Root growth of cauliflower (*Brassica oleracea* L. *botrytis*) under unstressed conditions: Measurement and modelling

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Abstract

Root observations were carried out on cauliflower using the minirhizotron and the soil core method in two years on two locations with different soil types, a loess loam and a humic loamy sand. Total root length (RL) (cm cm^{-2}) of cauliflower was correlated to total shoot dry weight (W_{sh}) (g m^{-2}) RL=0.0124(±0.005)*W_{sh}, r^2=0.76. There was an acceptable correlation (r^2=0.88) between the minirhizotron and the soil core methods for the sub-soil data, whereas the minirhizotron method underestimated rooting intensity for the top soil. Changes in rooting depth over time could be described for both soil types using a segmented function of temperature sum, consisting of an early exponential and a later linear phase. The increase of rooting depth during the linear phase was 0.107(±0.01) cm °C^{-1} d^{-1}. A simple descriptive root growth model based on the assumptions of a negative exponential decline of root length density (RLD) with soil depth, of a fixed ratio of RLD at the top of the soil profile and at rooting depth (r_{RLD}) and of a fixed fraction of dry matter increase allocated to fine-roots (f_{fR}) was formulated and used to describe the temporal and spatial variation of RLD found in the field. Slightly different estimates of f_{fR} and of r_{RLD} could be found for the different soil types, indicating a higher fraction of fine-root dry matter for the loess loam soil and a somewhat deeper root system for the humic loamy sand soil. A cross validation using the parameter values obtained from adjusting to the rooting data of one soil type for predicting RLD values of the other soil type, however, indicated that still quite satisfactory estimates (r^2=0.91 and 0.95) of RLD could be obtained.

Introduction

Fertilisation and irrigation supply regimes aiming to optimise resource use efficiency have to take into account the temporal and spatial rooting pattern of a crop (Schenk et al., 1991). The development of such strategies may strongly be facilitated by the use of well calibrated crop growth models which include modules that are able to predict these patterns with sufficient accuracy (Benjamin et al., 1996).

In intensively managed vegetable cropping systems the relevance of appropriate root growth models is high, because under these conditions often considerable amounts of nitrate are leached into the subsoil (De Neve and Hofman, 1998; Hähndel and Iser-

mann, 1993) where nitrate availability may become low because of low root length density (Kage, 1997; Kuhlmann et al., 1989; Van Noordwijk et al., 1993; Wiesler and Horst, 1994a). The amount and the time when these nitrogen amounts become available can only be predicted with detailed knowledge of the root growth patterns of a particular crop in combination with appropriate models for nutrient transport to the root system (Baldwin et al., 1973; De Willigen and Noordwijk, 1987; Kage, 1997; Van Noordwijk and Van de Geijn, 1996). Because of the higher mobility of water compared with nitrate, critical values of root length density for water uptake are very low (De Willigen and Noordwijk, 1987; Kage and Ehlers, 1996) and models which predict rooting depth (Chapman et al., 1993; Groot, 1987) may be sufficient for many practical purposes like irrigation scheduling despite

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the fact that absolute rooting density and spatial arrangement of the roots influences water availability (Droogers et al., 1997; Tardieu et al., 1992).

The availability of rooting data for vegetable crops is still limited, but older studies (Fröhlich, 1956; Greenwood et al., 1982) are now supplemented by more recent work (Jackson and Bloom, 1990; Jackson and Stivers, 1993; Smit et al., 1996; Thorup-Kristensen, 1998; Thorup-Kristensen and Van den Boogaard, 1998) often using the minirhizotron technique (Taylor, 1987). This method has several advantages like moderate time consumption, non destructivity and the possibility to study root turn-over (Cheng et al., 1991; Van Noordwijk et al., 1994). However, it needs to be calibrated using core sampling methods (Box and Ramseur, 1993; Majdi et al., 1992; Upchurch, 1987) if absolute values of RLD are desired.

According to Van Noordwijk and Van de Geijn (1996) approaches for root growth models within crop growth models may be categorised in (a) simple descriptive functions of the temporal and spatial root distribution without any feed back between shoot growth and root growth and distribution (Gerwitz and Page, 1974), (b) models including the interaction of root and shoot growth based on their functional equilibrium (Brouwer and De Wit , 1969; Savin et al., 1994) but describing spatial root distribution still with empirical functions and (c) models which also take into account responses of root expansion to local growing conditions. e.g. nutrient or water supply (Asseng et al., 1997; Grant, 1993; Jones et al., 1991; Manschadi et al., 1998; Pages and Jordan, 1991). Van Noordwijk and Van de Geijn (1996) state that for most applications quantifying the root effects on above ground processes, models of type 'b' may be more appropriate because they are more robust and more easily parameterised than models at a higher level of complexity.

The aim of the presented study is to quantify root growth and distribution of field grown cauliflower on different soil types in relation to above ground dry matter production. Thereby the minirhizotron and soil core method were used. The obtained data were used to elaborate and parameterise a root growth model for cauliflower. This was done within the context of an existing crop growth model for cauliflower (Kage and Stützel, 1999b). Such a calibrated root growth model may contribute to model based optimisations of fertilisation strategies.

Materials and methods

The field experiments were carried out on two different locations. One location (Hannover) was on the campus of the department of horticulture in Hannover, Germany. There, the soil type is a loamy humic sand with 1.5% C, 78% sand, 10% silt and 6% clay in the plough layer, 0–30 cm depth. The second location (Ruthe), on an experimental station situated about 15 km south of Hannover, has a loess loam with 1% C, 10% sand, 80% silt and 10% clay in the plough layer of 30 cm depth.

The experimental layout at Hannover in 1994 was a two factorial split plot design with two nitrogen fertilisation (normal/reduced) as sub-units, two irrigation levels (irrigated/not irrigated) as main units and four replications as randomised blocks. Rooting data were collected only from the irrigated treatment. In this experiment birds attacked the plants shortly before the last harvest, which resulted in some underestimation of crop productivity during the last part of the growth period. In 1996, the experiment was a completely randomised block design with three irrigation treatments and four replications from which only data of the optimally irrigated treatment are presented. The experiment at 'Ruthe' is a long-term rotational experiment consisting of two crop rotations, two tillage regimes, and two nitrogen fertilisation levels with three replications. In this experiment, root data were collected only from the mouldboard tillage plots. Nitrogen was given in all experiments as ammonium nitrate according to the N_{min}-fertilisation schedule (Scharpf and Wehrmann, 1975). For cauliflower, this defines a target supply level of 300 kg N/ha including the soil nitrate from 0 to 60 cm depth. Reduced fertilised plots received 70% of this supply. The planting density was 4 plants m^{-2} in a 0.5*0.5 m pattern for all experiments except for the experiment in 1996 at Hannover were the planting density was 3.3 plants m^{-2} (0.5*0.6 m). The cultivar 'Fremont' was used in all experiments. Planting dates are summarised in Table 1. General crop husbandry was as described in (Kage and Stützel, 1999b).

Soil cores were extracted on one or two sampling dates per experiment (Table 1) with a special root auger of 8 cm diameter (Eijkelkamp Agriresearch Equipment, Giesbeek, NL) down to a depth of 90 cm. Cores were divided into 10 cm depth increments except for the loess loam experiment in 1996, were 15 cm increments were used. Samples were taken at two positions within a field plot, one beneath a cauliflower

Year	Activity	Loamy sand	Loess loam
1994	Planting	March 31	April 7
	Installation of tubes	April 6	April 8
	Minirhizotron observations	May 26	June 1
		June 08	June 14
		June 23	June 29
		July 04	June 12
	Soil core extractions	July 5	June 15
			July 11
1996	Planting	June 27	April 9
	Installation of tubes	July 9	April 17
	Minirhizotron observations	August 2	June 1
		August 9	June 14
		August 15	June 29
		August 22	July 12
		August 27	
	Soil core extractions	August 29	July 1

plant and one in a mid-row position. Soil cores were stored at 4 °C until roots were washed out over a 1.25 mm sieve and root length was determined after removing organic debris from the sample using the method of (Newman, 1966).

Two minirhizotron tubes made of polyacryl with an outer diameter of 4.6 cm and a total length of 120 cm were installed per plot at an angle deviating 30° from the vertical to avoid preferential root growth along the tubes (Bragg et al., 1983). The upper parts of the tubes were painted black and closed with a rubber stopper to avoid light penetration (Levan et al., 1987). Holes for the tubes were drilled by hand-driven soil augers in a two step procedure. First, an auger of a diameter of 4 cm was used for a pilot hole, followed by a second spiral auger of 4.5 cm diameter. The minirhizotron tubes usually could be installed manually into the resulting hole with slight pressure indicating a close fit of the tube to the soil without severe soil compaction in the vicinity of the tube.

For root observations, an endoscope equipped with a glass fiber light source (Richard Wolf GmbH, Knittlingen, Germany) of a total length of 180 cm and a diameter of 1.8 cm was used. The view of the endoscope was at the right angle to its main axis and the aperture angle of the endoscope lens was 60°. To ensure a constant distance between the endoscope lens and the tube surface the endoscope was fixed within
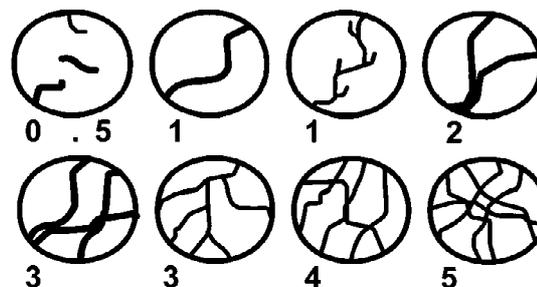

Figure 1. Scoring scheme according to Maertens (1987) used to in the minirhizotron observations. One root totally crossing the visible tube sector is equivalent to a scoring of 1. Maximum scoring is 5 even for observations with very dense rooting.

the tube by means of two PVC rings attached 15 cm from the bottom of the endoscope 10 cm apart. To facilitate an inspection of the minirhizotron tubes in effective soil depth increments of 5 cm at an installation angle of 30°, the endoscope was marked with rings in 5.77 cm spacings. Observations were taken from every tube in two view directions each deviating 45° from of the perpendicular in effective vertical increments of 5 cm. In 1994, all inspections were recorded using a video camera mounted on top of the endoscope, whereby video as well as audio data for location identification were stored using a battery driven video recorder. Thereafter, video tapes were analysed in the laboratory, using the scoring scheme of
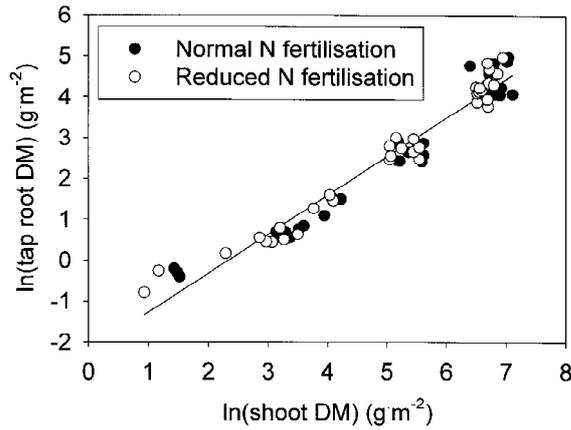
Figure 2. Relationship between the natural logarithms of the dry weight of the tap root of cauliflower, W_{tR}, and the shoot dry matter, W_{sh}. The regression line shown is: $\ln(W_{tR}) = -2.221$ (±0.133)$+0.9501$ (±0.0246) $\cdot \ln(W_{sh})$, $r^2=0.96$, $n=72$. Data are from the loess loam experiments only.

Maertens (1987) (Figure 1). In 1996, root observations were directly converted into root score values at the field plot. For correlation with soil core measurements, the scores were pooled according to the respective spatial aggregation of the soil core data.

Tap root extraction was performed using a spade by excavating a single cauliflower plant to a soil depth of 30 cm. The above-ground plant parts were cut off for further analysis and the remaining tap root was washed thoroughly using an intensive jet of water until all soil was removed. Afterwards the root parts were oven dried at 70° and 105 °C and weighed.

Model

The model module outlined in the following section aims to calculate the root growth and distribution of cauliflower based on a given total dry matter production rate, a simple dry matter partitioning scheme and some easily determined relationships describing the increase of rooting depth and the vertical root distribution. Thereby the root system of cauliflower is divided into two parts, a tap-root part mainly fulfilling supporting functions for the stem and a fine-root part responsible for water and nutrient uptake. Fine-root growth is modelled with respect to total length, depth increase and vertical root distribution.

Tap root growth

The whole-plant dry matter growth rate, $\mathrm{d}W_t/\mathrm{d}t$, (g m^{-2} d^{-1}) is the sum of the growth rate of the shoot, $\mathrm{d}W_{sh}/\mathrm{d}t$, the growth rates of the tap root, $\mathrm{d}W_{tR}/\mathrm{d}t$, and the fine-roots, $\mathrm{d}W_{fR}/\mathrm{d}t$:

$$\frac{\mathrm{d}W_t}{\mathrm{d}t} = \frac{\mathrm{d}W_{sh}}{\mathrm{d}t} + \frac{\mathrm{d}W_{tR}}{\mathrm{d}t} + \frac{\mathrm{d}W_{fR}}{\mathrm{d}t} \tag{1}$$

If allometric growth of the shoot and the tap root is assumed, as was found for the relationship between leaf and stem dry matter in cauliflower (Kage and Stützel, 1999b) the relationship between the natural logarithms of shoot and tap root dry matter is linear:

$$\ln W_{tR} = p_{tR} + o_{tR} \cdot \ln W_{sh} \tag{2}$$

The parameters o_{tR} and p_{tR} represent constants, which may be easily derived from linear regression analysis of double logarithmic plots of tap root *versus* shoot dry matter. Following the analysis of Kage and Stützel (1999b) and assuming that a certain fraction of total dry matter growth rate, f_{fR}, is allocated to the fine roots the following equation is obtained (for details of derivation see 'Appendix'):

$$\frac{\mathrm{d}W_{sh}}{\mathrm{d}t} = \frac{\mathrm{d}W_t}{\mathrm{d}t} \left(\frac{1 - f_{fR}}{1 + \mathrm{e}^{p_{tR}} o_{tR} W_{sh}^{o_{tR}-1}} \right) \tag{3}$$

which expresses the shoot dry matter growth rate as a function of the whole-plant growth rate, the standing shoot dry matter, and the fraction of dry matter allocated to the fine roots.

Assuming that a certain fraction of total dry matter growth rate, f_{fR}, is allocated to the fine root fraction the fine root growth rate simply is:

$$\frac{\mathrm{d}W_{fr}}{\mathrm{d}t} = f_{fR} \frac{\mathrm{d}W_t}{\mathrm{d}t} \tag{4}$$

Tap root growth then simply is calculated by inserting Equation (3) and Equation (4) into Equation (1), and solving for $\mathrm{d}W_{tR}/\mathrm{d}t$:

$$\begin{aligned} \frac{\mathrm{d}W_{tR}}{\mathrm{d}t} &= \frac{\mathrm{d}W_t}{\mathrm{d}t} - \frac{\mathrm{d}W_t}{\mathrm{d}t} \left(\frac{1 - f_{fR}}{1 + \mathrm{e}^{p_{tR}} o_{tR} W_{sh}^{o_{tR}-1}} \right) \\ &\quad - \frac{\mathrm{d}W_t}{\mathrm{d}t} \cdot f_{fR} \end{aligned} \tag{5}$$

which may be further simplified to:

$$\frac{\mathrm{d}W_{tR}}{\mathrm{d}t} = \frac{\mathrm{d}W_t}{\mathrm{d}t} \left(\frac{\mathrm{e}^{p_{tR}} o_{tR} W_{sh}^{o_{tR}-1} (1 - f_{fR})}{1 + \mathrm{e}^{p_{tR}} o_{tR} W_{sh}^{o_{tR}-1}} \right)$$
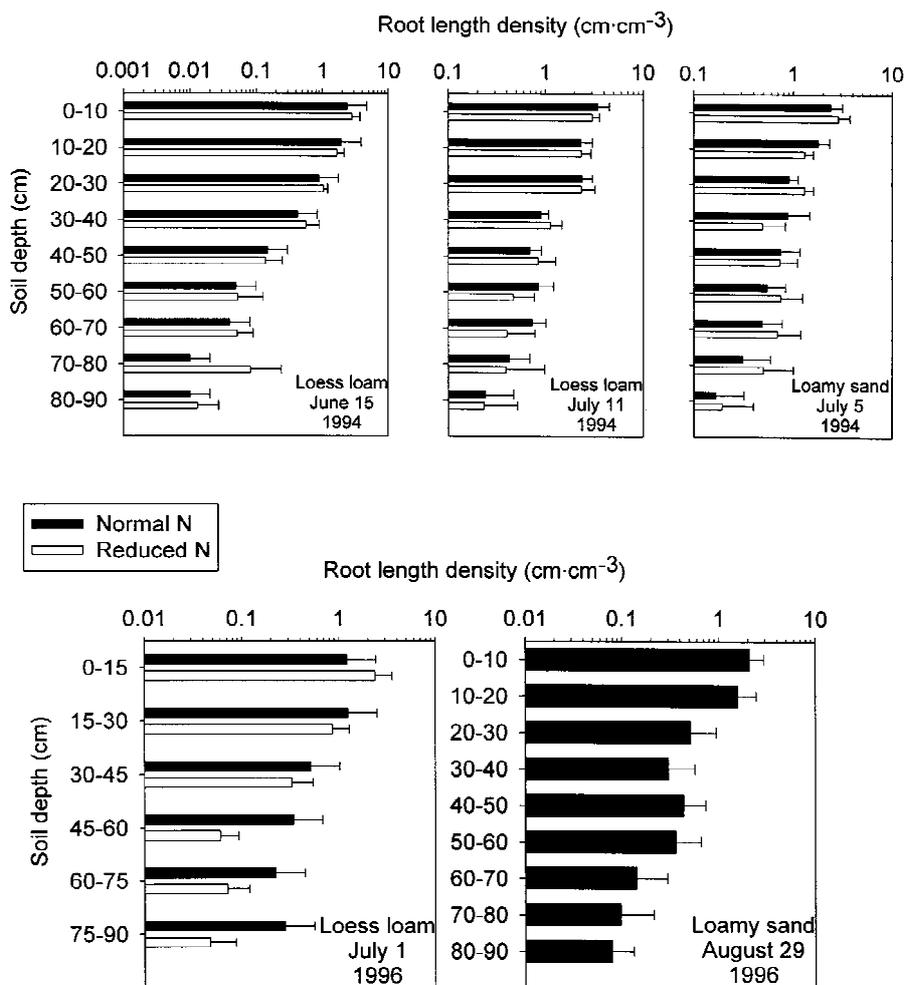
Root length density (cm·cm^{-3})

Figure 3. Root length density of cauliflower determined by the soil core method from 2 years and two locations in northern Germany. Bars indicate sample standard error.

Fine-root growth

If the fraction of dry matter increase attributed to fine-root growth, f_{fR}, is known, the increase of total fine-root length dRL/dt (cm m^{-2} d^{-1}) may simply be calculated from the total dry weight increase (g m^{-2} d^{-1}) and the average specific root length SRL (cm g^{-1}).

$$\frac{dRL}{dt} = \frac{dW_t}{dt} \cdot f_{fR} \cdot SRL \qquad (6)$$

The value of SRL may be regarded as a parameter or calculated from the average diameter and the average dry matter content of the roots. Here, a constant value of 7000 cm g DM^{-1} was used which was derived from experiments with cauliflower grown in large containers filled with loess loam soil (Kochler, unpublished results).

Rooting depth

Rooting depth z_r (cm) is often found to increase linearly with temperature sum within certain development stages, but lag phases in rooting depth increase (Thorup-Kristensen, 1998; Thorup-Kristensen and Van den Boogaard, 1998) as well as diminishing rooting depth increases in later developmental stages (Jaafar et al., 1993; Masse et al., 1991) have been observed. As physiological maturity is not reached in cauliflower crops for commercial vegetable production, we used a combination of an early exponential

increase followed by a linear increase in rooting depth for rooting depth description.

During the first phase rooting depth increase, dz_r/dt (cm d^{-1}) therefore is:

$$\frac{dz_r}{dt} = a_{zr} \cdot (T_a - T_b) \cdot z_r \tag{7}$$

Where T_a (°C) is the daily mean of air temperature, T_b (°C) is the base temperature for root growth and a_{zr} is a constant (°C^{-1} d^{-1}).

This equation can be integrated:

$$z_r = z_{r0} \cdot e^{a_{zr} \cdot \text{TSum}} \tag{8}$$

where z_{r0} is the rooting depth at the day of transplanting and TSum the sum of average daily temperatures above the base temperature, which we assumed to be 0 °C.

During the linear phase rooting depth increase is simply:

$$\frac{dz_r}{dt} = b_{zr} \cdot (T_a - T_b) \tag{9}$$

where b_{zr} (cm °C^{-1} d^{-1}) is another constant.

In order to obtain a continuously derivable function the exponential and the linear part of the function have to predict the same rooting depth increase at the switching point from one part to the other. Therefore, by combining the right hand sides of Equation (7) and (9) and solving for z_r at this switching point, z_{rc}, where maximum rooting depth increase is reached can be calculated:

$$z_{rc} = \frac{b_{zr}}{a_{zr}} \tag{10}$$

The temperature sum at which the rooting depth increase switches from the exponential to the linear phase, $\text{TSum}_{\text{crit}}$, is obtained by substituting z_{rc} from Equation (10) for z_r in Equation (8). Rearranging gives:

$$\text{TSum}_{\text{crit}} = \frac{\ln\left(\frac{z_{rc}}{z_{r0}}\right)}{a_{zr}} \tag{11}$$

The rooting depth at any time after the plants received the critical temperature sum can now be calculated with the following equation:

$$z_r = z_{rc} + b_{zr} \cdot (\text{TSum} - \text{TSum}_{\text{crit}}) \tag{12}$$

Vertical root distribution

The root length density, RLD, (cm cm^{-3}) of many annual arable and vegetable crops decreases approximately exponentially with soil depth (Barraclough, 1984; Gerwitz and Page, 1974; Greenwood et al., 1982):

$$\text{RLD} = \text{RLD}_0 \cdot e^{-k_r \cdot z} \tag{13}$$

where the constant k_r (cm^{-1}) is the fractional decrease in RLD per unit increase of soil depth and RLD_0 is the root length density at zero soil depth.

Integration of Equation (13) from $z=0$ to a depth $z = z_r$ were the root length density is very low yields the root length RL (cm cm^{-2}):

$$\begin{aligned}
\text{RL} &= \int_{z=0}^{z=z_r} \text{RLD}_0 \cdot e^{-k_r \cdot z} \cdot dz \\
&= \frac{\text{RLD}_0}{k_r} \cdot (1 - e^{-k_r \cdot z_r})
\end{aligned} \tag{14}$$

The second term of Equation 14 approaches 1 if the product of k_r and z_r is high.

To calculate the average rooting density RLD_{av} (cm cm^{-3}) within a certain soil layer located between two soil depths z_1 and z_2 Equation (14) may be set up for both depths. The difference between RL at z_2 and z_1 divided by the distance $z_2 - z_1$ gives the desired value of RLD_{av}:

$$\text{RLD}_{av} = \frac{\text{RLD}_0 \cdot (e^{-k_r \cdot z_1} - e^{-k_r \cdot z_2})}{k_r \cdot (z_2 - z_1)} \tag{15}$$

At the moment, k_r and RLD_0 remain unknown parameters.

Equation (14) may then rearranged to calculate RLD_0 from z_r, which is given from Equations (7) to (12) and RL which can be derived from numerical integration of Eq. (6):

$$\text{RLD}_0 = \text{RL} \cdot k_r \frac{1}{1 - e^{-k_r \cdot z_r}} \tag{16}$$

Using Equation (13) for the depth $z = z_r$ and introducing a new parameter, r_{RLD}, describing the ratio of RLD at z_r, RLD_{z_r}, and RLD_0 the following identity can be found for the parameter k_r:

$$k_r = -\frac{\ln\left(\frac{\text{RLD}_{z_r}}{\text{RLD}_0}\right)}{z_r} = -\frac{\ln(r_{\text{RLD}})}{z_r} \tag{17}$$

Thereby, the introduction of r_{RLD} avoids the necessity of using an iterative solution of the above set of equations.

Parameter estimation and statistics

The above algorithms were implemented as a submodel for root growth and as a modified partitioning submodel for cauliflower within the HUME modelling environment (Kage and Stützel, 1999a) and combined with other submodels for light use efficiency based calculation of dry matter production (Kage et al., 1999) and development (Kage and Stützel, 1999b). The HUME modelling environment supports parameter estimation based on the Marquardt algorithm (Marquardt, 1963) using an algorithm from Press et al. (1986).

To calculate the increase of total root length (Equation (6)) the fraction of dry matter increase attributed to fine root growth, f_{fR}, the specific root length and the total dry matter growth rate need to be known. An estimate of total dry matter growth rate may be obtained from derivatives of fitted growth curves or from more complex crop growth models. We used the latter approach and adopted for this purpose a light use efficiency (LUE) based dry matter production module (Kage et al., 1999) in combination with model modules for predicting development and dry matter partitioning of cauliflower (Kage and Stützel, 1999b). The dry matter production model module used assumes a linearly decreasing LUE with increasing levels of daily radiation according to the equation:

$$\frac{dW_t}{dt} = Q \cdot (LUE_0 - LUE_{dec} \cdot PAR) \tag{18}$$

where Q is the amount photosynthetic radiation intercepted by the canopy (MJ m^{-2} d^{-1}). LUE_0 (g DM MJ^{-1}) and LUE_{dec} (g DM MJ^{-2} m^{-2} d^{-1}) are parameters describing a function of a linear decrease of LUE with the daily sum of photosynthetically active radiation, PAR (MJ m^{-2} d^{-1}). The parameter LUE_0 had to be re-adjusted to take into account the growth of the tap root and the fine-roots, which the previous version of the module did not consider. As objective function the un-weighted squared sum of measured and simulated shoot dry weight of all normal fertilised treatments was used. The value of LUE_{dec}, however, was left unchanged at 0.36 (g DM MJ^{-2} m^{-2} d^{-1}).

The parameters f_{fR} (Equation (6)) and r_{RLD} (Equation (17)) were estimated by minimising the unweighted square sum of measured and simulated RLD values. Measured values are obtained either directly from soil core measurements or are derived from minirhizotron observation data using an empirical regression equation.

The parameter estimation procedure for the parameter LUE_0 from the dry matter production module and the parameters f_{fR} and r_{RLD} from the root growth module were performed separately in an iterative way for the whole data set, until no further change of parameter values occurred. Specific estimates of f_{fR} and r_{RLD} for parts of the data set then were made using the LUE_0 value obtained for the whole data set.

All other statistical analyses were performed using the procedures ANOVA, REG and NLIN from the SAS system (SAS Institute, 1988).

The descriptive and predictive power of a model can be evaluated by linear regression of output and measured data and several other statistical measures. One of them is the modelling efficiency EF (Smith et al., 1997):

$$EF = 1 - \frac{\sum(y_i - \hat{y}_i)^2}{\sum(y_i - \bar{y})^2} \tag{19}$$

Where y_i is the value of the *i*th observation, $\hat{y}_i$ is the *i*th model prediction and $\bar{y}$ is the average of the observations. Modelling efficiency approaches one for complete agreement between simulated and measured values, but may also become negative if the model describes the data less well than the observation mean.

Results

A close linear relationship exists between the natural logarithms of tap root and shoot dry weight (Figure 2), which was not significantly influenced by the level of nitrogen supply in our experiments. From this linear regression the parameters of p_{tR} and o_{tR} of Equation (2) are estimated to be −2.221 (±0.0133) and 0.9501 (±0.0246) (Figure 2).

Likewise, the root length density data from all experiments showed no significant difference between the nitrogen treatments (Figure 3), even for the 1996 experiment on the loess loam location where a slight tendency towards higher RLD values of the normal-fertilised treatment in the subsoil could be found. The 30% reduction of N supply had no significant effect on total plant dry matter production in our experiments (data not shown). The differences between the RLD values for the two sampling positions (near plant, inter row) were not significant (data not shown). The

Table 2. Parameters RLD_0 and k_r ($\pm$SE) together with the coefficient of determination, r^2, of the negative exponential function describing the decrease of root length density with soil depth (Equation 13). Also shown are the corresponding calculated total root length $RL=RLD_0/k_r$ (Equation 14) and the simulated total above-ground dry matter, W_{sh}, of the cauliflower crops. Data from two years at two different soil types (loess loam, loamy sand) with two different N-supply levels (normal/reduced)

Date	Soil	Fert.	RLD_0 (cm cm^{-3})	k_r (cm^{-1})	r^2	RL (cm cm^{-2})	W_{sh} (g m^{-2})
1994 June 15	Loess loam	Norm.	3.31 ($\pm$0.32)	0.052 ($\pm$0.007)	0.96	64	539.3
1994 June 15	Loess loam	Red.	3.78 ($\pm$0.16)	0.056 ($\pm$0.003)	0.99	67	421.9
1994 July 11	Loess loam	Norm.	4.00 ($\pm$0.37)	0.032 ($\pm$0.004)	0.93	127	1257.4
1994 July 11	Loess loam	Red.	3.73 ($\pm$0.32)	0.031 ($\pm$0.004)	0.94	122	1045.1
1994 July 05	Loamy sand	Norm.	2.74 ($\pm$0.18)	0.032 ($\pm$0.003)	0.96	86	948.9
1994 July 05	Loamy sand	Red.	2.96 ($\pm$0.42)	0.033 ($\pm$0.007)	0.84	89	812.8
1996 July 01	Loess loam	Norm.	1.60 ($\pm$0.27)	0.025 ($\pm$0.006)	0.86	64	752.7
1996 July 01	Loess loam	Red.	3.93 ($\pm$0.10)	0.068 ($\pm$0.002)	0.99	58	647.7
1996 August 29	Loamy sand	Norm	2.74 ($\pm$0.29)	0.049 ($\pm$0.007)	0.94	55	647.7

absolute values of RLD at the end of the growing season were in the range of 1–3 cm cm^{-3} in the upper 10 cm and about 0.1 cm cm^{-3} in 80–90 cm soil depth. The decrease with depth is in general linear on a logarithmic scale or negative exponential for non-transformed values. Increase of RLD from June 15 to July 11 on the loess loam experiment in 1994 was substantial. In the soil depth of 50–60 cm, for instance, the RLD increased from about 0.1 cm cm^{-3} to nearly 1 cm cm^{-3}. Equation (13) then was used to summarise the soil core observations from different soil depths, giving estimates of RLD_0 and k_r for the different sampling dates from which also RL may be estimated (Equation (14)). Thereby the median depth of the soil cores was taken for z_r. Again, there were no significantly different estimates of k_r and RLD_0 for the

different fertilisation treatments, with the exception of the 1996 loess loam data. Here significant different estimates of RLD_0 and k_r were obtained for the normal and reduced fertilised treatment. There was substantial variation in total root length (Table 2). This variation is related to differences in shoot dry matter (Table 2, Figure 4). Because for some soil core measurement data no corresponding measured shoot dry matter were available, we used the model interpolation from measured values of shoot dry matter (Figure 4). There is an indication that the ratio of total root length–shoot dry matter is higher for the reduced fertilisation plots, but this effect was not significant (Figure 5).

The data obtained from the minirhizotron observations showed no significant differences between the nitrogen treatments. The differences between the
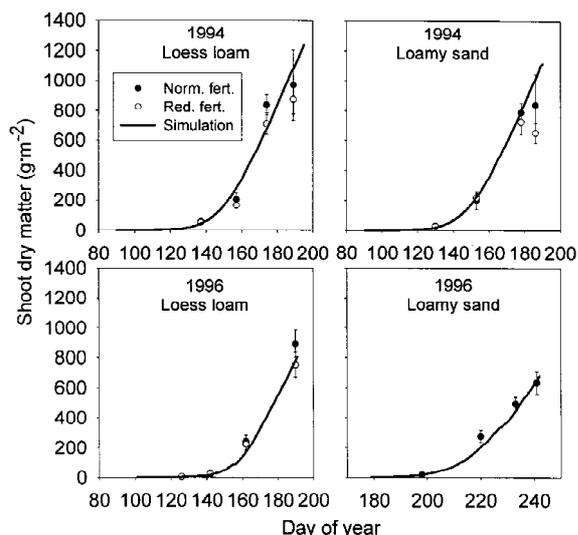
Figure 4. Simulated and measured shoot dry matter of cauliflower from 2 years and two different soil types. Error bars indicate standard error of the sample. Simulations are performed with a light use efficiency adjusted to the measured data from the normal fertilised plots.
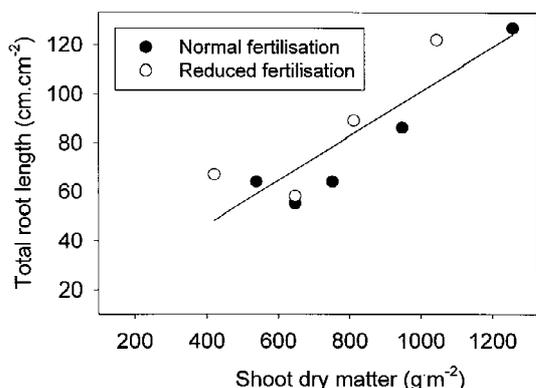

Figure 5. Relationship between total root length (RL) obtained from fitting a negative exponential equation to data from soil cores (Table 2) and simulated shoot dry matter (W_{sh}) of cauliflower for two different nitrogen supply rates. Data are from experiments in two years and on two soil types. Regression equation for all data shown is RL=0.1024 (±0.0053) · W_{sh}, r^2=0.76.

Figure 6. Root length density scores for cauliflower observed in minirhizotrones from two years and two locations in northern Germany.

Figure 7. Rooting depth (z_r) of cauliflower as a function of accumulated temperature sum (T_{sum}) after transplanting. Data are from two year (1994 and 1996)and two soil type (loess loam, LL, loamy sand, SL). The regression line shown is $z_r = z_{r0}^* \exp(a_{zr}^* T_{sum})$ for $T_{sum} < \ln((b_{zr}/a_{zr})/z_{r0})/a_{zr}$ and $z_r = b_{zr}/a_{zr} + b_{zr}^*(T_{sum} - \ln((b_{zr}/a_{zr})/z_{r0})/a_{zr})$. Parameter values: z_{r0}=6.04 (±1.52), a_{zr}=0.00394 (±0.000384), b_{zr}=0.107 (±0.00953), r^2=0.953, n=14.

sampling locations (near plant, mid row) were also not significant although there was an indication of fewer roots at the inter row position at early observations dates (data not shown). Therefore, all data for one soil depth class were pooled giving one value for each day and observation date. Except for the early sampling dates, where a steadily decrease of score values with soil depth could be found, root scores increased from 0 to about 40 cm soil depth and decreased from there on (Figure 6). This decrease was strongly dependent on
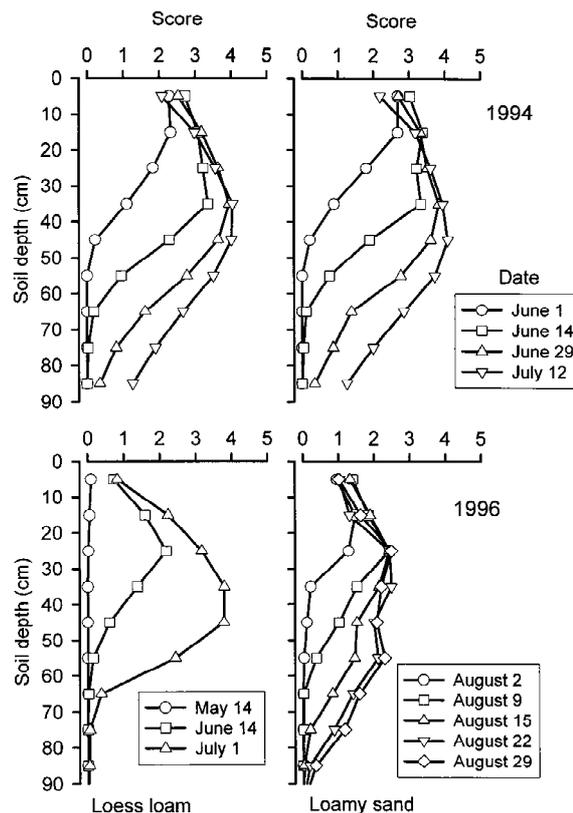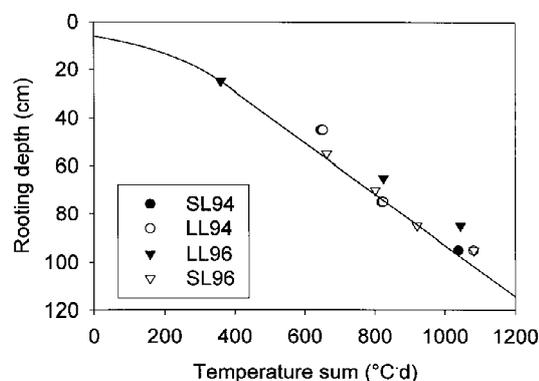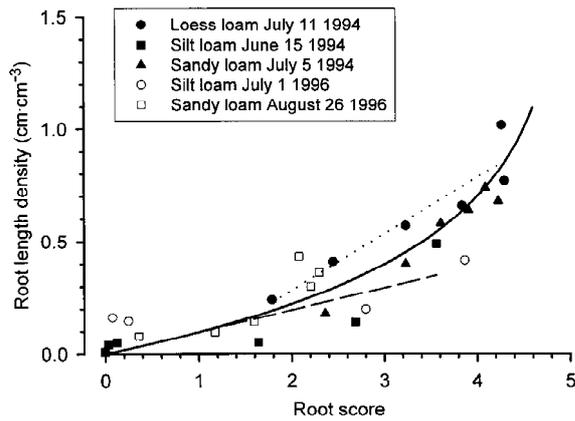
Figure 8. Correlation between root scores (sc) from minirhizotron observations and root length density (RLD) of cauliflower as determined by soil core measurements for two different locations and two years for soil depths >30 cm. The nonlinear regression line for all data is: RLD=ln(1-sc/5)/f, f = −2.299 (±0.099), r^2=0.83, n=28. The linear regression for loess loam, July 11 1994 (···) is y = −0.2191 (±0.1581)+0.2510 (±0.0460)·x, r^2=0.88, n=6 and for loess loam, June 15 1994 (- - -) is y = −0.0021 (±0.0632)+0.0985 (±0.0326)·x, r^2=0.70, n=6.

Table 3. Estimates for parameters r_{RLD} (±SE) (ratio of root length densities at soil surface to RLD at rooting depth) and fraction of fine root dry weight, f_{fR}, (±SE) correlation between the parameters, C, and modelling efficiency, EF. Data set from four field experiments: two years and two locations with different soil types (loess loam, loamy sand)

Data set	f_{fR} (-)	r_{RLD} (-)	C	EF
Loess loam	0.120 (±0.00530)	0.0180 (±0.00395)	0.59	0.95
Loamy sand	0.0984 (±0.00512)	0.0286 (±0.00706)	0.49	0.90
1994	0.110 (±0.00539)	0.0257 (±0.00615)	0.55	0.91
1996	0.114 (±0.00577)	0.0127 (±0.00331)	0.58	0.95
All Data	0.117 (±0.00441)	0.0210 (±0.00384)	0.55	0.92

sampling date. The absolute values of the root scores and the observed rooting depth increased substantially with time for the subsoil. The increase of rooting depth could well be described using the approach outlined in Equations (6) to (11), indicating a lag phase of rooting depth increase followed by a linear increase with temperature sum (Figure 7). There were no significant differences in this relationship between years and soil types. Interrow sampling positions tended towards a slightly, but insignificantly longer lag phase than inrow positions (data not shown).

A highly significant relationship could be found between the minirhizotron root scores below 30 cm soil depth and the corresponding RLD values from the soil cores (Figure 8). The non-linear function used here was motivated by the upper limit of root scores of 5. Again, there were no significant differences between years and soil types. Parameters of linear regressions fitted to different sampling dates on the loess loam soil were quite different (Figure 8).

The non-linear function shown in Figure 8 was used to convert the root scores from soil depths >30 cm into root length density values for all sampling dates where no core measurements were available. These RLD's and the available RLD data from soil core measurements were used to estimate the fraction of dry matter increase attributed to the fine-roots f_{fr}

and the ratio of RLD at the rooting depth to the RLD at the soil surface, r_{RLD}, as described above.

The value of LUE₀ obtained by adjustment to the measured shoot dry matter data is 7.36 (±0.06) g DM MJ^{-1} for total plant dry matter instead of 6.66 (Kage et al., 1999) for above ground dry matter production. The resulting prediction of shoot dry matter gives a linear regression with an insignificant intercept of Y=0.96 (±0.03) · X, r^2=0.96, n=16 for the data of the normal fertilised treatments (Figure 4).

The estimated values of f_{fR} and r_{RLD} indicate that the fraction of dry matter increase attributed to fine-root growth was higher in the loess loam soil than in the humic loamy sand and that in the humic loamy sand a greater percentage of roots is in the deeper soil layers. There were also marked differences between the two experimental years with respect to the value of r_{RLD}, r_{RLD} being higher in 1994 than in 1996 (Table 3). The model described the total variation found in the experimental data with parameter values obtained from the same data set (Figure 9a), but again the two soil types behaved differently. The descriptive value of the model was generally better for the medium soil depth than for either the upper soil and deeper soil layers (Table 4). However, the parameter values obtained from an adjustment to either the data from the experiments on humic loamy sand or to the loess loam

Table 4. Slope and intercept of the linear regression of the calculated vs. observed root length density values of cauliflower plants for the different soil depths from the parameterisation procedure as well as r^2 of the linear regression, residual mean square error, RMSE, and modelling efficiency, EF

| Soil depth (cm)	Slope	Intercept	r^2	n	RMSE	EF
0–10	0.4383	1.5665	0.4422	5	0.3745	−0.4115
10–20	0.2148	1.4995	0.1450	5	0.4358	−1.9545
20–30	1.1773	−0.2201	0.5593	5	0.4155	0.5466
30–40	0.7681	0.0719	0.7336	15	0.2026	0.6476
40–50	0.9469	0.0349	0.8022	15	0.1357	0.7966
50–60	0.9935	0.0365	0.8649	13	0.0881	0.8400
60–70	1.1574	0.0089	0.7653	12	0.1093	0.7097
70–80	1.0766	0.0085	0.6112	11	0.0990	0.5890
80–90	0.7271	0.0113	0.7759	11	0.0473	0.5001
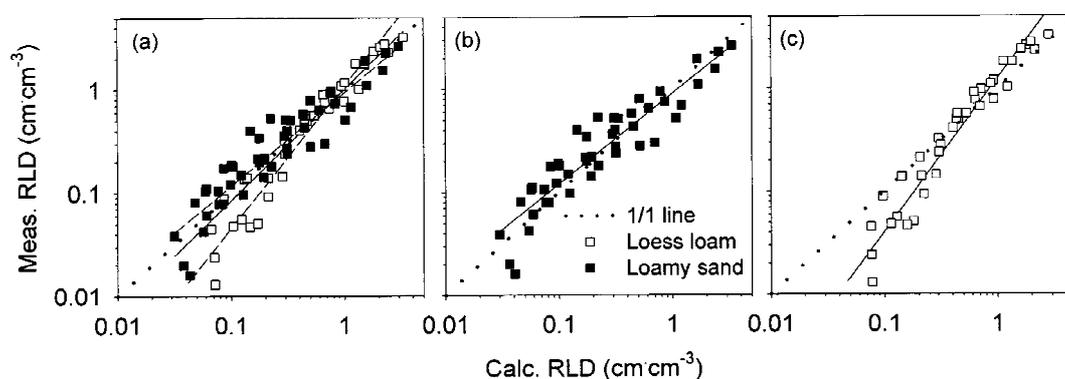
Figure 9. Calculated vs. measured root length density (RLD) of cauliflower (a) parameterisation using the whole data set for both soil types, (b) Evaluation of the model using the data from the loamy sand soil and the parameter estimations derived from the loess loam soil experiments (c) validation of the model using the data values from the loess loam soil and the parameter estimates derived from the RLD values of the loamy sand soil experiments. The regression equations shown are (a) $y=0.0233$ (± 0.0299)$+0.9824$ (± 0.0321)$\cdot x$, $r^2=0.92$ for parameterisation, all data, $y = -0.0272$ (± 0.0425)$+1.1031$ (± 0.0403)$\cdot x$, $r^2=0.95$ parameterisation, data from the loamy sand experiments, $y=0.0686$ (± 0.0335)$+0.8274$ (± 0.0411)$\cdot x$, $r^2=0.90$ parameterisation for the data from the loess loam experiments, (b) validation $y=0.0710$ (± 0.0279)$+0.7669$ (± 0.0341)$\cdot x$, $r^2=0.91$ for loamy sand, (c) validation for loess loam $y = -0.0819$ (± 0.0420)$+1.3040$ (± 0.0462)$\cdot x$, $r^2=0.95$.

also gave an acceptable prediction for the other data group (Figures 9b and c).

Discussion

The aim of the presented paper was to characterise rooting dynamics of cauliflower in relation to shoot growth using the soil core and the minirhizotron method. The collected rooting data were used to develop and parameterise a simple empirical root growth model module which describes and predicts rooting pattern of cauliflower as determined by temperature sum and crop growth rate.

The minirhizotron method gave unrealistic estimates of the root distribution in the topsoil (Figures 3 and 6). This drawback of the method has been previously observed (Vos and Groenwold, 1987; Wiesler and Horst, 1994b) and may be caused by several factors e.g. soil compaction due to agitating the tube during the measurement, soil drying in the vicinity of tubes due to gaps between soil and tube or light penetration into the minirhizotron tube. However, the method seemed to give reliable values of the rooting depth (Figure 7) and root scores for the subsoil correlated quite well with the RLD values of the soil coring method (Figure 8). The linear regression between the soil core data and minirhizotron scores obtained for the loess loam in 1994 indicate that the relationship

between the data from both methods may vary with time even within one crop (Bragg et al., 1983; Wiesler and Horst, 1994b). This problem may partly be overcome by using a non-linear relationship between root scores and root length density values (Figure 8). The limitations of the minirhizotron method in the topsoil region is not in every case very critical since here root length density is usually high enough to rapidly exhaust mobile resources like water and nitrate. The sub-soil region, where the method gives more reliable results seems more relevant for this resources because here low RLD may be critical for uptake (Kuhlmann et al., 1989; Kage & Ehlers, 1996; Kage, 1997).

From Equation (14) follows that k_r decreases with increasing rooting depth. This is in accordance with the results from June 15 and July 11 in 1994 obtained at the loess loam (Table 2) and those of Greenwood et al. (1982) who found k_r for cauliflower and other vegetable crops to decrease with increasing total root length. Also, the absolute k_r values of Greenwood et al. (1982) ranging from about 0.1 for early sampling dates with low total root length to about 0.05 for later states agree quite well with our data (Table 2). But their reported values of total root length and the ratio of total root length–shoot dry weight for cauliflower are considerably higher. From their data the relationship RL=0.215 ($\pm$0.012) $\cdot$ W_{sh}, r^2=0.97 was calculated, which predicts almost twice the amount of root length per unit shoot dry weight than we found (Figure 5). This may partly be explained by the fact that the experiments of Greenwood et al. (1982) were carried out with direct-drilled cauliflower seeds and not with transplants as in our experiments. Root growth may substantially be reduced due to the limited volume of the peat cubes in which the cauliflower plants were cultivated during the plant nursery period.

Linear increases of rooting depth with accumulating thermal time (Figure 7) have been found by several authors (Barraclough and Leigh, 1984; Jaafar et al., 1993; Pellerin and Pages, 1994; Thorup-Kristensen, 1998; Thorup-Kristensen and Van den Boogaard, 1998). The finding of Thorup-Kristensen and Van den Boogaard (1998) that rooting depth of cauliflower increases after a lag phase with a rate of 0.102 cm d^{-1} $°C^{-1}$ agrees strikingly well with our data from two different soil types (Figure 7). This indicates that rooting depth development of cauliflower is not strongly dependent on soil conditions as long as critical parameters like bulk density and soil water content are within a certain range optimal for root growth (Barber et al., 1988; Vepraskas, 1988). The

lag phase in rooting depth development of cauliflower may be explained by limited assimilate supply to the root system at early growth stages (Aguirrezabal and Tardieu, 1996) or by the transplanting shock and the root system disturbance caused by using transplants instead of direct-drilled plants.

One critical point of our model approach may be fact that root density at rooting depth is, according to Equations (14) and (12), changing with changing values of RLD_0 and, therefore, with total root length and time, because we assume a constant ratio, r_{RLD}, between rooting density at zero soil depth and rooting depth. Rooting depth, however, as we describe it with Equations (7) to (12) using our minirhizotron data (Figure 7) is operationally defined as the deepest soil depth where roots could be detected. This should imply a more or less constant value of RLD at z_r. But this approach avoids the need for an iterative solution of the equation system describing the root distribution (Hansen et al., 1990) and is obviously still able to describe and predict our data with sufficient accuracy (Figure 9, Table 3). Furthermore, the ratio of root density at the soil surface and at rooting depth is quite low (Table 3) and, therefore, the absolute calculated values of RLD at rooting depth are also low.

Models of root growth can be motivated by the aim to achieve a fundamental understanding of the complex interactions between soil, plant and climatic factors resulting in the immense complexity and plasticity of a plant root system (Grant, 1993; Jones, 1991; Pages, 1991). More applied approaches like the one presented here aim at acceptable descriptions of rooting patterns in time and space (Barraclough and Leigh, 1984; Greenwood et al., 1982) which may facilitate the prediction of the main functional aspects of root growth, like water and nutrient uptake with mechanistic models (De Willigen and Noordwijk, 1987). The presented model is simple and needs only four parameters, i.e. f_{fR}, the fraction of dry matter increase attributed to fine-roots, a_{zr} and b_{zr} describing the increase of rooting depth during the early exponential and the later linear phase, respectively, and r_{RLD}, the ratio of root length density at the top of the soil profile and at rooting depth. Additionally, an average value of the specific root length is needed. Such a simple model may be successfully parameterised even with the limited amount of data which are usually available from rooting studies in field experiments. Our parameterisation approach was successful with one examination of root length distribution with the soil core method at the end of the growing season of the crop accompan-

ied by some minirhizotron observations throughout the growing season. Whereas the more time consuming soil core method gives reliable estimates of total root length and its vertical distribution, the minirhizotron method is able to give additional information needed to identify the parameter values for describing the rooting depth development and the change of the vertical root distribution during time. If this approach is able to describe and predict root distribution pattern under altered nitrogen and water limitations remains to be proven. Problems will arise for soil profiles with compacted layers (Barraclough and Weir, 1988; Tardieu, 1988) or under extreme stress situations (Klepper and Rickman, 1990).

Conclusions

Fine and tap root growth of cauliflower are closely coupled to shoot growth, as indicated by an allometric relationship of tap root and shoot dry weight and a linear relationship of root length–shoot dry weight. The development of rooting depth could successfully be described using an expo-linear function of temperature sum. The vertical root distribution follows the negative exponential decline which has been observed for many other annual agricultural crops. Using this relationships it was possible to construct a simple empirical root growth model module for cauliflower which may facilitate further analysis of root function as a key characteristic for nutrient and water use efficiency. Further refinements of the model may include a value of f_{fR} and rooting depth development depending on the nutrient and water supply of the crop.

Acknowledgements

References

Aguirrezabal L A N and Tardieu F 1996 An architectural analysis of the elongation of field-grown sunflower root systems. Elements for modelling the effects of temperature and intercepted radiation. J. Exp. Bot. 47, 411–420.

Asseng S, Richter C and Wessolek G 1997 Modelling root growth of wheat as the linkage between crop and soil. Plant Soil 190, 267–277.

Baldwin J P, Nye P H and Tinker P B 1973 Uptake of solutes by multiple root systems from soil. III. A model for calculating the solute uptake by a randomly dispersed root system developing in a finite volume of soil. Plant Soil 38, 621–635.

Barber S A, Mackay A D, Kuchenbuch R O and Barraclough P B 1988 Effects of soil temperature and water on maize root growth. Plant Soil 111, 267–269.

Barraclough P B 1984 The growth and the activity of winter wheat roots in the field: root growth of high-yielding crops in relation to shoot growth. J. agr. Sci. (Camb.) 103, 439–442.

Barraclough P B and Leigh R A 1984 The growth and activity of winter wheat roots in the field: the effect of sowing date an soil type on root growth of high yielding crops. J. agr. Sci. (Camb.) 103, 59–74.

Barraclough P B and Weir A H 1988 Effects of a compacted subsoil layer on root and shoot growth, water use and nutrient uptake of winter wheat. J. agr. Sci. (Camb.) 110, 207–216.

Benjamin J G, Ahuja L R and Allmaras R R 1996 Modelling corn rooting patterns and their effects on water uptake and nitrate leaching. Plant Soil 179, 223–232.

Box J E J and Ramseur E L 1993 Minirhizotron wheat root data: comparisons to soil core root data. Agron. J. 85, 1058–1060.

Bragg P L, Govi G and Cannell R Q 1983 A comparison of methods, including angled and vertical minirhizotrons for studying root growth and distribution in a spring oat crop. Plant Soil 73, 435–440.

Brouwer R and De Wit C T 1969 A simulation model of plant growth with special attention to root growth and its consequences. Neth. J. agr. Sci. 10, 399–408.

Chapman S C, Hammer G L and Meinke H 1993 A sunflower simulation model: I. Model development. Agron. J. 85, 725–735.

Cheng W X, Coleman D C and Box J E 1991 Measuring root turnover using the minirhizotron thechnique. Agr. Ecosyst. Environ. 34, 261–269.

De Willigen P and Van Noordwijk M 1987 Roots, plant production and nutrient use efficiency. Ph.D. thesis, Agricultural University Wageningen.

De Neve S and Hofman G 1998 N mineralization and nitrate leaching from vegetable crop residues under field conditions: A model evaluation. Soil Biol. Biochem. 30, 2067–2075.

Droogers P, Van der Meer F B W and Bouma J 1997 Water accessibility to plant roots in different soil structures occurring in the same soil type. Plant Soil 188, 83–91.

Fröhlich H 1956 Die Bodendurchwurzelung seitens verschiedener Gemüsearten. Archiv für Gartenbau 5, 389–417.

Gerwitz A and Page E R 1974 An empirical mathematical model to describe plant root systems. J. appl. Ecol. 773–782.

Grant R F 1993 Simulation model of soil compaction and root growth. 1. model structure. Plant Soil 150, 1–14.

Greenwood D J, Gerwitz A and Stone D A 1982 Root development of vegetable crops. Plant Soil 68, 75–96.

Groot J J R 1987 Simulation of nitrogen balance in a system of winter wheat and soil. Simulation report CABO-TT, Wageningen, NL. 69 p.

Hähndel R and Isermann K 1993 Soluble nitrogen and carbon in the subsoil in relation to vegetable production intensity. Acta Hortic. 339, 193–206.

Hansen S, Jensen H E, Nielsen N E and Svendsen H 1990 DAISY – Soil plant atmosphere system model. Miljomimisteriet, Kopenhagen. 272 p.

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Jaafar M N, Stone L R and Goodrum D E 1993 Rooting depth and dry matter development of sunflower. Agr. J. 85, 281–286.

Jackson L E and Bloom A J 1990 Root distribution in relation to soil nitrogen availability in field-grown tomatoes. Plant Soil 128, 115–126.

Jackson L E and Stivers L J 1993 Root distribution of lettuce under commercial production: Implications for crop uptake of nitrogen. Biol. Agr. Horticul. 9, 273–293.

Jones C A, Bland W L, Ritchie J T and Williams J R 1991 Simulations of Root Growth. In Modeling Plant and Soil Systems. Ed. American Society of Agronomy. Vol. no. 31, pp. 91–123. Madison.

Kage H 1997 Is low rooting density of faba beans a cause of high residual nitrate content of soil at harvest? Plant Soil 190, 47–60.

Kage H, Alt C and Stützel H 1999 Predicting dry matter production of cauliflower (Brassica oleracea L. botrytis) under unstressed conditions II. Comparison of light use efficiency and photosynthesis-respiration based model modules. Scientia Horticulturae (submitted).

Kage H and Ehlers W 1996 Does root length density limit water uptake of field crops? Z. Pflanzenernähr. Bodenkde. 159, 583–590.

Kage H and Stützel H 1999a HUME: An object oriented component library for generic modular modelling of dynamic systems. In Modelling Cropping Systems. Eds. CSM Donatelli, F. Villalobos and JM Villar. pp 299–300. European Society of Agronomy, Lleida.

Kage H and Stützel H 1999b A simple empirical model for predicting development and dry matter partitioning in cauliflower (Brassica oleracea L. botrytis). Sci. Horticult. 80, 19–38.

Klepper B and Rickman R W 1990 Modeling crop root growth and function. Adv. Agron. 44, 113–132.

Kuhlmann H, Barraclough P B and Weir A H 1989 Utilization of mineral nitrogen in the subsoil by winter wheat. Z. Pflanzenernähr. Bodenk. 152, 291–295.

Levan M A, Ycas J W and Hummel J W 1987 Light leak effects on near-surface soybean rooting observed with minirhizotrons. In Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics. Ed. HM Taylor. Vol. 50, pp. 89–99. American Society of Agronomy, Madison.

Maertens C 1987 Ways of using edoscopy to determine growth and quality of root systems. In Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics. Ed. American Society of Agronomy. Vol. 50, pp 31–37. American Society of Agronomy, Madison.

Majdi H, Smucker A J M and Persson H 1992 A comparison between minirhizotron and monolith sampling methods for measuring root growth of maize (Zea mays L.). Plant Soil 147, 127–134.

Manschadi A M, Sauerborn J, Stutzel H, Gobel W and Saxena M C 1998 Simulation of faba bean (Vicia faba L.) root system development under Mediterranean conditions. Eur. J. Agr. 9, 259–272.

Marquardt D W 1963 An algorithm for least-squares estimation of nonlinear parameters. J. Soc. Ind. Appl. Math. 11, 431–441.

Masse J, Tardieu F and Colnenne C 1991 Rooting depth and spatial arrangement of roots in winter wheat. In Plant Roots and their Environment. Eds. B L McMichael and H Persson. pp 480–486. Elsevier, Amsterdam.

Newman E I 1966 A method of estimating the total root length in a sample. J. appl. Ecol. 139–145.

Pages L and Jordan M O 1991 Root structure of corn (Zea mays L.). II. A three-dimensional simulation model. Dev. agricult. managed-forest ecol. 24, 608–619.

Pellerin S and Pages L 1994 Evaluation of parameters describing the root system architecture of field grown maize plants (Zea mays L.). 1. Elongation of seminal and nodal roots and extension of their branched zone. Plant Soil 164, 155–167.

Press W H, Flannery B P, Teukolsky S A and Vetterling W T 1986 Numerical recipes, Cambridge University Press, Cambridge. 735 p.

SAS Institute 1988 SAT/STAT User's Guide. Cary, North Carolina.

Savin R, Hall A J and Satorre E H 1994 Testing the Root Growth Subroutine of the CERES-Wheat Model for 2 Cultivars of Different Cycle Length. Field Crops Res. 38, 125–133.

Schenk M, Heins B and Steingrobe B 1991 The significance of root development of spinach and kohlrabi for N fertilization. Plant Soil 135, 197–203.

Smit A L, Booij R and Van der Werf A 1996 The spatial and temporal rooting pattern of Brussels sprouts and leeks. Neth. J. Agricult. Sci. 44, 57–72.

Smith P, Smith J U, Powlson D S, McGill W B, Arah J R M, Chertov O G, Coleman K, Franko U, Frolking S, Jenkinson D S, Jensen L S, Kelly R H, Klein-Gunnewiek H, Komarov A S, Li C, Molina J A E, Mueller T, Parton W J, Thornley J H M and Whitmore A P 1997 A comparison of the performance of nine soil organic matter model using datasets from seven long-term experiments. Geoderma 81, 153–225.

Tardieu F 1988 Analysis of the spatial variability of maize root density I. Effect of wheel compaction on the spatial arrangement of roots. Plant Soil 107, 259–267.

Tardieu F, Bruckler L and Lafolie F 1992 Root clumping may affect the root water potential and the resistance to soil-root water transport. Plant Soil 140, 291–301.

Taylor H M, ed. 1987. Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics, Vol. 50. ASA/CSSA/SSSA, Madison, WI.

Thorup-Kristensen K 1998 Root growth of green pea (Pisum sativum L.) genotypes. Crop Sci. 38, 1445–1451.

Thorup-Kristensen K and Van den Boogaard R 1998 Temporal and spatial root development of cauliflower (Brassica oleracea L. var. botrytis L.). Plant Soil 201, 37–47.

Upchurch D R 1987 Conversion of minirhizotron-root intersections to root length density. In Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics. Ed. HM Taylor. Vol. 50, pp 143. American Society of Agronomy, Madison.

Van Noordwijk M, Brouwer G and Harmanny K 1993 Concepts and methods for studying interactions of roots and soil structure. Geoderma 56, 351–375.

Van Noordwijk M, Brouwer G, Koning H, Meijboom F W and Grzebisz W 1994 Production and decay of structural root material of winter wheat and sugar beet in conventional and integrated cropping systems. Agric. Ecosyst. Envir. 51, 99–113.

Van Noordwijk M and Van de Geijn S C 1996 Root, shoot and soil parameters required for process-oriented model crop growth limited by water or nutrients. Plant Soil 183, 1–25.

Vepraskas M J 1988 Bulk density values diagnostic of restricted root growth in coarse-textured soils. Soil Sci. Soc. Am. J. 52, 1117–1121.

Vos J and Groenwold J 1987 The relation between root growth along observation tubes and in the bulk soil. In Minirhizotron Observation Tubes: Methods and Applications for Measuring Rhizosphere Dynamics. Ed. HM Taylor. Vol. 50, pp 39–49. American Society of Agronomy, Madison.

Wiesler F and Horst W J 1994a Root growth and nitrate utilization of maize cultivars under field conditions. Plant Soil 163, 267–277.

Wiesler F and Horst W J 1994b Root growth of maize cultivars under field conditions as studied by the core and minirhizotron method and relationships to shoot growth. Z. Pflanzenernähr. Bodenk. 157, 351–358.

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Appendix

Equation (2) may be transformed to:

$$W_{tR} = e^{p_{tr}} W_{sh}^{o_{tR}}$$

Differentiation of Equation (A1) with respect to W_{sh} results in:

$$\frac{dW_{tR}}{dW_{sh}} = e^{p_{tR}} o_{tR} W_{sh}^{o_{tr}-1}$$

Applying the chain rule to the left hand side of Equation (A2) and rearranging leads to:

$$\frac{dW_{tR}}{dt} = \frac{dW_{tR}}{dW_{sh}} \frac{dW_{sh}}{dt}$$

Assuming that a certain fraction of total dry matter growth rate, f_{fR}, is allocated to the fine-root fraction the fine root growth rate simply is:

$$\frac{dW_{fr}}{dt} = f_{fR} \frac{dW_t}{dt}$$

From this Equation (1) may be rewritten:

$$\frac{dW_{sh}}{dt} = \frac{dW_t}{dt}(1 - f_{fR}) - \frac{dW_{tR}}{dt}$$

Introducing Equation (A2) into Equation (A3) and substituting for dW_{tR}/dt in Equation (A5) and some rearranging gives:

$$\frac{dW_{sh}}{dt} = \frac{dW_t}{dt}\left(\frac{1 - f_{fR}}{1 + e^{p_{tR}} o_{tR} W_{sh}^{o_{tr}-1}}\right)$$