but these differences were not statistically significant.

Table 1. Duration of growth (accumulated temperature sum), dry matter production and nitrogen uptake of the cauliflower crops at mid season and at final harvest

	Temperature sum (day °C)		Dry matter (t/ha)		N uptake (kg N/ha)	
	Mid season	Harvest	Mid season	Harvest	Mid season	Harvest
<i>Spring 1993</i>						
N1	487	998	0.74	8.4	37	160
N2	487	998	0.78	8.3	41	202
N3	487	1014	0.75	9.3	39	262
<i>Spring 1994</i>						
N1	453	887	0.61	5.5	24	132
N2	453	887	0.67	5.7	26	179
N3	453	887	0.66	6.4	28	241
<i>Summer 1993</i>						
Plana	470	912	1.70	6.8	85	253
<i>Summer 1994</i>						
Plana	600	1158	2.37	8.5	107	252
Siria	600	1059	2.12	6.6	95	235
<i>Summer 1995</i>						
Plana	520	1271	1.13	8.1	57	305
Siria	520	1212	0.82	6.9	41	293

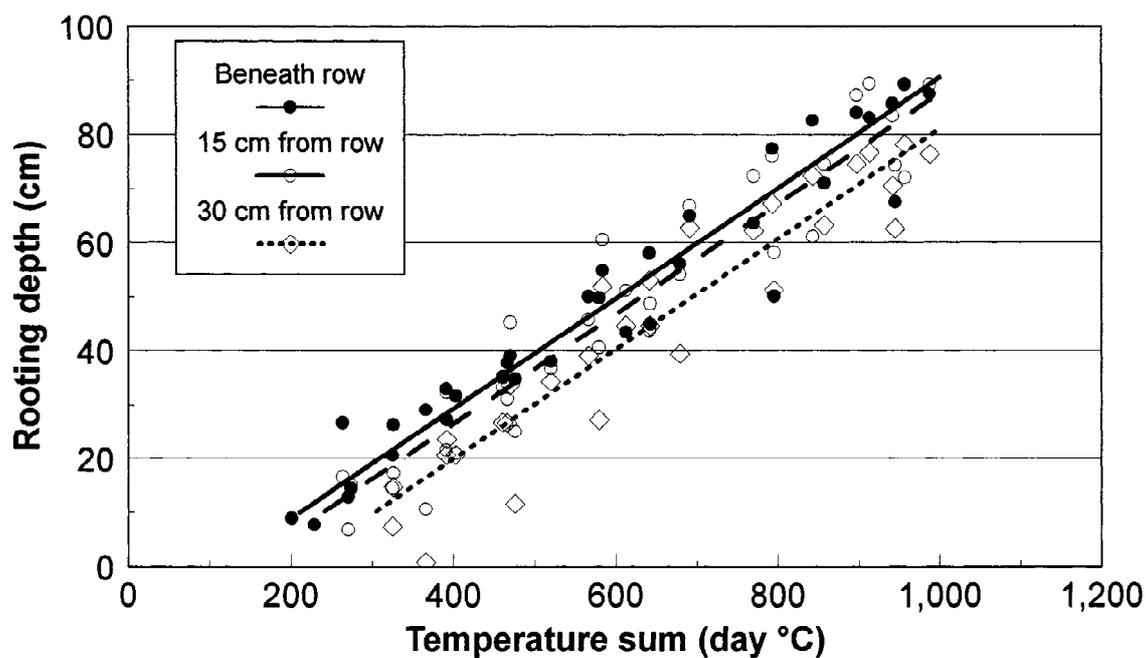


Figure 2. Relationship between thermal time and rooting depth measured on five cauliflower crops (cv. Plana). The regression line for rooting depth beneath the crop row was: $\text{Depth (mm)} = -115 \text{ mm} + 1.02 \text{ mm day}^{-1} \text{ }^{\circ}\text{C}^{-1} \times \text{Tsum (day }^{\circ}\text{C)}$ with intercepts of -144 mm and -209 mm , respectively, at 15 and 30 cm from the crop rows.

Table 2. Root depth and root intensity (fraction of observation squares with visible roots) of cauliflower crops, beneath the row (row), 15 cm from the row (15 cm) and in the interrow soil 30 cm from the crop rows (IR). Figures in brackets are S.E.

	Rooting depth (cm)			Root intensity (%)					
	Row	15 cm	IR	0–100 cm			80–100 cm		
				Row	15 cm	IR	Row	15 cm	IR
<i>Average of five Plana crops</i>									
Mid season	39 (1)	38 (5)	30 (6)	17 (1)	13 (3)	11 (4)	0	0	0
Harvest	89 (2)	89 (4)	83 (5)	53 (4)	54 (4)	54 (7)	24 (7)	23 (7)	16 (10)
<i>Cultivar experiments</i>									
Plana, mid season	41 (3)	44 (7)	40 (5)	20 (3)	16 (7)	18 (6)	0	0	0
Siria, mid season	50 (5)	41 (6)	33 (4)	24 (4)	14 (5)	9 (4)	0	0	0
Plana, harvest	90 (6)	95 (2)	86 (15)	51 (11)	59 (6)	59 (21)	33 (20)	40 (10)	31 (24)
Siria, harvest	93 (5)	82 (10)	76 (13)	52 (6)	37 (10)	32 (8)	32 (6)	12 (8)	9 (5)

Table 3. Soil nitrate (calculated on a kg N ha⁻¹ basis) beneath the crop plants (P) and in the interrow soil (IR). Average of measurements under Plana at the N2 fertilizer level in all five experiments. Figures in brackets are S.E.

	P		IR		P		IR	
	0–25		25–50		50–75		75–100	
At planting	32 (10)		13 (4)		11 (5)		8 (1.6)	
Mid season	61 (9)	112 (20)	21 (5)	26 (4)	15 (2)	17 (2)	10 (0.9)	13 (1.8)
At harvest	23 (5)	12 (3)	6 (1.3)	7 (2.1)	6 (1.0)	6 (1.0)	6 (1.0)	6 (0.7)

At midseason there are significant effects of depth (***) and position (***). At harvest there are significant effect of depth (***) but not of position.

Soil nitrate

Measurements of soil nitrate content at mid season showed a strong effect of the spatial distribution of the root system, as much less nitrate was found beneath the plants than at maximum distance from the plants. On average, this difference was only statistically significant in the top 25 cm soil layer, but in some of the experiments it was also significant in the 25–50 cm soil layer. The level of soil nitrate N in the top metre of the soil was increased from 65 kg N/ha at planting to 110 kg N ha⁻¹ beneath the plants and 167 kg N ha⁻¹ in the interrow soil at mid season and fell again to 41 and 31 kg N ha⁻¹ at these positions at harvest. The increase from planting to mid season was mainly found in the top 25 cm soil layer, and mainly at maximum distance from the crop plants, but increases were found in all four layers at both positions (Table 3).

From mid season until harvest, soil mineral nitrogen content decreased to a low level in all soil layers. At harvest, approximately 6 kg nitrate N ha⁻¹ was found in each 25 cm soil layer below the top 25 cm (Table 3). This was more variable in the fertilizer ex-

periment where between 2 and 9 kg nitrate N ha⁻¹ was found (Table 4). The absence of fertilizer effects on root growth was also reflected in the observed depletion of soil nitrogen. More nitrate N was left in the soil where high levels of fertilizer had been applied, but this increase was observed at all depths at both positions.

Siria was found to leave more nitrogen in the soil than Plana (Table 5), but this difference was also found in all depths and both positions, and thus, it did not reflect the differences in rooting pattern.

At final harvest, differences in nitrate content between soil from beneath the plants and interrow samples were absent in the deeper soil layers, whereas in the topsoil layer the nitrate content was generally highest beneath the plants.

Growth and branching of individual roots

Studies of the growth of individual root tips showed that many of the observed root tips did not grow at all, and that the frequency of growing root tips fell with time. 31 days after planting almost half of the root tips

Table 4. Soil nitrate concentration (as kg N ha⁻¹ per 25 cm soil layer) beneath the crop plants (P) and in the interrow soil (IR) in the fertilizer experiment. Figures in brackets are S.E.

Sample	Nitrogen level	P		IR		P		IR	
		0–25		25–50		50–75		75–100	
At planting		12 (4)		7 (1)		6 (0.1)		6 (0.3)	
Mid season	N1	51 (5)	96 (26)	12 (3)	14 (2)	11 (0.8)	16 (2.9)	9 (1.0)	10 (1.4)
	N2	76 (11)	113 (31)	21 (11)	19 (4)	14 (1.6)	15 (0.9)	10 (2.7)	12 (3.8)
	N3	123 (14)	137 (12)	23 (10)	24 (7)	13 (2.4)	13 (0.1)	11 (5.1)	11 (1.9)
At harvest	N1	12 (2)	8 (2)	2 (0.4)	2 (1.0)	4 (0.9)	4 (1.7)	4 (1.8)	5 (1.0)
	N2	17 (3)	14 (9)	5 (3.6)	7 (5.2)	6 (2.5)	6 (3.1)	6 (2.4)	6 (1.2)
	N3	28 (7)	21 (8)	8 (5.7)	8 (4.0)	7 (3.2)	6 (1.4)	6 (2.2)	9 (3.2)

At midseason there are significant effects of fertilizer level (**), depth (***) and position (*). At harvest there are significant effects of fertilizer level (***), depth (***) and interaction between depth and position (*).

Table 5. Soil nitrate concentration (as kg N ha⁻¹ per 25 cm soil layer) beneath the crop plants (P) and in the interrow soil (IR) beneath the two cultivars Plana and Siria. Figures in brackets are S.E.

	Cultivar	P		IR		P		IR	
		0–25		25–50		50–75		75–100	
At planting		36 (1)		18 (11)		8 (2.4)		7 (0.7)	
Mid season	Plana	47 (16)	120 (54)	25 (9)	34 (8)	12 (1.3)	16 (1.9)	10 (1.3)	15 (2.5)
	Siria	62 (31)	128 (62)	27 (16)	35 (11)	10 (3.3)	15 (1.5)	10 (1.8)	20 (4.9)
At harvest	Plana	25 (15)	12 (1)	6 (2)	9 (4)	5 (1.3)	6 (0.2)	5 (1.7)	6 (0.4)
	Siria	21 (9)	24 (11)	7 (2)	12 (5)	6 (1.6)	8 (0.9)	7 (1.7)	8 (1.1)

At midseason there are significant effects of depth (***), position (***), and interaction between depth and position (*). At harvest there are significant effects of cultivar (*) and depth (***).

were growing (Figure 3), at day 47 the frequency was less than 0.25 and at day 74 it was less than 0.1. At all dates the growth frequency of the thick roots was higher than that of the thin roots.

The average growth rate of all root tips fell during time, as the fraction of root tips which did not grow increased (Figure 3). The growth rate of the individual root tips varied strongly, from no growth up to more than 3 cm day⁻¹ for some of the thick roots. The average growth rate of the actively growing tips of the thick roots were relatively constant at 1.5 cm day⁻¹ at all three dates, whereas for the thinner roots it increased from 0.5 cm day⁻¹ at the first measurement to more than 1 cm day⁻¹ at day 74 (Table 6).

There were large differences in the growth activity in the different soil layers. At all dates approximately 70% of the root tips were growing in the deepest soil layer with active root growth, but at the other layers the activity was much lower (Figure 3). At 74 days

Table 6. Average growth rate of actively growing root tips across all soil layers. Figures in brackets are S.E.

	Day 31 (cm day ⁻¹)	Day 47 (cm day ⁻¹)	Day 74 (cm day ⁻¹)
'Thick roots'	1.37 (0.15)	1.63 (0.13)	1.41 (0.15)
'Thin roots'	0.53 (0.07)	0.73 (0.12)	1.07 (0.17)

after planting only 1% of the observed root tips were growing in the 0–60 cm soil layer, 13% were growing in the 60–80 cm soil layer and 64% of the root tips were growing in the 80–100 cm soil layer.

The number of branching roots and their branching frequency were the only root measurements which showed significant effects of fertilizer level (Table 7). The observed branching frequency (laterals per cm root) increased from 3 laterals cm⁻¹ at N1 to almost

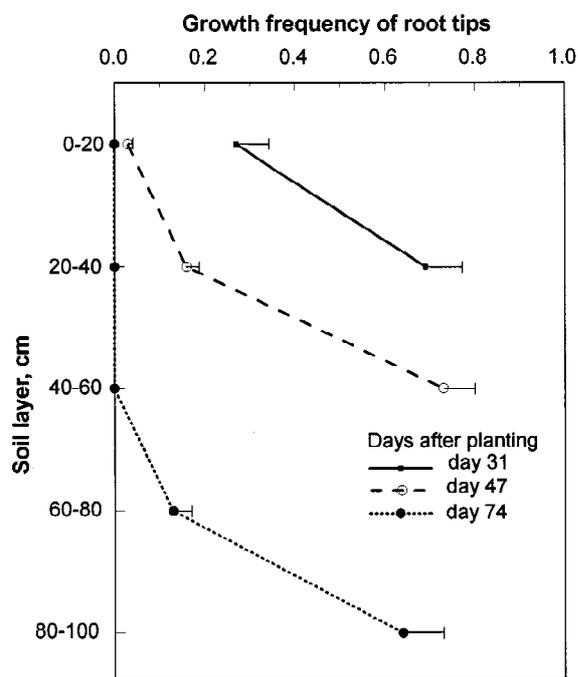


Figure 3. Growth frequency (fraction of observed root tips that were actively growing) in different soil layers, 31, 47 and 74 days after planting, data represented as mean + S.E.

5 laterals cm^{-1} at N3 (Table 7). As only the laterals which approach the minirhizotron surface can be observed, the real branching frequency must be assumed to be twice as high, i.e. from 6 laterals cm^{-1} at N1 to between 9 and 10 laterals cm^{-1} at N3. The branch-

Table 7. Observed branching frequency of actively branching roots at the three N fertilizer levels. As only the laterals approaching the minirhizotron surface are observed, the actual root branching frequency will be approximately twice the recorded values. Figures in brackets are S.E.

	No. of observed lateral roots per cm main root		
	N1	N2	N3
<i>Day 31</i>			
0-50 cm	3.0 (0.00)	4.3 (0.15)	4.7 (0.33)
<i>Day 47</i>			
0-50 cm	3.1 (0.15)	4.6 (0.09)	4.6 (0.13)
<i>Day 74</i>			
0-50 cm	3.2 (0.04)	4.8 (0.04)	4.8 (0.06)
50-100 cm	3.2 (0.03)	4.0 (0.27)	4.6 (0.02)
0-100 cm	3.2 (0.03)	4.4 (0.22)	4.7 (0.05)

ing frequency was almost constant during time, and constant across the soil layers (Table 7), even though fertilizer additions increased nitrogen availability only in the topsoil.

The total number of branching main roots observed in the top 50 cm of the soil was higher at N2 and N3 than at N1 at all three dates, whereas in the 50-100 cm soil layer the number of branching roots decreased with higher N supply. The decrease in the number of branching roots in the 50-100 cm soil layer was so marked, that the total number of observed lateral roots was lower at N3 than at N1, even though the branching frequency of the main roots was highest at N3. Thus increasing N supply led to a large increase the total number of observed laterals in the top 50 cm of the soil, but a decrease in the total number of observed branchings in the subsoil.

Discussion

Linear relationships between temperature sum and rooting depth have previously been observed by Barraclough and Leigh (1984) for wheat, by Thorup-Kristensen (1998) for pea and by Pellerin and Pagès (1994) for maize, though for maize a base temperature of 6 or 10 °C was used instead of the base temperature of 0 °C which we estimated for cauliflower.

Generally cruciferous crops are found to have very fast rooting depth development (Barraclough, 1989; Böhm, 1974; Thorup-Kristensen, 1993) compared to e.g. cereal crops. This was not found in the present experiments, where a rooting depth development rate of 1.02 mm day^{-1} was estimated for cauliflower which is significantly less than the rate of 1.8 mm day^{-1} found by Barraclough and Leigh (1984) for wheat, but in accordance with previous measurements on vegetable crops such as broccoli (Thorup-Kristensen, 1993) or green pea where a rate of 0.8 mm day^{-1} °C was estimated (Thorup-Kristensen, 1998).

The horizontal spread of the root system was estimated to be approximately three times as fast as the depth development, and clear differences in rooting depth and root intensity between the row and interrow positions were only observed during the early growth phases. Some investigations have shown similar results for other row crops like cotton (Prior et al., 1994) and onion (Hösslin, 1954). In contrast clear horizontal differences have been observed in lettuce (Steingrobe and Schenk, 1994) or celeriac (Hösslin, 1954). Garz et al. (1992) found vertical and horizontal rates of

root system development of 1.4 and 0.9 cm per day respectively for young sugar beet plants. The extent of differences in root growth beneath crop rows and the interrow soil will depend on row width as well as on crop age, as for all row crops a clear horizontal difference in root growth will exist during the early growth stages. Also the choice of cultivar seems to be important for horizontal root growth as found here and by Kujira et al. (1994) for cultivars of winter wheat.

At mid season the soil nitrate levels were significantly lower beneath the plants than in the interrow soil down to 25 cm and in some of the experiments down to 50 cm, though the effect in 25–50 cm was not significant across all five experiments. This result is in accordance with the average rooting depth beneath the crop rows of 39 cm at the time of the mid season soil sampling.

The observed rooting depths both at mid season and at harvest are somewhat deeper than predicted by the equation used by Greenwood et al. (1987):

$$\text{Rooting depth (cm)} = 18 + \text{DW} \times 8.59 \quad (2)$$

where rooting depth is predicted on the basis of the above ground dry weight of the crop (DW, t/ha). This equation would predict a rooting depth of approximately 27 cm at mid season and between 63 and 103 cm at harvest.

Cauliflower has been found to be a relatively deep rooted crop compared to other vegetable crops (Burns, 1980; Greenwood et al., 1982), but still the rooting depth at harvest estimated here is also deeper than the 60–77 cm estimated by Burns (1980). The present estimates of rooting depth is supported by results of soil analysis, showing that soil nitrate concentration also in the 75–100 cm soil layer fell to a low level at harvest. Cauliflower did not deplete the deeper soil as efficiently as found by some other cruciferous crops as white cabbage (Sørensen, 1993) or cover crops of fodder radish, white mustard, or winter rape (Thorup-Kristensen, 1993, 1994). This was not even the case at the N1 level where the crop had a clearly sub optimal nitrogen supply (Van den Boogaard and Thorup-Kristensen, 1998). This result could be due to the short growing period of the cauliflower crop which may not allow the roots enough time for a complete depletion of the subsoil. This idea is in accordance with the results of Strebel and Duynisveld (1989) who found that during growth, sugar beet assimilated N from progressively deeper soil layers, down to 150 cm, but that uptake from the deeper soil layers occurred at

a lower rate and for a longer period than in the upper soil layers.

The higher amount of nitrate left at all soil layers and positions with higher nitrogen supply, shows that the nitrogen left in the soil was not left due to inability of the roots to take up this nitrogen, as, at low nitrogen supply a more efficient depletion was found by a similar root system. When the N supply was so high that the sink capacity of the plant limited nitrogen uptake, more nitrogen was left, also in parts of the soil volume where the root density was sufficient for efficient nitrogen depletion. As in the present results, Everaats et al. (1996) found that cauliflower was able to take up nitrogen from row and interrow soil almost equally efficient (measuring down to 60 cm) even though they grew their crop with row intervals of 75 cm.

Though more nitrate was found in the soil under Siria than under Plana, this effect did not seem to be due to differences in rooting pattern. The extra nitrate found under Siria was found at all positions and depths, and not mainly in the interrow soil where the difference in root growth between the two cultivars were found. This is in contrast to the result reported by Wiesler and Horst (1994) for maize cultivars, where they found that more nitrogen was left in the subsoil layers under cultivars with lower root densities. Siria grew less dry matter and assimilated less nitrogen than Plana, and this difference, rather than a poor ability to deplete any of the sampled soil layers of nitrogen, seems to be the reason for the higher nitrate content in the soil after harvest of Siria as compared to Plana.

Detailed studies of root growth

The finding that during development, root growth moves downwards in the soil profile while new growth is reduced and finally stops in the topsoil, contradicts the approach used in many of the simpler root growth models (e.g. Petersen et al., 1995). In these models root length density is assumed to decrease logarithmically with depth, and rooting depth is then defined as the soil depth where a certain critical root length density is predicted. The logarithmic pattern is also contradicted by results such as those obtained by Engels et al. (1994) who found that root growth continued mainly in the subsoil without irrigation but moved to the topsoil with irrigation after drought. For simple model approaches, using linear relations between rooting depth and temperature sum or between rooting depth and crop dry weight as done by Greenwood et al. (1987), seem to be better justified

by experimental results. As crop dry matter production is strongly related to temperature sum, these two approaches are not very different.

More detailed root growth models often work with fixed root growth rates for each class of roots (e.g. Diggle, 1988; Pagès et al., 1989), but in the present results large differences were found in the growth rates of individual root tips, with many roots not growing at all. Root growth rate was dependent on soil layer and time of measurement, but even within a specific soil layer at a specific date variation was large. This result is in line with the observations of variable growth rate and absolute growth of single roots of maize (Aguirrezabal and Tardieu, 1996).

Many results on branching frequency have been published, and most of these results show a lower branching frequency than observed here (e.g. Diggle, 1988; Pagès et al., 1989) but Bingham and Stevenson (1993) found a distance of 1–2 mm between branches of wheat and Pagès and Pellerin (1994) found 1–3 mm between branches on maize, close to the 1–1.7 mm between branches that we observed with cauliflower. Pagès and Pellerin (1994) found that the branching frequency of maize was much higher in the topsoil than in the deeper soil layers in contrast to our results with cauliflower.

Several results have shown that roots are able to proliferate in soil volumes with higher nutrient supply (e.g. Drew, 1975) and this is supported by the present result that branching frequency was increased by higher nitrogen supply, even in a situation where the overall growth of the root system was not significantly affected. As the number of actively branching roots in the topsoil was highest at high N supply whereas in the subsoil it was highest at low N supply, the overall result was in accordance with such results. The increased branching in the fertilized soil layer and the reduced branching in the non fertilized soil layers were due to two mechanisms, a systematic effect of N supply on branching frequency found all through the root system, and an effect on the number of branching roots which was influenced by local nutrient supply.

Conclusion

The present study shows that cauliflower during most of its growing period increased its rooting depth with approximately $1 \text{ mm day}^{-1} \text{ }^{\circ}\text{C}^{-1}$ and obtained a final rooting depth of approximately 100 cm. Significant differences between root growth in row and interrow

soil was only found during early growth with Plana, whereas with Siria such differences were maintained until harvest. Still, both cultivars were able to utilize soil nitrogen down to 100 cm both beneath the rows and in the interrow soil. Increasing the nitrogen supply to the crop was found to increase root branching in the upper soil layers and decrease it in the deeper soil layers, but no significant effects on rooting depth or root intensity of the root system as such could be found. Higher nitrogen supply increased the amount of nitrate left at all soil depths in both row and interrow soil.

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