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Effects of temperature on parameters of root growth relevant to nutrient uptake: Measurements on oilseed rape and barley grown in flowing nutrient solution

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Summary Effects of root temperature on the growth and morphology of roots were measured in oilseed rape (*Brassica napus* L.) and barley (*Hordeum vulgare* L.). Plants were grown in flowing solution culture and acclimatized over several weeks to a root temperature of 5°C prior to treatment at a range of root temperatures between 3 and 25°C, with common shoot temperature. Root temperature affected root extension, mean radius, root surface area, numbers and lengths of root hairs. Total root length of rape plants increased with temperature over the range 3–9°C, but was constant at higher temperatures. Root length of barley increased with temperature in the range 3–25°C, by a factor of 27 after 20 days. Root radii had a lognormal distribution and their means decreased with increasing temperature from 0.14 mm at 3°C to 0.08 mm at 25°C. The density of root hairs on the root surface increased by a factor of 4 in rape between 3 and 25°C, but in barley the highest density was at 9°C. The contribution of root hairs to total root surface area was relatively greater in rape than in barley. The changes in root system morphology may be interpreted as adaptive responses to temperature stress on nutrient uptake, providing greater surface area for absorption per unit root weight or length.

Introduction

Recent mechanistic models of nutrient uptake by plants[5, 9, 14, 20] include one or more parameters of root growth and morphology, such as rate of root extension, mean root radius, mean root hair density and length. The likely importance of root morphology to nutrient uptake can be examined by sensitivity analysis[2, 14, 22]. These models usually describe plants that are not subjected to environmental perturbations and the dependence of parameters of root growth on factors such as temperature, pH and soil moisture have been characterized in relatively few studies[16, 17, 18].

The effects of root temperature on growth and uptake of nutrient ions by plants are complex and change with time, presumably because the balance of responses to temperature changes with the extent to which the plant becomes temperature adapted and with ontogenetic state. An understanding of root morphological response to temperature

is important if observed changes in shoot:root ratios and rates of nutrient uptake per unit root are to be interpreted. Clearly, if temperature affects relative rates of root surface area expansion and root extension differentially then the overall temperature responses of mean inflow (rate of uptake per unit root length) and flux (rate of uptake per unit surface area of root) of ions will differ. The present work was undertaken with these points in mind in order to study the effect of temperature on root growth and morphology. Root length, radius, surface area and root hairs were measured in oilseed rape (*Brassica napus* L.) and barley (*Hordeum vulgare* L.) grown in flowing nutrient solutions of different temperatures. Differential shoot and root temperatures were maintained, because they occur frequently under field conditions[6].

Flowing nutrient solution techniques allow the nutritional status of the root surface to be maintained relatively constant so that any morphological change in the roots is not in part a response to altered nutrient supply. Responses shown in solution culture may, however, differ from those in soil due to effects arising from growth in a liquid as opposed to a solid matrix.

Materials and methods

Plant growth

Oilseed rape (*Brassica napus* L. cv. 'bien venu') and barley (*Hordeum vulgare* L. cv. 'atem') were grown in a system of flowing nutrient solution that has been described in detail previously[7,13]. Briefly this system comprises 'plant culture units' linked to automatic monitoring and control equipment. A plant culture unit contains 300 l of nutrient solution which is circulated through 24 'culture vessels' of 1.2 l capacity arranged in parallel. Each culture vessel received solution at 1.2 $l\,min^{-1}$ giving vertical flow past roots of 2.4 $mm\,s^{-1}$. The system incorporates means for automatically monitoring, recording and maintaining the concentration of H, NO_3, NH_4 and K ions in solution. Solution temperature may be controlled between 2.5 and 2.5 ± 0.1°C[13].

Rape seed was sown directly into the system on August 17 1983 and thinned on emergence to 3 plants per culture vessel. Barley seed was germinated in aerated solution of 2 m*M* $CaSO_4$ for 24 hours prior to sowing on March 7 1984 and thinned to 6 plants per vessel. Eight plant culture units were used with each species. Plants were grown for several weeks before treatments were imposed. Solution temperature in all culture units was reduced decrementally to reach 5°C which was then maintained for 14 days prior to treatment. Details of temperature reductions are as follows. Rape was grown prior to treatment for seven weeks; the initial solution temperature of 20°C was reduced by decrements of 3°C on a weekly basis, reaching 5°C at the start of the sixth week. Barley was grown for four weeks prior to treatment; the initial temperature of 14°C was reduced by decrements of 3°C on days 7, 11 and 14 after sowing.

Nutrient concentrations and growth conditions are summarized in Table 1. At the start of the treatment period solution temperatures were changed to either 3, 5, 7, 9, 11, 13, 17 or 25°C to give one culture unit at each temperature. These root temperatures were held constant over 14 days for rape and 20 days for barley. Air temperatures were common to all treatments (Table 1). Concentrations of nutrient ions to be maintained during treatment were introduced to the solutions one week before treatment started (Table 1) to allow acclimatization. NO_3, NH_4, K and H ions were monitored automatically every 27 minutues and independently

Table 1. Composition of flowing nutrient solution and environmental details

Nutrient	Source	Concentration of ion (mmol mm^{-3}) in solution	
		1–3 weeks (barley) 1–6 weeks (rape)	4–6 weeks (barley) 7–9 weeks (rape)
Potassium	K_2SO_4	250	2.5
Ammonium	$(NH_4)_2SO_4$	250	10
Nitrate	$Ca(NO_3)_2 \cdot 4H_2O$	250	10
Calcium	$CaSO_4 \cdot 2H_2O$	100	198
	$Ca(NO_3)_2 \cdot 4H_2O$	125	5
	$Ca(H_2PO_4)_2 \cdot H_2O$	25	0.25
Magnesium	$MgSO_4 \cdot 7H_2O$	100	100
Phosphate	$Ca(H_2PO_4)_2 \cdot H_2O$	50	0.5
Sulphate	K_2SO_4	125	1.25
	$CaSO_4$	100	197.9
	$MgSO_4$	100	100
	$(NH_4)_2SO_4$	125	5
Iron	$FeSO_4 \cdot 7H_2O$	5.4	5.4
Micronutrients	As in Clement, Hopper and Jones[8]		
pH	$H_2SO_4/Ca(OH)_2$	pH 6.0 ± 0.1	pH 6.0 ± 0.1
Air temperature day/night (°C)		20/15	20/15 (rape) 25/15 (barley)
Light[a]		natural light	artificial light 14 h photoperiod
Relative humidity[b] day/night (%)		40/60	40/60

[a] Artificial light supplied by 4 × Philips HPI/T, 2 kW mercury halide lamps, giving on average 16 MJ m^{-2} d^{-1} total radiation measured on a Kipp solarimeter.
[b] Humidity was not controlled and values are means for experimental period.

maintained constant[7,13]. Other nutrient ions were supplied in an appropriate ratio to the required supply of NO_3 and NH_4 ions.

Measurements of root morphology

Rape plants were harvested on days 0 and 14 of treatment. Barley was harvested on days 0, 5 and 20. Root systems of individual plants in a culture vessel were intertwined and were not separated at harvest. All measurements were therefore made on bulked samples of roots from either three (rape) or six (barley) plants. Shoots were removed and roots blotted dry, weighed and preserved in 1:1:9:9 formalin, acetic acid, ethanol, water[15] prior to measurement. Samples were freeze dried for determination of dry weight. Root length was determined using a grid intersection method[24] after cutting root systems into 1 cm segments, mixing and subsampling in duplicate. Duplicate counts (~ 1000) were made on each subsample. Root diameter was determined on further subsamples using a microscope with a calibrated eye piece graticule and measuring 200 randomly chosen diameters per treatment. Surface density of root hairs was calculated from counts along 24 randomly chosen 1 mm lengths of root and round exactly one quarter of the root circumference (assuming cylindrical geometry). On each occasion root hair lengths and radii were measured.

Results

Root length

Both rape and barley responded to root temperature with respect to changes in root length (Fig. 1). After 14 days treatment total root

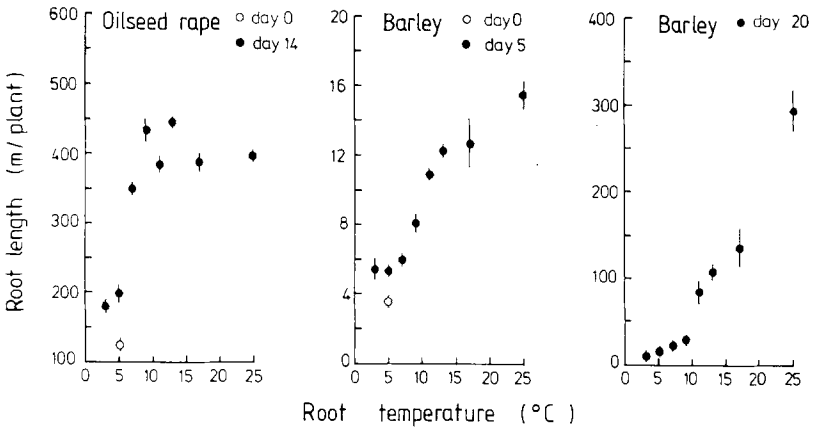

Fig. 1. Effect of root temperature on total root length of oilseed rape and barley plants grown in flowing nutrient solution. *Vertical error bars* are ± S.E.

length per rape plant was greatest at 9 and 13°C (433 and 446 m, respectively) and least at 3 and 5°C (182 and 199 m), compared to the day 0 length of 127 m. Root length on day 14 doubled with temperature over the range 3–9°C, but did not increase significantly with temperature above 9°C. Total root length of barley plants, 3.6 m on day 0, increased with temperature over the range 3–25°C (Fig. 1). The root system at 25°C was greater than that at 3°C by a factor of 27 on day 20.

Relative rates of root extension, (L_R) were calculated assuming exponential increase in total root length with time during the treatment period (Fig. 2)[18]. For rape, L_R was independent of temperature above 9°C, but decreased as temperature decreased below 9°C. Q_{10} coefficients were 3.5 and 1.1 respectively, for intervals 3–13 and 7–17°C. For barley there was an apparent break in the temperature response between 9 and 11°C. Above 11°C L_R was linearly related to temperature (T) as $L_R = 0.096 + 0.0041\,T$, with $r^2 = 0.998$. Between 3 and 9°C L_R increased with T as $L_R = 0.0228\,T - 0.0013\,T^2 - 0.0049$, with $r^2 = 0.997$.

Specific root lengths (root length per unit dry weight) were calculated using root weights (Table 2). They increased with temperature over the range 5–25°C in rape and barley (Fig. 3). Specific root lengths of rape showed a net increase with time at 9°C and above; in barley this increase was greater above 11°C.

Root radius

After 14 days of treatment, arithmetic mean and median root radii in rape decreased with increasing temperature, the values halving over

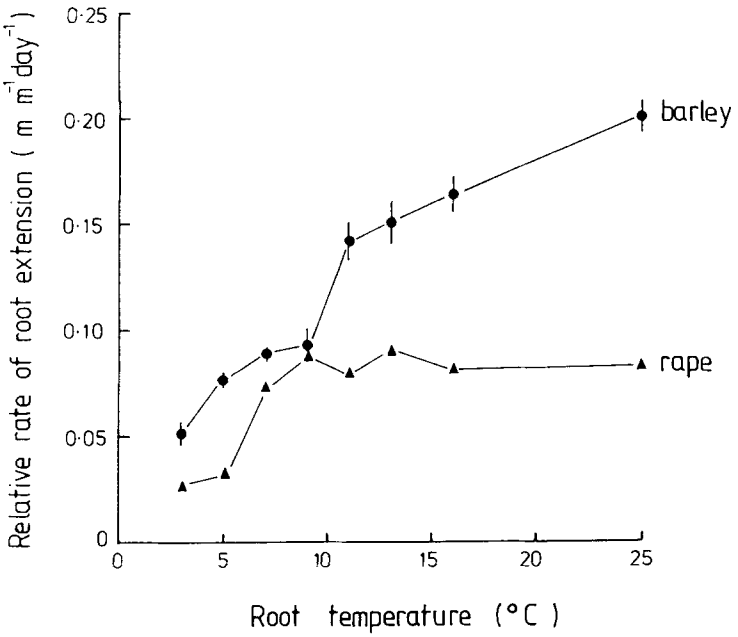

Fig. 2. Effect of root temperature on the relative rate of root extension of rape and barley, assuming exponential increase in total root length with time. *Error bars* for barley are ± S.E.

Table 2. Dry and fresh weight of roots of rape and barley plants grown at different root temperatures in flowing nutrient solution. Weights are arithmetic means of n plants bulked

Weight basis fresh/dry	Root temperature (°C)	Root weight (g plant^{-1}) Rape		Barley		
		Day 0	Day 14	Day 0	Day 5	Day 20
Fresh	3		9.08		0.42	0.87
	5	4.78	11.29	0.30	0.51	1.37
	7		18.91		0.54	1.70
	9		17.29		0.69	2.45
	11		18.47		0.70	4.31
	13		15.39		0.83	6.14
	17		11.05		0.94	6.97
	25		9.25		1.24	13.58
Dry	3		0.80		0.049	0.095
	5	0.33	0.81	0.033	0.053	0.137
	7		1.17		0.056	0.162
	9		0.98		0.064	0.227
	11		1.09		0.058	0.360
	13		0.92		0.064	0.473
	17		0.79		0.063	0.463
	25		0.58		0.072	0.812
Plants sampled (n)		48	18	48	18	6

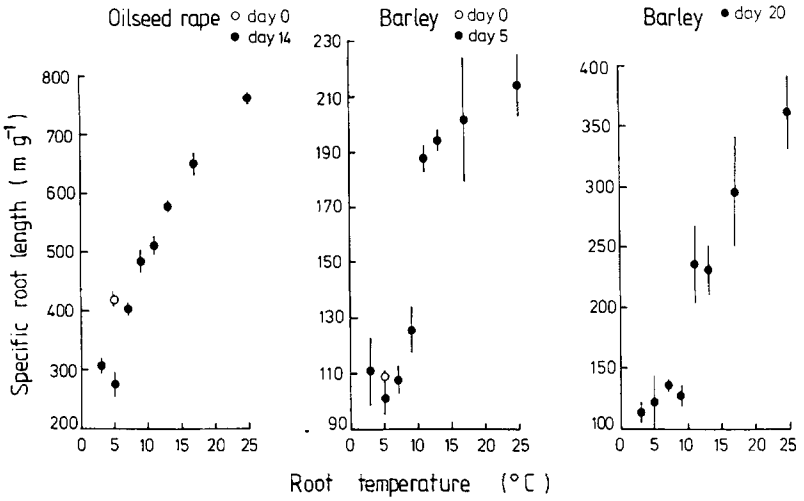

Fig. 3. Effect of root temperature on specific root length (length per unit root dry weight) of rape and barley. *Error bars* are ± S.E.

the range 3–25°C (Table 3). Barley showed an irregular trend in the same direction on days 5 and 20. Sample frequency distributions of root radii in both species were positively skewed at all temperatures and showed considerable kurtosis (Table 3). At all times and temperatures samples were distributed lognormally, based on χ^2 goodness of fit tests comparing normal, gamma and lognormal distributions.

Root hairs

The mean density of root hairs per unit surface area of root increased with time in rape at temperatures of 9°C and above (Fig. 4) and with temperature up to 25°C, the relationship approaching linearity in the range 5–25°C. Roots at 25°C had four times as many root hairs per unit area as roots at 3°C after 14 days. For barley, the relationship between density and temperature was irregular. After 20 days, density increased by a factor of six between 3 and 9°C, but decreased slightly above 9°C.

Root systems having a greater surface density of root hairs did not, on average, have longer root hairs. The length of rape root hairs was inversely correlated with density after 14 days. Root hairs were on average longest (Fig. 5) at 7°C (0.53 mm) and shortest at 17 and 25°C (0.13 mm), showing a net increase in length with time at temperatures of 9°C and below. In barley, root temperatures 3–13°C had little effect on root hair length. Values were highest at 25°C on day 5 and at 17°C on day 20. Root hair density, when expressed as numbers per unit root

Table 3. Sample statistics (n = 200) for root radius measurements (cm × 10^3) on rape and barley grown at different root temperatures in flowing nutrient solution

Root temperatures (°C)	Mean	Median	Coeff. skewness	Coeff. kurtosis
Oilseed rape[a] *(day 14)*				
3	14.0 ± 0.4*	12.6	1.30	1.50
5	13.3 ± 0.4	11.9	1.58	2.90
7	11.7 ± 0.4	10.2	1.61	2.70
9	10.3 ± 0.4	8.8	5.42	4.43
11	10.1 ± 0.4	9.0	2.36	7.10
13	9.8 ± 0.3	8.5	1.97	5.08
17	8.8 ± 0.4	7.3	2.22	4.75
25	7.9 ± 0.3	6.1	2.56	9.73
Barley[b] *(day 5)*				
3	16.2 ± 0.4	14.3	2.86	10.61
5	16.2 ± 0.3	15.3	1.94	4.61
7	17.2 ± 0.4	15.6	1.94	9.01
9	15.5 ± 0.3	13.9	1.76	3.93
11	14.4 ± 0.3	13.6	1.36	2.86
13	14.3 ± 0.3	13.6	1.80	5.72
17	13.5 ± 0.3	12.2	2.12	5.89
25	12.8 ± 0.4	11.1	2.02	4.53
Barley (day 20)				
3	13.1 ± 0.3	12.2	1.37	3.65
5	13.9 ± 0.4	12.6	3.76	19.83
7	12.9 ± 0.2	12.1	1.16	4.35
9	11.6 ± 0.3	10.9	3.27	15.11
11	11.3 ± 0.3	10.2	2.35	9.73
13	12.5 ± 0.4	10.5	3.32	12.59
17	11.4 ± 0.4	9.7	2.16	5.08
25	11.1 ± 0.4	9.9	2.49	8.90

[a] Day 0 mean radius = 12.4 ± 0.4; median = 10.2; coeff. skewness = 1.62; coeff. kurtosis = 2.58.
[b] Day 0 mean radius = 15.8 ± 0.3; median = 14.3; coeff. skewness = 1.321, coeff. kurtosis = 1.47.
* Standard error of mean.
Standard error of coeff. skewness = 0.172; standard error of coeff. kurtosis = 0.342.

length, showed a similar trend with temperature to density expressed on a unit surface area basis, although the magnitude was less because of the inverse relationship between root radius and temperature. Rape root hair density increased from 884 cm^{-1} length of root at 3°C to 2017 cm^{-1} at 25°C, on day 14.

The radii of root hairs appeared to vary little with either time, temperature or position of the root hair, and ranged from 0.0036 to 0.0052 mm rape and from 0.0038 to 0.0047 mm in barley.

Root surface area

Total root surface area with (A_{RH}) and without (A) root hair contributions was calculated assuming cylindrical geometry throughout,

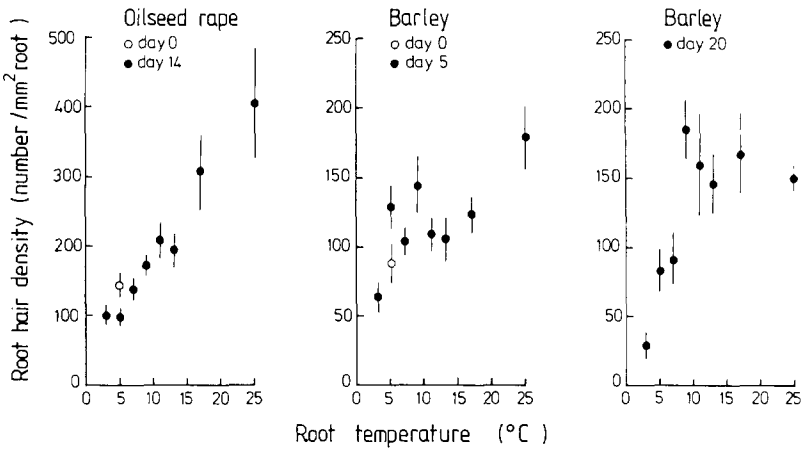

Fig. 4. Mean surface density of root hairs of rape and barley plants at different root temperatures. *Error bars* are ± S.E.

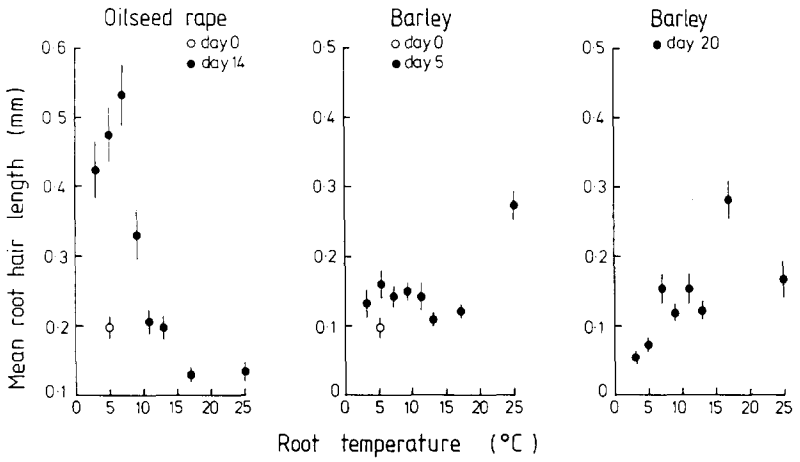

Fig. 5. Mean root hair lengths of rape and barley plants at different root temperatures. *Error bars* are ± S.E.

using sample arithmetic means of the necessary root dimensions and considering the entire surface area of root hairs for A_{RH} (Fig. 6). For rape, values of A_{RH} : A (day 14) were, 2.4, 2.4, 3.1, 2.5, 2.1, 2.0, 1.9 and 2.5, respectively, at temperatures 3, 5, 7, 9, 11, 13, 17 and 25°C. They were generally higher than the corresponding values for barley (day 20) which were, respectively, 1.1, 1.2, 1.4, 1.6, 1.7, 1.5, 2.1 and 1.7. The greatest relative increase in surface area attributable to root hairs was at 7°C in rape and at 17°C in barley (day 20).

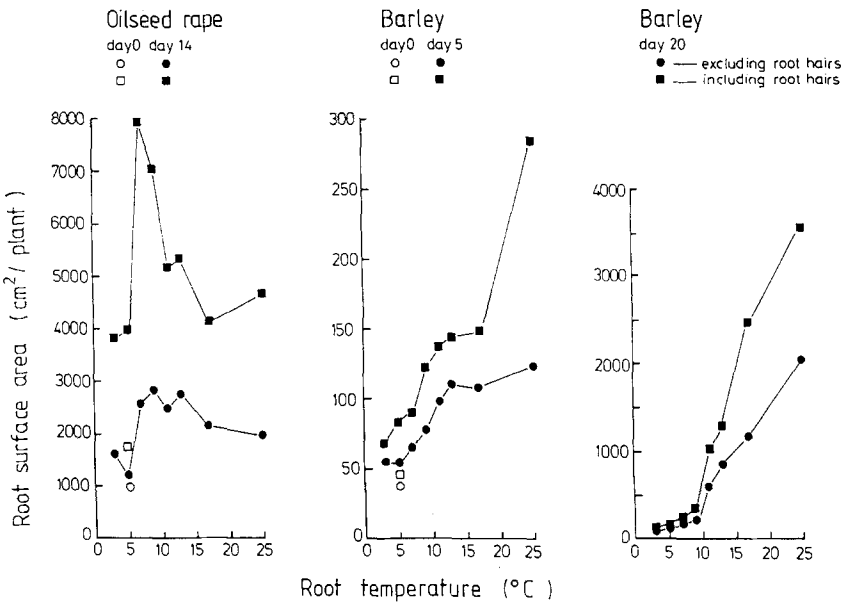

Fig. 6. Effect of root temperature on the total root surface area of rape and barley plants grown in flowing nutrient solution.

Surface area (excluding root hairs) per unit root length decreased progressively with increasing temperature in rape, from 8.8 mm^2 cm^{-1} at 3°C to 5.0 mm^2 cm^{-1} at 25°C. In barley the trend was irregular with temperature, ranging from 6.9 to 8.8 mm^2 cm^{-1}, respectively, at 25 and 5°C (day 20). The inclusion of surface area attributable to root hairs in the calculation gave values ranging from 10.5 to 22.8 mm^2 cm^{-1}, respectively, at 17 and 7°C, in rape, and from 8.6 to 18.1 mm^2 cm^{-1}, respectively, at 3 and 17°C, in barley.

Discussion

Root growth

The effects of root temperature on root length of *Brassica napus* L. cv. 'bien venu' were similar to those reported for *Brassica napus* L. cv. 'emerald' grown in a nutrient film system at 5, 10, 15 and 25°C[18]. However, relative rates of root extension for 'bien venu' were lower than for 'emerald' at the same temperature. The contrasting behaviour of barley cv 'atem', with relative rates of root extension increasing with temperature above 9°C, may be related to tillering, which also increased with temperature. As root branching was not measured it is uncertain whether root temperature affected root length by changes in the frequency of branching as well as the rate of root extension. However,

with 'emerald' no significant difference between numbers of laterals per unit length of root at 10 and 23°C was reported, and reduced growth at low temperatures was attributed to decreased rate of extension[18]. The assumption of simple exponential increase in total root length of rape with time is supported by data for 'emerald'[18] and in the case of barley by data for wheat root growth between 14 and 30 days[25]. Exponential functions have also been used to describe the growth of corn roots in soil[1,4], but have on occasion underestimated it[17]. Furthermore, it has been predicted that relative rates of root extension in barley may fall throughout development; for example from 0.34 d^{-1} to 0.10 d^{-1} between days 10 and 40 of growth[23].

The increasing specific root length in rape with temperature (3–25°C) accounts for the stability of the total root length per plant at temperatures above 11°C, despite the decreasing total root dry weight. Roots were on average thinner at higher temperatures. In contrast, with barley, both the relative rate of root extension and specific root length increased with temperature (3–25°C), while mean root radius decreased.

Measurements of root hair density are usually expressed as numbers per unit root length[11,12,17,22]. However, these units confound the effect of root radius (proportional to surface area), although they are convenient for modelling purposes. The density and lengths of root hairs measured in rape and barley were of the same order as those reported by other authors[11,12,17,22].

The present work shows that temperature influences production and growth of root hairs, in addition to other factors including soil moisture[17], nutrient supply[12,17], pH[26], microorganisms and soil impedance[21]. Root hairs are likely to be important to the uptake of ions having an effective diffusion coefficient of 10^{-9} cm^2 s^{-1} or less in soil[2]; thus uptake of phosphate should be greatly enhanced but there should be little effect with NO_3 ions[19]. Sensitivity analysis[14] of root hair parameters suggests that length has the greatest effect with P uptake, which quadruples as average length increases from 0.05 to 0.6 mm. Density of root hairs and maximum influx into root hairs are relatively less important. In our study root hairs were, on average, longest at temperatures of 3–7°C in rape and 17–25°C in barley.

The inverse relationship between density (Fig. 4) and length (Fig. 5) of root hairs in rape suggests that at low temperature the rate of initiation of root hair outgrowths from epidermal cells may be depressed, but that the availability of carbon substrates per root hair is high. Consequently, root hair extension is greater at low temperature, although general metabolic activity within the root may be low. Alternatively,

the turnover time for root hairs may be shorter at high temperatures; resulting in growth of short hairs only.

Morphological adaptation

Change in the ratio of shoot:root dry weights has frequently been observed in response to temperature change, generally with a decrease at low temperatures[3]. This has given rise to the concept that change in shoot:root ratio compensates for low specific ion fluxes into the root through the production of a relatively large root[10]. However, adaptation to temperature stress in relation to nutrient uptake may also include increased transport capacity per unit root, through the development of more ion carriers per unit root[6]. Whether this occurs only in newly synthesized root tissue, in old tissue, or both, is not clear. Increased partitioning of dry matter, into the roots relative to the shoots is unnecessary if morphological changes result in increased surface area per unit length and root length per unit dry weight[22]. Production of root hairs may be viewed as an adaptation providing maximum root surface area per unit weight and per unit length[22]. It is important that apparently adaptive changes in specific rates of nutrient uptake (*e.g.* mean flux and inflow) resulting from morphological change, and which increase root properties such as surface area per unit root length, are distinguished from changes caused by increased transport capacity per unit of root already present. However, the reasons behind changes in root morphology with temperature are unproven and may or may not relate primarily to nutrient uptake. It remains to define the primary sites and processes (*e.g.* availability of carbon substrate, cell water relations, cell wall synthesis, production of growth regulator compounds) that are transducers of the apparent effects of temperature on root growth and root morphology.

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References

1 Anghinoni I and Barber S A 1984 Predicting the most efficient phosphorous placement for corn. Soil Sci. Soc. Am. J. 44, 1016–1020.

2 Barber S A and Silberbush M 1984 Plant root morphology and nutrient uptake. *In* Roots, Nutrient and Water Influx, and Plant Growth. Soil Sci. Soc. Am., Crop Sci. Soc. Am. and Am. Soc. Agron., Madison, Wis. pp 65–87.

3 Berry J A and Raison J K 1981 Responses of macrophytes to temperature. *In* Physiological Environment. Eds. O L Lange, P S Nobel, C B Osmond and H Ziegler. Springer-Verlag, Berlin. pp 227–338.

4 Ching P C and Barber S A 1979 Evaluation of temperature effects on K uptake by corn. Agron. J. 71, 1040–1044.

5 Claasen N and Barber S A 1976 Simulation model for nutrient uptake from soil by a growing plant root system. Agron. J. 68, 961–964.
6 Clarkson D T and Deane-Drummond C E 1983 Thermal adaptation of nitrate transport and assimilation in roots. *In* Nitrogen as an Ecological Factor. Eds. J A Lee, S McNeil and I H Rorison, pp 211–224. Blackwell, Oxford.
7 Clement C R, Hopper M J, Canaway R J and Jones L H P 1974 A system for measuring the uptake of ions by plants from solutions of controlled composition. J. Exp. Bot. 25, 81–99.
8 Clement C R, Hopper M J and Jones L H P 1978 The uptake of nitrogen by *Lolium perenne* from flowing nutrient solution. 1. Effect of NO_3-concentration. J. Exp. Bot. 29, 453–464.
9 Cushman J H 1979 An analytical solution to solute transport near root surfaces for low initial concentration. 1. Equations development. Soil Sci. Soc. Am. J. 43, 1087–1090.
10 Davidson R L 1969. Effect of root/leaf temperature differentials on root/shoot ratios in some pasture grasses and clover. Ann. Bot. 33, 561–569.
11 Drew M C and Nye P H 1969 The supply of nutrient ions by diffusion to plant roots in soil. 11. The effect of root hairs on the uptake of potassium by roots of rye grass. Plant and Soil, 31, 407–424.
12 Foehse D and Jungk A 1983 Influence of phosphate and nitrate supply on root hair formation of rape, spinach and tomato plants. Plant and Soil 74, 359–368.
13 Hatch D J and Canaway R J 1984 Control of pH in a system of flowing solution culture using a microcomputer. J. Exp. Bot. 35, 1860–1868.
14 Itoh S and Barber S A 1983 A numerical solution of whole plant nutrient uptake for soil-root systems with root hairs. Plant and Soil 70, 403–413.
15 Johansen D A 1940 Plant Microtechnique, McGraw-Hill New York.
16 Mackay A D and Barber S A 1984 Soil temperature effects on root growth and phosphorous uptake by corn. Soil Sci. Soc. Am. J. 48, 818–823.
17 Mackay A D and Barber S A 1985 Effect of soil moisture and phosphate level on root hair growth of corn roots. Plant and Soil 86, 321–332.
18 Moorby H and Nye P H 1984 The effect of temperature variation over the root system and root extension and phosphate uptake by rape. Plant and Soil 78, 283–293.
19 Nye P H 1966 The effect of nutrient intensity and buffering power of a soil, and the absorbing power, size and root-hairs of a root, on nutrient absorption by diffusion. Plant and Soil 25, 81–105.
20 Nye P H, Brewster J L and Bhat K K S 1975 The possibility of predicting solute uptake and plant growth response from independently measured soil and plant characteristics. 1. The theoretical basis of the experiments. Plant and Soil 42, 161–170.
21 Nye P H and Tinker P B H 1977 Solute Movement in the Soil-Root System. Blackwell, Oxford.
22 Robinson D and Rorison I H 1983 Relationships between root morphology and nitrogen availability in a recent theoretical model describing nitrogen uptake from soil. Plant, Cell and Environ. 6, 641–647.
23 Rose D A 1983 The description of the growth of root systems. Plant and Soil 75, 405–415.
24 Tennant D 1975 A test of a modified line intersect method of estimating root length. J. Ecol. 63, 995–1001.
25 Tennant D 1976 Root growth of wheat. 1. Early patterns of multiplication and extension of wheat roots including effects of levels of nitrogen phosphorous and potassium. Aust. J. Agric. Res. 27, 183–196.
26 Wood M, Cooper J E and Holding A J 1984 Soil acidity factors and nodulation of *Trifolium repens.* Plant and Soil 78, 367–379.