

Effect of variety, irrigation regime and planting date on depth, rate, duration and density of root growth in the potato (*Solanum tuberosum*) crop

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SUMMARY

Experiments were conducted over the period 1987–94 at Cambridge University Farm and two other sites to examine the effect of various husbandry factors, particularly variety and irrigation regime, on rate, depth and density of rooting in potatoes. Maximum rooting depth ranged from 59 to 140 cm, indicating that potatoes can root to considerable depths and thereby have access to large volumes of water to satisfy the potential demand for water created by the atmospheric conditions and the size of the canopy. Root extension vertically through the soil profile was best described as a three-phase process: an initial rapid period lasting 3–5 weeks with growth rates *c.* 1.2 cm/day, a second period of slower growth (*c.* 0.8 cm/day), followed by cessation of root extension for the rest of the life of the crop. Variety had a major influence on the ultimate depth of rooting, primarily owing to variations in the length of the different periods of rooting rather than the rate in each period. It was observed that changes in the rate, or the cessation of root penetration were always preceded 4–9 days earlier by a change in the rate, or cessation, of leaf appearance. This feature should make it possible to characterize the duration of rooting of varieties through measurement of leaf emergence. Varieties which ceased leaf production early, such as Atlantic, were found to have a duration of root growth of *c.* 60 days, with Cara rooting for *c.* 30 days longer. Maximal total root length (TRL) and root length density (RLD) in the experiments reported were 16.9 km/m² and 5.5 cm/cm³, respectively, similar to those found previously in potatoes and crops such as sugar beet, but considerably greater than many other vegetables. Rooting density decreased with depth, but the root systems were not as surface-oriented as many other studies have shown. When TRL was close to its maximum, the vertical distribution of RLD showed that between 40 and 73% was confined to the upper 30 cm, with irrigated crops possessing a greater proportion of their roots in the plough layer. Despite being planted in rows 70–91 cm apart, rooting systems were homogeneously distributed in a horizontal direction by *c.* 35 days after emergence, at which time the roots had reached a depth of *c.* 50 cm. Therefore, apart from a short period after emergence, the potato crop is capable of accessing considerable volumes of soil from which to extract water and nutrients. Ensuring that soil conditions are conducive to maximal rates of root growth should be the target for growers, since this will lead to a more efficient use of soil water and irrigation.

INTRODUCTION

It has long been recognized that the potato crop is frequently responsive to irrigation (North 1960; Llewelyn 1967; Smith 1977; Harris 1978; Van Loon 1981; Anon. 1982; Bailey 1990; Gregory & Simmonds 1992), and in the UK the proportion of the crop area which is irrigated has increased from 15% in 1977 to 54% in 1999 (Anon. 2000). In this period the crop has

increasingly been grown on light, sandy soils on which irrigation is essential for both yield and quality. Potatoes consume far more irrigation water than any other crop in the UK. In 1995, 51% of all irrigation by volume was applied to potatoes, whereas the crop only accounted for 40% of the irrigated area (Anon. 1996). The widespread use of irrigation on such soils has raised concerns about the efficiency of water use and the risks of nitrogen leaching leading to pollution of groundwater. These concerns are largely based on the oft-repeated assumption that potatoes are shallow rooting and the consequential need to apply water

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frequently to maintain small soil moisture deficits (SMDs).

The perception of potatoes as a relatively shallow-rooted crop, similar to some temperate legume crops e.g. field beans (Gregory 1988), but falling well short of the penetration (150–200 cm) achieved by many winter cereal or sugar beet crops (Gregory *et al.* 1978; Brown *et al.* 1987) is, however, quite contrary to the early work of Weaver (1926). He showed that in soil without serious increase in resistance to root penetration with depth, potato root systems reach at least 1 m in depth and for most of that depth achieve a lateral structure of similar length. Apart from Weaver's work, which was pictorial in that entire root systems were extracted using pin-boards and then photographed or traced, there have been few quantitative studies of the growth and development of potato root systems, although there are other data showing that rooting depth can be considerable (Inforzato & Nobrega 1962; Fulton 1970; Durrant *et al.* 1973; Stone 1982; Allen & O'Brien 1985; Parker *et al.* 1989). However, owing to the vertical distribution of root produced by potato crops there may be little correlation between the maximum depth of root penetration achieved and the quantity of water taken up to satisfy the atmospheric demand (Gregory & Simmonds 1992).

The distribution of a crop rooting system can be defined by measurements such as root length density (RLD, cm/cm³), root dry weight (RDW, g/m²), total root length (TRL, km/m²) in the soil profile, or maximum depth of rooting (D_{\max} , cm). The combined influence of these root system parameters on water uptake in potatoes is not well understood, and therefore more detailed knowledge of the root system of potatoes (i.e. its size and extension and the position of roots in relation to water and nutrient supply) is required. This should provide understanding of how adequately the root system fulfils its role under a range of conditions, and whether below-ground limitations in accessing soil water account for any discrepancy between potential and actual growth of the crop. Measurements relating to rooting density are difficult to obtain and, therefore, there is a paucity of data pertaining to spatial and particularly chronological changes in root growth and distribution in potatoes. Since the growing season of most potato crops is short compared with winter cereals, D_{\max} might be expected to be shallow. However, the ultimate depth of rooting of any crop is a function of the duration of active root growth and the rate at which root growth occurs. The shorter growing season of potatoes compared with winter cereals could be compensated by more rapid rates of rooting. From the literature, there appear to be conflicting reports on the temporal pattern of root growth in potatoes.

Lesczynski & Tanner (1976) observed that RDW and TRL increased until 49–89 days after emergence

(DAE), depending on their irrigation and fertilizer regime. Irrigation regime altered both the maximum size of the root system and the time when this peak occurred. In one season, Vos & Groenwold (1986) found that RDW and TRL increased rapidly until 45 DAE then, following a slight (10%) decrease, remained constant until 101 DAE. In the succeeding season, RDW increased until the final sampling (80 DAE). In contrast, Asfary *et al.* (1983) observed that TRL did not change significantly from 2 weeks after emergence in 1977, whereas in the following season TRL peaked at *c.* 8 weeks after emergence. Opena & Porter (1999) found that TRL increased from 22 to 50 DAE, then decreased. Peak TRLs vary considerably between authors, but are substantially in excess of those for field beans and most vegetable crops, similar to cotton and sugar beet, but lower than the maximum values for winter wheat (Table 1).

Several reports in the literature also indicate that the potato crop appears to have a large proportion of its root system concentrated in superficial horizons. Most authors report that 80–90% of TRL is concentrated in the uppermost 30 cm of soil (Lesczynski & Tanner 1976; Asfary *et al.* 1983; Parker *et al.* 1989; Gregory & Simmonds 1992). The latter authors suggested that an explanation for the surface orientation might be the greater sensitivity of potato roots to unfavourable subsoil conditions and pans caused by cultivation compared with other crops such as cereals. Bishop & Grimes (1978) similarly reported that RLD was very sensitive to compaction in the subsoil. Since potato crops tend to be grown on widely spaced rows, it is possible that rooting is heterogeneous, being mainly concentrated under the plant rows, with only sparse rooting under the furrow. This has obvious implications for the efficiency of extraction of water from the soil. However, Lesczynski & Tanner (1976) observed that RLD was similar directly underneath rows and furrows after only 33 DAE. Vos & Groenwold (1986) found that RLD both within the hill (top 20 cm) and down to 1 m was higher between plants within the ridge than directly underneath plants by 53 DAE. By 80 DAE, root growth under the furrow had increased but was still less than under the ridge.

Without detailed knowledge of root growth it is inevitably difficult to schedule the application of irrigation as the estimation of potential soil supply of water is constrained irrespective of crop demand. The implicit need for frequent irrigation of potatoes on light sandy soils may therefore be exaggerated. This paper reports studies of root growth in relation to varying agronomic and environmental conditions over the period 1987–94 conducted at Cambridge University Farm (CUF) and two other sites. From these data the relationship between crop demand for water and soil supply of water has been established as the basis for efficient irrigation scheduling.

Table 1. Maximal total root length (TRL) in contrasting crop species

Species	Variety	TRL (km/m ²)	Sample depth (cm)	Source
Potato	Russet Burbank	8.4-11.4	70	Lesczynski & Tanner (1976)
	White Rose	1.6-4.6	91	Bishop & Grimes (1978)
	Vanessa	13.6-18.3	90	Asfary <i>et al.</i> (1983)
	Bintje	4.0-7.1	70	Vos & Groenwold (1986)
	Record	7.8-20.9	100	Parker <i>et al.</i> (1989)
	Norin 1	12.5-24.1	90	Iwama <i>et al.</i> (1993)
	Konafubuki	7.8-12.8	90	Iwama <i>et al.</i> (1993)
	Superior	3.8-8.7	45	Opena & Porter (1999)
Sugar beet	Regina	12.9	150	Brown <i>et al.</i> (1987)
Winter wheat	Maris Huntsman	23.5	200	Gregory <i>et al.</i> (1978)
	Avalon	19.3-32.1	180	Barraclough & Weir (1988)
Winter oilseed rape	Bienvenu	24.8	180	Barraclough (1989)
Field bean	*	1.7	80	Gregory (1988)
Broad bean	*	1.8	85	Greenwood <i>et al.</i> (1982)
Cauliflower	*	11.9	85	Greenwood <i>et al.</i> (1982)
Lettuce	*	2.4	85	Greenwood <i>et al.</i> (1982)
Onion	*	1.8	85	Greenwood <i>et al.</i> (1982)
Parsnip	*	5.7	85	Greenwood <i>et al.</i> (1982)
Pea	*	5.6	85	Greenwood <i>et al.</i> (1982)
Turnip	*	15.4	85	Greenwood <i>et al.</i> (1982)
Cotton	GSA 71	5.8-11.7	90	Kamara <i>et al.</i> (1991)

* Not given.

MATERIALS AND METHODS

This paper reports the effects of agronomic factors and variety on rooting parameters (rate of root extension, D_{\max} , RLD and TRL) and the relationship between leaf appearance and root extension. Experiments were conducted at CUF and two other sites (Gleadthorpe Experimental Husbandry Farm, Meden Vale, Mansfield, Nottinghamshire and Terrington Experimental Husbandry Farm, Terrington, King's Lynn, Norfolk) over the period 1987-94 (Table 2). The experiments were subjected to natural rainfall, except during 1989-93 when crops were grown under permanent polythene rainshelters (Polybuild Ltd) of dimensions 16 m × 8 m. Temperatures were increased under the rainshelters compared with ambient, but both ends of the shelter were left open and the sides were only clad to a height of 30-50 cm above the ground so air flow was good. Global radiation under the rainshelters was reduced by *c.* 23% (Stalham 1989), but crops grew normally compared with crops grown outside the shelters. Soil cultivations involved ploughing, spring tining and rotavating to 20 cm depth before drawing up ridges (unless planting was on the flat) prior to planting seed tubers using hand dibbers. Techniques for studying root growth were modified throughout the experimental programme, but a general outline of the methods is given before the details of individual experiments are discussed.

Maximum depth of rooting

Maximum depth of rooting (D_{\max}) was determined by

digging profile pits at the end of the season using a spade or JCB digger. At least two harvest rows were exposed and the depth of the deepest roots recorded in all rows. Measurements were taken from the top of the ridge or the soil surface for flat plantings.

Rate of rooting

Rate of vertical root growth was determined from periodic observations of profile pits. At 50% plant emergence profile pits were dug by hand using a spade across two harvest rows and D_{\max} recorded. The pits were enlarged both down the length of the plot, leaving two discard plants between each successive digging, and vertically. The number of determinations of D_{\max} varied between experiments.

Leaf appearance

The number of leaves on the mainstem greater than 5 mm in length and at least partially unfurled were counted from plant emergence, initially at 3-4 day intervals, and then weekly until leaf emergence ceased. The 10th, 15th, 20th, 25th and 30th leaves were tagged with coloured wire so that they could easily be identified to aid counting. The positions of visible floral initials were noted and leaf counting continued on subsequent sympodial branches.

Root length density and total root length

Total root length is calculated from the sum of all horizons of RLD, and is therefore dependent on plant

Table 2. *List of experiments and treatments*

Expt	Year	Site	Variety	Irrigation regime	Date of planting
1	1987	CUF	Record	None, 30 mm @ 40 mm SMD	15 April; 6 May
2	1987	Gleadthorpe	Record	15 mm @ 20 mm SMD 16–44 DAE, then 25 mm @ 35 mm SMD (Early); 25 mm @ 35 mm SMD (Late)	6 April; 5 May
3	1987	Terrington	Record	Rained only	5 May
4	1988	CUF	Record	15 mm @ 20 mm SMD 16–44 DAE, then 30 mm @ 40 mm SMD (Early); 30 mm @ 40 mm SMD (Late)	8 April; 6 May
5	1988	Gleadthorpe	Record	15 mm @ 20 mm SMD 16–44 DAE, then 25 mm @ 35 mm SMD (Early); 25 mm @ 35 mm SMD (Late)	11 April; 5 May
6	1988	Terrington	Record	Rained only	6 May
7	1989	CUF (Rainshelter)	Record	None (Dry); 15 mm @ 20 mm SMD 16–44 DAE, then 30 mm @ 40 mm SMD (CUF*); 5–6 mm @ 10 mm SMD (Wet)	6 April
8	1990	CUF (Rainshelter)	Cara	None (Dry–Dry); 20 mm starting 44 DAE whenever limiting SMD reached (Dry–Wet); SMD < 20 mm from planting to 44 DAE (Wet–Dry)	30 March
9	1991	CUF (Rainshelter)	Cara; Estima; Record	None (Dry); Irrigated (CUF)	15 April
10	1992	CUF (Rainshelter)	Cara	No irrigation (W1); dry until 44 DAE, then irrigated at same frequency as W6 (W2); irrigated as W6 from 21–72 DAE (W3); irrigated as W6 from emergence until 72 DAE (W4); irrigated according to CUF (W5); irrigated to maintain SMD at 10–25 mm (W6)	7 May
11	1993	CUF (Rainshelter)	Cara; Estima	No irrigation (W1); 12–20 mm at CUF Limiting SMD (W2); 4–12 mm @ 25 mm SMD (W3)	22 April
12	1994	CUF	Arran Comet; Atlantic; Cara; Desiree; Erntestolz; Estima; Hermes; Lady Rosetta; Maris Piper; Panda; Pentland Dell; Pentland Squire; Record; Russet Burbank; Saturna; Shepody	Irrigated according to CUF	29 April (P Dell, 3 May)

* CUF, Cambridge University Farm Potato Irrigation Scheduling Scheme; irrigation applied when Limiting SMD reached. 'Limiting' was defined as the amount of water available within the rooting zone held at a tension of less than 60 kPa.

Table 3. *Soil texture and Series, row width, plant spacing, profile and irrigation method*

Expt	Soil texture (Series)*	Row width (cm)	Plant spacing (cm)	Planting depth (cm)	Profile	Irrigation method
1	Slightly stony sandy loam/sandy clay loam (Milton)	71	26	10	Ridge	Overhead
2	Slightly stony medium loamy sand/sand (Cuckney)	86	21	12	Ridge	Overhead
3	Stoneless silt loam (Agney)	91	20	10	Ridge	None
4	Stony sandy loam/sandy clay loam (Milton)	71	26	10	Ridge	Overhead
5	Slightly stony medium loamy sand/sand (Cuckney)	86	21	12	Ridge	Overhead
6	Stoneless silt loam (Newchurch)	91	20	10	Ridge	None
7	Very slightly stony sandy loam (Milton)	67	30	10	Ridge	Drip
8	Stony sandy loam/clay loam (Milton)	72	18	9	Flat	Drip
9	Slightly stony sandy loam/sandy clay loam (Milton)	71	20	10	Flat	Drip
10	Stony sandy loam/sandy clay loam (Milton)	71	20	10	Flat	Drip
11	Stony sandy loam (Milton)	71	20	9	Flat	Drip
12	Slightly stony sandy clay loam/clay loam (Milton)	71	20	8	Ridge	Overhead

* Soil series taken from Anon (1983).

population density, which was generally similar across all experiments (Tables 2 and 3). The measurement of RLD in all experiments was made using different combinations of hand-made corers and gouge augers. In order to prevent soil contamination between horizons, the immediate area to be soil sampled was wetted to depth 2–3 days previously to prevent dry soil falling into the hole made by the auger after withdrawal or loss of soil from the auger on its removal. Wetting also aided penetration of the auger in unirrigated plots. The extracted core was divided into either 10 or 20 cm horizons depending on depth. Unless several cores were taken in different spatial positions across the profile, the different horizons of replicate cores were bulked together and frozen in sealed polythene bags until analysis could take place. Details of the sampling positions are given under the individual experiments.

Roots were extracted from the cores in the laboratory by a modified hydro-elutriation system (Cahoon & Morton 1961; Smucker *et al.* 1982) using a series of diminishing mesh grids (2, 1, 0.5, 0.2 mm) to collect the roots following initial tests after the recommendation of Böhm (1979). Roots were floated off using filter paper and washed into a plastic tray, or collected from the meshes using tweezers. Newman's (1966) grid intersection technique as modified by

Marsh (1971) and Tennant (1975) was used to estimate total root length per sample. For large samples of roots, a 1 × 1 cm grid formed from graph paper was taped to the bottom of a 30 × 21 cm transparent plastic tray, whilst for smaller samples a 0.5 × 0.5 cm grid was attached to a 17 × 11 cm tray. Dead, brown root material of potato origin was included in RLD determinations, but owing to the fragility of these older roots, recovery on extraction from the soil was inherently low.

Root dry weight

Root dry weight (RDW) was measured after drying washed samples of roots subjected to RLD determinations for 48 h at 90 °C. Horizons were kept separate so that relationships could be established between RLD and RDW.

Individual experiments

Details of the experimental treatments and methods are presented in Tables 2 and 3. Experiments 1 and 4 used randomized block designs involving all combinations of 2 irrigation regimes, 2 dates of planting (see Tables 2 and 3) and two physiological ages of seed (0 and 330 °Cdays > 4 °C) as treatments. The experimental design in Expts 2 and 5 was a split plot,

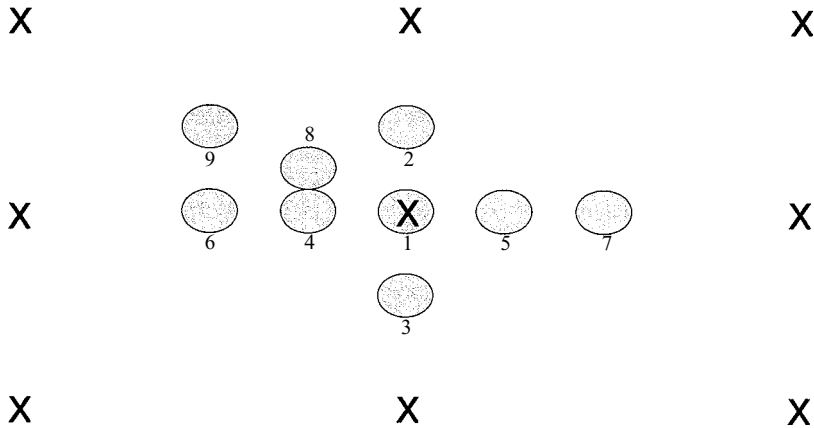


Fig. 1. Core sampling positions for rooting density (O) in relation to position of plants (X).

with irrigation regime \times date of planting as the main plots. In Expts 3 and 6, the sole treatments were the two physiological ages. Physiological age had no effect on rooting parameters and data were averaged (means) over this treatment combination. Experiments had four replicates, except for Expts 3 and 6 (eight), and Expts 9–12 (three). The experimental design in Expts 7–12 was a randomized block, with the treatments appearing in Table 2. Variates were analysed by analysis of variance using the Genstat 5 statistical package (Payne *et al.* 1993). Treatment means are stated to be significantly different only if the probability of differences occurring by chance were less than 5% ($P < 0.05$).

Experiments 1–6

Measurements of D_{\max} were taken at the end of the season. RLD was measured on all sites in Expts 4–6 using two different corers to sample the root system. In the upper 40 cm of soil, a cut-off length of 7.6 cm diameter aluminium irrigation pipe was pushed 10 cm into the soil and excavated after pushing a builders trowel underneath the leading edge to prevent the soil escaping. This was repeated four times, excavating the soil around the pipe as the depth increased. The auger was changed to a 2-part steel gouge auger (cutting diameter 5.8 cm) for depths greater than 40 cm. The auger was hammered into the soil in 20 cm increments, before being withdrawn using a 'tommy bar'. The gouge auger was lined with perspex sleeves to aid soil removal upon splitting the auger into two halves. From 60 to 100 cm depth, cores were split into 10 cm increments. In the April-planted, early irrigated treatments at CUF and Gleadthorpe cores were taken from seven positions to examine the spatial variability in RLD:

1. Directly below the 'central' plant (or as close to the seed tuber as possible).

2. Half-way between the 'central' and neighbouring plant on one side in the same ridge.
3. Half-way between the 'central' and neighbouring plant on the other side to (2) in the same ridge.
4. In the flanks of the ridge half-way between the 'central' plant and furrow bottom.
5. In the flanks of the ridge half-way between the 'central' plant and opposite furrow bottom.
6. In the furrow bottom on one side of the 'central' plant.
7. In the furrow bottom on the other side of the 'central' plant.

The sampling positions are depicted graphically in Fig. 1.

Two replicates of each position were taken from each plot and bulked together. A similar spatial sampling technique was used in potatoes by Leszczynski & Tanner (1976) and Vos & Groenwold (1986), and by Brown *et al.* (1987) in sugar beet. For all other treatments, RLD was determined by taking two replicate cores from each plot from positions 1 and 2 only. The sampling in these experiments was *c.* 65–70 and 49–55 DAE for April and May plantings, respectively.

Experiment 7

Maximum depth of rooting, D_{\max} , was estimated from breaking open cores during the estimation of rooting density, as well as digging profile pits at the end of the season. Spatial variation in RLD was measured in similar fashion to Expts 4–6, but only across the ridges (positions 1, 4, 5, 6, 7 in Fig. 1). Positions 2 and 3 in Fig. 1 were not sampled since RLD was assumed to have been homogeneous at the same depth within the ridge from an early stage, and certainly well before the root cores were taken (86 DAE). The same augers were used as in Expts 4–6.

Experiment 8

Planting in Expts 8–11 was changed to a flat profile in order to improve the accuracy of the neutron probe measurements of soil water content near the soil surface, so there were no ridges or furrows, but the relative positions of plants were the same. Maximum rooting depth, D_{\max} , was measured only at final harvest. Roots were sampled on 20–21 August (104–105 DAE) by coring to a depth of 100 cm using a gouge auger (diameter 6.0 cm) driven into the soil using a petrol-driven percussion hammer (Atlas Copco Cobra). The auger was extracted using a jack/ball-clamp arrangement (Eijkelkamp) and the core sectioned into segments: 0–10, 10–20, 20–30, 30–40, 40–60, 60–80 and 80–100 cm. This augering method was used for all subsequent experiments. Two cores were taken in each plot immediately between two plants within the row (position 2, Fig. 1) and bulked together.

Experiment 9

Maximum rooting depth, D_{\max} , was measured on five occasions by extending a profile pit into the plot. On two occasions, 28 June (46 DAE) and 26 July (74 DAE), roots were sampled by coring to a depth of 100 cm from position 2 (Fig. 1). Two replicates were taken from each plot and bulked together.

Experiment 10

Maximum rooting depth, D_{\max} , was measured on eight occasions as in Expt 9. Root length density was measured to a depth of 100 cm on two occasions, 14 July (54 DAE) and 11 August (82 DAE). The sampling position was mid-way between two plants within the row (position 2, Fig. 1), and the soil from two cores per plot was bulked together. In the uppermost 40 cm of soil, RLD was determined in 10 cm increments, below this depth soil cores were bulked together over 20 cm horizons.

Experiment 11

Maximum rooting depth, D_{\max} , was measured on seven occasions as in Expt 9. Three batches of root cores were taken to determine RLD. The samples were taken earlier than in previous experiments (20, 37 and 79 DAE), since the previous work had shown that initial root growth was rapid and short-lived in determinate varieties such as Estima. At 20 DAE sampling position was likely to be more critical than later in the season, since roots might be less homogeneous with respect to horizontal distance from the plant. Therefore it was decided to take an additional core from position 8 (Fig. 1), which was half way between position 1 (initially the greatest RLD) and position 9 (the lowest RLD). An assumption was made that the distribution of roots horizontally would be the same as that measured

vertically until the RLD in the region furthest from two pairs of plants in adjacent rows (position 9, Fig. 1), was the same as that close to the plant. It was found that mean RLD at 20 DAE would have been only 87% of that estimated from the two core positions taken owing to the rapid decrease in RLD between 25 and 35 cm radially from the plant centre. Therefore, both TRL and RDW were adjusted by this factor for the earliest sampling, but the data from the two later samplings were taken from position 2 only, thereby permitting comparisons with earlier experiments.

Experiment 12

In order to further test the effect of variety on the dynamics of rooting, this experiment tested 16 varieties of varying determinacy. A total of 11 determinations of D_{\max} were made weekly until mid-August, with the final rooting depth measured on 26 August, using the method of Expt 9.

RESULTS

Maximum depth of rooting (D_{\max})

Tables 4 and 5 show that D_{\max} was usually more than 60 cm and in several cases more than twice this depth. Overall, the results are much closer to the depths found by Weaver (1926) than the depths which might be described as from a shallow-rooting crop. The depth of rooting of all varieties was affected by soil water regime in many experiments. Forcing crops to exist solely on soil water reserves rather than having access to rainfall or irrigation produced the deepest rooting. The maintenance of small SMDs throughout growth reduced D_{\max} compared with no supplementary irrigation (Table 5). There was a trend in Expts 2 and 5 for the use of irrigation early in the season to reduce D_{\max} compared with the use of irrigation only later in the season, but the differences were not significant. Where there was little effect of irrigation regime on D_{\max} , as at CUF in Expts 1 and 4, the roots were prevented from growing deeper by the water table at *c.* 90 cm.

Varieties differed markedly in D_{\max} . Cara consistently produced deeper rooting systems than other varieties and on favourable sites was capable of rooting well beyond 1 m. Estima was consistently shallower rooting than Cara and was one of several varieties which only rarely approached a D_{\max} of 1 m. There are, therefore, potentially large differences between varieties in access to soil water supplies if D_{\max} were to be used as the criterion for potential water uptake.

Rate of root penetration

The data for root penetration of all varieties and irrigation regimes visually conformed to a broad

Table 4. *Effect of season, site, date of planting and irrigation regime on maximum rooting depth (D_{max}) in the variety Record (Expts 1-6)*

Expt	Season	Site	Date of planting	Irrigation regime	D_{max} (cm)	S.E. (D.F.)
1	1987	CUF	15 April	None	90	1.2 (21)
			6 May	Late	87	
				None	87	
2		Gleadthorpe	6 April	Early	59	8.8 (9)
			5 May	Late	71	
				Early	93	
			Late	106		
3	1988	Terrington	5 May	—	117	12.1(7)
4		CUF	8 April	Early	89	0.8 (21)
			6 May	Late	88	
5		Gleadthorpe		11 April	Early	105
			5 May	Late	127	
				Early	100	
6		Terrington	6 May	Late	102	8.9(7)
			—	109		

Table 5. *Effect of irrigation regime and variety on maximum rooting depth (D_{max}) in Expts 7, 8, 9 and 11*

Expt	Variety	Irrigation regime	D_{max} (cm)	S.E. (D.F.)
7	Record	Dry	118	8.4 (6)
		Moist	99	
		Wet	88	
8	Cara	Dry-Dry	140	8.3 (6)
		Dry-Wet	115	
		Wet-Dry	120	
9	Estima	Dry	90	3.1 (10)
		Wet	88	
	Record	Dry	100	
		Wet	97	
	Cara	Dry	110	
		Wet	104	
11	Estima	Dry	88	4.5 (10)
		Moist	89	
		Wet	80	
	Cara	Dry	118	
		Moist	115	
	Wet	105		

pattern comprising three periods. Initially there was a rapid rate of penetration for *c.* 3-5 weeks post-emergence, followed by a longer period of slower growth culminating in a cessation of further penetration (Fig. 2). Root functioning continued for some weeks after D_{max} had been achieved, as shown by changes in soil water content measured with a neutron probe.

In order to determine whether there were significant

differences in patterns or rates of root penetration caused by irrigation regime or variety, linear regressions were fitted between depth of rooting and time after emergence for individual varieties and irrigation regimes (where relevant) for different periods. In order to determine the point where the rate of rooting changed between the initial rapid period (1) and the slower second period (2), a Genstat split-line programme was used to analyse the data on rate of penetration from Expts 10-12 where sequential measurements of D_{max} were made. The data were constrained in Expts 11 and 12 to rooting depths measured up to 66 and 59 DAE, respectively, since these experiments included varieties which ceased root penetration *c.* 60 DAE. The programme calculated the point between period 1 and 2 to be *c.* 18-38 DAE (Table 6).

Although the Genstat split-line programme calculated the position of any break point, it did not test if the split line was a significantly better fit than a single straight line. To enable comparison, the two parts of the split line were considered as two separate lines and the regression of two lines through the data, separated according to the break point calculated by the split-line programme, was compared with a single line through all the data. In running the comparison, equal weighting was given to the residuals of the deviations from the fitted lines as the two lines did not individually cover the same range as a single line through all the data. This analysis showed that the effects of variety or irrigation regime on rate within individual periods were not significant, but that the length of each period and the time of cessation of rooting were dependent on variety. There was a

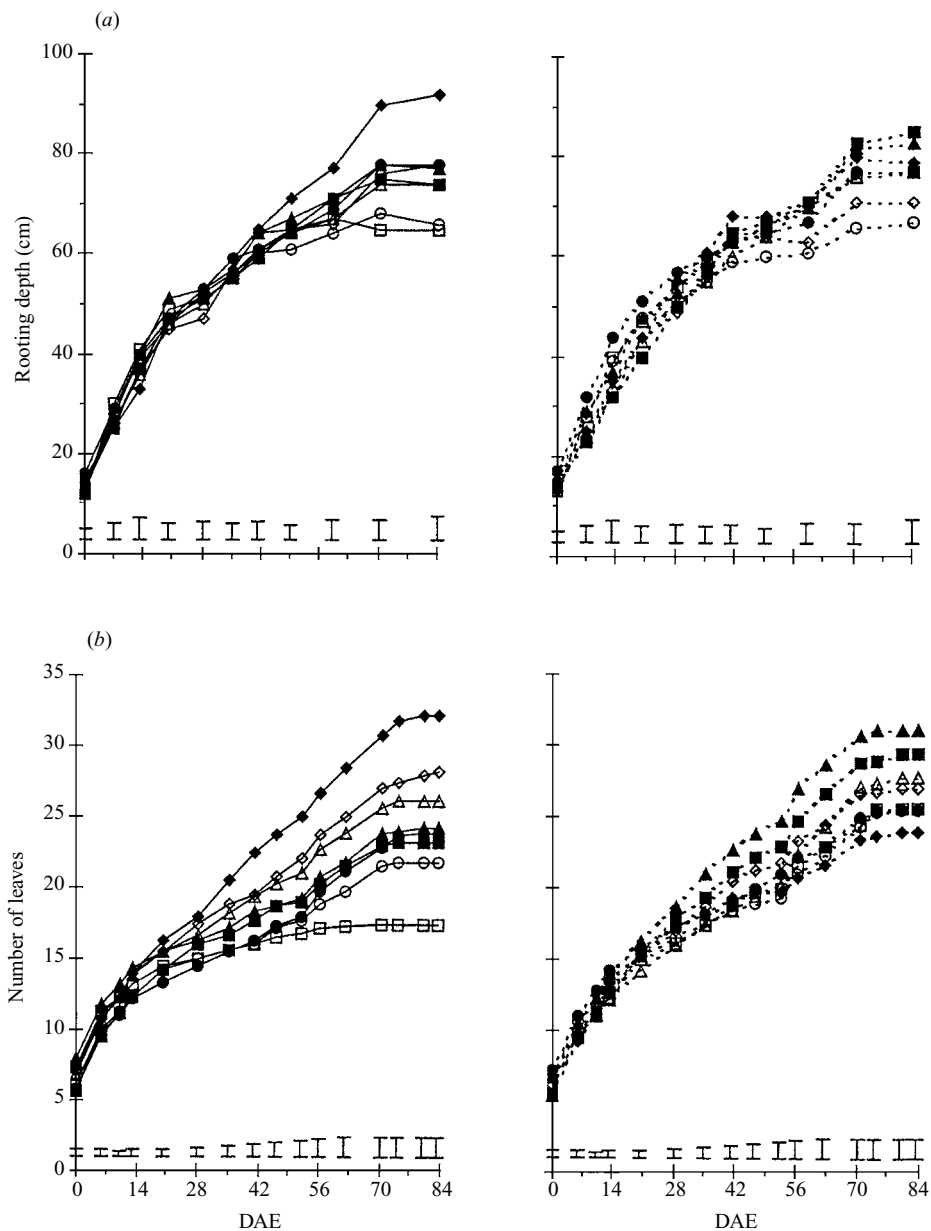


Fig. 2. Rooting depth (a) and number of emerged leaves (b) with respect to time after emergence for 16 varieties in Expt 12. A Comet (—■—), Atlantic (—□—), Cara (—◆—), Desiree (—◇—), Erntestolz (—▲—), Estima (—△—), Hermes (—●—), L Rosetta (—○—), M Piper (—■—), Panda (—□—), P Dell (—◆—), P Squire (—◇—), R Burbank (—▲—), Record (—△—), Saturna (—●—), Shepody (—○—). Error bars are S.E.

significant improvement when describing the rate of rooting as two distinct periods in Expts 11 and 12 as opposed to a single period, but the rate of rooting in periods 1 and 2 in Expts 9 and 10 was not significantly different, although it was numerically faster in period 1 than period 2 in Expt 9 (Table 6).

In Expt 11, Cara and Estima had the same rate of rooting in periods 1 and 2, and the same break point separating the two periods. Cara continued to extend its roots for longer than Estima which ultimately led to deeper rooting (Table 5). In Expt 12, there were significant differences between varieties in the length

Table 6. Rate of root penetration in different periods in Expts 9–12 (averaged (means) across varieties in all Expts, and irrigation regimes in Expts 9–11)

Expt	Period (DAE)*	Rate (cm/day)	S.E.	D.F.
9	0–34	1.26	0.099	10
	34–65	0.99	0.122	
	0–65	1.14	0.109	
10	0–29	0.78	0.121	10
	29–67	0.83	0.128	
	0–67	0.81	0.118	
11	0–38	1.28	0.107	10
	38–66	0.90	0.247	
	0–66	1.22	0.116	
12	0–26	1.59	0.188	30
	26–59	0.40	0.104	
	0–59	1.12	0.094	

* Duration of first period was determined by Genstat split-line programme.

of periods 1 and 2 (Table 7). Despite there being differences in the duration of the first phase of root penetration, there were no significant differences between varieties in the rate of root penetration during this phase. However, there were significant differences in rate of rooting between varieties in period 2.

Irrigation regime did not alter the timing of the change between the 1st and 2nd periods of rooting in Expts 9–11. Overall, differences in D_{\max} between varieties were caused mainly by differences in the

Table 8. Slope of the relationship between rooting depth and number of emerged leaves after emergence of 7th leaf for 16 varieties in Expt 12

Variety	Slope (cm/leaf)
A Comet	3.74
Atlantic	6.32
Cara	3.16
Desiree	2.99
Erntestolz	4.08
Estima	3.18
Hermes	3.46
L Rosetta	3.60
M Piper	3.09
Panda	3.17
P Dell	3.98
P Squire	2.82
R Burbank	2.59
Record	2.92
Saturna	3.11
Shepody	2.66
Mean	3.43
S.E. (30 D.F.)	0.464

duration of active root growth rather than by differences in rate of root penetration, although Expt 12 indicated that root extension rate in period 2 was affected by variety. The rate of root penetration in the 1st phase and the overall rate to cessation were broadly similar to published values for other potato crops.

Table 7. Break point, rate of rooting in periods 1 and 2, and duration of root penetration in 16 contrasting varieties in Expt 12

Variety	Break point Period 1–2 (DAE)	Rate (period 1) (cm/day)	Rate (period 2) (cm/day)	Duration of root growth (DAE)
A Comet	17.6	1.90	0.64	71
Atlantic	19.6	1.87	0.43	58
Cara	27.8	1.51	0.69	90
Desiree	37.8	1.19	0.08	80
Erntestolz	18.2	1.98	0.57	73
Estima	22.1	1.55	0.46	70
Hermes	25.2	1.45	0.43	72
L Rosetta	22.9	1.70	0.31	61
M Piper	35.8	1.31	0.47	73
Panda	21.5	1.73	0.54	81
P Dell	34.4	1.48	0.24	75
P Squire	37.9	1.24	0.03	63
R Burbank	24.2	1.58	0.38	77
Record	26.7	1.42	0.57	75
Saturna	20.8	1.86	0.30	72
Shepody	25.6	1.62	0.19	74
Mean	26.1	1.59	0.40	73
S.E. (30 D.F.)	4.19	0.188	0.104	4.0

Table 9. *Effect of irrigation regime and variety on total root length (TRL) in Expts 4–11*

Expt	Variety	Irrigation regime	TRL (km/m ²)	S.E.(D.F.)
4	Record	Early (8 April planting)	13.4	1.16 (21)
		Early (6 May planting)	12.8	
		Late (8 April planting)	13.7	
		Late (6 May planting)	13.4	
5	Record	Early (11 April planting)	14.2	1.20 (9)
		Early (5 May planting)	13.6	
		Late (11 April planting)	14.6	
		Late (5 May planting)	13.9	
6	Record		12.8	0.93 (9)
7	Record	Dry	12.1	0.64 (6)
		CUF	15.7	
		Wet	15.4	
8	Cara	Dry–Dry	7.1	0.99 (6)
		Dry–Wet	11.4	
		Wet–Dry	8.3	
9	Estima	Dry	8.4	1.95 (10)
		CUF	11.5	
	Record	Dry	8.5	
		CUF	15.7	
10	Cara	Dry	9.8	1.78 (10)
		CUF	18.1	
		W1	7.1	
		W2	7.3	
		W3	13.9	
		W4	12.2	
11	Estima	W5	15.6	1.15 (10)
		W6	14.9	
		Dry	9.1	
	Cara	CUF	14.1	
		Wet	13.7	
		Dry	11.1	
		CUF	16.9	
		Wet	16.4	

Relationships between root growth and leaf appearance

The general observation was that there was a change in rate of root penetration around the time of a change in the rate of appearance of new leaves, so that the patterns of growth between roots and leaves were similar. However, a change in rate of rooting was always preceded by a change in rate of leaf appearance (Fig. 2). Therefore, prior to the reduction in rate of rooting after phase one, there was a slowing in rate of leaf appearance. In order to determine the point at which the rate of leaf appearance decreased, a similar analysis to that used for rate of rooting was used. This showed that there was a decrease in rate of leaf appearance 5 days before a change in rooting was observed, and that there were no significant differences between varieties, although the error variation was large (S.E. = 3.1 days). The observation that changes in the rate of leaf appearance preceded changes in rate of rooting extended throughout the period of active

root growth. Therefore, if a variety had ceased root penetration completely it had already stopped producing new leaves *c.* 9 days (Expt 11) and 4 days (Expt 12) prior to this. Since Cara continued to produce new leaves for most of its life, rooting also continued to increase in depth throughout the season, leading to the deepest roots.

In Expt 10–12, it was apparent that the slowing in rate of root growth at the end of period 1 was preceded by a slowing in the rate of appearance of new leaves. It was found that close-fitting linear relationships (mean $R^2 = 0.95$) could be established between number of leaves and depth of rooting for the period of growth after *c.* seven leaves had emerged. Analysis of variance performed on the slope of the lines calculated in Expt 12 showed that all varieties except Atlantic had similar slopes (Table 8).

Whilst the relationships between rooting depth and number of emerged leaves in Cara and Estima had the same slope in Expt 12, the slope was steeper than in Expt 11. Thus, it is not possible to determine rooting

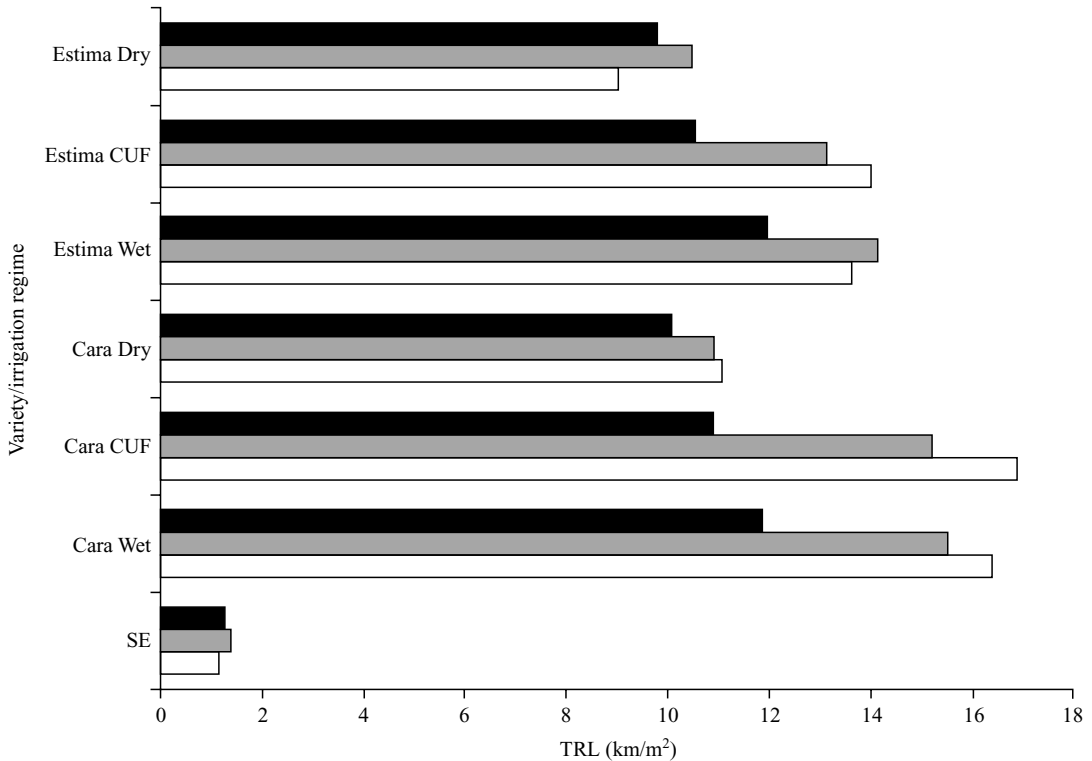


Fig. 3. Effect of time of sampling, irrigation regime and variety on total root length in Expt 11. 20 (■), 37 (▒), 79 (□) days after emergence.

depth from a simple procedure, e.g. counting the number of emerged leaves, because this is affected by variables such as soil conditions, but the characterization of the period of root penetration of different varieties is possible from such a technique.

Rooting density

Total root length (TRL)

The measurement of TRL indicated that potatoes are capable of producing very large rooting systems. Peak TRL varied from 7.1–18.1 km/m² (Table 9), with the range in values and maxima similar to the data produced by other authors working with potatoes (Table 1). Total root length increased as the season progressed (Fig. 3), although withholding irrigation completely reduced the increase substantially. The data from Expts 9 and 10 with only two later dates of sampling are not presented but show the same trend, although in Expt 9 the TRL of irrigated Estima decreased considerably between 51 and 79 DAE. With irrigation, Cara continued to increase its TRL until later in the season than Estima, ultimately producing a larger TRL (Fig. 3). The maximal TRL of the variety Record was in-between Estima and

Cara (Table 9). Keeping the soil close to field capacity as occurred in Expts 7, 10 and 11 did not produce larger rooting systems than crops kept much closer to their limiting soil moisture deficit (Table 9).

Completely dry crops produced very limited TRLs, except in Expt 7 where very favourable soil conditions produced prolific rooting, and the ratio of dry TRL to fully irrigated TRL was *c.* 78% compared with only 47–66% in Expts 8–11 (Table 9). Withholding irrigation for prolonged periods (Wet–Dry in Expt 8 and W2 in Expt 10) was deleterious compared with full irrigation in terms of producing a large TRL (Table 9). Early irrigation in Expts 4 and 5 had very little detrimental effect on TRL, and TRL was similar irrespective of date of planting in these two experiments (Table 10). Growing crops inside polythene rainshelters had little effect on the ultimate size of root system produced when compared with uncovered crops (Expts 4–6).

Homogeneity of rooting density (RLD)

Horizontal. Despite planting in widely spaced rows (70–91 cm), once the rooting system had reached its maximum size (during July and August for typical plantings) rooting was homogeneously distributed

Table 10. Effect of sampling position on root length density (cm/cm^3) at 65 days after emergence in early-irrigated, early-planted Record in Expt 5. (a) Inter-row; (b) Intra-row. Positions correspond to sampling locations detailed in Fig. 1

(a)

Depth (cm)	Position					S.E.
	6	4	1	5	7	
10		4.07	4.47	3.67		0.417
20		4.08	3.18	5.45		0.409
30	S	2.80	4.55	5.08	3.16	0.339
40	1.94	2.22	2.01	2.36	2.74	0.240
50	0.84	1.12	0.90	1.24	1.38	0.127
60	0.96	0.91	0.95	0.81	0.86	0.106
70	0.31	0.35	0.28	0.38	0.24	0.028
80	0.15	0.17	0.14	0.14	0.11	0.016
90	0.08	0.12	0.00	0.10	0.06	0.008
100	0.03	0.01	0.01	0.00	0.01	0.003

(b)

Depth (cm)	Position			S.E.
	2	1	3	
10	3.70	4.47	4.64	0.417
20	3.11	3.18	3.15	0.409
30	3.33	4.55	3.53	0.339
40	1.98	2.01	2.05	0.240
50	0.86	0.90	0.75	0.127
60	0.99	0.95	0.81	0.106
70	0.27	0.28	0.36	0.028
80	0.13	0.14	0.24	0.016
90	0.05	0.00	0.08	0.008
100	0.02	0.01	0.00	0.003

S, Stone layer.

horizontally, irrespective of irrigation regime. There were no significant effects of sampling position either within or between ridges on RLD in any particular horizon, even on wide rows such as used at Gleadthorpe (86 cm). A typical set of data is presented in Fig. 4 using the position notation described in Fig. 1.

Whilst crops grown without water had sparser rooting systems in the upper horizons than irrigated crops, irrigation regime had little effect on the horizontal distribution of RLD (Table 11).

In Expt 11, where sampling for RLD was more frequent, it was established that RLD would not become homogeneous horizontally until *c.* 35 DAE (see Materials and Methods). The data therefore indicate that, apart from a short period after emergence, the rooting system of potatoes is not confined to areas immediately underneath the row,

Table 11. Effect of sampling position and irrigation regime on root length density (cm/cm^3) at 86 days after emergence in Expt 7. (a) Dry; (b) CUF; (c) Wet. Positions correspond to sampling locations detailed in Fig. 1

Depth (cm)	Position					S.E.
	6	4	1	5	7	
(a)						
10		2.22	2.36	1.89		0.503
20	1.88	2.03	1.87	1.84	2.32	0.501
30	1.43	1.01	1.66	1.39	1.77	0.444
40	2.09	2.22	2.07	2.14	2.12	0.687
50	1.09	1.18	1.00	1.07	1.21	0.229
60	1.03	1.04	0.87	0.73	0.99	0.302
70	1.10	0.46	0.89	1.02	0.94	0.142
80	0.53	0.57	0.77	0.62	0.55	0.059
90	0.36	0.47	0.30	0.37	0.09	0.039
100	0.45	0.60	0.32	0.39	0.59	0.041
(b)						
10		2.79	2.41	2.22		0.503
20	2.13	2.17	2.17	3.66	2.22	0.501
30	3.69	2.77	1.54	1.89	2.00	0.444
40	3.80	3.69	4.13	5.10	3.61	0.687
50	1.08	1.21	1.24	1.79	2.00	0.229
60	1.18	1.06	1.42	1.43	1.30	0.302
70	1.17	0.88	1.00	1.23	0.77	0.142
80	0.19	0.41	0.22	0.21	0.23	0.059
90	0.16	0.08	0.12	0.16	0.23	0.039
100	0.13	0.10	0.06	0.11	0.26	0.041
(c)						
10		2.99	3.16	2.55		0.503
20	2.64	2.76	3.11	2.99	4.00	0.501
30	2.78	2.50	2.69	2.82	2.81	0.444
40	4.60	5.00	3.03	3.79	4.12	0.687
50	0.51	0.39	1.47	0.90	1.23	0.229
60	1.44	1.40	1.41	1.08	1.27	0.302
70	0.14	0.17	0.20	0.51	0.13	0.142
80	0.04	0.07	0.07	0.17	0.10	0.059
90	0.03	0.06	0.05	0.09	0.07	0.039
100	0.00	0.00	0.00	0.00	0.00	0.041

but (given favourable soil conditions) will spread horizontally to considerable distance so that roots can access considerable volumes of soil in search of both water and nutrients. In Expt 5 there was an apparent shift in RLD to one side in the 20–30 cm horizon (data not shown), since stone-windrowing had deposited a 10–15 cm layer of pebbles in the furrow bottom, and as a consequence root growth was very sparse in this region.

Vertical. It was observed that subterranean nodes close to the soil surface produced few root initials, which showed little branching. Therefore, there was generally an increase in RLD between 10 and 20 cm in depth, with the peak at 20–30 cm depth followed by a rapid decrease (Fig. 4).

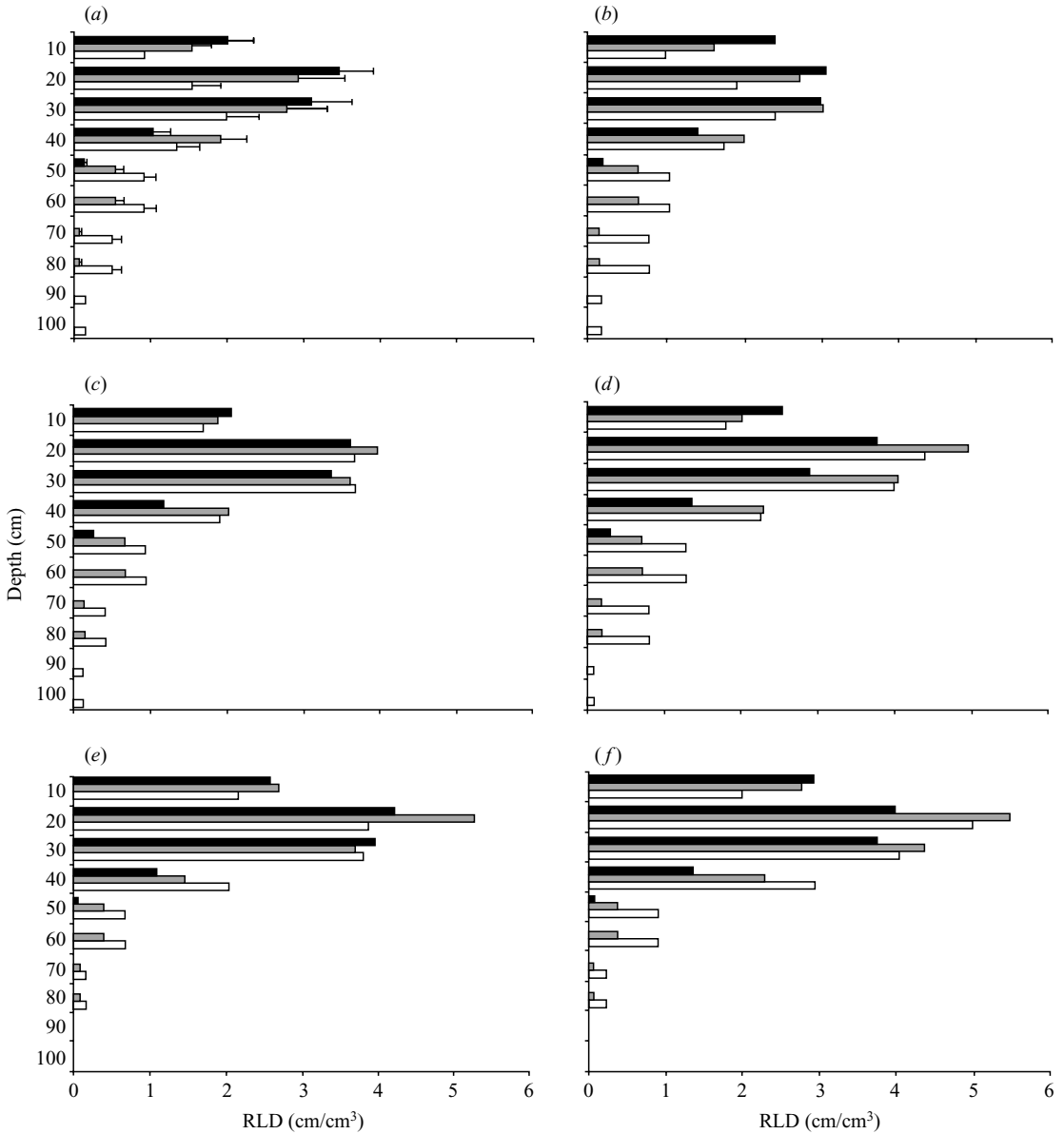


Fig. 4. Effect of depth and time of sampling, irrigation regime and variety on root length density in Expt 11. (a) Dry Estima; (b) Dry Cara; (c) CUF Estima; (d) CUF Cara; (e) Wet Estima; (f) Wet Cara. 20 (■), 37 (▨), 79 (□) days after emergence. Error bars are S.E.

In our experiments, some of the crops had only a slow decrease in RLD between 20 and 40 cm, with the marked decrease occurring at greater depths (e.g. Expt 7; Table 11). This contrasts with the results of Greenwood *et al.* (1982) working with a range of vegetable crops (see Table 1), who observed an exponential decrease in RLD with increasing depth from the soil surface depth, but the roots originated much closer to the surface than in the experiments

reported here owing to the deeper planting depth of potatoes compared with the vegetable species used by Greenwood *et al.* (1982).

The maximum RLD recorded was in Expt 11 (5.5 cm/cm³). This is a high value, but well below some of the values reported in the literature in the top 15 cm of soil, 9.7 cm/cm³ (Parker *et al.* 1989) to 19.1 cm/cm³ (Iwama *et al.* 1993).

Many authors have commented on the surface

Table 12. *Effect of irrigation regime and sampling date on root length density (RLD) (cm/cm³) in 0–30 and 30–100 cm horizons in Expt 10*

Depth (cm)	Sample date	Irrigation regime						S.E. (10 D.F.)
		W1	W2	W3	W4	W5	W6	
0–30	54 DAE	1.60	1.60	3.16	3.13	3.29	3.64	0.459
	82 DAE	1.34	1.67	2.99	2.54	3.23	3.58	0.476
	Change	-0.26	+0.07	-0.17	-0.59	-0.06	-0.06	
30–100	54 DAE	0.38	0.38	0.46	0.61	0.61	0.73	0.105
	82 DAE	0.44	0.33	0.71	0.65	0.77	0.60	0.109
	Change	+0.06	-0.05	+0.25	+0.04	+0.16	-0.13	

orientation of the rooting system of the potato crop, with 80–90% of rooting concentrated in the top 30 cm of soil (Lesczynski & Tanner 1976; Asfary *et al.* 1983; Parker *et al.* 1989; Gregory & Simmonds 1992). The data from our experiments generally indicated that although a large proportion of the root system ramified within the ploughed layer, the root system was less surface-orientated than much of the literature suggests. Examining vertical distribution of RLD when TRL was close to its maximum, showed that only 40–73% of the root system was located in the upper 30 cm of the profile. Unirrigated crops had only *c.* 50% of their rooting system in the upper 30 cm compared with *c.* 61% in crops receiving irrigation throughout their life.

Changes with time

Generally, the crop produced maximal RLD in the superficial horizons (< 30 cm) within 3–5 weeks after emergence (Fig. 4). The RLD of horizons closest to the surface decreased at the same time as it was increasing in the deepest horizons where roots were present. There was an interaction with irrigation regime in the time course of changes in RLD in each horizon. Crops growing solely on soil reserves began to lose roots in the upper 30 cm between 3 and 5 weeks after emergence, whereas RLD increased over the same period in crops kept irrigated.

Effect of variety and irrigation

If sampling occurred before root death caused a reduction in RLD in the upper horizons, then the rate of increase and maximum RLD in any horizon appeared to be similar for any of the three varieties measured during the course of these experiments. Since Cara continued to produce roots after Estima and Record had ceased, the RLD in deeper horizons increased beyond that measured for Estima and Record.

Visually, the rooting systems of dry crops late in the season were markedly different from irrigated crops, being sparser in surface horizons, with a slower decrease in RLD with increasing depth. As mentioned

earlier, in crops not receiving water throughout their life, rooting was less superficially orientated than in those receiving irrigation. In Expts 7, 10 and 11 where irrigation was scheduled to maintain the soil close to field capacity in the wettest treatment, there was a slight (but nonsignificant) increase in the proportion of roots in the uppermost 30 cm of soil (68%) compared with the treatment irrigated throughout the season at a much higher SMD (59%).

In Expt 10, plots which received irrigation throughout, or during early season only, produced the greatest RLD, which were almost double those where water was withheld during early growth (Table 12). There was a slight decrease in RLD in the upper 30 cm between the two root core samplings, except in W2. However, where irrigation was withdrawn during this period (W4), considerably more root death occurred in the upper 30 cm than where irrigation continued (Table 12).

Although W2 was irrigated from the end of tuber initiation, the soil was very dry by this stage and little root ramification occurred in the upper profiles after application of water. Therefore, the RLD in the upper 30 cm of soil was more similar to a completely unirrigated crop than to those which received irrigation. In W2, RLD below 30 cm did not increase after irrigation commenced, even though rooting conditions were more favourable in the deeper, wetter horizons. The completely dry plots (W1) did appear to have ramified more completely in the 80–100 cm horizon than the other treatments by August, although the differences were not significant (data not shown).

Root dry weight

The relationship between root dry weight and root length

In Expt 11 linear regressions were fitted to the data of RDW of all samples and their RL. More limited data from a preliminary study in Expt 4 were also used, but were similar to the data from Expt 11 and have been left out of the analysis. Initially, separate regressions were fitted for each variety and irrigation regime, and

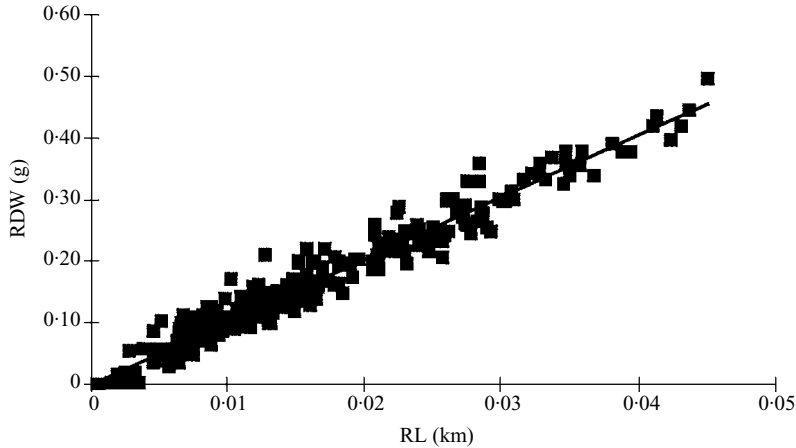


Fig. 5. The relationship between root dry weight (RDW) and root length (RL) in Expt 11. The formula of the relationship was $RDW = 10.22 RL$, $R^2 = 0.94$.

all depths were kept separate and the differences in slope analysed using ANOVA. Despite visually thicker roots in the more superficial horizons, there was no significant effect of depth of sampling, irrigation regime or variety on the slope of the regression. Therefore, all data were combined to establish the relationship shown in Fig. 5.

Root dry weight as a proportion of total dry weight

The relationship between RDW and RL was used to calculate the contribution of RDW to total dry weight (TDW) at the sequential harvests taken in Expts 7–11. The proportion of TDW contained in the root system was *c.* 11% in irrigated crops at final harvest (78–87 DAE). At earlier harvests, the proportion of roots was higher, *c.* 63% at 20 DAE in Expt 11. There was a decrease in the proportion of TDW contained in the roots, which was best fitted by the following equation:

$$\begin{aligned} \% \text{ of TDW as RDW} &= -34.67 \ln(\text{DAE}) + 162.9 \\ R^2 &= 0.90 \end{aligned}$$

DISCUSSION

Over the 12 experiments, maximum rooting depth ranged from 59 to 140 cm, indicating that significant water uptake could be achieved over a depth of 100–110 cm where rooting is unrestricted. This has great implications for the calculation of the limiting soil moisture deficit at which irrigation should commence at all times during the growing season. Whilst it cannot be concluded that the few roots which penetrate such deep horizons contribute massively to water uptake, it does emphasize the importance of maintaining edaphic conditions conducive to root growth, especially in dry seasons when such roots would enable crop growth to continue for

longer without severe water restriction. Obviously, if the crop could obtain a significant quantity of water from a deep root network, the irrigation requirement to maintain optimum crop growth rates could be much reduced or even eliminated if the zone of capillary rise from a water table could be penetrated by roots (e.g. Expts 1, 4 and 12; Boone *et al.* 1978; Parker *et al.* 1989).

Previous work at Gleadthorpe has indicated that rooting rarely exceeds 70 cm on these sandy soils (Bailey 1990), but our experiments showed that D_{\max} could be deeper by 30 cm or more. With the low water-holding capacity of the soil at this site, this additional depth of rooting would reduce the requirement for irrigation, although the crops were scheduled to the deficits normally used for the other experimental and commercial crops of potatoes at Gleadthorpe (35 mm SMD). The deeper rooting may also have allowed the crops to take up extra water to satisfy potential atmospheric demand more fully, and could explain why tuber yields in 1988 (where D_{\max} was greater than 1 m) were substantially higher (ware yield > 40 mm; 67.2 t/ha) than other crops of the variety Record planted at similar times at this site over a number of years (ware yield 1983–87, 40.4 t/ha). At Terrington (Expts 3 and 6), D_{\max} was substantial, and given the high available water holding capacity of the silt loam subsoil (21 mm/100 mm) would indicate that a large soil water reservoir would be usable by the crop.

Irrigation was used as a treatment in the majority of experiments, since this was expected to have an effect on patterns of root growth (e.g. Weaver 1926). In some field experiments irrigation applied early reduced D_{\max} compared with withholding irrigation until later in the season when higher SMDs had accumulated. Taking this further, growing crops solely

on soil reserves without the additional inputs of rainfall or irrigation resulted in deeper, albeit sparser, rooting. If irrigation can reduce the depth of rooting, then the target must be to find regimes that have the least effect on this parameter of rooting. Ultimately, the objective has to be to obtain the deepest rooting in conjunction with a large TRL that is distributed as homogeneously as possible, which should lead to a more efficient use of soil water and a reduced need for irrigation. In Expt 10, there were no significant differences between the irrigation treatments in D_{\max} which suggests that it is indeed possible, with judicious use of irrigation, to achieve the maximum possible depth of rooting.

Roots were recovered from exceptional depths in Expt 8, and almost without exception, roots measured with lengths in excess of 1 m had completed part or all of their journey downwards via inter-ped fissures or worm-channels. However, the effectiveness of these roots in taking up water when surrounded by, or close to, an air void is questionable.

A major component influencing final depth of rooting is the rate at which roots penetrate vertically. The data from this series of experiments suggest that the rates of vertical elongation of potatoes grown in good soil structural conditions can be similar, at their most rapid, to those of winter cereals (e.g. 1.6 cm/day in Expt 12). Parker *et al.* (1989) found mean rates of 0.9–1.3 cm/day when comparing cultivation and irrigation treatments, whilst Boone *et al.* (1978) observed very rapid rates of penetration of *c.* 1.6 cm/day rising to 2.0 cm/day following penetration of a compacted horizon at 50 cm. In winter wheat, Gregory *et al.* (1978) observed rates of vertical elongation of 1.8 cm/day during the linear phase of shoot growth in the spring (April–June), whilst Barraclough & Leigh (1984) indicated that root extension rate during the period September–December would have been at least 1.2 cm/day. Since potatoes have a short growing season when compared with winter cereals, where the size of the root system increases until anthesis (early June; Barraclough & Weir 1988), it might be expected that the poor root penetration often reported for potatoes is a consequence of the short duration of active root growth. The duration of root penetration of our maincrop potato varieties extended over a period of 70–100 DAE, therefore, the ultimate depth of rooting would be expected to be considerable (90–120 cm) given that rates of rooting averaged 1.07 cm/day in these experiments over the first 64 DAE.

The observation that changes in rate, or cessation, of rooting were always preceded by changes in rate of leaf appearance or the cessation of new leaves appearing on sympodial branches allows characterization of the longevity of root growth of a variety based on its aerial determinacy. Since it appears that varieties differ in the duration rather than rate of

rooting, this could reduce the time involved in assessing the limiting SMD for new or existing varieties. The key value of this relationship is that for any variety the period of leaf emergence, and therefore the factors which influence it, also determine the period available for root growth.

The absolute values of the components of root growth in any crop will be determined by the extent to which soil conditions and crop growth rate influence extension and proliferation of roots during the period of leaf emergence. These experiments, and those of Rosenfeld (1997) in compacted soils, show the effects of soil conditions on all aspects of root growth. The effect of crop growth rate on rooting is less clear, but still likely to be substantial. As many factors which influence the number of emerged leaves (e.g. soil conditions again, soil water and nutrient status, physiological age), and hence the duration of root growth, also affect leaf expansion and the size of the canopy, it appears likely that the relationship of canopy size to potential water supply in potato crops will be greatly affected by growing conditions in the initial stages of growth, since there is scope to generate very different root systems. This may lead to different responses to supplementary irrigation. Severe water stress in unirrigated crops reduced the number of leaves compared with those which were irrigated, but dry crops almost universally had deeper rooting than irrigated crops. It appeared that unirrigated crops continued to root at faster rates than irrigated crops in response to exhausting the water in horizons close to the surface, despite having slower rates of leaf appearance during the stage when they were short of water.

Peak TRLs were generally large, at the maximal end of the scale found by other authors, and compared very favourably with all other crop species with the exception of winter cereals, dispelling the belief that the rooting system of potatoes is sparse as well as shallow (Tables 1 and 9). Early in the crop's life, the root system comprised a large fraction of TDW, *c.* 63% at 20 DAE. There was a decrease in the proportion of TDW contained in the roots as the season progressed, but it was still *c.* 11% in irrigated crops at final harvest. Reports in the literature show a similar range. Asfary *et al.* (1983) found 64% of TDW as root at 14 DAE, which decreased to 6% at 84 DAE. Iwama & Nishibe (1989) and Iwama *et al.* (1995) working with a range of Japanese and wild species of potato grown both in pots and the field recorded much lower RDW:TDW ratios, *c.* 1.3–15.4% at 60–70 DAE. The close-fitting relationship in our experiments between RL and RDW, universal over depths and varieties, combined with the modelled decrease in the proportion of TDW existing as root material, allows a potential estimate to be made of the TRL of a crop if the non-root TDW were measured, but clearly the ratio of RDW:TDW varies widely

across the genetic base of potato clones. If the rooting systems of the Japanese selections have similar hydraulic characteristics (i.e. resistance to water flow within the root system) to the varieties used in the UK, then clearly their uptake of water may be hindered by a lack of rooting.

In order to sample the root system when close to its maximum depth, sampling was relatively late in many experiments (70–104 DAE). Net root production may have been decreasing in the uppermost horizons, especially of April plantings, and the density of rooting in these surface layers may well have been greater earlier in the season. Lesczynski & Tanner (1976) observed that irrigation and fertilizer regime had a marked influence on the time after emergence when root senescence and death exceeded new root production in the top 30 cm of soil. Net root production in the plough layer began to decrease approximately 50 DAE where the crops were irrigated every 3 days, compared with the equilibrium in RDW from 33–89 DAE in crops irrigated at 5-day intervals. Vos & Groenwold (1986) observed that *c.* 50–60 DAE decay of roots commenced in the top layers of soil, starting with the oldest roots. The timing of the onset of root death is important in that RLD is decreasing in the upper horizons during July for typical UK maincrops when canopies are closed, radiation levels high and tuber bulking rates rapid. If this process of root death continues, then surface horizons will increasingly become devoid of active roots.

In our experiments, keeping the superficial horizons wet (but not over-wet) with surface-applied irrigation led to a maintenance of roots in these horizons as well as a proliferation in deeper horizons. Several authors have stated that favourable edaphic factors encourage root growth in the most superficial horizons, and where these conditions are maintained throughout the life of the crop, very little deterioration in the size of the root system occurs (Klepper *et al.* 1973; Lesczynski & Tanner 1976; Brown *et al.* 1987; Gregory & Simmonds 1992). Clearly there is a point at which root growth and turnover are slowed by drying of the soil to the extent that considerable root death occurs and RLD decreases. From our experiments, it was difficult to determine the precise soil water status that caused the premature onset of root death, but clearly it was higher than 40 mm since the CUF-scheduled crops were irrigated to this deficit and suffered no premature decrease in RLD compared with crops grown in wetter soils. It would be useful to know the extent to which the root system can regenerate following rainfall or irrigation, but it appears that if soils dry out sufficiently to cause a decrease in RLD, subsequent irrigation results in only limited regeneration of roots near the soil surface, even in an indeterminate variety like Cara.

Our spatial sampling in July and August supports Weaver's (1926) view that root systems in potatoes

have very homogeneous horizontal distributions. Visual observations of the path of individual roots showed that some roots emanating from one row could be found underneath adjacent rows of both sides even on the widest rows (91 cm), which indicated that root growth rates were similar in horizontal and vertical directions. This suggests that if inflow rates of nutrients and water into individual roots are similar to other crop species, potatoes should not suffer a penalty in terms of their use of soil reserves because they are planted on widely spaced rows. However, these experiments indicated that RLD would not become homogeneous horizontally until *c.* 35 DAE, similar to the 33 DAE observed by Lesczynski & Tanner (1976). Therefore, during early canopy expansion, when root growth is confined to areas close to the plant, the sparseness or absence of rooting in more distant areas can potentially hinder uptake of nutrients and water. At 35 DAE ground cover would be *c.* 70% in many maincrop varieties, and therefore atmospheric demand for water on the rooting system would be substantial but lower than if full canopy cover had been achieved. This emphasizes the importance of good soil conditions in the upper profiles in minimizing the time that the roots take to meet across the rows.

A considerable fraction of the root system was contained within the intensively cultivated ploughed layer, but the root system was less surface-orientated than much of the literature suggests. Only 40–73% of the TRL at its maximum was found in the upper 30 cm of the profile, with irrigated crops possessing more superficial rooting than unirrigated crops. Vos & Groenwold (1986) observed a similar distribution pattern with depth. They found that 61% of TRL at 24 DAE was contained in the 0–30 cm horizon, and by 80 DAE, it was only 31%. These data should be compared with much of the literature which states that 80–90% of TRL is concentrated in the uppermost 30 cm of soil (Lesczynski & Tanner 1976; Asfary *et al.* 1983; Parker *et al.* 1989; Gregory & Simmonds 1992).

When evapotranspiration demand on the plant is high, the soil is depleted most rapidly in the horizons with high RLD given that water is not limiting in any one horizon (Gregory & Simmonds 1992). This feature is of critical importance if edaphic factors (e.g. loose soil conditions, fertilizer concentration, early irrigation and unfavourably high soil resistances in the subsoil) encourage superficial root systems to form early in the life of the crop. In the absence of rainfall or irrigation, a very shallow, dense root network, such as might be created by compaction or frequent over-irrigation, rapidly dries the superficial horizons. Therefore, the entire crop root system is likely to experience greater fluctuations between low soil water potentials and extremely high ones, increasing the propensity of older roots to suberize and eventually die. This obviously has implications for uptake of

nutrients (especially nitrogen) since the soil nutrient concentration decreases considerably below the cultivated layer. This may be less significant in potatoes since cultivations tend to be deeper than for most other crops. Rosenfeld (1997) showed that shallow compaction restricted rooting to such an extent that irrigation could only partially compensate for the reduced uptake by roots in compacted soil, but could not remove the effect completely. Additionally, there are disadvantages in trying to maintain a shallow-rooted crop at close to its optimum soil water potential owing to the increased frequency of drainage likely under both the poorly distributed aerially applied irrigation systems currently servicing the majority of the UK potato crop, and the uneven distribution of local thunderstorms that occur during the summer months. Most of the experiments reported here suggest that accurately scheduled and applied irrigation is of vital importance in producing a deep, well-ramified root network so that together they can sustain the crop under conditions of high atmospheric demand.

The obvious extension of this work on rooting is to examine the relationships between rooting parameters discussed and water uptake in relation to the demand for water created by the atmospheric evaporative

demand on the crop canopy. Irrigation strategy has been shown to have an effect on the distribution and longevity of the rooting system, and optimizing the efficiency of any irrigation scheduling system must involve establishing the largest possible rooting system in the shortest possible time, which is homogeneously distributed across the entire row width of the crop. Two further papers will follow, one dealing with the effects of soil conditions and compaction on rooting and water uptake and another attempting to quantify water uptake in relation to root distribution and crop demand leading to the calculation of limiting SMDs for use in irrigation scheduling. Understanding of these areas will undoubtedly improve the efficiency of scheduling irrigation.

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