
**PROJECT REPORT 316**

# INVESTIGATING THE SCOPE FOR MANAGING THE ROOT SYSTEM OF SPRING BARLEY CROPS TO IMPROVE PERFORMANCE ON DROUGHT-PRONE SOILS

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# INVESTIGATING THE SCOPE FOR MANAGING THE ROOT SYSTEM OF SPRING BARLEY CROPS TO IMPROVE PERFORMANCE ON DROUGHT-PRONE SOILS

by

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**CONTENTS**

**Abstract**

Water availability can significantly limit cereal yields in the UK in some regions in some years. Predictions of climate change suggest that the frequency and severity of water-limitation is likely to increase over the coming years. It is important, therefore, to develop management strategies to improve crop performance at drought prone sites. One approach is to try and modify the root system so that it can access more water. The aims of this project were to investigate the potential for managing the root system of spring barley, through variety choice and the use of plant growth regulators. A particular objective was to provide the industry with targets for the scale of change needed to a cereal root system to access more water, and the possible yield benefits that might arise. The project involved a combination of controlled environment, glasshouse and field experiments.

A range of genotypes, including several modern UK semi-dwarf varieties, an older tall variety, and wild barley from the Middle East, were screened for differences in root characteristics under well-watered conditions. There was relatively little variation amongst the different genotypes. Chalice, a modern variety had the fastest growth rate and hence produced the largest root length and mass. There was no consistent difference between the semi-dwarf varieties and the tall variety. Four 'modern' varieties were selected for further study (Chalice, Optic, Chariot and Derkado). The varieties did not differ in their response to drought, or their ability to utilize water from wet soil zones deep in the soil profile, although they did differ in their accumulation of the plant stress hormone, abscisic acid. Optic accumulated very little in its roots compared to Chalice. This raises questions about the nature of its role in controlling shoot functions under drought. From the results, there appears to be little scope at present for matching varieties of spring barley to the drought risk of a site on the basis of their root traits. A specific breeding programme is likely to be needed to make significant genetic improvements to the root system.

The effects of an anti-gibberellin plant growth regulator (trinexapac-ethyl, Moddus®, Syngenta) and a biostimulant growth promoter (Route®, Loveland Industries) on root growth and the drought response of cv Optic were studied in detail in field and outdoor lysimeter (large drums of soil) experiments. In the field experiments, there was no effect of either treatment on yield at three contrasting sites. Detailed measurements of root growth at one site revealed no effect on root number, total root length and the length and mass at any soil depth. Drought in lysimeters reduced yield by 1 t per ha, but there was no effect of Moddus or Route on water extraction and drought tolerance of the crop. There is no evidence from these experiments, and little in the scientific literature, to show that growth regulators have a significant effect on root growth of cereals and water capture from the important deep soils layers.

Simple models have been developed to predict the effects of changes in root distribution on wheat yield on different soil types and under different seasonal weather patterns. The model provides the

industry with targets to work towards for making genetic improvements to the root system. Some further development is needed to consider possible interactions between water and nutrient uptake.

## Summary

### Introduction

Water availability can seriously limit UK cereal production at some sites and in some seasons. Estimates made in the 1970's and supported by more recent studies suggest that up to 17% of the potential yield of wheat may be lost each year through lack of water. Cereals differ in their risk of drought limitations. Winter barley crops often avoid serious drought because they mature early before limiting soil water deficits develop. Wheat on the other hand matures later and, particularly on light soils, limiting soil water deficits can coincide with the grain filling period. Spring barley is also at risk because of its late maturity. In addition its later sowing means that there is less time for it to develop a deep root system.

Climate change predictions suggest that in the UK, winters will become wetter and summers drier. There are already indications that the frequency of droughts is increasing. On the loamy sand soils of ADAS Gleadthorpe, drought-limited wheat yields occurred in 13 out 19 years of measurements between 1980 and 2000. There is a need therefore to improve the access of cereal crops to water. An obvious approach is to modify the root system to promote root production in deeper soil layers. However, before this can be achieved we need to know 1) whether we have the husbandry tools available for manipulating the root system and 2) what scale of change we need to make.

The aim of research reported here was to investigate the potential for managing root systems of spring barley to improve crop performance on dry soils. The specific objectives were to:

- Investigate the extent of variation in root characteristics and response to drought amongst current UK genotypes. This was to identify whether there is scope for matching varieties, on the basis of their root traits, more effectively to site conditions.
- Investigate the effects of selected plant growth regulators and promoters on root growth, water capture and the response to drought of spring barley.
- Develop simple models linking root distribution, to plant available water and yield and use them to investigate the likely yield returns from managing the root system on a range of contrasting soil textures and under different seasonal weather patterns.

The first two objectives will help determine whether variety choice and growth regulator/promoters are effective husbandry tools for managing the root system of spring barley. The third objective is to provide the industry with the necessary targets to work towards in terms of improving cereal root systems, and the costs and benefits involved. There

is evidence that in many species, as the soil dries, a plant hormone known as abscisic acid (ABA) is synthesized by the root and delivered to the shoot where it contributes to the control of the shoot's response to drought i.e. the reduction in leaf expansion, closure of stomata and possibly the early senescence of the canopy. The above objectives were therefore addressed in the context of this possible ABA signalling.

**Genotypic variation in root traits and drought tolerance**

Eight genotypes were grown under controlled environment conditions in columns of sandy loam soil 75 cm deep. The plants were kept well irrigated throughout and harvested at the start of stem extension. The genotypes included modern varieties, some current, some now outclassed, differing in earliness, height and reported suitability for light soils. These were Chalice, Chariot, Optic, Derkado and Dandy. Chalice, Chariot, Optic, Derkado are all semi-dwarf varieties possessing the sdw1 semi-dwarfing gene. Dandy, in contrast, is a tall variety. In addition a breeding line from the Scottish Crops Research Institute (B83-12/21/5) and two exotic genotypes from the Middle East (Dudiah from Syria and Mehola from Israel) were included for comparison. It was expected that the exotic lines might have root characteristics conferring greater tolerance of drought than the UK commercial varieties.

There was relatively little variation amongst the genotypes in root characteristics at stem extension. Chalice had the largest total length and mass of root system of all genotypes and the greatest length in the deep soil layers. This was the result of a faster growth rate because shoot dry weight and leaf area were also larger than the other genotypes. Derkado invested its dry matter in shorter (thicker and/or denser) roots compared to the other genotypes. Some genotypes (e.g. Optic and Dudiah) tended to locate a greater proportion of their root length slightly deeper in the soil (i.e. 20-30 cm) than others (e.g. Chalice and Chariot). With the exception of Chalice and Derkado, there was no appreciable difference in root characteristics between the modern varieties and the exotic genotypes. Nor was there any consistent difference between the modern varieties on the one hand, and Dandy on the other, which suggests that the sdw1 gene has little effect on the morphology of the root system.

On the basis of these results it was hypothesized that Chalice would be more tolerant of topsoil drying because its faster rate of growth would enable its root system to extend more rapidly into the deep soil layers ahead of the drying font. It was also hypothesized that Derkado would be relatively intolerant of drought because its investment of biomass in short roots would not be conducive to good soil exploration. However, any effect these root characteristics might have on water use will depend on possible genotypic differences in other

traits, for example differences in ABA production and threshold soil moisture deficits for eliciting shoot responses to drought.

Genotypic variation in the capacity for root ABA accumulation and threshold soil moisture contents for stomatal closure were investigated by growing plants in sandy loam soil until mid-tillering and then withholding water. The experiment was conducted on four varieties (Chalice, Chariot, Optic and Derkado) in a heated glasshouse using relatively shallow pots so that the soil around the roots would dry reasonably uniformly, thus avoiding any confounding effects of genotypic differences in root distribution.

All varieties had similar soil moisture thresholds for stomatal closure. Stomata began to close at around 22% moisture content (volume/volume). At this point 50% of the plant available water had been depleted. However, varieties differed markedly in root ABA concentrations. In Chalice and Derkado root ABA concentrations increased as the soil moisture content declined, whereas in Optic and Chariot there was little or no change. These results show that there is no consistent relationship between root ABA concentration and stomatal conductance, and highlight the complexity of any involvement of root-produced ABA in controlling shoot responses to drought. Consequently, attempts to improve crop productivity on dry soils through simple selection for genotypic differences in ABA production are unlikely to be successful.

The ability of the same varieties to utilize water located deep in the soil profile was investigated in a further glasshouse experiment. Plants were grown in 120 cm deep columns packed with a loamy sand soil to facilitate a normal spring barley root distribution. The bottom 25 cm of each columns was hydraulically isolated from the top with a layer of gravel that allowed roots to grow between the compartments, but prevented any upward movement of water. In one treatment (referred to as the water-table treatment) water was provided in unlimited quantities to the bottom compartment only. In the other (control) columns were irrigated from the soil surface to maintain the soil close to field capacity. The exposed soil and water reservoir surfaces were covered with polythene. Water loss from the system through transpiration was monitored by frequent weighing and used to calculate irrigation requirements. Transpiration, above-ground dry matter production and grain yield were all reduced when the supply of water was confined to bottom of the soil profile. However, there was no significant interaction between varieties and irrigation regime on any of the above implying that the varieties did not differ in their ability to utilize deep supplies of water. Thus our hypothesis that Chalice would be better able to exploit deep sources of water and that Derkado would be less tolerant of drought, was not supported by these results.

Varieties did differ in their yield components. In Optic and Chariot, mean grain weight was more stable under drought (i.e. unchanged) than in Chalice and Derkado. The stability was associated with a greater sensitivity of ear number and hence grain number per column, to drought than in the other varieties. Thus, there was a greater reduction in ear and grain number in Optic and Chariot which ensured that there was adequate assimilate for grain filling in spite of the likely (though not measured) reduction in photosynthetic activity during this period.

Collectively the results demonstrate that the variation between current spring barley varieties in root characteristics and response to drought is relatively small, and hence there would appear to be little scope at present for matching varieties more effectively to site conditions on the basis of their root traits. However, we appreciate that only a relatively small number of varieties has been studied, and we have not considered shoot traits that may influence drought tolerance such as the capacity for storage and remobilization of soluble carbohydrates.

**Effects of plant growth regulators and promoters**

There is considerable interest within the industry in the use of plant growth regulators and promoters to modify root growth and reduce the risk of drought limitations to yield. There have been a number of reports that early applications of growth regulators can stimulate rooting and enhance yield in the absence of lodging. A preliminary experiment was conducted under controlled environment conditions to screen a range of growth regulators and promoters for their effects on root growth of spring barley cv Optic. The growth regulators and promoters selected represent some of the most popular or most heavily marketed products. Two without label recommendations for use on spring barley were selected on the basis of reports in the literature and to serve as a comparison. The treatments were, Moddus (trinexapac-ethyl), Meteor (chlormequat chloride, choline chloride and imazaquin), Route (Zn and N complexes) and FTC-1 (undisclosed active ingredients). The treatments were applied during early tillering at rates recommended by the manufacturers. Plants were kept well watered and harvested at the start of stem extension (Zadoks growth stage 31). None of the treatments had any significant effect on shoot growth. Root fresh weight and length was increased significantly by Route, but not by any of the other treatments.

The effects of Route were investigated in more detail in field and outdoor lysimeter experiments. Even though Moddus had no effect on root growth in the preliminary screen it was included in the field and lysimeter experiments as a comparison treatment. In each

experiment, Route (0.8 l $ha^{-1}$) and Moddus (0.2 l $ha^{-1}$) were applied to cv Optic when the crop was at growth stage 13/14.

The field experiments were conducted at three sites of differing soil textures. Soils ranged from a coarse-textured loamy sand over sand, to a finer textured sandy loam over deep clay. All three sites were located in the Montrose area of Angus, Scotland. Yield varied between the sites from 5.12 t $ha^{-1}$ to 6.98 t $ha^{-1}$. However, Moddus and Route had no significant effect on yield at any of the sites. Detailed measurements of root and canopy growth were made only at one site, which turned out to be the highest yielding site. Again there was no effect of the treatments on any of the crop attributes measured. Tillering, the number of adventitious roots produced, the depth and spread of structural roots (and hence anchorage strength), the total length and dry weight of the root system, and the length and weight of roots in any particular soil layer were all unaffected. In addition, there was no effect on water extraction from the soil.

The effects of Moddus and Route on the drought response of spring barley (cv Optic) were investigated in a lysimeter experiment. Lysimeters were 30 cm diameter plastic columns, 120 cm deep, packed with a loamy sand subsoil and 40 cm deep sandy loam topsoil. They were located under a fixed rainshelter to enable the water supply to the crop to be controlled. The soil moisture content was measured at 5 depths in the lysimeters by TDR probes inserted through the side. Seeds were sown at high density to ensure rapid canopy cover and depletion of soil water. Moddus and Route were applied at the same rates and timings as the field experiments. A week after application, water was withheld from one set of lysimeters when the crop was at mid-tillering. The other set was irrigated twice weekly.

Neither Route nor Moddus had any significant effect on the rate of soil water depletion or maximum soil moisture deficit achieved by the droughted crops. Drought reduced the grain yield by about 1 t $ha^{-1}$ largely by reducing the number of ears per $m^2$ and number of grains per ear. There was no significant interaction between growth regulator/promoter treatment and irrigation implying that Route and Moddus had no effect on the drought tolerance of the crop.

There is no evidence from these experiments that the growth regulators and promoters studied significantly influence root growth and drought tolerance of spring barley under field or outdoor lysimeter conditions. The earlier promise, therefore, shown by Route in laboratory experiments on young plants was not substantiated in crops grown under more realistic field conditions. Further we have been unable to find convincing evidence in the scientific

literature that any of the anti-gibberellin growth regulators alter root length of cereals at depths in the soil necessary to increase water availability to the crop.

Route gave a small (5%) increase in yield in the lysimeter experiment when averaged over the irrigation and drought treatments (although it was at the margins of statistical significance). Thus, there may be some small yield enhancement with this product, but the effect is not the result of improvements in water capture, nor is it consistent because it was not found at any of the three field sites.

**Modelling root distribution, plant available water and yield**

In order to provide targets for future improvements in root systems a modelling approach was taken to identify the scale of changes needed to produce a worthwhile increase in yield on contrasting soils and under different weather patterns. The modelling was conducted in two stages. The first was the development of a simple dynamic simulation of canopy expansion, senescence and transpiration as a function of plant available water and the soil moisture deficit. Yield was then estimated from the amount of water transpired over the season and the harvest index. The second stage was to use a recently developed empirical model (King et al. 2003) to estimate plant available water from root distribution and soil texture. Linking the two enabled the effects of changes in root distribution on yield to be predicted.

The model was developed for winter wheat using data from irrigation experiments conducted at ADAS Gleadthorpe in 1994 and 1995. Wheat was the focus rather than spring barley because more data were available for crop growth, water use and yield of modern cultivars. The model predicted well the soil moisture deficit between April and July in moderate and severe drought years. Although there was some discrepancy between the predicted and actual yields, the relative yield reductions resulting from drought were predicted reasonably well.

The model predictions suggest that doubling the root length of a typical wheat crop below 50 cm could give yield increases of 0.6 – 1.0 t $ha^{-1}$ in a severe drought year on clay and medium sand soils respectively, and 0.3 – 0.5 t $ha^{-1}$ in a moderate drought year. The yield gains depend on the distribution of the additional root length down the soil profile; the deeper the location, the greater the effect on water availability. We consider that increases in root length of this scale are potentially achievable given the extent of genotypic variation in root characteristics reported in the literature and that being found amongst current UK wheat varieties in other HGCA funded research (project number 2422). However, it will be necessary to consider possible trade-offs involved in modifying the root system including the additional dry matter requirements and the effects on the acquisition of nutrients, especially phosphate. This must

also include a consideration of the effects on grain quality. For example if a change is made to the root system that increases water availability to the crop, it could result in enhanced tiller survival as soil moisture deficits develop, without providing sufficient water to sustain the crop to harvest. As such grain filling may not be assured and high screenings could result. Thus, an improvement in yield could be at the expense of quality.

Model calculations show that for a typical wheat crop there is little additional water that can be made available by increasing its root length density if the soil depth is less than about 80-100 cm, assuming the soil to be well structured. This highlights the importance of maximising the depth of rooting to secure water and thus emphasizes the necessity for careful management of soil structure to avoid physical restrictions to root growth.

With some further development, the model can be adapted for use with other cereals including spring barley.

**Implications and key messages**

- In the present study there was no significant effect of Route or Moddus on root growth and water capture of spring barley under field conditions. Nor is there any compelling evidence in the scientific literature to indicate that anti-gibberellin growth regulators have functionally significant effects on cereal root growth. Independent studies of the beneficial effects on cereal roots of other commercially available bio-stimulants are scarce or lacking. As such we conclude that there is little evidence to support the use of plant growth regulators and promoters to modify root growth and improve water capture by cereals.
- At present there appears to be little variation in root characteristics amongst current UK varieties of spring barley. As such there is little scope for matching varietal root traits more effectively to the risk of drought at a site. There may be greater scope for matching shoot traits, such as the capacity for accumulating and remobilizing stem soluble carbohydrate reserves, but for the most part these were not investigated in this work.
- Glasshouse experiments suggest that current varieties differ in the stability of mean grain weight to drought. Chalice appears to be less stable, than Optic and this regard may be less suitable for drought-prone sites.
- A specific breeding programme may be needed to modify root growth and distribution sufficiently to improve water availability to the crop. Based on the

findings of previous studies, it is probable that by screening a wider range of germplasm, and utilizing more exotic sources, the necessary variation in root traits will be found.

- The models developed here for wheat, when extended to spring barley, can be used to provide targets for these improvements and the likely benefits in terms of yield.
- Before any change is made to the root system to improve yield, possible trade-offs must be considered, including the effects on nutrient uptake and the potential impact on grain quality. This can be done through further development of the models.

***Reference***

King J, Gay A, Sylvester-Bradley R, Bingham I, Foulkes J, Gregory P and Robinson D. 2003. Modelling cereal root systems for water and nitrogen capture: towards an economic optimum. *Annals of Botany* 91: 383-390.

# 1. Introduction

## 1.1 Drought limitations to UK cereal production

Water availability can seriously limit UK cereal production at some sites and in some years. Austin (1978) estimated that on average 17% of potential wheat yield is lost each year through lack of water. In an average year, a typical winter wheat crop uses approximately 300-330 mm of water between tillering and the end of grain filling (Goss et al. 1984; Gales et al. 1984; Foulkes et al. 1994). This must be supplied by the current rainfall and soil moisture reserves. For the major arable areas, average monthly rainfall is distributed relatively uniformly throughout the year (Smith 1984). The evaporative demand of the atmosphere, which drives crop transpiration, is a function of the solar radiation, air temperature, humidity and wind speed. It is greatest near the coast, decreases with altitude inland, and tends to be lower in the north than the south. However, in general it varies less between regions and seasons than rainfall (Smith 1984). From about April to July potential evaporation from the crop (transpiration) and the soil surface (soil evaporation) exceeds rainfall and the crop relies increasingly on water stored in the soil.

In the UK winter wheat tends to be grown on the finer textured, moisture retentive soils and is therefore often regarded as not being particularly susceptible to drought (Cannell 1981). However, a significant percentage of wheat crops in the central and eastern counties of England may be grown on the lighter soils of low water holding capacity (Foulkes et al. 1994). On these soils drought may be more common and, in especially dry years, potential yield losses can be severe (2-4 t $ha^{-1}$; Foulkes et al. 2001). With soils typically at field capacity at the beginning of April, limiting soil moisture deficits occur most frequently towards the end of summer. This coincides with the post anthesis period in wheat. Limiting deficits before anthesis are much less frequent (Foulkes and Scott 1998).

Barley tends to be grown on lighter, less moisture retentive, soils than wheat. However, since winter barley matures early before major soil moisture deficits develop, the worst drought problems are often avoided (Gales et al. 1984). Spring barley, on the other hand, is more susceptible because, like wheat, it matures late. Moreover, because of its later sowing its maximum rooting depth and hence access to water is less (Cannell 1981) and there is potentially less time for the accumulation of stem carbohydrate reserves to buffer against the effects of late season drought. There is also a greater loss of water from the soil surface during

early summer, as a result of the incomplete canopy cover at this time. If soil water is limiting, loss from the soil surface is wasteful as there is less available for transpiration (Passioura 1983; Richards et al. 2002). These differences between the major cereal crops are reflected in their relative yields in dry years compared to average years (Orson 1999). According to current predictions of climate change, summers in the UK are set to become warmer and drier and thus the frequency of droughts is likely to increase over the coming years (Ministry of Agriculture Food and Fisheries 2000).

**1.2 Crop responses to soil drying**

With a sufficiently large root length density (root length per unit volume of soil), roots are able to extract water from soil to a tension of 1.5 MPa (the permanent wilting point) (Bailey 1990). The amount of soil water potentially available to a crop is, therefore, that held between field capacity and 1.5 MPa. This is determined largely by soil texture. However, when the root length density is low, only the water held at lower tensions (< 0.2 MPa) can be extracted with ease (Bailey 1990). In addition to the effects of soil texture, the amount of water in a soil profile that is readily available for crop growth also depends on the structural condition of the soil, as this influences the spatial distribution of roots, and on the maximum rooting depth. In some literature the term available water capacity (AWC) has been used to refer to the water easily available to the crop (Foulkes et al. 1994; 2001), elsewhere it is used simply to describe the amount of water held between field capacity and the permanent wilting point (Bailey 1990; Rowell 1994) without regard to root depth and distribution. Throughout this report we use the term plant available water (PAW) to refer to water that is easily available to the crop, and AWC for water that is *potentially* available (that held between field capacity and a tension of 1.5 MPa). PAW is equivalent the term *root zone capacity* used by Bailey (1990).

As long as there is sufficient soil water available, crops can transpire at the rate determined by the evaporative demand of the atmosphere (known as the potential rate). As water is depleted from the soil, a limiting soil moisture deficit is reached beyond which canopy function is impaired and the transpiration rate falls. Leaf expansion is reduced and leaf senescence accelerated restricting the final canopy size and duration (Henson et al. 1989; Foulkes et al. 2001). Stomatal closure is induced decreasing leaf conductance to water vapour and $CO_2$ (Day et al. 1981). The effects of stomatal closure on the availability of $CO_2$ within the leaf, is generally believed to be the primary cause of the decrease in photosynthetic efficiency associated with drought, but non-stomatal limitations can also occur (Escalona et al. 1999). The sensitivity of the above processes to developing water stress differs. Thus leaf expansion is usually reduced before stomatal conductance (Ritchie 1981; Sadras and Milroy 1996). Experimentally determined threshold soil moisture deficits at which leaf expansion, stomatal

conductance and transpiration are reduced vary widely depending on the plant species and experimental conditions adopted. Foulkes et al. 2001 estimated the threshold for canopy expansion in winter wheat to be when 50% of PAW had been depleted and 64% for canopy senescence. Transpiration of field-grown wheat under a fixed rainshelter was reduced below the potential rate when 45% of the extractable water had been removed (Weir and Barraclough 1986) and for spring barley when 50% had been depleted (Day et al. 1978). In experiments on wheat grown in lysimeters transpiration was reduced after 70-75% of PAW was depleted (Gales et al. 1984). Averaged over a range of species grown in controlled environment and field experiments, thresholds of 40% for leaf expansion and 60% for stomatal conductance and gas exchange have been reported (Sadras and Milroy 1996).

Root growth is less sensitive to a developing water stress than shoot growth. Root extension may be maintained for longer as the soil water potential declines (Sharp et al. 1988). Preferential extension and branching of roots in zones of higher water availability, as other parts of the soil dry, helps the root system keep pace with the shoot's demand for water (Asseng et al. 1998; Molyneux and Davies 1983; Reid and Renquist 1997).

### 1.3 Physiological control

The traditional view of the sequence of events occurring during the onset of drought was that soil drying restricted water uptake which in turn reduced leaf water content, water potential and turgor pressure, thereby reducing growth and stomatal conductance (Davies et al. 2002). Research over the last decade, however, suggests that roots may be able to sense the soil water status and 'signal' this directly to the shoot contributing to the induction of the drought response. This is most pronounced in 'isohydric' species where soil drying may reduce leaf expansion and stomatal conductance before any change in leaf water status occurs (Tardieu and Simonneau 1998; Davies et al. 2002). The signal most widely implicated in these responses is absiscic acid (ABA), which is synthesized by the roots as the soil dries and delivered to the shoot in the xylem sap. The level of complexity involved in the control of the shoot responses to soil moisture deficits is now beginning to be appreciated. For example, there is evidence that hydraulic effects and root-derived signals interact to control stomatal conductance and that sensitivity of stomata to ABA concentrations in the xylem sap can be modified by a range of factors including the prevailing vapour pressure deficit and pH of the xylem sap.

### 1.4 Improving crop performance in drought-prone situations

There are several possible avenues for improvement of crop performance in drought-prone situations. These include, adopting management practices or selecting varieties to increase

water capture, water use efficiency or harvest index under drought (Passioura 1983; Loss and Siddique 1994; Araus et al 2002; Richards et al. 2002). Above-ground plant traits that may confer improved drought-tolerance of cereals under UK conditions have been discussed previously (Foulkes et al. 1993, 2001; Foulkes and Scott 1998). Here we focus on below-ground attributes.

The appropriate strategy for a given situation depends on soil characteristics and the seasonal pattern of water availability. Where water is stored deep in the soil profile and remains untapped at the end of the season because of insufficient root length density (Passioura 1983), increasing the depth of rooting to improve capture is a suitable approach. But where the rainfall is uncertain and water is available only to the depth of the rains' wetting front, a reduction in the size of the root system or increase in its hydraulic resistance may help conserve water for the vital flowering and grain-filling period (Brown et al. 1987; Passioura et al. 1993). In the UK, winter rainfall is usually sufficient to recharge the soil water reserves, and thus increasing water capture may be a viable strategy providing the soil is deep enough. Only if winter rainfall is lower than average following an exceptionally dry summer, such as 1976, is there a risk of incomplete recharge. Current predictions of climate change in the UK suggest that winter rainfall will increase and hence annual recharge should be assured.

Another approach for increasing capture of the available stored water is to increase the water potential gradient between leaf and soil through osmotic adjustment of leaves and roots, or by reducing the axial resistance to water flow through the root xylem (Taylor 1983). Early closure of stomata in response to a developing soil moisture deficit (i.e. low soil moisture threshold for closure), will help conserve water in situations where water is bound to be exhausted before the end of grain filling. However, where there are relatively large supplies of water a low threshold may be over conservative and restrict photosynthetic activity unnecessarily early. Increasing the threshold could sustain photosynthetic activity at high rates for longer during the grain filling period and still enable grain filling to be completed.

The above strategies are appropriate where soils are deep and there is additional water to be exploited. In contrast, crop production on shallow soils will require a more conservative strategy of soil water management.

**1.5 Tools and targets**

Many researchers and agronomists have argued the need for deep, vigorous, root systems in drought-prone situations, but without quantifying how deep or vigorous they should be. In order for improvements to be made, the industry needs both the tools to modify the root

system and quantifiable targets to work towards. The financial benefits in terms of yield or quality must more than offset the costs incurred managing the root system (Bingham and Hoad 2000). Genetic variation exists in a number of root attributes (O'Toole and Bland 1987; Bingham 2001), which may provide opportunities for variety selection or targeted breeding. Crop and soil management can also influence root growth (Hoad et al. 2001). However, at present there is little information on the scale of change we may be able to make through choice of variety or husbandry practice and whether it is likely to be economically worthwhile.

**1.6 Aims and Objectives**

The aim of the work reported here was to investigate the potential for managing root systems of spring barley, through variety choice and plant growth regulators to improve crop performance on dry soils. The specific objectives were to:

1. Investigate the extent of variation amongst current UK genotypes in root characteristics and response to drought.
2. Investigate the effects of selected plant growth regulators and promoters on root growth, water capture and the response to drought of spring barley.
3. Develop simple models linking root distribution, to plant available water and yield and use them to investigate the likely yield returns from managing the root system on a range of contrasting soil textures and under different seasonal weather patterns.

Objectives 1 and 2 addressed the question of whether we have the necessary husbandry tools, in variety selection and PGR use, to manage spring barley root growth and activity effectively. They were investigated in the context of ABA production by roots and possible root-shoot signalling. Objective 3 addressed the issue of targets for management of cereal root systems.

The research involved both controlled environment and field experimentation. Controlled environments have a number of advantages: ease of management, ease of access to the root system and the facility for 'out of season' experimental work. But they can suffer from a number of drawbacks and extrapolation of results to the field has to be done with caution (Bingham 2001). However, the focus of the experimental part of the project was to identify potential tools for management. The intention was that any treatment that showed particular promise could then be investigated more thoroughly in the field over several sites and seasons.

## 2. Root Characteristics and Drought Response of Spring Barley Varieties

### 2.1 Introduction

There is considerable genotypic variation in root morphological characteristics of crop species that might be exploited to improve crop performance in water-limited environments (O'Brien 1979; O'Toole and Bland 1987; Ludlow and Muchow 1990, Ellis et al. 2000). Variation has been reported in the depth of rooting, the rate of root extension, the distribution of roots, penetration ability and specific root length (Hurd 1968, 1974; O'Brien 1979, Wahbi and Gregory 1989a; Atkinson 1989; Blum and Johnston 1993).

Where crops are grown on deep soils and water is stored throughout the profile, deeper rooting will provide access to more water (Jordan and Miller 1980). In these situations deeper rooting cereal varieties have been shown to be more drought tolerant (Hurd 1974; Jordan and Miller 1980). Deeper rooting might be achieved through an increase in the rate of main root extension and/or a greater duration of extension. However, an increase in main root extension into deeper soil layers must be accompanied by branching at these depths to increase the root length density sufficiently to enhance water uptake. In the UK, root length density may limit water uptake below about 70-80 cm for winter cereals and about 50 cm for spring cereals (chapter 3 this study; Bailey 1990). Thus in many situations an increase in maximum rooting depth is not essential to secure more water. Rather it is an increase in root length density that is needed which could be achieved through greater production and extension of lateral roots close to the apex of the main roots.

A greater rate of root extension might be advantageous for spring sown crops that are sown into relatively dry soils as this would help ensure the rate of root extension exceeds rate of the soil drying front (Cannell 1981). If soil dries ahead of the rooting depth, soil strength increases thereby offering greater impedance to further root extension. This may be less of an issue with winter cereals in the UK, as roots are likely to have penetrated to depths of at least 80-100 cm before the evaporative demand begins to exceed rainfall in April-May (Gregory et al. 1978a; Weir and Barraclough 1986).

Root systems are major sinks for photosynthates during vegetative growth. Estimates made for spring wheat gown under temperate W. European conditions indicate that as much as 2.3 t $ha^{-1}$ of C (equivalent to 6.4 t $ha^{-1}$ dry matter) may be transferred below-ground during the season (Swinnen et al. 1994). Biomass allocation to the root system is at the expense of the

shoot, and potentially grain yield (Bingham et al. 2002). Thus a higher specific root length (SRL, length per unit weight) represents a potentially better investment of the plant's biomass, as there is a proportionally greater length of root for soil exploration. However, there may be trade offs if a greater SRL is associated with anatomical changes that increase the resistance to water transport, such as a reduction in xylem vessel diameter (Atkinson 1989).

There is evidence that the distribution of roots down the soil profile can influence soil water extraction and the shoot's response to soil water deficits. In model simulations of soil water extraction Gregory and Simmonds (1992) have demonstrated that it is the relative distribution of roots that determines the effective soil water potential as the soil water deficit increases. Simulations were conducted for model crops with a comparable maximum rooting depth, but different root length density in the upper layers of the soil. The crops with the largest proportion of their roots in the upper soil reduced the soil water potential more for a given soil water deficit. Blum and Johnston (1993) grew several wheat varieties in soil columns that permitted the topsoil to dry, whilst maintaining an unlimited supply of water to the bottom part of the soil profile. Varieties with a small root biomass in the topsoil and a relatively uniform distribution throughout the profile maintained a greater stomatal conductance and produced a larger plant biomass and grain yield than varieties with a large proportion of their root system in the topsoil. The results were interpreted in terms of a greater ABA production and delivery to the shoot by varieties with more roots in the topsoil. Thus a relatively uniform distribution of root length might be advantageous for crop performance on dry soils, providing there is an adequate supply of water available at depth, as it would enable stomata to remain open for longer as the soil moisture deficit develops.

At present there is little information available regarding the root morphological characteristics and responses to soil drying for current UK spring barley varieties. Such information is needed by the industry for two reasons. Firstly, to determine whether existing varieties might be better matched to soil and regional climatic conditions. Secondly, to identify whether there is sufficient variation amongst current (commercial) genotypes to make selection for specific root traits a feasible proposition.

### *Objectives*

The objectives of experiments reported here were:

1. To quantify the root morphological characteristics of a range of spring barley genotypes differing in shoot characteristics, phenology or reported suitability for dry conditions.
2. To investigate the shoot's response to soil drying and its relationship to root ABA production in selected UK varieties.
3. To investigate the ability of selected UK varieties to access water and grow when provided with an unlimited supply from a deep water table, but a drying topsoil.

These objectives were addressed in three separate experiments conducted under controlled environment or glasshouse conditions.

## 2.2 Experiment 1- Root morphological characteristics

Several genotypes were selected for study on the basis of their phenology, shoot phenotype, date of introduction (commercial varieties), geographical origin and reported suitability for drought prone areas. These included several modern UK commercial varieties, plus for comparison, a breeding line, and two exotic genotypes from drought susceptible regions of the Middle East. The genotypes were as follows: Chalice, Optic, Chariot, Derkado, Dandy, B83-12/21/5, Dudiah, and Mehola.

*Cultivars*

Chalice, Optic, Chariot, and Derkado are modern semi dwarf varieties possessing the sdw1 semi-dwarfing gene. Dandy, in contrast is an older, tall variety. A view held amongst some agronomists is that tall varieties are better suited to drought prone sites than short varieties (D. Cranstoun, SAC personal communication). The view is based on field experience rather than any robust experimental evidence. Chalice and Chariot tend to mature a little earlier than Derkado, and Optic a little later (SAC and HGCA 1998). Chalice is susceptible to high screenings. Derkado is reported to be less suited to stress situations (SAC and HGCA 1998). Currently, Chalice and Optic are widely grown, whilst Chariot and Derkado, being older varieties, have been outclassed.

*Breeding lines and exotic genotypes*

B83-12/21/5 (abbreviated to B83 in this report) is a breeding line used at the Scottish Crops Research Institute (SCRI). It carries the Golden promise ari-e. GP semi-dwarfing gene. Derkado and B83 are the parents of a double haploid mapping population established at SCRI. The population is being used to map QTLs for several roots traits to barley chromosomes. If significant differences between Derkado and B83 were observed in the current study, the genes responsible could be located and tested in further work using the mapping population. Of the exotic genotypes studied, Dudiah is a landrace (*Hordeum vulgare*) from N.E. Syria and Mehola is a wild barley (*Hordeum spontaneum*) from Israel. They were selected for study for two reasons. Firstly to extend the germplasm screen to more exotic types with the possibility of identifying phenotypes better suited to drought conditions as occur in the Middle East. Secondly because SCRI are currently introgressing part of their chromosomes into a modern cultivar, which opens up the potential for genetic analysis of any interesting root traits observed in the exotic genotypes.

Seeds of Dandy, B83, Dudiah and Mehola were provided by Brian Forster of SCRI. The others were obtained commercially. Morphological characteristics of their roots systems were investigated under well-watered conditions. The rationale for growing plants under well-watered conditions was to identify root traits that might enable the root system to establish or explore the soil more effectively in advance of any drought, thereby enhancing its ability to avoid or minimise drought-induced yield losses by improved exploitation of stored water.

**Materials and methods**

A sandy loam soil was collected from Sunnybrae Farm near Aberdeen, and was air dried for seven days and then passed through a 2 mm sieve to remove stones and plant debris.

Plastic cylinders (referred to hereafter as columns) measuring 10.5 cm (internal diameter) x 75 cm (depth) were lined with PVC sleeves to facilitate the removal of intact soil and root cores. Each column was filled with 8.5 kg of air-dried soil (over a three day period, to allow for settling). The soil was then saturated with water, covered with a polythene sheet to prevent evaporation, and left to drain for forty-eight hours to reach field capacity. Columns were placed in a controlled environment cabinet.

Seeds of spring barley (that had been pre-treated with Raxil-S 1.5ml $kg^{-1}$) were imbibed in aerated distilled water for twenty-four hours, and then germinated on moist germination paper for four days at 20$^{o}$C then transplanted, at a density of one seedling per column. Varieties were allocated to columns according to a randomised block design.

Columns were watered with distilled water three times each week, so that excess drained freely from the bottom of the column. Measurements with a theta probe (Delta-T Devices Ltd., Cambridge, UK) of the surface 10 cm of the soil indicated that the soil water content never fell below 20 % v/v. Temperature in the cabinet was maintained at 20 ± 0.5 $^{o}$C day and 15 ± 0.5 $^{o}$C night. Light was provided over a 16 hour photoperiod by fluorescent lamps giving a photon flux at initial plant height of 500-900 µmol $m^{-2}$ $s^{-1}$ PAR depending on location in the cabinet.

Plants were harvested after 33 days, at the start of stem extension. Shoots were excised from the roots and the green area of leaf and shoot bases (leaf sheaths) were determined using a WinDias leaf area measurement system (Delta-T Devices, Cambridge, UK). Dry weights

were determined after drying plant material in a forced draft oven at 80 $^{o}$C for one hour, and then 60 $^{o}$C until constant weight was achieved.

Soil and root cores were removed intact from the columns, and stored at 4 $^{o}$C. Roots were washed within three days of harvesting. Cores were cut into seven, 10 cm thick and one, 5 cm thick sections, and soil was gently washed from the roots of each section by hand, over a 500 μm sieve. The root samples were then frozen between moist germination paper and stored at – 20$^{o}$C prior to analysis. For analysis samples were defrosted at room temperature, sub-sampled according to fresh weight, spread in dishes of water, scanned and digital images stored as tiff files. The images were later analysed using the image analysis software WinRhizo (Regent Instruments, Inc., Quebec). Sub- and main samples of root were dried at 80$^{o}$C for 48 h and weighed. Root lengths of the main sample were calculated from the sub-sample measurements after correcting for the difference in weight.

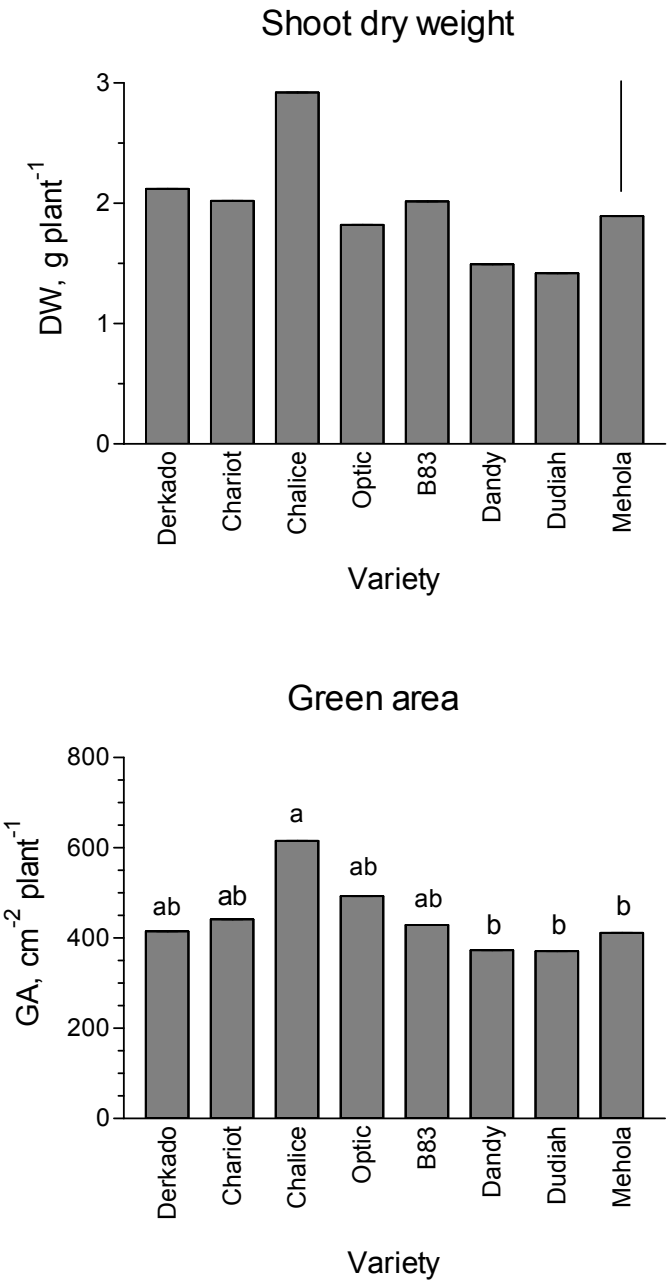


Fig. 2.1. Shoot biomass and green area of spring barley genotypes. Values are means of 5 replicate plots. Vertical line for shoot dry weight represents LSD (P=0.05) calculated after one-way ANOVA. Green area did not conform to a normal distribution. Columns denoted by a different letter are significantly different at P<0.05 as shown by a non-parametric equivalent of the Tukey test on the rank sums from a Kruskal Wallis test.

**Results**

Shoot dry weight at the start of stem extension ranged from just under 1.5 g plant$^{-1}$ for Dandy and Dudiah to nearly 3 g plant$^{-1}$ for Chalice (Fig. 2.1). Most of the other varieties produced around 1.8-2.0 g plant$^{-1}$. The difference in biomass between Chalice and Optic, Dandy, Dudiah and Mehola was significant at $P<0.05$. Shoot biomass did not differ significantly between the other varieties. Green area, which included the leaf laminae and leaf sheaths, differed between varieties in the same way as soot biomass. Thus, Chalice had the largest green area whilst Dandy, Dudiah and Mehola had the smallest ($P<0.05$).

In general there was a greater variation between genotypes in root characteristics than in shoot biomass and green area. (Fig. 2.2). There was a 2.9 and 3.4 fold difference in root dry weight and total root length respectively, between the largest and smallest varieties, compared with only a 2 and 1.5 fold difference for shoot biomass and green area. Chalice produced the largest root system. Root biomass and length were significantly greater than all the other varieties ($P<0.05$). Dandy, Dudiah and Mehola were amongst the smallest in terms of both root biomass and length. Derkado was unusual in that it was ranked 2$^{nd}$ for root biomass but last for root length. This is reflected in the substantially lower specific root length (SRL) of Derkado compared with the other genotypes (Fig. 2.2). Analysis of variance revealed no overall significant difference between varieties in their shoot:root dry weight ratio ($P=0.142$). However, it is worthy of note that Chalice, ranked first in terms of shoot and root biomass, had the lowest S:R ratio.

The distribution of root length down the soil profile is shown in Fig. 2.3. The data have been normalised to account for differences in total root length. Lengths in each soil layer are presented as a fraction of the total length. Analysis of variance on arcsine transformations of the data for each soil depth indicated significant differences between varieties at depths of 10-20 and 20-30 cm, suggesting that varieties differed in their root distribution. Two broad categories of distribution are apparent. The first is where the greatest proportion of the total root length is located in the uppermost soil layer, with the proportion decreasing steadily with soil depth. This was found with Derkado, Chalice, Chariot and Mehola. The second is where there is less of the root system located in the uppermost soil layer and a greater fraction located in the 10-20 and 20-30 cm layers. This is most pronounced in the case of Dudiah and to a lesser extent Optic and B83.

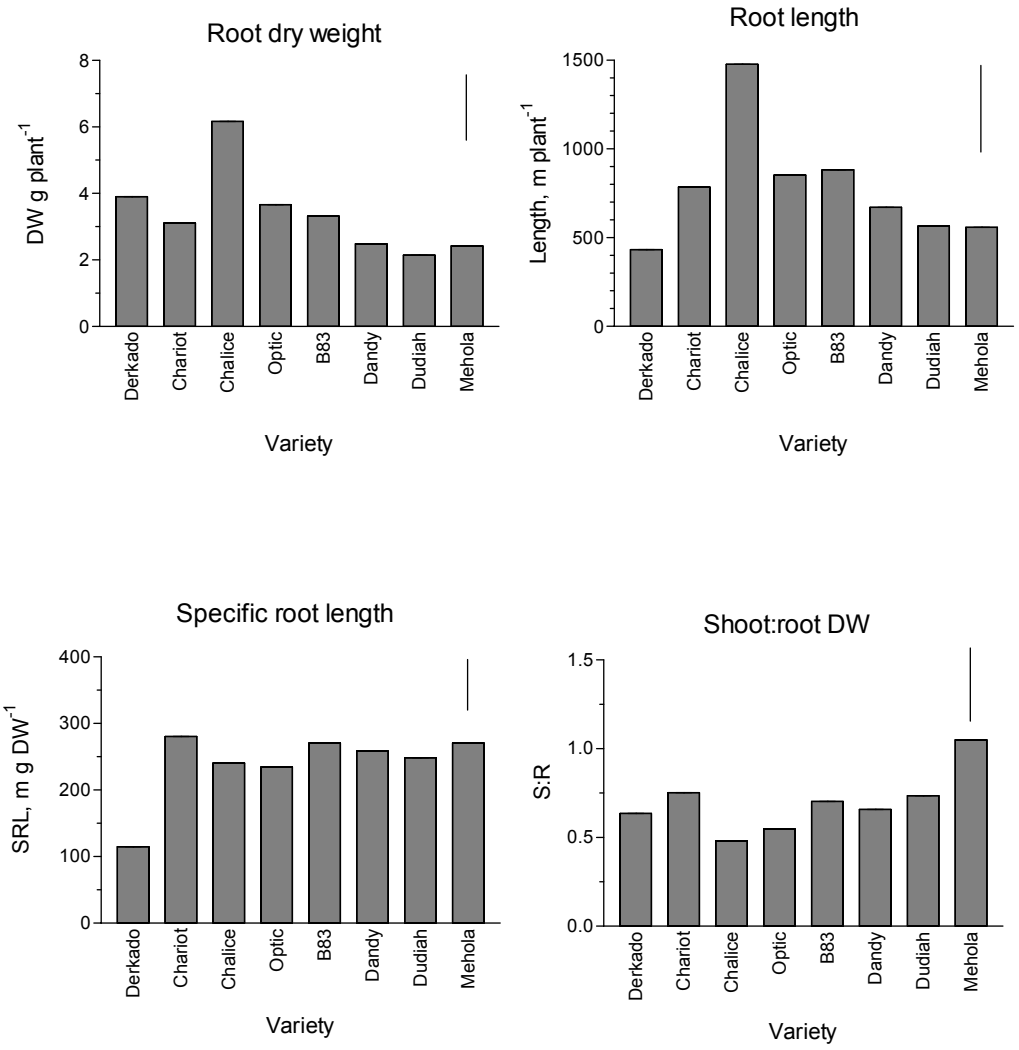


Fig. 2.2. Root characteristics and shoot:root biomass partitioning of spring barley genotypes. Values are means of 5 replicates. Vertical lines represent LSD (P=0.05) calculated after one-way ANOVA.

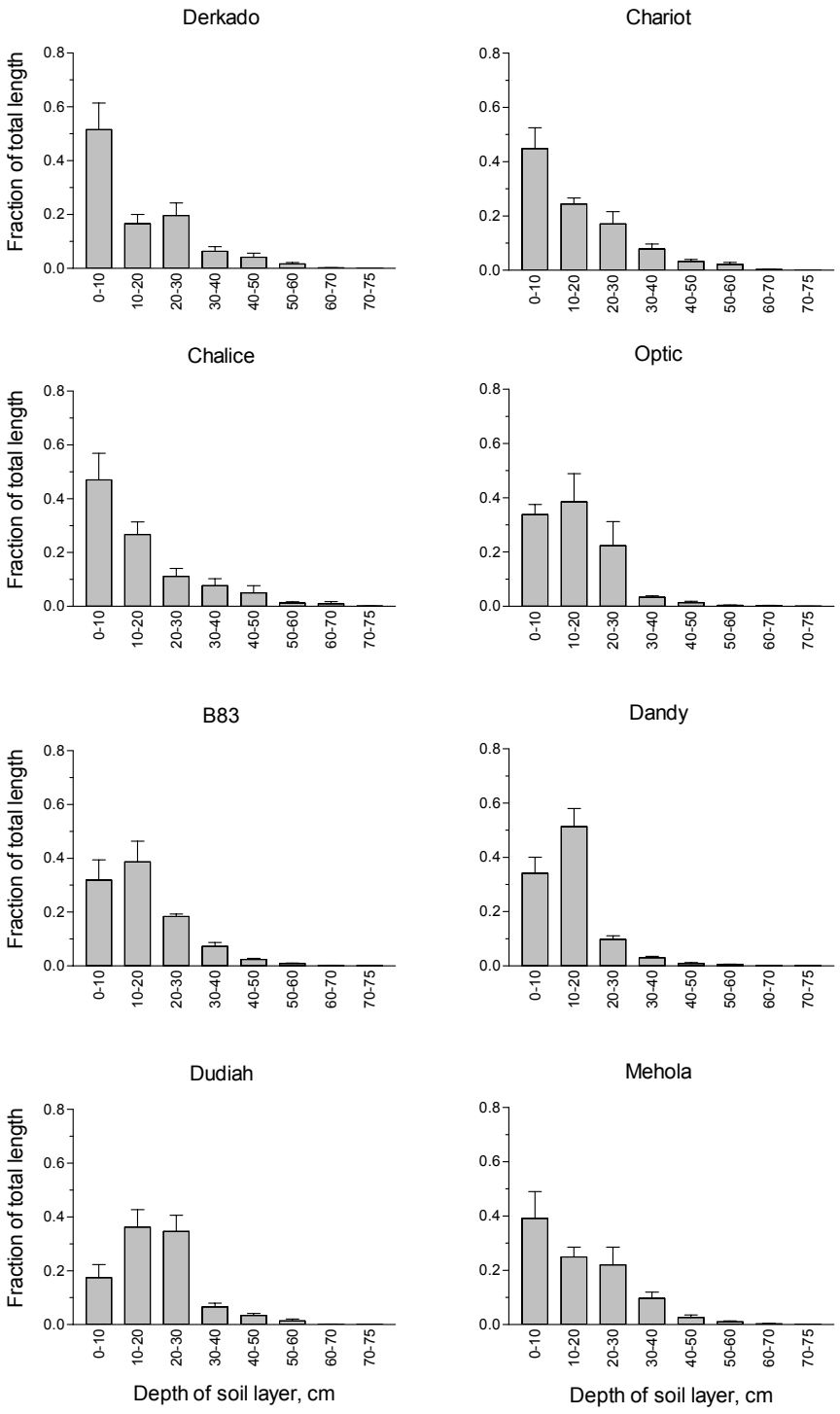


Fig. 2.3. Fraction of total root length with depth down the soil profile. Depth of a soil layer is measured from the soil surface. Values are means (+ SEM) of 5 replicates. One-way ANOVA on arcsine transformed data at each soil depth gave: 0-10 cm P=0.137; 10-20 cm P=0.009; 20-30 cm P=0.045; remaining depths P>0.15.

With the exception of Chalice, there was little difference between varieties in the amount of root located in the deepest layers of soil. Chalice had the greatest root length below 50 cm in absolute terms (Fig. 2.4) though not in terms of the proportion of the total root length (Fig. 2.3). Dudiah had an absolute and proportional root length below 50 cm comparable with most of the other genotypes, in spite of its proportionally deeper location of roots in the top 30 cm.

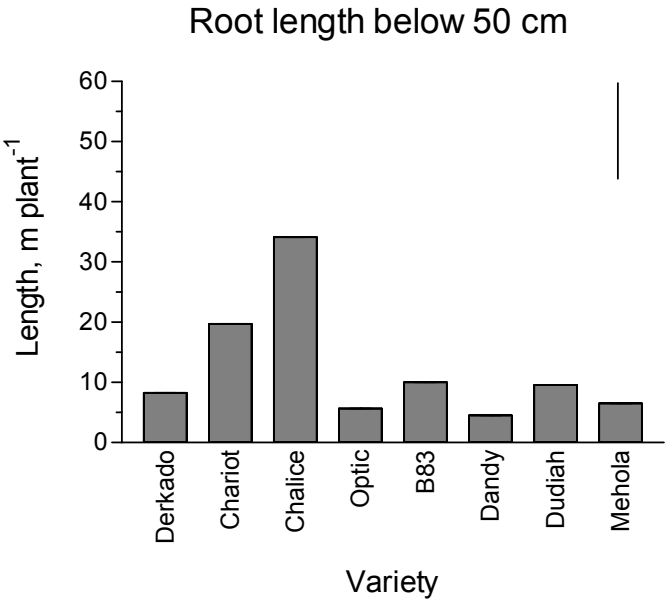


Fig. 2.4. Root length below 50 cm in the soil profile. Values are means of 5 replicates. Vertical line represents LSD (P=0.05) calculated after one-way ANOVA.

## 2.3 Experiment 2 – Response to uniform soil drying

The response of selected UK varieties to soil drying was initially investigated in plants grown in shallow pots. This approach was taken to identify any genotypic variation that might be present in the threshold soil moisture contents for stomatal closure and capacity for ABA signal production by roots. The use of shallow pots enabled the root systems to be exposed to uniform soil drying, avoiding the confounding effects that would arise in the field, or in soil columns, from genotypic differences in root distribution. The response of the same genotypes to variation in soil water availability down the soil profile was investigated in experiment 3.

### Materials and methods

*Plant growth*

Seeds of Derkado, Chalice, Optic, and Chariot were imbibed in aerated distilled water for eighteen hours, and germinated on moist germination paper for four days at 20$^{o}$C. Seedlings were then transplanted, one per pot, into pots measuring 18 cm (top rim diameter) x 16 cm (deep), with a volume of 3,000 cm$^{3}$. Pots were filled with a sandy loam soil, sieved to pass a 2 mm mesh, and packed to a dry bulk density of 1.4 g cm$^{-3}$.

The evaporation of water from each pot was minimised by covering the surface of the soil of with a 3 cm deep layer of gravel (nominal diameter 5 mm). To simulate the shading effects of a crop canopy, and to restrict tillering, at Zadoks GS 12 the shoots of each plant were enclosed in a cylinder of green mesh (mesh size, 4mm; manufacturers, Netlon). The cylinders were 10 cm in diameter giving an equivalent plant density of 127 plants m$^{-2}$. The height of the mesh cylinders was 10-20 cm below that of the top of the plant and the cylinders were extended as the plants grew.

The experiment was conducted in a heated glasshouse during November and December. Temperature control was good (appendix 2.1). Day time temperature averaged 20.5 $^{o}$C with a range of 19-22$^{o}$C; night time temperature was 19$^{o}$C with range of 16-21$^{o}$C over the course of the experiment. Day time relative humidity ranged from 50-70 %, but during the soil drying period was generally close to 55%. Supplementary lighting was provided over a 16 h daylength from sodium lamps (400 W Sonta/agro). Light intensity varied with changes in sunlight, but the photon flux at plant height was in the order of 450-650 μmol m$^{-2}$ s$^{-1}$ PAR during measurements of stomatal conductance.

*Soil drying regime*

26 replicates of each variety were grown in a completely randomised design for three weeks, until plants were at GS 31. Pots were watered every 3 days to replace water losses. Water was then withheld from 20 replicates of each variety and the soil allowed to dry, while 6 were watered daily with distilled water (controls) until water drained freely from the base of the pot. Four drying and two control replicates of each variety were harvested every one or two days during the stress period. The drying period lasted up to 8 days. For a particular variety the harvests were spaced according to the soil moisture content.

Soil moisture contents were monitored daily using a theta probe (Delta-T devices). A separate experiment, in which pots were enclosed in polythene to prevent evaporation from the surface, showed that the soil moisture content at field capacity was 38% and that plants could extract water down to a soil moisture content of 5% v/v.

*Stomatal conductance and net photosynthesis*

Stomatal conductance and net photosynthesis were monitored once a week prior to the initiation of soil drying, and then daily during the period of soil drying, using an LCA 4 infra red gas analyser fitted with a narrow leaf chamber (Analytical Development Company, Ltd., Hoddeston, UK). Measurements were made around midday on the youngest fully expanded leaf.

*Leaf water potential and xylem sap pH;*

Leaf water potential was measured on the newest fully expanded leaf of each plant, and xylem sap expressed from this leaf was used to measure pH. Leaf water potential was recorded using a SKPM Skye pressure chamber (Skye Instruments, Powys, UK). Approximately 20 microliters of xylem sap were then exuded from the leaf, and the pH of the xylem sap was measured using a micro combination pH electrode (model no. PHR-146; Lazar research Laboratories Inc. Los Angeles, CA, USA).

*Root ABA concentrations*

After making the leaf measurements, the remaining shoot material was excised at the soil surface, and pots transferred to a cold room at 4$^{o}$C to await root extraction. Roots were washed from soil by hand over a 500 μm sieve, within five hours of the plants being harvested. A representative sub-sample of the root system was rapidly frozen in liquid nitrogen, and stored temporarily at –80 $^{o}$C before freeze drying. Root tissue was ball milled and ABA determined on aqueous extracts by radioimmunoassay using the monoclonal

antibody MAC252 (Quarrie et al. 1988). Insufficient xylem sap was expressed from the leaves to enable its ABA concentration to be determined.

Where possible, measurements of soil moisture content, stomatal conductance, net photosynthesis, leaf water potential, and xylem sap pH were done on an individual plant in immediate succession, so that for each plant all of these measurements were made within thirty minutes of each other. One plant from each variety was harvested in sequence, and the sequence repeated until all the replicates had been harvested. However, due to time constraints it was not possible to measure leaf water potential and xylem sap pH, nor extract root tissue for ABA determination on all replicates.

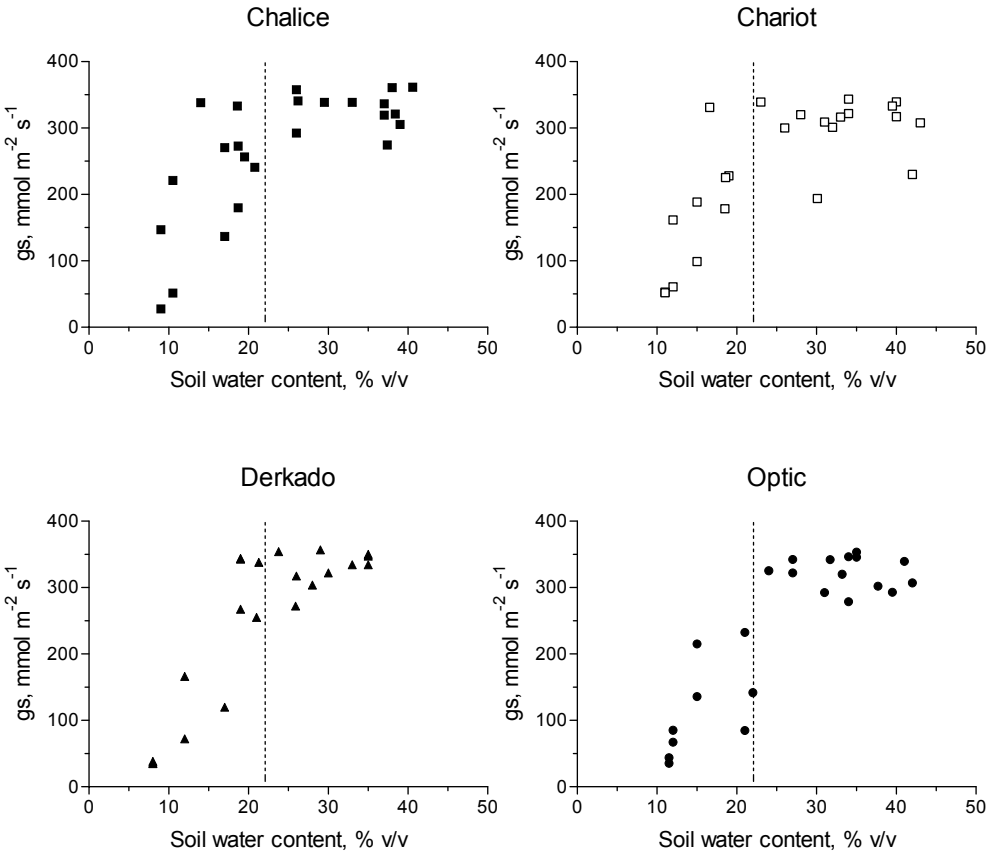


Fig. 2.5. Relationship between stomatal conductance to water vapour ($g_s$) and volumetric soil water content. Vertical line shows soil water content at 50% PAW. Each point represents a single determination on a separate replicate plant.

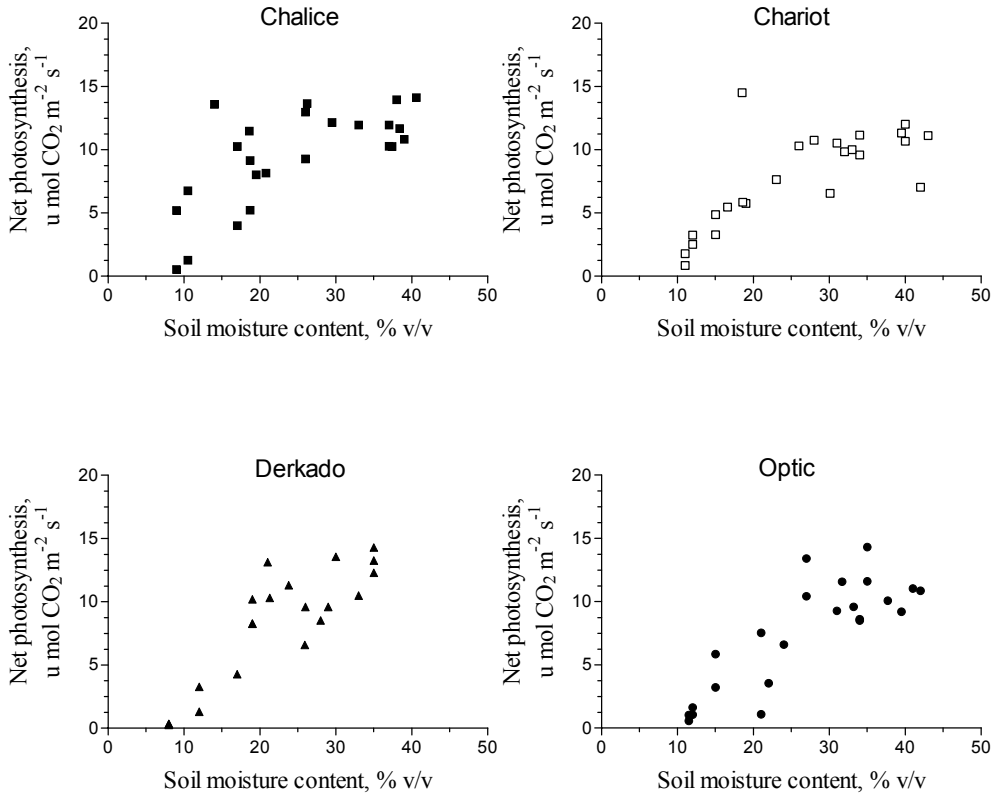


Fig. 2.6. Relationship between net photosynthetic rate of the youngest expanded leaf and volumetric soil water content. Each point represents a single determination on a separate plant.

**Results**

The soil dried relatively quickly after withholding water and almost all the plant available water was depleted within 6 – 8 days. Chalice, being largest of the varieties, depleted the water most rapidly, whilst Optic depleted water the slowest (data not shown). Under well watered conditions the stomatal conductance of all varieties was between 300 and 350 mmol $m^{-2}$ $s^{-1}$ (Fig. 2.5). The conductance declined when the soil water content decreased below about 22%. This represents the point at which 50% of PAW has been depleted. The data are quite scattered, which is typical for this type of measurement (Borel et al. 1998), and thus it is not possible to define precisely a threshold soil moisture content for stomatal closure for each variety. All varieties, appeared to have similar thresholds. For Chalice it may have been slightly lower than 22% and for Optic slightly greater, but the difference if any was small. The net photosynthetic rate followed the same pattern with soil moisture content as stomatal conductance (Fig. 2.6). By the end of the drying period, the leaf water potential was reduced to between –1.0 and –1.5 MPa depending on the variety (Fig. 2.7).

The bulk tissue ABA concentration of the roots showed surprising differences between varieties (Fig. 2.8). The concentration in roots of well water plants (soil moisture contents 25-40 %) was in the region of 100 ng g $DW^{-1}$ for Chalice, Chariot and Derkado, and slightly higher for Optic at an average of about 150 ng g $DW^{-1}$. Derkado showed the expected response of an increase in ABA concentration as the soil moisture content declines, reaching concentrations of up to 300 ng g $DW^{-1}$ in the driest soil. If the single outlying point is ignored (open square, Chalice, Fig 2.8), the response of Chalice is comparable. In Optic and Chariot on the other hand, there was very little change in the ABA concentration over the entire range of soil moisture contents. There was no discernable change in pH of the xylem sap during soil drying for any of the varieties. The pH ranged from 5.8-6.5 with the majority of measurements lying between 6.1 and 6.4 (Fig. 2.9).

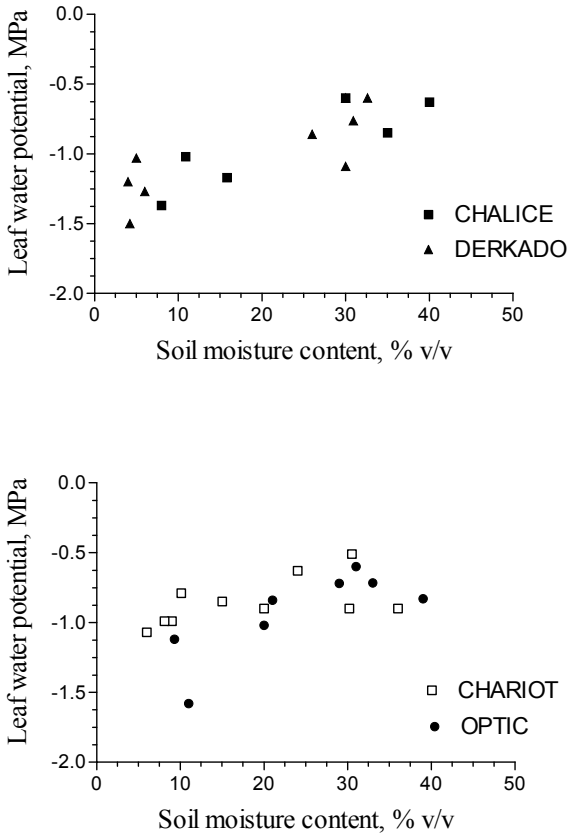


Fig. 2.7. Leaf water potential as a function of soil moisture content for 4 spring barley varieties. Each point represents a single determination on a separate plant.

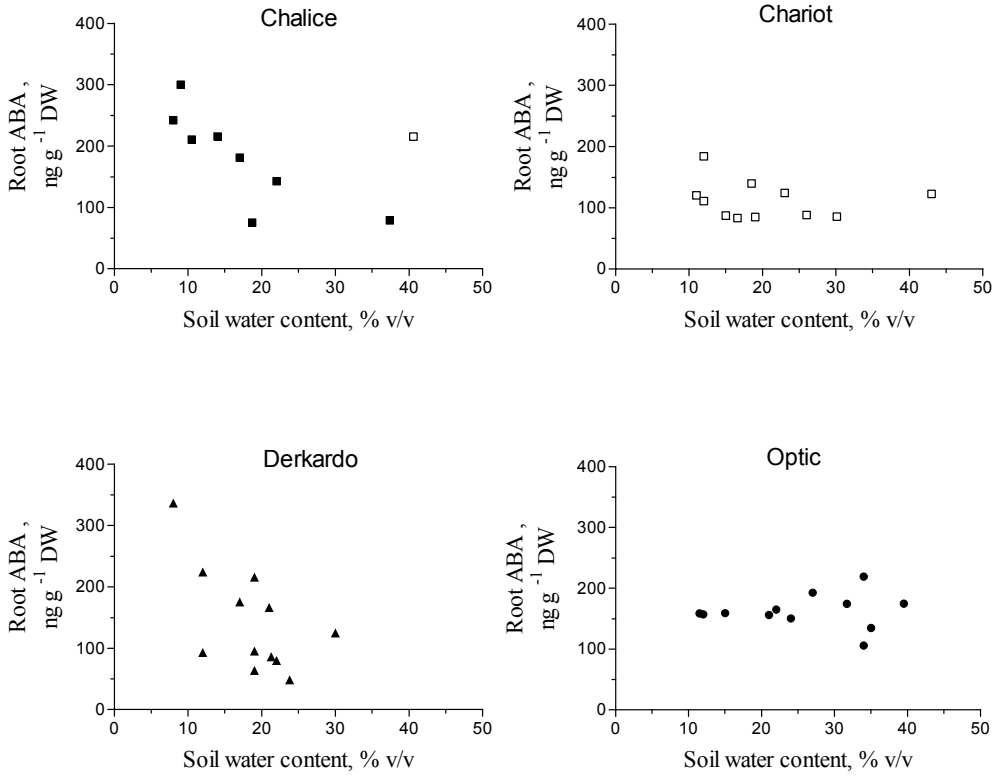


Fig. 2.8. Root ABA concentration at different soil water contents. Each point represents a single determination on a separate replicate plant. For Chalice, open square highlights an outlying point.

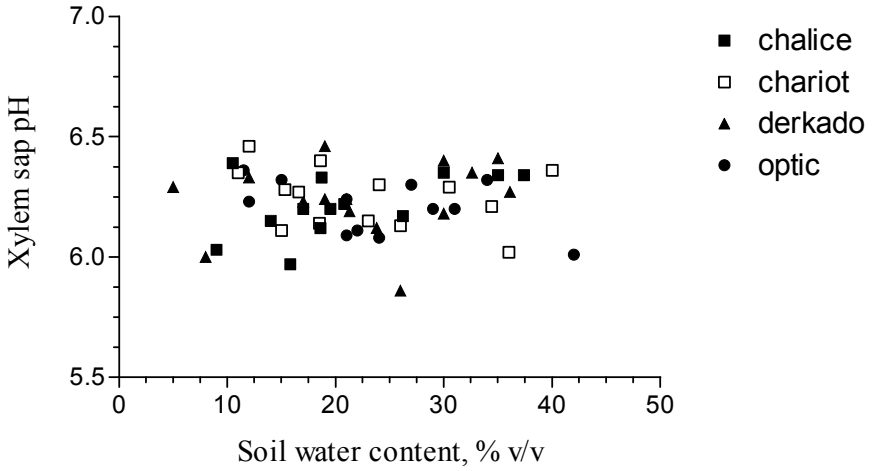


Fig. 2.9. pH of xylem sap expressed from excised leaves. Each point represents a single determination on a separate replicate plant.

## 2.4 Experiment 3 – Response to a drying top soil and deep water table

Preliminary experiments of ours have shown that barley is able to tolerate extreme drying of the topsoil without affecting stomatal conductance and net photosynthesis providing at least 50% of the root system is well supplied with water (i.e. soil moisture contents close to field capacity; data not shown). As such those varieties that either, establish deep roots more rapidly, have a greater plasticity of root growth so that compensatory root proliferation occurs in moist soil layers when the top soil dries, or have a more uniform distribution of roots down the soil profile reducing the possible production of chemical signals by roots in the drying soil, would be expected to exploit stored soil water more effectively as the top soil dries. In the following experiment, a system was designed (after Blum and Johnston 1993) that would discriminate between varieties that differ in one or more of the above characteristics. Plants were grown with water supplied throughout the soil profile, or only to the bottom 20%. From the results of experiment 1, we hypothesized that Chalice would be better able to exploit these deep supplies of water compared to Derkado, Chariot and Optic.

### Materials and methods

*Plant growth*

Plastic columns (10.5 cm internal diameter x 120 cm deep) were lined with PVC sleeves to facilitate in the removal of soil cores at the end of the experiment. The bottom 20 cm of the columns was packed with a loamy sand soil (appendix 2.2). A 5 cm deep layer of gravel (nominal diameter 5 mm) was placed on top of this soil layer. The gravel acted as a hydraulic barrier, preventing the conduction of water from the lower layer of soil into the upper layer, when water was supplied via the base of the column. Previous experiments of ours had shown that a gravel layer provides effective hydraulic isolation without restricting root growth between the soil sections. A 5 cm layer of sandy loam soil (appendix 2.2) was added next. This was to ensure the following loamy sand topsoil did not fill the pore spaces between the gravel and circumvent the hydraulic isolation between the top and bottom sections of the column. The top 85 cm of the columns were packed with the loamy sand to a dry bulk density of 1.35 g $cm^{-3}$. NPK fertilizer was applied at rates recommended for malting spring barley (90:50:50 kg $ha^{-1}$ NPK respectively). The columns were then watered to field capacity, and stood in 13 cm deep pots for three days to drain prior to transplanting the seedlings. The columns and pots were placed inside polythene bags that were sealed around the base of the column to prevent direct evaporation of water from the surface of the reservoir. The surface of the soil was also covered with a thin polythene sheet followed by a 2 cm deep layer of gravel, to prevent direct evaporation of water from the soil.

Seeds of spring barley (cv Chalice, Chariot, Derkado and Optic) were imbibed in aerated distilled water for eighteen hours, and then germinated on moist germination paper for four days at 20°C. Two seedlings were transplanted into each column to give an equivalent field density of 234 plants $m^{-2}$. A 10 cm diameter cylinder of green mesh (mesh size, 4 mm; manufacturers, Netlon) was placed around the plants in each column at GS 22 to simulate the shading effects in a crop canopy. The mesh cylinders were extended in height as the plants grew so that the top of the cylinder was 10-20 cm below the top of the plant.

The experiment was conducted in a heated glasshouse between December 2002 and April 2003. Supplementary light was provided by sodium lamps over a 16 hour photoperiod. Photon flux at plant height varied according to daily changes in sunlight, but was typically in the order of 400 - 450 μmol $m^{-2}$ $s^{-1}$ PAR during measurements of stomatal conductance. Daily maximum and minimum temperatures are shown in appendix 2.3. A malfunction of the RH sensor meant that RH was recorded only for the period 26-40 days after planting. Mean daily RH was 53% (VPD 1.02 kPa) and ranged from a minimum of approximately 40% RH during the day to a maximum of 60% at night.

During establishment plants were watered twice a week from the soil surface to maintain the soil close to field capacity. Irrigation treatments were imposed 26 days after planting, when the plants were at GS 30.

*Treatments*

At GS 30 each variety was subjected to two types of irrigation regime. Half the plants (controls) were watered twice a week from the soil surface (under the plastic sheet and gravel layer) to replace transpiration losses. The other half were supplied with water via the pots at the base of the column. The pots were filled with water to give a reservoir 8 cm deep. The reservoir was replenished at least twice a week to maintain the depth close to 8 cm. The hydraulic barrier within the columns meant that water was in free supply only 95 cm below the soil surface. Five replicates of each variety/irrigation combination were grown in a randomised block design. The quantities of water supplied were measured accurately and a water balance sheet kept for each column.

*Soil moisture contents*

Columns, including their pots (plus water reservoir in the case of water table treatments) were weighed to the nearest 0.02 kg at the start of the growing period, and then weekly throughout

to record transpiration losses and calculate irrigation requirements. In addition, one replicate of each variety/irrigation regime combination was fitted with four sets of 7 cm long wave guides at equidistant depths from the soil surface (15, 45, 75, 105 cm), and the soil moisture contents at each depth measured once a week, using Trease TDR equipment (Ele. International, Hemel Hempstead, UK).

*Stomatal conductance*

Midday stomatal conductance to water vapour was measured on the youngest fully expanded leaf using an LCA 4 infra red gas analyser fitted with a narrow leaf chamber (ADC Ltd, Hoddesdon, UK). Due to time constraints, these measurements were only made during the first five weeks after imposing the irrigation treatments.

*Harvest biomass and yield components*

Plants were harvested at grain maturity. From the end of grain filling to final harvest any senescent leaf tissue that was shed from the plants was collected and retained for inclusion in the total biomass measurements. Shoot tissue was severed from the root below the soil surface. Ears were cut from the straw and each fraction dried in a forced draft oven at 80$^{o}$C until constant weight. Ear number and grains per column were counted. Ears were threshed by hand and the weight of grain and chaff recorded.

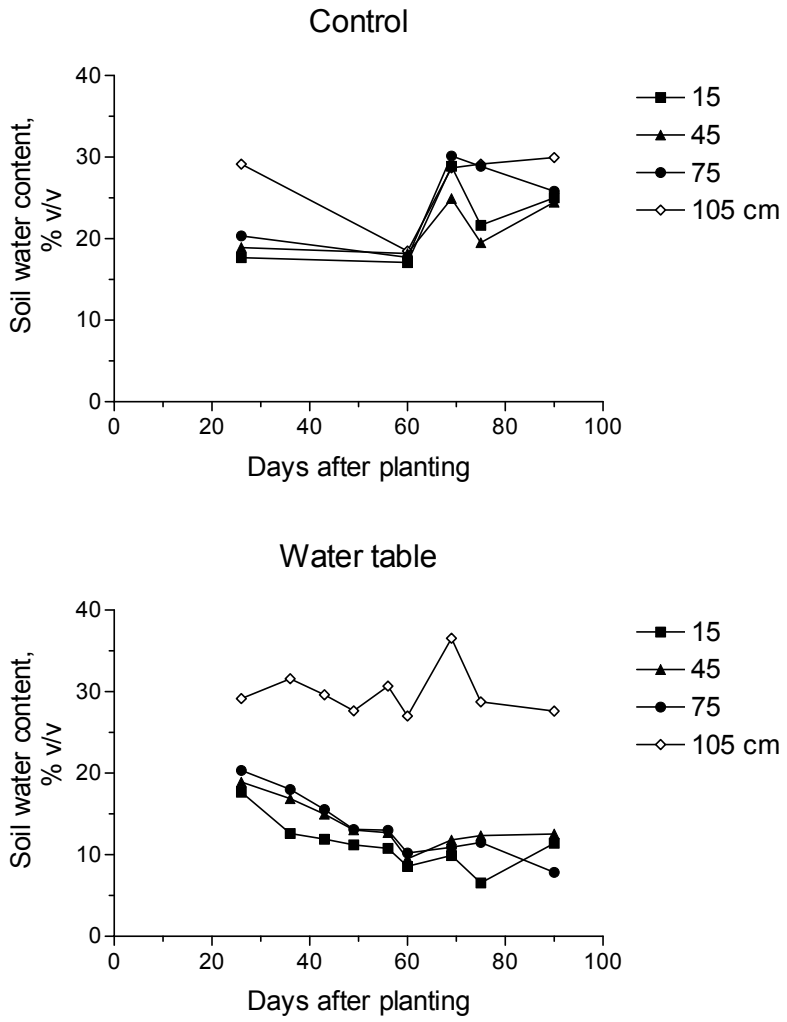


Fig. 2.10. Soil water content measured at 4 depths within the soil column. Controls were irrigated from the soil surface. From day 26 onwards, water table columns were supplied with water only to the bottom section (95-120 cm). Values are means across varieties of one replicate per variety.

**Results**

*Soil water content and transpiration*

The total amount of water transpired during the experiment did not differ significantly between varieties (Table 2.3). Thus the time courses for the soil moisture content of different soil layers and for the cumulative transpiration have been averaged over the varieties. The water table treated plants received their final irrigation from the soil surface 25 days after planting. From day 26, they were supplied with water only at the base of the column. Water was depleted most rapidly from the top of the soil as shown by the rapid decrease in soil water content at 15 cm (water table, Fig. 2.10), but the soil water content in all layers above the hydraulic barrier was reduced to around 10% v/v by day 60, which represents the complete extraction of PAW. Thereafter the soil water content in these layers remained relatively constant. The soil water content at 105 cm was close to field capacity (30% v/v) throughout the experiment. The large difference in soil water content measured at 105 cm compared to the layer above it at 75 cm, illustrates the effectiveness of the hydraulic isolation of the two layers. Direct measurements of root length and biomass were not made, but visual inspection at the end of the experiment showed that the plants had generated a significant amount of root tissue in the bottom section. In control columns, irrigated from the soil surface, the water content of all layers was maintained between field capacity and approximately 18% v/v (Fig. 2.10).

Measurements of stomatal conductance were made only for first 5 weeks after imposing the irrigation treatments. There was no significant difference between treatments for any of the varieties (data not shown). However, there was an indication that in Derkado, Chalice and Optic, the conductance was beginning to decline between day 55 and day 62 under the water table treatment compared to controls. These observations are consistent with the cumulative transpiration rates. Water-table plants transpired at a similar rate to controls until approximately day 62. Thereafter, the rate fell below that of controls (Fig. 2.11). By this time, each variety was at ear emergence (GS 59), with the exception of Chariot, which was at the late booting stage. There was some indication that on average Chalice might have transpired more rapidly than the other varieties especially during the early stages of the experiment, but variation between replicates was high and differences were not statistically significant (data not shown).

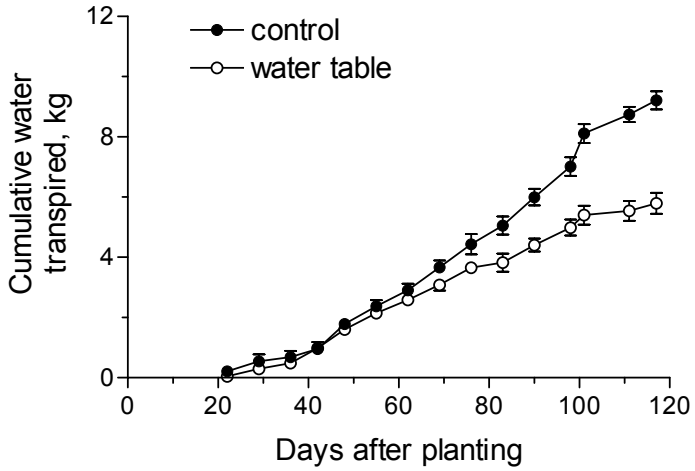


Fig. 2.11. Cumulative transpiration of spring barley grown with water supplied to the entire root system (controls) and to the layer 95 cm below the soil surface (water table). Values are means across varieties (± SE).

*Plant growth and yield*

Varieties differed ($P<0.05$) in their above-ground biomass at harvest (Table 2.1). When averaged over irrigation treatments, Chalice, Chariot and Optic had a comparable biomass, but that of Derkado was 16-23% lower. Restricting the supply of water to the upper part of the root system (water table treatment) reduced biomass production by 32%. There was no significant interaction between variety and irrigation regime indicating that the varieties did not differ in their response to the restricted water supply.

The ranking of varieties for grain yield was the same as that for biomass. In each irrigation regime, Chalice was the highest yielding followed, in order, by Optic, Chariot and Derkado. The yield differed by up to 48% between varieties, when averaged over irrigation treatments. The range was considerably larger than that found with biomass. The mean grain yield across varieties was reduced by 32% when the upper soil profile was allowed to dry, but as with biomass there was no significant interaction between variety and irrigation regime.

Harvest index (HI) followed the same ranking between varieties as biomass and grain yield, but irrigation regime had no significant effect on HI.

*Transpiration and transpiration efficiency*

Control plants transpired between 8.30 and 9.90 kg water during the course of the experiment, depending on the variety (Table 2.2). The average across varieties was 9.33 kg. This represents a mean transpiration rate of 9 mm $d^{-1}$. The high rate is indicative of the high evaporative demand in the glasshouse, resulting from warm temperatures and low relative humidity, coupled to a large leaf area. Confining the supply of water to bottom of the soil profile reduced the total amount of water transpired by nearly 40%. There was no significant difference between varieties in the amount of water transpired, nor any interaction between variety and irrigation regime. Similarly, the transpiration efficiency for biomass production (biomass produced per unit of water transpired) did not differ significantly between varieties or irrigation treatments, although it was slightly and consistently (i.e. for all varieties) greater in the water table treatment compared with controls. When, on the other hand, the transpiration efficiency was calculated on the basis of grain weight, the efficiency of Derkado was significantly lower than that of Chalice and Optic. This is a reflection of the lower HI of Derkado.

*Table 2.1. Final harvest biomass, grain yield and harvest index. WT refers to water table irrigation treatment. LSD are for P=0.05.*

| | Above ground biomass, g column$^{-1}$ | | | Grain yield, g column$^{-1}$ (100% DM) | | | Harvest Index | | |
|---|---|---|---|---|---|---|---|---|---|
| Variety | Control | WT | mean | Control | WT | mean | Control | WT | mean |
| Chalice | 21.98 | 16.92 | 19.45 | 10.38 | 7.89 | 9.14 | 0.47 | 0.46 | 0.47 |
| Chariot | 22.02 | 13.68 | 17.85 | 9.01 | 5.25 | 7.13 | 0.41 | 0.37 | 0.39 |
| Optic | 21.36 | 15.10 | 18.23 | 9.27 | 6.80 | 8.03 | 0.43 | 0.45 | 0.44 |
| Derkado | 18.75 | 11.37 | 15.06 | 6.04 | 3.72 | 4.78 | 0.32 | 0.32 | 0.32 |
| mean | 21.03 | 14.27 | | 8.68 | 5.91 | | 0.41 | 0.40 | |
| SED var | 1.189 (P=0.007) lsd 2.422 | | | 0.620 (P=0.000) lsd 1.261 | | | 0.068 (P=0.000) lsd 0.139 | | |
| SED irrig | 0.841 (P=0.000) | | | 0.438 (P=0.000) | | | 0.048 (P=0.650) | | |
| SED var x irr | 1.681 (P=0.552) | | | 0.876 (P=0.628) | | | 0.0967 (P=0.714) | | |
| rdf 32 | | | | | | | | | |

*Table 2.2. Cumulative transpiration and transpiration efficiency. WT refers to water table irrigation treatment. LSD are for P=0.05.*

| | Transpiration, kg $H_2O$ $column^{-1}$ | | | Transpiration efficiency (biomass), g DW $kg^{-1}$ $H_2O$ | | | Transpiration efficiency (grain), g DW $kg^{-1}$ $H_2O$ | | |
|---|---|---|---|---|---|---|---|---|---|
| Variety | Control | WT | mean | Control | WT | mean | Control | WT | mean |
| Chalice | 9.85 | 5.73 | 7.79 | 2.30 | 3.06 | 2.68 | 1.09 | 1.44 | 1.27 |
| Chariot | 9.90 | 5.56 | 7.73 | 2.23 | 2.62 | 2.43 | 0.91 | 0.96 | 0.94 |
| Optic | 8.30 | 5.90 | 7.10 | 2.58 | 3.06 | 2.82 | 1.11 | 1.37 | 1.24 |
| Derkado | 9.27 | 5.72 | 7.49 | 2.03 | 2.17 | 2.10 | 0.67 | 0.70 | 0.68 |
| mean | 9.33 | 5.73 | | 2.29 | 2.73 | | 0.94 | 1.12 | |
| SED var | 0.706 (P=0.399) | | | 0.387 (P=0.280) | | | 0.179 (P=0.007) lsd 0.365 | | |
| SED irrig | 0.499 (P=0.000) | | | 0.274 (P=0.116) | | | 0.127 (P=0.181) | | |
| SED var x irr | 0.999 (P=0.751) | | | 0.547 (P=0.878) | | | 0.253 (P=0.765) | | |
| rdf 32 | | | | | | | | | |

*Yield components*

The two plants per column in the control treatments, produced on average 10.6 ears between them (Table 2.3). Chalice, produced significantly less (8.2) than the other varieties. Under the water table treatment the average number of ears was reduced to 7.4, but here there was no difference between varieties. Thus there was a significant reduction in ear number with restricted watering in each variety except Chalice.

In contrast to its effects on ear number, the irrigation regime had no significant effect on the number of grains per ear in Chalice, Chariot and Derkado. In Optic, grain number per ear was *increased* by restricted watering. Grain number per ear differed markedly between varieties. Derkado was the most unusual, producing only 10 grains per ear.

The effects of irrigation regime on the total number of grains produced per column were largely a reflection of its effects on ear number. Although there was no significant interaction between variety and irrigation treatment on the total number of grains, restricted watering reduced grain number to a greater extent in Chariot and Optic than in Chalice and Derkado.

Mean grain weight was significantly reduced by restricted watering in Chalice and Derkado, but not in Chariot and Optic. There was a wide range in mean grain weight between varieties, particularly in the control irrigation regime. Chalice and Derkado had significantly higher mean grain weights under this regime than Optic and Chariot (Table 2.3).

*Table 2.3. Yield components. WT refers to water table irrigation treatment. LSD are for P=0.05.*

| | Ears column$^{-1}$ | | | Grains ear$^{-1}$ | | |
|---|---|---|---|---|---|---|
| Variety | Control | WT | mean | Control | WT | mean |
| Chalice | 8.2 | 7.8 | 8.0 | 23.7 | 21.3 | 22.5 |
| Chariot | 10.8 | 7.2 | 9.0 | 19.8 | 17.6 | 18.7 |
| Optic | 11.8 | 6.8 | 9.3 | 16.4 | 20.2 | 18.3 |
| Derkado | 11.6 | 7.8 | 9.7 | 9.7 | 10.5 | 10.1 |
| mean | 10.6 | 7.4 | | 17.4 | 17.4 | |
| SED var | 0.702 (P=0.115) | | | 1.048 (P=0.000) lsd 2.13 | | |
| SED irrig | 0.496 (P=0.000) | | | 0.740 (P=0.986) | | |
| SED var x irr | 0.993 (P=0.017) lsd 2.023 | | | 1.479 (P=0.017) lsd 3.01 | | |
| rdf 32 | | | | | | |

| | Grains column$^{-1}$ | | | Mean grain weight, mg (100% DM) | | |
|---|---|---|---|---|---|---|
| Variety | Control | WT | mean | Control | WT | mean |
| Chalice | 194.2 | 166.6 | 180.4 | 53.6 | 47.3 | 50.4 |
| Chariot | 213.2 | 128.4 | 170.8 | 42.6 | 40.0 | 41.3 |
| Optic | 193.2 | 137.2 | 165.2 | 48.3 | 49.2 | 48.7 |
| Derkado | 110.0 | 80.0 | 95.0 | 55.0 | 46.3 | 50.6 |
| mean | 177.7 | 128.1 | | 49.8 | 45.7 | |
| SED var | 13.27 (P=0.000) lsd 27.03 | | | 1.591 (P=0.000) lsd 3.24 | | |
| SED irrig | 9.39 (P=0.000) | | | 1.125 (P=0.001) | | |
| SED var x irr | 18.77 (P=0.129) | | | 2.249 (P=0.025) lsd 4.58 | | |
| rdf 32 | | | | | | |

## 2.5 Discussion

The productive conditions in experiment 1 resulted in large individual plants by the start of stem extension. Wide spacing within the growth cabinet, resulting in a low effective plant density, coupled with high light intensities over a long photoperiod, encouraged profuse tillering, leaf area and biomass production. However, there was relatively little variation in root or shoot traits amongst the eight genotypes studied.

Chalice produced the largest root system of all the genotypes in terms of total biomass and length (Fig. 2.2). This was mostly the result of a faster growth rate, since shoot biomass and green area were also significantly greater (Fig. 2.1). There was no significant difference between genotypes in their shoot:root ratio, but there was a tendency for Chalice to allocate slightly more biomass to the root system as it had the lowest S:R ratio of all the genotypes.

Specific root length (SRL) was remarkably consistent between genotypes, with the exception of Derkado (Fig. 2.2). Values are comparable with those reported for older varieties of spring barley (Atkinson 1989). In a study of 25 varieties, that included Proctor, Triumph, Goldthorpe and Karu, most had SRLs between 200 and 290 m $g^{-1}$, though the range was 133-635 m $g^{-1}$ (Atkinson 1989). In the present study, Derkado produced an SRL of only 115 m $g^{-1}$, just outside the range found by Atkinson (1989). Variation in SRL is often thought to reflect differences in the thickness of roots. However, the genotypic variation in diameter can be less than that in SRL, because differences in tissue density contribute to the variation in SRL (Atkinson 1989).

Some variation was observed amongst genotypes in the relative distribution of the root system down the soil profile. This occurred mostly in the top 30 cm (Fig. 2.3), with the commercial variety Optic and the landrace Dudiah locating a relatively greater proportion of their total length between 10 and 30 cm than the other genotypes. However, there was little difference between genotypes in root length in deeper soil layers, with the exception of Chalice, which had the greatest root length at depth owing to its greater overall growth rate (Fig. 2.4).

The lack of any detectable difference in depth of rooting and total root length between Dandy (the tall variety), B83, and some of the varieties possessing the sdw1 gene (Optic, Chariot and Derkado) suggests that the ari-e.GP and swd1 genes have little effect on root growth and distribution, at least under the conditions used in our experiments. Comparisons of semi dwarf and tall varieties of wheat have also found only minor differences in root size and distribution (Lupton et al. 1974; Miralles et al. 1997). In winter wheat, root growth in tall and semi-dwarf

varieties was similar; although there was some indication from $^{32}P$ labelling experiments that semi-dwarf varieties had a slightly greater root activity at depth (Lupton et al. 1974). In near isogenic lines of dwarf, semi dwarf and standard height spring wheat, dwarf lines produced a larger root mass and length than the other lines in some seasons, but the differences were largely confined to the upper 30 cm of the soil profile (Miralles et al. 1997). An increase in root mass in the surface layers, such as this, may be detrimental to productivity under drought conditions (Blum and Johnston 1993).

Inevitably the morphology of the shoot and root system found in screening experiments depends to a large extent on the growth conditions adopted (Wahbi and Gregory 1989a). However, the general ranking of genotypes for particular traits has been found to be reasonably consistent (Wahbi and Gregory 1989a). Thus in some studies the relative rooting depth of varieties in the field have been found to correlate with their root length in laboratory screening experiments on young vegetative plants (Hurd 1974), although the differences may be much smaller in the field compared to controlled environments (Wahbi and Gregory 1989b). As such we might predict from the results of experiment 1 that Derkado would be more sensitive to drought than the other commercial varieties because of its lower SRL and potentially poorer soil exploration. Similarly we might predict that Chalice would be relatively more drought tolerant because its more rapid root growth might result in a deeper final distribution of the root system. The hypothesis for Derkado is certainly consistent with field observations that Derkado is less well suited to light, drought prone soils (SAC and HGCA 1998). However, these predictions were not supported by the results from experiment 3 (discussed later). The overall response of a variety to drought will be determined by the integration of numerous physiological and morphological responses, any one of which may be more influential than another. For example, the benefit or disadvantage of any difference between varieties in root distribution may be offset by differences in sensitivity of stomata to increasing soil moisture deficits through variation in hydraulic or chemical signalling between roots and shoots.

The responses of stomata to soil moisture deficits, and the contribution of root-generated ABA to the response, were investigated in experiment 2. Plants were grown in large volumes of soil, but in relatively shallow pots so that the whole root system was exposed to relatively uniform soil drying. This was to separate any effect arising from differences in the variety's inherent capacity for root ABA production and root to shoot signalling, from those resulting from differences in root distribution. Each of the varieties studied responded similarly to soil drying. Stomatal closure commenced when approximately 50% of the PAW had been depleted (Fig. 2.5). This is consistent with field experiments on spring barley in which the

transpiration rate deviated from the potential rate also after 50% of PAW had been depleted (Day et al. 1978). Further, the stomatal conductance and net photosynthetic rate of leaves of well-watered plants differed little between varieties (Figs 2.5 and 2.6).

Roots of several species have been shown to accumulate ABA as their relative water content or tissue water potential falls (Tardieu et al. 1992, Kulkarni et al. 2000, Borel et al. 2001). In the present work, there was a clear inverse relationship between the soil moisture content and the bulk tissue ABA concentration for Derkado and, with the exception of a single outlying point, for Chalice. In contrast, Chariot and Optic whilst having comparable baseline ABA concentrations, failed to accumulate significant amounts of ABA as the soil dried (Fig. 2.8), and yet the response of stomatal conductance and net photosynthesis to soil moisture content was the same in each variety.

We can only speculate as to why there is not a more consistent relationship between stomatal conductance, root ABA and soil moisture content across our spring barley varieties. Stomata appear to respond to the concentration of ABA in the xylem sap, but the sensitivity of the response is dependent on other factors including the leaf to air vapour pressure difference and the composition and pH of the xylem sap (Tardieu et al. 1993, Davies et al. 2002). Increases in pH of the xylem sap of some species have been observed during soil drying and after nitrate deprivation (Davies et al. 2002, Dodd et al. 2003). However, no change in xylem sap pH was seen with any of the varieties studied here, over a wide range of soil moisture contents. So variation in xylem sap pH cannot explain why the stomatal response to soil drying is the same in Derkado, Chalice, Optic and Chariot in spite of their different root ABA concentrations. Other possible explanations include genotypic differences in the partitioning of ABA between bulk tissue and xylem sap. Optic and Chariot, may synthesise ABA at a lower rate than Chalice and Derkado, but deliver it more rapidly to the xylem, or ABA in the tissue may turn over more rapidly. Thus, they may accumulate less in root tissue, but as the soil dries, be able to raise the xylem ABA concentrations in the same way as the other varieties. Alternatively, the relative contribution of hydraulic and hormonal (ABA) signals to stomatal control may differ in the two groups of varieties, with Chariot and Optic being less dependent on a root-derived ABA signal than Chalice and Derkado.

In experiment 3, plants were grown with an unlimited supply of water, but the supply was located deep in the soil profile (below 95 cm). The rationale was that the experimental design would provide a means of identifying varieties with improved drought tolerance resulting from one or more of the following traits. 1) rapid root growth establishing an extensive root length density deep in the soil profile in advanced of any soil drying. 2) greater plasticity of

root growth so that greater proliferation of root growth occurs in moist soil layers as the topsoil dries. 3) more uniform root distribution resulting in less signalling from roots in the dry soil layers, and as such an ability to sustain a larger stomatal conductance and higher rate of transpiration (*cf* Blum and Johnston 1993). The results from experiment 1 indicated that Chalice had the greatest rate of growth, and thus may, potentially, be more tolerant of drought than the other varieties through the first mechanism listed above.

After ear emergence, plants whose water supply was confined to the bottom of the soil profile were unable to sustain transpiration at the same rate as control plants irrigated from the soil surface (Fig. 2.11). Measurements of leaf expansion were not made and stomatal conductance was measured only up to day 60, so it is not possible to determine whether a smaller leaf area or reduced stomatal conductance were primarily responsible for the slower transpiration rate. However, it seems likely that both were involved. Ear number at the final harvest was reduced which suggests that leaf area would have been lower because of the lower shoot number, and there was some indication of a gradual closure of stomata before day 60.

The lower transpiration rate when the water supply was confined to the bottom of the profile was associated a smaller total water use, biomass production and grain yield. But there was no significant interaction between variety and irrigation regime, which implies that none of the varieties had any particular advantage in terms of accessing more water or utilising the soil water more efficiently when water was available only deep in the profile. Transpiration efficiencies were low, but consistent with the high evaporative demand in the glasshouse. Typically, transpiration efficiencies increase as the evaporative demand falls (Richards et al. 2002). The lack of any significant difference between Chalice and the other varieties in water use and biomass production under restricted watering suggests that either the difference in rate of root growth seen in experiment 1 was less pronounced in experiment 3, or that it did not confer any particular advantage. Other factors may have offset the benefits of a more rapid rate of root growth, such as high root length densities in the dry topsoil, or lower plasticity of root growth in response to the localised water supply compared to the other varieties.

Although the varieties did not differ in their response to restricted water supplies in terms of grain yield, they did differ in their yield components. Ear number was the component most affected for Chariot, Optic and Derkado and this significantly reduced the number of grains produced per column. In contrast ear number in Chalice was unaffected by irrigation regime, although it is noteworthy that Chalice had a significantly lower ear number in the control irrigation regime compared to other varieties (Table 2.3). This is surprising as Chalice is

generally regarded as being a relatively high tillering variety (SAC and HGCA 1998). In field experiments on spring barley where drought was imposed during specific developmental stages, ear number was reduced by drought during stem extension and not earlier during the tiller production phase (Day et al. 1978). Thus it was enhanced tiller mortality that was responsible for the lower ear number (Day et al. 1978). In the same study, grain number per ear was affected mostly by drought during the period of spikelet initiation. In the present work, spikelet initiation would have been largely complete before the restricted watering regime was imposed which probably accounts for the lack of any significant reduction in grain number per ear. The greater number under the water-table treatment in Optic may have been a consequence of reduced competition for assimilates resulting from enhanced tiller mortality.

The mean grain weight was reduced in Chalice and Derkado, but not Optic and Chariot. The reduction in mean grain weight was associated with a smaller relative change in grain number per column in Chalice and Derkado. This implies that these varieties were source limited during grain filling; current photosynthesis and storage reserves were insufficient to fill their relatively larger grain number. These varieties also had the largest mean grain weight in plants irrigated from the soil surface (controls), suggesting they may have a larger potential grain weight than Chariot and Optic. Chariot and Optic on the other hand, had a more pronounced reduction in the number of grains to fill when irrigation was confined to the bottom of the profile. The lack of any change in mean grain weight with restricted watering implies that these varieties were sink limited during grain filling. Thus in spite of an anticipated (though not measured) reduction in rate of photosynthesis during grain filling, the rate in conjunction with remobilisation of storage reserves appears to have been sufficient to meet the requirements of the grain. Differences between varieties in their ability to remobilise stem reserves and to sustain high photosynthetic rates under drought may have also contributed. Chalice has a reputation in the industry for being at risk of high screenings under late season stress. The results presented here are consistent with these field observations.

When averaged over irrigation regimes, the yield of Derkado was significantly lower than that of the other varieties. This is partly in line with its earlier date of introduction and lower yield potential than the younger varieties, but it may not account for the scale of the difference. There was quite a large proportion of empty grains under both the well water and restricted watering regimes, and it is possible that this variety may be particularly sensitive to high temperature stress. The maximum temperature in the glasshouse exceeded 30$^{o}$C on days 78 and 79, which coincided with ear emergence, and again during early grain development (appendix 2.3). This could account for the significantly lower harvest index and grain weight

transpiration efficiency of Derkado compared with the other varieties under each irrigation regime (Tables 2.1 and 2.2).

### 2.6 Conclusions

In conclusion, results from the current experiments have demonstrated that there is relatively little variation in root characteristics amongst modern UK varieties of spring barley. No evidence was found that root traits of tall varieties, represented by Dandy, differ from those of semi-dwarfs. The faster growth rate of Chalice observed in experiment 1, was either not repeated, or did not confer any advantage over the other varieties in experiment 3 in terms of water capture from deep soil layers. Therefore, based on the limited number of varieties studied, there would appear to be little scope for improving yield on drought-prone soils by matching current varieties more effectively to soil conditions. However, the results do suggest that varieties differ in their stability of mean grain weight under drought. Although, screenings were not measured specifically, a more stable mean grain weight in particular varieties could have implications for grain quality, as screenings and specific weight might also be more stable.

# 3. Effects of Growth Regulators and Growth Promoters on the Response of Spring Barley to Soil Drying.

## 3.1 Introduction

Plant growth regulators (PGRs) are widely used in UK cereal production to reduce stem length and increase resistance to lodging. Most commercially available PGRs exert their effects through the inhibition of gibberellin biosynthesis, although ethephon (2-chloroethylphosphonic acid) releases ethylene within plant tissue which may have direct growth regulatory effects, in addition to disrupting tissue auxin concentrations. To reduce straw length, treatments are applied at the beginning of (e.g. chlormequat) or during the later stages of stem extension (ethephon and trinexapac ethyl). Earlier applications during tillering have been advocated to promote root growth and there is considerable interest amongst growers in using PGRs to improve the tolerance of crops to root lodging and drought (Humphries et al. 1967; De et al. 1982). In addition to the anti-gibberellin PGRs, there is a range of growth promoting substances on the market that are reported, by the manufacturers, to stimulate root growth.

However, independent evidence of the effects of PGRs and growth promoters on root growth is limited. Most studies have been conducted on young plants under controlled environment conditions (Cooke et al. 1983; Enam and Cartwright 1990; Guckert et al 1992; Rajala and Peltonen-Sainio 2001) or using unreliable root sampling techniques such as hand pulling (Humphries et al. 1967). There have been few studies in which root growth and resource (water and nutrient) capture have been measured in the field using robust sampling procedures that enable roots to be recovered efficiently from deep soil layers (Bragg et al. 1984). Cooke et al. (1983) reported that chlormequat chloride (CCC) application increased the root:shoot ratio in young winter wheat plants grown in hydroponics, but the effects on root growth *per se* were inconsistent. Chlormequat chloride plus choline chloride and imazaquin increased overall root length of winter wheat plants grown in vermiculite moistened with nutrient solution by 10% (Guckert et al 1992). Root surface area, biomass and root:shoot ratio were also increased. In contrast, CCC and ethephon had no significant effect on root biomass of spring barley, oats or wheat grown in pots of clay topsoil over sand (Rajala and Peltonen-Sainio 2001). In the same study, trinexapac-ethyl increased the root:shoot dry weight ratio in barley and wheat, but it was the result of a decrease in shoot biomass rather than an increase in root growth. However, measurements were made only 14 days after treatment and thus there may have been insufficient time for any growth effects to manifest themselves. Early

applications of CCC to field grown wheat in the UK increased the density of roots in spring, but the effects had disappeared by July. In winter barley, a small increase in the density of roots at soil depths of 40-80 cm was observed in July (Bragg et al. 1984).

There is clearly a need for more information on the effects of plant growth regulators and promoters on the root growth of crops under field conditions. In particular there is a need for measurements of their effects on root growth in deeper soil horizons where root length density can be limiting for water uptake.

The objective of experiments reported in this chapter was to investigate the effects of selected growth regulators and promoters on root growth of spring barley grown in the field and on the crop's response to drought. Three experiments were conducted. The first was a preliminary screen of four growth regulators/promoters to investigate their effects on root growth under controlled environment conditions. Its purpose was to identify treatments that might merit more detailed investigation in the field. Two treatments were taken through to the field where their effects on, root growth and distribution, canopy growth, water capture and yield were determined. The third experiment investigated the effects of the growth regulator/promoters on the response of spring barley to drought. This experiment was conducted in lysimeters under a rainshelter because it enabled greater control to be achieved over the crop's water supply.

The growth regulators and promoters were selected on the basis of their biochemical mechanism of action, and their reported effects on the growth of roots (Table 3.1). Moddus (Table 3.1) has been reported, by the manufacturers, to increase root mass and length in winter cereals (Anon 1995). There are no data available regarding its effects on the roots of spring barley, although some farmers claim that early, low rate applications can increase yield in the absence of lodging (J. Tatnell, Syngenta; personal communication). Meteor does not have a label recommendation for use on spring barley, but in view of its reported effects on the growth of wheat roots (Guckert et al. 1992) it was decided to include it as an experimental comparison. Route is marketed as a growth promoter to improve cereal establishment, increase yield, stabilise grain quality and improve rooting. In the USA, it is widely marketed as a tool for increasing drought tolerance of crops. FTC-1 is sold commercially for improving the root growth and yield of potatoes. It was included in here to determine its effects on cereal roots.

*Table 3.1. Growth regulators and growth promoters used in preliminary screen*

| Product | Active ingredient(s) | Manufacturer | Accepted/putative mechanism of action | Recommended uses |
|---|---|---|---|---|
| Moddus | Trinexapac ethyl | Syngenta | Inhibits gibberellin biosynthesis | Lodging control in wheat and barley |
| Meteor | Chlormequat chloride, choline chloride and imazaquin | BASF | Inhibits gibberellin biosynthesis | Lodging control in winter wheat |
| Route | ZC Technology - incorporating Zn and N complexes | Loveland Industries Ltd | Increases auxin concentrations & photosynthetic efficiency | Improved establishment, rooting, yield and grain quality of cereals |
| FTC-1 | Undisclosed | Dalgety | | Improved rooting and yield of potatoes |

### 3.2 Experiment 1 - Preliminary treatment screen

**Materials and methods**

*Plant growth and treatments*

PVC columns measuring 10.5 cm internal diameter by 100 cm deep were lined with PVC sleeves to facilitate the removal of intact cores of soil, and then packed with a sandy loam soil to a dry bulk density of 1.1 g $cm^{-3}$. Prior to packing, the soil was passed through a 2 mm sieve to remove stones. Fertilizer was applied at rates recommended for malting spring barley (N, P, K and Mg at 90, 50, 50 and 7 kg $ha^{-1}$ respectively). P, K and Mg were applied as top dressings before planting, N was applied after planting at GS 14.

Seeds of spring barley (cv Optic) were imbibed in aerated distilled water for eighteen hours, and then germinated on moist germination paper for four days at 20°C. Seedlings were transplanted, one per column, when their roots were approximately 4 cms long.

Appropriate rates and timings of growth regulators were determined after consultation with the manufacturers. Route (0.8 l /ha), Meteor (1.0 l/ha) and FTC-1 (30 l/ha), were applied at GS 12. Moddus (0.3 l/ha) was applied at GS 23. Controls were sprayed with the same volume of distilled water at GS 12. Treatments were arranged in a randomized block design, and growth regulators/promoters were applied using a hand held pump with a medium spray setting. The experiment was conducted in a controlled environment growth room. Temperature was maintained at 21 ± 1°C, and light supplied at a photon flux of 450-500 μmol $m^{-2}$ $s^{-1}$ PAR from PLL fluorescent lamps over a 16 h photoperiod. Humidity was not controlled, but ranged from 80-85% RH. The soil was irrigated three times a week, to restore the soil to field capacity. Excess water was allowed to drain from the columns. Plants were harvested at GS 31.

*Measurements*

At GS 31, shoots were severed from the roots and weighed fresh. The area of the leaf lamina area was then determined automatically using a WinDias leaf area measurement system (Delta-T Devices, Cambridge, UK). For measurement of roots, soil cores within PVC sleeves were removed intact from the columns, and stored at 4 °C for up to 3 days. Cores were cut into four 25 cm long sections, and soil was washed from the roots of each section by hand, over a 0.5 mm sieve. After separating live roots from dead roots and debris, root tissue was gently blotted dry and weighed fresh. The root sections were then frozen between moist tissue paper, and stored at –20°C to await analysis. Sections were defrosted at room temperature, sub

samples of known weight were spread in dishes of water, scanned on a flat bed scanner, and the digital images stored as tiff files. The images were then analysed using WinRhizo software (Regent Instruments, Inc. Quebec), which determined the total root length in the subsample. Data were analysed for statistical significance by oneway ANOVA using the software Minitab (Minitab Inc, USA).

**Results**

None of the growth regulator or promoter treatments significantly altered plant leaf area or shoot fresh weight compared to the untreated controls (Table 3.2). Moddus, Meteor and FTC-1 had no significant effect on the fresh weight or total length of roots produced over the time-scale of this experiment (Table 3.2). In contrast Route-treated plants had a significantly greater root fresh weight and root length (Table 3.2). The greater total root length was associated with an increase in each soil layer compared to controls (data not shown).

*Table 3.2. Effects of growth regulators and promoters on root and shoot growth. Values are means of 4-5 replicate columns (except FTC-1 root length where n = 2). Treatments followed by a different letter differ significantly (P<0.05) as shown by LSD.*

| Treatment | Leaf area, $cm^2$ $plant^{-1}$ | Shoot FW, g $plant^{-1}$ | Root FW, g $plant^{-1}$ | Root length, m $plant^{-1}$ |
|---|---|---|---|---|
| Control | 549 | 29.7 | 18.0 a | 380 a |
| Meteor | 579 | 30.3 | 16.4 a | 465 a |
| FTC-1 | 481 | 27.1 | 18.0 a | 334 a |
| Moddus | 473 | 20.3 | 13.4 a | 326 a |
| Route | 593 | 33.4 | 29.4 b | 688 b |
| *Significance* | ns | ns | P=0.012 | P=0.003 |

On the basis of the above results, Route showed the most potential for manipulating root growth. This treatment was, therefore, selected for further investigation in the field and in lysimeters subject to drought. Although Moddus had no significant effect on growth in the screening experiment, it was decided to include it in the field and lysimeter experiments to serve as a comparison treatment for Route and because of the interest shown in it by agronomists.

### 3.3 Experiment 2 - Effects of early applications of Moddus and Route on field crops

The main objective of this experiment was to test the hypothesis that root growth of spring barley can be modified significantly by early application of Moddus and Route to field-grown crops. A second objective was to conduct detailed measurements of the canopy to determine the physiological basis of any yield-enhancing effect these growth regulators/promoters may have.

**Materials and methods**

Field experiments were conducted at 3 sites, which differed in soil characteristics. Two of the fields were located on the same farm; the third was at a neighbouring farm approximately 1 mile away.

*Table 3.3 Site location*

| Site | Farm | Field no. | OS map ref |
|---|---|---|---|
| 1 | Charleton farm, Montrose | 12 | NO/72193/61174 |
| 2 | Charleton farm, Montrose | 7 | NO/71534/61142 |
| 3 | Borrowfield farm, Dubton, Montrose | 1 | NO/70415/60232 |

*Table 3.4. Soil texture*

| Site | Soil texture |
|---|---|
| 1 | Loamy sand to 35 cm, over lying sub soil of medium sand grading to coarse sand below 50 cm |
| 2 | Sandy loam to 45 cm over sandy loam subsoil, with a deeper layer of clay at approximately 80 cm |
| 3 | Sandy loam top soil to 40 cm relatively stone free, overlying medium sand |

Variations in soil physical properties, pH and depth were assessed by auger sampling before drilling. Crops of spring barley cv Optic were drilled within 2 weeks of each other. Plots (2 m x 16-18 m depending on the site), were marked out after the crop had established. Plots were

located where crop establishment and soil properties were relatively uniform. Route (0.8 l $ha^{-1}$) and Moddus (0.2 l $ha^{-1}$) were applied on the 1st May at growth stage 13/14 using a hand held Azo-sprayer with 2 m boom. Treatments were applied in a volume of 198 l $ha^{-1}$ @ 3 bar, with a medium spray quality. Control plots were walked, but not sprayed. Treatments were applied in early morning under humid conditions with a light breeze. A short spell of heavy rain occurred 5 hours after application. Treatments were completely randomised within 6 blocks. The experimental plots received the same husbandry as the commercial crop. Husbandry details are given in Appendix 3.1.

Extensive crop measurements were made at site 3 only. At site 1 some less detailed measurements were made on the canopy, and at all sites grain yields were recorded after combining.

*Crop measurements at site 3*

Plots were divided to give two sub-plots measuring 2 x 10 m. In each block one of the subplots was designated for destructive sampling, the other was used for combining. The arrangement of combining and sampling sub-plots was alternated from block to block.

*Canopy growth and crop biomass*

Four destructive samples were taken between Zadoks growth stage 14/15 and the end of anthesis (GS 69). Above ground biomass was harvested from 0.25 $m^2$ quadrats (0.5 x 0.5 m) for determination of fresh and dry weight. Plots from 4 blocks were sampled. Plant tissue was dried in a forced draft oven at 80°C for 48 h prior to measurement of dry weight. Light interception and leaf area index were measured on the same 4 blocks using a SunScan Canopy Analysis System (Delta T Devices, UK).

*Soil moisture content*

Volumetric soil moisture content was measured every week or two weeks to a depth of 1 metre using a Diviner capacitance probe. Access tubes were sunk in each plot in 5 of the 6 blocks after the plots had been treated with Route or Moddus. An additional tube was sunk in a guard plot for determination of field capacity. Plants within a radius of 1 metre from the tube were cleared, the soil soaked with water, and covered with black polythene sheeting. The soil moisture content was then measured at regular intervals for up to 7 days to follow drainage through the profile.

*Root and tiller measurements*

At GS31, 10 plants were taken at random from the quadrat samples and the number of tillers counted. The numbers of adventitious roots on the main stem and each of the tillers were also recorded. The same measurements were made at GS71 on plants carefully dug out of the soil to retain as much of the structural root length as possible. In addition, the spread and depth of structural roots was determined according to Berry et al. (1998).

At GS71 soil cores, 8 cm diameter, were taken to 1 metre using a petrol driven percussion hammer (Cobra, UK). The cores were divided into 10 cm slices and each slice placed in a separate polythene bag. In all two cores were taken from each plot; one from within a row of plants and one from between the rows. The cores were stored frozen at –20$^{o}$C prior to root extraction and analysis.

For a particular depth interval, the soil slices from the within- and between-row cores were defrosted and pooled. Roots were washed from the soil using an automatic root washer and collected on a 0.56 mm mesh. The root tissue was back-washed into a dish of water and dead roots and debris separated by hand and by floatation. Live roots were distinguished from dead roots by their elasticity (dead roots break easily when stretched or bent) and their paler colour.

Cleaned root samples were then spread in a dish of water and placed on a scanner. Images were saved as Tiff files and the length and diameter of roots measured using computerised image analysis. The quantity of roots in each of the top 3 slices was too great for reliable image analysis. Roots from these slices were therefore sub-sampled on the basis of fresh weight prior to scanning. After scanning, samples and sub-samples of roots were weighed fresh before drying at 80$^{o}$C for 48 h and reweighing.

*Flag leaf lifespan and crop height*

The time of flag leaf emergence was determined accurately by frequent visits (every 2-3 days) to the site. From then on the % green area of the flag leaf of 10 plants per plot was estimated in the field every 7 to 10 days, until complete senescence. At GS 75, crop height was measured from the soil surface to the tip of the awns at 10 locations per plot

*Rate and duration of grain filling*

After GS 71, 10 ears were harvested at random from each plot and their dry weight determined (including awns). The increase in ear dry weight was taken as a measure of grain filling. No distinction was made between main stem ears and tiller ears.

*Ear number, harvest index and combine yields*

Immediately prior to harvest, 10 shoots per plot were harvested at random, divided into ear and stem tissue and dried. Ears were weighed before and after hand threshing to remove the chaff. Ear densities were determined by counting the number of ear bearing shoots in a 0.5 m length of a row. Five rows were measured per plot.

Plots were combined on 17th August using a Claas small plot combine. Samples were taken for determination of moisture content.

*Sites 1 and 2*

At site 1 plots were divided into two sub-plots for combining and destructive sampling as described for site 3. LAI and light interception were measured, plus less frequent measurements of above ground biomass. Flag leaf lifespan was also determined as described above. No measurements were made at site 2 before harvest. Plots at sites 1 and 2 were combine harvested on the same date (17th August 2002) as site 3.

*Statistical analysis*

Data were analysed by ANOVA using the statistical software Minitab (Minitab Inc, USA).

**Results**

*LAI & light interception*

At site 3, LAI increased to a maximum value of 4.8 by the end of anthesis (GS 65/69) (Fig. 3.1). At site 1, the peak LAI was less (3.3) and was reached around 16 days earlier at GS 49. In each case there was no significant effect of Route or Moddus on the maximum LAI, or on the rate of development of the canopy. The SunScan Canopy Analysis system only provides an indirect estimate of LAI based on measurements of the amount of light intercepted by the crop and certain assumptions about canopy architecture. In our experience, estimates of LAI using this system agree reasonably well with direct measurements of green area index (GAI) up to anthesis. As the canopy begins to senesce, it will continue to intercept light, but an increasing proportion of it will be by dead and dying leaves. Thus values of LAI after anthesis will not be reliable estimates of the functional leaf surface or GAI.

At site 3, the canopy at its maximum size intercepted approximately 94% of the incoming light, whilst at site 1 it was only 85% (Fig. 3.2). As with LAI, there was no significant effect of Route or Moddus on % light interception at either site.

*Biomass & Radiation Use Efficiency*

By GS 69, the crop had accumulated an average of 720 g DW $m^{-2}$ at site 3 (Borrowfield) and 650 g DW $m^{-2}$ at site 1 (Charleton field 12). There was no significant effect ($P>0.10$) of Route or Moddus on above-ground biomass at either site (Fig. 3.3). Radiation use efficiency (RUE) is the amount of above ground biomass produced per unit of light energy intercepted. RUE has not been calculated, but since, at a particular site, there was no significant effect of the treatments on light interception (Fig. 3.2) or biomass production (Fig. 3.3) up to anthesis, then RUE must also have been unaffected.

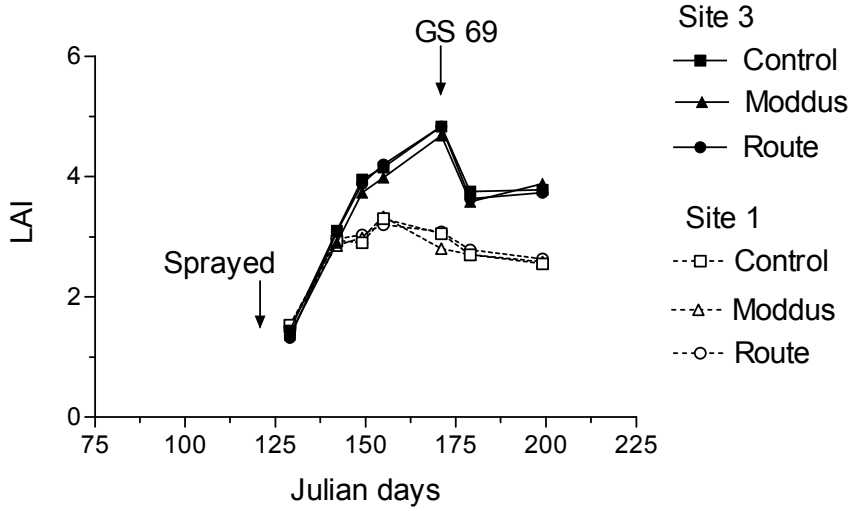


Fig. 3.1. LAI over time. Each point is the mean of 6 measurements on each of 4 replicate plots. Error bars omitted for clarity

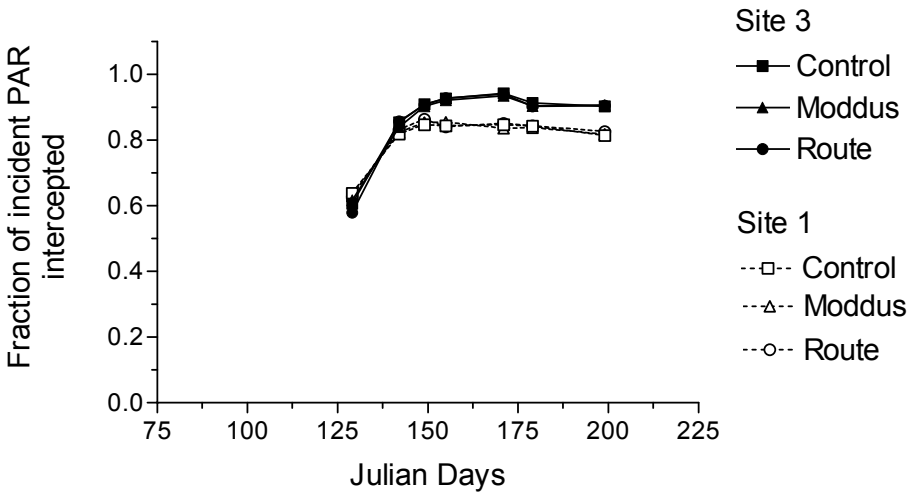


Fig. 3.2. Fraction of incident light (PAR) intercepted by the crop canopy. Each point is the mean of 6 measurements made on each of 4 replicate plots. Error bars omitted for clarity.

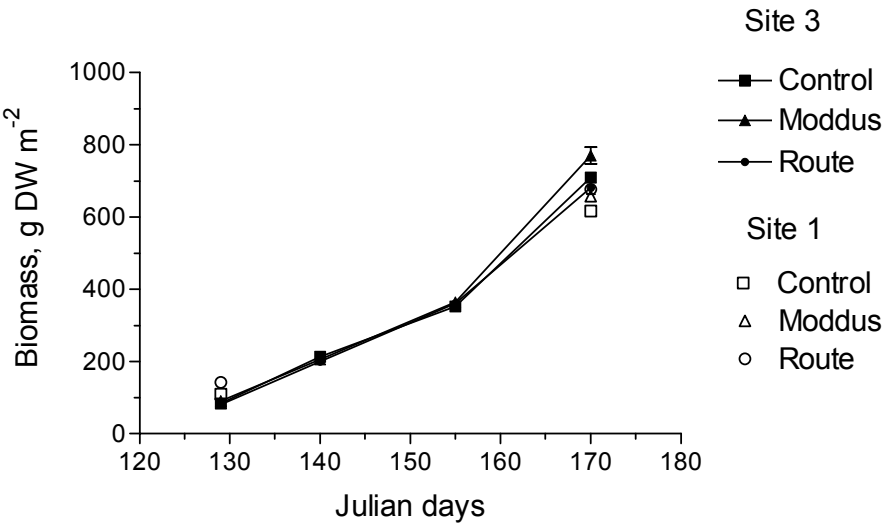


Fig. 3.3. Above ground biomass up to GS 69. Each point is the mean of 4 replicate plots. For clarity error bars omitted when symbols overlap.

*Tiller & adventitious root production*

At growth stage 31 the crop at site 3 (Borrowfield) had on average, 4.5 potentially fertile shoots per plant (main shoot plus 3.5 tillers; Table 3.5). The mean number of adventitious roots on the main stem was 5.9. The number on each of the tillers depended on the age of the tiller. The most recently emerged and hence smallest tillers had the fewest roots. Many of the T3 tillers had no adventitious roots. Tillers are named after the leaf axil from which they emerge (e.g. T3 is the tiller emerging from the axil of leaf 3) (Woodward and Marshall 1988). There was no significant effect of Route or Moddus on the number of tillers or on the number of adventitious roots produced.

Between GS31 and 71, a few emerged tillers died, leaving approximately 4 living shoots and 3 ears per plant in all treatments (usually the main shoot plus T1 and T2; Table 3.5). The number of adventitious roots on the main stem, T1 and T2 increased by 1 or 2 over this period, but was unaffected by Moddus and Route (Table 3.5). The living but non-ear bearing shoots, and the dead or dying shoots, at GS 71 rarely had roots. On average only 28% of these shoots possessed any adventitious roots; those that did generally had only 1 or 2 (data not shown). The anchorage strength of a cereal plant is influenced by the depth of the rigid portion of its adventitious roots and their spread. Route and Moddus had no effect on either of these characteristics of the root system (Table 3.6).

*Table. 3.5. Site 3 GS31 and GS 71. Effects of treatments on the number of emerged tillers and on the number of adventitious roots on the main shoot (MS) and the leading tillers (T1-T3). Values are means of 10 plants in each of 4 replicate plots ± SE of mean (n=4).*

| | | Control | Moddus | Route |
|---|---|---|---|---|
| GS 31 | | | | |
| No. tillers plant$^{-1}$ | | 3.5 ± 0.4 | 3.5 ± 0.2 | 3.5 ± 0.1 |
| No. roots on:- | MS | 5.9 ± 0.2 | 5.8 ± 0.2 | 5.7 ± 0.2 |
| | T1 | 3.3 ± 0.1 | 3.4 ± 0.2 | 3.3 ± 0.2 |
| | T2 | 2.0 ± 0.2 | 1.8 ± 0.2 | 1.7 ± 0.1 |
| | T3 | 0.3 ± 0.2 | 0.7 ± 0.1 | 0.4 ± 0.2 |
| GS 71 | | | | |
| No. roots on:- | MS | 8.1 ± 0.5 | 8.0 ± 0.3 | 7.8 ± 0.6 |
| | T1 | 4.5 ± 0.4 | 4.3 ± 0.4 | 4.8 ± 0.4 |
| | T2 | 3.5 ± 0.4 | 3.9 ± 0.4 | 3.3 ± 0.2 |

*Table 3.6. Site 3 GS71. Effects of treatments on the depth and spread of structural (adventitious) roots, number of living shoots and number of ears plant$^{-1}$. Values are means of measurements on 10 plants from each of 4 replicate plots. Differences between treatments not significant at P = 0.10.*

| Treatment | Root plate depth (mm) | Root plate spread (mm) | No. living shoots plant$^{-1}$ | No. ears plant$^{-1}$ |
|---|---|---|---|---|
| Control | 20.5 | 29.3 | 3.9 | 2.9 |
| Moddus | 19.6 | 31.2 | 4.0 | 2.9 |
| Route | 19.4 | 29.6 | 3.9 | 2.8 |
| SED, rdf 6 | 0.58 | 1.05 | 0.18 | 0.18 |

*Root system size and distribution*

The initial intention was to take soil cores to a depth of 1.2 m, but since very few roots could be seen by the naked eye below 70 cm, coring was stopped at 90 cm. The total biomass and root length of the crop, expressed per m$^2$ of ground surface, is given in Table 3.7.

*Table 3.7. Effects of treatments on crop root biomass and total root length at GS 71.*

| Treatment | Root biomass, g DW m$^{-2}$ | Root length, km m$^{-2}$ |
|---|---|---|
| Control | 130 | 22.7 |
| Moddus | 147 | 24.0 |
| Route | 152 | 26.0 |
| SED, 8df | 11.6 | 2.0 |

The general trend in total root system biomass and root length after treatment with Moddus and Route is in the direction expected from manufacturers' marketing literature, but the differences were not statistically significant (P>0.19).

The distribution of roots down the soil profile is shown in Figures 3.4 and 3.5. Over 97% of the root system was located in the top 50 cm of the soil. There was a steady reduction in both

root length density and root biomass with increasing soil depth. In the Route-treated, and to a lesser extent the Moddus-treated crops, the root length density and root biomass were greater between 20-30 cm than 10-20 cm. However the differences between treatments in the 20-30 cm layer were not statistically significant (P=0.111).

*Soil water*

The profile soil water content for the top 50 cm of soil shows a steady depletion of water during the experiment up to the final measurement at GS 85/87 (Fig. 3.6). The Route treated plots consistently had the highest water contents. The profile water content below 50 cm (50-100 cm) remained relatively constant at a value close to field capacity indicating that there was no appreciable water extraction from below 50 cm.

*Crop height*

The height of the crop at GS 75 was about 81 cm at site 3 (Table 3.8). It was shorter at site 1 (76 cm). There was no significant effect of Route or Moddus on crop height at site 3, but at site 1 the crop was increased slightly by Route ($P < 0.05$).

*Table 3.8. Effects of treatments on crop height. Height was measured in cm from the soil surface to the tip of the awns at GS 75. Values are means of 10 sampling points in each of 4 replicate plots per treatment.*

| | Site 1 | Site 3 |
|---|---|---|
| Control | 75.3 | 81.2 |
| Moddus | 75.8 | 81.4 |
| Route | 76.6 | 81.0 |
| SED, 6 df | 0.36 | 0.50 |

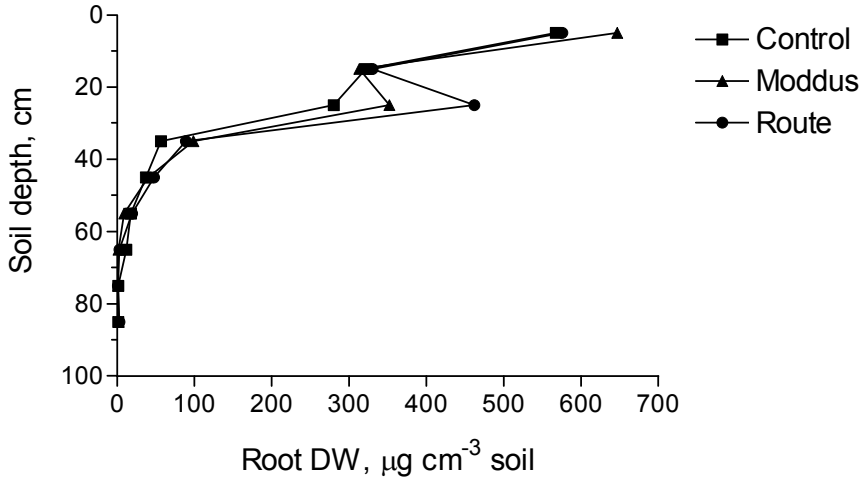


Fig. 3.4. Effect of treatments on the distribution of root biomass down the soil profile. Values are means of cores from 5 replicate plots. SE omitted for clarity

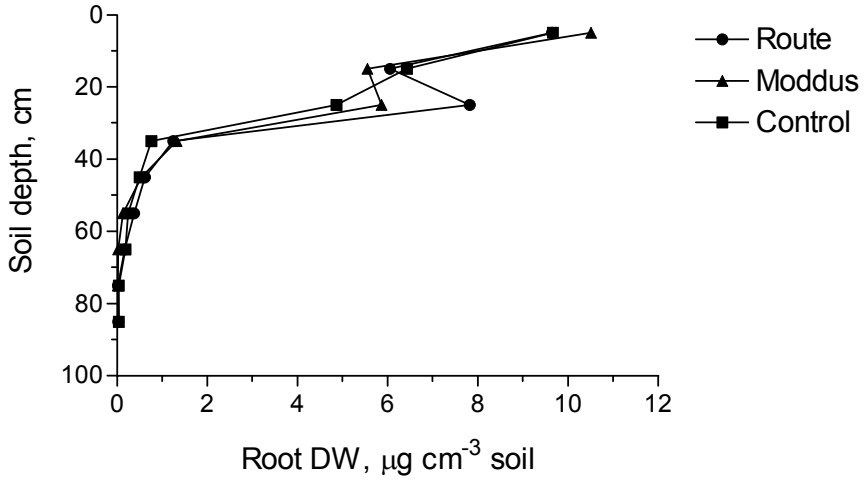


Fig. 3.5. Effect of treatments on the distribution of root length density down the soil profile. Values are means of cores from 5 replicate plots. SE omitted for clarity.

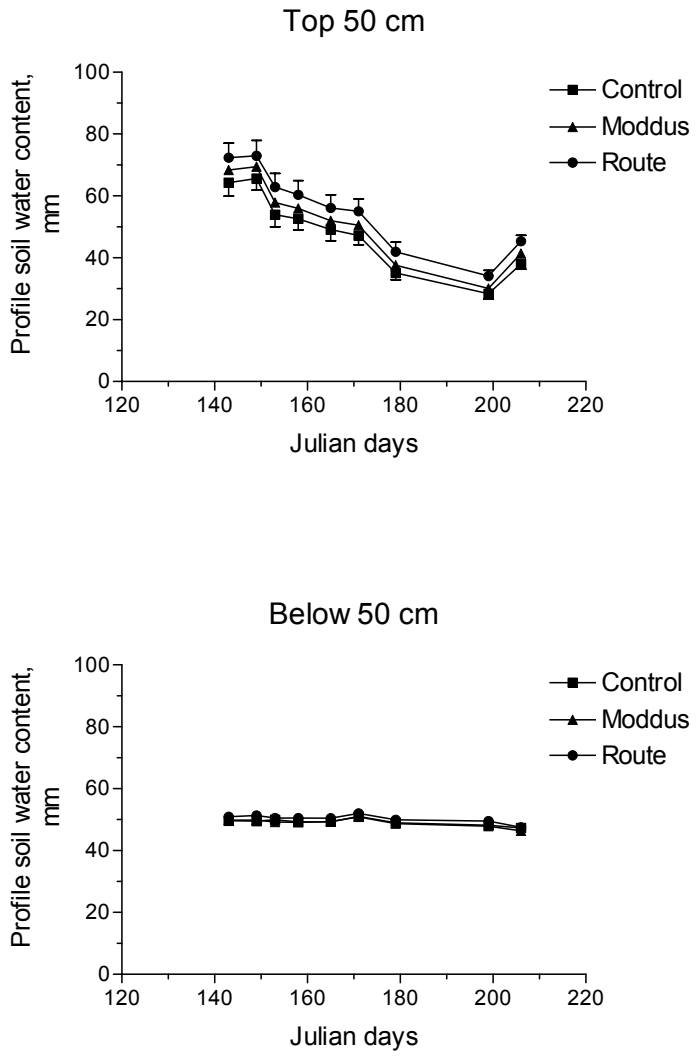


Fig. 3.6. Soil water content in top 50 cm of the soil profile and between 50 and 100 cm. Below 50 cm error bars omitted for clarity.

*Flag leaf lifespan*

The time period from flag leaf emergence to 50% green area was approximately 3 days less at site 1 compared to site 3, indicating that the leaf lifespan was less at this site (Fig. 3.7). There was no significant effect of Route or Moddus on the lifespan of the flag leaf at either site.

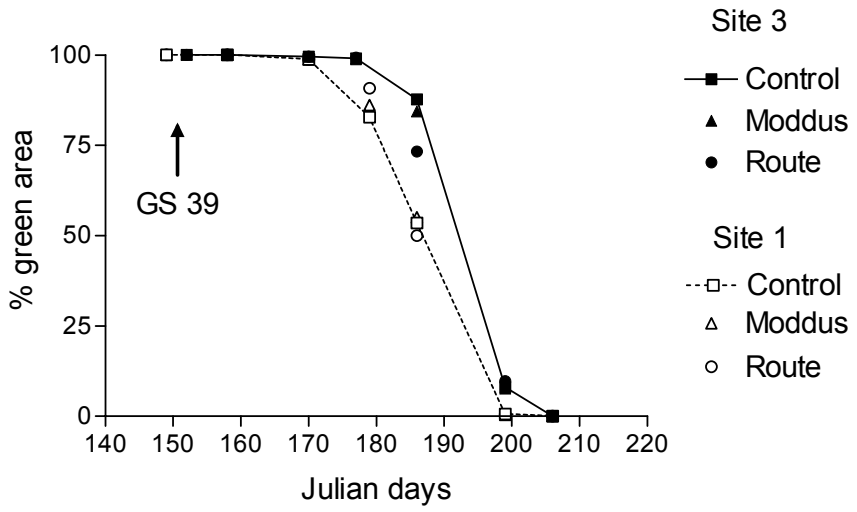


Fig. 3.7. Effects of treatments on the percentage green area of the flag leaf. Each point is the mean of 10 shoots in each of 4 replicate plots. For clarity error bars are omitted and lines shown only for controls.

*Grain filling*

Ear dry weight was measured at weekly intervals to provide an index of grain filling. The duration of grain filling was comparable at the two sites. Ear weight increased at a similar rate during the initial period of grain filling, but the rate was lower at site 1 during the middle to late stages, resulting in a lower final weight at maturity (Fig. 3.8). There was no clear effect of Route or Moddus on either the rate or duration of grain filling.

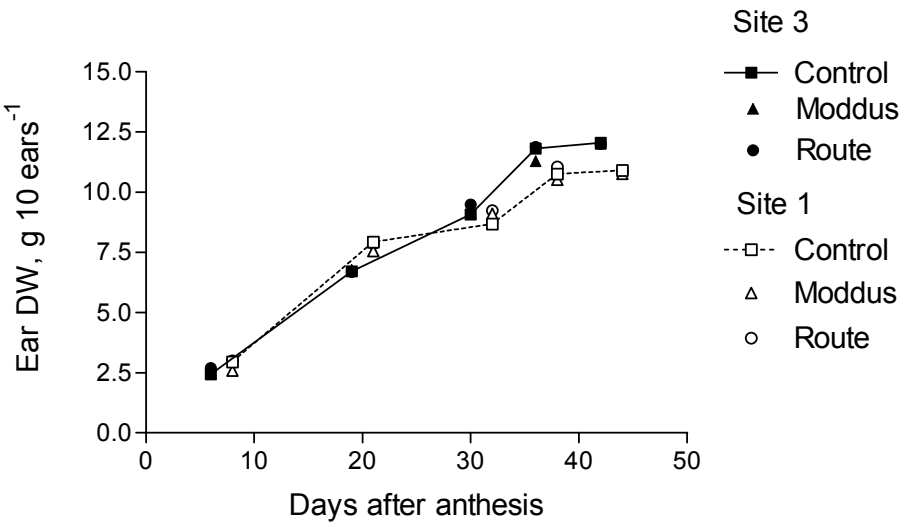


Fig. 3.8. Ear growth with time after anthesis. For clarity lines only shown for controls and SE omitted.

*Grain yield, ear population, and harvest index*

Yields differed significantly between sites, with site 1 giving the lowest yield and site 3 the highest (Table 3.9). There was no significant effect of treatment on the grain yield. Similarly, the treatments had no significant effect on the number of ears per $m^2$, or on the harvest index (Table 3.10). The ear population was appreciably higher at site 3 compared to site 1.

*Table 3.9. Combine harvested grain yields t $ha^{-1}$ @ 85% DM. Values are means of 6 replicate plots per site.*

| Treatment | Site 1 | Site 2 | Site 3 | mean |
|---|---|---|---|---|
| Control | 4.94 | 5.68 | 6.93 | 5.85 |
| Moddus | 5.17 | 5.74 | 7.00 | 5.97 |
| Route | 5.25 | 5.78 | 6.92 | 5.98 |
| mean | 5.12 | 5.73 | 6.95 | |
| SED site 0.069; SED treat 0.069; SED site x treat: 0.120; 45 rdf | | | | |

*Table 3.10. Effects of treatments on ear population and harvest index (HI).*

| Treatment | Site 1 | | Site 3 | |
|---|---|---|---|---|
| | Ears $m^{-2}$ | HI | Ears $m^{-2}$ | HI |
| Control | 562 | 0.58 | 958 | 0.59 |
| Moddus | 514 | 0.57 | 968 | 0.59 |
| Route | 586 | 0.57 | 900 | 0.59 |
| SED, rdf 6 | 26.5 | 0.008 | 62.2 | 0.006 |

## 3.4 Experiment 3 - Effects of Moddus and Route on the growth and water relations of spring barley subjected to drought

### Materials and methods

#### Lysimeter construction and crop growth

A rain shelter with a ground area of 35 $m^2$ was constructed from a polytunnel frame. The shelter was 4 m high at its centre, and the top surface and the top third of the sides of the shelter were lined with a transparent skin (720 gauge UVIEVA polythene with UV stabilizer and 91% transmission of the photosynthetically active radiation). The open sides were approximately 1.75 m high; sufficient to prevent rain falling on the lysimeters located in the centre of the floor area, whilst allowing good air movement over the crop. The shelter was protected with bird netting.

The lysimeters were constructed of PVC pipe 120 cm long with an internal diameter of 30 cm. The bottom of each pipe was covered with polythene sheeting, which was pierced to allow the drainage of water. A 5 cm deep layer of gravel was poured into the bottom of each lysimeter to facilitate drainage. Sixty-six lysimeters were then packed to a depth of 45 cms from the top surface with a loamy sand (dry bulk density 1.4 g $cm^{-3}$). This zone of soil was then well watered and left to settle for two days. A 40 cm layer of sandy loam was then added (dry bulk density 1.1 g $cm^{-3}$). The soils had low take-all risks, having not been farmed for over two years (the last crop being oilseed rape). Detailed soil chemical and particle size analyses are presented in appendix 2.2.

Fertilizer was added to the soil at the recommended rates for malting spring barley (NPK of 90:50:50 kg $ha^{-1}$ respectively). It was added to the sandy loam layer in two aliquots of solution, at depths of 9 and 22 cm. This was to ensure the fertilizer was well mixed in the lysimeter-equivalent of the plough layer. A 2 cm deep layer of sieved (2 mm mesh) sandy loam was then added to form a fine seed bed. Lysimeters were saturated with water and left to drain for two days prior to sowing. The crop was sown at a depth of 2 cm on 3rd April 2002, at a density of 430 seeds $m^{-2}$. The high density was to ensure there was rapid canopy development and sufficient plants to dry the soil effectively, even if the evaporative demand was atypically low.

The experimental design was factorial; 3 growth regulator treatments (Moddus, Route and Controls) each with and without irrigation. Treatments were arranged in a randomised block.

Ten replicates of each treatment were used, four of which were utilised for the destructive measurements of leaf water potential, and ABA quantification, and six of which were carried through to yield.

Moddus (0.2 l $ha^{-1}$), Route (0.8 l $ha^{-1}$) and distilled water (controls) were applied at GS 14, using a hand held pump set with a medium spray. Moddus was applied at an earlier growth stage than in the preliminary experiment following recommendations from the manufacturers (Jason Tattenall, Syngenta personal communication). After the treatments were applied, lysimeters were irrigated with 14 mm of water, every second day, for six days, to ensure that chemicals on the surface were washed into the soil. Water was withheld from non-irrigated treatments thirty seven days after planting, when the crop was at GS 21.

All crops were subjected to a prophylactic fungicide programme consisting of Opus (0.3 l $ha^{-1}$) plus Corbel (0.4 l $ha^{-1}$) at GS 22, and then again 4 weeks later; followed by Amistar (0.4 l $ha^{-1}$) plus Unix (0.4 l $ha^{-1}$) at GS 40.

*Soil moisture contents and PAW*

Volumetric soil moisture contents were recorded weekly at depths of 10; 25; 50; 80; 100 cm using a TDR Trease soil moisture measurement system (Ele International, Hemel Hempstead, UK), fitted with 17 cm long waveguides. Waveguides were permanently installed in 5 lysimeters per treatment and had been calibrated for the specific soils. Irrigated crops were re-watered twice a week so that the lysimeters were brought up to approximately 85% of field capacity. Field capacity values were determined by saturating four additional unplanted lysimeters with water, covering the soil surface with a plastic sheet to prevent evaporation, and monitoring soil water contents during and following drainage. The permanent wilting points of the soils were determined by withholding the water from a further two densely planted columns, and measuring how dry the soil became in the densely rooted zones of top and sub soil. Values corresponded well with those recorded in laboratory experiments, and also with published values for these soil textures (Bailey 1990; Rowell, 1994). PAW of the soil was estimated according to Bailey 1990 assuming good structural conditions in the subsoil and a topsoil depth of 42 cm.

*Net photosynthesis and stomatal conductance*

Stomatal conductance to water vapour and net photosynthesis were measured once a week (commencing 68 days after sowing, at GS 45), on leaf 2 using an ADC LCA 4 infra red gas analyser (Analytical Development Company Ltd., Hoddesdon, UK) fitted with a narrow leaf chamber. This leaf was selected in preference to the flag leaf because of its larger size.

Measurements were made 2 h either side of midday on 1-2 plants from each of 6 replicate lysimeters per treatment.

*Leaf water potential and stem base ABA*

Leaf water potential of leaf 2 was measured once a week, on three replicates, using a SKPM 1400 pressure chamber (Skye Instruments, Powys, UK) following the procedure described by Turner (1981). We were unable to extract sufficient xylem sap for determination of its ABA concentration. Instead bulk tissue ABA concentration in the stem base was determined. After the measurement of water potential on an individual leaf had been completed, an approximately 6 cm length of the shoot base of the same plant was excised, quickly frozen in liquid nitrogen, and then stored in a freezer at -80 $^{o}$C before freeze drying for ABA analysis. Leaf water potential measurements and tissue sampling for ABA analysis were conducted within 2 h of midday. ABA was determined as described in section 2.4.

*Growth and yield data*

Mean plant height and tiller numbers per plant were recorded at GS 39. The progress of flag leaf senescence was recorded from GS 39 onwards using a visual scoring system. Six plants in each of 6 replicate lysimeters were assessed three times a week, and the percentage of the leaf area that was visibly yellow was noted.

Four replicate lysimeters were harvested at growth stage 59, and the green areas of the leaves, stems and ears were measured using a WinDias leaf area measurement system (Delta-T Devices, Cambridge, UK). The dry weight of the same fractions was determined after drying tissue in a forced draft oven at 80$^{o}$C until constant weight.

The final harvest was at crop maturity. Above ground biomass was harvested and separated into ears and stems plus the remaining leaf tissue. Tissue was dried at 80$^{o}$C until constant weight was achieved and the weight of each fraction recorded. The numbers of grains per ear were then counted on a sub sample of 10 plants per lysimeter before hand threshing and determination of mean grain weight.

**Results**

*Soil moisture deficits*

Water was withheld from the unirrigated lysimeters on day 37. A technical fault was experienced with the TDR measurement system that meant measurements of soil moisture content were delayed for about 3 weeks. The first measurement after withholding water was on day 62, by which time crops had depleted between 63-70 mm of the available soil water depending on the growth regulator treatment (Fig. 3.9). The estimated PAW of the columns was 132 mm, thus approximately 50% of PAW had been depleted by this time.

There was no discernable effect of Moddus or Route on the rate of soil moisture depletion and the final SMD reached did not differ significantly from controls ($P>0.05$). If 50% depletion of PAW is taken as the onset of water stress, then the crops were droughted from about growth stage 37/39 onwards. Irrigated lysimeters had SMDs maintained well below 50 mm (<50% PAW depleted).

*Stomatal conductance and photosynthesis*

There was a small reduction in stomatal conductance ($g_s$) of irrigated crops over the course of measurements (day 68-106 after sowing, Fig. 3.10) This was apparent in controls and plants treated with Moddus and Route. The stomatal conductance of non-irrigated crops also declined, but to a greater extent than irrigated crops. By day 106, $g_s$ was approximately 25-30% of that of irrigated crops depending on the growth regulator treatment. There was some indication that Route may have delayed stomatal closure as the soil dried compared to controls and Moddus-treated plants. A significant reduction in $g_s$ relative to irrigated crops was observed only on day 106 (Fig. 3.10c). For controls and Moddus-treated crops, significant reductions were observed earlier (Fig. 3.10a and b).

When the relative $g_s$ ($g_s$ non-irrigated/$g_s$ irrigated) was plotted against the SMD for unirrigated crops, the apparent delay in stomatal closure of Route treated plants was further highlighted. At a comparable SMD of 110 mm, relative $g_s$ of Route-treated crops was greater than controls or Moddus-treated crops (Fig. 3.11). The data suggest that stomatal closure was elicited at an SMD of around 85 mm for Moddus-treated and 98 mm for Route-treated crops. This represents thresholds of approximately 64 and 74% PAW-depleted respectively. A threshold for controls is more difficult to determine, largely because of the temporal variation in $g_s$ of irrigated crops (Fig. 3.10a) and its effect on relative $g_s$, but the threshold probably falls somewhere between 60 and 74% PAW (80 and 98 mm SMD).

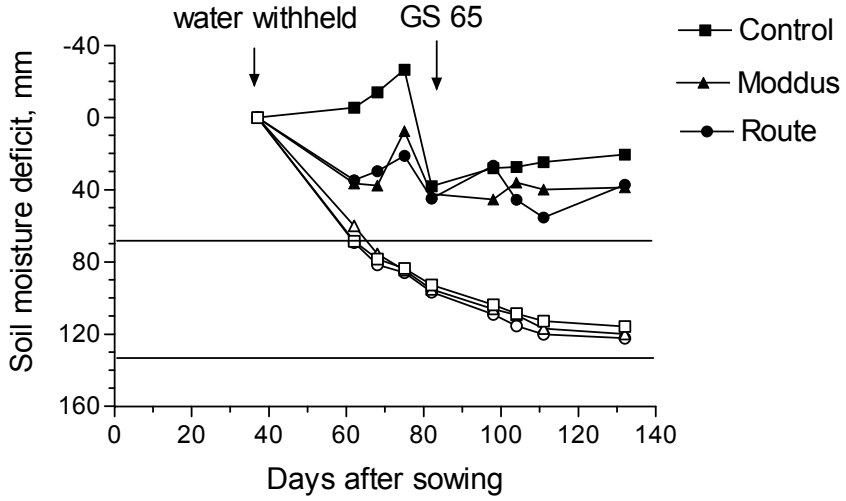


Fig. 3.9. Soil moisture deficits over time. Closed symbols are for irrigated- and open symbols for unirrigated crops. Horizontal lines represent SMD at 50% depletion of PAW (upper line) and 100% depletion of PAW (lower line). Values are means of 5 replicate lysimeters; error bars omitted for clarity. Arrows indicate time of imposing drought and Zadoks growth stage 65.

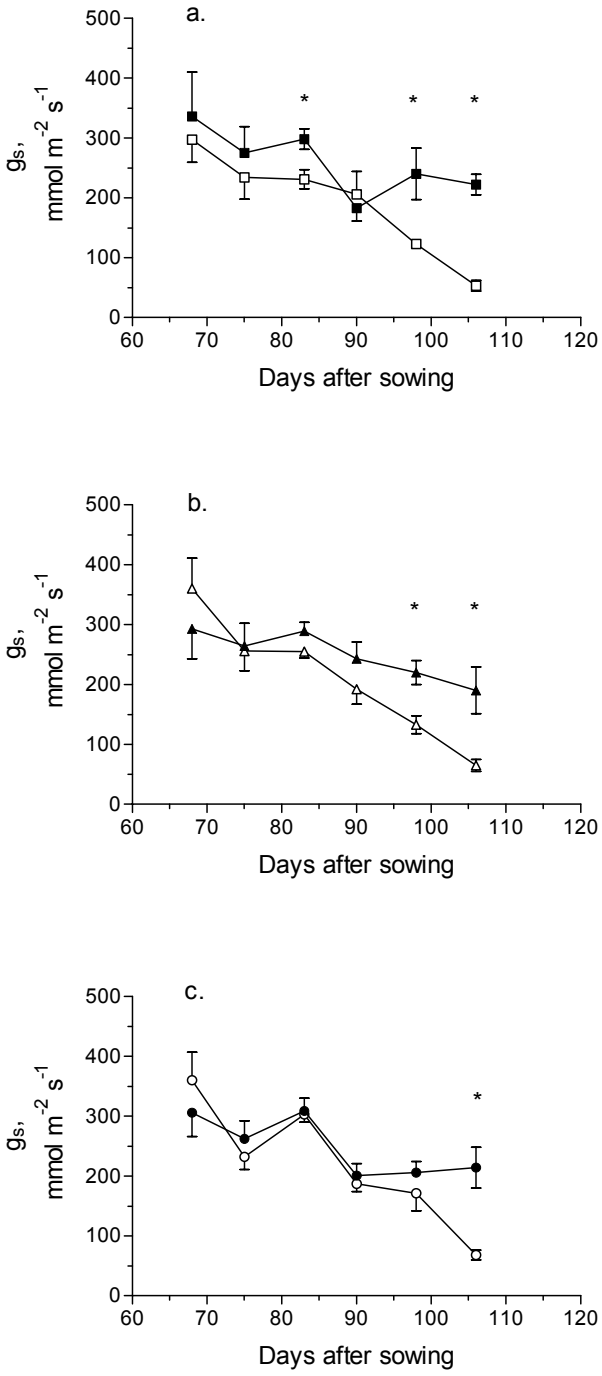


Fig. 3.10. Stomatal conductance to water vapour of leaf 2; a) Controls, b) Moddus and c) Route-treated crops. Closed symbols are irrigated crops, open circles are unirrigated. Points are means ± SE. * indicates means significantly different at $P<0.05$.

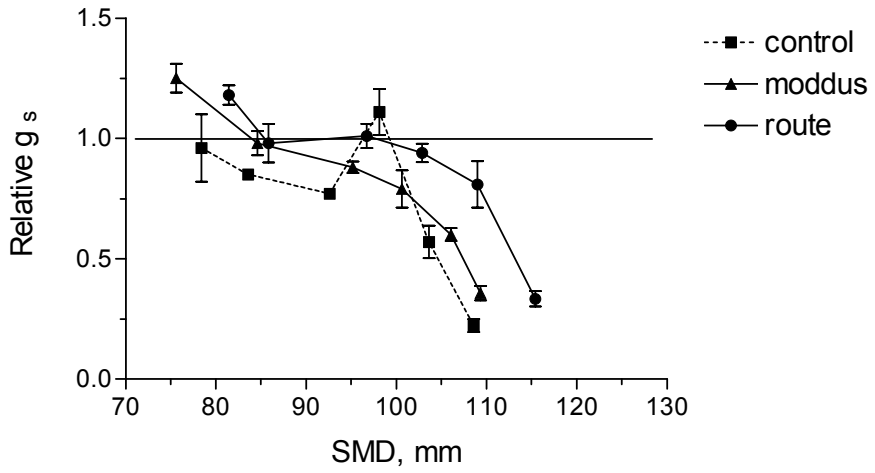


Fig. 3.11. Stomatal conductance of unirrigated crops as fraction of irrigated crops. Points are means ± SE. Horizontal line at relative $g_s$ of 1.0 shown for reference.

In irrigated controls the rate of photosynthesis of leaf 2 declined from approximately 19 μmol $m^{-2}$ $s^{-1}$ 68 days after sowing to 7 μmol $m^{-2}$ $s^{-1}$ at the final measurement on day 106 (Fig. 3.12). The decline may be the result of both environmental controls and the effects of leaf ageing. The same pattern was observed in irrigated Moddus- and Route-treated crops, and on any particular date rates were comparable with those of controls. The effects of drought on photosynthesis tended to follow those on stomatal conductance. Thus, the rate was reduced below that of irrigated crops earlier in controls and Moddus-treated crops than crops treated with Route.

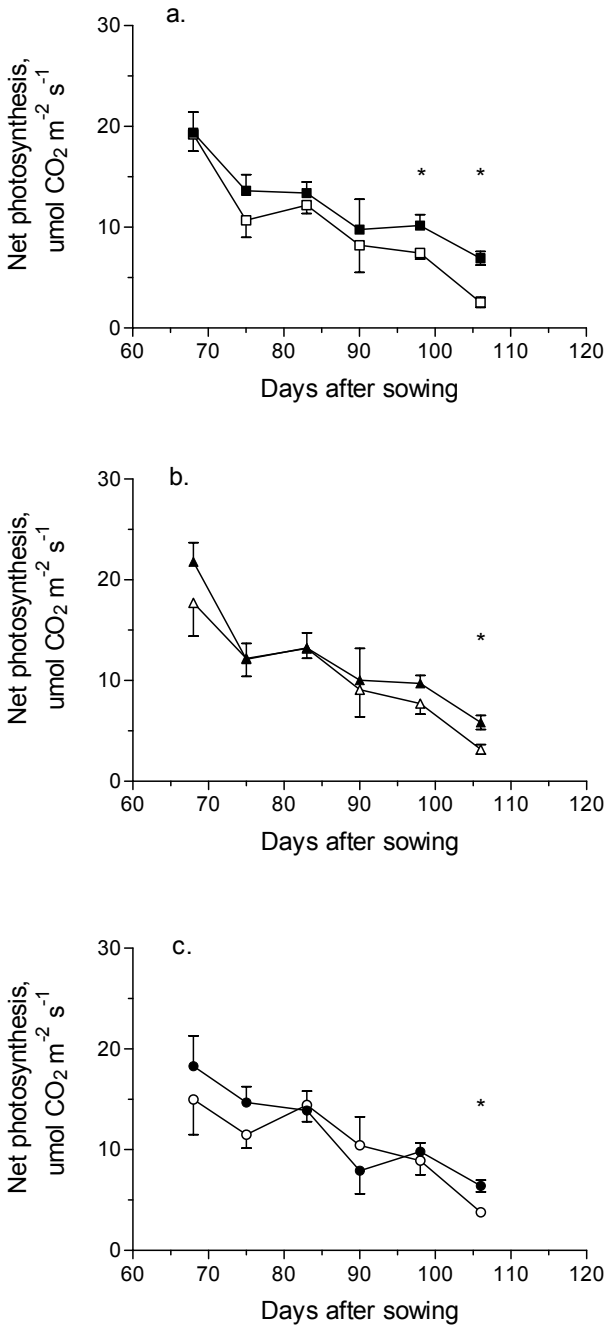


Fig. 3.12. Net photosynthetic rate of leaf 2; a) Controls, b) Moddus and c) Route-treated crops. Closed symbols are irrigated crops, open circles are unirrigated. Points are means ± SE. * indicates mean for unirrigated crops significantly lower than irrigated crops at $P<0.05$.

*Leaf water relations*

The midday water potential of leaf 2 of irrigated crops ranged from –1.0 to –1.4 MPa irrespective of the growth regulator treatment (Fig. 3.13). In droughted crops, the same pattern of water potential was found in controls, Moddus- and Route-treated plants. It fell to its lowest value (< –1.5 MPa) 83 days after sowing before returning to values similar to irrigated crops by day 106. The lowest potential coincided with a period where SMD was large and stomatal conductance relatively high ($g_s$ broadly comparable to irrigated crops). The restoration of the water potential to values found in irrigated crops was associated with the closure of stomata (reduction in $g_s$) (Figs 3.13 and 3.10).

*Stem base ABA concentrations*

Changes in the bulk tissue ABA concentration of the stem base during soil drying are shown in Fig. 3.14. Control and Moddus-treated crops showed only small increases in ABA concentration as the SMD increased. In contrast the ABA concentration of Route-treated crops more than doubled over the same range of SMD. Data from the SMD ranges 25-50 (irrigated) and 100-125 mm (unirrigated) were pooled for statistical analysis.

*Table 3.11. Effects of drought and growth regulator treatment on the ABA concentration (ng ABA g $DW^{-1}$) of the stem base.*

| Irrigation | Growth regulator/promoter | | | |
|---|---|---|---|---|
| | Control | Moddus | Route | mean |
| Irrigated | 69.56 | 84.14 | 70.12 | 74.62 |
| Unirrigated | 91.42 | 119.32 | 169.17 | 126.64 |
| mean | 80.49 | 101.75 | 119.64 | |
| LSD irrigation x growth regulator, 28.6 (P=0.05, rdf 73) | | | | |

The results show that there was a significant interaction between growth regulator treatment and drought. Drought had no significant effect on the ABA concentration of controls, but increased it significantly in Moddus and Route-treated crops. Moreover, concentrations in Route treated crops subjected to drought were significantly greater than those treated with Moddus (Table 3.11). There was no significant effect of growth regulator treatment on the ABA concentration in the absence of drought.

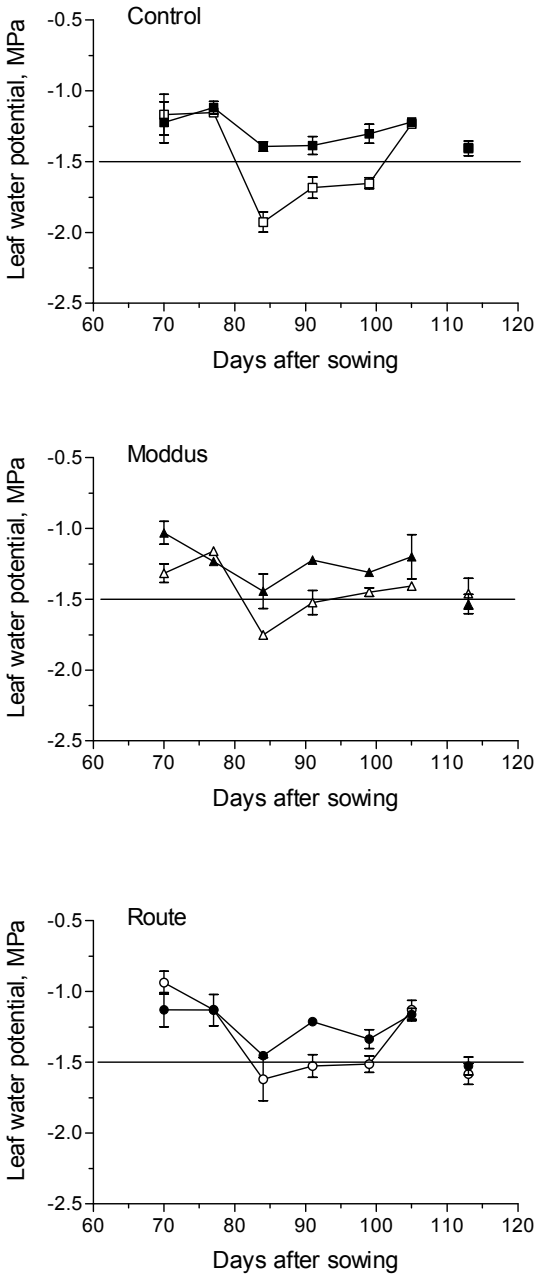


Fig. 3.13. Midday leaf water potential. Closed symbols are irrigated crops, open symbols are unirrigated. Points are means ± SE of 3 replicates. Points connected by lines are measurements made on leaf 2. Detached points are for measurements made on the flag leaf. Horizontal line at –1.5 MPa is for reference.

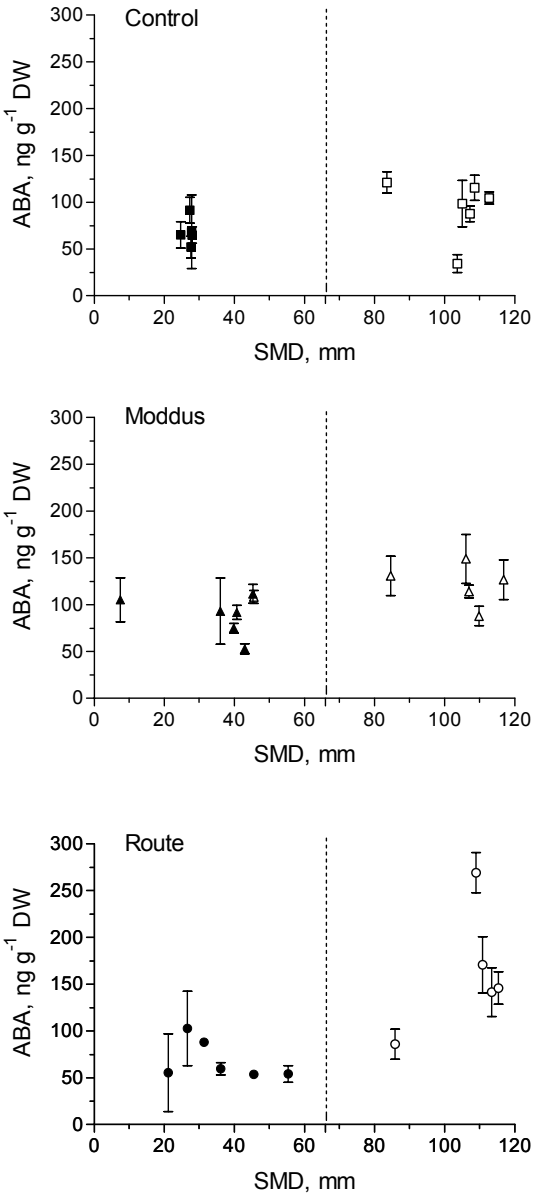


Fig. 3.14. Concentration of ABA in the stem base as a function of soil moisture deficit and growth regulator/growth promoter treatment. Closed symbols are for tissue taken from irrigated plants, and open symbols for tissue from unirrigated plants. Plant tissue was sampled for analysis at several times during the experiment and data are plotted against the SMD at the time of sampling. Vertical line represents SMD at 50% depletion of PAW.

*Plant growth*

Tiller number and plant height were measured at GS 39. There was no significant effect (P>0.05) of irrigation or growth regulator treatment on these aspects of growth (Table 3.12). Nor was there any significant effect on GAI and its component fractions (leaf lamina, stem and ear) at growth stage 59 (Table 3.13). However, by this growth stage drought had reduced total above ground biomass by 0.75 t $ha^{-1}$, an effect largely attributable to a reduction in stem dry weight (Table 3.14), plus a small contribution (11%) from a lower, ear dry weight. However, the reduction in ear dry weight on its own was not statistically significant. There was no significant effect of Moddus or Route on the total biomass or its components, nor any significant interaction between growth regulator/promoter and irrigation.

*Table 3.12. Number of tillers per plant and mean plant height at GS 39.*

| | Control | | Moddus | | Route | |
|---|---|---|---|---|---|---|
| | Irrig | Unirrig | Irrig | Unirrig | Irrig | Unirrig |
| Tiller no. $plant^{-1}$ | 1.2 | 1.4 | 1.3 | 1.2 | 1.24 | 1.6 |
| Plant height, cm | 49.8 | 48.4 | 49.8 | 52.8 | 50.8 | 48.2 |
| Tiller no. SED & significance: Irrig 0.10 (ns); pgr 0.12 (ns); irrig/pgr 0.17 (ns). Height SED & significance: Irrig 1.18 (ns); pgr 1.45 (ns); irrig/pgr 2.05 (ns). | | | | | | |

*Flag leaf lifespan*

Drought advanced the onset of senescence of the flag leaf to the same extent in controls and crops treated with Moddus and Route (Fig. 3.15). The mean time to 50% loss of green area was reduced by 7.9 days in controls, compared to 7.0, and 7.9 days for the Moddus and Route-treated crops respectively. In each case the reduction was statistically significant (P<0.05). There was no significant effect of growth regulator treatment on flag leaf lifespan in either irrigated or unirrigated crops.

*Grain yield, yield components and harvest index*

Analysis of variance showed no significant interactions of relevance (P>0.05) between growth regulator treatment and irrigation on grain yield or its components. This implies that Moddus and Route had no significant effect on the response of the crop to drought. Thus only main effects of growth regulator and irrigation treatments are presented in Table 3.13. When averaged over growth regulator treatments, drought reduced grain yield by approximately 1 t

$ha^{-1}$. This was associated with a significant reduction in the number of ears $m^{-2}$ and grains $ear^{-1}$. There was no effect on the mean grain weight or harvest index. When averaged over irrigation treatments, Route increased grain yield by nearly 0.5 t $ha^{-1}$. The increase was significant only at P=0.067 and was the result of a combination of small, (though on their own not statistically significant) increases in ear number $m^{-2}$ and grain number $ear^{-1}$. There was no significant effect of Moddus on yield or its components.

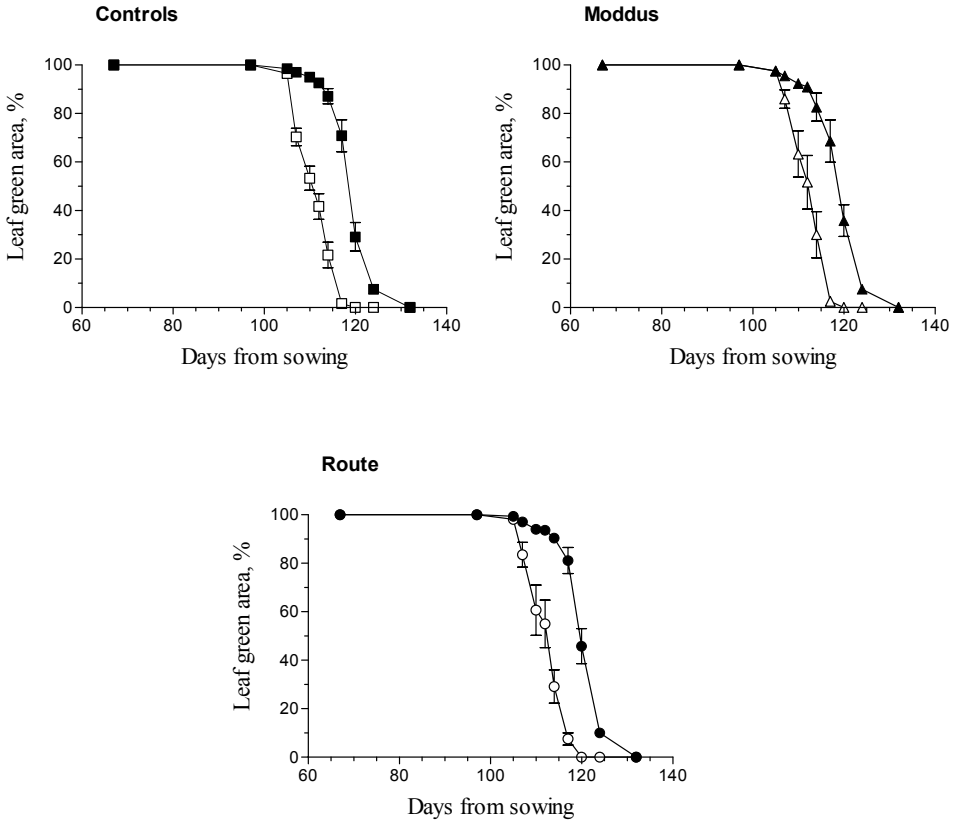


Fig. 3.15. Flag leaf green area. Closed symbols are controls, open symbols are unirrigated crops. Points are means ± SE of 6 replicate lysimeters.

*Table 3.13. GAI of different plant fractions at GS 59. Values are means of 4 replicate lysimeters per treatment combination*

| Fraction | Control | | Moddus | | Route | |
|---|---|---|---|---|---|---|
| | Irrig | Unirrig | Irrig | Unirrig | Irrig | Unirrig |
| Leaf | 4.36 | 3.99 | 4.10 | 3.88 | 4.52 | 4.10 |
| Stem | 1.57 | 1.56 | 1.57 | 1.39 | 1.54 | 1.30 |
| Ear | 0.67 | 0.78 | 0.65 | 0.60 | 0.63 | 0.57 |
| Total | 6.59 | 6.32 | 6.31 | 5.87 | 6.69 | 5.98 |
| Leaf irrig (ns); PGR (ns); irrig/PGR SED 0.473 (ns); Stem irrig (ns); PGR (ns); irrig/PGR SED 0.175 (ns); Ear irrig (ns); PGR (ns); irrig/PGR SED 0.111 (ns); Total irrig (ns); PGR (ns); irrig/PGR SED 0.650 (ns) | | | | | | |

*Table 3.14. Above ground biomass (t ha$^{-1}$ dry weight) of different plant fractions at GS 59. Values are means of 4 replicate lysimeters per treatment combination*

| Fraction | Control | | Moddus | | Route | | mean | |
|---|---|---|---|---|---|---|---|---|
| | Irrig | Unirrig | Irrig | Unirrig | Irrig | Unirrig | Irrig | Unirrig |
| Leaf | 1.59 | 1.53 | 1.42 | 1.46 | 1.60 | 1.60 | 1.54 | 1.53 |
| Stem | 6.71 | 5.97 | 6.94 | 6.31 | 6.77 | 6.17 | 6.81 | 6.15 |
| Ear | 1.90 | 1.76 | 1.68 | 1.75 | 1.90 | 1.70 | 1.83 | 1.74 |
| Total | 10.21 | 9.27 | 10.03 | 9.51 | 10.26 | 9.47 | 10.17 | 9.42 |
| Leaf irrig (ns); PGR (ns); irrig/PGR SED 0.108 (ns); Stem irrig SED 0.192 (P=0.005) ; PGR (ns); irrig/PGR SED 0.332 (ns); Ear irrig (ns); PGR (ns); irrig/PGR SED 0.096 (ns); Total irrig SED 0.277 (P=0.021); PGR (ns); irrig/PGR SED 0.480 (ns) | | | | | | | | |

*Table 3.15. Grain yield, harvest index and yield components. Only the main effects of the treatments are presented.*

| | Yield, t $ha^{-1}$ @ 85% DM | Ears $m^{-2}$ | Grains $ear^{-1}$ | Mean grain weight, mg | HI |
|---|---|---|---|---|---|
| PGR/Promoter | | | | | |
| Control | 8.24 | 842 | 19.32 | 44.4 | 0.494 |
| Moddus | 8.25 | 837 | 19.34 | 43.8 | 0.500 |
| Route | 8.70 | 857 | 19.42 | 44.1 | 0.507 |
| Irrigation | | | | | |
| Irrig | 8.88 | 899 | 19.75 | 44.4 | 0.504 |
| Unirrig | 7.91 | 792 | 18.97 | 43.8 | 0.497 |
| SED pgr (signif), rdf 25 | 0.215 (P=0.067) | 29.0 (ns)_ | 0.553 (ns) | 0.593 (ns) | 0.0068 (ns) |
| SED irrig (signif), rdf 25 | 0.175 (P=0.000) | 23.7 (P=0.001) | 0.319 (P=0.022) | 0.484 (ns) | 0.0055 (ns) |

## 3.5 Discussion

**Effects of growth regulators and promoters on root growth and resource capture**

An increase in the root:shoot biomass ratio of cereals has been observed after application of anti-gibberellin treatments in several controlled environment studies. In some, the increase in ratio is associated with a stimulation of root growth (Guckert et al. 1992), but more often it results from a reduction in shoot growth rather than any increase in growth of the root system (Cooke et al. 1983; Enam and Cartwright 1990; Rajala and Peltonen-Sainio 2001). Early applications (Zadoks GS 13) of PGRs can even *reduce* root biomass in some species. Trinexapac-ethyl reduced root biomass in spring oats and CCC reduced biomass in spring wheat (Rajala and Peltonen-Sainio 2001). In the present study, no effect of the gibberellin biosynthesis inhibitors trinexapac-ethyl (Moddus) and CCC plus choline chloride and imazaquin (Meteor) was found on the root or shoot growth of spring barley (Table 3.2). Trinexapac-ethyl-treated plants had the lowest mean leaf area, root length, shoot and root biomass, of all the treatments, but the reductions were not statistically significant. In contrast the growth promoter Route significantly increased root fresh weight and length by GS 31, without influencing leaf area or shoot biomass.

However, when tested in the field and in outdoor lysimeters, we found no significant effect of Moddus or Route on root growth and water capture by spring barley. A number of root characteristics were measured in the field experiment. There was no effect of treatment on the production of adventitious roots. This may have been associated with the lack of effect on tiller production and survival in this experiment. Nor was any significant effect found on the spread and depth of the root plate (i.e. the structural roots). This implies that the early application of Moddus or Route would have had little impact on the anchorage strength of the crop.

The total crop root biomass and root length at anthesis was also unaffected by the treatments. Route and to a lesser extent Moddus-treated crops had a slightly greater root length than controls at a depth of 20-30 cm in the profile, but the differences were not statistically significant. Moreover, the difference would have little impact on water uptake. Root length densities of 1-2 cm $cm^{-3}$ are thought to be sufficient to extract, with ease, all the available soil water (Brown et al. 1987). Consequently, any increase above this value is unlikely to have much benefit in terms of water capture; the root length density of 5 cm $cm^{-3}$ found in controls would be more than adequate for the purpose.

The overall depth of rooting at anthesis was surprisingly shallow in this experiment. There was little rooting beyond 50 cm. This is unusual for spring barley, which can normally root to at least 120 cm, with appreciable root length densities between 50 and 80 cm. The reasons for the lack of sub-soil rooting are unknown. Sub-soil pH was not limiting (6.2). It could result from the manner in which the sand is packed leading to a high impedance to root penetration. Quantitative measurements of roots were not made at the other sites, but at site 1, examination of the soil profile revealed a similar lack of root penetration into the sand subsoil. However, this is not always found with sand, and at many sites crops are able to root deeply and extract water from medium and coarse sands (e.g. Foulkes at al. 2001).

The pattern of water extraction confirms the measured root distribution. There was no detectable depletion of soil water below 50 cm. Above 50 cm, in spite of periods of heavy rainfall in summer, there was a substantial depletion of water from the soil leading to the development of a significant soil water deficit. Based on the calculated plant available water content and the measured soil moisture deficit, it is estimated that the crop experienced some water stress between anthesis and the end of grain filling. However, there were no visible signs of water stress in the crop, such as wilting or leaf curling. Although Route-treated plots had consistently higher soil moisture contents than control and Moddus-treated plots, this is probably not the result of a more efficient use of water by the crop after application of Route, since the difference between Route-treated plots and controls did not increase over time.

In the lysimeter experiment root length was not determined, but Moddus and Route had no effect on the rate of water extraction and the final soil moisture deficit in the droughted crops, suggesting there was again little effect on the growth of the root system. Here too, Moddus had no significant effect on the growth of the shoot or on grain yield, whereas Route did increase yield to a small extent.

The general lack of growth response to trinexapac ethyl in these experiments cannot be readily explained in terms of application technique, rainfall after application or poor growing conditions. The results were comparable in both sets of experiments in which application technique (field versus lysimeter), weather after application (rainshelter versus field), soil depth (field versus lysimeter) and crop yield potential (field sites 1-3; lysimeter drought/irrigated) differed. The rate applied was that recommended by the manufacturers (J. Tattenall personal communication). A later, or higher rate of application might have reduced stem length and increased tiller number (Rajala and Peltonen-Sainio 2001). In turn, additional tillering might increase the number of adventitious roots a little, but in spring barley we would not expect this to alter root length density in the deeper parts of the soil appreciably.

Firstly, any effect on adventitious root number is likely to be small because later formed tillers that survive have relatively few roots (Table 3.5; Anderson-Taylor and Marshall 1983) and secondly the roots on these later formed tillers will not have sufficient time to extend and branch into the deeper soil layers where the additional root length is required for water capture.

**Response to drought**

The impact of drought on yield depends on its severity and timing in relation to the crop's phenology (Passioura 1983). Early drought occurring before anthesis can reduce ear number and grain number per ear. If the drought is severe during the grain filling period, grain filling can be impaired and mean grain weight reduced. Crops may be particularly susceptible to rapid development of water stress during flowering as this can impair spikelet fertility and hence grain set (Salter and Goode 1967). Day et al (1978) reported yield reductions of up to 50% for spring barley crops grown under rainshelters on a silty clay loam soil, depending on the duration of the drought. The greatest yield losses were associated with the longest periods of limiting soil moisture deficits (i.e. when drought occurred pre and post-anthesis). The experiment was conducted in 1976, an exceptionally hot dry year in the UK. The main cause of the reduced biomass production and yield was the reduction in light interception resulting from reduced canopy expansion and premature senescence (Legg et al. 1979). In a similar experiment on a deep silt loam soil in New Zealand, yield losses of up to 62% were found (Jamieson et al. 1995a). Here, reductions in radiation use efficiency were associated with the decreased crop growth rate but only when the drought was imposed early after emergence. When the drought was imposed from two weeks before anthesis or later, the main cause of the lower growth rate was a decrease in light interception resulting from the earlier canopy senescence (Jamieson et al. 1995b). In a separate modelling exercise, using data from the same experiment, it was concluded that stomatal control was more influential than reduced radiation interception in reducing canopy transpiration (Jamieson et al. 1995a)

In the present study drought reduced grain yield by 11% (approximately 1 t $ha^{-1}$) when averaged over the growth regulator treatments (Table 3.15). The lower yield was the result of both a smaller number of ears $m^{-2}$ and grains $ear^{-1}$. There was no significant effect on the mean grain weight or on the harvest index. In this respect the response to drought was the same as that found with Optic in the glasshouse where the temperature and evaporative demand were greater. As discussed in section 2.5, ear number and grain number per ear are determined through the initiation and survival of tillers and spikelets respectively. Competition for assimilates during stem extension is believed to be an important factor governing tiller and spikelet mortality (Hay and Walker 1989).

After withholding water, the soil dried rapidly, so that by GS39, 50% of PAW had been depleted. At GS 59, the biomass of the stem was significantly reduced by drought. However, there was no effect on GAI indicating that canopy expansion was not impaired. Moreover, leaf water potential, stomatal conductance and leaf photosynthetic rate were comparable to irrigated plants until the end of anthesis and the start of grain filling, which implies that the crop was not discernibly water stressed at ear emergence. The results suggest that radiation interception and radiation use efficiency are unlikely to have been restricted in non-irrigated crops prior to anthesis.

So what was the cause of the reduction in stem weight, ear number and grain number? We consider a plausible explanation to be that soil drying during stem extension altered the partitioning of assimilates away from the stem to the root system. Drought is known to increase the root:shoot biomass ratio (Passioura 1983; Gregory 1994) and as part of the soil dries, root production can be stimulated preferentially in the moist soil horizons (Sharp and Davies 1979; Reid and Renquist 1997). Diversion of assimilates to additional root production could lead to a reduction in deposition of stem storage reserves, thereby lowering stem weight at GS 59 without significantly influencing leaf biomass or GAI (Table 3.14). In spring barley, primary tillers are an important source of photoassimilates for the seminal and adventitious roots of the main stem (Anderson-Taylor and Marshall 1983). Diversion of assimilates could also have resulted in enhanced spikelet mortality. A reduction in spikelet number, especially if small, is unlikely to be detected in measurements of ear biomass at GS 59.

From the present data we cannot determine precisely at what growth stage the ear number was reduced by drought. However, since GAI at GS 59 was not significantly affected by drought, it seems likely that shoot number was also unaffected at this time. The reduction in ear number seen at harvest may, therefore, have resulted from either a) a smaller percentage of the shoots at GS 59 bearing ears, in which case the effect occurred before any measurable effect on the plant water status, or b) late mortality of ear-bearing tillers (i.e. after GS59) at a time when leaf water deficits developed (Fig. 3.13). If the former hypothesis is correct, it is significant that a drying soil can limit yield potential before there is any impact on plant water status and canopy function. Restricted uptake of N, and other, less mobile, nutrients such as P, from a drying topsoil might contribute to the response (Day et al. 1978). However, there is evidence from other work that droughts imposed after anthesis can reduce ear number (Lawlor et al. 1981; Morgan and Riggs 1981) and as such, the lower ear number in the present study may well be a direct consequence of the reduction in plant water status.

During grain filling, leaf water potential of non-irrigated crops fell, stomatal conductance decreased and leaf photosynthetic rate decreased and the canopy senesced prematurely, all of which indicate that the crop was water stressed during this period. But, as found in the glasshouse experiment (Table 2.4), there was no effect of drought on the mean grain weight, which implies that grain filling was not restricted by the above drought-induced responses. Presumably, the effect of the soil drying on ear number and grain number limited the sink capacity to such an extent the crop was able to complete grain filling in spite of the stomatal closure and accelerated canopy senescence. Enhanced mobilisation of stem storage reserves may have helped buffer grain filling from a reduction in photosynthetic activity. In addition there is evidence that in barley the photosynthetic rate of the ear is less sensitive to drought than that of the leaves (Sanchez-Diaz et al. 2002). The weather during grain filling was relatively dull, with below average daily sunshine (appendix 3.2). Had the conditions been brighter, and the evaporative demand greater, a reduction in grain filling and mean grain weight may have been observed. Interestingly, the yield loss of 1 t $ha^{-1}$ is comparable with that reported by Day et al (1978) for crops subjected to pre-anthesis drought then irrigated during grain filling.

The stomata in the current work exhibited typical 'anisohydric' behaviour (Tardieu and Simonneau 1998). Leaf water potential fell before stomatal closure occurred (Figs 3.13 and 3.10). The eventual recovery of the water potential to that found in irrigated plants was probably the result of the reduced stomatal conductance and relatively low evaporative demand at this time.

Again we were unable to extract enough xylem sap for determination of ABA. Instead the ABA concentration of the stem base was measured. It was reasoned that changes in concentrations here might reflect changes in concentrations of ABA delivered from the root system to the leaves, although this hypothesis has not been tested. In control plants, soil drying had no significant effect on the ABA concentration of the stem base. This is consistent with the results reported for cv Optic in the previous chapter, where no clear relationship was observed between the soil moisture content and root ABA concentrations. However, treatment with Route, significantly increased the stem base ABA concentration at high soil moisture deficits (Fig. 3.14). In spite of the increase, there was no major difference between controls and Route-treated plants in the response of their stomata to soil moisture deficit. The reasons for this are unknown. The difference between control and Route-treated plants in stem-base ABA concentrations could result from effects of Route on ABA production or its partitioning between stem tissue and xylem sap. Whatever the reason, the results further highlight the complexity of the control of stomatal conductance and the role of hormonal signalling. It

seems unlikely, therefore, that the response of stomata to soil drying can be modified genetically through simple selection procedures based on bulk tissue ABA concentrations.

### 3.6 Conclusions

Early applications of Route and Moddus, applied according to the manufacturers' recommendations, had no significant effect on root growth and water capture by spring barley under field and outdoor lysimeter conditions. There was evidence in the case of Route applied to crops in lysimeters, that the product was absorbed by plants and induced a physiological effect response. There was a small increase in grain yield after treatment, and changes in stem-base ABA accumulation in response to drought. However, neither Route nor Moddus improved the drought tolerance of the crop. Drought reduced yield by about 1 t $ha^{-1}$, largely by reducing the number of ears per $m^2$. Ear number may have been reduced at the end of anthesis by effects of drought on plant water status, or earlier through effects of soil drying on the uptake of nutrients such as N and P. Further research is needed to elucidate the role of P in the response of spring barley to drought, as this has implications for the design of an appropriate root system for improving crop performance on drought-prone soils.

# 4. Modelling Root Distribution and Water Capture to Identify Targets for Management

In collaboration with MJ Foulkes, University of Nottingham

## 4.1 Introduction

Development of the concept of canopy management in cereals and oilseed rape has enabled growers to rationalise inputs such as seed and N fertilizer (Sylvester-Bradley et al. 1998; Spink et al. 2000). Canopy management is founded on the basic principle that there is an optimum size of canopy for radiation interception that can be defined in economic terms. Thus, as the size of the canopy is increased, a point is reached beyond which the returns from the additional radiation intercepted are outweighed by the costs of the additional inputs (e.g. seed, N, fungicide) needed to produce and maintain the canopy. The canopy management approach has, therefore, provided growers with quantifiable targets to work towards.

Similar targets are needed for plant breeders, agrochemical companies and growers wishing to improve the performance of a root system through either genetics or crop husbandry. To provide such targets we must have an appreciation of the optimum size and distribution of root system for a particular situation, the scale of any changes we may need to make to the root system, and the likely economic returns from those changes. Here we deal specifically with targets and potential economic benefits from improving water capture by cereal crops under UK conditions.

Modelling is a useful approach for investigating crop responses to water stress and the likely impact of changes to particular plant traits. Numerous models of crop water relations exist which range in complexity from the simple models used for irrigation scheduling to the dynamic simulation models of crop growth (Bailey 1990; Jamieson et al. 1998; Mandal et al. 2002). The concept of a soil reserve of plant-available water (PAW) and threshold PAW at which crop responses to water stress are triggered, forms the basis of many of these models. Several methods have been proposed for estimating PAW. These are usually based on generalisations about the depth of ‘dense’ and ‘sparse’ rooting for given types of crop (Bailey 1990). Whilst these are perfectly acceptable for irrigation purposes, they are not precise enough for setting targets for improvements to the root system, or evaluating the scale of any economic return.

Recently King et al. (2003) have developed a simple model of root distribution and water capture for wheat. The amount of water that can be captured is calculated as a function of the root length density and expressed as a fraction of the available water capacity. Thus the model can be used to estimate the PAW of a soil profile with different lengths and distributions of root system. The model also predicts the possible economic return from a given increase in water capture during grain filling. However, this component of the model is restricted to the situation where there is a terminal drought, and that the crop is bound to exhaust the plant available water before the end of grain filling. In its drive for simplicity, the model does not consider the effects of the timing or severity of drought on canopy expansion, photosynthesis, transpiration rate and senescence. Under UK conditions complete exhaustion of PAW might occur in particularly dry seasons and with certain soil textures. But canopy growth and function is restricted before all the PAW is exhausted, and there will be many cases, for example on soils of greater water holding capacity and in seasons of higher rainfall, where extractable water remains at the end of the season. Further complexities arise from the buffering of grain filling by stem carbohydrate reserves and increases in water use efficiency with increasing intensities of drought.

The aim of work reported in this chapter was to extend the scope of the King et al. (2003) model and use it to investigate the potential benefits of modifying the root system for soils of differing PAW and under contrasting UK seasonal weather patterns. The approach taken was to use the existing model to determine the PAW for different soil textures and root distributions and to estimate the effects of changing the root distribution on yield by developing a new model for predicting biomass and yield as a function of crop evapotranspiration and PAW. We have sought to use the minimum amount of crop and soil information as possible, to adhere to the original goal of simplicity and practical utility (King et al. 2003).

The modelling was conducted for winter wheat crops as there are good data sets available for the growth and drought response of modern wheat varieties under UK conditions. By contrast there are relatively few data available for modern spring barley varieties. However, the general principles developed here will be applicable for a range of small grain cereals.

### 4.2 Predicting transpiration and grain yield - model development

***Root growth***

The effective rooting depth of winter wheat is assumed to be 80 cm at the beginning of April and increases at a constant rate until anthesis, giving a final effective rooting depth of 165 cm. Accordingly, PAW is increased as the effective rooting depth is increased to a final maximum value at anthesis. Maximum rooting depths in the UK are about 1 m at the beginning of April and 2 m by anthesis (Gregory et al. 1978a; Weir and Barraclough 1986)

***Canopy growth and senescence***

Initially canopy growth is considered in the absence of water constraints. Canopy expansion and senescence are considered in 5 phases:

- Slow expansion from 1st April to 17th April (approx GS 30) @ 0.0266 GAI $d^{-1}$
- Rapid expansion from 17th April to 24th May (flag leaf emergence GS39) @ 0.12 GAI $d^{-1}$
- Constant canopy size from 24th May to 12th June (ear fully emerged GS59)
- Slow senescence from 12th June to 27th June (GS71) removing leaf surface @ 0.04 GAI $d^{-1}$
- Rapid senescence from 27th June until 31st July (GS87) removing green area @ 0.16 GAI $d^{-1}$

The benchmark dates and values of GAI are taken from the Wheat Growth Guide (Sylvester Bradley et al. 1997). They are derived from detailed measurements on crops of cv Mercia, grown under the same husbandry regime, averaged over 18 site seasons in the UK. They are taken to represent the potential growth and lifespan of the canopy in the major wheat production areas of the UK, when water supplies are non-limiting. The general pattern of canopy growth and senescence is consistent with that of irrigated crops reported by Foulkes et al. (2001). For simplicity, differences in crop phenology resulting from variety and sowing date are not considered.

***Effects of soil moisture deficits (SMD)***

The rate of canopy expansion and senescence are modified by a drought factor defined in terms of the intensity of water stress. This approach is similar to that used in a range of crop simulation models such as Sirius and CERES-wheat (Jamieson et al. 1998).

The intensity of drought is determined from the current SMD and PAW expressed as:

$$F_D = 1-(SMD/PAW) \quad (1)$$

Thus, when $F_D = 1$ the soil is at field capacity and when $F_D = 0$, all the plant available water has been exhausted. The rate of canopy expansion is reduced below the benchmark rate, when $F_D$ falls below a critical threshold value (0.65). It then ceases altogether after a second threshold value is reached (0.2). The potential rate of expansion is multiplied by a factor ($F_L$) that ranges linearly between 0 and 1 according to the value of $F_D$. $F_L$ is 1 at $F_D \geq 0.65$ and 0 at $F_D \leq 0.2$

The reduced rate of canopy expansion is applied until GS39 at which point the maximum GAI is reached. The canopy size then remains constant until GS 59 irrespective of the intensity of drought. Slow senescence commences at GS59 removing GAI at a fixed rate. After GS61, the slow rate can be accelerated by drought. The rate of GAI removal between GS61 and 71 is increased by a factor $F_S$ that is dependent on $F_D$. The rate of senescence during this phase therefore ranges from the potential rate at $F_D \geq 0.6$ to the maximum rate (i.e. the rate during the phase of rapid senescence) at $F_D = 0.2$. During the phase of rapid senescence, the rate is not increased by drought. This has the effect of advancing the time of complete canopy senescence without increasing its maximum rate. This is consistent with field observations for cereals in the UK (Chapter 3; Foulkes et al. 2001).

Root growth is assumed to remain at the potential rate during the onset of water stress. This is a reasonable simplifying assumption. Rates of root extension are less sensitive to soil drying than leaf expansion and biomass partitioning is often adjusted in favour of the roots (Sharp et al. 1988; Gregory 1994).

***Potential crop transpiration***

Potential evapotranspiration is determined from meteorological data using the Penman equation (French and Legg 1979). The contributions made by transpiration and soil evaporation to the potential evapotranspiration depends on the relative amounts of radiation intercepted by the crop and transmitted to the soil surface. This in turn depends on the current size of the canopy. Potential transpiration ($E_{TP}$) is given by:

$$E_{TP} = E_P [1-\exp(-kGAI)] \quad (2)$$

Where $E_P$ is the potential evapotranspiration, GAI is the current value of green area index and *k* is an extinction coefficient of 0.46 (Jamieson et al. 1998). The expression in parentheses gives the fraction of radiation intercepted by a canopy of given GAI.

***Actual transpiration***

The actual transpiration rate ($E_T$) is calculated from the potential rate after accounting for the effects of soil moisture deficits on canopy transpiration. If $F_D$ (equation 1) exceeds a threshold value ($F_{Dthr}$), $E_T$ is set to $E_{TP}$. When $F_D$ falls below the threshold, $E_T$ is given by:

$$E_T = E_{TP} [F_D/F_{Dthr}] \quad (3)$$

This has the effect of reducing the transpiration rate below the potential rate once a critical soil moisture deficit has developed. The rate is reduced linearly from the potential rate at $F_{Dthr}$ to zero when all the plant available soil moisture has been exhausted ($F_D = 0$). The default value of $F_{Dthr}$ is set to 0.5.

***Evaporation from the soil surface***

Soil evaporation ($E_S$) is determined separately following Tanner and Jury (1976) and Jamieson et al. (1995a). Briefly, when the soil surface is wet, $E_S$ is limited by the amount of energy reaching the soil surface. The rate is given by:

$$E_S = E_P [\exp(-k\text{GAI}] \quad (4)$$

where the expression in parentheses is the fraction of radiation transmitted to the soil. Once the soil surface has dried sufficiently to provide a barrier to water vapour diffusion, $E_S$ becomes diffusion-limited. $E_S$ during this phase is calculated according to Jamieson et al. (1995a):

$$E_S = 2C^2/\Sigma E \quad (5)$$

where C is the soil diffusion constant and $\Sigma E$ is the accumulated soil evaporation since the diffusion-limited phase began (Jamieson et al. 1995). In the absence of specific soil data, C is assumed to be 3.5 mm $d^{-1/2}$ (Loomis and Connor 1992) and diffusion limited evaporation assumed to commence after a cumulative $E_S$ of 9 mm following the last significant rainfall event (Jamieson et al. 1995a). Rainfall occurring after the start of the diffusion-limited rate is

subtracted from ΣE and if ΣE < 0, $E_S$ is set back to the energy-limited rate. Actual $E_S$ is taken to be the lesser of equations 6 and 7. This accounts for periods when radiation reaching the soil surface is too low to drive $E_S$ at the diffusion-limited rate (Tanner and Jury 1976; Jamieson et al. 1995a).

***Soil moisture deficit***

The soil moisture deficit is calculated as the cumulative sum of actual transpiration and soil evaporation minus rainfall. Rainfall above that required to restore the soil to field capacity is regarded as drainage or runoff. For simplicity no account is taken of the infiltration characteristics of the soil and instantaneous distribution of water within the soil is assumed.

***Estimating yield***

Transpiration occurring between GS 30 (benchmark date 14th April) and complete canopy senescence is used to calculate the increase in above ground biomass.

The transpiration efficiency (TE; biomass gain $mm^{-1}$ water transpired) was derived from the data of Foulkes et al. (2001) for crops in grown in 1994 and 1995. $E_T$ was calculated from measured values of crop evapotranspiration ($CE_P$) by multiplying $CE_P$ by model values of $E_T/E_T + E_S$. Measured values of $CE_P$ could not be used for the irrigated crops, because an unknown proportion of the water applied in irrigation is evaporated from the canopy surface and is therefore not available for transpiration. Instead, the model was run with high values of PAW to ensure there was no restriction by soil water on canopy growth and transpiration. Model values then represented the transpiration by non-stressed crops. In general model predictions of $E_T + E_S$ under conditions of high PAW were about 10 % lower than the measured water use of irrigated crops reported by Foulkes et al. 2001.

Since WUE and hence TE increases with drought (Foulkes et al 2001; Clover et al. 2001), values of TE were plotted against the relative transpiration (transpiration under drought/transpiration of non-limited crops) to give a TE that varies with the intensity of drought.

Harvest biomass is then calculated after adjusting for the biomass produced before GS30 and that 'lost' between GS87 and harvest. A benchmark value of 100 g $m^{-2}$ is used for pre- GS 30 biomass and a fixed reduction of 70 g $m^{-2}$ post GS 87. The latter has been found to be broadly comparable for both droughted and non-droughted crops (Foulkes et al. 2001).

Grain yield is estimated from the biomass at harvest by multiplying by the harvest index (HI). HI can also vary with drought. Under UK conditions, where droughts tend to occur either post-anthesis or both pre- and post-anthesis, the HI is often reduced. Measured values of HI (Foulkes et al. 2001) were plotted against the relative transpiration to give an HI that is dependant on the intensity of drought. Yields are reported at 85% dry matter.

***Model structure***

The model is written as an Excel spreadsheet. Calculations are made in daily timesteps commencing on the 1st April when the soil is assumed to be at field capacity and the SMD is zero. The previous day's SMD is used first to calculate current GAI and then the potential transpiration, actual transpiration, soil evaporation and current SMD.

### 4.3 Model parameterisation and evaluation

The 1994 and 1995 data sets of Foulkes et al. (2001) were used to parameterise the canopy growth component of the model. The data are from irrigation experiments conducted on wheat cv Mercia at ADAS Gleadthorpe. The model was run using measured values of SMD. In 1994 canopy growth of irrigated crops was comparable to the benchmark values taken from the Wheat Growth Guide (Fig. 4.1). Drought had no significant effect on the maximum canopy size achieved, but advanced complete canopy senescence by about 8 days. In 1995, canopy expansion was slower than in 1994 and slower than the benchmark crops resulting in a smaller maximum canopy size (Fig. 4.2). This was considered to be the result of inadequate N supply (Foulkes et al. 2001). Drought reduced the maximum canopy size by about 1.5 units of GAI and advanced canopy senescence by nearly 17 days.

After careful parameterisation, the model was able to correctly predict the relative effects of drought on the maximum canopy size and canopy lifespan. In 1994, no reduction in canopy size was predicted and a reduction in lifespan of 8 days was indicated. In 1995, although the absolute canopy size was larger than observed, the predicted reduction in both maximum GAI and lifespan in response to drought was similar to that measured (1.5 units and 18 days respectively). Threshold values of $F_D$ for the reduction in canopy expansion and acceleration of senescence that gave the best compromise between maximum canopy size and canopy duration in droughted crops were; rate of expansion limited at $F_D$ 0.65, expansion ceases at $F_D$ 0.2, accelerated senescence occurs at $F_D$ 0.6 and the maximum rate is achieved at $F_D$ = 0.2.

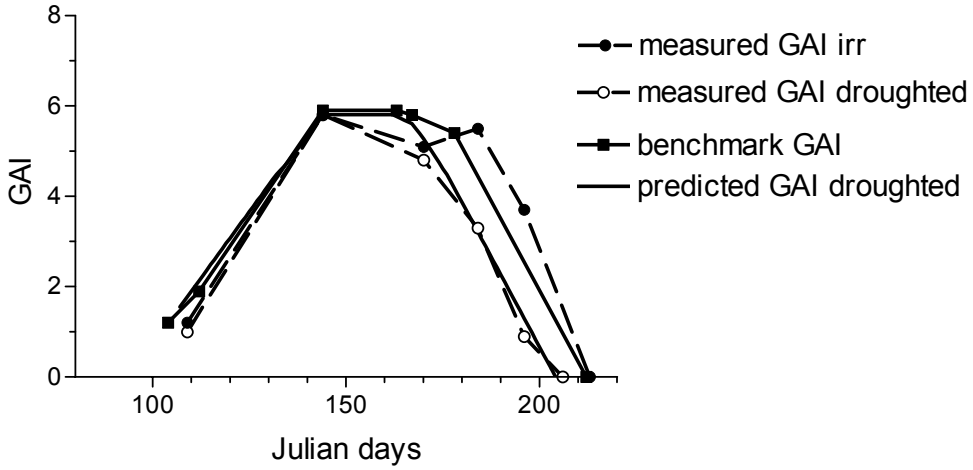


Fig. 4.1. Measured and predicted GAI for 1994. Measured values are from crops of Mercia winter wheat grown under irrigated and non-irrigated (droughted) conditions. Benchmark GAI is the GAI for conditions of no water stress (equivalent to predicted GAI for non-droughted crops). GAI under drought was predicted from measured records of SMD.

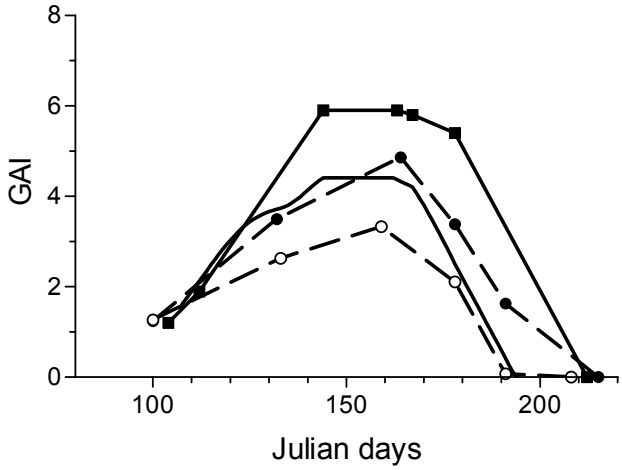


Fig. 4.2. Measured and predicted GAI for crops of wheat cv Mercia in 1995. Treatments and symbols as for Fig 4.1.

Model predictions of SMD have been compared to field measurements for crops grown at ADAS Gleadthorpe between 1993/94 and 1995/96. In 1993/4 the PAW to 165 cm was 160 mm, whilst in 1994/5 and 1995/6 it was 137 mm when calculated according to Bailey (1990).

In 1993/94, the model over predicted SMD especially during the first month (data not shown). However, after resetting the model to the measured SMD on 22$^{nd}$ April, it predicted the SMD well for the remainder of the season (Fig. 4.3). This suggests that the assumption that the soil was at field capacity on 1st April may not have been valid for this year. In 1995/96, the predictions were good over most of the season. In 1994/95, the model predictions were again accurate up to grain filling, after which SMD was over predicted for a short while. The accuracy could be improved over the grain filling period if the threshold for reduced transpiration ($F_{Dthr}$) was raised to 0.6 so that transpiration was restricted at a lower SMD (after 40 % of PAW had been depleted). However, this reduced the accuracy of predictions during the period of canopy expansion and after complete canopy senescence. Using specific values of GAI for 1995 instead of the benchmark values had little effect on the seasonal pattern of SMD. This is because the lower transpiration that resulted from the smaller canopy was offset by greater evaporation from the soil (data not shown). Overall the results indicate that using general parameter values, the model can provide a reasonably good estimate of crop water use over a number of contrasting seasons.

The model was parameterised using data taken from field experiments in 1994 and 1995. It was tested against independent data sets from experiments conducted in 1995/96, 1997/98 and 1998/99. Table (4.1) compares the harvest biomass, HI and grain yields from these experiments with those predicted by the model.

1996 was an extremely dry year, with the monthly rainfall from March to July consistently below the long-term average. This resulted in a pre- and post-anthesis drought. By contrast in 1998, April and June were significantly wetter than average and although May and July were drier than the norm, no significant period of drought occurred. 1999 was drier than 1998 and a limiting SMD developed after flowering. Yield responses to irrigation reflected these seasonal differences in the onset and duration of drought. Drought reduced yield by 44% in 1996 and 18% in 1999. There was no response to irrigation in 1998 (Table 4.1).

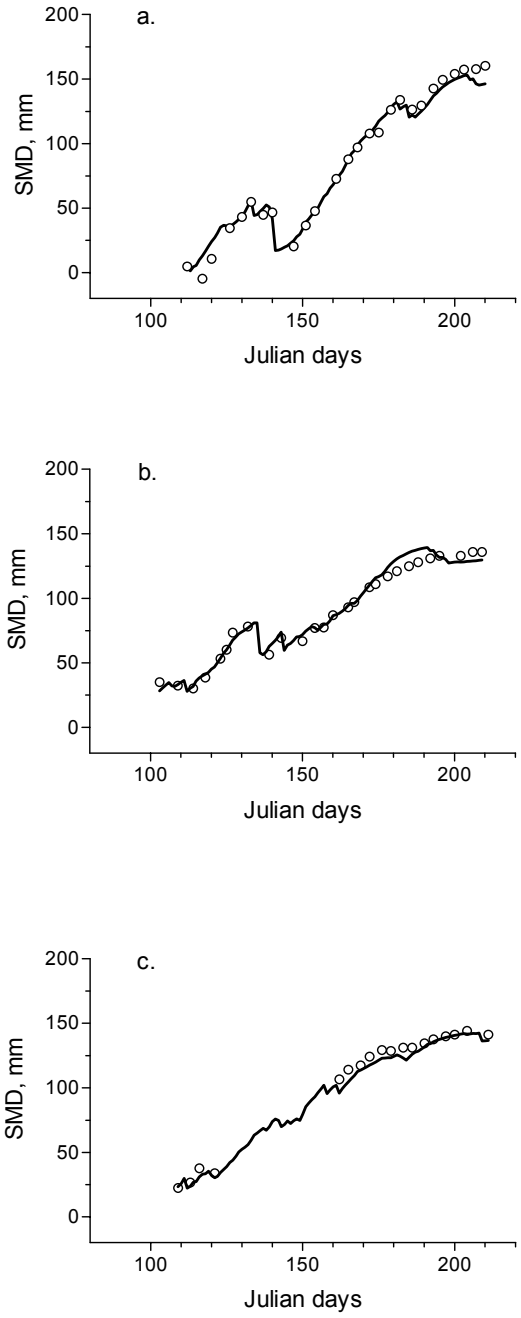


Fig. 4.3. Measured (open symbols) and predicted (solid lines) soil moisture deficits for (a) 1994, (b) 1995 and (c) 1996.

*Table 4.1 A comparison of measured and predicted above-round biomass at harvest, HI and grain yields. 1996 measured values are means of 6 varieties (data from Foulkes et al. 2001); 1998 and 1999 are means of two varieties Mercia and Maris Huntsman (lines carrying Rht2 gene; Foulkes unpublished results). Relative biomasses and yields are the values for unirrigated crops expressed as a fraction of those for irrigated crops.*

| | | Measured | | | | | Predicted | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Biomass t ha$^{-1}$ | HI | Yield t ha$^{-1}$ | Rel biomass | Rel yield | Biomass t ha$^{-1}$ | HI | Yield t ha$^{-1}$ | Rel biomass | Rel yield |
| 1996 | Irrigated | 16.5 | 0.53 | 10.27 | | | 17.1 | 0.52 | 10.47 | | |
| | Unirrigated | 10.9 | 0.45 | 5.72 | 0.66 | 0.56 | 12.8 | 0.46 | 6.94 | 0.75 | 0.66 |
| 1998 | Irrigated | 15.7 | 0.44 | 8.11 | | | 14.4 | 0.52 | 8.83 | | |
| | Unirrigated | 15.7 | 0.47 | 8.69 | 1.00 | 1.07 | 14.2 | 0.50 | 8.44 | 0.99 | 0.96 |
| 1999 | Irrigated | 16.3 | 0.54 | 10.34 | | | 15.8 | 0.52 | 9.68 | | |
| | Unirrigated | 14.8 | 0.50 | 8.69 | 0.91 | 0.84 | 14.7 | 0.48 | 8.43 | 0.93 | 0.87 |

Model predictions of grain yield agreed reasonably well with measured values for some treatment x season combinations, but not others. Thus for unirrigated crops in 1996, the predicted and actual yields differed by over 1 t $ha^{-1}$ and for irrigated crops in 1998 and 1999 by about 0.6 – 0.7 t $ha^{-1}$. A large proportion of the variation is likely to arise from the model not accounting for seasonal differences in actual transpiration efficiency (TE) and HI sufficiently accurately. The HI of irrigated crops ranged from 0.54 to 0.44 between 1996 and 1999. Differences in TE can be inferred from data for unirrigated crops in 1996. Here the model predicted well, the crop water use (Fig 4.3) and HI (Table 4.1), but overpredicted the biomass (Table 4.1). This suggests that the actual TE of the crop was lower than that of crops used to parameterise the model (i.e. those in 1994 and 1995).

Although the predictions of absolute yields must be treated with some caution, the model was able to predict with acceptable accuracy the *relative* response of above-ground biomass, HI and yield to water limitation across seasons at Gleadthorpe with contrasting timings and intensities of drought. Assuming responses of TE and HI to intensity of water stress at Gleadthorpe are representative of those over the range of UK soil types with differing PAW, it should be robust enough to predict the relative response to drought of crops grown under the same climatic conditions (as might occur in the same geographical region and season), but different soil water availabilities. As such the model can be used to explore the potential benefits of improving the water availability through modifications to the root system.

### 4.4 Modelling root distribution and PAW

***Root distribution***

In the model of King et al. (2003) the distribution of root length down the soil profile is described the equation:

$$Y = 1 - \beta^d \qquad (6)$$

Where Y is the fraction of the total root length accumulated from the soil surface to a given depth d and β is a parameter that describes the shape of the root distribution curve. A value of 0.97 was found to describe well the root distribution of Maris Huntsman wheat grown on Astley Hall series sandy loam soil overlying clay (Gregory et al. 1978a and b). Fig. 4.4 shows the effects of varying the value of β on the distribution of root length density for a crop whose total root length is 31.9 km $m^{-2}$. This is the estimated size of root system for a typical Mercia

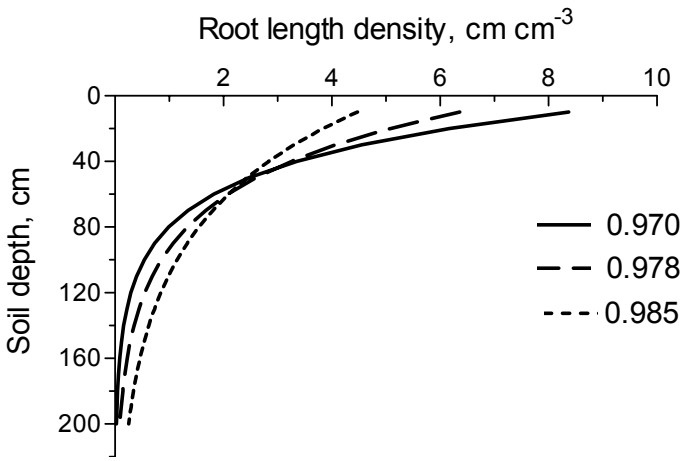


Fig. 4.4. Distribution of root length density (Lv) with depth down the soil profile. Different values of β (0.97, 0.978 and 0.985) describe the different distributions. A typical crop of winter wheat growing in deep soil of uniform structure is taken to have a β of 0.97.

crop grown in the reference crop trials upon which the Wheat Growth Guide is based (Sylvester-Bradley et al. 1997, King et al. 2003). An increase in β represents a reduction in root length in the upper layers of the soil and a greater proportion of roots deeper in the profile.

***Estimating PAW***

King et al. (2003) describe the effect of root length density on potential water capture by:

$$\phi = 1 - e^{-kLv} \qquad (7)$$

Where ϕ is the amount of water captured from given a soil layer as a fraction of the total available, Lv is the root length density in the layer and *k* is a 'resource capture coefficient'. An estimate of *k* was obtained by fitting the relationship to field measurements of seasonal water extraction by dryland barley reported by Gregory and Brown (1989). It was necessary to use data for barley as there were no suitable data available for wheat. A value of 2 fitted the data reasonably well (King et al. 2003).

Potential capture of water by the whole root system can be estimated by summing the potential capture by roots in each individual layer. The potential capture can be estimated in terms of mm of water, for any soil texture, by multiplying ϕ by the available water capacity of the soil (i.e. that held between field capacity and 1.5 MPa) assuming that *k* is relatively stable across different soil textures. This provides a method for estimating the plant available water (PAW) of a soil that can account for differences in root distribution.

To test the validity of the above technique, estimates of PAW for different soil textures are compared with those derived using the method of Bailey (1990). The distribution of Lv with depth for a typical wheat root system (total length 31.9 km $m^{-2}$ and a $\beta = 0.97$) was calculated using equation 6 and used in equation 7 to calculate the fraction of the total profile available water that can be captured. Values of topsoil and subsoil available water capacity (assuming good structural conditions) were taken from Bailey (1990 table 2.3) for use with equation 7. Topsoil depth was taken to be 30 cm. Estimates of PAW made using the Bailey method were based on effective rooting depths of 165 and 200 cm, assuming average structural conditions in the subsoil.

Average structural conditions are assumed for the subsoil in the Bailey method, because these, along with the sparse rooting in the subsoil, will more accurately reflect the *actual*

available water in field soils. The assumption of good structural conditions was used to derive values for use in equation 2, because this provides a better estimate of the *potentially* available water (i.e. available water capacity) without restrictions imposed by root distribution. The model itself then imposes the condition of restricted root length density to estimate the *actual* available water (PAW).

Overall there was good agreement between estimates of PAW derived from the model and those derived using Bailey's method when, in the latter, an effective rooting depth of 165 cm was assumed (Fig 4.5). The slope of the relationship was 1.02 ± 0.03. When a rooting depth of 200 cm was used, the Bailey method overestimated PAW compared to the model (data not shown). Although some roots of wheat may penetrate to depths of 180-200 cm, the root length density below 160 cm is small (Gregory et al. 1978a; Weir and Barraclough 1986), and contributes relatively little to the overall water availability and uptake. This is reflected in the model predictions of water availability below 160 cm (<4 % of the total PAW from below 160 cm), but not those estimated according to Bailey. This is because in the Bailey method all roots of winter cereals in the subsoil below 80 cm are treated the same and assumed to be able to extract water to a tension of 0.2 MPa. This 'average' condition is appropriate if an 'effective' rooting depth is considered, rather than the maximum. An 'effective' rooting depth of 150-160 cm is consistent with field measurements of root distribution and water extraction by winter wheat on deep soils in the UK (Gregory et al. 1978b; Goss et al 1984).

Although the model and the Bailey estimates of PAW agreed reasonably well overall, there were some disparities. The model tended to underestimate PAW for silty soils and overestimate it for soils of high clay content compared to the Bailey method (Fig. 4.5). It is not possible to determine which of the methods provides the most accurate estimate of PAW for these soil textures. Differences in the way the two methods deal with resource capture or root distribution between different soil textures might contribute to the variation. Not withstanding these disparities, the model provides a reasonably good method for estimating the PAW of soils over a range of textures and has the advantage that it allows the effects of altering the root length distribution on PAW to be investigated.

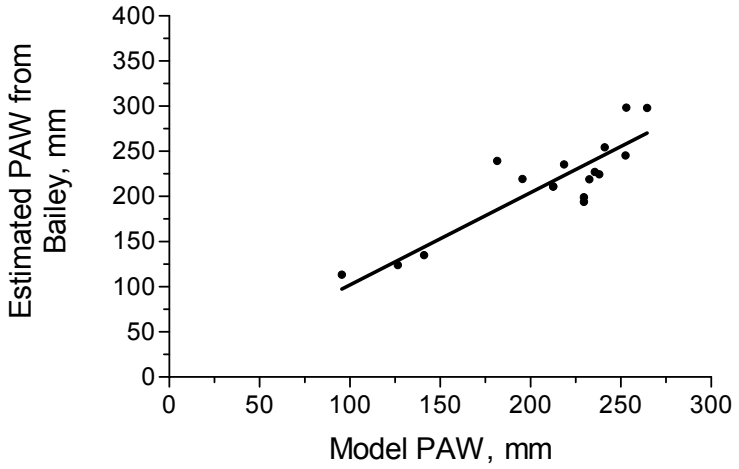


Fig. 4.5. Relationship between the plant available water (PAW) determined by the model and that estimated using the method of Bailey assuming an 'effective' rooting depth of 165 cm. Line fitted by regression forced through the origin ($y = 1.02\ x$; $r^2$ 0.988).

## 4.5 Model applications

The canopy growth/transpiration and root distribution/PAW models described above were used to investigate the yield responses to variations in PAW and the modifications required to the root system to effect given changes in PAW.

***Predicting yield responses to variations in PAW***

Figure 4.6 compares the predicted yields for crops grown on soils of differing PAW under the climatic conditions occurring at ADAS Gleadthorpe in 1994 (a post-anthesis drought year), 1995 (a pre- and post-anthesis drought year) and an average year. For 1994 and 1995, site specific meteorological data were used. For the average year, potential evapotranspiration and rainfall data for the site were averaged for the years 1986-1999. The range of PAW used in the model has been extended above that normally associated with wheat crops, to investigate the benefits of increasing PAW even on soils with high moisture retention characteristics.

In a severe drought year such as 1995 not only were substantial yield reductions (>50%) predicted for soils of low PAW, but some limitation to yield was predicted at high PAW (>250 mm). This would include the soils with a high water retention capability such as silt loams. In 1994, yield reductions on soils of low PAW were smaller, but still appreciable; some limitation was again predicted over the range 150-250 mm. In an average year, the yields were unrestricted by water availability until the PAW fell below about 180-200 mm. Small reductions in yield (nearly 1 t $ha^{-1}$) were predicted at a PAW of about 140 mm (Fig. 4.6). This agrees well with the average yield response to irrigation at Gleadthorpe over the same time period (see below).

Threshold values of PAW for reductions in transpiration may vary with evaporative demand and possibly soil type. They tend to be lower (higher $F_{Dthr}$) when high demand is coupled with coarse textured soils (Sadras and Milroy 1996). In the UK evaporative demand is lower and less variable than in Mediterranean climates. A value of 0.5 is consistent with the average for a range of experiments (Sadras and Milroy 1996) and for crops under UK conditions (Weir and Barraclough 1986). Fig. 4.6 illustrates the effects of varying the threshold value over the range $F_{Dthr}$ 0.3-0.7. At the lower end, transpiration is sustained for longer and potential yield reductions from drought are reduced for soils of mid-high PAW. At the higher end, more soil water is conserved, but yield reductions larger over the mid PAW range because less is transpired and more is left in the soil at the end of the season.

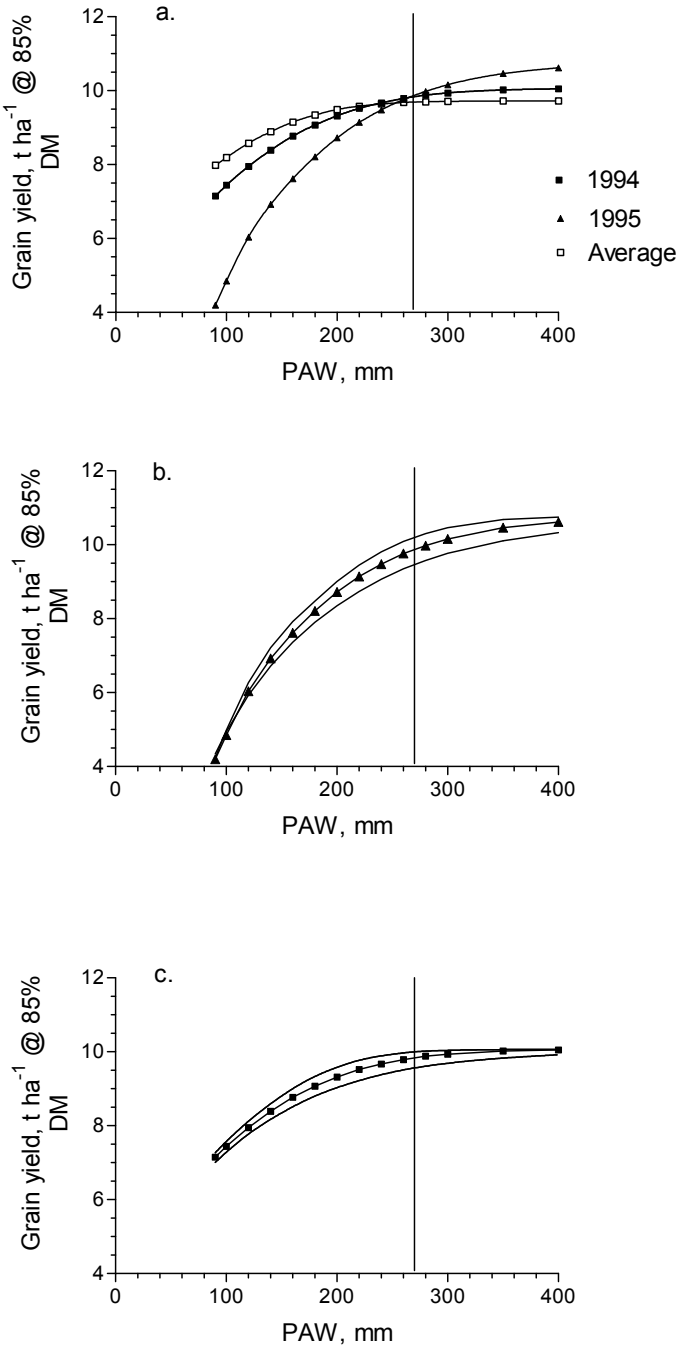


Fig. 4.6. (a) Predicted grain yields for crops grown on soils of differing PAW in a moderate drought year (1994), severe drought (1995) and average year. The vertical line represents the upper limit of PAW normally found for wheat in the UK. To the right of the line represents the predicted response range were the range of PAW to be increased further. (b) and (c) shows the predicted yields for 1995 and 1994 respectively using a threshold $F_{Dthr}$ for canopy transpiration of 0.5 (centre line and symbols), 0.7 (lower line) and 0.3 (upper line).

The results suggest that the minimum PAW for wheat in central England should be around 180-200 mm to maximise yield in an average year, and preferably higher to reduce the risk of yield reductions in dry years.

We estimate that, on average, 16% of wheat crops are affected by drought in the UK (Foulkes et al. 2001), and we expect this percentage to increase as climate change progresses in coming decades.

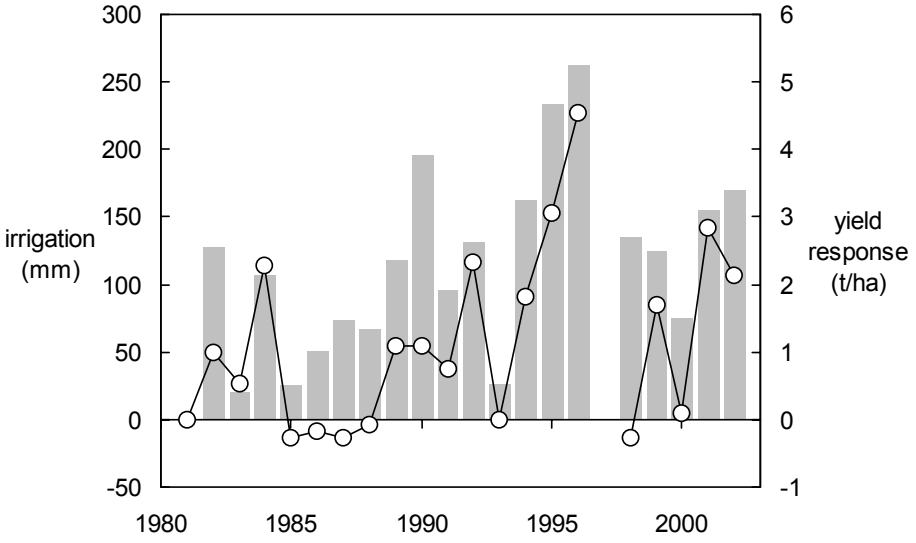


Fig. 4.7. Responses in grain yield of winter wheat to irrigation over the last 20 years at ADAS Gleadthorpe (updated from Bailey 1990 by data of Foulkes et al. 2002 and Foulkes, unpublished data). Columns are rainfall and circles are yield.

ADAS Gleadthorpe represents the more extreme sites for droughts in the UK. Over the past 20 years, irrigation results there (Fig. 4.7) indicate that drought effects are probably becoming more serious and frequent. Almost 5 t $ha^{-1}$ grain yield was lost in the worst season (1996) and the average yield loss due to drought was 1.2 t $ha^{-1}$ each year. Droughts of 2 t $ha^{-1}$ or more are likely to arise about 2 years in every 5 at sites such as Gleadthorpe.

***Effects of modifying root distribution on PAW***

For a root system with a maximum rooting depth of 180-200 cm, a large proportion of the soil water is unavailable to the crop because of limiting Lv. Consequently increasing the proportion of roots at depth can have a large effect on PAW. Fig. 4.8 shows the increase in PAW resulting from a given increase in β for different soil textures. A visual impression of

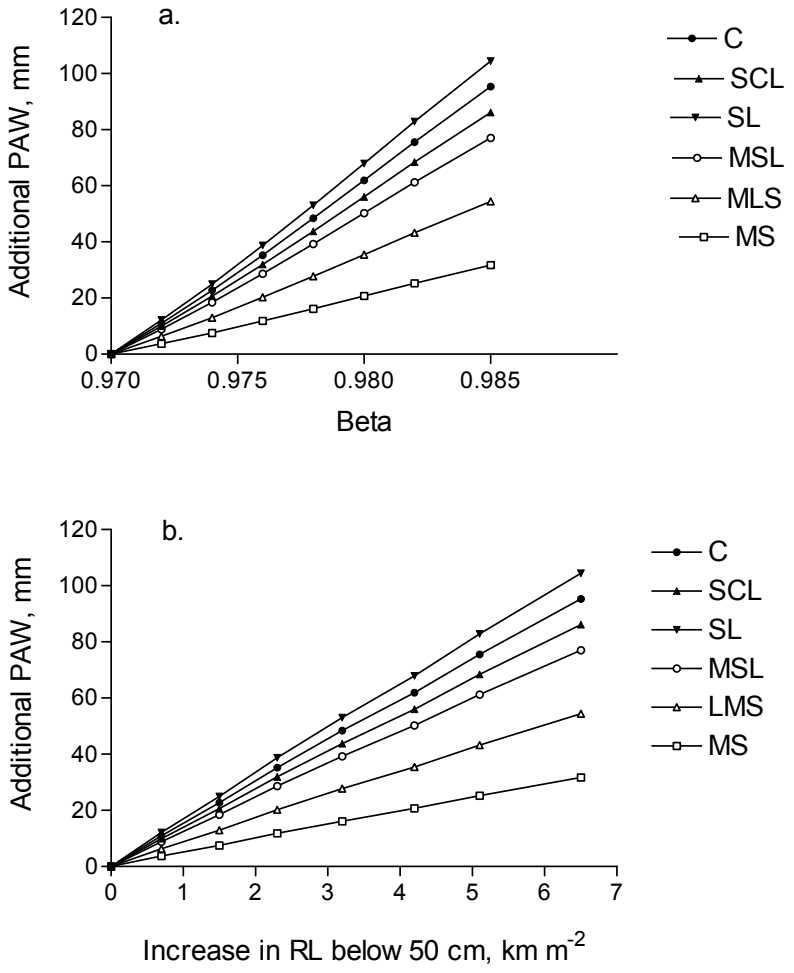


Fig. 4.8. (a) Effects of altering the root distribution on the PAW of soils of contrasting texture. In (b) the altered β is expressed as an increase in root length between 50 and 200 cm. Soil textures are: C clay; SCL sandy clay loam; SL silt loam; MSL medium sandy loam; LMS loamy medium sand; MS medium sand.

the distribution of Lv as β is increased is given in Fig 4.4. Not surprisingly, for a given increase in β, the greatest increase in PAW occurs on the fine textured soils (clay, sandy clay loam, and silt loam). This is because they have a greater water holding capacity than coarse textured soils. Thus increasing β from 0.970 to 0.985 results in an increase in PAW of 104 mm on a silt loam, but only 32 mm on a medium sand. The increase in β represents an increase in root length below 50 cm of 6.5 km $m^{-2}$ (Fig. 4.4); a 1.9 fold increase. Because of the non-linear nature of the distribution of Lv down the soil profile and the relationship between Lv and water capture, a given increase in root length will have a relatively larger effect on PAW the deeper it occurs in the soil.

***Effects of modifying root distribution on yield***

The predicted increases in PAW resulting from changes in root length illustrated in Fig. 4.8 were translated into potential yield gains using the relationship between PAW and yield in Fig. 4.6. In a severe drought year like 1995, yield increases in the order of 1.0-1.8 t $ha^{-1}$ might be expected for an increase in root length of 6.5 km $m^{-2}$ on clays and medium sands respectively (Fig. 4.9). A smaller increase in length of 3.2 km $m^{-2}$ could give yield gains of 0.6-1.0 t $ha^{-1}$ on the same soil types. In less severe droughts (e.g. 1994), the yield response is, not surprisingly, lower. Nevertheless, worthwhile yield increases of 0.3-0.5 t $ha^{-1}$ could be achieved with an increase of 3.2 km $m^{-2}$. Even in an average year, yield gains in the order of 0.35 t $ha^{-1}$ are predicted for the same increase in root length on loamy sand and sands (with an $F_{Dthr}$ of 0.5). Fig 4.10 shows, for 1994, how these yield gains vary with changes in the threshold PAW for reductions in transpiration. The effect of varying the threshold depended on the soil texture, but useful yield increases were predicted from an increase in root length on all soil textures irrespective of the threshold value.

***Soil depth***

Soils vary considerably in their depth. Root penetration may be prevented by a physical barrier such as underlying rock or indurated soil layer, or may be restricted because of adverse sub-soil conditions such as low pH. PAW for soils of different depth have been estimated (Table 4.1). The model predictions are for the situation where a physical barrier determines the soil depth and where roots can penetrate easily up to the barrier. We have assumed that the total size of the root system remains the same as that in deep soil, but that its distribution becomes truncated. The root length that would, in a deep soil, be located lower than the depth of the barrier is instead allocated in proportion to the root length in each 10 cm layer above the barrier. The root distributions used are shown in Fig 4.11.

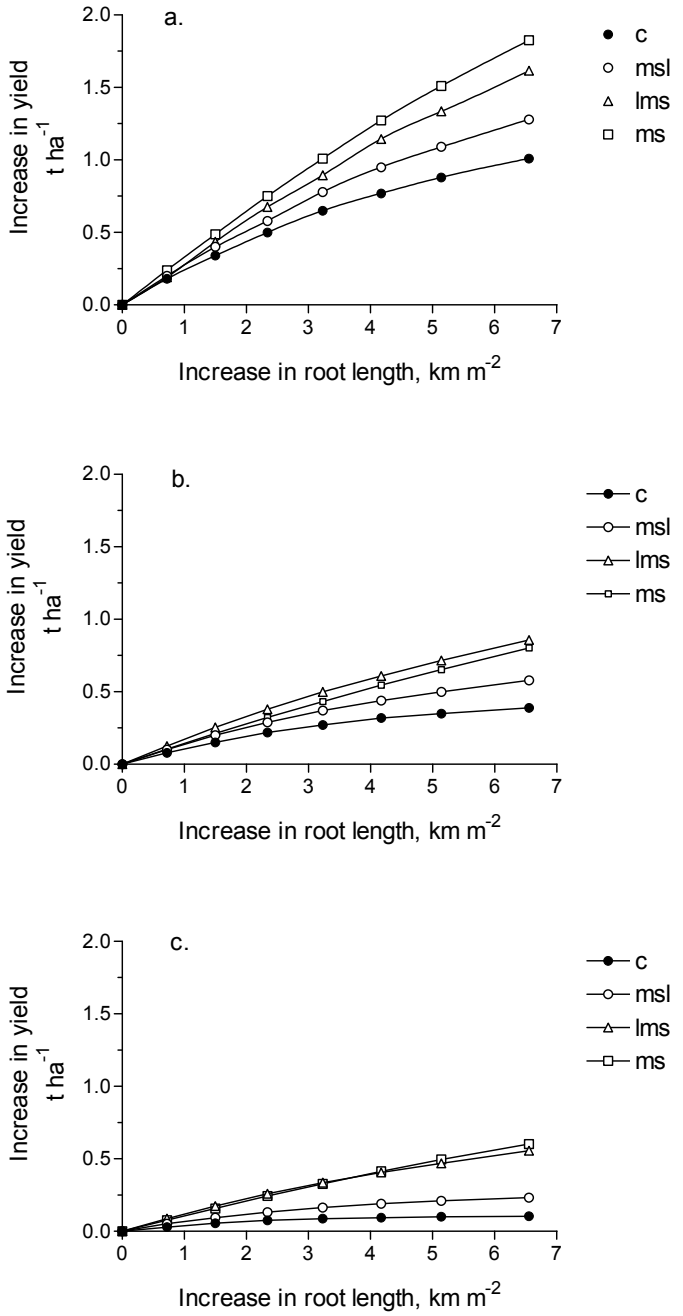


Fig. 4.9. Predicted increases in yield resulting from increases in root length effected by altering the root distribution (increasing β from 0.970-0.985). Predictions are for: (a) severe drought year 1995, (b) moderate drought year 1994, (c) average year. Predictions were made using a threshold $F_{Dthr}$ for canopy transpiration of 0.5. Soil textures are as listed in Fig. 4.8.

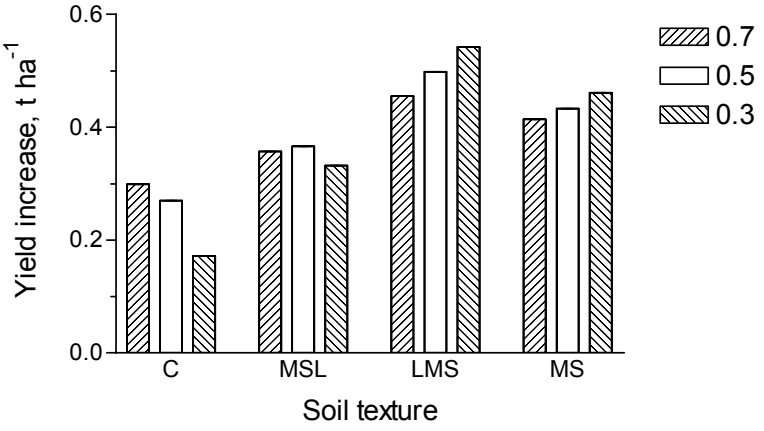


Fig. 4.10. Effects of altering the threshold $F_{Dthr}$ for canopy transpiration on the predicted yield response from an increase in root length of 3.23 km $m^{-2}$ ($\beta = 0.978$). Predictions are for a moderate drought year (1994). Soil textures as listed in Fig. 4.8.

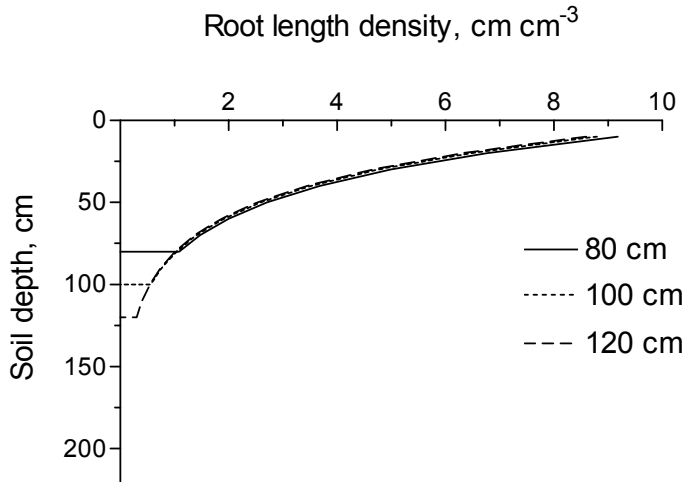


Fig. 4.11. Root length density distributions used to determine PAW for soils of different maximum depth

In soils of only 80 cm depth, Lv is large enough to capture most of the available water. PAW is about 97% of AWC and hence there is little additional water to be captured if Lv were increased. With soil depths of 100 and 120 cm, significant amounts of additional water might be made available to the crop (5-17 and 12-41 mm respectively) depending on the soil texture (Table 4.2)

*Table 4.2. Estimated PAW (mm) for soils of different depths and texture. Additional potentially available water (mm) is the difference between the estimated PAW and AWC of the soil. Estimates are based on a root system of total length 31.9 km $m^{-2}$ and whose distribution becomes truncated by a physical barrier to penetration at the given soil depth. Soil textures are as in Figure 4.8. Root distributions are shown in Fig. 4.11.*

| Soil texture | Soil depth (cm) | | | | | |
|---|---|---|---|---|---|---|
| | 80 | | 100 | | 120 | |
| | PAW | Additional | PAW | Additional | PAW | Additional |
| C | 152 | 4.0 | 182 | 15.7 | 203 | 37.1 |
| SCL | 142 | 3.6 | 170 | 14.2 | 188 | 33.5 |
| MSL | 133 | 3.2 | 157 | 12.7 | 174 | 30.0 |
| LMS | 97 | 2.3 | 114 | 9.0 | 126 | 21.2 |
| MS | 70 | 1.3 | 80 | 5.2 | 87 | 12.4 |

**4.6 Discussion**

***Implications of model outputs***

Soil PAW for the major winter wheat production areas of the UK ranges from about 120 mm to over 250 mm, assuming an effective rooting depth of 1.5 m (Foulkes et al. 1994). In years with below average rainfall, yield responses to irrigation in the order of 2- 4 t $ha^{-1}$ have been reported for soils at the bottom of the range such as loamy sands (Bailey 1990; Foulkes et al. 2001). On soils of higher PAW including silt loams and silty clay loams, yield losses from drought, and responses to irrigation, are smaller and less frequent (French and Legg 1979; Gales and Wilson 1981; Weir and Barraclough 1986). However, when they occur they represent a large loss to growers because they occur over a larger area. Whilst most soils of

the eastern counties of England fall within the middle of this range of PAW, a significant proportion of wheat, in the order of 15-16% (MAFF, 1999), may be grown on light soils, especially in Nottinghamshire and Suffolk (Foulkes et al. 1994).

Model predictions of yield in a moderate drought year such as 1994 suggested some limitation from drought on soils of PAW <250 mm. This upper limit is higher than would be expected from field experiments on moisture retentive soils. However, over the range 180-250 mm the predicted change in yield is small, and likely to be at, or beyond, the limits of detection in field experiments. Also, over this range, the predicted yield is sensitive to variations in the threshold PAW for reductions in transpiration (Fig. 4.6). In the severe drought year of 1995, yield reductions were predicted over the entire range soil PAW found in the UK. In an average year, yield losses close to 1 t $ha^{-1}$ were predicted for soil PAW of 140 mm. Thus, in general the model predictions are consistent with conclusions from previous analyses that yield may be limited by drought on loamy sands and sands of eastern England in most years and on finer textured soils in some years (Gales 1983). Between 1980 and 2000, water limitation to yield has been observed on the loamy sands at ADAS Gleadthorpe in 13 out of the 19 years for which data are available (Fig 4.7).

The model predicted that increasing the root length below 50 cm in a typical wheat crop by 3.2 km $m^{-2}$ (doubling Lv) could increase yield by up to 0.5 t $ha^{-1}$ on sands and loamy sands in a moderate drought year and up to 1.0 t $ha^{-1}$ in a more severe drought (Fig. 4.9). Larger increases in root length could increase the potential yield gains further. Small potential yield improvements are also predicted for the finer textured soils such as sandy loams and clays. Although yield losses from drought are smaller on these soils, because they have a greater water holding capacity, a given increase in root length will make available a larger amount of water. Hence the benefit in terms of water capture from increasing root length may be worthwhile. It must be emphasized, however, that the scale of any additional water capture depends on the distribution of the extra rooting. Proportionally greater gains can be made the deeper in the profile the additional root length is located. Doubling the root length density in deeper parts of the profile is potentially achievable. Differences of this order have been found between modern wheat varieties at soil depths of 80 cm, the deepest layer measured (Ford, Gooding and Gregory, HGCA project number 2422).

The potential gain in yield does not take into account the cost to the crop of producing the additional roots. At a typical specific root dry weight of 4.57 g $km^{-1}$ (Gregory 1978a), an increase in length of 3.23 km $m^{-2}$ represents an additional dry matter investment of 15.3 g $m^{-2}$ (0.15 t $ha^{-1}$). If allowances are made for the respiratory costs associated with producing and

maintaining the tissue, plus losses resulting from exudation and root death, much of the potential yield gain is negated (Bingham et al. 2002). Thus there would seem to be little advantage in modifying the crop so that it invests more total dry matter in the root system. A more profitable approach would be to try and alter the distribution of rooting so that fewer roots are located in the top soil and more are produced deeper in the profile (Bingham et al. 2002; King et al. 2003). This might also have the advantage of reducing the potential signal production by roots in the topsoil and raising the threshold PAW at which stomatal conductance and transpiration are reduced. On soils of mid range PAW this could contribute to yield in drought years by promoting greater utilization of the soil water reserve (Fig. 4.6). But delaying stomatal closure would be a risky strategy on soils of low PAW as it could lead to exhaustion of PAW before or during the early grain filling period.

On the other hand, altering the root distribution and reducing root length in the top soil may have detrimental effects on the uptake of P. If drought responses such as enhanced tiller mortality are mediated through P deficiency, a reduction in root length might exacerbate the problem. An alternative approach might be to utilize, for additional root production, the dry matter wastefully allocated to the production of non-fertile tillers (Berry et al. 2003).

Potential gains from manipulating the root system to improve water capture are limited on shallow soils. Improvements are only likely to be worthwhile if the potential soil depth is greater than 100-120 cm. The calculations emphasise the importance of maintaining good soil structure to maximise root penetration and the ability of the crop to proliferate roots at depth.

***Limitations and further developments***

Outputs from models can only provide an indication of the likely scale of changes needed to a root system and the economic returns. The model assumes the soil is homogeneous in structure enabling roots to explore according to their genetic potential. Some root distributions may be restricted by non-uniformity in soil physical and chemical properties, and not-conform to that described by the β function. Nevertheless, PAW can be predicted from any root length distribution providing $L_V$ at any particular depth interval is known, and thus potential gains from modifying the distribution can still be determined. The model is not applicable to soils that are imperfectly drained or those with a high water table from which there might be significant replenishment of the soil water reserve in the root zone.

Grain yield is estimated on the basis of transpiration from GS 30 to GS87. By estimating transpiration over a long period it minimises the impact of errors in prediction during the relatively short period of grain filling. However TE can vary between seasons and climatic

regions. Some of the variation may be reduced by adjusting values for the prevailing vapour pressure deficit (Clover et al. 2001). Use of a season-long estimate of transpiration to calculate yield integrates the effects of drought pre and post anthesis. By doing so it avoids the necessity to determine the effects of drought on the contribution of current photosynthesis and stem storage reserves to grain filling. This aspect is catered for in an empirically determined harvest index. However, its reliability in conditions of extreme drought where water is exhausted at or shortly after anthesis, and hence affects grain set, may not be adequately accounted for. Further developments to model transpiration, transpiration efficiency and remobilisation of storage reserve during grain filling may improve the reliability here, but at the expense of simplicity.

In its current form the model is based on standard benchmark values for canopy development and crop growth. These apply well to the large majority of the UK wheat producing areas. The model can be applied equally well to other regions by simple adjustment to the benchmark dates for crop development. However, some adjustment will also be needed to account for regional variations in TE and possibly HI.

### 4.7 Conclusions

The model developed here extends the utility of that developed by King et al. (2003) and provides a tool for assessing the scale of changes needed to a root system to improve water capture from a range of different soil textures. It allows the economic returns to be estimated for a range of different soil types, soils depths and prevailing climatic conditions. Relatively small increases in root length may give significant gains in yield in drought years, particularly on the light textured soils. These gains are only likely to be realized through a modified distribution of root system or allocation of dry matter normally wasted in the production of non-fertile tillers rather new additional dry matter investment. The model emphasises the importance of careful soil management for ensuring maximum root penetration in order to make full use of the soil's potential.

# 5. Summary Conclusions and Implications

## 5.1 Tools for managing the root system

Early applications of the anti-gibberellin Moddus (trinexapac-ethyl) and growth promoter Route had no significant effect on root growth and drought tolerance of spring barley cv Optic grown in the field and in outdoor lysimeters. Although only a limited range of growth regulators and promoters were investigated, the results are consistent with reports in the scientific literature. There is little compelling evidence that any of the anti-gibberellin growth regulators provides significant improvements in the tolerance of cereals to drought. Effects on root growth are often small and inconsistent (Steen and Wünsche 1990, Rajala and Peltonen-Sainio 2001). Where the growth regulator increases tillering, there may be an associated increase in number of adventitious roots (Crook and Ennos 1995) and this may result in small increases in root length and biomass in the upper layers of soil (Steen and Wünsche 1990, Rajala and Peltonen-Sainio 2001). However, we must be cautious when interpreting the functional significance of such effects. Cereals generally have ample root length in the topsoil for capture of the available water and N, and consequently increases here are unnecessary unless immobile nutrients such as P are limiting. Greater root length is required in the deep soil layers (>50-80 cm) in order to access more water (Chapter 4). The effect of growth regulators on root length in deep soil layers has rarely been investigated and where it has, the effects are small or absent (Bragg et al. 1984; Rajala and Peltonen-Sainio 2001). The small and inconsistent effects of anti-gibberellin growth regulators on root growth are consistent with the general lack of effect dwarfing genes (that induce insensitivity to gibberellins) have on deep rooting in wheat (Lupton et al. 1974; Miralles et al. 1997). In contrast to research on the anti-gibberellins, there have been few independent studies into the effects of bio-stimulant growth promoters on cereal roots.

On basis of the scientific literature and experiments reported here we conclude that the scope for using plant growth regulators to modify root growth and improve water capture by cereals is limited.

There was relatively little variation in root traits amongst the genotypes of spring barley studied in Chapter 2. Under the conditions of the screening experiment, Chalice had the most rapid rate of root growth, and Derkado produced the shortest roots for a given investment of biomass. However, these varieties did not differ from other modern varieties in their response to drought when water supply was confined to the bottom of the soil profile. Thus, at present

there seems to be little scope for improving crop performance on dry soils by matching varieties more effectively to site conditions on the basis of their root traits.

A specific breeding programme is likely to be needed to significantly improve the ability of UK spring barley crops to capture water. Screening a wider range of germplasm than was possible here, should reveal greater variation in root traits that might be exploited (Wahbi and Gregory 1989a; Ellis et al. 2000), and use of genetic mapping techniques should simplify the task of selection. There are examples where selection for yield under drought conditions has led to an increase in depth of root system (Hurd 1974). However, it will be necessary to convince breeders of the potential benefits of improvements to the root system before progress can be made.

**Targets for management**

Modelling is a useful approach for investigating the possible cost and benefits associated with modifying the root system. The model developed for winter wheat in Chapter 4 allows predictions to be made of the yield response to given changes in root length and distribution for different combinations of soil texture and different UK climatic conditions. It can be used, therefore, to provide geneticists and breeders with specific targets to work to. In the same way it can be used by agronomists and researchers to assess the scale of changes they would need to make to the root system through changes in agronomic practice, to have any impact on the capture of water and yield.

Relatively small increases in root length density of wheat at soil depths of 50-200 cm are predicted to give yield gains of up to 0.5 t $ha^{-1}$ on light soils in an average to moderate drought year. These increases are potentially achievable. In contrast to spring barley, other work in progress, suggests that significant variation in root length density at soil depths below 50 cm already exists amongst current UK wheat varieties (HGCA project 2422).

The model predictions also suggest that wheat crops on many soils in the eastern counties, normally regarded as having a reasonably high PAW, may become water-limited more frequently as summers become drier. The model emphasizes the importance of maximizing the depth of rooting to secure sufficient supplies of soil water. This highlights the need for careful management of soil structure in order to avoid potentially damaging restrictions to the root system. The model has been developed for wheat, but with the necessary data for parameterization, it can be adapted for barley.

Before changes can be made to the root system, further consideration must be given to the possible trade-offs involved. We have argued that investment of more biomass in the root system would be at the expense of the shoot and hence an altered distribution of root length is preferable. However, the impact of reducing the length of roots in the topsoil on uptake of immobile nutrients, especially P needs to be considered. Further research is needed to establish the causes of tiller mortality during drought, the role of P supply in the process, and the likely impact of changes in root distribution.

In situations where there is unused water remaining in the soil profile at the end of the season, delaying stomatal closure as the soil moisture deficit develops could result in a greater total water capture and yield. However, modifying stomatal control is unlikely to be a worthwhile strategy for two reasons. Firstly, it is risky in terms of grain yield and quality because in unusually dry conditions water may be exhausted before grain filling is completed. Secondly, because stomatal control is complex (Davies et al. 2002) simply manipulating ABA signal production is unlikely to be effective. The results presented here provide further evidence of the complexity. Varieties have been shown to differ in root ABA accumulation, but not the response of their stomata to soil moisture deficits. ABA accumulation in the stem base of cv Optic during drought can be increased by plant growth regulator/promoter treatments, but without appreciably influencing the stomatal response.

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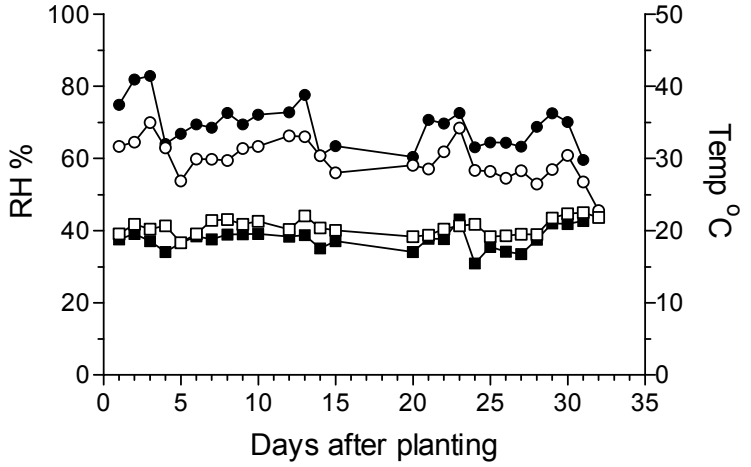
## Appendix 2.1




Average daily day (open symbols) and night (closed symbols) temperature (squares) and relative humidity (circles) in the glasshouse during experiment 2, chapter 2.

**Appendix 2.2**

Analysis of soil used in experiment 3 (chapter 2) and lysimeters (chapter 3).
Chemical analysis was by the modified Morgan method

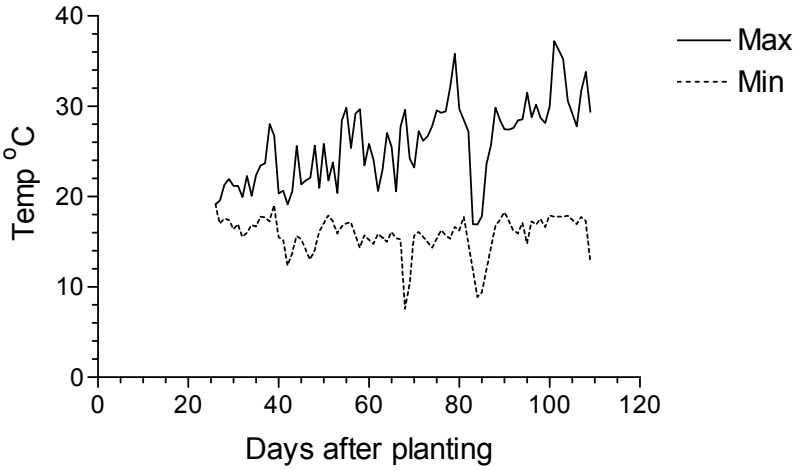
*Particle size analysis*

| | Size, mm | Soil | | Units |
|---|---|---|---|---|
| | | Loamy sand | Sandy loam | |
| V coarse sand | > 1 | 6.51 | 6.91 | % |
| Coarse sand | 0.5-1.0 | 18.27 | 16.61 | % |
| Medium sand | 0.25-0.50 | 23.95 | 20.47 | % |
| Fine sand | 0.125-0.25 | 22.19 | 18.22 | % |
| V fine sand | 0.063-0.125 | 11.76 | 10.79 | % |
| Total sand | | 82.68 | 73.00 | % |
| Silt | | 10.35 | 13.10 | % |
| Clay | | 6.97 | 13.90 | % |
| Organic matter (LOI) | | 2.5 | 8.1 | % |
| Stone content | 2.0-3.65 | 9.9 | 3.6 | % wt |
| (% wt) | >6.35 | 10.3 | 4.0 | % wt |

*Chemical analysis*

| | Loamy sand | | Sandy loam | |
|---|---|---|---|---|
| | Analysis | Status | Analysis | Status |
| | | | | |
| pH | 6.1 | | 6.2 | |
| Extractable P | 2.6 | Low | 4.4 | Low |
| Extractable K | 52.3 | Low | 94.2 | Moderate |
| Extractable Mg | 37.2 | Low | 164 | Moderate |

**Appendix 2.3**




Daily maximum and minimum temperature in the glasshouse during the 'water-table' experiment.

**Appendix 2.4**

Chemical analysis of soils used in the other controlled environment experiments. Analysis was by the modified Morgan method

| | A | | B | |
|---|---|---|---|---|
| | Analysis | Status | Analysis | Status |
| | | | | |
| pH | 6.0 | | 6.0 | |
| Extractable P | 10.0 | Moderate | 9.7 | Moderate |
| Extractable K | 73.6 | Low | 105 | Moderate |
| Extractable Mg | 81.2 | Moderate | 184 | Moderate |

Soil A Experiment 1, chapter 2
Preliminary screen of growth regulators, chapter 3

Soil B Experiment 2, chapter 2

## Appendix 3.1

Site and husbandry details for field experiments

*Site 1. Charleton Field 12*

| | |
|---|---|
| Previous cropping | 1998 set-aside, 1999 set aside, 2000 spring barley, 2001 potatoes |
| Cultivations | Minimum tillage |
| Sowing date | 5 March 2002 |
| Seed rate | 240 kg $ha^{-1}$ |
| **Variety** | Optic |
| Fertilizer:<br>Seed bed NPK<br>17/March/02<br>10/April/02 | Total N 130 kg $ha^{-1}$<br>370 kg $ha^{-1}$ 14-14-21<br>5 kg $ha^{-1}$ manganese sulphate<br>212 l $ha^{-1}$ Nuram (foliar N) |
| Herbicide:<br>29/Mar/02<br>Pre-harvest | Roundup pre-em<br>1.5 l $ha^{-1}$ MCPA, 0.7 l $ha^{-1}$ Foundation<br>Roundup |
| Fungicide<br>29/Mar/02<br>7/Jun/02 | <br>Charisma 0.6 l $ha^{-1}$, Torch 2.5 l $ha^{-1}$<br>Bumper P 0.3 l $ha^{-1}$, fenpropimorph 0.25 l $ha^{-1}$ |

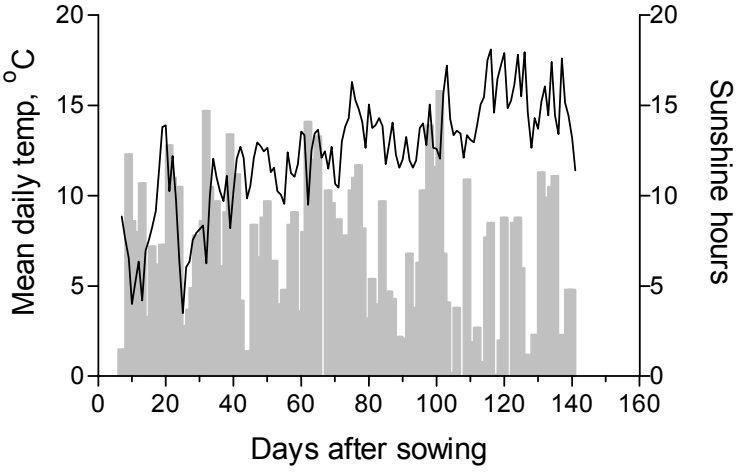
*Site 2. Charleton F7*

| | |
|---|---|
| Previous cropping | 5 years spring barley |
| Cultivations | Ploughed, harrowed |
| Sowing date | 7 March 2002 |
| Seed rate | 240 kg $ha^{-1}$ |
| Variety | Optic |
| Fertilizer:<br>Seed bed NPK<br>17/March/02<br>10/April/02 | Total N 130 kg $ha^{-1}$<br>370 kg $ha^{-1}$ 14-14-21<br>5 kg $ha^{-1}$ manganese sulphate<br>212 l $ha^{-1}$ Nuram (foliar N) |
| Herbicide:<br>29/Mar/02<br>Pre-harvest | <br>1.5 l $ha^{-1}$ MCPA, 0.7 l $ha^{-1}$ Foundation<br>Roundup |
| Fungicide<br>29/Mar/02<br>7/Jun/02 | <br>Charisma 0.6 l $ha^{-1}$, Torch 2.5 l $ha^{-1}$<br>Bumper P 0.3 l $ha^{-1}$, fenpropimorph 0.25 l $ha^{-1}$ |

*Site 3. Borrowfield*

| | |
|---|---|
| Previous cropping | Spring barley |
| Cultivations | Ploughed, harrowed |
| Sowing date | 12 March 2002 |
| Seed rate | 188 kg $ha^{-1}$ |
| Variety | Optic, seed dressing Anchor |
| Fertilizer:<br>Seed bed NPK<br>8/April/02<br>30/April/02 | Total N 100 kg $ha^{-1}$<br>250 kg $ha^{-1}$ 20:10:10<br>250 kg $ha^{-1}$ 20:10:10<br>3 kg $ha^{-1}$ manganese sulphate |
| Herbicide:<br>14/May/02 | <br>30 g $ha^{-1}$ Harmony M, 0.6 l $ha^{-1}$ Oxytril CM |
| Fungicide<br>14/May/02<br>28/May/02<br>19/Jun/02 | <br>Ensign 0.2 l $ha^{-1}$<br>Unix 0.4 kg $ha^{-1}$<br>Amistar 0.5 l $ha^{-1}$ |

**Appendix 3.2**




Weather conditions during lysimeter experiment, chapter 3. Bars represent sunshine hours and line represents mean daily temperature.