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**MANAGEMENT OF CEREAL ROOT SYSTEMS**

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# MANAGEMENT OF CEREAL ROOT SYSTEMS

by

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# MANAGEMENT OF CEREAL ROOT SYSTEMS

## PART A: PROJECT ABSTRACT

### **Background**

At present we do not know how to manage root systems in the way that we can manipulate canopies. We know that management decisions can affect cereal roots but in many cases do not know what the result is for yield and quality. The project was a desk study and consultation to find out what is known already so that future research can be appropriately targeted.

### **Situations where rooting can limit yield**

Poor rooting can limit growth due to low uptake of water or nutrients or by increasing the risk of lodging. Root systems respond dynamically to soil conditions and there is usually a large enough system to support the above-ground parts. The clearest examples of yield losses due to poor rooting come from studies on soil compaction and from the poor control of root diseases such as Take-all and pests such as cereal cyst nematode. Even in these cases, however, the effect on yield depends on other factors such as rainfall. The risk of root lodging is increased where the root system is not strong enough. It is not clear whether cereal root systems could be modified to allow the crops to make better use of water and nutrients, particularly nitrogen.

### **Diagnosis of rooting problems**

Some problems will occur equally throughout a field and are thus not obvious. Others may occur in patches characterised by a lower or yellower crop cover, shorter crops or premature ripening. Rooting problems are best seen by digging soil pits down to a depth of between 0.5 to 1.2 m (depending on soil type) and examining them for signs of harder layers of soil and areas of poor rooting. Pits are normally dug after harvest when the soil is moist but this will miss any temporary problems that occurred earlier in the growing season.

### **Farming operations that affect rooting**

Farmers can modify the root system either deliberately or as a consequence of other actions. The operations that influence rooting include: rotation, variety choice, cultivations, seed rate, sowing date, nitrogen rate and timing and plant growth regulator application. However, for some of these farmers have no real choice and others take place too late to have a significant effect. On heavier soils a key decision is whether or not to carry out expensive cultivations such as sub-soiling and better guidance is needed. Problems are likely to be greatest for spring crops when roots compete strongly with the shoots for the products of photosynthesis, particularly in dry springs.

### **Varietal differences in rooting**

Varieties differ in rooting pattern in the same way as there are differences in straw length and canopy characteristics. Differences in nitrogen scavenging ability have been noted and there are differences in the response to pH. However, there is insufficient knowledge to identify good characters for use in a plant breeding programme.

# MANAGEMENT OF CEREAL ROOT SYSTEMS

## PART B: SUMMARY REPORT

### Contents

1. Introduction
2. Linking practice to yield via the rooting environment
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9. Genotypic variation in rooting
10. Technology Transfer: *Research in Action* demonstration at the HGCA Arable Farming Event, Cereals 1999
11. Identifying measures to improve yield by manipulation of root systems
12. Recommendations for research

### 1. Introduction

At present we do not know how to manage root systems in the way that we can manipulate canopies. We know that management decisions can affect the rooting pattern of cereals (and oilseed rape) but not whether these changes are beneficial. The aim of this desk study was to abstract and synthesize our existing knowledge of cereal root systems so that it could be used to answer farmers' questions about how best to improve yield when it is thought to be limited by soil conditions.



The original objectives of the work were kept under review during the project and modified on the basis of discussion with researchers and farmers. The final list is given below:

- To develop a conceptual model linking farming practices, root system characteristics and yield.
- To specify the key features of the soil environment that might influence rooting and decision making.
- To identify the circumstances in which crop yield can be limited by rooting characteristics.
- To identify measures and practices that improve root performance of cereals.
- To consider the importance of the root system in reducing the risk of lodging in cereals.
- To identify measurements that provide indicators of the effectiveness of the rooting system.
- To indicate genotypic variation in rooting that affects the exploitation of soil resources and responses to soil properties.
- To indicate where knowledge is lacking for effective management decisions.

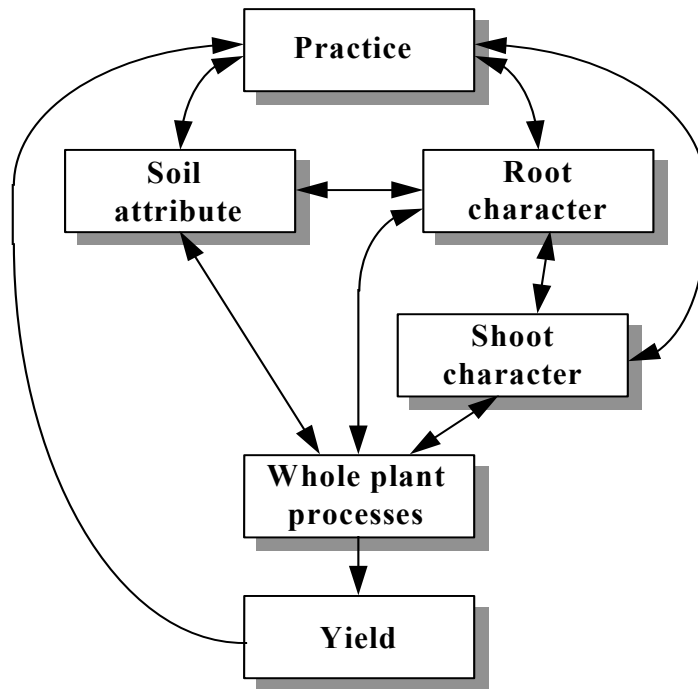
## **2. Linking practice to yield via the rooting environment**

A conceptual model of the key linkages between agronomic practices and yield, as influenced by changes in the rooting environment or the root system are shown in Figure 1. This model provides a framework within which the other results are placed. Effects of these practices on rooting might be direct or mediated through changes in the soil or on the above-ground parts of the crop. Influences in Figure 1 are more often bi-directional than one-way only. For example, the soil type and chemical environment affect root growth and uptake rates of nutrients and water, but the roots can also affect the structure and chemical environment of the soil, although these effects may not be apparent till the following season.

There is a complex and incompletely understood functional inter-dependence of the shoot and root. Above-ground conditions can affect the growth of plant roots as a consequence either of the size of the plant or the relative sink strengths of the above and below-ground parts of the plant. The shoot relies on the root for a supply of nutrients and water while the roots depend on the shoot for a supply of carbohydrate. For example, conditions that are favourable for photosynthesis but not to leaf growth can result in an increase in root growth.

Interpretation of field experiments is complicated by the difficulty of making accurate measurements below ground and the uncertainty associated with the contributions of the rhizosphere flora (fungi and bacteria) to the supply and uptake of nutrients and water. Although these contributions are thought to be small in normal arable situations, the close association between plants and the rhizosphere flora blurs the distinction between root and soil.

**Figure 1.** Linkages between agronomic practice and yield as mediated by the rooting environment and root system or shoots



### 3. The cereal root system

The root system of wheat, barley and oats consists of three to six primary (or seminal) roots growing from the seed and the secondary roots (also called nodal, crown or adventitious roots) that arise from nodes at the base of the main stem and tillers. Each tiller (shoot) develops its own roots and can thus become independent of other shoots.

The primary roots are 0.2-0.4 mm thick and in a fully grown crop occupy 5-10% of total root volume: they develop first, second and third order lateral branches. Secondary roots develop once tillering starts, i.e. 4-12 weeks after germination. They are 0.3-0.7 mm thick and form lateral roots (0.1-0.2 mm thick) with abundant root hairs. Laterals may have a horizontal spread of up to 1 m from the main-stem.

Root extension rate depends on temperature and is typically 5 mm day<sup>-1</sup> for autumn sown cereals. In spring, extension is 15-25 mm day<sup>-1</sup>. The maximum rooting depth for winter cereals is 1.5 to 2.0 m and the maximum weight (at full ear emergence) is approximately 1t ha<sup>-1</sup>. Total root length at maximum canopy size is between 16-32 km m<sup>-2</sup>.

Fewer data are available for oilseed rape which has a taproot from which laterals branch and which reaches similar depths to the cereals.

Most root mass is found in top 25-50 cm of the soil where the concentration of mineral nutrients tends to be highest. When water is in short supply the deeper roots become more important. The genetic pattern of root growth is modified by cultural conditions. For example, roots can proliferate in areas of moisture (at any level in the soil profile) or nutrient availability (e.g. caused by uneven fertiliser distribution).

#### 4. The soil environment

The soil type has an important influence on management, especially for decisions up to the flag leaf stage (or the onset of flowering in oilseed rape) by which time most treatments have been applied. After this, the weather has a dominant effect on growth rate, yield and quality. Being able to describe the soil and climate of a field is important in the choice of practices and for optimising inputs, as well as for modifying experiences and trial results from other places. Earliness, accessibility and droughtiness are three virtually permanent features of a soil as there is limited scope for ameliorating any problems. A farmer is able to base decisions at least on observations of surface soil conditions and localised crop growth, even if soil pits have not been dug to expose the subsoil.

Earliness depends on large scale climatic differences, but also local factors, such as aspect, that affect soil heating in spring. Accessibility relates to soil structure and soil water. Once surplus water has drained and the soil is at field capacity, tractors and farm implements can be driven over most UK arable soils without damage. Working the land when the soil is wetter can cause serious compaction although the consequences for yield vary with situation. Droughtiness is partly a meteorological phenomenon although crops depend to a large extent on water stored in the soil. The amount of water available to a crop in the main arable areas of the UK before the canopy begins to senesce is usually less than a month's worth and is sometimes much less. This may not be obvious in a rainy area, where soil reserves of water are only important in dry years.

Water availability, nutrient availability and soil temperature vary seasonally while the consequences of low availability depend on the sensitivity of the phase of development. For example, the early availability of water may determine the success or failure of seedling establishment, particularly in oilseed rape.

Spatial variability, which can be classified into two types, is an important attribute of soils. Firstly, there is variation with depth in the field. For example, levels of organic matter are higher at the surface and decline with depth. In some cases, the change is continuous while in others there are step changes such as when there is a cultivation pan. The second type of spatial variation occurs across a field. Yield mapping and soil testing have shown that soil variation over a distance of a few metres can be as much as that across the whole field.

Roots penetrate the soil through gaps between the soil aggregates. The bulk density is the weight of dry soil per unit volume and, since most soil mineral particles have a density of about 2.5 tonnes/m<sup>3</sup>, can be used as an index of the soil porosity. The pores are filled either with air or with water. However, the pore volume is not the whole story as the pore size

distribution is also important. In some clay soils, for example, most of the porosity is in the cracks between otherwise impenetrable peds.

Aeration is closely linked to bulk density. Oxygen is required for respiration by plant roots and by soil micro-organisms. In a well-drained soil, its uptake is balanced by diffusion from the surface through the soil pores.

Differences in temperature between soils are most marked near the surface. Soils containing a large amount of water heat up more slowly in spring and cool less quickly in autumn. Although this phenomenon is only really important in the plough layer, this is the zone that influences the rate of development of the above-ground parts of the plant and the uptake of much of the nitrogen.

## **5. Effects of the soil environment on root growth**

The availability of water affects the growth of the whole plant and also the relative allocation of assimilate to the above-or below-ground parts of the plant. The actual amount of water available depends on soil texture, organic matter content, rooting depth or depth to an impeding layer, and stone content. Thus, there is more water available in deep clay or silt soils without stones. In some clay soils, rooting in the subsoil is only possible through structural cracks and wormholes and this means that not all the 'available' water can be accessed by crops. On the other hand, crops growing in shallow soils over soft parent materials such as chalk can root down into the soil parent material itself.

Bulk density high enough to restrict rooting can occur naturally towards the bottom of the soil profile or because of incorrect cultivations. The latter includes both plough pans caused by ploughing in wet conditions at the same depth year after year in vulnerable soils and cultivation pans, which are a feature of over-cultivation of sandier soils. Problems caused by cultivation are made worse where the organic matter level of the soil is low.

If the oxygen falls to too low a level, root growth can be reduced and death rates increase. Saturated soil is not necessarily anaerobic since oxygen will be dissolved in the water although this will soon be used up. Thus cereal roots can survive short periods of flooding without adverse affects. The effect of waterlogging is least at low temperatures when more air can be dissolved in water and biological activity is depressed leading to a lower oxygen requirement. Because the rate of diffusion of oxygen depends strongly on pore size it is possible for there to be anaerobic patches in an otherwise well aerated soil.

Crop development depends strongly on temperature and rooting is no exception. During winter, the air temperature may be too low for significant above-ground growth but the temperature in the soil may be high enough for root growth of winter cereals, which occurs at the expense of carbohydrate reserves built up in the autumn.

Roots branch profusely when they come into contact with a layer of soil with a high concentration of available nitrogen or phosphorus. Crops grown in nutrient-rich soils have roots which are shorter, more branched and more compact than those grown in similar but poorer soils. Root weight is also a smaller proportion of the total biomass in fertile conditions. The feeding roots are more vulnerable than the structural roots to local

deficiencies in soil nutrients. Although experiments have shown the importance of phosphorus for root development, most UK arable soils contain sufficient available phosphorus for adequate root growth.

## 6. Circumstances in which crop yield can be limited by rooting

It is clear that the key factor is the depth of soil available to the plants for uptake of water and nutrients. In many circumstances plant roots are able to take up most of the available water and nutrients in the root zone. However, the pattern of uptake over time is important because the availability of nutrients can be diminished by leaching losses from the system (particularly nitrogen) down the soil profile, and by drying out of the soil. We would expect differences to show up most in spring crops where the shorter period of growth and greater overlap of shoot and root growth reduce the range of plant responses.

The potential rooting depth increases with stage of development up until about anthesis. The amount of water taken up by plants from below the rooting zone is relatively small unless there is a water table immediately below. If the soil of the plough layer is continuously wet during the early stages of growth, shallow rooting is encouraged which can exacerbate the effect of dry weather later. On the other hand prolonged waterlogging, i.e. anaerobic conditions, can cause root death. When the soil is wetter than field capacity and drainage is occurring, soluble nutrients such as nitrate are leached to lower levels in the soil profile.

Soil structure strongly influences a crop's utilisation of below-ground resources, and climatic factors such as the amount of rainfall can increase or diminish the effects of root limitations on crop growth. The timing of root system development appears to be crucial since the requirements for water and nutrients changes during the growing season. It is also important for there to be sufficient water in the soil in the later stages of development for good grainfill. In well structured soils cereal crops can abstract most of the available water during extended dry spells. However, layers of soil compaction may render large volumes of the subsoil inaccessible to root growth until too late in the growing season, and this precludes the exploitation of stores of water and nutrients in the deep soil layers. Shallow rooting systems characteristic of compacted soils result in a reduction in nutrient and water uptake to the detriment of yield.

## 7. Lodging

Weak root systems can predispose cereals to root lodging. However, the treatments needed to strengthen them are not known with certainty. Good anchorage strength depends on the number and angle of crown root spread and crown root length. Root systems which have many fibrous roots growing downwards and which are progressively strengthened towards their base are less susceptible to lodging. Selective breeding for crops with shorter stems and more widely spread, stronger crown roots will therefore be useful to farmers in areas with a high lodging risk. Farm practices are also important because the condition of the crop has at least as much influence on the probability of lodging as does the weather. Practices which have an influence on lodging resistance include the date of sowing (early drilling improves rooting although it also increases tiller production), plant population density (as this affects

the root: shoot ratio), depth of drilling, rate of nitrogen application (affects the root: shoot ratio and stem strength) and the use of plant growth regulators.

## **8. Indicators of root system performance**

Root attributes which are repeatedly linked to resource capture are root length, root depth, and degree of root-soil contact. Although researchers can use mini-rhizotrons (root periscopes) to monitor the evolution of root systems during the growing season, digging a soil pit (See Appendix 1 *in* Part C: The Review, page 67) is a cheap and effective way of estimating rooting depth and rooting length, at least in qualitative terms (sparse, common, profuse). They are also not subject to the problems of representativeness posed by the permanent access tube installations needed for mini-rhizotrons.

## **9. Genotypic variation in rooting**

There is evidence for varietal differences in response to increasing site fertility. This may be associated with differing ability to scavenge for nitrate. We know that there are significant varietal differences in root system attributes including morphology and response to pH, though not the consequences for yield in particular situations. Selective breeding for favourable root attributes may be used to increase yields in stressful environments and to reduce yield losses through lodging. However, we still do not know enough to be able to attempt this with confidence. Modern genetic methods such as the development of genetic mutants and gene mapping provide an opportunity to test the advantages and disadvantages of different morphologies in particular environments and to separate out the effects of genotype and phenotype. Root plasticity is important for coping with temporal and spatial variation in soil conditions. A root system that is unable to adapt to changing conditions is likely to be the least satisfactory in our unpredictable climate and heterogeneous soil environment.

## **10. Technology Transfer: *Research in Action* demonstration at the HGCA Arable Farming Event, Cereals 1999**

The review on management of root systems was presented as part of the *HGCA Research in Action* at Cereals '99. A soil trench across a plot of winter wheat was used to demonstrate the effect of compaction on rooting characteristics. Considerable interest was aroused and many useful comments were received from farmers. The questions asked fell into four main categories:

- when is it most beneficial to carry out expensive cultivations such as subsoiling?
- what is the normal structure and function of root systems?
- what is the best way to dig a soil pit and what should be looked for?
- what procedures should be used to sample soils and roots in the field?

## 11. Identifying measures to improve yield by manipulation of root systems

The clearest examples of improved growth due to an improvement of the root system come from reduction in soil compaction and from the control of root diseases such as Take-all and pests such as cereal cyst nematode. There is some evidence that varieties differ in their ability to scavenge nitrate from deep in the soil profile. It may be possible to improve the amount or timing of water uptake by manipulating root characteristics, e.g. by adjusting the target plant population density or by choosing an appropriate variety. However, there is no good experimental evidence for this yet under UK conditions. Counts of roots below a depth of 0.60 m suggest that only a proportion of plants actually root below that depth although some root very much deeper.

In contrast to leaf canopies, it is difficult to define an 'optimal' root system for a particular site-season combination. This is because of permanent differences in soil characteristics coupled with inter-seasonal variations in rainfall and temperature. However, in some cases it is possible to use a detailed knowledge of the interactions between soil attributes and root and how these affect shoot growth and yield to select the most appropriate farming practices.

For progress to be made we need to understand the functioning of root systems in the field better so that appropriate combinations of treatments can be tested in field trials. Fine tuning will require measurements to be made on farms because of the spatial heterogeneity of soils. However, some measures should be part of normal best practice such as ensuring the correct pH throughout a field and taking action, e.g. by crop rotation, to minimise the effects of root pathogens.

Neighbouring roots, either from plants of the same crop or of weeds, can lead to a more rapid depletion of nutrients and water, particularly in the plough layer. In a Mediterranean climate, the target plant population density for cereals is often rather less than in a wetter climate. This is said to reduce the rate of water uptake by the crop so that an adequate amount of water remains at flowering. However, availability of nitrogen may be even more important.

Crops which do not invest enough assimilate in the roots may produce a root system which is insufficient to satisfy the water requirements of the plants during dry conditions in the latter part of crop development.

Chemicals applied to the above-ground parts of the plant can affect rooting. Although plant growth regulators are normally applied too late to have a significant effect on root development, there is some evidence that some growth regulators applied at mid tillering can affect root mass and strength. However, the effects of PGR's on roots need to be more widely examined across different soil types and climatic conditions. It is also possible that there are inadvertent effects of herbicides on rooting, although these are likely to be temporary.

Fertiliser application influences the development and distribution of roots. For example, nitrogen application to low nitrogen index soils can increase root length. However, excess fertilising of soils in drought prone areas can result in proliferation of surface root production.

Root dry mass is influenced by plant population. At high plant densities, a greater proportion of the roots is concentrated in the upper parts of soils. High plant density can also reduce root strength and thus increase the risk of lodging. It can also increase the risk and earliness of infection from soil borne disease.

Direct drilling can encourage the formation of stable soils with a network of biopores, though after several years some soils have more compact surface layers than under conventional tillage. Periodic ploughing is then required to improve root penetration. Soils which are more resistant to compaction are better suited to direct drilling i.e. those with good drainage and relatively high organic matter content. Adding manure or other organic material to the soil also has the effect of encouraging earthworm activity which helps to create biopores to depths of up to 2 m.

Rooting of winter crops is generally increased by early drilling, though this increases the risk of Take-all. Normal sowing depths have little effect on rooting. Rotations can be modified so that deep rooting crops such as oilseed rape are planted before crops such as wheat which have a relatively poor penetration ability and thus may not achieve their genetic rooting potential.

Effects of soil compaction are most severe during dry years and periods of drought and the effects of compaction in winter wheat may not be noticed in a wet year. Because compaction reduces the ability of winter wheat to cope with water shortages in the spring and summer, the detrimental effects of soil compaction may be reduced by improving root development by sowing earlier in autumn. Beneficial effects of subsoiling are likely to be largest for spring crops in years when a dry summer follows a wet spring.

In naturally well-structured soils, e.g. some clays, the effect of compaction becomes less over the growing season as wetting and drying cycles re-activate planes of weakness. Thus rooting may be impeded in the early part of the growing cycle but not later on. When water is not limiting the adverse effects of compaction can be eliminated by the application of top dressings of nitrogen fertiliser. Appropriate use of nitrogen fertiliser can ameliorate the effect of soil compaction on above-ground growth and yield. Severe or temporary water logging may be managed by drainage, but permanent water logging offers little or no scope for improvement.



## 12. Recommendations for research

In many cases we probably do not need to modify the root system. The root system itself is able to adjust, to a limited extent, to changes in soil conditions. Focused research is required to improve our understanding of the role of roots in limiting conditions, particularly in terms of water and nitrogen uptake. We need to identify situations in which there is scope for manipulating root systems to improve yield and quality, or reduce inputs. Since, in most cases, management decisions will have to be made before sowing, techniques must be developed to enable farmers to assess the *risk* of limitations to yield and quality occurring at their site. Action might only be justified economically if the risk of yield loss is high.

At present there is incomplete knowledge of the target root size and distribution for optimum crop growth under a particular set of soil conditions, and indeed the scope for manipulating the root system by variety choice, fertilisation policy, plant population density and sowing date. Thus, there are no general approaches to root management that will have benefits for crop growth and yield in a way such as that provided by ‘canopy management’. Many of the recommendations below relate to management of roots or soils under sub-optimal conditions and the need for better use of existing information and technology transfer.

**(1) Improving crop management in areas of high drought risk.** There is a need for a better understanding of how root systems respond to, and function in, drying soils. In particular, information is needed on how roots exploit sub-soil water and nutrients and how this might be improved. Since water and nitrogen availability are closely associated, the supply of both water and nitrogen to the canopy can be impaired as the soil dries. Research is needed to determine effective and reliable ways of encouraging deeper rooting to provide access to greater supplies of water and nitrogen. Problems of water shortage may be associated with particular sites at the end of the season (late season drought on light soils). Water deficits may also be temporary or very localised (e.g. parts of fields).

**(2) Improving crop management on ‘difficult’ soils.** Difficult soils include those which are unstable and susceptible to a loss of structure and those with a blocky sub-soil in which roots can become clustered in cracks or large pores. Layers of soil compaction may render large volumes of the subsoil inaccessible to root growth until too late in the growing season, and this precludes the exploitation of stores of water and nutrients in the deep soil layers. It can also result in a perched water table and anaerobic conditions in the top soil. It is important to confirm whether soil physical properties cause poor crop yields because of a lack of oxygen or because poor root growth induces a shortage of water or nitrogen. Shallow root systems, characteristic of compacted soils, may result in a reduction in nutrient and water uptake to the detriment of yield. We suggest that a better understanding of the way a root system responds to changes in availability of, water and nitrogen could lead to better targeting of expensive cultivations, such as sub-soiling, according to local conditions.

Research is needed to determine how much of the root system should be in the top-soil and how much in the sub-soil to avoid any limitation on the canopy. Soil layers vary in their degree of compaction and the extent to which they are perforated by pores. The pores provide pathways for roots to deeper soil horizons. Varieties might also differ in their ability to penetrate hard soil layers. These factors should be considered when assessing the probability of roots reaching the sub-soil under particular soil conditions and hence the risk of yield limitation.

**(3) Refining advice on cultivations.** In the light of current cereal prices and the desire to reduce establishment costs, there is a need to review advice on cultivations. There is still much uncertainty on when and where cultivations can be reduced, especially in wetter areas and on soils which are susceptible to structural damage. There is a considerable amount of information in the literature that can be utilised to provide targeted advice. This might need to be supported by additional focussed research. Cultivations need to be considered in relation to the requirements of the root system for oxygen, water and adequate root-soil contact, and the risk of limitations to the canopy. We suggest that a more flexible approach to cultivations be investigated, which could involve the rotational application of minimum cultivation techniques.

**(4) Remedial action for shallow-rooted crops.** Temporary water-logging during spring can lead to shallow rooting. This can place the crop at risk from a shortage of water and nutrients later in the season. Management options for shallow rooted crops should be investigated. Plant growth regulators might be a useful tool for stimulating rooting in these situations. Some growth regulators have been shown to increase crown root proliferation and resistance to root lodging, but their effects on root distribution and rooting depth are less well known. Whether they can enhance the depth of rooting sufficiently to reduce the risk of water and nitrogen shortage later in the season needs to be determined.

**(5) Establishment.** It is often suggested that good root establishment is essential for successful over-wintering of cereals, but there are few quantitative data to support this claim. The optimum size and distribution of root system at the start of winter should be investigated for winter cereals, together with the possible action that can be taken to address any deficiency.

**(6) Use of species and varietal strengths.** There appears to be scope to reduce or remove below-ground limitations to crop growth by use of genotypic variation in root growth and morphology and the uptake of water and nitrogen. The measurement of root characteristics in variety trials should therefore be encouraged. In particular, varieties need to be compared under sub-optimal soil conditions as it is under these conditions that the greatest benefits from superior varietal attributes are likely to arise. Species, e.g. winter barley and winter wheat, should also be compared in terms of rooting in order to understand better the circumstances in which one would perform better than the other.

**(7) Soil and root system assessments.** Development of effective root management strategies will require the routine assessment of root systems. At present the techniques available are time consuming and labour intensive, and this limits their widespread use. There is an urgent need to develop more rapid, less expensive, techniques to quantify root length and distribution. These can then be used by researchers for the measurement of root characteristics in variety trials and specific research projects. Farmers are unlikely to have the time or facilities for quantitative measurements. Soil pits which provide semi-quantitative or qualitative information on root and soil conditions are likely to be sufficient for advisory purposes. The optimum number and dimensions of soil pits needs to be investigated as well as the indices of root growth to be assessed.

**(8) Root lodging.** There has been good progress in the prediction and management of lodging. Root lodging is more common than stem lodging and a critical factor in root lodging is the shear strength of the soil. However, the weakest link in the model of lodging is the prediction and control of soil strength. Further research on the factors determining soil strength is required to improve the reliability of advice on the management of lodging.

**(9) Root pathogens.** There has also been good progress in identifying varietal traits associated with tolerance of Take-all. The work to date has focussed on shoot characteristics; tolerance appears to be associated with good economy of tillering and large stem storage reserves. Root characteristics linked to tolerance require more detailed investigation to improve opportunities for minimising the impact of the disease.

**(10) Experimental approaches.** We consider it essential to combine the use of field and controlled environment methods. However, care should be taken when using pots: although experiments in pots and tubes can provide valuable insights into root growth, it is difficult to apply the results to field situations. This is because conditions in the pots, particularly soil structure, bulk density, nutrient distribution and temperature profile, often differ significantly from those in the field.

**(11) Molecular biology.** In the longer term, the genetic basis of root system morphology and function should be investigated. Research programmes to link ideotypes for rooting for particular situations to the molecular understanding of plant growth should be established. Genetic mapping of root (and whole plant) structural and physiological traits will enable breeders to select desirable characteristics more easily.

**(12) Technology Transfer:**

**(a)** There is considerable scope to use existing knowledge to develop clearer guidelines for matching agronomy to soil type. For example there should be a farmer's guide to soil management, including subsoiling, emphasising the costs and benefits.

**(b)** Advice about and demonstrations of examination of soil and root systems should be provided. This should include methods of exposing soil profiles and root systems and the use of shallow soil profiles to examine root spread and number of primary or secondary roots. Advice for cultivations and managing root systems needs to be matched closely to conditions on each farm. Considerable progress could be made by improving the dissemination of existing knowledge to farmers, for example how to examine a soil to identify possible problems.

**(c)** Participative Research (or Farmer-Focused Research) in which the farmer is a participator and beneficiary could be used to improve technology transfer between researchers and farmers and overcome the problems associated with soil variability. The experimental approach is summarised as follows:

- Develop participative farmer groups and establish priorities of local farmers.
- Set up on-farm demonstrations within an integrated core programme.
- Assess the benefits and disbenefits that arise from the Farmer Focused Research.
- Assess how optimum technologies could be transferred more widely amongst farmers and crop consultants.

# MANAGEMENT OF CEREAL ROOT SYSTEMS

## PART C: THE REVIEW

### 1. SUMMARY

The soil-root-shoot system is analysed to highlight the importance of root growth to above-ground cereal growth and yield. The system is complicated by two way interactions, for example the soil environment has major impacts on root growth, but root growth can have profound effects on the soil itself. We conclude that in most situations roots are not limiting to crop growth, but they may become limiting under sub-optimal climatic or soil conditions. The unpredictability of climatic events and their interaction with soil type makes it difficult to prescribe the best farming practices, although an understanding of how root systems behave in changing environments allows the risks of root limitation to be minimised. Optimality is difficult to define for root systems since they serve many functions and limitations depend on a heterogeneous environment – an optimal root system in one field may be limiting to yield in another. The most common scenarios to give rise to root limitations are extreme weather events which cause mechanical failure (root lodging), a shortage of resources (drought or low nutrient availability) or soil conditions which physically impede the progress of root growth (horizons of soil compaction). Management practices are identified which may help farmers to lessen the effects of these unusual situations.

### 2. INTRODUCTION

While the contribution of canopy size to yield is now well understood, we do not know how yield is affected or limited by the root system. We know that management decisions can affect the rooting pattern of cereals, but it is not clear whether these changes are beneficial. This review aims to synthesise the existing knowledge of root systems so that it can be used to identify the most appropriate farming practices for use in a temperate climate with soil limitations. The conceptual model shown in Figure 1. provides the framework for the review (Appendix 2). A description of soil attributes and their affects on rooting is followed by an analysis of rooting attributes and their affect on resource capture. We investigate the effect of the root system on shoot growth and yield and consider whole plant processes which give rise to allocation patterns. We then investigate the effects of various farm practices on the soil, root system and yield of cereal crops.

### **3. SOIL ATTRIBUTES**

#### **3.1. Classification of climate and soils**

Farmers know that crop growth varies within a field and from year to year. The former is more likely to be caused by variation in soil characteristics whilst the latter is strongly influenced by the weather. Variability in soil type and weather, and interactions between them, will also affect a crop's response to treatments. The soil type is an important factor in decision making. After the flag leaf stage, by which time most treatments have been applied, weather has a large effect on growth rate, yield and quality. Regional climatic variability can be taken into account when choosing varieties and application rates. However, being able to describe the soil and climate of a field is important in fine tuning practices and optimising inputs, as well as for modifying experiences and trial results from other places. Likewise, researchers can use this information to decide how transferable results are from one place to another.

#### **3.2. Climate classifications**

Although the UK has been mapped in terms of agroclimatic regions (Francis 1981; Smith 1984), the criteria used are not necessarily appropriate for decision making and for the arable areas inter-annual variation is large compared with spatial variation. With a few exceptions, such as coastal locations and areas separated by high ground, climate changes relatively slowly with distance and a detailed classification is unnecessary. The major climatic gradients in the UK are east-west (winter temperatures and annual rainfall) and north-south (summer temperatures). In the absence of more detailed information, the arable areas of the UK can be divided into six regions, north-east, north-west, east, west, south-east, south-west. Particular locations in these regions can be referenced to the typical climatic values (e.g. wetter than the typical regional value in summer), either on the basis of actual observations or by inference from altitude or distance from the sea.

#### **3.3. Soil classifications**

Soil types have been mapped for all the arable areas of the UK. However, the categories and scale are not necessarily appropriate for a farmer, who is able to base decisions at least on observations of surface soil conditions and localised crop growth, even if soil pits have not been dug to expose the subsoil. The farmer can also differentiate fields in terms of observed earliness, accessibility and droughtiness which are virtually permanent features of a soil as there is limited scope for amelioration. Although not formal scientific terms, these features can be semi-quantified for use in decision support systems.

Clearly fields in Devon are earlier in absolute terms than those in Aberdeenshire for large scale climatic reasons as described above. However, earliness is used as a relative term within a farm or region referring to the rate at which a soil heats up in spring. It is a common observation in the UK that sandy soils on south-facing slopes warm up earlier than clay soils on the level. The reasons are the increased solar radiation load on the slope and the generally lower thermal conductivity and heat capacity of sandy topsoil. At any soil water potential, clay soils contain more water than sandy soils and the bulk density is usually greater so the surface layers warm up more slowly in spring (and cool down more slowly in autumn).

Moreover, poor drainage, which is more likely to occur on clay soils, leads to a higher water content and a slower rate of change of temperature. Thus, one of the benefits of drainage is to speed up the rate of warming in spring.

Once the soil has dried to field capacity, tractors and farm implements can be driven over most UK arable soils without damage. The consequences of traversing the land when the soil is wetter, particularly where cultivations are involved, vary from soil to soil. In some strongly structured soils with a high organic matter level, the damage may be minimal. In others, a cultivation pan can form in the plough layer restricting root penetration at least temporarily. In others again, a plough pan can form below the plough sole and this again restricts rooting. The following three broad categories can be identified, based on the work of Cannell *et al* (1978).

1. Well drained soils with a stable structure such as those on chalk or limestone, well drained loamy soils and coarse sands with a high organic matter content.
2. Chalky clays, and clay soils with a clay or loam topsoil which have been improved by drainage.
3. Sandy soils with a low organic matter content, silty soils, wet alluvial soils, clayey soils that return to field capacity before November, clay soils with a clay or loam topsoil which have not been improved by drainage.

Like earliness, droughtiness is partly a meteorological phenomenon and so, other things being equal, fields in south-east England are more droughty than those in south-west Scotland. Of course other things are never equal and differences between soils can be much greater than those between regions. The profile available water in UK cereal fields varies from about 60 mm to more than 250 mm, equivalent to 20 to 80 days of potential transpiration in June. In soils at the upper limit, such as the silty clay loams of Rothamsted Experimental Station, drought symptoms will rarely be seen provided there are no structural problems. On the other hand, in a high rainfall area at the margins of arable agriculture, even soils at the lower end of the range may only show an effect of drought in dry years. The actual amount of water available to the crop depends on the texture of the soil (higher in clay and silt soils), the organic matter content, the rooting depth (depth to an impeding layer) and the stone content. In some clay soils, rooting in the subsoil is only possible through structural cracks and wormholes and this means that not all the 'available' water can be accessed by crops. On the other hand, crops in shallow soils over chalk can root down into the soil parent material itself.

### **3.4. Soil types**

The soil type can have a large impact on all of the factors which affect the growth and distribution of roots (Andrén *et al* 1993). For example, clay soils and sandy soils differ from each other in their available water capacity (because of the pore size distribution of the soil), nutrient retention and delivery (pore structure, organic matter content, pH and water availability), penetration resistance and even temperature. In a survey of 50 spring barley root profiles taken over a range of soil types, plants grown on sandy soils had a mean maximum rooting depth of 70 cm as compared to 140 cm on loamy soils (Madsen 1985) and low root length densities could be explained by soil texture. Andrén *et al* (1993) found that the root

number, root length and mean rooting depth of barley were greater on sand than on clay even though there were no differences in root system or plant dry mass. They also found that the crop grown in sand contained more N and P than the crop grown in clay. P availability on clay soils is reduced because P is easily adsorbed onto the surface of clay particles.

There is evidence that the size of soil aggregates has an influence on the rate of plant growth which is independent of the ability of the root system to take up adequate quantities of water and nutrient (Passioura & Stirzaker 1993). Crops grown on finer aggregates tend to grow better than those grown on large aggregate sizes and this phenomenon may explain the observed lower growth rates and yields of crops grown on excessively loose soils (Hakansson *et al* 1998).

### **3.5. Soil attributes affecting roots and soil heterogeneity**

The general classification described above can be related to factors which can be measured in the field. Some factors vary considerably temporally and spatially. Temporal variations are particularly important for water availability, nutrient availability and soil temperature and tend to be the result of irregular timing of farm practices or unpredictable weather events. Farm practices such as tillage, ploughing in of crop residues, fertiliser spreading, liming and farm traffic all contribute to the heterogeneous spatial distribution of resources. Placement of fertiliser is not now common with cereals. However, few spreaders give completely even distributions. Spatial heterogeneity is important because crop roots may respond very differently to different soil conditions. However, the scale of heterogeneity is crucial because if it can be sensed by a crop root then the root can respond meaningfully to it. The plant may be even more efficient at using resources than if they are homogeneously distributed (van Noordwijk & van de Geijn 1996). In contrast, scales of heterogeneity which are larger than the individual crop plants cannot be sensed by the root systems and this usually results in a less efficient use of resources.

Two types of spatial heterogeneity are important. In the first instance there is variation with depth. This variation can be continuous or can occur in steps such as when there is a cultivation pan. The changes are often more rapid towards the surface soil layers when compared to the deeper soil layers. This is reflected in root growth models which divide the soil into horizontal layers which increase in depth towards the bottom of the soil profile. Yield mapping and soil testing have shown that horizontal soil variation over a distance of a few metres can be as much as that across the whole field (Beckett & Webster 1971). Recent developments in precision farming aim to optimise inputs by taking account of these variations.

Resources which have a heterogeneous distribution through the soil include organic matter (van Noordwijk *et al* 1993; vanVuuren *et al* 1996), mineral nutrients (Robinson *et al* 1994; vanVuuren *et al* 1996; Robinson & vanVuuren 1998) and water (Barraclough 1989; Tardieu & Katerji 1991; Gregory 1994a; Droogers *et al* 1997; Brisson *et al* 1998). Soil structure and bulk density may also vary heterogeneously, for example when there is a layer of soil compaction induced by farm traffic (Davies *et al* 1972; Ehlers *et al* 1983; Lipiec *et al* 1991).

Crop root systems demonstrate mechanisms for coping with a heterogeneous distribution of resources. Soil conditions which inhibit root growth in one part of the soil may lead to compensatory growth in other soil zones where conditions are more favourable (Barracough 1984; Barracough & Weir 1988; Lipiec *et al* 1991; Unger & Kaspar 1994; Gregory 1994a). Similarly, when the availability of nutrients is low, plants will increase the rate of absorption per unit length of root in zones of relatively high nutrient availability (Robinson *et al* 1994). Atkinson (1990) suggests that highly branched root systems are more efficient at exploiting heterogeneous soils while Robinson and van Vuuren (1998) concluded that fast growing plants showed a greater plasticity of root growth in response to nutrient patches. In an experiment using localised patches of N<sup>15</sup> labelled organic matter in otherwise N-deficient soil (van Vuuren *et al.* 1996), exploitation of the mineralised nitrogen by wheat occurred mainly from an increase in N uptake rate per unit root length, i.e. N inflow. Root proliferation in the patch occurred most vigorously only after most of the mineralised n had been captured and therefore had a limited impact on N capture. Increased N inflow during the first five days after roots entered the patch accounted for 8% of the patch-derived N that the wheat eventually captured. A combination of increased inflow and modest proliferation in the following seven days captured 63% of the total N. The remaining 29% of the N was captured during the period of greatest root proliferation, inflow had decreased to the rate of the controls. Root proliferation response to localised N appears to be correlated strongly with N capture only when plants with different rooting responses compete for N (Robinson *et al.* 1999). Therefore, attempts to manipulate this response by management or genetics are unlikely to greatly affect N capture in intensively managed cereal monocultures except in the case of competition with weeds.

#### **4. PHYSICAL ENVIRONMENT**

##### **4.1. Water availability**

Not all the apparently available soil water can actually be taken up by plants (Droogers *et al* 1997). The bulk density, organic matter content and porosity of the soil as well as the rooting characteristics of the crop define a hypothetical extraction zone around each root. In some circumstances accessibility can be increased by appropriate management of the soil and cultivar selection. For example, in a comparison of several different barley cultivars, the proportion of available water abstracted varied from 95% to only 68%.

Some authors have found a disparity between the amount of available water and the actual soil water depletion (Tardieu & Katerji 1991) once rainfall is taken into account (Brisson *et al* 1998). This is because on highly conductive soils, deeper layers which do not contain any roots may still contribute substantially to the water balance and the uptake of nutrients by capillary rise of water.



#### **4.1.1. Waterlogging**

Waterlogging occurs when the soil is saturated leading to low oxygen concentrations and the production of toxic compounds which inhibit root growth (Ellis 1997). Anaerobic conditions also encourage denitrification and reduce the available soil nitrogen. This is compounded because soluble nutrients such as nitrate are leached to lower levels in the soil profile unless the saturated hydraulic conductivity is low. Cereal roots can survive short periods of flooding without adverse effects because oxygen dissolves in water in small quantities and because they are capable of anaerobic metabolism when oxygen supply exceeds demand. It has also been reported (Varade, Stolzy & Varade 1970) that at least some cultivars of wheat are capable of oxygen transport from the shoot to the roots through aerenchyma tissues. The effect of waterlogging is least at low temperatures when more air can be dissolved in the water and biological activity is depressed leading to lower oxygen requirements by the plant. The importance of aeration of the roots during aggregate penetration has been discussed by van Noordwijk *et al* (1992). The oxygen requirements are highest for the growing tip of the root, which, during penetration of soil aggregates may be a long way from the nearest oxygen source. Anaerobic breakdown of plant residues can lead to the production of harmful substances, such as acetic acid, that can inhibit rooting. However, roots may follow the channels left by decaying roots of previous crops.

Weaver (1926) warned that raising the depth of the water table may cause death of the deeper roots and usually results in a decrease in yield. He also noted that if the subsoil was waterlogged deeper roots would not develop and this would predispose crops to drought and agricultural disturbance. In addition to reducing soil nutrient availability, waterlogging disrupts the uptake of nitrogen and this manifests itself as a plant nutrient deficiency (Gales 1983; Huang *et al* 1995). Physiological processes such as photosynthesis, water uptake and root-shoot hormone relations are affected (Pezeshki 1994). Comparisons of wheat cultivars show that in waterlogged soils, intolerance is accompanied by high concentrations of Fe and Mn in the shoot (Huang *et al* 1995). The effects of waterlogging seem to be reduced by increasing nutrient availability through fertiliser application (Gales 1983; Huang *et al* 1995).

#### **4.1.2. Aeration**

Aeration is closely linked to bulk density since the soil consists of mineral matter, water and air. Oxygen is required for respiration by plant roots and by soil micro-organisms. In a well drained soil, oxygen uptake is balanced by diffusion from the surface through the soil pores. Root growth may be reduced and death increased if the amount of oxygen reaching the roots falls below a critical level. Because the rate of oxygen diffusion depends strongly on pore size it is possible for there to be anaerobic patches in an otherwise well aerated soil.

#### **4.1.3. Drought**

During drought, soil water becomes less than required for potential transpiration by the plant. There are also changes in the physical condition of the soil such as increases in strength (Ehlers *et al* 1983; Martino & Shaykewich 1994) and the formation of air gaps between the root and the soil, which reduce the amount of contact and which can lead to large increases in the resistance to water and nutrient uptake (Nye 1992). Drying of the soil surface may also inhibit normal development of the nodal root system (Gregory *et al* 1978; Gregory 1994a).

The root number of five barley cultivars was reduced by drought, and the root volume was reduced by between 56.3% and 51.6% when compared to a well-watered treatment (Khaldoun *et al* 1990). Root and shoot growth of winter wheat were also reduced by the imposition of an artificial drought (Barraclough & Weir 1988) even though water use was not affected until after anthesis. An increase in winter wheat root length at heading from 7.8 km m<sup>-2</sup> to 14.9 km m<sup>-2</sup> in two successive years was attributed to warmer and wetter conditions in the second year (Haberle *et al* 1996).

Water and nutrient availability should be considered together. In one experiment on a silty clay loam soil at Rothamstead (England), the combined effect of low water and nitrogen availability reduced the yield of winter wheat from 9.7 t ha<sup>-1</sup> with fertiliser and adequate water to just 3.8 t ha<sup>-1</sup> (Barraclough 1989). Since drought alone reduced the yield to 7.9 t ha<sup>-1</sup> and low nitrogen availability alone to 4.8 t ha<sup>-1</sup>, the effects are almost additive. Drought reduced the amount of root growth in the topsoil although there was some compensatory growth in the subsoil as long as there was available nitrogen. Drought increased the depth of rooting from 140 cm to 160 cm although the root density at depth was low (<0.1 cm cm<sup>-3</sup>) compared to the topsoil (5-9 cm cm<sup>-3</sup>). In droughted conditions and with a supply of nitrogen, a rooting density of 1 cm cm<sup>-3</sup> was found sufficient to allow all the available water to be extracted to a depth of 0.8 m. Below this depth water uptake was limited by root growth.

Winter cereals are probably less susceptible to water shortage than spring cereals because of their earlier and more extensive root development (Gales 1983). Weaver (1926) suggested that keeping the surface soil too moist during the early life of a plant would promote a shallow rooting habit which would make the plant vulnerable to drought at later stages of the life cycle.

#### **4.2. Bulk density**

The most important soil conditions to affect root growth appear to be the presence of an appropriate system of pores for roots to grow through combined with a soil structure which allows penetration and a supply of all the resources required for growth (Gregory 1994a). The bulk density is the weight of dry soil per unit volume. Since most soil mineral particles have a density of approximately 2600 kg m<sup>-3</sup> (silica), bulk density can be used as an index of the spaces in the soil. These spaces are filled with either air or water. Stirzaker *et al* (1996) point out that bulk density alone is insufficient to explain root penetration to depth. Even in a soil of high bulk density, there may be pores which make exploration of deeper soils possible. Hence, the pore size distribution is also important. In some clay soils, most of the porosity is in cracks between otherwise impenetrable peds (soil structural units). In a study on the effects of aggregate size on the growth of wheat roots, coarse aggregates and compacted soil structures were found to decrease the root length, root surface area, root fresh weight, shoot weight and seed yield (Keita & Steffens 1989). Where there were fine aggregates, roots tended to be thicker and root hairs were longer. Bulk density high enough to restrict rooting can occur naturally towards the bottom of the soil profile or because of cultivation practices.

### 4.3. Compaction

Intensification of UK farming systems in the 1960's led to widespread problems of compaction which were reviewed for England and Wales in a report of the Agricultural Advisory Council (1970). Subsequent changes to machinery and farming practice reduced these problems considerably. A soil may have 60% of its volume as pore space, of which 20-30% is occupied by air at field capacity (Davies *et al* 1972). Soil compaction occurs when the structure of a soil is changed so that there are fewer large pore spaces. Thus, a heavily compacted soil may have only 30-40% pore space, of which just 5% is filled by air at field capacity, and the bulk density will be higher than in the uncompacted state. However, for a given bulk density, soil shear strength rises with decreasing soil moisture content so that the penetration resistance of a soil increases as it dries (Ehlers *et al* 1983; Martino & Shaykewich 1994). The soil shear strength is predicted to have a very large influence on the probability of root lodging (Crook & Ennos 1993).

Zero tillage tends to lead to a higher soil bulk density and penetration resistance in the surface layer when compared to a tilled soil (Ehlers *et al* 1983). However, the highest bulk densities and penetration resistances occur in soils which have been regularly subjected to passes by heavy farm machinery (Ehlers *et al* 1983). These areas of high penetration resistance occur in zones known as 'plough pans' which are situated immediately below the tilled layer. For example, Hakansson *et al* (1996) found that 'ordinary' farm traffic increased penetration resistance by an average of 40% at a depth of 40 cm while Ehlers *et al* (1983), working on a loessial soil, found that tillage had induced a plough pan in the 25-30 cm soil layer with a bulk density of 1.5 g cm<sup>-3</sup> compared to a bulk density of 1.28 g cm<sup>-3</sup> in the 1-5 cm layer. Lipiec *et al* (1991) showed that the use of a five wheel compaction treatment changed the soil structure by reducing the air filled porosity and increasing the penetration resistance. Slipping farm vehicle wheels may cause compact layers with a pronounced platy structure (Davies *et al* 1972).

Because of structural differences between soil types, bulk density is not an appropriate measure of compaction when comparing sites with different soils. For this reason, the concept of 'degree of compactness' was developed (Hakansson 1990; Lipiec *et al* 1991). The degree of compactness of a soil refers to the ratio (as a percentage) of the dry bulk density of the soil and the dry bulk density of the same soil in a compacted reference state. The reference state is determined by loading the soil with a pressure of 200 kPa until drainage ceases (Hakansson 1990). The usefulness of this measure was confirmed in a series of 100 field experiments on spring barley where it was shown that the maximum crop yield was obtained at the same degree of compactness regardless of soil type. The optimum degree of compactness (87 %) was virtually independent of the soil particle size distribution but varied with crop type.

Roots grown on soils with a high penetration resistance show characteristic changes in morphology. Cell walls are thickened and there is a decrease in the rate of cell production (Bengough *et al* 1997). Mechanically impeded roots are thicker, as they continue to increase in diameter further behind the growing tip than in unimpeded roots. Their surface is less regular, they tend to be flatter and their growth tends to follow a more convoluted path through the soil (Lipiec *et al* 1991).

It has been claimed (Pietola 1991) that in most fields which are subject to ordinary farm traffic, penetration resistance reaches values which restrict root growth (Hakansson *et al* 1996). As Barley, Farrell & Greacen (1965) point out, soil strength can be regarded as a property which has a general influence on root elongation rather than as a limiting factor which is only encountered in unusual situations. Root penetration is controlled chiefly by the strength of the soil, and a number of authors have suggested a strong relationship between the rate of vertical root growth and the penetration resistance (Barley *et al* 1965; Ehlers *et al* 1983; Martino & Shaykewich 1994). Drying out and the resulting hardening of a clay loam soil may entirely inhibit the penetration of roots into the subsoil (Pietola 1991).

It was recognised relatively early on that the importance of compaction on crop yield depended on the amount and distribution of rainfall during the growing season (Fisher *et al* 1975). Tardieu (1994) suggested that under some climatic conditions, the effects of soil compaction on whole plant growth rate and allocation could be pronounced, while under more favourable conditions only small changes occurred. This was confirmed by Unger & Kaspar (1994) who noted that even if compaction limited root growth, weather events could enhance or diminish the effect of root limitations on crop growth. There are data which support the suggestion that the

beneficial effects of subsoiling are largest for spring sown crops in years when a dry summer follows a wet spring (Barraclough 1984; Barraclough & Weir 1988). In contrast, a mid September sowing date, followed by an unusually wet spring resulted in a relatively small effect of compaction on yield (Barraclough & Weir 1988). With cereals sown late in the autumn or in the spring, penetration of the compact soil layer would be later and the potentially increased supply of water from the subsoil delayed. Barraclough & Weir (1988) concluded that soil compaction is most detrimental during dry years and periods of drought. A further consideration is that when the zone of compaction is deeper in the soil, the amount of water available to the roots is larger, and there is less likelihood of severe water stress (Barraclough 1984). The responses of crops to subsoil loosening seems to depend on the patterns of rainfall distribution in relation to root growth and the developmental stage of the crop (Bamford *et al* 1991).

It has been shown that variations in root growth can be explained mainly by differences in soil water content, whereas variations in bulk density may be of minor importance (Ehlers *et al* 1983). This issue has been contentious in the literature - Some have found that root elongation was partly a function of the soil water potential and not solely a function of the penetration resistance (Eavis 1972; Mirreh & Ketcheson 1973; Baryosef & Lambert 1981), while others have found that soil water *per se* had no influence on the rate of root penetration and that this was solely accounted for by soil strength (Barley *et al* 1965; Taylor & Ratliff 1969; Greacen & Oh 1972). In a review of the evidence, Ehlers (1980) concluded that for sorghum the extension rates of roots were directly related to the penetration resistance and not to the soil water content *per se* unless the matrix potential dropped below -0.5 or -1.0 MPa.

Soil horizons rarely have a uniform bulk density, and roots tend to follow zones of relatively low penetration resistance (Barraclough & Weir 1988). Zero tillage can intensify the soil shrinkage process, leading to heterogeneity of soil structure characterised by vertical planes of weakness, or by the presence of channels created by previous plant roots and soil fauna (Ehlers *et al* 1983; Stirzaker *et al* 1996). Martino & Shaykewich (1994) found that although zero tillage increased the penetration resistance in the top 10 cm of soil, there was an increase in the proportion of macropores ( $>100 \mu\text{m}$ ) close to the soil surface. These channels are known as 'biopores' and although they typically occupy less than 1% of the soil volume, they allow crop roots to penetrate compact layers of soil (Ehlers *et al* 1983; Martino & Shaykewich 1994; Stirzaker *et al* 1996). However, growth inside pre-existing biopores involves a trade off between the increased access to soil resources and the poor root-soil contact. The walls of biopores also tend to be relatively impenetrable to lateral root growth.

Stirzaker *et al* (1996) showed that in a growth chamber, barley was found to grow best on soil with a bulk density of  $1400 \text{ kg m}^{-3}$ . This represents a compromise between soil which was soft enough to allow good root development but was sufficiently compact to give good root-soil contact. Quantitative measures of the limits of plant tolerance to root compaction are reported in a number of different units. Bowen (1981) showed that when soils were at field capacity, the critical maximum bulk densities for root penetration ranged from  $1.55 \text{ g cm}^{-3}$  on clay loams to  $1.85 \text{ g cm}^{-3}$  on loamy sands. They quote a critical air filled porosity of 10% v/v and a penetration resistance of 3 MPa. In a review of the literature Ehlers *et al* (1983) found that root growth ceased at soil strengths between 2 and 2.5 Mpa, although their own data showed that the limiting penetration resistance for root growth in a tilled  $A_p$  horizon was 3.6 MPa and in the untilled  $A_p$  horizon 4.6-5.1 MPa. They attribute these higher values of critical penetration resistance to the development of a continuous pore system in the soil, created by worms and the roots from previous crops. Martino & Shaykewich (1994) also suggest a soil strength critical for root penetration of 2 MPa and found that this value was independent of soil type. However, the only measure of soil compaction which is truly independent of soil type is the 'degree of compactness' (see page 21): in a wide ranging test, Lipiec *et al* (1991) found that when it exceeded 88% there was a sharp decline in LAI and yield of barley.

#### **4.4. Temperature**

Crop development depends strongly on temperature and rooting is no exception. Differences in temperature between soils are most marked near the surface. Soils containing a large amount of water heat up more slowly in the spring and cool less quickly in the autumn while increases in compaction have been found to reduce daily soil temperature fluctuations (Lipiec *et al* 1991). During winter, the air temperature may be too low for significant above-ground growth but the temperature in the soil may be high enough for root growth. Daytime temperature has more effect than nighttime temperature because this is when these processes are active. Higher root temperatures lead to increases in root length density ( $\text{cm cm}^{-3}$ ) (Sharratt 1991; Haberle *et al* 1996).

## 5. CHEMICAL ENVIRONMENT

### 5.1. pH

In wheat, there is evidence that root hair growth is reduced below a pH of 7 and by low calcium concentrations but that it is increased by low nitrate concentrations. Low calcium availability is usually correlated with low pH. The root length and root fresh weight of wheat plants grown at pH's ranging from 6.0 to 4.0 were all decreased with decreasing H<sup>+</sup> concentration (Johnson & Wilkinson 1992). There was a similar decrease in the root length between cultivars which indicated a uniform response of wheat to excess H<sup>+</sup> concentration in the soil solution.

### 5.2. Nutrient availability

Nutrient availability has a strong interactive effect with the availability of other soil resources (see *drought*). Higher soil nutrient availability increases the nitrogen uptake rate of a wide range of wheat genotypes (Greef & Kullmann 1992) and this is usually associated with an increase in yield.

Application of nitrogen to soils with low available nitrogen can cause an increase in root length throughout the root system (Robinson *et al* 1994) although is not invariably the case. There is also an increase in the number of laterals and branching (Weaver 1926; Feil & Geisler 1988; Gregory 1994a), the average length of each lateral root (Welbank *et al* 1974; Gregory 1994a), the depth of rooting (Hansson & Andren 1987) and in the rooting density (Hansson & Andren 1987). In contrast, some authors report a decrease in the length of the main axes and laterals (Weaver 1926; Greef & Kullmann 1992). It has long been known that nutrient rich soil patches lead to localised root proliferation (Gregory 1994a) and surface applications of nitrogen fertiliser tend to result in high root densities in the surface layers of the soil. In one case the effect of fertiliser on the rooting depth of barley gave no access to mineral nitrogen below 25 cm where only scarce unbranched primary roots could be observed (Welbank *et al* 1974). Weaver (1926) warned against fertilising the soil surface with nitrates in regions which are susceptible to drought because of the stimulation of surface root production.

Nitrogen is not the only important nutrient, and phosphorus in particular is crucial to proper root development. In addition, P is more likely to be scarce because of its low mobility in the soil. The importance of phosphorus for roots has been known since the 19<sup>th</sup> century. Weaver (1926) appreciated its importance and recommended that a dressing of phosphate enhanced root production and was valuable whenever greater root development was required. Phosphates induce the young roots to penetrate rapidly into the layers of soil beneath the surface which imparts a higher resistance to water shortages later. After 100 days, Weaver (1926) found that the depth of rooting of wheat grown with phosphates was twice that of wheat grown on similar soils with a low phosphate status. This is consistent with Gregory *et al* (1994a) who note that banding of P close to the seed during drilling may stimulate growth and result in fast early development of the crop. There is some evidence that low P availability increases the production of root hairs on oilseed rape (Bhat & Nye 1974). Root hairs are especially important in the uptake of nutrients such as P which only have low

mobility in the soil. Other research has shown that the length of root hairs is inversely proportional to the phosphorous status of the plant (Foehse & Junck 1983). Potassium was not found to stimulate lateral branching in the same way as nitrates.

### **5.2.1. Transport of water and solutes through the soil**

While shoots take up rapidly replenished resources such as CO<sub>2</sub> from the air surrounding the leaves, roots tend to deplete resources in the rhizosphere immediately surrounding them (Gregory 1994a). The rate of uptake is therefore also dependent on the rate at which nutrients and water are able to move through the soil medium to the root surface.

The mobility of nutrients varies considerably so that while nitrate can move distances of between 1 and 10 cm through the soil to an absorbing root, phosphates can effectively only diffuse from within 1 mm of the root surface (Ellis 1997). The diffusion of nitrate through the soil medium is also about one order of magnitude faster than the movement of ammonium (Clarke & Barley 1968).

Whereas nutrients move through the soil down concentration gradients, the movement of water is driven by a water potential gradient. In a homogeneous soil, the water content close to the root surface will be lower than in the bulk soil. This difference depends on the rate of transpiration which drives the uptake of soil water by the roots. The average rate of water uptake per unit length of root is found by dividing the total length of the root system by the transpiration rate. However, not all parts of the root system are equally active in water uptake. It follows that crops with relatively small root systems will have the largest draw-down in soil water content close to the root (Kage & Ehlers 1996). Stomata will therefore tend to close at a higher average soil water content in plants which have a lower total root length. The root length density and rate of water transport through the soil limit the rate of water uptake by the root when the soil close to the root reaches permanent wilting point. Adopting the assumptions of the 'single root model', the most important factors in determining the rate of water transport to the roots are volumetric water content and root length density (Kage & Ehlers 1996). Root diameter was found to be less important. In practice Kage and Ehlers (1996) found that the rate of water movement through the soil was only limiting in deeper soil layers with very low rooting densities (<0.1 cm cm<sup>-3</sup>). They commented that a plant which is well adapted to drought stress should develop its root system rapidly to exploit all depths but should not over develop its root length density in the surface soil layers. The most efficient investment of carbon is in thin roots which are more efficient at water uptake than thicker roots, although the root should be large enough to maintain root-soil contact and to not have a prohibitive xylem transport resistance.

Some studies seem to confirm that the water content close to the root is substantially reduced and that the rate of water uptake is therefore closely dependent on the root length density (Gardner 1960; Cowan 1965), while others have shown that only small water gradients in the soil are necessary to maintain water transport to the roots (Molz 1975; Bristow *et al* 1984; Reid & Hutchinson 1986).

The degree of root-soil contact is particularly important for the uptake of resources which are scarce or have a low mobility such as P (Gahoonia *et al* 1997). Root-soil contact of wheat increases with soil bulk density (Schoonderbeek & Schoute 1994). However, in very wet conditions, the degree of aeration can decrease with increasing root-soil contact.

## **6. BIOLOGICAL ENVIRONMENT**

### **6.1. Soil micro-organisms**

Soil micro-organisms have an important influence on the availability of nitrogen to the crop.

Mycorrhizal symbiosis may be a way for the plant to overcome the limits of root fineness for phosphorus uptake as the thin fungal hyphae increase the volume of exploited soil in return for relatively small investments in biomass (Marschner 1998; Ryser 1998). In fact Ryser (1998) suggests that the evolution of the fine root system may be a means of serving the same purpose when development of a mycorrhizal association is not possible. The branching order of mycorrhizal plants is typically increased from three to five because of increased branching of the root axes (Atkinson & Hooker 1993). One other benefit of the arbuscular mycorrhizas of grasses such as cereals is that they tend to decrease the effects of soil borne diseases (Atkinson & Hooker 1993).

Spring and winter wheat cultivars show varying degree of dependence on mycorrhizal associations (Hetrick *et al* 1993; Hetrick *et al* 1996) and modern breeding (since 1950) may have reduced the reliance on mycorrhizal symbiosis. Mycorrhizal colonisation in the absence of dependence was beneficial to six out of ten wheat cultivars (Hetrick *et al* 1996). The response to mycorrhizal infection decreased with increasing P fertilisation which suggests that responsiveness to P availability may be a good predictor of mycorrhizal dependence. Most cereal soils in the UK have a high enough phosphorus status that mycorrhizal infection is not thought to play a significant role in P uptake.

Incubation of wheat seedlings with *Azospirillum* dramatically increases the formation of lateral roots, probably because it releases nitrite close to the root which acts as a phytohormone to encourage root branching (Bothe *et al* 1992).

### **6.2. Soil borne pathogens and pests**

Several pathogens can seriously affect the rooting of cereals. Take-all is the most damaging root disease of cereals; with wheat suffering more so than barley. At harvest, Take-All (*Gaeumannomyces graminis*) increased the proportion of soil mineral nitrogen which originated from applied fertiliser from about 10 % to 21 % (Macdonald *et al* 1997) showing that the stunted roots were less effective in taking up nitrogen from the soil. High nitrogen supply increased the infection rate of Take-All on the primary roots of wheat and the severity of the primary infection cycle but decreased the infection of secondary roots and the severity of the secondary infection cycle (Colbach *et al* 1997).



Effects of Take-all on cereals and strategies for its management have been reviewed by Hornby and Bateman (1991). Some methods of control relate directly to root development. For example, correcting poor drainage or soil structural problems that affect rooting and avoidance of high seed rates which can reduce root development. Other key factors are ranking soils/fields according to the level of Take-all risk, avoiding major nutrient deficiencies, avoiding second or third wheats in high risk situations, modifying rotations, use of adequate nitrogen fertiliser and preventing patches of low pH.

Cereal cyst nematode (*Heterodera avenae*) can have dramatic negative effects on the growth of wheat roots (Amir & Sinclair 1996) although its most important effect in the UK is on oat roots (Ellis 1997).

### **6.3. Roots of neighbouring plants**

The roots of neighbouring plants may compete for soil resources such as water and nutrients. Reducing the planting density reduces the amount of competition from neighbouring plants and is a strategy that may conserve soil water for use in the later stages of development of the crop.

## **7. ROOT CHARACTERISTICS**

As early as 1926, Weaver (1926) warned of the difficulties in interpretation of root data. Accurate measurement of the root system presents practical difficulties which many root scientists have struggled to overcome (Knof 1990; Bengough *et al* 1992; Vetterlein *et al* 1993; van de Geijn *et al* 1994; Kucke *et al* 1995; Majdi 1996; Pages & Bengough 1997). Observation of the root system *in situ* can skew results and sampling the soil with cores or permanent access tubes is subject to problems of representativeness (Andren *et al* 1991; Parker *et al* 1991; Hansson *et al* 1992; Jordan 1992; de Ruijter *et al* 1996). Despite this, measurements of the rate of growth and consequent distribution of roots within the soil profile are very important because of their role in nutrient and water uptake.

### **7.1. Root growth**

In small grain cereals such as wheat, barley and oats the seed contains relatively large reserves of storage carbohydrate and nutrients (Marschner 1998) which allow the initial root system to grow rapidly to considerable depth. Branching often begins before the leaves have unfolded so that the plant can establish an early contact with water (Weaver 1926). There is evidence that the final root biomass and length of barley roots does not vary much between seasons although there are differences in the rate of root growth between years (Welbank *et al* 1974). Typically, the root mass of winter wheat increases exponentially until the end of March and then linearly until anthesis (Gregory *et al* 1978). Under UK growing conditions translocation of carbon to the roots of cereals effectively stops after anthesis (Gregory 1994a). Thus the root mass remains constant for about one month and then decreases slightly towards harvest due to root death. It is important to note that new root growth may be occurring

in

one

layer whilst root death is happening in another. Total measures give an apparently static situation whereas the observed root mass is the net outcome of dynamic changes in the root system. The final masses of winter wheat grown on UK soils typically range between 97 g m<sup>-2</sup> and 170 g m<sup>-2</sup> (Gregory 1994b).

For winter wheat, a survey of total root length showed values between 15.4 km m<sup>-2</sup> and 32.0 km m<sup>-2</sup>. The maximum root length of spring barley (10.2 km m<sup>-2</sup>) was attained within 100 days of sowing (Welbank *et al* 1974) after which it decreased slightly. High nitrogen availability increased the root length relative to treatments with lower nitrogen availability (Welbank *et al* 1974) and sand also increased the root length of barley (24 km m<sup>-2</sup>) when compared to clay (16 km m<sup>-2</sup>) (Andr n *et al* 1993). The time of sowing has a large impact on root length so that wheat sown in September always had more root length than wheat sown in October (Barraclough 1984) even though the root masses converged between March and June. Despite differences in total root mass and total root length, the mean length of cereal root members is relatively constant across a wide range of growing conditions (Gregory 1994a).

## 7.2. Root depth

There is a genetically determined maximum depth of rooting although the actual depth of rooting is largely determined by soil conditions (Gregory 1994a). The rooting depth increases until anthesis when it usually becomes constant (Gregory 1994a). Winter wheat roots reach depths of 0.75 – 1.0 m by the beginning of April and keep growing rapidly downwards to reach approximately 2.0 m by the end of May (Gregory *et al* 1978; Gales 1983). Sixty days after sowing, spring barley roots had reached a depth of 0.3 m (Welbank *et al* 1974) while reports of maximum barley depth range from 0.7 m on sandy soils (Madsen 1985) through 1.2 m (Bragg *et al* 1984), 1.32 m (Kirby & Rackham 1971), 1.4 m on loamy soils (Madsen 1985) to 1.6 m for spring barley and 1.7 m for winter barley (Vetter & Scharafat 1964). Other studies showed maximum rooting depth for wheat varied from 1.4 m for winter wheat when water availability was high to 1.6 m under drought conditions (Barraclough 1984). Spring wheat (Vetter & Scharafat 1964) had a depth of 1.6 m compared to 1.9 m for winter wheat (Gregory *et al* 1978). (Vetter & Scharafat 1964) Oat roots penetrate to a depth of 1.8 m (Vetter & Scharafat 1964). Individual roots of cereal crops can reach a depth of over 2 m (Kirby & Rackham 1971; Ellis 1997) while laterals can extend to a distance of 1 m from the plant.

Root depth is affected by date of sowing in a similar way to root length, with September sown crops having a deeper root system than those sown in October (Barraclough 1984). Mechanical impedance can have a large impact on rooting depth. The proportion of roots penetrating the soil was found to be inversely related to the soil penetration resistance (Martino & Shaykewich 1994), and this led to an associated reduction in the rooting depth on compact soils (Ehlers *et al* 1983; Barraclough 1984; Barraclough & Weir 1988; Lipiec *et al* 1991; Unger & Kaspar 1994). Typically the rooting depth of winter wheat in a compacted light sandy loam soil reached a maximum of 1.0 m at anthesis, compared to 1.4 m in an unimpeded soil (Barraclough & Weir 1988) - while on a loess-like soil in Poland, the rooting depth of spring barley was reduced by compaction from 0.6 m to 0.30 m (Lipiec *et al* 1991).

### 7.3. Extension rate

Barracough and Weir found vertical root extension rates in winter wheat growing in an unimpeded soil of 12, 5 and 18 mm day<sup>-1</sup> in autumn, winter and spring respectively. Gregory *et al.* (1978) found the same spring value and an average value of 6 mm day<sup>-1</sup> over the whole season. However, the rates of root extension found by Barracough & Weir were severely reduced by the presence of a plough pan, falling to just 1.5 mm day<sup>-1</sup> during February, March and April. During May and June, when the plough pan had been extensively penetrated, the rate of vertical extension increased to 9 mm day<sup>-1</sup> which was still far short of the rate in unimpeded soils. Barracough (1984) plotted root depth against thermal time to obtain a single extension rate of 1.8 mm °C day<sup>-1</sup>.

### 7.4. Root distribution

Many authors have reported that cereal and oilseed rape roots are distributed unevenly with the bulk of their length in the surface layers (Welbank & Williams 1968; Welbank *et al* 1974; Gregory *et al* 1978; Barracough 1984; Madsen 1985; Hansson & Andren 1987; Barracough 1989; Smukalski & Obenauf 1990; Ellis 1997). Growth occurs sequentially down the profile and this leads to an exponential decrease in root length density with depth (Barracough 1984; Barracough & Leigh 1984; Haberle *et al* 1996). The distribution of roots through the profile also changes through the season, with about 60-70 % of the root mass of winter wheat in the 0-0.3 m layer in April and a large amount of growth in deeper layers (0.1-0.5 m) between May and mid-June (Gregory *et al* 1978). Barracough (1984) described the general distribution of a mature wheat root system with depth: 60-70 % of the root length occurred in the top 0.3 m, another 20-25 % within the next 0.3 m and less than 1-2 % below 1 m. However, many growth conditions significantly alter the root distribution from the generalised pattern. For example, compacted layers of soil may impede root growth in deeper layers (Gregory 1994a). Analysis of the patterns of root distribution in experiments where there was a layer of compaction reveal consistent trends. Roots of plants tend to be confined to the surface layers of soil above the plough pan (Barracough 1984; Barracough & Weir 1988; Lipiec *et al* 1991; Unger & Kaspar 1994).

Although the rooting depth is reduced, it has been consistently found that there is no effect of soil compaction on the total root length (Barracough 1984; Barracough & Weir 1988; Lipiec *et al* 1991; Unger & Kaspar 1994). Instead, there is a compensatory growth of roots in the surface layers and Lipiec *et al* (1991) attribute this to more horizontal mode of root growth.

Accumulation of nutrients close to the soil surface is well known to cause an accumulation of roots in the top layers of soil (Gregory 1994a). Application of nitrogen fertiliser to barley caused an accumulation (90-97%) of the root mass in the top 0.3 m of the soil (Hansson & Andren 1987) while there were only scarce unbranched primary roots below a depth of 0.2-0.25 m in fertilised winter wheat (Haberle *et al* 1996). Barracough (1984) found that nitrogen fertilisation increased root growth down to 0.8 m in the presence of adequate supplies of water and to 1.2 m in drought conditions.

Qualitative estimates of rooting of cereals have been made routinely as part of the process of soil descriptions in England and Wales. These measurements were generally made after harvest and show that there is enormous variation in the degree of rooting below the plough layer. For example root abundance was classed as 'common' to 1.0 m in a Eufibrous earthy peat of the altcar series while on a glazed brown earth of the Worcester series rooting was classed as 'few' below 0.30 m.

### **7.5. Genetic variations in root system morphology and function**

The root attributes of cereals vary significantly between cultivars (Stoppler *et al* 1991; Kujira *et al* 1994; Gregory 1994a; Marschner 1998), and selecting varieties which are less prone to resource limitations is important in maximising crop yield in extreme environments (Gregory 1994a). Choice of the appropriate variety is influenced by the expected growth conditions and agronomic limitations and is therefore specific to the field and local climate. The effects of genotypic variations on root characteristics of crop plants are reviewed by O'Toole and Bland (1987).

Surveys of old and new cereal cultivars show that modern cultivars are more responsive to high nutrient availability than old cultivars (Haberle 1993; Haberle *et al* 1995) although they tend to have a lower root fraction (Wahbi & Gregory 1995). Stoppler *et al* (1991) found that of four winter wheat varieties, the modern cultivars developed a more extensive and deeper root system which was observed to confer a better drought resistance. In contrast Feil and Geisler (1988) showed that the relative yield ranking of new and old cultivars was independent of soil nutrient status. Although some authors have suggested that dwarfing genes are associated with a decrease in the biomass of the root system (Benlaribi *et al* 1990), there is evidence that dwarfing-genes do not influence the spread of the root system or the total root length (Kujira *et al* 1994).

Atkinson (1990) found variations in the speed of root penetration, specific root length, branching patterns, root density, total root mass, and root hair development of 25 spring barley varieties. The number of root axes and length growth of lateral roots differs between barley genotypes (Wahbi & Gregory 1995). Leon & Schwang (1992) used the grid intersection method (Newman 1966) to evaluate differences in total root length between cultivars of oats and barley and found that yield stability was correlated with root system length. Adaptability to growing conditions is an important genotypic trait in its own right and this can be selected for in plant breeding programmes (Zeniseva 1990). Cranstoun and Hoad (1997) categorised cereals according to their 'yield sensitivity', which is a measure of the variety's ability to exploit an increase in site yield potential. It is possible that a component of this yield sensitivity is related to the root systems of these varieties – they may have inherently larger root systems, or they may have a higher degree of root plasticity.

The variations in root system morphology described above can lead to differences in structural and mechanical strength of the root system which determine the susceptibility to lodging events. Crops with shorter stems and with more widely spread, stronger secondary roots are more resistant to lodging (Ennos 1991; Crook & Ennos 1993; Crook *et al* 1994; Crook & Ennos 1995).

There are also variations in physiological characteristics between varieties and these can be important in determining the outcome of processes such as nutrient acquisition (Marschner 1998). The rate of uptake of nutrient per unit root length varies considerably between cultivars and depending on the nutrient availability (Römer 1985). At the whole plant level there can be differences in the efficiency of water use which relate to allocation of resources between the root and shoot (van den Boogaard *et al* 1997) and to the rate of photosynthesis per unit of leaf nitrogen (van den Boogaard *et al* 1996). There is evidence for genotypic differences in N uptake which are determined by N absorption per unit of root length (Greef & Kullmann 1992).

The increases in root surface area because of root hairs ranged from 95 % to 341 % for winter wheat and 112 % to 245 % for barley (Gahoonia *et al* 1997). The differences in these area enhancements were the result of cultivar differences in the number and length of root hairs. Root hairs of wheat grown in nutrient solution are typically 2.5 to 3 mm long while those of oilseed rape are only 0.2 mm in length (Gregory 1994a). However, the length and number of root hairs in the field depends on soil conditions. Root hairs are thought to be especially important in the uptake of less mobile nutrients such as P.

Divergent selection has been used to test the use of morpho-physiological traits including root attributes in selection and to evaluate the resulting effects on yield (Al Hakimi *et al* 1998). Results showed that the use of modified bulk breeding using related species was a promising technique for increasing durum wheat yield in drought prone environments and for improving yield stability in a range of conditions.

### **7.6. How do root attributes affect nutrient uptake?**

An increase in allocation to the below-ground portions of cereal plants increases the volume and depth of soil explored (Atkinson 1990) which increases the potential for nutrient uptake. However, Haberle *et al.* (1996) found that at heading, wheat crops were unable to make use of substantial amounts of N which had been leached below 0.8 m depth. In the Champagne region of Northern France, Boiffin *et al.* (1982) found that where the rooting depth of winter wheat had been deep, there was less available soil nitrogen at depth than when the rooting depth had been shallow. They suggested that the nitrogen content of different soil horizons in late winter was best explained by the depth of winter wheat roots.

Root length is the most obvious attribute to relate to the rate of nutrient uptake as it has a clear functional significance and is closely related to the volume of soil explored (Atkinson 1990; Ryser 1998). Root length is especially important for the uptake of relatively immobile ions such as P (Nielsen & Schjorring 1983; Gregory 1994a). However, other authors argue that despite being the most commonly quoted root attribute, uptake rates of phosphate, calcium and potassium from solution are poorly related to root length (Russell 1977; Gregory 1994a; Gao *et al* 1998). This may be because root length is only significant if the uptake of these elements is limiting. For typical nitrate concentrations in the soil solution, the total root length is usually more than sufficient to allow the maximum rate of uptake (Robinson & Rorison 1983) while it is much more important in the uptake of less mobile ammonium ions. Some estimates put the fraction of root length that is apparently involved in nitrate uptake as

low as 3.5-11% (Robinson *et al* 1991), figures similar to those estimated for water uptake by cereals (Passioura 1980). These estimates assume uniform distribution of roots in the soil and, because this is never true, should not be taken literally. Forde & Clarkson (1999) stated that there was no convincing evidence for significant age-dependent changes in the physiological capacity of roots to absorb nitrate or ammonium ions. However, measures of root length which take some account of root age have been found to be more effective at predicting nutrient uptake activity than root length *per se* (Gao *et al* 1998) while van Noordwijk and de Willigen (1987) have proposed the use of a root area index as a functionally appropriate measure of root growth. The specific root length ( $\text{m g}^{-1}$ ) varies substantially and this probably relates to differences in allocation between the cell walls and root diameter (Atkinson & Hooker 1993). Changes in the cell walls are closely related to the surface area available for nutrient exchanges between the soil and root. Root diameter is important because if it is too small then the increased resistance may limit the rate of transport of water and solutes towards the stem.

Haberle *et al.* (1997) found that the pattern of water and nutrient depletion by winter wheat mirrored the distribution of root length through the soil profile. The effect of rooting density on nutrient uptake depends on the mobility of the required ions (Atkinson 1990). Ions such as nitrate can be depleted at relatively low rooting densities because they are so mobile whereas depletion of P only occurs at high root densities. As the soil is dried around roots, the hydraulic conductivity declines dramatically thus reducing the flux of nutrients towards the root. High rooting densities themselves have an affect on the water potential of the soil and this can reduce the movement of nutrients towards the root. Roots proliferate when they come into contact with soil layers which have a high nutrient content (Weaver 1926; Russell 1977).

Older roots contribute proportionally less to the uptake of nutrients and this relates to the total number of root axes and to the root order (Gregory *et al* 1978). In barley, the contribution of seminal roots to total nutrient uptake falls from more than 50% in vegetative plants to less than 5% during grain filling (Ehlers *et al* 1981). Specific root length may increase with decreasing nutrient availability and this allows a better exploration of the soil volume (Ryser 1998). Root hairs increase the soil-root contact, which is crucial to improving the absorption of the least mobile nutrients. Root hairs have been observed to increase the absorbing area of winter wheat roots by as much as 341% (Gahoonia *et al* 1997).

### **7.7 How do root and plant attributes affect water uptake?**

The uptake of water by a root system depends on the root characteristics of the variety (Dib & Monneveux 1992). Uptake of water takes place over most of the profile, although in drought conditions the bulk of absorption takes place in the younger portions of the root in deeper soil (Weaver 1926). Depth of water extraction is often less than the rooting depth in wet conditions, and tends to be more closely related to soil depths where root branching occurs (Mcgowan *et al* 1984). The potential for uptake of water and nutrients from the subsoil cannot be realised without adequate rooting depth (Fisher *et al* 1975). Winter wheat in a sandy loam and clay can extract water to a depth of at least 1.5 m and have been known to extract water to a depth of 2 m (Gales 1983). Spring barley has been observed to abstract

81% of the soil water to a depth of 1 m although the crop only took up 46% of the available water from the entire rooting zone (Russell 1976). Even when roots extend deep into the soil, there is a preferential uptake of water from the surface layers (Gregory 1994b). Water uptake from depth takes place only after there has been a substantial depletion in the surface layers. If the surface is re-wetted, uptake from the shallow layers is resumed provided the surface roots are still alive and only moves back through the deeper layers as it depletes them. Barraclough (1984) found that irrigated wheat used no water from below 0.8 m whereas droughted plants removed water from the entire soil profile where roots were found.

Root characteristics moderate the effects of drought both directly by increasing the rate of water uptake and indirectly by increasing the rooting depths (Gregory & Brown 1989). They may affect the rate of water uptake directly or have an effect on the rate at which the soil water supply becomes available. Deep rooting allows a crop to make use of the deeper water stores later in the season. Consequently, drought resistance in wheat has been found to be correlated with the rapid downward growth of roots (Hurd 1968; Hurd 1974). Rooting depth is thus important in conferring a degree of protection from drought, although the timing of the drought is crucial. For example, in the UK, drought in spring can seriously decrease growth rates of spring-sown cereals.

In regions where crops normally utilise virtually all the profile available water, high resistance to water flow in root systems reduces the rate of water extraction from the soil and helps to preserve soil water for key phases of development such as anthesis (Richards & Passioura 1989). High resistance to water flow occurs when there are fewer root axes or when the xylem diameter is small. Selection of varieties with narrow xylem vessels increased yields in these conditions by between 3 and 11%.

Wheat cultivars with the highest rates of root growth also tend to have the lowest rates of transpiration per unit root mass and this tends to decrease the rate of water uptake per unit root length (van den Boogaard *et al* 1996).

Actual transpiration rate remains close to the potential until 70% of the available soil water has been used, but with a large root system this may occur after a decline in available soil water of only 50%. Having a well-developed root system does not guarantee full use of the soil water reserves if the plants fail to make any osmotic adjustments and consequently close their stomata (Mcgowan *et al* 1984). Even in the UK, low rainfall on shallow, sandy or stony soils can result in an inadequacy of water. A larger or more efficient root system could result in excessive leaf area index and reduced canopy photosynthesis after anthesis. This can lead to poor grain fill, especially in winter barley (Passioura 1976).

The influence of root distribution on water uptake has been modeled by comparing the soil moisture deficit with the extractable soil water which is available to the root system (Francis & Pidgeon 1982a). When the ratio of soil moisture deficit to extractable soil water is less than 0.7 then the supply factor is 1 but in the range 0.7-1.0 the supply factor drops linearly to 0. The maximum extractable water is defined as the sum of all the available water capacities in each 0.1 m layer down to 0.8 plus a linearly decreasing proportion of the available water

capacity between 0.8 and 1.2 m in depth for spring cereals. For winter cereals this decrease is more gradual and extends deeper to 1.4 m. This gives a simplified approximation of rooting depth distribution and water uptake. Validation of this approach using a number of test crops showed that the model out-performed the other three models used (Francis & Pidgeon 1982b) and this is attributed to the inclusion of soil and rooting parameters.

### **7.8. How do roots affect the soil?**

Roots create biopores in the soil which increase the aeration and the infiltration of water to the subsoil. These biopores also provide conduits for root growth through soils with high penetration resistance (Ehlers *et al* 1983; Passioura 1991; Passioura & Stirzaker 1993; Stirzaker *et al* 1996). However, researchers have suggested that the poor root-soil contact in biopores may reduce the absorption of nutrients and water and that there may even be a release of an inhibitory signal when more than one root occupies the same pore (Passioura 1991; Passioura & Stirzaker 1993; Stirzaker *et al* 1996).

By extracting water from the soil, roots may enhance the drying-wetting cycle which modifies soil structure (van Noordwijk *et al* 1992) particularly in clay-rich soils. Root uptake of water may even dry the soil enough to increase the soil strength so that it cannot itself penetrate it. Root movement through the soil tends to loosen the structure which increases its accessibility to micro-organisms and increases the mineralisation rate. Although in the long term, roots increase the aggregate stability through formation of pores and the release of exudates and decaying tissues, in the short term, roots can reduce aggregate stability.

### **7.9. Rhizodeposition**

Martin and Kemp (1986) showed that a high proportion of radioactively labeled carbon that was translocated to the root was lost as rhizosphere respiration. Seven weeks after emergence this figure stood at 65% while at ten weeks it had decreased to 45%. In other experiments the amounts of carbon transferred below ground were 40-58% of net assimilate (Liljeroth *et al* 1994) and 52% of above ground production (Swinnen 1994). Total rhizodeposition was estimated to constitute 29-50% of carbon translocated below ground (Swinnen 1994). Some materials may be lost from the roots to the rhizosphere where they provide a substrate and food source for soil micro-organisms and enhance the availability of essential resources such as mineral nutrients (Gregory 1994b). Exudates can represent a significant flow of carbon from roots into the soil (Darrah 1998). However, other estimates suggest that only 7-15% of net carbon assimilation is deposited in the soil during the growth of wheat and barley (Swinnen *et al* 1995).

It is only comparatively recently that rates of root turnover have been reliably quantified for cereals (van Vuuren *et al.* 1997; Fitter *et al.* 1997). Changes in biomass hide losses from the root system by root death, leakage and exudation. Some material is lost by the root as the mucigel sheath sloughs off into the surrounding soil. The mucigel sheath may have a role in stabilising soil aggregates and in the maintenance of root-soil hydraulic contact. The rhizosheath of wheat is significantly wetter than the surrounding soil (Young 1995). Roots may die because of damage by below-ground herbivores or pathogens or because of frost or



drought (Ryser 1998). In an analogous manner to leaves, roots may die when respiration losses outweighed gains of nutrient or water. It was found that more than 50% of oilseed rape roots decompose in the process of root turnover (Klimanek 1990). Root turnover increases with soil temperature.

Soluble exudates include simple sugars, amino acids, organic acids and many other intermediates of metabolism (Swinnen *et al* 1995). A large amount of the released material appears to serve no definite function and is just consumed by rhizosphere organisms. Exudation may be viewed as a penalty required in return for the capability of taking up water and nutrients or it may fulfill a functional role – for example the release of organic acids increase the solubility of P when there is a deficiency and the release of phytosiderophores increases the uptake of iron or zinc (Awad *et al* 1994; Swinnen *et al* 1995; Marschner 1998; Schilling *et al* 1998). Phytosiderophores can increase the mobility of iron over a distance of as much as 4 mm from the source (Awad *et al* 1994). Exudation from plant roots increases the soil micro-organism population and may result in higher rates of mineralisation (Gregory 1994a). The resulting increases in available soil nutrients may contribute significantly to crop nitrogen supply (Reydellet *et al* 1997) under conditions of low nitrogen fertiliser inputs.

Roots change the pH of the soil by releasing H<sup>+</sup> ions, by the production of CO<sub>2</sub>, the release of organic acids and by encouraging microbial production of acids from carbon sources released by the root (Nye 1992; Gregory 1994a; Marschner 1998). Acidification of the rhizosphere may bring relatively insoluble nutrients such as calcium into solution although in soils which have high levels of free iron and aluminum oxides the effect may be to reduce phosphate availability. Plants have proton pumps in the cell membranes that acidify the apoplast relative to the cytoplasm. In oilseed rape roots this mechanism can lead to the rhizosphere being acidified by as much as 0.68 pH units when P is in short supply (Moorby *et al* 1988).

## **8. DO ROOTS LIMIT SHOOT GROWTH AND YIELD?**

There have been relatively few studies which have investigated how the growth and yield of cereals and oilseed rape can be limited by rooting. Gregory *et al* (1984) state that after the initial seed reserves have been exhausted, the size and activity of the root system determines the rate at which the shoot system can grow. There is also evidence that wheat cultivars which have higher rates of root growth and higher proportions of their biomass in their roots also have higher leaf growth rates, higher leaf area ratios and higher proportions of their biomass in their leaves (van den Boogaard *et al* 1996). Using data from winter wheat growth, total root length was found to be positively correlated with grain yield (Barraclough 1984) although similarly yielding crops could have different sized root systems. In contrast, total root dry mass is poorly correlated with grain yield.

Increases in nutrient availability in the soil appear to have no effect on root growth but strongly affect shoot and grain weight (Smukalski & Obenauf 1990; Greef & Kullmann 1992). This is probably because the shoot is such an important site for the conversion and incorporation of nitrates into dry matter. Other experiments report an effect of fertilisation on

biomass and yield. Typically, a crop supplied with optimal N will achieve double the yield of an unfertilised crop (Hansson & Andren 1987; Sylvester-Bradley 1993; Haberle *et al* 1997). Retarded root growth of winter wheat resulting from a high planting density was correlated with reduced ear weight. However, high plant population density is also correlated with a low harvest index of the above-ground parts. It was concluded that a high root length per stem seems to be most important in achieving a high ear weight (Stoppler *et al* 1991). Nutrient availability affected grain yield by influencing the number of grains per ear rather than the weight of each grain as is the case with changing water availability (Barraclough 1984). This may be a reflection of the timing of the stresses. Nutrient stress tends to start at the time of heading whereas water shortages usually occur later in the growing season.

Cereal cyst nematode damages wheat roots sufficiently that shoot growth and transpiration are reduced (Amir & Sinclair 1996). The wheat crop's ability to obtain water depends on the health and extent of the root system and the detrimental effect of root damage on shoot growth does suggest that the roots can limit shoot growth. The main deleterious effect was associated with a modification of rooting depth, which implies that root depth is of crucial importance during periods of low water availability. Similarly, the fungal disease Take-All invades the roots and causes significant reductions in yield (Ellis 1997). However, Take-All can also disrupt the movement of assimilate from the shoot to the root so that limitations to growth are not so easily identified.

Genotypic differences in root traits have been linked to differences in yield especially under unfavourable growing conditions. For example, above-ground growth and yield were affected by differences in the root systems of oats and barley when the plants were grown in a drought environment or with a very low N availability (Leon & Schwarz 1992). This suggests that root systems are not usually limiting to shoot growth but that they may be in conditions of low resource availability. On the other hand, coefficients of variation in field trials are rarely less than 10% so agriculturally-significant differences may not be detected.

A decrease in the transport rate between the root and shoot has been observed following damage to the root system of barley plants although this effect was quickly counteracted by an increase in xylem pressure which was presumably brought about by an increase in root efficiency (rate of uptake per unit root length) (Bajorat *et al* 1995). This suggests that undamaged roots do not necessarily function at full capacity and are therefore not limiting to shoot growth. Brisson *et al* (1998) summarised a number of experiments which have demonstrated that only half the root system is required to meet the demands of the plants. This is shown by an increase in nutrient and water uptake in zones of high availability when compared to zones of low availability. In other words, the rate of uptake per unit root can 'upregulate' in response to low overall resource availability.

There is general agreement in the contemporary literature that soil compaction causes reductions in above-ground growth and crop yield (Russell 1956; Hull & Webb 1967; Fisher *et al* 1975; McEwen & Johnston 1979; Barraclough 1984; Barraclough & Weir 1988; Lipiec *et al* 1991; Pietola 1991; Hakansson *et al* 1996). A decrease in LAI is likely to be the driving mechanism (Barraclough 1984; Barraclough & Weir 1988; Lipiec *et al* 1991; Unger & Kaspar 1994). These adverse effects are attributed to the shallow rooting systems characteristic of compacted soils which result in a reduction below optimality in the rates of nutrient and water uptake (Barraclough & Weir 1988; Lipiec *et al* 1991; Unger & Kaspar 1994). Reduced penetration of roots

into the subsoil renders large zones of soil nutrients and water inaccessible to plants, and over a period of time, soluble nutrients particularly nitrate may be leached from the soil (Barraclough 1984). The suggestion that it is a paucity of nutrients that is responsible for reductions in above ground growth and yield is supported by the observations of Fisher *et al* (1975) who showed that the increase in yield caused by double digging a soil was associated with a 26% increase in phosphorus content and a 72% increase in potassium content of the leaves.

The time course of leaf area index which has been found to be an important determinant of yield in cereals and oilseed rape depends strongly on the degree of water and nutrient stress (Gales 1983). On UK arable farms, sub-optimal uptake of nitrogen is particularly important. There is evidence that the shoot responds to adverse soil conditions before they are actually affected by a reduced supply of resources from the root (Passioura & Stirzaker 1993). For example, when roots become restricted by compact soils, leaf growth is also retarded even though the leaves are receiving the quantities of water and nutrients required for rapid growth. There is also evidence that leaves close their stomata and stop photosynthesising well before there is any detectable change in the leaf water potential. These apparent 'feedforward effects' are due to signals from the root to the shoot in response to the onset of water shortage. Since conditions often become more adverse over time, any decrease in the crop's demand for water will be advantageous and appear to be the consequence of the plants anticipating drought.

The concept of root limitation is difficult to quantify because roots perform several functions. For example, the proliferation of lateral roots does not necessarily increase the exploitation of mobile resources such as nitrate, but it may be important for the uptake of less mobile resources such as P (Robinson 1996). Because there may be differences in the relative resource availability between sites, a root system which can supply the shoot adequately in one place may be limiting in another. It is important to note that it is not the absolute sizes of the root system which determine a limitation to the shoot. Hence a root system which is usually adequate may become limiting in a period of drought (see 10. Root : Shoot Allocation). In addition there is a dynamic feedback, so that if a root system starts to limit the uptake of essential resources, the balance is redressed in favour of root growth. Generally, the root systems of cereals grown in the intensive arable systems of western Europe are regarded as being larger than they need to be for absorption of water and nutrients in normal conditions. This may be an insurance policy so that if part of the root system becomes damaged or redundant, then the rest of the root system can supply the shoot (Gales 1983).

One irregular occurrence where root systems indirectly limit yield is in root lodging of cereals. Weak root systems predispose crop plants to being blown over. When conditions conducive to lodging are present, a rigid cone of secondary roots together with the soil within the cone move together as a block to compress the soil beneath (Crook & Ennos 1993). Plant genotypes with many fibrous roots growing downwards which are progressively strengthened towards their base, with shorter stems and more widely spread, stronger secondary roots are less likely to lodge (Crook *et al* 1994). Cereal lodging has large effects on crop yield, with losses reaching 45% (Mulder 1954; Laude & Pauli 1956; Weibel & Pendleton 1964). Harvests may also be delayed, grain drying costs increased and grain quality decreased (Baker *et al* 1998). The severity of loss depends on what stage of growth lodging occurred at. The largest effect is seen when lodging occurs at anthesis or soon after the start of grain filling. This accounts for 25-50% of losses. Lodging before anthesis reduces the number of

grains per ear whereas lodging after anthesis reduces the weight of the grain. The severity of losses also depends on the angle at which the plants are lodged because an increase in tilt angle reduces the amount of radiation which can reach the leaves (Fischer & Stapper 1990). Although both stem and root lodging occur it has been consistently found that root lodging is more likely than stem lodging (Pinthus 1973; Easson *et al* 1993; Baker *et al* 1998) because the stem is stronger than the root anchorage (Ennos 1991).

## **9. DOES THE SHOOT CONTROL ROOT GROWTH?**

The influence of root growth and shoot growth are inextricably linked because root system growth and maintenance depends on the shoot to supply it with carbohydrates which are essential to growth. Situations where root growth limit shoot growth have already been discussed and there are also many cases when the shoot appears to control root growth. A reduction in the rate of canopy photosynthesis by a disease such as powdery mildew, leads to an overall decrease in crop growth rate (Hibberd *et al* 1996). Likewise, changes in intercepted radiation, CO<sub>2</sub> concentration (Aguirrezabal *et al* 1993), shoot pruning and defoliation (Bingham & Stevenson 1993; Bingham *et al* 1996; Bingham *et al* 1997) have been extensively used to manipulate the carbohydrate supply to the root.

Reducing the carbohydrate supply to the roots has been found to decrease the root mass, root length (Aguirrezabal *et al* 1993), the rate of extension of seminal axes and first order laterals (Bingham & Stevenson 1993; Bingham *et al* 1996) and the number of primary roots and their rate of branching (Aguirrezabal *et al* 1993). Bathing roots in a solution with additional glucose seems to increase the rate of root primordium formation (Bingham & Stevenson 1993; Bingham *et al* 1997; Bingham *et al* 1998). Changes in root biomass may be mediated through changes in the rate of carbohydrate supply to the roots (Demotesmainard & Pellerin 1992; Palta & Gregory 1997).

Roots do not act as simple pumps, since their activity is regulated by conditions in other parts of the plant (Gregory 1994a). For example, water uptake is determined by a combination of water availability and potential transpiration. Similarly, roots are able to discriminate in the uptake of ions from solution and this selective uptake changes temporally suggesting that there is a feedback control on root activity from other parts of the plant. Variations in the availability of nutrients and water primarily affect leaf growth and assimilation (Greef &

Kullmann 1992) but it is not known to what degree nutrient limitations affect root growth directly or as indirect effects of reduced assimilation and transport of carbohydrates to the root. The observation that shoot and root growth of winter wheat are oppositional led Schipper (1996) to believe that growth may be organised by variations in meristem activity which are influenced by hormonal control.

Tardieu (1994) has proposed that changes in the rate of root growth in response to soil compaction may be a consequence of an integrated whole plant response - and not merely a result of direct local root impedance. He argued that at the individual root level, high penetration resistance could not account for observed reductions in the root elongation rate and showed that soil compaction also affected the elongation rates of other organs such as leaves and non-impeded roots. There is evidence that unimpeded roots in surface soil layers grow faster than normal to compensate for the relatively slow growth of impeded roots (Unger & Kaspar 1994). Tardieu (1994) suggests that chemical messengers could be released by roots in contact with a compact soil layer, or that the observations may be a result of changes in resource allocation.

The dependence of root growth on shoot growth has been the basis for a number of developmental models which exploit the regularity of root growth when compared to shoot growth (Klepper *et al* 1984; Gregory 1994a). These are based on linear relationships which link the number of nodal root axes on a stem with the number of leaves on the stem. The state of development of the root system may be inferred from the degree of above ground development. There is a parallel here with above-ground development and growth where leaf development and tiller initiation are tightly controlled by environment but LAI depends on leaf expansion and tiller survival.

## **10. ROOT : SHOOT ALLOCATION.**

The ratio between the amount of root dry mass and the amount of shoot dry mass is a measure of the allocation of resources between different plant components. Since the aim of farmers is to increase the quality and yield of grain from their crops, there is a trade off between the amount of investment in the root structure and the amount of assimilate partitioned to the development and filling of grain. In wheat and barley the number of spikelets at anthesis depends on the proportion that survive and on the number of fertile tillers. Competition by roots could lead to fewer tillers or perhaps lower survival after the onset of stem extension. Root allocation is sometimes insufficient to produce a root system capable of maintaining a plant - particularly in extreme climatic events such as drought (Gregory *et al* 1996) or lodging.

Allocation is not a process in its own right, but the outcome of many processes including assimilation, translocation, respiration, growth, storage, hormone synthesis and other biochemical conversions (Cannell & Dewar 1994). Although most data in the literature is in the form of instantaneous values for the root: shoot ratio, an analysis of the dynamics of root: shoot allometry can be more revealing since a large change in partitioning may have a relatively small effect on the ratio in the first instance.

While some authors have found little difference in root : shoot allocation at maturity between wheat, barley and oats (Bingham 1995) some have found large differences between species (0.2 winter wheat, 0.4 oats and 0.5 barley) but no intra-species variation (Bolinder *et al* 1997) and others have found significant intervarietal differences (Haberle *et al* 1995). Older cultivars tend to have lower root : shoot ratios than the newer varieties which suggests that there has been a relative increase in the root mass or a decrease in the stem mass with time (Haberle *et al* 1995).

The root : shoot ratio typically decreases steadily and with an exponential decay from emergence to maturity (Smukalski & Obenauf 1990; Baret *et al* 1992; Katterer *et al* 1993; Wahbi & Gregory 1995; Gregory *et al*

1996). During early vegetative growth, up to 50% of assimilated carbon may be translocated below ground, although as much as 50% is consumed in respiration or lost from the plant in exudation and rhizodeposition (Gregory *et al* 1996). The principle direction of resource allocation changes markedly at flowering, with considerably less assimilate transfer to the roots (Gregory *et al* 1996). After anthesis, the net size of the root system barely increases at all - and the amount of assimilate translocated to the root system is very small (Gregory 1994a). In winter wheat, the exponential growth phase of roots begins before the exponential growth of shoots, and it ceases earlier (Gregory *et al* 1978). This is reflected in the root : shoot ratio which was 0.33 and 0.39 in winter and rose to 0.52 during early spring. From April to mid-May this ratio decreased rapidly to 0.1 coincident with the linear phase of shoot growth. Barraclough (Barraclough & Leigh 1984) reports root : shoot ratios for winter wheat varieties which decreased from 0.43-1.0 in winter and early spring to 0.09-0.19 at anthesis.

### 10.1. Functional balance

Brouwer (1962) observed that for a particular developmental stage plants of a species maintain a constant ratio of root dry mass to shoot dry mass for a given set of environmental conditions and will over time return to the original ratio if either the root or the shoot are pruned. However, a change in environmental conditions may be accompanied by a shift in allocation between the root and shoot. For example, it is reported that a decrease in planting density leads to an increase in root : shoot ratio (Easson *et al* 1995), while an increase in the nutrient availability leads to a decrease in the root : shoot ratio (Hansson & Andren 1987). The functional balance hypothesis (Brouwer 1962) which states that the amount of tissue capable of CO<sub>2</sub> fixation will be balanced by the amount of tissue capable of nutrient uptake is a useful concept for interpreting these observations.

$$\sigma_c.W_s = K.\sigma_n.W_r \quad (1)$$

where  $W_s$  is the shoot mass,  $W_r$  is the root mass,  $\sigma_c$  is the rate of carbon fixation per unit of shoot mass,  $\sigma_n$  is the rate of nutrient uptake per unit of root mass and  $K$  is a constant equal to the carbon to nutrient ratio of the plant dry matter. The functional balance hypothesis is based on the interdependence of two resources. Nutrients are required in the leaves for carbon assimilation to occur, and the amount of carbon fixed determines the amount of root for nutrient uptake.

It follows from the functional balance hypothesis that if a plant is to grow in a balanced way, then the rates of carbon and nutrient acquisition must be maintained. The increase in quantity of nutrient taken up by the plant is directly related to the rate of increase of the root dry mass. Assuming that the root : shoot ratio remains constant it follows that the rate of increase in total nutrient uptake is equal to the rate of increase of the total plant dry mass.

Ingestad & Agren (Ingestad & Agren 1992) derived the same relations from first principles. The importance of Ingestad nutrition is that if nutrients are not supplied at the same rate as the plant is growing then there will be a nutrient limitation and there may be a shift in allocation to compensate. In practice, the nutrient which is required in the largest amount for healthy growth is nitrogen and allocation behaves in accordance with predictions of the functional balance hypothesis when the rate of supply of nitrogen is changed. Limiting the supply of phosphorus and sulphur has similar effects on allocation (McDonald *et al* 1991). However, there is evidence that allocation does not respond in the same way to shortages of other elements. For example, it does not respond to the rate of supply of magnesium, iron and manganese (McDonald *et al* 1991). McDonald, Ericsson and Ingestad (1991) suggests that where the nutrient availability limits the rate of carbon uptake, there is no shift of allocation in response to low rates of supply. For instance, reducing the value of  $\sigma_{mg}$  (rate of uptake of magnesium; Equation (1)) also reduces the value of  $\sigma_c$  (Equation (1)) and there is therefore no shift in allocation.

Experimental results confirm that crop plants do tend to behave in accordance with the functional balance hypothesis. For example, when winter wheat plants were grown at two levels of nitrogen nutrition, it was found that the lower supply of nitrogen was associated with an increase in the root : shoot ratio (Barraclough 1984). Similarly, the root : shoot ratio of barley decreased with increasing nitrogen fertilisation (Welbank & Williams

1968). In contrast, potassium and phosphorus limitations did not affect the partitioning of barley plants (Welbank *et al* 1974).

## **10.2. The functional balance and climate change**

Atmospheric CO<sub>2</sub> concentrations are predicted to double to approximately 700 μmol mol<sup>-1</sup> by the mid to late 21<sup>st</sup> century and continue to rise at a rate of approximately 1.2 μmol mol<sup>-1</sup> yr<sup>-1</sup> (Conway *et al* 1988). The atmospheric CO<sub>2</sub> concentration is important because it may have a large impact on crop growth and because CO<sub>2</sub> is a greenhouse gas. Models predict that increased concentrations of greenhouse gases may cause global warming in a phenomenon reported in the press and literature as the *greenhouse effect*.

Whereas it is only at the extreme ranges of nutrient concentration that there is an effect of concentration on the rate of uptake from the soil, the concentration of CO<sub>2</sub> is important in determining the uptake rate of carbon ( $\sigma_c$  Equation (1)). By experimentally changing the CO<sub>2</sub> concentration we can lower or raise the value of  $\sigma_c$  (Equation (1)) and predict the effect on allocation between the root and shoot.

In an investigation of the effects of elevated CO<sub>2</sub> concentrations on winter wheat, it was found that elevated CO<sub>2</sub> concentrations increased grain yield by 12.6% (Batts *et al* 1998). This can be attributed to an increase in the assimilation rate of plants in higher CO<sub>2</sub> concentrations. The increase in assimilation rate was accompanied by an increase in root allocation of 56% (Gregory *et al* 1996; Batts *et al* 1998) - an observation which is compatible with the predictions of the functional balance hypothesis.

In contrast, the effect of warming was to decrease grain yield and root allocation in winter wheat cultivars (Gregory *et al* 1996; Batts *et al* 1998). Warming increases the rate of respiration by more than it increases the rate of photosynthesis, so that the net assimilation is reduced. The observation that root allocation was reduced in a warmer environment is also in accordance with the functional balance hypothesis.

### 10.3. The functional balance and water use

The functional balance is also appropriate for describing the relative balance between root and shoot allocation in relation to water availability and use (Cannell & Dewar 1994) because the acquisition of carbon and water are highly dependent on each other. There is experimental evidence that plants do respond to changes in water availability with changes in allocation. For example, in an experiment on wheat plants grown in soil columns, it was found that limited water availability increased the allocation of C<sup>13</sup> to roots (Gregory *et al* 1996). Spring barley reacts to soil moisture deficit by increasing allocation to the root biomass (Zenisceva 1990).

Crop species and cultivars differ in water use efficiency (*WUE*) defined as the ratio of water lost through evapotranspiration to carbon assimilated (*E/A*). The effects of drought may be ameliorated in plants which have a high water use efficiency because the amount of water loss per unit of carbon fixed is relatively low. However, because plants with a higher *WUE* may be larger than other plants (particularly in drought conditions), the total amount of water lost per plant may not be smaller (Rogers & Dahlman 1993). Care is therefore needed in interpreting the effects of *WUE* on crop growth during seasons of low water availability particularly since it depends on the atmospheric condition as well as the genotype. Rogers and Dahlman (1993) reviewed the effects of elevated CO<sub>2</sub> concentrations on crop growth. They report that there is an increase in the *WUE* in crops because of a decrease in the transpiration rate which results from reduced stomatal conductance, and an increase in the rate of carbon assimilation. In an investigation of the relationships of plant growth and water use efficiency with the pattern of biomass allocation, van den Boogaard *et al* (1996) found that there was a link between allocation pattern and water use efficiency.

Because compaction limits the accessibility of soil nutrients and water to roots, the effects of soil compaction on allocation are likely to mimic the effects of low water or nutrient availability. Results from an experiment on winter wheat (Barraclough & Weir 1988) show that plants grown on a soil with a plough pan had a root : shoot ratio which was higher (0.75) than for a soil with no plough pan (0.39). It has also been shown that direct drilled spring barley has higher root : shoot ratios than on soil with shallow cultivation (Bram *et al* 1992). Hamblin, Tennant & Perry (1990) showed that there was an increase of the root : shoot ratio from low soil strength, high soil water and high nitrogen availability through to high soil strength, low soil water and low nitrogen availability. The root : shoot ratio at anthesis increased from 0.19 to 1.33 through this sequence of conditions.

Bingham (1995) was unable to find any significant differences in root : shoot ratio between wheat and wild oats although wheat showed a greater specific root length than wild oats. This was interpreted as a more efficient use of the dry matter allocated to the roots. A number of alternative relationships may be more useful than the root : shoot ratio - especially under the framework of the functional balance hypothesis. For example, it may be useful to consider the fine root : leaf mass which focuses more on a comparison of the tissues which have a functional significance in carbon, nutrient and water uptake. Modifications may replace root mass with other measures - for example the total root length, root area or absorbing area. Similarly a more appropriate measure



of shoot activity may be provided by leaf area. Nye and Tinker (1977) claimed that root length : shoot dry weight is the best representation of the absorbing ability of a whole plant.

## **11. FARMING PRACTICES AND ROOTING**

### **11.1. Nutrient uptake, fertilisation and recovery**

The total amount of nutrient uptake over a growing season is related to the length of time over which it occurs (Atkinson 1990). Nitrogen availability depends on the balance between the rate of mineralisation and losses from leaching and de-nitrification. There is a strong seasonal cycle of availability and during some months soils cannot accommodate the potential for uptake. For example, spring barley is capable of taking up nearly 80% of its total nitrogen content during one month (Dyson 1986) at a rate of  $4.5 \text{ kg N day}^{-1}$  although the amount available is rather less. Uptake by winter cereals takes place over a longer period of time. Winter wheat is more likely to experience shortages of naturally available nitrogen because of the effect of cold temperatures on mineralisation. The uptake activity is also temperature dependent (Barraclough 1984)

Increases in yields of grains with a high nutrient content have lead to a dramatic increase in the amount of nitrogen fertiliser used between 1960 and 1990 (Atkinson 1990) although there has been no increase since 1985. The increased grain yield of winter wheat has been coupled with an increase in grain nitrogen offtake of  $42 \text{ kg N ha}^{-1}$  over the past 20 years (Foulkes *et al* 1998).

Nitrogen uptakes for barley grown on sandy soils and clay were 150 and 120 kg N ha<sup>-1</sup> although this increased to 270 kg N ha<sup>-1</sup> in the presence of fertilisation and irrigation (Andrén *et al* 1993). These figures compare well with those of Hansson and Andren (1987) who found that nitrogen uptake of barley grown with or without fertiliser (120 kg N ha<sup>-1</sup>) were 150 kg N ha<sup>-1</sup> and 58 kg N ha<sup>-1</sup> respectively.

In a typical winter wheat crop fertiliser nitrogen recovery is about 55% (range 40-70%) in the crop year of application (Gales 1983). For example, whole crop recovery of added nitrogen averaged 52% for winter wheat compared with 45% for oilseed rape (Macdonald *et al* 1997). However, offtake in the grain was only 33% for wheat and 25% for oilseed rape. The recovery of nitrogen from applied fertiliser depends on previous applications. Wheat which had not previously been fertilised captured 73% of a nitrate application while previous fertilisation reduced this figure to just 13% (Robinson *et al* 1994). The soil type also affects the recovery of nitrogen. Barley grown on sandy soil took up 61% of the applied nitrogen fertiliser (25 g m<sup>-2</sup>), 65% P (3.5 g m<sup>-2</sup>) and 82% K (19 g m<sup>-2</sup>) while on clay the corresponding values were only 46%, 33% and 77% (Andrén *et al* 1993). These figures compare with N recoveries for barley of 75% (Hansson & Andren 1987) and 71-83% (Dowdell 1982). The nitrogen offtake in the grain was 24% (Hansson & Andren 1987).

Nitrates leach easily into the deeper layers of soil, but in contrast it is difficult to get potassium and particularly phosphorus fertilisers into the deeper soil horizons where the newly formed roots are located later in the season (McEwen & Johnston 1979). Leaching of added nitrogen fertiliser was higher from a sandy soil (110 kg ha<sup>-1</sup>) than on clay (32 kg ha<sup>-1</sup>). On lighter soils, there may be some P leaching where large dressings are applied over a period of years, although the largest amounts of P movement into the subsoil occur with the use of farmyard manure. Nitrate losses in drainage water have increased from 11 to 67 kg ha<sup>-1</sup> in the last sixty years (Parsons 1987). In recent years there has been a growing interest in the use of more sustainable low input agricultural systems which have lower quantities of fertiliser leaching into the drainage water. Planting winter cover crops whose deep roots scavenge residual nitrates may reduce the amount of nitrate leached into the groundwater (Sainju *et al* 1998).

### **11.2. Plant population density**

The total root dry mass of individual crop plants tends to increase in response to plant density (Kirby & Rackham 1971). This is because of increased competition for soil resources and an accompanying shift in allocation. The increment in root dry mass was smaller at high (800 plants m<sup>-2</sup>) than at low (200 plants m<sup>-2</sup>) densities, suggesting that root dry mass may have an asymptotic relationship with density. At higher plant densities roots tend to be increasingly concentrated in the upper part of the soil profile. Increasing seeding rate decreases the diameter and strength of the secondary roots which are important determinants of lodging susceptibility (Easson *et al* 1995). High planting density increases the risk of infection from Take all and the earliness of onset of the disease (Colbach *et al* 1997).

### **11.3. Sowing date**

Sowing date depends on the accessibility of the soil. Rooting of winter crops is generally increased by early drilling. However, drilling may be delayed by surface wetness (Cannell *et al* 1978) because of the risk of compacting surface soils. If sowing is too early there is also a danger of poor establishment and crops may suffer damage if there is a wet or cold spell. Sowing date has been identified as a determinant of disease risk for Eyespot, Take-all and sharp eyespot on wheat (Colbach *et al* 1997). Early sowing always increased disease frequency of Take-all on wheat.

### **11.4. Crop rotation**

The rotation appears to have a large effect on the risk of soil-borne disease (Colbach *et al* 1997). Various agronomic practices have been suggested to ameliorate small root systems, caused by Take-all induced root loss, in second or subsequent wheats. These include adjusting nitrogen fertiliser rate, seed rate and the use of fungicides. The previous crop can also affect the soil structure by encouraging biopore formation (Cresswell & Kirkegaard 1992). The ameliorating effects of a grass ley on the structure of the plough layer have long been recognised. However, crops with a tap root system, such as oilseed rape, are better able to penetrate compact subsoils than are cereals because single thick roots are more effective at soil penetration than the large number of fine roots more typical of cereals. Although biopores increase the infiltration of water, nutrients and roots into the deeper soil layers, they may have some deleterious effects because of their tendency to concentrate pathogenic micro-organisms which would harm crop roots. Cultural practices may be manipulated so that deep rooting crops such as oilseed rape are planted prior to crops such as wheat which have a relatively poor penetration ability (Cresswell & Kirkegaard 1992).

### **11.5. Direct drilling vs conventional tillage**

Direct drilling has been designed to encourage the formation of stable soil structures which are infiltrated by biopores (Stirzaker *et al* 1996; Ellis 1997). The biopores which develop under direct drilling are more likely to be continuous from the soil surface through to deeper levels which encourages infiltration of water and air to the subsoil (Pearson *et al* 1991). Under this system there is no tillage and the surface soil tends to be more compact than under conventional tillage (Braim *et al* 1992; Ellis 1997). In some soil types periodic ploughing is required to allow adequate root penetration.

The increases in surface soil compaction in direct drilling may inhibit water infiltration into deeper layers of soil and under conditions of high rainfall the surface may become waterlogged (Ellis 1997). Direct drilling is therefore less appropriate during wet years or in areas which habitually get high rainfall (Cannell *et al* 1978). Wet soils are more prone to compaction and the date of sowing and harvest may also be delayed. Soils which are resistant to soil compaction are better suited to direct drilling. These tend to be soils with good drainage which have an high organic matter content.

On some soils direct drilling reduces the growth rate of wheat (Braim *et al* 1992; Kirkegaard *et al* 1995). Reductions in root growth were associated with a lower N uptake and a 20% decrease in shoot mass (Braim *et al* 1992). Since the rates of nitrogen inflow per unit root length may be higher in direct drilled soils the reduction in root growth does not necessarily result in lower uptake of nitrogen. Minimum tillage can lead to lower root lengths in the seedling stages and a recovery in later periods of growth (Pearson *et al* 1991). Other researchers - e.g. (Ellis 1997) - have shown that root density of crops at depth is increased causing an increase in water extraction and subsequently yield. On the other, Wulfsohn *et al.* (1996) found that the root distribution and biomass of winter wheat were higher only in the upper layer of untilled soil when compared to conventional tillage (Wulfsohn *et al* 1996).

Generally, integrated farm systems use less pesticides and mineral fertilisers as well as less intensive soil tillage compared to conventional farming (van Noordwijk *et al* 1994). Van Noordwijk *et al.* (1994) indicated that the amount of root was increased by integrated management while in another study rooting density was reduced when compared to conventional tillage (Schoonderbeek & Schoute 1994). Soil macroporosity was larger for integrated farm management than for conventional systems (Schoonderbeek & Schoute 1994) and in the upper layers of conventional farmed soil the number of pores was very small. The distribution of roots in the surface layers was the same for the two systems. However, the root-soil contact was higher in the conventional system.

#### **11.6. Sowing depth**

The effects of sowing depth on rooting seem to be small within the normal range of sowing depths of cereals, although Kirby (1993) found that deep sowing (200 mm) resulted in a reduced mass of the seminal root of barley which was associated with a decrease in the rate of leaf elongation and stage of development. The time to seedling emergence of barley increases with increased sowing depth (Kirby 1993). The seedling survival rate was not affected between the depths of 23 and 83 mm although it did decline to about 6% at a depth of 143 mm.

## 12. SELECTING APPROPRIATE FARMING PRACTICES

In contrast to leaf canopies, it is difficult to define an 'optimal' root system for a particular site-season combination. This is because of permanent differences in soil characteristics coupled with inter-seasonal variations in rainfall and temperature. However, in some cases it is possible to use a detailed knowledge of the interactions between soil attributes and root and how these affect shoot growth and yield to select the most appropriate farming practices. Two case studies analyse appropriate farming practices to (i) reduce damage by root lodging and (ii) to alleviate the effects of soil compaction.

### 12.1. Farming practices which ameliorate lodging damage

The condition of a crop has at least as much influence on the probability of lodging as does the weather, and the ability to manipulate the characteristics of a crop by different farming practices allows lodging to be controlled to an extent, despite the weather's inherent unpredictability (Baker *et al* 1998). Choice of the most appropriate variety is important. In areas with soils which have a low strength, there may be benefits to choosing varieties which have stronger rooting systems, and there may be advantages to manipulating the seed rate so that growth of the root system is encouraged. The date of sowing and the planting density as well as the depth of drilling have an influence on the incidence of lodging (Baker *et al* 1998).

Early drilling increases rooting although this benefit may be offset by a larger tiller production which increases the turning force at lodging. Crop height tends to be increased by an early sowing date and this magnifies the chances of lodging. Increased seeding rate tends to decrease the diameter and strength of the important secondary roots (Easson *et al* 1995) although it also tends to decrease the production of tillers which reduces the overturning force. A higher seed rate significantly increases the chances of root lodging. In one series of trials, a seed rate of 150 seeds m<sup>-2</sup> caused 10% lodging whereas a seed rate of 250 seeds m<sup>-2</sup> caused 76% lodging.

A high soil water content reduces the strength of the soil and this increases the likelihood of root lodging (Baker *et al* 1998). Soils which have a higher water content at wilting point and at field capacity have a higher lodging risk because less rainfall is required to wet the soil to its weak state. Wet soils should therefore be avoided in areas which are particularly prone to lodging. Crops which are sown later in spring are least likely to experience wet soils. The clay content of a soil is also predicted to have a very large influence on the probability of lodging since as the clay content of the soil increases, so does its strength (Baker *et al* 1998). Also, a higher 'visual score' increases the chance of lodging because it indicates looser and weaker soils.

Rolling in spring tends to increase the soil strength which may benefit some of the higher risk crops with poor root anchorage. The incidence of lodging is not evenly spread throughout fields. This may be because of variations in soil characteristics through a field or because of edge effects. For example, the highest probability of lodging is in the headlands, whereas areas close to tramlines are seldom affected.

The rate of nitrogen application and the use of plant growth regulators can have a large impact (Baker *et al* 1998). Higher levels of nitrogen fertilisation lead to shifts in allocation away from the roots and towards the above ground portions of the plants which increases the susceptibility to lodging. Nitrogen applications should reflect the structure of the variety selected, so that a variety with a relatively weak stem might benefit from smaller spring nitrogen applications to reduce the above canopy size and increase allocation below ground. In an experiment on the effects of nitrogen and plant growth regulators on crop characteristics associated with lodging resistance, Crook & Ennos (1995) found that high levels of nitrogen increased the height of the stem and centre of gravity which increased the force of the turning moment on the base of the stem and roots. High levels of nitrogen also weakened the stems and secondary roots. In contrast, growth regulators had no effect on the stem or secondary root bending strengths although they did reduce the stem height and therefore the force of the turning moment on the base of the stem and roots. In a separate experiment, it was found that the levels of nitrogen and plant growth regulators had no effect on the tensile strength of the roots (Easson *et al* 1995). Plant growth regulators allow farmers to artificially manipulate plant growth to favour changes in dry matter allocation. For example the spread and depth of the root system may be enhanced by use of specific growth

regulators such as *Chlormequat*, *Meteor* or *Moddus*. Plant growth regulators should be applied during stem extension to increase the strength of the stems. As well as having the usual effects of reducing stem heights, the manufacturers of some plant growth regulators claim that they can influence a number of key morphological and physiological characteristics in cereals: for example, thickening and strengthening the stem and significantly increasing the root mass. Other effects include increases in the spread of the crown root system. Generally, applications made during the tillering stage have the largest effect on secondary root structure while those made during stem extension had the largest effect on height reductions.

## **12.2. Farming practices to alleviate compaction**

The risks of soil compaction adversely affecting crop growth and yield can be reduced by efficient application of nutrients, by managing soils through the use of tillage and by growing deep rooted crops in rotation (Unger & Kaspar 1994). These practices help to improve root distribution and increase the rooting depth. Because compaction reduces the ability of winter wheat to cope with water shortages in the spring and summer, the detrimental effects of soil compaction may be reduced by earlier autumn sowing dates which have a greater chance of avoiding summer droughts (Barraclough & Weir 1988).

Soil strength is reduced in wet soils, so a growing season in which the soil is moist during the time when roots explore the upper part of the soil profile tends to reduce the impact of compaction (Unger & Kaspar 1994). On the other hand, soils which are moist are more vulnerable to compaction by farm machinery. Incorporating organic matter into the soil decreases the penetration resistance of a soil when it is compacted (Unger & Kaspar 1994). Adding manure or other organic material to the soil also has the effect of encouraging earthworm activity which helps to create biopores to depths of up to 2 m.

As early as 1956, Russell (1956) had presented data from experiments that suggested that there might be some benefits to deep ploughing and subsoiling. Although, he warned that deep ploughing was risky in situations where the subsoil was sandy or where there was a high content of stones in the subsoil these situations are rare in the UK. He also warned against deep ploughing when the water table was close to the surface or in deep undrained clays which are unable to carry tractors or crops. More recently, Unger & Kaspar (1994) reviewed a wide range of mechanical options for reducing compaction. Above 30 cm they recommended the use of a mouldboard or disk plough, although they stress that disk ploughs are less efficient and may inadvertently contribute to compaction as they rely on their weight to penetrate the soil. Tine implements were effective for working the soil to a greater depth and operated by 'shattering' the compact soil. They advised that most mechanical interventions work more efficiently on a dry soil than a wet soil. In addition, Davies, Eagle & Finney (1972) recommended that for operations requiring heavy draught, tractors should have ballast added to reduce wheelslip - but that this ballast should be removed whenever it is not needed. They also suggest the use of crawler tractors when possible and cage wheels or half-tracks to reduce ground pressures.

Davies, Eagle & Finney (1972) make the apparently obvious point that traffic should be reduced to the absolute minimum for growth of the crop. A more sophisticated approach is the use of a controlled traffic system which restricts tractor wheels to specific lanes or inter-rows (Unger & Kaspar 1994). After research in the 60's showed the widespread effects of compaction on cereal growth and yield tramlines were universally adopted to minimise damage. Using inter-row cropping increases the soil area which remains uncompacted when compared to a random or uncontrolled traffic pattern and has been shown to boost the root length in the 0-15cm layer of non-traffic rows by three times. On soils which are suitable for direct drilling (Cannell *et al* 1978) the soil structure may be improved in the long term by minimum tillage.

Barraclough & Weir (1988) showed that as long as water was not limiting, the adverse effects of compaction could be eliminated by the application of top dressings of nitrogen fertiliser. Appropriate use of nitrogen fertiliser can ameliorate the effect of soil compaction on above ground growth and yield. In naturally well-structured soils, e.g. many clay soils, the effect of compaction becomes less over the growing season as wetting and drying cycles re-activate planes of weakness. Thus rooting may be impeded in the early part of the growing cycle but not later on.

### **13. CONCLUSIONS**

In many conditions the root system does not limit crop growth or yield and it is more than adequate for maintenance of the supply of nutrients and water to the shoot. The limit to rooting is generally not the genetic potential of the crop but rather a physical barrier such as a horizon of high bulk density, a water saturated zone or, much less commonly, bedrock. However, reductions in the rate of uptake of soil resources lead to feedback responses in allocation which increase the size of the root system. There is no discernible optimum rooting strategy as conditions for growth change within a field, between fields and over time. Limitations are most likely to occur when a plant experiences unusual or extreme growth conditions such as drought or damage inflicted by diseases like Take-all. Soil factors which have the largest effect on root growth are the penetration resistance, pore distribution, water and nutrient availability's. Root attributes which are repeatedly linked to resource capture are root length, root depth and degree of root-soil contact. Cultural practices can have a large effect on the development and function of root systems. Matching the appropriate farming practices to soils, climate and crop will therefore lessen the probability of root limitations.

Roots are important in provide mechanical strength and support to the shoot, and selective breeding may confer increased protection from lodging damage. Selection of the appropriate cultivar may also lessen yield reductions during stressful events such as drought. Root plasticity is an important factor for coping with spatial and temporal heterogeneity. A root system that is unable to adapt to changing conditions is likely to be the least satisfactory in our unpredictable climate and heterogeneous soil environment.

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## **APPENDIX 1:**

### **Digging a soil pit**

It is usually convenient to examine the soil after harvest. However, the soil must be moist and neither very dry nor very wet as these conditions give a misleading indication of soil structure. Several pits should be dug in representative parts of the field, avoiding headlands. The pits should be at least two feet (60 cm) deep although it is often advantageous to dig deeper as soil inevitably falls in from the side. They should be large enough for you to stand in. Once the pits have been dug you should take a thin spit of soil from the edge of the pit with a spade. Then, holding the spade horizontally, gently bump it on the ground to see how the soil breaks up. Danger signs are large angular clods or horizontal cracking into plates. This process may have to be repeated to cover the whole depth of interest. Note the depth of any compacted layer. The next thing to do is to use a penknife or builder's trowel to stick into one of the faces of the soil pit to test for compaction and remove any surface smeared by the digging. You are looking for any layers that feel firmer than the rest. Sometimes dragging the blade down the profile allows you to feel a compacted layer. Finally look for roots. The topsoil generally shows profuse rooting. In a well-structured soil, roots will be fairly frequent at a depth of two feet and, for a winter cereal, a few will reach four feet (1.2 m). The key thing to watch out for is a sharp reduction in rooting with depth. Since most soils are rather variable it is important to dig several pits.



APPENDIX 2:

**Figure 1**

A schematic representation of the linkages between agronomic practices and yield, mediated by changes in the rooting environment or the root system.

