Physical effects of soil drying on roots and crop growth

Andrew P. Whitmore\textsuperscript{1,2,*} and W. Richard Whalley\textsuperscript{1}

\textsuperscript{1} Cross Institute Programme for Sustainable Soil Function (SoilCIP), Centre for Soils and Ecosystem Function, Department of Soil Science, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK
\textsuperscript{2} Centre for Bioenergy and Climate Change, Department of Soil Science, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK

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Abstract

The nature and effect of the stresses on root growth in crops subject to drying is reviewed. Drought is a complex stress, impacting on plant growth in a number of interacting ways. In response, there are a number of ways in which the growing plant is able to adapt to or alleviate these stresses. It is suggested that the most significant opportunity for progress in overcoming drought stress and increasing crop yields is to understand and exploit the conditions in soil by which plant roots are able to maximize their use of resources. This may not be straightforward, with multiple stresses, sometimes competing functions of roots, and conditions which impact upon roots very differently depending upon what soil, what depth or what stage of growth the root is at. Several processes and the interaction between these processes in soil have been neglected. It is our view that drought is not a single, simple stress and that agronomic practice which seeks to adapt to climate change must take account of the multiple facets of both the stress induced by insufficient water as well as other interacting stresses such as heat, disease, soil strength, low nutrient status, and even hypoxia. The potential for adaptation is probably large, however. The possible changes in stress as a result of the climate change expected under UK conditions are assessed and it appears possible that wet warm winters will impact on root growth as much if not more than dry warm summers.

Key words: Crop, drought, hypoxia, mechanical impedance, physical stress, root, root environment, root growth, soil, water-logging.

Introduction

The purpose of this review is to examine what is known about the interactions between stresses on root growth induced by drying in soil. The ability of roots to penetrate strong soil has been reviewed by Clark \textit{et al.} (2003), the response of roots to soil physical stresses by Bengough \textit{et al.} (2006), the management of root systems by Hoad \textit{et al.} (2001), and means to sense the root environment by Clark \textit{et al.} (2005). Biophysical processes in the rhizosphere have been comprehensively reviewed (Gregory and Hinsinger, 1999; Gregory, 2006; Hinsinger \textit{et al.}, 2009) and the process of root-shoot hormonal signalling by Dodd (2005) and Davies \textit{et al.} (2000, 2002). Our review concentrates on neglected or poorly understood phenomena which have been overlooked, as well as on more recent findings. Although water stress is almost certainly the most intensively-researched physical stress to root growth, field data show that it alone may not be the critical stress. This review will explore the sometimes overlooked problem of the effect of several different physical stresses on roots acting in combination or in sequence. This problem has received more attention in the soil science literature than it has in the plant science community. Hypoxia, water stress, and mechanical impedance to root growth all change when the water content of the soil is altered. Both laboratory and field data will be cited to show that even well-watered soil can be sufficiently strong to impede root elongation. If we are interested in drought avoidance, then the most productive line of research is likely to be connected to the effects of high soil strength on root and plant growth. Soil type affects the balance between water stress and high soil
strength and it is possible that whether a soil shrinks or not as it dries determines this balance. The ability of shrinking soils to stay mechanically weak when they dry may contribute significantly to the greater yields found on clay soils, although this is conventionally attributed to better nutrient status. The rhizosphere interfaces directly with the root (for a review see Hinsinger et al., 2009), but there is much that even the properties of bulk soil can tell us about the processes at the root–soil interface. Still less is known about the way different stresses interact in soil. This review has three main sections. Firstly, it examines the ways in which the scientist is able to study roots and the root environment. Because this region is difficult to access many techniques involve inference, and the limitations of methodology on our understanding will be discussed. Secondly, it explores several poorly-understood or neglected processes in soil, which nevertheless impact strongly on root growth. Thirdly, it reports on the response of plants to stress, including a number of less well-known responses. In conclusion, the implications of climate change are assessed, taking account of the stresses and plant responses discussed in this review.

Studying the physical root environment

Sensing the root growth environment

Progress on understanding how roots and plants respond to their environment is hindered by our ability to measure the physical stresses they encounter in soil accurately. In the field, measurement of matric potential can be inaccurate and misleading (Whalley et al., 2001, 2007a, 2009). Water-filled tensiometers can report matric potentials, \( \psi \), of the order of \(-90\) kPa even though the soil has actually become much drier than this (Marinho et al., 2008; Whalley et al., 2009). An example of such misleading output from a tensiometer is shown in Fig. 1. As soil dries (with time) the output from the water-filled tensiometer reads to a minimum potential (maximum tension) of \(-90\) kPa and eventually fails. That the soil dries during this time is shown by the output from a porous matrix sensor (Or and Wraith, 1999; Whalley et al., 2009) and measurements of the degree of saturation based on the water content, \( \theta \). Porous matrix sensors infer matric potential from the water content of a porous ceramic with a known water-release characteristic. The measurement range of these sensors is determined by the pore sizes of the ceramics used in the sensor. The sensors have the advantage that they do not fail at low matric potentials, but they can be inaccurate if used outside their calibration range and are sometimes criticized because they give an indirect measurement of matric potential. The difficulty with the commonly-used water-filled tensiometers is not only that they are not accurate in dry soil, but more importantly that it is not clear when the tensiometer is providing reliable data and when it has failed. It seems likely that improved porous matrix sensors (Or and Wraith, 1999; Whalley et al., 2009) will be used increasingly to provide more reliable matric potential data over a much wider range of matric potentials relevant to root growth.

The mechanical strength of soil can easily be measured with a penetrometer. Here the force needed to push a cone through the soil is expressed as a pressure by dividing the force by the area of the base of the cone. Figures 2a and b show how penetrometer resistance and matric potential are related to each other. Typically, penetrometer pressures of \(2\)–\(2.5\) MPa or more are sufficient to impede root elongation significantly (Bengough and Mullins, 1990; Da

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Fig. 1. Soil water status plotted against time at a depth of 20 cm in a soil that is being dried by the roots of winter wheat (Whalley et al., 2007a). Note that the water-filled tensiometer records a lower limit to soil drying of approximately \(-90\) kPa, whereas a porous matrix sensor (PMS) reports that the soil continues to dry, which is supported by estimates of the degree of saturation determined from a soil moisture meter.

Fig. 2. The mean penetrometer resistance at a depth of 20 cm (a), the matric potential at a depth of 20 cm plotted against time (b). Note that when soil dries to \(-80\) kPa the penetrometer resistance exceeds 2 MPa. These data are redrawn from Whalley et al. (2006) with kind permission from Springer Science+Business Media: Plant and Soil, Does soil strength play a role in wheat yield losses caused by soil drying? Vol. 280, 2006, pages 279–290, Whalley WR, Clark LJ, Gowing DJG, Cope RE, Lodge RJ, Leeds-Harrison PB, Fig. 1, © Springer. Part of Springer Science+Business Media.
Silva and Kay, 1997; Bengough et al., 2006). However, it is misleading to think of this as a threshold value, since the elongation rate of roots decreases in an approximately linear fashion until high penetrometer pressures are encountered.

Of all the measurements to characterize the soil environment in recent years, the greatest advances have been made in the measurement of soil water content. Unfortunately, soil water content is not itself a stress, but it is correlated with other stresses such as water stress (potential), oxygen stress, and soil strength. Furthermore, water content and physical stresses are related in highly non-linear ways and differ between soil types. In drying soils, for example, very small changes in water content can lead to very large changes in water potential. The accuracy of the water content sensor severely restricts the range where meaningful inferences on matric potential can be obtained.

Oxygen stress is relatively easy to measure, although it is more helpful to consider it in terms of oxygen flux to the root (Blackwell and Wells 1983). Key papers in this area have been published by Armstrong and coworkers (Armstrong, 1994) which describe how the polarographic method can be used to measure the flux of oxygen to a platinum electrode. This method works well in wet soil, but as soil dries the measurement can become flawed (Whalley et al., 2000).

Experimental difficulties in the investigation of the effects of physical stresses on plant growth

As Mittler (2006) has observed, the uptake of results by the industry from laboratory data on the effects of water stress on plant growth has been disappointing. This is almost certainly due to the fact that the several stresses on root growth are not independent of each other. Mittler (2006) remarked that for progress to be made, the plant scientist should study stress combinations relevant to field conditions. Few would disagree with this goal, but, in practice, this is not easy to achieve. Much of the work on the effects of water stress on plant growth have used model systems in which water stress is varied independently of other stresses in a root growth environment that is well-aerated and mechanically weak (see Whalley et al., 2000, and references therein). This produces data which can be interpreted more easily but it is less helpful for understanding plant growth in the field. The results of even simple laboratory model systems can be confounded by interactions between different stresses. For example, Verslues et al. (1998) report that when polyethylene glycol solution is used to simulate the effects of water stress (via the osmotic rather than matric potential), it is likely that reduced oxygen availability will affect root elongation.

To gain some insight into the interaction between the effects of oxygen availability and water stress on root elongation in the context of the soil physical condition, it is instructive to consider the maximum growth pressure on roots. When roots elongate in soil, assuming they are not in large pores, they must generate a growth pressure from cell turgor and the relaxation of the cell walls in the root (Greacen and Oh, 1972; Clark et al., 1996). In drying soil, the ability of roots to generate growth pressure is impaired (Whalley et al., 1998) while the strength of the soil (i.e. that growth pressure required) increases. In very wet soils, the flux of oxygen to the roots is restricted, impairing further the ability of a root to generate growth pressure (Eavis et al., 1969).

It is tempting to think that if soil is used in experimental systems, the results will have direct field relevance. However, the difficulty with this line of logic is that the interpretation of plant responses remains specific to that soil type, because they are pertinent to a certain and often unique combination of stresses. There is a significant body of literature (Hakansson and Lipiec, 2000), for example, that relates soil bulk density to plant growth, and in recognizing the limitation of this approach, attempts have been made to generalize by developing the concept of a reference bulk density to allow comparison between soil types. It remains very difficult, however, to relate plant physiological functions to what is, in effect, a soil condition rather than a plant stress. While such data may well be important as an empirical management tool, they are less useful for identifying critical physical stresses or combinations of stresses that limit plant growth or for deciding how to optimize soil–plant interactions in order to maximize yield. Thus, the concerted effects of several stresses and the fact that certain properties of soil that can readily be observed are not in themselves stresses suggests that a modelling approach could help in understanding the effects of soil drying on plants and their roots.

Modelling the effects of drying on roots

Bengough et al. (2006), in reviewing the response of roots to soil physical conditions, cite the use of da Silva and Kay’s (1997) succinct and practically-relevant Least Limiting Water Range (LLWR). This concept expresses the range of water contents in soil in which roots are able to grow and penetrate the soil matrix. Da Silva and Kay (1997) analyse the effect of the LLWR in different soils on rooting in the top 20 cm. The range has proved a useful concept, but inevitably attracts criticism because it is so succinct. Bengough et al. (2006) point out that the deeper layers may be important too and that the LLWR will be affected by agricultural practices such as tillage and compaction or by environmental conditions that change soil structure such as wet–dry and shrink–swell cycles. Measurements of penetration resistance in three contrasting soils made by Gregory et al. (2007) found that the strength of a sandy loam, sandy clay, and clay soil in the UK was greater than 2 MPa below 40 cm throughout the year and that soil below 30 cm was stronger than 2 MPa for the majority of the spring and summer. This has been verified using a computer simulation model (Whitmore, 1995, 2007) coupled with a pedotransfer function to estimate strength (see below; Whalley et al., 2007b). Even in surface soil, Betz et al. (1998) found that the LLWR could become very small under zero tillage, that is to say the range of water contents supporting root
Root extension is very small. Root impedance is probably not the threshold that the LLWR suggests, however. McKenzie and McBratney (2001) suggest a concept they call the Partial LLWR whereby the range is extended. Nonetheless, use of LLWR would suggest that root extension into the soil matrix below 40 cm is possible on few days of the year only. Roots extend most easily through macropores or regions of weakness in the soil and the importance of structure is thus likely to be in maintaining large pores into which roots can elongate (see below). A correction would appear to be needed to LLWR to express the greater homogeneity of exploitation of the soil volume by roots in sandier and structured soils.

As a first approximation in loose soil, there is a common relationship between matric potential and soil strength, $Q$, for a range of different soils. In agricultural soils, it is the capillary forces between particles that give soil its strength. These forces are expressed by the matric potential but clearly the more fine capillaries there are that are filled with water the stronger the soil will be and so if the matric potential is then multiplied by the degree of saturation $S$ (defined as $\theta/\theta_{\text{max}}$ where $\theta$ is the water content and $\theta_{\text{max}}$ is the maximum water content or soil porosity), there is statistical improvement (Fig. 3).

$$Q \propto |\psi S|$$  \hspace{1cm} (1)

What these data show is that even if loose soil is used in growth experiments to provide a water stress, it is not possible to discount the effects of high soil strength on root and plant growth. A seemingly anomalous prediction of Equation 1 is that as soil becomes increasingly dry and $S$ approaches zero, the soil is predicted to become weaker, decreasing from a maximum. Indeed, for sand–kaolinite mixtures this has been shown to be the case (Mullins and Panayiotopoulos, 1984) and beach sand behaves in a similar manner. However, in agricultural soils, strength does not decrease from the maximum probably because of cementation by biological exudates and mineral precipitation as soil dries. Provided it is applied within the range of the agricultural soils from which it is derived, a more general relationship between water stress and soil strength for soils of various densities was derived by Whalley et al. (2007b).

$$\log_{10}Q = 0.35\log_{10}(|\psi S|) + 0.93p + 1.26$$  \hspace{1cm} (2)

This pedotransfer function was developed for a large number of Canadian soils and UK data. It provides two important messages which are illustrated conceptually in Fig. 4. Firstly, even wet soils can be strong. Secondly, dense soils become too strong for roots to penetrate at relatively high matric potentials (i.e. in well-watered soils). An important feature of equation (2) is that it is not specific to soil type, which has been achieved, in part, by expressing soil water status as the product $|\psi S|$. Soil density is included and subsumes the internal friction which needs to be overcome in order to rearrange soil particles. This friction increases as soil becomes more dense. Although it is possible to calculate penetrometer pressure precisely (Farrell and Greacen, 1966), too much information is needed from geotechnical soil tests, which are time-consuming to make in practice. Moreover few laboratories are sufficiently well-equipped to make these tests. Thus equation (2) is a compromise, can be improved as more data become available, but provides a relatively simple and robust method to explore the interaction between water stress and soil strength.
### Effects of drying

**Soil structure**

There is no consensus on how soil structure benefits crop growth (or otherwise), although it is frequently assumed that a ‘well structured’ soil allows deep root penetration and access to water at depth (Passioura, 1991) and possibly to air (see below; Kooistra and Van Noordwijk, 1996). In this context well-structured usually refers to the existence of continuous pores from the surface to soil at depth, which allow roots to by-pass compacted or damaged soil. Structure, however, is a state, not a stress, which has sometimes led to confusion in the literature. The difficulty of arriving at a consensus on the effects of soil structure on plant growth is that soil structure is a soil condition which affects the balance of stresses (water, air, and soil strength) that directly affect crop growth. Soil structure can also influence the root length distribution with depth and most research effort has been directed towards the identification of impenetrable layers. Table 1 emphasizes the importance of structure in supplying root accessible pores. Without structure, only a very light soil has an appreciable number of pores into which roots or root hairs can penetrate without expanding a cavity. Such pores also offer the root a means to anchor itself in soil thus providing the necessary purchase against which to exert pressure elsewhere. Interestingly, root length (but not mass) has been found to be greater in sand than clay soils (Hoad et al., 2001) supporting the idea that root extension into pores is easier in soils with pores of the optimal size. As Table 1 shows, unstructured soils tend to have little pore space into which roots can grow directly and the creation of pores between structures in medium and heavy textured soils is likely to be important for root growth. Even root hairs seem able to expand slightly into a clay matrix (Champion and Barley, 1969). There is an extensive literature describing the interaction between plant roots and soil structure (Ball et al., 2005) and crops. Roots exert an effect on soil structure in their turn.

Good structure is critical for crop establishment because an optimal seedbed for root exploration should contain a wide variation of aggregate sizes with a mean roughly the same size as the seed (Dexter, 1988). This facilitates both exploration and anchorage by the seminal root system. Winter crops in the UK are sown into a dry but wetting environment. Generally, however, there is sufficient water vapour in the soil atmosphere for germination (Wuest, 2007).

### Shrinking and swelling

Soils with appreciable amounts of clay minerals tend to shrink when they dry but swell on rewetting. Typically, at the surface of the soil, shrinkage is isotropic and, on drying, shrinkage leads to a change in height of the land as well as the opening of cracks in soil, some of which can reach surprising depths (1 m or more; observation by the authors). Roots bridge the cracks and have been observed to be snapped as a crack expands, but it is not clear to what extent this affects plant growth. Rainfall may penetrate more deeply than would otherwise be the case, which can facilitate the rewetting of shrinking soils (Armstrong et al., 1999). When shrinking soil dries, despite the fact that the bulk density increases, the value of \( \psi \) in equation (2) remains small in comparison with its value in a drying rigid soil. This is because the drying, shrinking soil remains relatively saturated and has a higher value of \( \psi \) (i.e. closer to zero) as the soil shrinks. By contrast, as a non-shrinking sandy soil dries, \( \psi \) will become low (i.e. large and negative) and \( S \) decreases after only a relatively small amount of water is removed by roots. Gregory et al. (2007) found that a clay soil remained weak enough for roots to penetrate whilst continuing to supply water to a growing wheat crop throughout much of the growing season whereas a neighbouring lighter soil, also cropped to wheat, soon became too strong for roots to penetrate in the early spring. The ability of heavier soils to yield substantially more than lighter soils is often attributed to their ability to supply nutrients or avoid simple drought. Figure 5 suggests that the ability of the roots to continue to penetrate soil (and

### Table 1. Volume (% by volume) available for anchorage and root exploration in the stated soils in the stated ranges

<table>
<thead>
<tr>
<th>Volume of pores (% by volume)</th>
<th>% Composition of soils</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5–5 kPa</td>
<td>5–30 kPa</td>
</tr>
<tr>
<td>Clay</td>
<td>Silt</td>
</tr>
<tr>
<td>Silty clay loam</td>
<td>3</td>
</tr>
<tr>
<td>Sandy clay</td>
<td>2</td>
</tr>
<tr>
<td>Light sand</td>
<td>3</td>
</tr>
<tr>
<td>Sandy loam</td>
<td>1</td>
</tr>
<tr>
<td>Clay</td>
<td>.1</td>
</tr>
</tbody>
</table>

Fig. 5. Measured differences in strength (kPa) in June 2005 to 50 cm depth between soils cropped to winter wheat and those kept fallow: a clay (dotted line) and sandy loam (solid line). The dashed line is the SED for the comparison between soils at each depth. Data reworked from Gregory et al. (2007). The clay soil thus remains weaker relative to its control (unplanted) as it dries than the sandy loam soil.
provide fewer root-sourced signals) as it dries is likely also to play an important role in allowing the crop to exploit available nutrients and water.

**Hysteresis**

On wetting, the change in water potential, $\psi$, follows a different relationship with the change in water content, $\theta$, from that when the soil dries (Fig. 6). Strictly known as the soil water characteristic, soil scientists conventionally think of a soil water release curve because measurements of this relationship are made more easily on soil that is progressively dried. Measurements of soil water uptake are less common because the standard equipment in soil physics laboratories does not allow the soil to be rewetted at matric potentials smaller than –80 kPa. There are a number of reasons why soil water exhibits hysteresis: one of the main ones being the ‘ink-bottle’ effect, where a pore drains in accordance with the diameter of its entrance but refills according to the diameter of its body. For any given water content, soil water can be held at one of many matric potentials bounded by the main drying and the main wetting curves (Fig. 6A). Raats and Duijn (1995) have gone as far as to argue that water can move from a ‘drier’ to a ‘wetter’ region in soil (as determined by $\theta$) if the potential gradient in $\psi$ is favourable.

In practice, water and shrink–swell hysteresis interact since the change in pore size distribution with shrinking and swelling affects the water characteristic. Full wetting up of a soil that shrinks and swells probably occurs only after the end of the growing season. This offers an explanation for the observations of Gregory *et al.* (2007) that soil resistance to a penetrometer persisted into the autumn even after sufficient rain had fallen to reduce the soil water deficit caused by the growing wheat.

Hysteresis is only one aspect of the uncertainty in employing the water release characteristic in order to help understand the plant response to dry soil. Gallipoli *et al.* (2003) show how it may be better to think of matric potential as a function both of water content and porosity (Fig. 6A). It is usually assumed implicitly that porosity is a fixed parameter, but unfortunately this is not the case, because porosity changes due to shrinkage or in response to external stresses on the soil. The external stresses may be due to the impact of machinery or indeed due to growth pressures from roots themselves. The effects of soil deformation on the water release characteristic and related hydraulic properties need to be understood. In Fig. 6B the relationship between the degree of saturation $S$ and matric potential $\psi$ is given by Gallipoli *et al.* (2003) as

$$
S = \left( \frac{1}{1 + \left( A(\nu - 1)^b \psi \right)^n} \right)^m \tag{3}
$$

where $\nu$ is the specific volume of soil and the remaining quantities ($A$, $b$, $n$, and $m$) are fitted parameters. In practice, the water release characteristic will trace a path along the surface plotted in Fig. 6B. The void ratio will be determined by shrinkage or external forces on the soil, such as compaction or shear deformation. How well equation (3) captures the effect of shear deformation on the soil water characteristic remains to be tested for agricultural soils, although it does give good predictions for mixtures of sand and kaolinite.

While the effects of shrinkage and exudates on soil structure have received much attention (Czarnes *et al.*, 2000) there is a requirement to understand how deformation of the capillary matrix affects soil hydraulic properties (Berli *et al.*, 2008).

The water release characteristic and hydraulic properties for any soil do not follow a unique relationship with the amount of water in soil. For this reason, matric potential inferred from soil water content measurements using a water release characteristic can only be treated as approximate and, as noted earlier, there are limits to the accuracy with which stresses can be inferred because of the non-linear

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**Fig. 6.** Water release characteristic as influenced by hysteresis (A) and deformation (B). Both these sets of data were obtained with a published model for hysteresis and for the effects of soil deformation on the water release characteristic. The figures illustrate that even for a given soil, the water release characteristic is not a unique relationship.
nature of these relationships. Although Wraith and Or (2001) advocate this approach, it may nevertheless be better to measure matric potential with an appropriate sensor rather than measure \( \theta \) and rely on the water release characteristic.

Waterlogging

Strangely, prior waterlogging may indirectly exacerbate stress from drying. Dickin and Wright (2008) showed that wheat that became waterlogged shortly after sowing suffered yield losses of between 20% and 24%. Although these authors found no additional yield loss from plants that were first waterlogged and then droughted, they did notice a reduction in roots at most depths in the waterlogged treatment and, in particular, below 60 cm. They suggested that, without deep roots, crops could be more susceptible to prolonged summer drought. They observed a delay in plant development to the extent that only about 30–40% of ears had emerged 93 d after sowing in the waterlogged treatment compared with 80–90% in the controls. Belford (1981) also found a short delay in ear emergence of 2–5 d as a result of waterlogging. Clark et al. (2003) observed that predicting the ability of roots to overcome mechanical impedance depends on the stress history of the root as well as the nature of the impedance. By this they mean the impedance history, but it seems possible that roots waterlogged early in growth may be weaker than similar, unstressed roots. There seems to be a delay of 2–3 d after the relief of the stress before roots are able to extend once more. Although wheat roots are able to develop aerenchyma as a result of either water or nutrient stress (Lynch, 2007), further root extension does not seem to occur if the exposure to an oxygen-free environment occurs once the length of a root exceeds 10 cm (Thomson et al., 1990). Roots growing into waterlogged subsoils would therefore appear to be particularly susceptible.

Surface layers of soil are usually well oxygenated, even when wet, since the diffusion coefficient of \( O_2 \) in air is between 1 and \( 2 \times 10^4 \, \text{cm}^2 \, \text{d}^{-1} \) depending on temperature. However, in water it is much less \( (1–2 \, \text{cm}^2 \, \text{d}^{-1}) \). In soil, the tortuous nature of the pore network means that effective diffusion constants are rather less than in air alone. An increase in temperature will lead to a sharp increase in respiration of both roots and soil and, as a result, subsoils may be less well-aerated. Most roots contain porous internal channels to some extent, however, and De Willigen and van Noordwijk (1989) estimate that typically up to 30% of a root’s oxygen demand may be met via internal transport depending on root thickness.

Lodging

Roots provide anchorage in soil. In high winds, it is advantageous for a plant to be anchored in a strong medium such that the stresses imposed by the wind can be borne over a large part of the root system. If the surface soil is weak and wet, it is likely that the upper root system will bear the brunt and could rupture even if the stem is able to withstand the strain. Baker et al. (1998) model lodging in wheat but relate soil strength partly to water content alone. It is possible that better separation between soils might be obtained with the use of equation (1) rather than \( \theta \) or \( \psi \) alone.

Adaptive responses of plants to drying

The water regime in the soil appears to lead to quite harsh conditions for roots. The environment can change quickly from too wet to respirate to too strong to penetrate; so how do roots reach the subsoil or extract the water that is present? Some plant responses that may help mitigate the effects of extremes in the stresses experienced by plants in a drying soil are discussed here.

Exudation

Exudation of carbon rich substrate into soil and other rhizodeposition as a result of root turnover have been the subject of various reviews (Hoad et al., 2001; Hinsinger et al., 2009). Roots are thought to emit polysaccharides and organic acids in order to enhance the solubility of poorly-accessible nutrients such as phosphorus, or to chelate \( Al^{3+} \) so reducing aluminium toxicity (Lynch, 2007). Exudation probably reduces the frictional component of the resistance to root extension into soil (Ijima et al., 2000). However there are other possibilities. Whalley et al. (2005b) showed that aggregates taken from the rhizosphere of maize and barley plants retained significantly less water at \(-6 \, \text{kPa} \) matric potential than aggregates taken from the bulk soil. By implication, the rhizosphere was more aerated at this potential. Although a similar experiment with winter wheat plants did not find significant differences between rhizosphere and bulk soil, there was, nonetheless, an increase in aeration in the rhizosphere soil, which was greatest at \(-6 \, \text{kPa} \). Read et al. (2003) found a similar change in the water release curve when bulk soil was treated with a phospholipid typical of exuded compounds. A matric potential of about \(-6 \, \text{kPa} \) is close to the critical value at which root-sized pores will be full of water making external transport of air difficult. So plants that are able to enhance the aeration around their roots may well be able to continue growing into soil that is weak, because it is wet, without the restriction of being unable to respire. Although wheat can produce aerenchyma, their production is thought to have a cost to the plant (Lynch, 2007) and certainly makes roots thicker. Conversely, Young (1995) has argued that, because \( \theta \) was greater in soils below \(-6 \, \text{kPa} \), more water is available to the plant. These conclusions are not necessarily contradictory, they simply suggest that the plant is able to access greater amounts of water for any given effort against the local potential in soil.
Wilting occurs if the leaf water potential exceeds the integral of the water potential at the soil–root interface modified by a resistance to transport term in the plant. Although Barraclough et al. (1989) showed that droughted soils at Rothamsted could produce comparable yields of wheat using less water than control plots, there is undoubtedly a minimum transpiration stream needed for full productivity. Liste and White (2008) have reviewed the mechanism known as hydraulic lift. Roots are a highly conducting medium, often having a far greater internal hydraulic conductivity than the external dry soil. Thus, they may be able to act as a passive conduit at night for the transport of water along the potential gradient from subsoil to topsoil, from a sparse to a dense root system. The amount of water that it is possible to move in this way is estimated to be between 14% and 33% of the daily evapotranspiration demand (Liste and White, 2008). This range is sufficient to explain the difference in the water use between droughted and undroughted wheat found by Barraclough et al. (1989). Direct evidence for hydraulic lift comes from the fact that deuterated water supplied to the roots of one plant was found in the stems of another (Caldwell et al., 1998) suggesting an explanation for a part of the more efficient resource capture found under intercropping. Inverse hydraulic lift, where water transport to deep, dry soil is enhanced by roots in excess of matrix flow has also been demonstrated (Caldwell et al., 1998). McCully (1995) suggested that roots release and hydrate mucilage which, in turn, coats and stabilizes soil structures in the rhizosphere but that this differed from passive hydraulic lift in that the hydration was driven by internal pressure from within the root.

Support for the idea of hydraulic lift in wheat is shown in Fig. 7. Matric potentials are very sensitive to small changes in water content, especially in a sandy soil, as is the case here, making the effect easier to detect. Interestingly, penetrometer pressure, as predicted with equation 2, decreases slightly overnight, because the soil rewets (Fig. 7B). It is not impossible that matrix flow could account for these observations, but it is difficult to explain how intermediate soil layers show little evidence for the passage of water en route to the surface.

Root growth and distribution

Ho et al. (2005) suggest that plants which increase the density of their roots in the topsoil are able to acquire phosphorus more effectively than those which do not. They argued further that genotypes with roots that proliferate deep in the soil are better able to withstand drought stress. Lynch (2007) asserts that crops tend to develop roots in the surface soil for nutrient acquisition (particularly P) and in the subsoil for water. Liu and Li (2005) found that reduced root activity induced by drying early in growth enhanced grain production from which they deduced that photosyntheticate was reserved for enhanced exploration of the growing medium later. However, these authors grew their spring wheat plants in vermiculite which remains weak when dry. Growth regulators are applied in practical farming to improve the harvest index of cereals and the breeding of short-strawed varieties has achieved a similar outcome. The genes associated with reduced height do not seem to affect the ability of roots to penetrate soil (Kubo et al., 2005), nor do growth regulators seem to reduce the tensile strength of roots (Hoad et al., 2001). Mycorrhiza often enhance the drought tolerance of plants able to form such associations compared with non-mycorrhizal plants and have been shown to improve the uptake of water by wheat in dryland areas (Al-Karaki et al., 2004), but the costs of maintaining high density relationships with mycorrhiza can reduce yields.
of the host wheat plant (Ryan et al., 2005) presumably through the consumption of photosynthate by the fungus. Van Noordwijk and de Willigen (1987) reviewed much of the older literature showing that growing a large root system often penalized above-ground growth, although a large root system seemed to reduce the risk of crop failure as a result of nutrient or water stress. Van Noordwijk et al. (1998) argue that a plant cannot afford to continue to invest in root maintenance during dry periods and that the plant may be better served by allowing part of the root system to die and reinvest in new growth when favourable conditions return. By contrast, Hoad et al. (2001) suggest that root length and mass tend to be conserved between seasons. Hoad et al. (2001) offer an explanation for these different views in that root extension rate can vary considerably and so, presumably, root demand could conflict temporarily with shoot demand at a critical developmental stage, leaving the shoots permanently retarded. Waines and Eghdaie (2007) conclude that the root systems of modern wheat cultivars are small, having perhaps two-thirds of the root mass of the landraces from which they derive. Doubtless this lack of root is a result of selection for larger yields of grain when grown under optimal management, nutrient and water supply. Over the long-term it seems likely that crops can influence soil properties with the organic carbon that they leave behind (Watts et al., 2001, 2006).

The diameter of a typical root hair is unlikely to be much less than 10 µm, yet pores of this size drain under a suction of 30 kPa. Such suction is often quoted as field capacity, i.e. pores of this size drain under gravity within a few days. This being so, root–water contact can rarely be complete without the risk of hypoxia from standing water. A simple calculation of the root surface area cannot therefore be taken as a guide to access by the plant to water unless uptake from the vapour phase is appreciable (Dalton, 1988). Van Noordwijk et al. (1993) and van Noordwijk and de Willigen (1984) have developed a methodology for assessing root–solid and root–air contact. Veen et al. (1992) suggest that roots might try to optimize root–water and root–air contact and that the local distance between air gaps could be important in determining this optimum. Recently, Segal et al. (2008) have argued on the basis of modelling that root hairs do not increase the root surface area but function by effectively increasing the radius of the parent root. The effective root area is then a cylinder bounded by the tips of the root hairs. It is this area then that will require optimization for root–soil and root–air contact.

**Root–shoot signalling**

Root-sourced signalling that controls shoot elongation and stomatal conductance has recently been reviewed comprehensively (Davies et al., 2000, 2002; Clark et al., 2005; Dodd, 2005). A key question to resolve in a multi-stress environment is what physical stress (or combinations thereof) trigger the signalling processes. Although most work has been directed at the effects of water stress, the impacts of high soil strength on shoot growth are well documented (Masle and Passioura, 1987) and they can be observed at matric potentials much higher (i.e. less negative) than those frequently used by plant scientists to investigate the effects of water stress. For example, Sharp (2002) used water potentials as low as −1.5 MPa, whereas clay and sandy soils can be too strong for root penetration at matric potentials of −100 and −250 kPa, respectively (Whalley et al., 2005a). To explore the effects of high soil strength per se, Whalley et al. (2006) grew wheat in a sand culture system that allowed the mechanical strength of the root growth environment to be increased without affecting aeration or the hydraulic environment. They found that, simply by increasing the mechanical strength of the root zone, shoot growth was approximately halved. Since there was no change in the stomatal conductance this suggests that the reduction in shoot growth was mediated by chemical signalling. It is generally accepted that shoot growth responses to stress in the root zone are determined by a combination of hydraulic and chemical signalling. To make progress at interpreting how root-sourced signalling can affect crop growth, the question of how the root system as a whole responds to the conditions within the soil profile needs to be addressed. Interestingly, in laboratory experiments, Blum et al. (1991) concluded that shoot growth was not limited by water availability per se, but by drying of the surface soil. In field experiments, the increased strength of the soil surface (Whalley et al., 2008) appeared to give the best explanation for reduced yield of winter wheat and, by comparison with previous work (Whalley et al., 2006), yield loss appeared to be related to soil strength rather than to low matric potential. It is too simplistic to say that we simply need to focus on conditions in the soil surface, since deep roots are important for accessing water at depth. In Fig. 8 a conceptual model is illustrated, outlined in narrative by Whalley et al. (2008), of how stresses on deep and shallow roots may interact to determine shoot elongation. Recently, Dodd et al. (2008) have shown, by experiment, that if soil heterogeneity is taken into account, it is possible to explain more of the variation in xylem ABA.

Our conceptual model shown in Fig. 8 has been partly parameterized in the sense that Sperry et al. (1998) have developed a model that allows it to be determined whether soil or xylem conductance is limiting water uptake for a given root to shoot ratio. There seems to be an urgent need to include signalling processes in such models, since this would allow optimal root length distributions that maximize yield in drying soils to be identified. A prerequisite would seem to be a model of the root water potential (Bruckler et al., 2004). Despite this, few models exist which calculate the root water potential, approximating it instead with the soil water potential. Nor do most modellers seem aware of the hormonal response of the plant to this parameter (an exception being Lafolie, 1991).

**Climate change**

The climate in most parts of the UK is forecast to become warmer and wetter in the winter with warmer but drier summers. We can interpret the effect of these changes on
roots and crops by means of the stresses and responses to stress discussed in this review (Table 2). Note that, in compiling this table of effects on roots, no account is taken of wider plant system responses such as an acceleration of phenology (Semenov, 2009).

In Table 2 an attempt has been made to score the stress on a plant, the effect of climate change on soil water, i.e. an impact or the response a plant can make. Thus a stress scores negatively but a response scores positively if it is something that is likely to alleviate a particular stresses. It is clearly difficult to make a quantitative judgement as to the relative effect of each stress without detailed experimentation or at least modelling. The scores must be treated with caution therefore and probably represent little more than a tally of processes having a relevant impact. With this reservation, however, plants look to have some ability to deal with drier conditions during spring or summer. This is not to say that this or that plant or this or that variety will cope. Nor is it to say that crop yields might not be impacted. It simply says that from what we know about plants, mechanisms exist which may help alleviate drying stresses. It is more surprising to look at this table and see that wetter winters may have a more serious impact on crop yields than drier summers. This is partly because of the wet period itself and partly because the early stress may make the plant more susceptible to subsequent drought. It may also be that the more mature crop is capable of ameliorating its environment in the spring and summer to a greater extent.

**Table 2.** The possible effects of climate change on the ability of crops to withstand drought and continue to yield well

<table>
<thead>
<tr>
<th></th>
<th>Direct effect on plant of drying from</th>
<th>Indirect effect via soil</th>
<th>Importance of response to alleviate stress</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hypoxia&lt;sup&gt;a&lt;/sup&gt; Strength Lodging Hysteresis Shrink-swell Root-shoot signalling&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Hydraulic lift Exudation Balance</td>
<td></td>
</tr>
<tr>
<td>Wetter autumn/winters</td>
<td>– – – –</td>
<td>+ (inverse) +</td>
<td>2+/3–</td>
</tr>
<tr>
<td>Drier autumn/winters</td>
<td>– – – ++</td>
<td>+</td>
<td>2+/-</td>
</tr>
<tr>
<td>Wetter spring/summers</td>
<td>– – ++ –</td>
<td>–</td>
<td>4+/2–</td>
</tr>
<tr>
<td>Drier spring/summers</td>
<td>– – ++ –</td>
<td>–</td>
<td>6+/3–</td>
</tr>
<tr>
<td><strong>Expected UK conditions</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Warmer wetter autumn/winters</td>
<td>– – – –</td>
<td>+</td>
<td>2+/4–</td>
</tr>
<tr>
<td>Warmer drier spring/summers</td>
<td>– – ++ –</td>
<td>++</td>
<td>++</td>
</tr>
</tbody>
</table>

<sup>a</sup> Hypoxia assumed to impact directly on waterlogged roots but also indirectly in association with later stress.

<sup>b</sup> Root-sourced signals probably ensure a plant’s survival in dry soil and might be thought of as having a positive effect. They probably reduce yield, however, and so the impact is negative on balance.
extent than the young seedling in autumn and winter. The lack of adaptive mechanism found in the literature for young plants to hypoxia may reflect a lack of research.

Conclusions

It is our view that drought is not a single, simple stress and that agronomic practice that seeks to adapt to climate change must take account of the multiple facets of both the stress induced by insufficient water as well as other interacting stresses such as heat, disease, soil strength, low nutrient status, and even hypoxia. The potential for adaptation is probably large. Above-ground components of plants are well studied because they are accessible. Roots are less well studied, not just because they are not visible but also because it is difficult to control completely the conditions in which they grow in a manner that is representative of the conditions under which they will be deployed.

The sum of these multi-faceted stresses, the stress history of both the root and the soil, together with the effects of the adaptive mechanisms put into place by the plant make up what we perceive as the effect of drought. In order to be able to understand and predict the yield response of crops, it is necessary to be able to measure, understand, and predict these effects quantitatively. Porous-matrix sensors will improve our knowledge of soil moisture potential from which stress can be inferred. To be able to breed effectively it is necessary to understand the separate and combined traits that cope with the stresses separately and in concert. To manage the crop effectively and to cope with climate change it is necessary to understand the combined effect of changes in soil and water on the various components of the stress on crops, not only as the soil dries but also the extent to which the plant is pre-disposed towards drought stress by prior exposure to hypoxia. Comprehensive measurements of all these stresses and responses for all crops are inconceivable and so it is clear that we need robust models founded upon a sound scientific understanding of the interacting processes in soil that impact on a crop.

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References


Dodd IC, Gregorio E, Davies WJ. 2008. Abscisic acid signalling when soil moisture is heterogeneous: decreased photoperiod sap flow from drying roots limits abscisic acid export to the shoots Plant, Cell and Environment 31, 1263–1274.


