

Modelling Cereal Root Systems for Water and Nitrogen Capture: Towards an Economic Optimum

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A quantitative model of wheat root systems is developed that links the size and distribution of the root system to the capture of water and nitrogen (which are assumed to be evenly distributed with depth) during grain filling, and allows estimates of the economic consequences of this capture to be assessed. A particular feature of the model is its use of summarizing concepts, and reliance on only the minimum number of parameters (each with a clear biological meaning). The model is then used to provide an economic sensitivity analysis of possible target characteristics for manipulating root systems. These characteristics were: root distribution with depth, proportional dry matter partitioning to roots, resource capture coefficients, shoot dry weight at anthesis, specific root weight and water use efficiency. From the current estimates of parameters it is concluded that a larger investment by the crop in fine roots at depth in the soil, and less proliferation of roots in surface layers, would improve yields by accessing extra resources. The economic return on investment in roots for water capture was twice that of the same amount invested for nitrogen capture. © 2003 Annals of Botany Company

Key words: Economic model, nitrogen, root depth, root distribution, water, wheat, barley, yield, *Triticum aestivum*, *Hordeum vulgare*.

INTRODUCTION

Cereal yields in the UK have increased steadily throughout the latter decades of the 20th century at approx. 0.1 t ha⁻¹ y⁻¹ through improved cereal varieties and husbandry (Scott *et al.*, 1998). Recently, husbandry improvements have been aimed at improving economic returns and reducing environmental impacts, rather than at just increasing production, such that yield increases have been sustained without increasing the amount of N applied. Confidence to constrain inputs has partly arisen through a new ability to recognize optimum crop canopies (Sylvester-Bradley, 2000), and estimate the returns from 'canopy management' (Sylvester-Bradley *et al.*, 1997b). The major advance in understanding required to achieve this was to consider canopy function as a whole rather than focus on a series of individual physiological attributes. In doing so, the functions of component systems were summarized using key variables (such as the green area index, GAI) which are amenable to management on a field scale and for which quantitative relationships can be described linking their size to inputs, e.g. in the case of GAI, soil and fertilizer N. This approach ignores much physiological detail, especially at cellular levels of organization and below.

Despite these advances in management of the above-ground crop, it has been shown that modern high-yielding varieties may actually be less efficient than their predecessors at capturing soil nitrogen (Foulkes *et al.*, 1998; Sylvester-Bradley *et al.*, 2001). One possible reason for this is that a key part of the plant, the root system, has so far been beyond the reach of management and has received little direct attention for genetic improvement.

The objective of the present work was therefore to develop a theoretical framework that could be applied to the genetic and agronomic improvement of cereal root systems. Specifically, the aim was to model the capture by root systems of two key resources, water and nitrogen, using the minimum amount of crop and soil information necessary to describe their structure and function.

Initially, the study was limited to water and nitrogen because these have the largest and most common effects on crop performance under UK conditions (Archer, 1985; Foulkes *et al.*, 2001). However, yield production goals are not the only motivation to improve the efficiency of resource capture by cereal root systems since there may also be significant environmental benefits. First, sustainable agricultural systems are being extended, and these aim to use soil resources more efficiently. Secondly, climate change may increase the frequency of droughts in temperate cereal-growing regions (Hume and Jenkins, 1998), making access to deep soil water and nutrients more important. In

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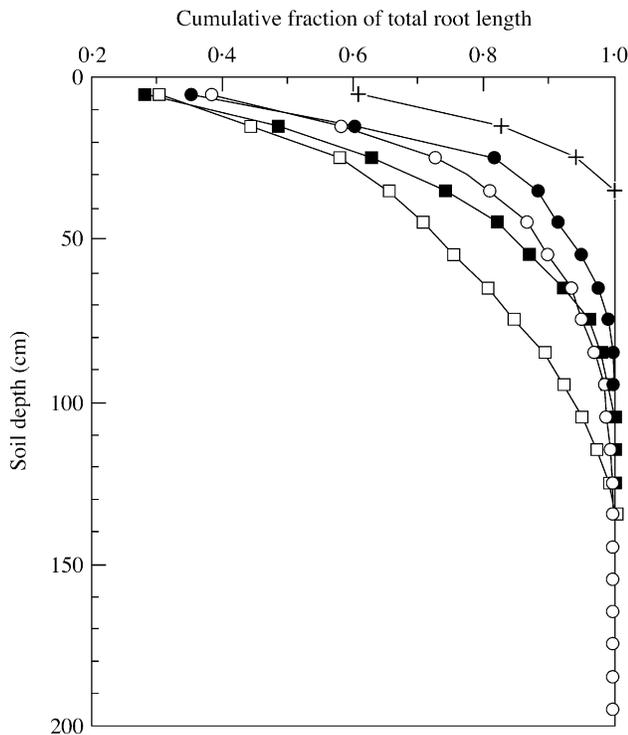


FIG. 1. Cumulative fraction of root length with soil depth on five representative dates (in 1975) during the growth of a winter wheat crop ('Huntsman') sown on 30 Oct. 1974 (Gregory *et al.*, 1978a, b). Crosses, 14 January; closed circles, 8 April (approx. GS31, stem extension); open circles, 10 June (maximum rooting depth achieved); closed squares, 17 June (GS61, anthesis); open squares, 5 August (crop maturity).

addition, agrochemicals, such as plant growth regulators, and fungicides able to control root diseases (e.g. take all), may be used more effectively if root systems are understood in terms of optimum sizes for economic performance of crops.

This paper reports the development of a model that uses minimal descriptions of the size, distribution and resource capture by a wheat root system to estimate the economic implications of changing key features of that system. Throughout the paper reference is made to the decimal code of Tottman and Broad (1987) to identify the stages of growth during the life cycle of cereals.

MODEL DEVELOPMENT

Rationale

The model was designed for winter wheat (*Triticum aestivum*) grown under typical UK conditions in deep soils of uniform texture and structure. Almost all UK wheat crops receive N fertilizer in order to meet the shortfall between canopy requirement and inherent soil supply. Hence, any additional capture of inherent soil N can be taken to reduce the fertilizer requirement. In the case of water, about 20 % of UK crops encounter drought; most often this occurs during grain filling. Hence, any additional capture of water due to improved rooting can be taken to

increase yields of these droughted crops. The primary impact of sub-optimal performance of the root system is assumed to be on grain yield, and the model currently only predicts below-ground resource capture over the grain-filling period. The model was fitted to data from the few detailed UK studies on wheat that include data on root system size and distribution with depth in the soil, and N and water uptake during growth (Gregory *et al.*, 1978a, b, 1979a, b; Barraclough, 1984; Barraclough and Leigh, 1984).

Recent studies have shown a uniform distribution of nitrogen with depth at the start of canopy development (Sylvester-Bradley *et al.*, 2001); this becomes skewed to a decline with depth at anthesis following uptake from lower soil layers and replenishment of surface layers through fertilizer addition and mineralization. However, based on the assumption that during canopy expansion nitrogen uptake from topsoils usually takes precedence over deeper uptake, a uniform distribution of nitrogen with depth has been assumed at anthesis here.

In addition, at the start of canopy development when soil is at field capacity, the distribution of soil water with depth is uniform. The development of a soil moisture deficit in the upper layers commences as evapotranspiration starts to exceed rainfall supply. However, this is not usually sufficient to alter significantly the uniformity of water supply with depth until after the time of anthesis in early June, when rainfall supply is no longer sufficient to maintain the upper soil layers, and crops depend more on subsoil resources.

Water and nutrient capture are usually calculated per unit soil volume, using relationships with root length density to quantify the crop's water- and nutrient-absorbing ability per unit volume of soil (Tinker and Nye, 2000). Total uptake is calculated by summing uptake from successive layers of soil within the rooting zone. Thus, information about root distribution with depth is required. Rootable depth defines the total volume of soil available for exploration (Baldwin, 1976; Gales, 1983). In the UK, 2 m is the approximate maximum depth achieved by most winter cereals (Gregory *et al.*, 1978b; Gales, 1983; Lucas *et al.*, 2000), and is generally achieved by the time of anthesis (Fig. 1). Thereafter, senescence can occur at extreme depths and in the upper layers (as in Fig. 1), though the basic pattern of distribution is maintained.

The basic morphology of cereal root systems is well known, and because cereal root systems develop in a consistent pattern, they have a relatively predictable architecture (when grown in an homogeneous soil) (Robinson, 1994). Methods are available to describe root development with time and ontogeny, down to the level of individual roots within a hierarchy (Klepper, 1987) and their demography (van Vuuren *et al.*, 1997). However, much of the detailed, dynamic morphology of cereal root systems can be summarized without reducing the resolution of the model significantly.

Similarly, it is possible to reduce much of the complexity of resource capture by crops to a few key variables, and this approach, for example, is routine when modelling light transmission through, and capture by, crop canopies (Percy and Valladares, 1999). Water uptake models are often based

TABLE 1. List of symbols, their definitions and units

Symbol	Definition	Unit
d	Depth in soil profile	cm
D_N	Demand for N during grain filling	kg ha ⁻¹ d ⁻¹
f	Fraction of crop dry matter partitioned to root system	—
G	Grain growth rate	g m ⁻² d ⁻¹
	Green leaf area index (GAI)	—
I	Incident photosynthetically active radiation	MJ m ⁻² d ⁻¹
k	Resource capture coefficient	cm ²
K	Light extinction coefficient in the canopy	—
L	Total root length	km
L_v	Root length density in soil	cm cm ⁻³
n	Crop growth stage	—
P	Price of grain	£ t ⁻¹
R	Total dry weight of roots	g m ⁻²
S	Total dry weight of shoot	g m ⁻²
V_N	Value of nitrogen for grain filling	£ kg ⁻¹
V_{water}	Value of water for grain filling	£ mm ⁻¹
	Water use efficiency (WUE)	g m ⁻² mm ⁻¹
Y	Fraction of the root system accumulated from the soil surface to depth d	—
β	Parameter describing the cumulative distribution of roots with depth	—
ϵ	Radiation use efficiency of the crop	g MJ ⁻¹
ϕ	Resource capture as a fraction of the amount available for capture	—
γ	Dry matter fraction of grain	—
σ	Specific root weight	g km ⁻¹
t	Julian date	—

on radial transport to a single cylindrical root, and the assumption of uniform arrays of such roots in the soil (Gardner, 1960). However, to a reasonable approximation, crop water uptake can also be reduced to an equation relating the amount of water extracted to the mean root length density [$\theta = \theta^* \exp(-kL_v t)$], where θ is the amount of water extracted, θ^* the maximum amount extractable and t is the elapsed time (not Julian date as in Table 1) (Passioura, 1983; Monteith, 1986), k and L_v are as defined in Table 1. This has been sufficient to show that mean root length densities (0.5–10 cm cm⁻³) of cereals in the upper layers of most soils are theoretically adequate to access most of the available soil water within the crop's yield-forming period, and that densities >1 cm cm⁻³ are associated with only small increases in the total amount of water taken up during this period.

With respect to the capture of mobile nutrient resources (water and N), complex models such as those developed by Baldwin *et al.* (1973) and de Willigen and van Noordwijk (1987) are based on radial flow into dispersed, single roots and then summed to give uptake for the whole root system. These models are probably unnecessarily detailed for our purpose; for example, the problems of radial transport are seldom relevant for crop growth, and can be ignored. The above type of modelling was also carried out by Barber (1995) on plants grown in pots. Sensitivity analyses showed that the length of root was largely unimportant for mobile nutrients (N), but became the most sensitive parameter in the model when considering the uptake of immobile nutrients (P and K). However, being derived from pot-work, the model lacked a term for the relative distribution of roots down a soil profile, which

prevented successful translation to field use. One resource capture model for both canopies and root systems that does take into account relative distribution with depth is the WaNuLCAS model of van Noordwijk and Lusiana (1999). Here, tree root length densities in four separate layers down a profile are modelled in relation to their competitive impact on neighbouring crop roots in four spatial zones of an inter-row agroforestry system. It may be that an approach such as ours to the depth distribution of roots would also be appropriate in this model.

Root system size

The present model is based on the following assumptions: (1) Adequate water and fertilizer are available during canopy and root system formation, such that crop growth is unrestricted by resource supply before anthesis. (2) The mass of the root system is predictable from that of the vegetative part of the shoot system throughout the crop's life, and that this partitioning is governed by crop development rather than being a response to the environment. (3) A mature root system is produced by the beginning of the grain yield forming period [i.e. anthesis, growth stage 61 (GS61), Sylvester-Bradley *et al.*, 1997a], when the main economic impact of the root system is exercised. (4) The functioning of the root system remains effectively unchanged during grain filling, although the overall size may decline towards harvest.

Typical shoot dry masses of winter wheat in the UK at the start of stem extension (GS31) and at anthesis (GS61) are 0.16 and 1.13 kg m⁻², respectively (Sylvester-Bradley *et al.*, 1997a). The root dry mass at GS61 for the above shoot mass

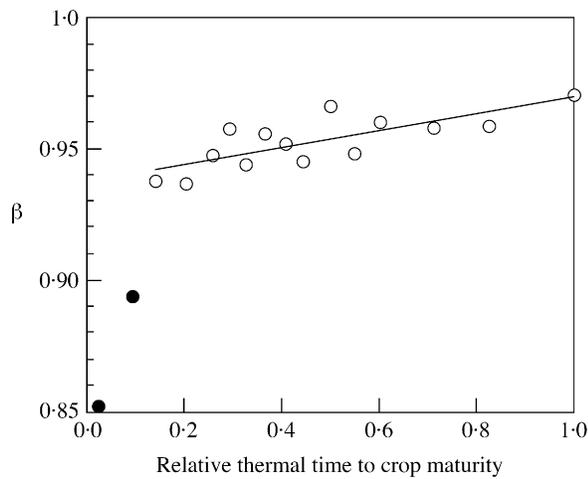


FIG. 2. Variation in β (which describes the distribution of root length with soil depth) with relative thermal time (τ_R) for the crop shown in Fig. 1. In this example, τ_R is the number of day-degrees accumulated at each harvest relative to the total accumulated between 1 January and crop maturity (5 August). The linear regression for data between 18 March and 5 August (open circles) is $\beta = 0.0313\tau_R + 0.938$, $R^2 = 0.583$; this period coincided with the major phase of crop growth. Two outlying data points for 14 January and 25 February (closed circles) were omitted from the regression.

is approx. 146 g m^{-2} , and the maximum root dry weights of UK winter wheat crops are typically between 97 and 170 g m^{-2} (Gregory, 1994).

Total root length (L) is related to root mass (R) by the specific root weight (σ) (Gregory, 1994). Assuming that σ for winter wheat is a constant 4.57 g km^{-1} (as measured by Gregory *et al.*, 1978b), then L at GS61 is 31.9 km m^{-2} . Maximum root lengths of winter wheat crops are between 15 and 32 km m^{-2} (Gregory, 1994).

Root distribution

It was assumed that: (1) rooting depth is not restricted by soil physical conditions, nor is it influenced by localized heterogeneities in the soil (cf. Robinson, 1994); and (2) the distribution of root material with depth is approximated by the Gale and Grigal (1987) equation:

$$Y = 1 - \beta^d \quad (1)$$

where Y is the fraction of the root system accumulated from the soil surface to depth d , and β is a parameter that describes the shape of the cumulative distribution with depth. This was first described by Gerwitz and Page (1974) as $Y = 1 - \exp(-\alpha d)$, where $\exp(-\alpha) = \beta$. As β approaches 1, there is a greater proportion of roots deeper in the profile. For $\beta = 0.920$, approx. 57 % of roots occur in the top 10 cm of the soil profile, whereas this layer contains only about 40 % of roots when $\beta = 0.950$. Equation (1) is sufficiently robust to summarize root mass and length distributions for a wide range of terrestrial biomes, including temperate grasslands and crops (Jackson *et al.*, 1996, 1997).

β was estimated using the most complete set of data available for the depth distribution of root length (Gregory

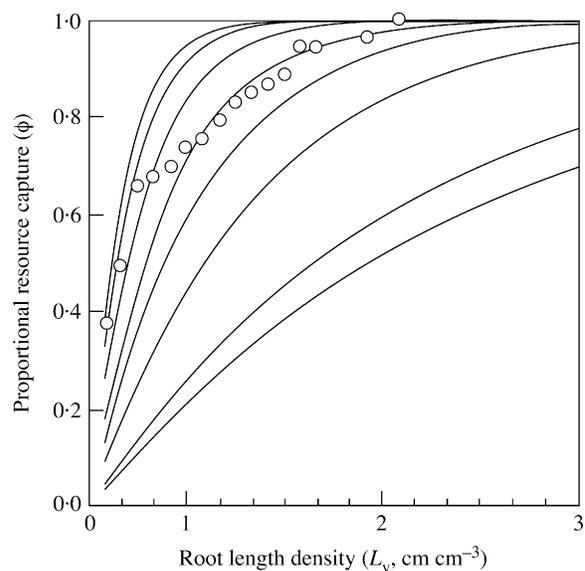


FIG. 3. Proportional resource capture (ϕ), calculated using eqn (3), in relation to root length density (L_v). Each curve is for a different resource capture coefficient (k). These are, from left to right, $k = 5, 4, 3, 2, 1.5, 1, 0.5$ and 0.4 cm^2 , respectively. Data points are for water capture by barley crops relative to total amount available in the soil, and for root length densities of those crops measured at anthesis (Gregory and Brown, 1989). The data fit reasonably well to the $k = 2 \text{ cm}^2$ line when $L_v > 0.6 \text{ cm cm}^{-3}$. N capture would be expected to follow a similar trajectory. The curve for $k = 0.4 \text{ cm}^2$ gives $\phi \approx 1$ at $L_v \approx 10 \text{ cm cm}^{-3}$ as would be expected theoretically for P capture.

et al., 1978b; Fig. 1). Figure 2 shows that β increased from 0.940 on 18 March (Julian date 77) to 0.970 by the time the crop reached maturity (5 August; Julian date 217). However, ‘parallel curve analysis’ (Ross, 1990) using a maximum likelihood program (Ross, 1987) showed that β in Fig. 2 did not change significantly after March. The stability of β during the main growth phase (mean \pm s.e. 0.953 ± 0.003) suggests that (in relative terms) root extension may proceed at a similar rate at all depths, and that eqn (1) may be applied before GS61 without altering β . Using the appropriate values of β , Y [eqn (1)] and R , root length density (L_v ; cm cm^{-3}) in each 10 cm layer of the soil profile can be estimated at each stage of crop growth:

$$L_v = (Y_d - Y_{d-10})R/\sigma \quad (2)$$

Water and nitrogen capture

The uptake of water is similar to that of nitrogen (as nitrate) in that, in moist soils used for crop production, both are transported to root surfaces mainly by the mass flow of soil solution (Tinker and Nye, 2000). A generic function was chosen to describe resource capture as a fraction (ϕ) of that which is potentially available for uptake during the full season:

$$\phi = 1 - e^{-kL_v} \quad (3)$$

where k is a ‘resource capture coefficient’ in units of cm^2 [i.e. $1/(\text{cm cm}^{-3})$]. k subsumes the many details of resource

uptake physiology (e.g. the molecular mechanisms of ion and water transport across membranes) and of soil transport (e.g. hydraulic conductivity, ion diffusivity). Larger values of k lead to a more rapid resource depletion for a given root length density. The value of L_v used in eqn (3) can be derived from eqn (2) to calculate ϕ for each soil layer. Alternatively, a mean L_v for the whole soil profile can be used, as in Fig. 3. To estimate k in the absence of suitable data for wheat, measurements of water and nitrogen use by dryland barley (Gregory and Brown, 1989), which were seasonal averages taken from a water limited system, were used. As such, k is a constant for resource-limited situations, such as those for which this model is intended. A value of $k = 2 \text{ cm}^2$ fitted the data for water uptake acceptably well when $L_v > 0.6 \text{ cm cm}^{-3}$, i.e. for all but the most sparse root systems.

Resource capture by the whole root system is the accumulated capture by roots in each soil layer. Assuming a maximum possible rooting depth (e.g. 2 m for UK winter cereals: Gregory *et al.*, 1978b; Gales, 1983; Lucas *et al.*, 2000), and a uniform distribution of available resources with depth, total capture is easily calculated as mean ϕ averaged over all soil layers, including those containing no roots. On this basis, a winter wheat crop could capture about 55 % of available water and N by anthesis, which is equivalent to all the resources contained within the top 1.1 m of the soil profile.

Economic evaluation

We consider the case where drought limits grain filling by reducing water capture compared with a well-watered crop, whilst N is not limiting. In this assessment it is assumed that all dry matter accumulation in the shoot post-anthesis is diverted to grain filling. The economic value (V_{water}) of water use during grain filling is:

$$V_{\text{water}} = WP/\gamma \quad (4)$$

where W is WUE, P is the price per tonne of grain and γ is the dry matter fraction at which the grain is sold. A typical recent price of wheat in the UK is £70 t^{-1} (P), and grain is sold at 85 % dry matter (γ). For a WUE of 5 $\text{g m}^{-2} \text{mm}^{-1}$ (Foulkes *et al.*, 2001), V_{water} was calculated by eqn (4) to be £4.12 $\text{mm}^{-1} \text{ha}^{-1}$.

In N-limiting conditions whilst soil water is abundant, it is assumed that extra N capture during grain filling delays the onset of senescence and the end of the grain-fill period. Grain growth rate (G) during grain fill can be calculated from eqn (5) (Sylvester-Bradley *et al.*, 1997b) where all growth is directed towards grain fill rather than vegetative biomass.

$$G = \varepsilon I(1 - e^{-KA}) \quad (5)$$

where A is GAI ε , I and k are as defined in Table 1. For typical values of $\varepsilon = 2.4 \text{ g MJ}^{-1}$, $I = 9 \text{ MJ m}^{-2} \text{d}^{-1}$, $K = 0.45$ and GAI = 6, the grain growth rate, G , during filling is about 200 $\text{kg ha}^{-1} \text{d}^{-1}$.

An equation analogous to eqn (4) was used to calculate the economic value (V_N) of N used in grain filling:

$$V_N = GP/\gamma D_N \quad (6)$$

where D_N is the daily demand for N during grain filling. If 200 kg N ha^{-1} [eqn (5)] is required over a typical grain-filling period lasting 40 d, D_N is about 5 $\text{kg ha}^{-1} \text{d}^{-1}$, which must be translocated from the canopy. Assuming a grain price of £70 t^{-1} , then the value of extra N during grain filling amounts to £3.32 $\text{kg}^{-1} \text{N}$.

The sensitivity of the net economic return to the values of the main variables was tested by varying the value of each over a defined range whilst holding the values of the others constant. These ranges were: β , 0.955–0.985; σ , 2.5–7.5 g km^{-1} ; k , 1–3 cm^2 ; and f , 0.05–0.2. The effects on water uptake of varying shoot dry weight at anthesis (S_{GS61} , 0.8–1.4 kg m^{-2}) and WUE (4–6 $\text{g m}^{-2} \text{mm}^{-1}$) were also tested, as were variations in grain growth rate (G , 0.15–0.25 $\text{t ha}^{-1} \text{d}^{-1}$) and grain demand for N (D_N , 3–5 $\text{kg ha}^{-1} \text{d}^{-1}$) for their effects on N uptake.

The parameters β , WUE and σ had the largest effects on economic yield in relation to water uptake (Fig. 4) and, in relation to N uptake, β and σ were again important (Fig. 5). The effects of all variables on economic yield in relation to N uptake were less than half those in relation to water uptake.

DISCUSSION

Outputs from the model and their significance.

The theoretical framework that is developed here allows: (1) the size and distribution of winter wheat root systems at anthesis to be described; (2) water and nitrogen capture, as a fraction of the amounts available for capture, to be estimated, along with the use of these resources in yield formation; and (3) the economic effects of changes in single root system characters on water and nitrogen capture to be evaluated.

According to the model, the vertical distribution of the root system, as described by β , can have a profound effect on yield. Larger values of β give a greater economic return for water and N capture. This implies that a more uniform distribution of roots with depth could, in theory, improve the economic return from a winter wheat crop. This is because such crops could more readily access resources deeper in the soil that would be unavailable to crops with smaller β values. If the same root mass is distributed more evenly with depth, roots in upper layers will, on average, be less concentrated. This will delay the point at which inter-root competition begins in these layers and, therefore, prolong the effectiveness of each of the roots in resource capture. At the same time, deeper layers would more quickly achieve root length densities adequate for maximum resource capture. The effectiveness of the whole root system is then increased, compared with that of a less evenly distributed root system. However, it should be noted that this enhanced effectiveness would be restricted if the resource also declined with depth, as N may do in many cases (Sylvester-Bradley *et al.*, 2001). Conversely, it may become even more important for resource distributions which increase with depth, as may be the case for water in drought years.

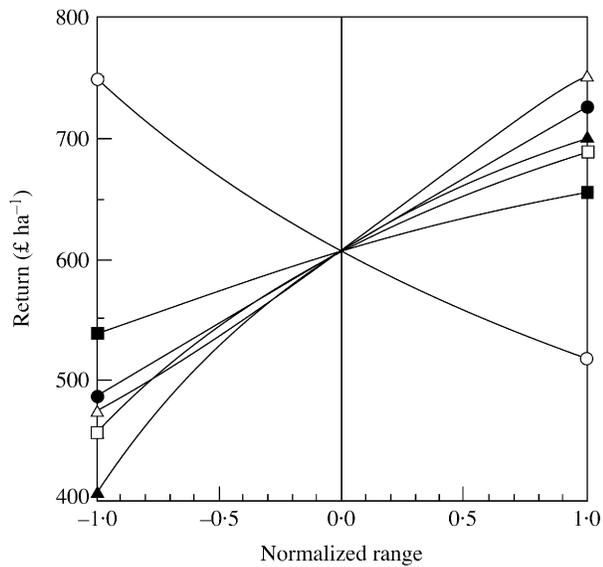


FIG. 4. The sensitivity of the economic return to variations in water capture during grain filling, as affected by individual variables in the model. The value of each variable was adjusted singly over a range normalized to zero at its mid-point. Open triangles, root distribution with soil depth (β , 0.955–0.985); closed triangles, dry matter partitioning to roots (f , 0.05–0.2); open squares, resource capture coefficient (k , 1–3 cm^2); closed squares, shoot dry weight at anthesis (S_{61} , 0.8–1.4 kg m^{-2}); open circles, specific root weight (σ , 2.5–7.5 g km^{-1}); closed circles, water use efficiency (WUE, 4–6 $\text{g m}^{-2} \text{mm}^{-1}$).

The partitioning (f) of dry matter between shoot and root systems was also influential on grain yield, as was the specific root weight (σ), which is approximately proportional to the square of the mean radius. The model predicts greater economic returns as a result of water and N uptake from crops with greater partitioning of dry matter to roots (larger f). This prediction agrees with one made by Baldwin (1976) who modelled total crop yields on the basis of a detailed treatment of soil transport, water and nutrient uptake, and root–shoot partitioning. However, our model also predicted maximum returns from crops with finer roots (smaller σ), contradicting Baldwin's (1976) conclusion: he predicted a 32% increase in yield for a doubling of mean root radius (roughly equivalent to doubling $\sigma^{0.5}$). Rather than the extra dry matter being invested in thicker roots to increase resource translocation (Baldwin, 1976), the model presented here suggests that it would be better invested in expanding the absorptive area (per unit mass) at lower depths in the soil to increase overall resource capture.

The implications of model outputs for the manipulation wheat root systems

If the location of appropriate characters can be identified in gene sequences then genotypes with more efficient root systems may be identified, bred or engineered. However, our model takes no account of possible genetic linkages or interactions between characters, and these could confound attempts to genetically manipulate one character independently of others. As cereal genetic maps become increasingly

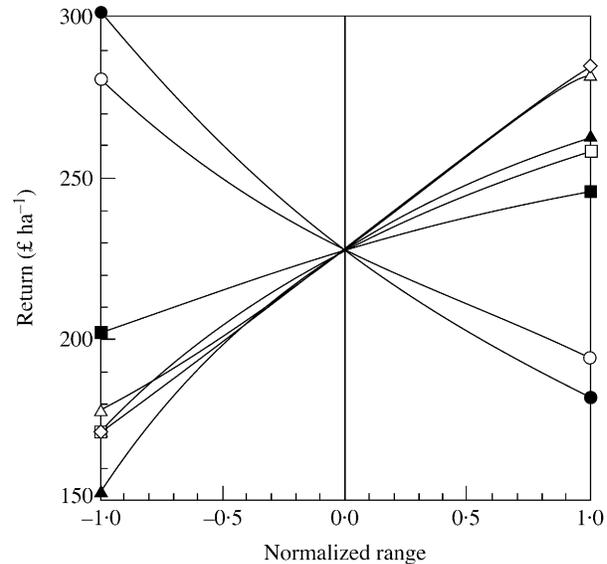


FIG. 5. Sensitivity of the economic return to variations in N capture during grain filling, as affected by individual variables in the model. The value of each variable was adjusted singly over a range normalized to zero at its mid-point. Symbols and ranges as for Fig. 4, with the exception of: closed circles, grain demand for N (D_N , 3–5 $\text{kg ha}^{-1} \text{d}^{-1}$); open diamond, grain growth rate (G , 0.15–0.25 $\text{t ha}^{-1} \text{d}^{-1}$).

detailed and include root traits, the potential for targeted trait manipulation can be assessed *a priori*. For example, root dry weight in barley (*Hordeum vulgare*) is mapped close to the locus of a major dwarfing gene (*ari-eGP*) with widespread developmental effects (R. P. Ellis pers. comm.). Attempts to manipulate root dry weight in that species could possibly be confounded by simultaneous and undesirable changes in other important characters. Whether the same constraint would apply to wheat would depend on the degree of synteny between the species (Freeling, 2001), but this remains to be determined.

Characters may also be constrained allometrically, or may vary with the environment, limiting the extent to which each could be manipulated independently, e.g. via plant growth regulators. For example, an increase in partitioning of dry matter to roots (f) is predicted to increase the economic return. Yet, logically, crop growth rate will begin to fall if f becomes too large and the canopy too small for maximum photosynthesis. It might prove impossible to simultaneously increase f and shoot weight at anthesis to maximize the economic return, at least beyond certain (as yet unknown) limits.

The resource capture coefficient (k) proved a less important influence on the economic return from water and N capture because the range of root length densities chosen to test its impact on resource capture (Fig. 3) was relatively small. Much greater variation has been reported for root systems in general, so it will be important to validate our assumption of smaller variation in commercial wheat crops within the UK.

One of the advantages of the present model is that it needs crop information for only one growth stage (GS61), and the

outputs from the model were achieved using minimal information about the crop and soil. In this respect, the model offers considerable practical utility: decisions in crop husbandry must necessarily be based on a few simple observations. The model predicts that at current costs, water is a more valuable resource than N in terms of the probable returns from managing the root system, but this will depend on circumstances; clearly, water will be the more important resource on light-textured soils, whereas N will be more important on deep, retentive soils. Particularly in the case of N, it may be useful to extend the use of the model to assess effects at other growth stages, to assist earlier decision making.

Future developments

The present model was based on several assumptions or 'typical' values. Some of these assumptions (e.g. a maximum rooting depth of 2 m) were derived, for expediency, from a limited set of experiments, and most of these assumptions need testing for a wider range of soil types and geographical locations. For example, it is extremely unlikely that physical impedances will not limit rooting depth in certain soils, e.g. shallow soils overlying rock, or waterlogged soils. The effects of such limitations on the capture of different resources are difficult to predict. The distribution of wheat in relation to climate and soil type must also be taken into account, as must the resource limitations that may be most important economically in different regions. In reviewing various constraints on yield in the UK, Gales (1983) noted that crop root systems could extract water to depths of 1.5–2.0 m on sandy loams and clay soils. Although the amount of water considered 'available' was that held between 0.005–1.5 MPa tension, abstraction below 0.5 m tended to be only of 'easily available water' held at tensions between 0.005–0.2 MPa. Taking this into account, Gale concluded that drought in the UK would be most likely to occur in crops on clay soils (i.e. with less easily available subsoil water), even though such soils contain ample total amounts of water.

Many soils have an uneven distribution of resources owing to fertilizer applications and the periodic saturation of topsoil with rainwater. Our assumption that water and N are distributed evenly throughout the whole rooting volume is an obvious oversimplification. However, it would be easy to relax this assumption and impose an initially non-uniform distribution if sufficient information were available. The effects of uneven initial distributions on the model's predictions can be tested using assumed patterns for water and N analogous to eqn (3), though a potential difficulty lies in defining the amounts available from rainfall and mineralization during crop growth. Inclusion of transport between soil layers would be more difficult, though simple algorithms exist to achieve this (e.g. Campbell, 1985).

A related issue concerns the effects of resource availability during the formative growth phases on β and k during yield formation. For instance, irrigation and N fertilizer can cause root proliferation in surface soil (Barraclough *et al.*, 1989; Robinson, 1994), so the distribution of water availability earlier in the crop's growth may alter β at anthesis. It

is possible that k also varies under drought or with N supply. This possibility will require testing, as will the determination of k as a function of root length density for different nutrients, but without the confounding effects of soil depth. Finally, the logical goal of developing such a framework is to consider whether root systems are actually optimal for resource capture. To do this, it will be necessary to calculate not only their ability to capture resources, but also the costs of resource capture, possibly in terms of carbon (cf. Robinson, 2001). The present model indicates a possible over-abundance of roots in the surface layers for water and N capture (though not necessarily for P) during later growth stages: it will be useful to test genotypes with larger β values.

Another obvious aspect of the model that requires further development is to consider P capture. Soil resources other than water and N may have only weak effects on wheat yield in most fields in the UK owing to regular fertilizer use (Archer, 1985). Nevertheless, it will be necessary to check that effects of changes in root system characters on P capture do not compromise the conclusions drawn for water and N. In most soils, equilibrium concentrations of P in soil solution, and diffusivities of P through the soil, are limited by buffering reactions (Tinker and Nye, 2000) and, consequently, the mean root length densities required to theoretically access all of the available P are about an order of magnitude larger than those needed to capture water and N (van Noordwijk, 1983). In Fig. 3, relative P uptake would probably follow trajectories described by $k < 0.5$ and, in theory, P uptake should be more closely correlated with root length density than are the uptake of water and N. However, this is not always borne out by experiments (Otani and Ae, 1996), and further investigation is required. P uptake will require a different conceptual approach from that used for N and water uptake because P concentrations in solution are low and absorption processes will have to be included. Rather than being based on total root length, P uptake may depend more on new root growth (Yanai, 1994). At a later stage, questions about K, S and micronutrients may also need to be addressed.

CONCLUSIONS

There remains considerable scope for exploring further simplifications in nutrient uptake models with the aim of improving their practicality. The approach adopted here has been guided by this aim. By constructing a summarizing framework of root resource capture, we have shown that it is possible to evaluate the value of the size and distribution of a wheat root system, and its water- and N-capturing functions, in terms of the crop's final economic performance. This is a major step forward and opens the way to assessing the efficiency of different root systems and, furthermore, to deriving an optimal root system, or ideotype (cf. Jones, 1983, p. 274), for UK conditions.

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