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'Soil conditions and plant growth'

J. B. PASSIOURA

CSIRO, Division of Plant Industry, GPO Box 1600, Canberra 2601, Australia

ABSTRACT

Plants can respond to soil conditions in ways that can not readily be explained in terms of the ability of the roots to take up water and nutrients. Roots may sense difficult conditions in the soil and thence send inhibitory signals to the shoots which harden the plants against the consequences of a deteriorating or restrictive environment, especially if the plants' water supply is at risk. Generally, this behaviour can be interpreted as feedforward responses to the soil becoming too dry or too hard, or to the available soil volume being very small as with bonsai plants, or to roots' becoming infected with pathogens. However, soil that is too soft or in which the roots are forced to grow in very large pores can also induce large conservative responses, the significance of which is unclear. The inhibitory signals may affect stomatal conductance, cell expansion, cell division and the rate of leaf appearance. Their nature is still under debate, and the debate is becoming increasingly complex, which probably signifies that a network of hormonal and other responses is involved in attuning the growth and development of a plant to its environment.

Key-words: biopores; bonsai; feedforward; inhibitory bacteria; root signal; soil structure; water potential.

INTRODUCTION

The title of this paper is in quotation marks because it comes from E. J. Russell's famous book (1912) which gave in its time a definitive account of soil as a medium for plant growth. A major theme of that book, and its later equally definitive editions by his son E.W. Russell, was the impact of soil conditions on the roots' ability to supply the shoot with adequate water and nutrients.

During the last 15–20 years it has become clear that plants can respond to soil conditions in ways that can not readily be explained in terms of the current ability of the roots to take up water and nutrients – that roots sense difficult conditions in the soil and thence send inhibitory signals to the shoots (Davies & Zhang 1991; Jackson 1993; Aiken & Smucker 1996). Such behaviour is known in control theory as feedforward. It contrasts with the more familiar feedback in that it involves direct sensing of the environment, and thereby provides advance warning of change. In plants it is usually a conservative response to a deteriorating or restrictive environment. The range of soil conditions that produce such responses includes: physical (hardness, dryness); chemical (hypoxia, salinity); biological (initial infection by disease organisms).

That plants may have evolved such responses if water supply is at risk makes sense. Once soil water potential has fallen to a level that directly affects leaf water potential there is typically so little available water left in the soil that the plant is in danger of severe wilting. There may be advantage in restricting the development of leaf area, say, well before nearly all of the water supply is gone. In the wild, conservative behaviour is likely to improve the plants' chances of success. In agriculture, the reverse is often true. The domestication of crop plants has favoured production over survival and has often involved removing various forms of conservative behaviour that are common in wild progenitors. Ear shattering in cereals, seed dormancy and excessive height are examples (Evans 1993). The response of irrigated crops to frequency of irrigation is another example. Very high frequencies are often needed to maximize production even when moderate frequencies maintain high leaf water status (Merrill & Rawlins 1979; Garside *et al.* 1992)

This paper explores the ecophysiology of conservative responses of plants to soil physical conditions together with some remarkable microbiological interactions with these conditions. Many such responses can plausibly be thought of as examples of feedforward, of conservative responses to a diminishing supply of water, or to a diminishing ability of the roots to access that water. However, some can not (for example plants may grow slowly in soil that is too soft), and their significance, if any, remains mysterious. The biochemistry and internal physiology of plants behaving in this way is covered by companion papers in this volume (Wilkinson & Davies, p. 195; Sauter *et al.* p. 223; Sharp, p. 211).

CONSERVATIVE RESPONSES TO PHYSICALLY INHOSPITABLE SOIL

Soil hardness

Hardness of soil strongly affects root growth. This hardness is usually expressed in terms of penetrometer resistance – the pressure required to push into the soil a cylindrical probe with a conical tip. Root growth slows markedly once this resistance exceeds about 1 MPa and falls away, roughly linearly, to almost nothing at a resistance of about 5 MPa (Bengough & Mullins 1990; Materechera, Dexter & Alston 1991). The hardness is strongly affected by soil compaction, whether by wheel traffic, the feet of stock, or even the wind-induced movement of large tree roots. It is also strongly affected by soil water content, and can vary many fold over

Correspondence: J. B. Passioura. E-mail: j.passioura@pi.csiro.au

the typical range of available water content in the soil (Bengough 1997).

Soil hardness may also affect shoot growth (Boone 1986; Brereton, McGowan & Dawkins 1986; Wolfe *et al.* 1995). Such effects are often explicable in terms of the inability of the hampered roots to supply the shoot with water or nutrients. However, there can also be a substantial feedforward response, i.e. a response to compaction that cannot be readily explained in terms of the supply of water and nutrients to the shoot (Masle & Passioura 1987; Andrade, Wolfe & Fereres 1993; Mulholland *et al.* 1996; Stirzaker, Passioura & Wilms 1996; Masle 1998)

Figure 1 shows the leaf area of plants whose roots were growing in soil of various hardness. The leaf area was closely related to the penetrometer resistance of the soil, even when this was varied by changing the bulk density or the water content of the soil. The elongation of the roots is strongly affected when the penetrometer resistance is large, but in these experiments there was no evidence that the roots were unable to extract enough water and nutrients for the needs of the leaves. Leaf water potential was unaffected by compaction, and there was no response to luxurious applications of phosphorus, the macronutrient whose uptake is most likely to be affected by a hampered root system. Indeed, leaves typically react very early to uniformly hard soil, even as the first leaf is emerging, when the seedling is still living off nutrients in the seed. Subsequent relative growth rate is much less affected, so that the relative size of plants growing in soft and hard soil remains roughly constant after the initial response, with consistently smaller leaves and consistently slower rates of leaf appearance with the hard soil (Masle & Passioura 1987; Masle 1998).

In the field, plants do not encounter uniformly compacted soil. There, hardness of the soil is spatially, and temporally because of changing soil water content, very variable (Tardieu 1988; Kirkegaard *et al.* 1992). Roots may grow into and out of a layer of hard soil, such as a hard pan, and also grow preferentially in cracks or biopores – large continuous pores made by previous roots or earthworms and other soil fauna (Ehlers *et al.* 1983; Wang, Hesketh & Woolley 1986; Volkmar 1996). Further, the uptake of water by roots dries the soil and thereby hardens it, making it more difficult for roots to grow in – a self-reinforcing process (Bengough 1997). On the other hand, the exudation of water from root tips (McCully 1995) may soften the soil in front of the growing root, thereby easing the passage of the root through the soil. The relative importance of these contrasting effects is yet to be determined.

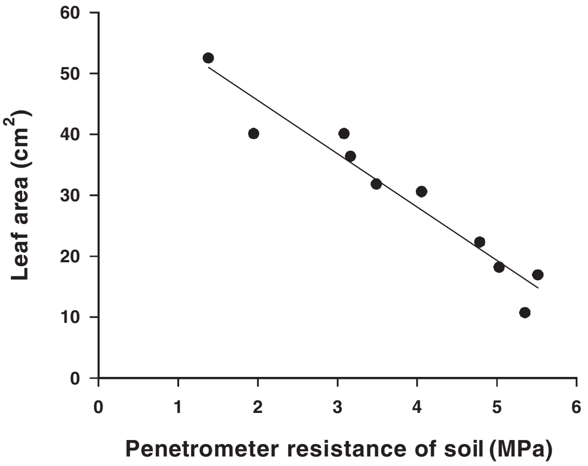

Figure 1. Effect of penetrometer resistance of soil on growth of young wheat plants (adapted from Masle & Passioura 1987).

Work with soil compacted differentially in layers (Masle 1998; Hussain *et al.* 1999) has shown noticeable effects on leaf growth and stomatal conductance as the roots encounter or leave a compacted layer of soil, generally with a delay of a few days between the first experience by the roots of the changed conditions and any effect on growth rate or stomatal conductance. This delay may result more from the time taken for a substantial proportion of the root system to experience the change rather than from a delay in response by individual roots, although even when the soil is suddenly softened by adding water the plants take several days to respond (Masle 1998). Young *et al.* (1997) developed a technique for rapidly and uniformly increasing the mechanical impedance to root growth throughout the rooting medium by squeezing the medium. This technique gave a remarkably rapid effect on leaf elongation rate – within minutes of increasing the impedance, which contrasts with the slow response of the plants in Masle's (1998) suddenly softened soil. Unfortunately, Young *et al.* (1997) did not report on the effect on their plants of removing the pressure they had applied to the rooting medium

The bonsai effect

Plants growing in small containers are typically much smaller than those growing in large, even when they have seemingly adequate supplies of water and nutrients (Richards & Rowe 1977; Peterson *et al.* 1984; Körner, Pelaez Menendez-Riedl & John 1989; Ismail & Davies 1998). The anatomical response of plants to bonsai conditions is startling and rather different from what one would expect from inadequate water or nutrients. Körner *et al.* (1989) showed that the leaves of bonsai plants were small entirely because they had fewer cells. The size of the cells was at least equal to that of control plants, which suggests that the plants had a specific response in cell division to their roots' being crowded. There must have been several fewer cycles of cell division during the formation of each organ in the bonsai plants compared with the normal plants. This response differs from that of plants growing in hard soil, which tend to have smaller leaf cells (Beemster & Masle 1996), though it is possible that the difference reflects the species examined rather than intrinsically different physiological responses to hard soil or to the totally impenetrable barriers that many roots experience when growing in small pots.

One does not normally associate bonsai with plants in the field, but the fact that direct-drilling, the sowing of plants without prior ploughing, often induces slow growth

(Barry & Miller 1986; Fischer, Mason & Howe 1988; Kirkegaard 1995) may reflect a similar response to that of bonsai plants. The roots emerging from the germinating seeds may have access to a very small volume of disturbed soil if the sowing implement has smeared the walls of the slot in the soil into which the seeds are dropped. The slot may thus act as an initially impenetrable container before the roots find comparatively rare pores through which they can access the rest of the soil.

Excessively large pores

Another physical feature of soil that affects the growth rate of plants without affecting the availability of water and nutrients is that of the size of the pores through which the roots are growing. Miller and colleagues (Donald, Kay & Miller 1987; Alexander & Miller 1991) sieved aggregates of different sizes from a loam and found that maize plants growing in pots filled with the smallest of the aggregates grew substantially better than plants growing in the larger aggregates in which the diameters of the inter-aggregate spaces probably exceeded that of the roots – the inter-aggregate spaces presumably had diameters about one fifth of that of the aggregates, as in packed spheres (Fig. 2). All plants had adequate supplies of water and nutrients, so we are left with the conclusion that, as with plants growing in hard soil or small pots, a signal from the roots was affecting the growth rate of the shoot.

These observations have implications for the performance of plants whose roots are growing in biopores, large continuous pores that have been made and maintained by previous roots or soil fauna. If the biopores are particularly large, for example wormholes, which have diameters many times that of a root, the plants may react adversely even if the roots are able to extract enough water and nutrients.

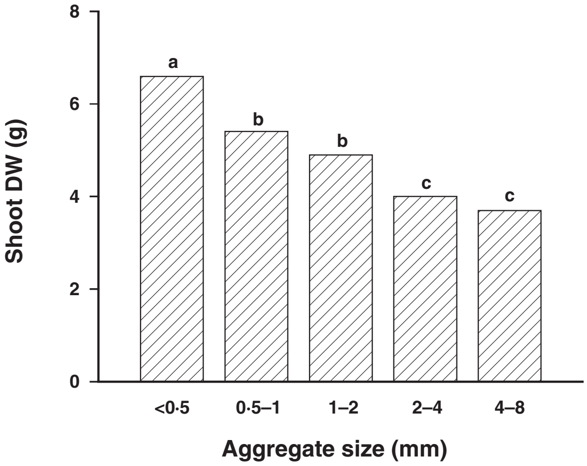

Figure 2. Shoot dry weight of maize plants grown in aggregates of different sizes sieved from the same batch of soil. Different letters above the bars signify statistically significant ($P < 0{\cdot}05$) differences among the treatments. (Adapted from Alexander & Miller 1991).

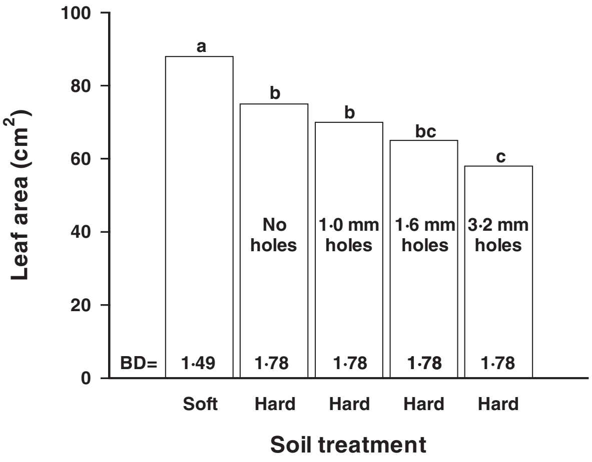

Figure 3. Leaf area of young barley plants growing in soil of moderate or high bulk density (BD, Mg m^{-3}) with holes of various diameters formed in the hard soil by pushing steel rods vertically into the soil. Different letters above the bars signify statistically significant ($P < 0{\cdot}05$) differences among the treatments (plotted from data of Passioura & Stirzaker 1993)

Figure 3 shows evidence that this might be so. Barley plants were grown in cylindrical pots in which soil was packed at a moderate and at a high bulk density. Within the latter, artificial 'biopores' were made by pushing sharpened steel rods of different diameters vertically into the soil to the depth of the pot, with eight holes per pot arranged equally spaced on a circle of 50 mm diameter concentric with the pot. A single seed of barley was sown in the centre of each pot. At the time of harvest, each plant had an average of seven seminal plus nodal root axes, and of these most were in the large pores (several times more than would be expected from chance exploration (Stirzaker *et al.* 1996)). The leaf area was much affected by the roots' having access to large pores in the hard soil, being about 30% smaller with 3·2 mm holes than with no holes in the hard soil.

A further example of the possible impact of biopores on growth comes from the work of Pierret, Moran & Pankhurst (1999) who grew wheat plants in undisturbed cores of soil (90 mm diameter by 1000 mm depth) collected from the field, and also in the same soil broken up, sieved, and repacked to the same bulk density into pots of the same dimensions. The various horizons in the undisturbed soil were treated separately and repacked in order. Remarkably, the plants grew almost twice as fast in the repacked soil as in the undisturbed. The roots in the undisturbed soil grew predominantly in cracks and biopores, and in soil adjacent to those cracks and biopores.

Although these examples show plants growing poorly when their roots are in large pores, such behaviour is overridden if the soil is allowed to dry, for then the ability of the roots in biopores to grow deeply and thereby to access wet subsoil turns the presence of biopores into an advantage (Cornish 1993). Nevertheless, although biopores may provide highways for the roots, their general sparseness, coupled with the roots' propensity to grow clumped together within them, can drastically slow the uptake of water in comparison with more widely distributed roots (Passioura 1991; Tardieu, Bruckler & Lafolie 1992).

Excessively loose soil

Experience in the field often shows that crops may grow poorly in soil that is too loose (Håkansson, Voorhees & Riley 1988; Kirkegaard *et al.* 1992). Many such examples can be explained in terms of poor establishment owing to inadequate contact between seed and soil. However, several examples cannot be explained in this way and may reflect similar processes to those that occur when roots are growing in large pores. Figure 4 shows the behaviour of young barley plants growing in soil of very low through moderate to high bulk density. The shoot weights at both very low and very high bulk density were about 15% smaller than those of plants growing at optimal bulk density, whereas the root weight was reduced only at the high bulk density and not at the low.

Although this behaviour seemingly involves a signal generated by the direct experience of the roots it is not so easy to interpret it as feedforward, as in the previous examples, because it is not clear that the future ability of the roots to extract water is in danger. Possibly this response reduces the risk of the plants lodging through uprooting (Goodman & Ennos 1999).

Soil drying

When a soil dries many changes take place within it. It not only holds water more strongly, but it also gets harder and it transmits solutes less readily so that deficiency of poorly mobile nutrients such as phosphorus is more likely. Plants eventually respond to the falling water potential of their leaves by slowing their growth and closing their stomata. However, plants can also react to a drying soil well before there is a detectable change in the water potential of the leaves. Stomatal conductance (Bates & Hall 1981) and the growth rate of the leaves (Saab & Sharp 1989) may fall, apparently in response to signals received from the roots in the drying soil (Davies & Zhang 1991). Further, both stomatal conductance and rate of leaf growth may fall as the soil dries even if the water status of the leaves is maintained high by pressurizing the roots (Gollan, Passioura & Munns 1986; Passioura 1988).

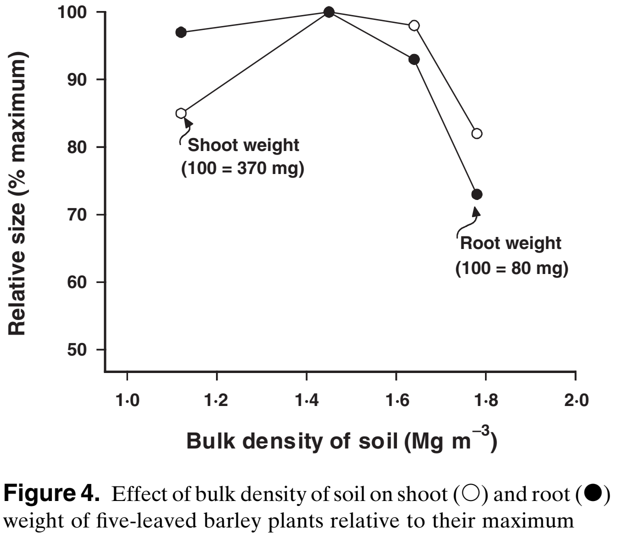

Figure 4. Effect of bulk density of soil on shoot (○) and root (●) weight of five-leaved barley plants relative to their maximum values. LSDs ($P < 0·05$) were 12% (45 mg) for shoot weight and 15% (12 mg) for root weight. (plotted from data of Stirzaker *et al.* 1996).

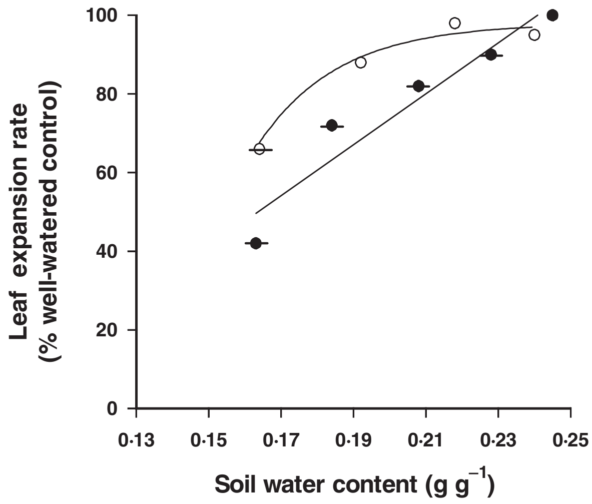

Figure 5. Expansion rate of leaves of young wheat plants (as a percentage of that in well-watered controls) growing in drying soil of two bulk densities, low (open symbols), and high (closed symbols). The plants were grown with their roots in pressurized chambers to keep the shoot water potential high at all times. The points marked with a short bar denote that the unwatered plants differed significantly ($P < 0·05$) in leaf expansion rate from the well-watered plants (adapted from Passioura & Gardner 1990).

Given the common connection between the hardness and the water content of soil it is conceivable that this early response of plants to soil drying may be as much a response to increasing hardness (see Fig. 1) as to falling water potential. Figure 5 illustrates how this may be so. It shows how the development of leaf area of wheat plants growing in drying soil is affected by both the drying and the hardness of the soil even when the leaf water potential of the leaves is prevented from falling. The plants were grown in pots that could be encased in pressure chambers. Applying pressure in these chambers effectively counterbalances the increasing suction in the soil water as the soil dries and prevents the leaf water potential from falling. The pots contained soil that was packed either loosely (bulk density, 1·0 $\mathrm{Mg\ m^{-3}}$) or firmly (bulk density, 1·38 $\mathrm{Mg\ m^{-3}}$). The soil was the same as that used in the experiment illustrated in Fig. 1. At the starting water content of 0·25 $\mathrm{g\ g^{-1}}$ the penetrometer resistance of the soil at the high bulk density was 2·0 MPa and was on the verge of having a significant effect on leaf growth (see Fig. 1). At the low bulk density the penetrometer resistance of the soil was negligible at all water contents. Figure 5 shows that soon after the soil started to dry the growth rate of the plants in the firm soil was affected, thereby implicating soil strength as the inducer of a signal from the roots to the leaves. Eventually the plants in the soft soil also slowed their growth, thereby implicating low soil water potential as the inducer of a signal. Thus soil drying may affect leaf growth through feedforward effects induced by both the hardness and the water potential of the soil.

Experiments with roots split between two containers have shown that growth rate of leaves may fall when one of the containers is allowed to dry even though the roots in the other well-watered container are able to supply enough water to the leaves to prevent their water potential from falling (Gowing, Davies & Jones 1990; Dry & Loveys 1999). This response has been developed into an effective irrigation technique for grape vines, in which parts of the root system are alternately allowed to wet and dry (Loveys *et al.* 2000).

INTERACTIONS BETWEEN SOIL STRUCTURE AND MICROBIAL ACTIVITY THAT INFLUENCE PLANT GROWTH

Widespread agronomic experience is that crops sown without prior cultivation, that is with seeds sown directly into a shallow narrow slot in the soil ('direct- drilled'), grow more slowly as seedlings. It is possible that this slow growth arises at least partly because the soil is too hard as discussed above. However, there is now strong evidence that the slow growth may often be due to microbial interactions (Chan *et al.* 1989; Kirkegaard *et al.* 1995). Figure 6a shows the leaf area of 40-day-old wheat seedlings grown in undisturbed cores collected from fields prepared either by cultivation or for direct-drilling, some of which had been sterilized by γ-irradiation. The plants were grown in a controlled environment designed to match the conditions of light and temperature during the early life of the crops in the field, and were given abundant nutrients to mask the flush of nutrients from dead organisms that typically accompanies sterilization. Sterilization improved the growth of plants in both tillage treatments, but much more so in the direct-drilled, with the result that it annulled the effect of tillage that was so evident in the unsterilized soil.

Micro-organisms known to be favoured by direct-drilling include *Rhizoctonia* root-rot and *Pythium* spp. (Cook, Sitton & Waldher 1980), both of which groups are pathogens, and some *Pseudomonas* spp. (Elliot & Lynch 1984; Simpfendorfer, Kirkegaard & Heenan 2001) which, while not pathogenic, nevertheless inhibit plant growth by releasing toxins. Why sterilization and tillage have similar effects may be related to the disruption of fungal hyphae by tillage, which could protect the plants against infection by, say, *Rhizoctonia* or *Pythium*. However, it is not clear why bacteria such as Pseudomonads are also affected. Possibly there is substantial reorganization of microbial ecology resulting from the general disruption of fungal hyphae.

Severe infection with *Rhizoctonia* or *Pythium* undoubtedly affects the ability of the roots to provide the leaves with adequate supplies of water and nutrients, but these tillage effects also occur even if only a few percent of the total root length is affected (James *et al.* 1997). Further, the effects evident in the unsterilized soil of Fig. 6a occurred even as the first leaf was developing, when the shoot was still presumably well supplied by nutrients from the seed. Thus, there is a prima facie case that the roots were sending inhibitors to the leaves. Such inhibitors may originate not in the plant but in the rhizosphere, as could be so with abscisic acid produced by micro-organisms (Müller, Deigele & Ziegler 1989; Hartung *et al.* 1996). This case is supported by further experiments (Kirkegaard *et al.* 1999) in which plants infected with *Rhizoctonia* were grown with their roots in a pressure chamber so that the leaves could be maintained highly turgid at all times (Passioura 1988); this pressure treatment had no effect on the growth of the infected plants (Fig. 6b), indicating that factors other than the supply of water to the shoot were reducing growth.

GENERAL COMMENTS

It is now clear that roots, when they are growing in physically inhospitable soil, send inhibitory signals to the leaves. The effects of the signals on the leaves are various. They may affect stomatal conductance, cell expansion, cell division, and the rate of leaf appearance. Generally, though not always, they act to harden the plant against falling water status. This is not to say that such responses necessarily predominate. Certainly leaf water status can in itself affect the behaviour of plants, perhaps interactively with non-hydraulic signals (Tardieu & Davies 1993). Nevertheless, although moderate changes in leaf water status arising from changes in humidity or light intensity may have substantial transient effect over tens of minutes, they have little sustained effect on elongation rates of leaves (Passioura & Munns 2000). By contrast, most of the phenomena discussed here induce sus-

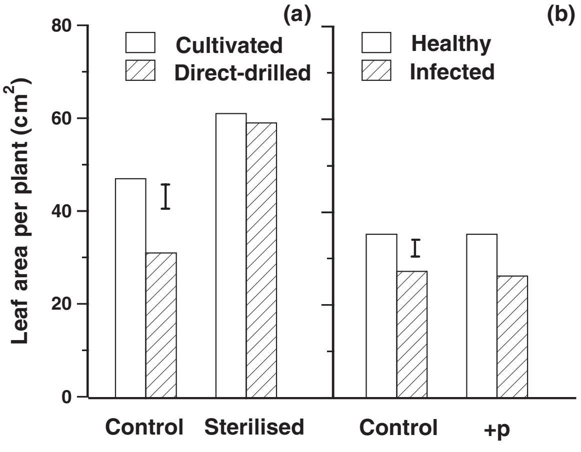

Figure 6. Leaf area of wheat seedlings as affected by (a) tillage and soil sterilization, and (b) infection with Rhizoctonia and root pressurization (+ p). The vertical markers in each group denote LSDs ($P < 0{\cdot}05$) (adapted from Kirkegaard *et al.* 1995, 1999).

tained changes in growth with undetectable changes in leaf water status.

Within the roots, the tips may be the main seat of signalling activity. They are isolated from the xylem and may have a low water potential when growing in large pores or excessively loose soil, even if the soil is well-watered, for they may be unable to extract the water necessary for their growth because of poor contact with the soil water. An intriguing alternative explanation is that there may be no induction of a signal, but that the root tips may continually produce a low level of inhibitor which in favourable soil conditions, but not in unfavourable, disperses by diffusing into the neighbouring soil. If soil dryness or poor contact with the soil (loose soil or roots in biopores) inhibits such dispersion, this putative inhibitor could build up in concentration within the tip and eventually find its way into the transpiration stream and thence to the leaves. This speculation is not without some evidence: pea roots growing in large pores become necrotic (Stirzaker *et al.* 1996).

Aeroponics also provides an environment in which roots have no contact with solid phase and in which any inhibitors released by roots may not readily disperse. It is notable that aeroponically grown maize has substantially smaller shoots and substantially larger roots than comparable plants grown in soil despite good nutrition and water supply in both media (Margaret McCully, personal communication). A build-up of putative inhibitors may also pertain where roots are crowded, as in small containers or in compact soil, although the bonsai effect does seem to persist even when the rooting medium is rapidly flushed with water or nutrient solution (Richards & Rowe 1977).

The comments in the previous paragraphs are speculative, but they do illustrate that there are important processes occurring in roots of which we are almost entirely ignorant and which, when we come to understand them, may provide powerful insights into the environmental biology of plants. The conservative behaviour of plants may be well justified if there is danger of the water supply running out. An exponentially growing plant is accelerating towards catastrophe if it does not slow its growth well before the soil water potential falls below the point at which it noticeably influences the water potential of the leaves, for by then little available water is left in the soil. By contrast, conservative behaviour of annual crop plants may often be inappropriate, especially when water is unlikely to be limiting, as with irrigation or with well-watered and well-fertilized direct-drilled crops. Removing such conservatism may substantially increase productivity. In perennial horticultural crops, which are prone to becoming too leafy, inducing conservative behaviour can be beneficial, as in partial root-zone drying with grape vines.

The nature of these signals from roots, how they are induced, and how they act, is under vigorous debate. Mooted mechanisms are becoming increasingly complex as evidenced by the companion papers in this volume (Wilkinson & Davies, p. 195, Sauter *et al.* p. 223; Sharp p. 211) Probably a rich network of hormonal and other responses is involved in attuning the growth and development of a plant to its environment. Unravelling the workings of such a network is very difficult (Trewavas 1986). In the field, plants experience very diverse environments, both temporally and, especially in relation to roots and soil, spatially. It is probably too much to expect that one or two simple chemicals can be the main agents for integrating this diverse experience.

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