

CHAPTER 3

ROOT GROWTH RESPONSE AND FUNCTIONING AS AN ADAPTATION IN WATER LIMITING SOILS

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Abstract: In this chapter we consider the advantages and disadvantages of different root growth patterns and root functional characteristics in terms of water and nutrient uptake from soils depleted of these resources. Impacts are considered within a framework of analysis which considers crop yield to be a function of water available to the crop during its life cycle, the amount of biomass produced by the crop for every unit of water available and the proportion of the biomass produced going into reproductive yield. Root properties will impact on all of these variables and can therefore impact substantially on yield in conditions where water and nutrients are limiting. We suggest that regulation of this kind can form an effective basis for crop improvement programs focused on dryland environments

Keywords: Water Deficit, stomata, root growth, water and nutrient uptake, chemical signaling, abscisic acid, pH, ethylene

1. INTRODUCTION

When plants first colonized land, the maintenance of a favorable shoot water status became a significant problem due to the evaporating power of the atmosphere surrounding the shoot and the resulting potential for substantial losses of water from an expanding transpiring surface. Evolution has solved the problem of shoot turgor maintenance by providing some control over water loss to the atmosphere through the influence of stomatal and cuticular properties (see chapter by Van der Straeten), and by ensuring that in many plants there is a ready supply of water to shoots to replace that lost through transpiration. This is achieved through the evolution of a vascular system which ramifies through plants from within a few cells of the water source in the soil to within a few cells of the sites of evaporation in the leaves. Vascular development provides a low resistance pathway for water and solute movement without which plants as we know them (more than a few

cms tall) could not exist. Soil provides most plants with a predictable supply of water (and nutrients) and some anchorage but the physical, biological and chemical properties of the rooting medium also mean that roots have had to evolve particular properties to ensure that much of the water in the soil within the potential rooting zone is made available to the plant.

Water availability from the soil becomes a particular issue if soil water is not replenished as it is used by the plant. Table 1 (modified from Robinson et al. 2003) lays out the basic design requirements for a root system faced with restricted availability of water. We focus here on desirable properties (for the point of view of sustained water uptake in drying substrate) of roots of crop plants where economic yield is an important issue. This is rather than focusing on survival of severe drought, which is an important component of drought resistance in wild plants but is largely irrelevant to the yielding of annual crops in particular. Here, yields are commonly restricted by soil moisture deficits well before the survival of the plant is at risk and therefore the mechanisms that contribute to the maintenance of yield are distinctly different from those that may contribute to plant survival of cellular desiccation. It is these mechanisms that can potentially be exploited in plant improvement programs for dryland agriculture. In the discussion that follows, we will use the framework laid out in Table 1. for an analysis of root properties that may be important for yield maintenance in situations where water supplies may be restricted.

Table 1. Summary of the design requirements of root systems of crop plants subjected to drought stress

1	Root growth and penetration of soil pores <ul style="list-style-type: none"> ● Growth and turgor relations ● Root proliferation ● Root system topology ● Impact of changes in root morphology and structure on the uptake of water and nutrients and yield.
2	Radial fluxes of water and ions into the root <ul style="list-style-type: none"> ● Aquaporins ● Water-proofing ● Hydraulic lift ● Impact of modified water and ion fluxes through roots
3	Root signals and the limitation of leaf growth and leaf functioning <ul style="list-style-type: none"> ● Root signals and the limitation of leaf growth and leaf functioning ● Abscisic acid synthesis, distribution and catabolism ● Xylem sap pH ● Ethylene and ACC
4	Signaling between substrate and roots <ul style="list-style-type: none"> ● Rhizosphere micro-organisms
5	Resolution of design conflicts and behavior of roots of plants in communities

2. PENETRATION OF SOIL PORES

As water is lost from the leaves of a plant into comparatively dry air, resulting water potential gradients will pull water first from the xylem and then from the roots to replace that lost by transpiration. A reduction in root water potential will pull water into the root from the soil and cause water to move to the root through the soil, again down a gradient of decreasing water potential. As long as transpiration rates are not too high and plants are rooted in soil that is well charged with water, such movement can be comparatively rapid and plant water uptake can effectively keep pace with transpirational water loss. In conditions where transpiration rates are substantial, however, and particularly if soil water is not replenished, depletion zones of water (and nutrients) will develop around roots and in these regions the movement of water can be greatly slowed with a consequent significant restriction in the rate of uptake of water and nutrients by the plant. More drying of the bulk soil further from the root will further increase the resistance to water movement to the roots. Soil resistances to water movement are in series with radial root resistances and if the former are large (for example when the soil dries) then there is little benefit to be gained by engineering plants with low water uptake resistance per unit of root surface area (high hydraulic conductivity). Rather, water uptake can be sustained if root growth can be sustained as the substrate water potential declines, such that root tips grow into areas of soil where water contents are higher, soil resistances to water movement are consequently lower and therefore water availability is sustained.

The importance of capturing more of the water available in the soil is apparent from an analysis produced by Passioura (1977) showing crop yield (Y), particularly in 'water limited' crop production is a function of three variables:

$$\text{(eqn 2) } Y = BWR \times W \times HI$$

BWR is the biomass to water ratio, W is the water available, and HI is the harvest index. The analysis is valuable for a variety of reasons, not least because it focuses attention on how to increase crop yield by increasing the water available to the crop, making more water available at key developmental periods so that a greater proportion of crop biomass is yield (HI) and how to improve the ratio of crop biomass produced to water lost (i.e increase water use efficiency). Root growth and functioning have important impacts on all of these variables.

2.1. Root Growth and Turgor Relations

Roots of most plants show reduced sensitivity to reductions in cellular water potential when compared to growth of shoot cells subjected to the same degree of dehydration, and the basis of this response is now comparatively well understood largely a result of an impressive body of work conducted by the Sharp laboratory using a model root system under growth conditions that can easily be

replicated (the maize primary root system subjected to osmotic stresses imposed in a vermiculite growing medium) (see Sharp, this volume). Root growth maintenance at low substrate water potential requires turgor maintenance (e.g. Spollen and Sharp, 1991) and the capacity to loosen cell walls for irreversible extension despite the potential growth limitation imposed by a range of chemical inhibitors (e.g. LeNoble et al. 2004). The potential benefits to be obtained in terms of sustained water uptake and sustained plant growth in drying soil mean that increased understanding and modification of properties limiting root growth provides an attractive target for those interested in improving plants for dryland agriculture. The maize primary root system (Sharp, this volume) provides a wealth of information on the mechanisms behind root growth maintenance at low water potential and is already being exploited for plant improvement through functional genomics (Sharp et al. 2004). One issue with this system, however, is that as water potential is decreased in the vermiculite medium, root diameter decreases. Commonly, as soil water potential declines, roots become thicker, presumably to counteract increasing soil strength (not an issue with vermiculite). It will be important to address this as an issue in plant improvement programs as it is well known that plants can increase their potential water and nutrient uptake by producing a greater length of root from a given dry mass (i.e. by increasing SRL (Specific root length)), the common response to low water potential, while thicker roots, the common response to increasing soil strength, will be of benefit for penetration of drying soils.

In some crops, high yield under dryland conditions can be associated with deep root penetration (e.g. Mohamed et al. 2002) but as we emphasize below, this will not always be the case if increased root growth and root shoot ratio (a result of differential sensitivity of root and shoot growth to soil drying and common response to water scarcity) are achieved at the expense of economic yield, and this must be born in mind for plant improvement programs based on a modification of root properties .

2.2. Root Proliferation

In nearly all soils, water, nutrients, soil strength and other properties show considerable heterogeneity. Localised proliferation of roots is generally thought to be advantageous to plants in foraging for water and nutrients and involves the use of morphological plasticity in response to resource heterogeneity to selectively place resource-acquiring structures in favorable patches of habitat (Hutchings and John, 2003). Drew (1975) was among the first to describe root proliferation into patches of soil with high nutrient status, while Zhang and Forde (1998) have recently identified the gene in *Arabidopsis* responsible for the sensing of localized high concentrations of nitrate. Localised proliferation of parts of a root system into nutrient-rich patches may involve reduced growth of other parts of the same root in soil where nutrients are in short supply (Gersani and Sachs, 1992).

Increase in soil strength as soil dries can impact on root branching and generally more lateral roots per unit length of main root axis are found (Bengough, 2003). In

some plants, however, total numbers of lateral roots may be decreased by higher mechanical impedance (Goss, 1977).

2.3. Root System Topology

The ecological literature (e.g. Kutschera (1960) shows us that the architecture of root systems is as varied as that of shoot systems. Perhaps as importantly, several authors have stressed the flexibility of architecture in response to changes in the local environment. Two extreme architectures that have been described (see e.g. Robinson et al. 2003) are the ‘Herringbone’ systems with a main axis and one or few developmental orders of laterals, and those systems with a ‘dichotomous’ architecture. Fitter et al. (1991) predicted that herringbone systems though more expensive to construct are more efficient at exploiting soil for water and nutrients. Importantly for crop improvement programs, Fitter (1987) showed that root systems of *Trifolium praetense* tended towards dichotomy when water was in ample supply but became more herringbone in structure as soil dried.

2.4. Impact of Changes in Root Morphology and Structure on the Uptake of Water and Nutrients and Yield

Local proliferation of roots can be shown to be advantageous in terms of growth of plants in soils with heterogeneous nutrient distributions. For example, Drew and Saker (1975) have shown that barley plants with only a few percent of roots in nutrient rich soil can achieve similar whole plant growth rates to plants with all of their roots exposed to high nutrient concentrations. Some of this apparent increase in uptake of nutrients from localized patches may be due to physiological adaptation of existing roots as well as to changes in root growth patterns (see below). Sharp and Davies (1979) have shown similarly that deeper rooting by only a few roots in maize plants can maintain substantial water uptake and vegetative growth as soil dries. Deeper rooting and sustained root growth late in the season in stay-green varieties can have beneficial effects on yield since water is then available during critical and sensitive phases of reproductive development (Borrell et al. 2001). The positive impact of this kind of response can be seen in equation 1 through an effect of extra water available on the *HI* component of yield.

It seems therefore that deeper rooting of individual plants or plants in competition for water with plants of other species can be beneficial in terms of extra water harvesting, particularly at critical stages of plant development. If this response can make what may be a relatively sustainable new source of water in the subsoil available to the plant then the effects of extra root production may be very positive. Proliferation in more superficial layers may increase water availability only rather temporarily, that is unless soil water is replenished. Such responses may be less obviously beneficial, particularly for plants in monoculture where extra investment in roots may yield little extra water for a crop of plants competing against themselves (see Passioura, 1977). Hutchings and John (2003) note that for mobile nutrients

such as nitrogen there often seems to be little benefit to proliferation, unless plants are competing for nutrients. Under these circumstances proliferators can recover more N (or water) than competitors (Robinson et al. 1999) but the costs of this behaviour can be high and might outweigh benefits, particularly in a mono-culture. Once produced, roots have to be maintained and the allocation of extra carbohydrate to root systems, particularly during periods of grain filling can have adverse effects on the grain yield to water used ratio (equation 1 above).

One other consideration in analysis of benefits of extra resource investment in roots is the placement of roots in the soil. In compacted soil or in soil where mechanical impedance increases due to drying, roots will clump in channels or fissures. Clumping can also be produced by the production of many short laterals (see above) (Tardieu, 1988). Such clumping can enormously restrict the scavenging capacity of root systems for water and nutrients (Passioura, 1991).

There is now a considerable body of work which suggests that rather than engineering root properties to increase scavenging capacity for water in the soil, in environments where yielding is dependent upon stored water, there is some benefit to be taken from breeding crops with narrow xylem vessels which should increase the resistance to water flux and force plants to use water in the subsoil more slowly (Passioura 1972). In cereals, seminal roots grow deep into the subsoil and because crops in dryland environments can rely largely on subsoil water, seminal roots can be of crucial importance in determining water use patterns. If plants use the subsoil water too rapidly during the development of the vegetative plant, then too little will remain for the crucial period of development when grain is filling and HI will be reduced even if biomass production is substantial (see Equation 1 above). Use of subsoil water can be slowed if seminal roots have higher hydraulic resistances.

Wheat breeding in Australia has reduced the xylem vessel diameter of two commercial wheat varieties from 65 μ m to less than 55 μ m (Richards and Passioura, 1981a, 1981b). Selections with narrow vessels yielded 8% more than the controls in the driest environments, while yield differences in the wetter environments were largely non significant (Richards and Passioura, 1989).

Taken together these effects of structural and morphological variation of root systems show that an apparently simple target of 'keeping roots growing as soil dries' can have many and varied consequences, some of which will impact adversely on yielding. It is likely that selection for particular root traits will be beneficial in some soils and some environments with particular rainfall patterns, but not in others and that design requirements will vary from cropping region to cropping region.

3. RADIAL FLUXES OF WATER AND IONS INTO THE ROOT

Generally, the radial resistance to water movement into plants is much greater than the resistance to axial flow (in young maize roots 2 or 3X while in older roots the difference may be several hundred fold, Tyree, 2003). The resistances of the various components of the pathway have been debated over the years and there is still some controversy over their identity and magnitude. Steudle et al. (1993) have

concluded that while the endodermis may be the major barrier to solute flow, this is not the case for water flow but this situation may vary with root age. In some plants (e.g. maize), apoplastic bypass to radial water flux can be important (Freundl et al. 1998) while in others (e.g. sunflower), the apoplastic pathway can be blocked due to lignification or suberisation. Steudle and Peterson (1998) have recently described a new model which helps our understanding of radial water flux. It is well known that root radial resistance to water uptake is apparently sensitive to the flux of water into the root with apparent resistance declining as the transpiration flux increases. Steudle and Peterson argue that this may be because of a change in the proportion of total water flux moving through different pathways into the root but there may also be changes in membrane properties to water flow (see Tyree, 2003).

3.1. Aquaporins

Channels in the membrane, analogous to those that are important for ion flux can influence the radial flow of water into roots. These are commonly referred to as aquaporins and Siefitz et al (2002) have demonstrated that these pores account for about half of the root conductance in tobacco. Activity of channels is under metabolic control (Tyerman et al. 2002; Maurel and Chrispeels, 2001). Steudle (2000) has suggested that this pathway can dominate water flux when movement is driven largely by osmotic gradients or when the apoplastic pathway becomes blocked, which can occur in response to some soil conditions. A variety of factors of soil and root factors will affect aquaporin activity, including pH, pCa and osmotic gradients. Clarkson et al. (2000) have shown how increased nitrogen availability increases the hydraulic conductivity of roots (Clarkson et al. 2000) and there may also be diurnal control of root hydraulic properties (see also Tsuda and Tyree, 2000).

3.2. Water Proofing

The role of stomata and cuticular development in the regulation of water loss is well known. However effective these mechanisms, they are of limited value if plants lose substantial quantities of water to the soil. Most species will show reduced root hydraulic conductivity as the soil dries and this change will restrict water loss from roots (e.g. Nobel and North, 1993; Nobel and Sanderson. 1984). As the soil dries, a vapour gap will develop between the root and the soil and this will also limit water loss. It appears that both of these changes are to some extent reversible when soil is rewetted and this property is referred to as rectifier-like activity. In some plants however water-proofed roots will not change their properties and increased water available in the soil can only be fully accessed if new roots are produced. Rectifier-like root properties may be of considerable significance for plants that grow in shallow soil which is prone to rapid and substantial variation in water status. Recent work suggests that aquaporins may help regulate water loss from very dry roots

3.3. Hydraulic Lift

In water-limited environments, one important feature of the survival of some plants is deep rooting (Canadell et al., 1996) with some woody plants rooting down to 10 metres or more. Under these conditions, hydraulic lift can be commonly observed. This is a passive mechanism where the water potential gradient transfers water through the root system, from deep wetter soil to shallower soil (Richards and Caldwell, 1987). With water moving in and out of roots on a daily basis, clearly this mechanism is not compatible with those mechanisms that contribute to water proofing of roots. During the night when transpiration rates are generally low, the mechanism can provide quite a lot of temporary stored water to the upper soil layers (more than the plant itself can store) During the following day, the roots of plants performing hydraulic lift (as well as of any neighbouring plants with shallower root systems) will extract this water from the soil and it can substantially increase plant transpiration in the following day and also contribute to enhanced carbon gain (Caldwell et al., 1998). A recent study by Kurz-Besson et al. (2006) shows that for cork oak trees in Portugal, hydraulic lift may provide between 17 and 81% of the water transpired.

3.4. Impact of Modified Water and Ion Fluxes Through Roots

The phenomenon of hydraulic lift described above is an excellent example of getting more water through the plant as a way of enhancing yield (see equation 1) when water is in short supply. Targets for a plant improvement programme might therefore include deeper rooting characteristics combined with shallow roots that do not show water proofing capacity.

Roots with high radial hydraulic conductivity can be beneficial for high biomass production where there is a lot of water available to the plant, or where water is regularly replenished by rainfall or by irrigation. Such plants may, however, have a tendency to use water too rapidly in water scarce situations, at least if water is required for reproductive development later in the season.

4. LONG-DISTANCE TRANSPORT BETWEEN ROOTS AND SHOOTS- ROOT SIGNALS

While the role of roots in scavenging for water and minerals in the soil is readily apparent and the contribution of water and ions as substrates for a variety of plant processes is well-discussed, roots also contribute other material to shoots in the form of signals, and the role of these signals in modifying plant growth and development is no less significant than that of the other root-sourced substrates. Roots signals have information content, for example allowing the plant to modify growth and functioning as a function of water and nutrient availability in the soil or soil mechanical impedance (see for example, Davies et al. 2002). Most importantly, canopy development and stomatal behavior can be restricted by root signaling, often

in circumstances where the water relations of the shoots are not obviously changed by any modification of soil properties. Effects can be dramatic and over-coming or in certain circumstances enhancing the effects of root signals can be an appropriate target for a plant improvement program. Perhaps the most obvious target in this regard is a manipulation to allow sustained or even increased rates of canopy development as the soil dries. This can have a number of potential benefits. Firstly, when water is still in relatively abundant supply, the extreme sensitivity of root signaling (see e.g. Davies and Gowing, 2001) can limit leaf development, the consequent interception of solar radiation and the production of biomass. Suppressing root signaling that limits leaf growth or reducing the sensitivity of leaf growth to root signals can therefore allow the grower to produce more biomass in relatively moist soils. Another benefit can be achieved by intervening in the same way to allow the young crop to cover the soil more rapidly (Passioura, 2004). In Mediterranean-type climates where crops will largely grow on stored water derived from rains during the previous autumn, the soil surface can be wet in spring. Direct evaporation from the soil can be substantial (e.g. Leuning et al. 1994) and this loss of water will therefore be relatively unproductive (this water loss from the plant would generate extra carbon fixation and biomass production). van Herwaarden and Passioura (2001) have shown clearly how faster coverage of the soil by crops in these environments in the spring can greatly reduce seasonal evaporation from the soil and therefore increase water use productivity and impact positively on yield (equation 1).

Agriculture already uses an unsustainable 70% of the world's water supplies (Bacon, 2004). Reducing the use of water in agriculture can be achieved in a variety of ways but the use of deficit irrigation (DI) (the application of only a predetermined percentage of calculated potential plant water use) is an attractive means of saving water. Ideally the application of DI must be achieved without substantial yield penalty otherwise the yield/water use ratio (water use efficiency) will not be increased. We have already noted above how even mild soil drying will limit plant growth and development and so if plants are to be kept growing under a reduced supply of water then a plant improvement programme to suppress root signaling or the responses to root signaling will be needed.

4.1. Root Signals and the Limitation of Leaf Growth and Leaf Functioning

When the soil around the roots dries, dehydration of the root cortex will act to generate a number of chemical signals that will impact on plant growth and functioning. Extra synthesis of a number of growth regulators can positively inhibit leaf growth, while restricted synthesis of other regulators can act as a negative signal, with the lack of a promoter of leaf growth also restricting canopy development. The plant hormones abscisic acid (ABA) and ethylene will act in the first of the above categories, while reduction in the supply of cytokinins and in some cases ABA can act to restrict growth. Other plant growth regulators will also act as root signals, as will inorganic ions (see e.g. Roberts and Snowman,) and changes in pH of the xylem

sap (Wilkinson and Davies, 2002). Not all hormonal root signals are synthesized in the root. Reductions in root turgor can act to more rapidly re-circulate hormones arriving in the phloem from the shoots and some hormonal signals may originate in the soil (see below). Some root-originated signals can act directly on the shoots and others act as part of a transduction chain to release or target shoot-sourced effectors.

4.2. Abscisic Acid Synthesis, Distribution and Catabolism

Of all of the so-called plant hormones, abscisic acid has received most attention as a compound mediating the effects of soil drying on plant growth and functioning. There is often a clear relationship between declining soil water availability and ABA content of the roots or ABA concentration in the xylem (Tardieu et al 1992). The extreme sensitivity of the stomatal response to ABA means that stomatal behavior can often be linked sensitively to changes in soil water availability (e.g. Zhang and Davies, 1990). One of the results of this is that as soil dries, sensitive responses of stomata can act to maintain shoot water status at a level comparable to that of the well watered plant. This turgor maintenance (or isohydric behaviour) can be important for plant development in drying soil.

ABA can act as a sensitive inhibitor of growth of shoots in drying soil (Bacon et al. 1998), but more recent work has suggested that this response is sensitive to the water status of the shoot, with ABA acting as an inhibitor of growth in plant parts where turgor is sustained but as turgor declines, this hormone is required to sustain some growth of both roots and shoots (see Sharp et al. 2004). This may be because ABA can suppress the run-away synthesis of ethylene, which itself acts as a growth inhibitor at low water potentials. The idea that the impact of a hormone can be either promotive or restrictive for growth, depending on the level of another variable is an intriguing one and suggests that manipulation of hormone action in plants can be achieved by a variety of means other than the manipulation of hormone synthesis itself.

The root-sourced ABA signal can improve instantaneous water use efficiency (A/E) and in the longer term can modify a range of developmental variables which may be of adaptive significance under drought (see Trewavas and Jones, 1989). While quite subtle increases in ABA delivery to sites of action in the shoot can act to regulate gas exchange and growth (Jia and Davies, 2007), more substantial increases in hormone synthesis may be required to modify gene expression to affect development. ABA accumulation in developing reproductive structures can have deleterious effects on flowering and fruiting (Morgan, 1980) and there may be some advantage to be gained from manipulating plants to avoid such accumulations. We have shown recently (Jia et al. 2007) that ABA catabolism can be much more rapid than had previously been shown to be the case and there may be a case for targeting catabolism of this hormone in programs designed to increase yield under drought.

4.3. Xylem Sap pH

Wilkinson and Davies (1997) have shown that soil drying can act to alkalinize the xylem sap of some plants, and more recently Jia and Davies (2007) have shown that as had previously been hypothesized, these changes in the pH of sap delivered to leaves from roots in drying soil, are translated into changes in the pH of the apoplast of the leaves of these plants. Because ABA is a weak acid, the dissociated form arriving in leaves will partition according to pH gradients, tending to move to alkaline compartments. In the well-watered plant, these are the symplast of the leaf cells and the phloem. Alkalinisation of the apoplast as a result of soil drying (and other environmental changes – Jia and Davies, 2007) will result in more ABA residing for longer in the apoplast and therefore penetrating to the sites of action on the guard cells (which have only an apoplastic connection with the other cells in the leaf). Such changes in pH therefore have the effect of increasing the apparent stomatal response to a given delivery of ABA (i.e. increasing the apparent sensitivity of stomata to the ABA signal). In many circumstances, an increase in xylem sap pH and an increase in ABA delivery occur together as an effect of soil drying and combine to generate a sensitive response to the change in soil conditions. The pH signal can be one of the most sensitive of all signals to a change in water availability in the soil (see e.g. Sobeih *et al.* 2004) and can occur without any extra ABA synthesis, purely by making more existing ABA available to sites of action in leaves. Changes in xylem sap and apoplastic pH are attributable to a range of changes in root, stem and leaf functioning (see e.g. Wilkinson and Davies, 2002) and some of these variables may be quite amenable, if not obvious, targets for the manipulation of stomatal behavior and water use efficiency.

4.4. Ethylene and ACC

Soil drying will increase concentrations of the ethylene precursor ACC (1-aminocyclopropane-carboxylic acid) both in the root and in the xylem (Gomez-Cadenas *et al.* 1996). Delivery of ACC to the shoot from the root system can account for shoot ethylene production (Else and Jackson 1998) and therefore can limit leaf growth under drought. The plant hormone ethylene can be involved in both the suppression of root growth during soil drying and the suppression of leaf growth via long-distance chemical signaling (Sharp *et al.* 2001). Drying of the soil around the roots of tomato plants can maintain leaf water potential at values equivalent to well-watered plants for up to 2 weeks (Sobeih *et al.* 2004), largely a function of partial stomatal closure following ABA/pH long distance signaling from roots in drying soil. Ethylene evolution of wild-type plants increases as soil dries but can be suppressed using transgenic (ACO1_{AS}) plants containing an antisense gene for one isoenzyme of ACC oxidase. Most importantly, ACO1_{AS} plants show no inhibition of leaf growth when soil dries, even though both ACO1_{AS} and WT plants show similar changes in other putative chemical inhibitors of leaf expansion (xylem sap pH and

ABA concentration). It seems likely that the enhanced ethylene evolution under PRD is responsible for leaf growth inhibition of WT plants. ACO1_{AS} plants showed no leaf growth inhibition over a range of soil water contents which significantly restricted growth of WT plants.

5. SIGNALLING BETWEEN THE SUBSTRATE AND THE ROOT

We have described above a range of long-distance signaling pathways that may be manipulated to modify plant growth and functioning in drying soil. The emphasis has been upon changes in soil water availability impacting on uptake of inorganic ions from soil and the subsequent transport of these to the shoots through the xylem stream or on the impact of variation in root water status on the production and/or transport of hormonal signals. Of course the root will impact on the availability of inorganic ions for uptake, with one of the best examples of this is the acidification of the rhizosphere by roots which can increase the availability of ions. Exudation of organic acids (OAs) and phytases into the rhizosphere have been shown to greatly increase the availability of inorganic phosphate in soils, where the unavailability of this ion can often be greatly inhibiting to plant growth. In fact, exudation of malate and citrate from roots is thought to be the principle mechanism in alleviating Pi deficiency stress in plants (e.g. Ryan et al., 2001)). Secreted OAs mobilise bound and precipitated forms of Pi by anion exchange and may also enhance the activity of extracellular acid phytases which hydrolyse organic P in the rhizosphere. Transmembrane transporters probably exert primary control over OA secretion from higher plant roots (Ryan et al., 2001), although there is little information in crop systems which relates the presence of anion channels directly to Pi-induced OA efflux from roots. It seems likely that variation in OA efflux will impact on ionic signaling between roots and shoots via its impact on ion availability to the root surface.

Hormone fluxes from roots to shoots are comprised mainly of plant-sourced hormones but significant concentration of hormones can be found in the soil (e.g. Hartung et al., 1996). Presumably some of this hormone will originate from the roots while some may arise as a result of microbial activity in the rhizosphere. In addition to this some soil bacteria contain enzymes that will metabolise hormones as a carbon and nitrogen source. This is important, as Slovik has shown that low concentrations of ABA in the soil are important to sustain ABA accumulations in plants and to maintain root to shoot signaling in response to soil drying. ACC and ABA accumulated in the soil solution from whatever source can also be a source of signal for xylem transport as well as impacting on the signalling process through an equilibration effect on transport. As water moves into the root system along water potential gradients, some ACC and ABA molecules will be dragged along and these can be transferred into the xylem. The efficiency of radial ACC and ABA transport across the root is likely to vary between the different genotypes.

5.1. Rhizosphere Bacteria

Although some bacteria (containing ACC deaminase) can utilise ACC as a carbon and nitrogen source, bacterial ACC synthesis does not occur. Thus rhizobacteria utilising ACC must rely on efflux of ACC from plant roots or from fragments of plant material in the soil. This efflux may be considerable, as the soil solution of even well-watered plants contains appreciable amounts of ACC (0.23 μM - Else *et al.* 1995). Although no direct comparisons of ACC and ABA efflux have been made, plant roots appear to be more “leaky” with respect to ACC since the concentration of ACC in the soil solution (0.23 μM) of well-watered plants is 3 orders of magnitude greater than the concentration of ABA (0.67 nM). Edaphic conditions that stimulate root ACC synthesis such as soil drying and flooding are likely to increase root ACC efflux and soil ACC concentrations (by increasing root ACC concentrations and also increasing production in other plant material incorporated in the soil). Interestingly, rhizobacteria can decrease root ACC concentrations (Penrose *et al.* 2001) presumably by stimulating ACC efflux and there are now a few data indicating that rhizobacterial treatments can sustain growth in drying soil, presumably by reducing the accumulation of ethylene (Dodd *et al.* 2006). Alkaline soils stimulate efflux of weak acids (such as ABA and ACC) from roots according to the anion trap concept (Degenhardt *et al.* 2000) and modifying soil pH may also be a means of reducing the sensitivity of shoot growth and development to soil drying..

There is now good evidence that some soil bacteria will synthesise cytokinins (Arkipova *et al.* 2005) and there is interest in determining whether addition of these micro-organisms to the soil might prevent or slow the decline in cytokinin production by droughted plants and thereby act to maintain plant growth at low soil water potentials.

6. RESOLUTION OF DESIGN CONFLICTS AND BEHAVIOUR OF ROOTS OF PLANTS IN COMMUNITIES

We have argued above that selection for particular root traits in plant improvement programmes will be beneficial in some soils and some environments with particular rainfall patterns and at particular times in the development of the crop, but not in others. In other words, design requirements for root systems with respect to yield will vary from crop to crop, depending on the nature of the economic yield and whether the crop is determinate or indeterminate, from cropping region to cropping region where rainfall patterns differ and with developmental stage where relative impact of drought on vegetative development and reproductive development will vary. This should not be surprising because the same kinds of considerations are also important in selection for shoot traits that might impact positively on yielding in drought-prone environments (e.g. Condon *et al.* 2002).

Figure 1 shows a proposed ideotype for a very specific combination of crop and drought (grain crop growing largely on stored water), with inter-relationships shown between putative signalling capacities and vegetative and reproductive development.

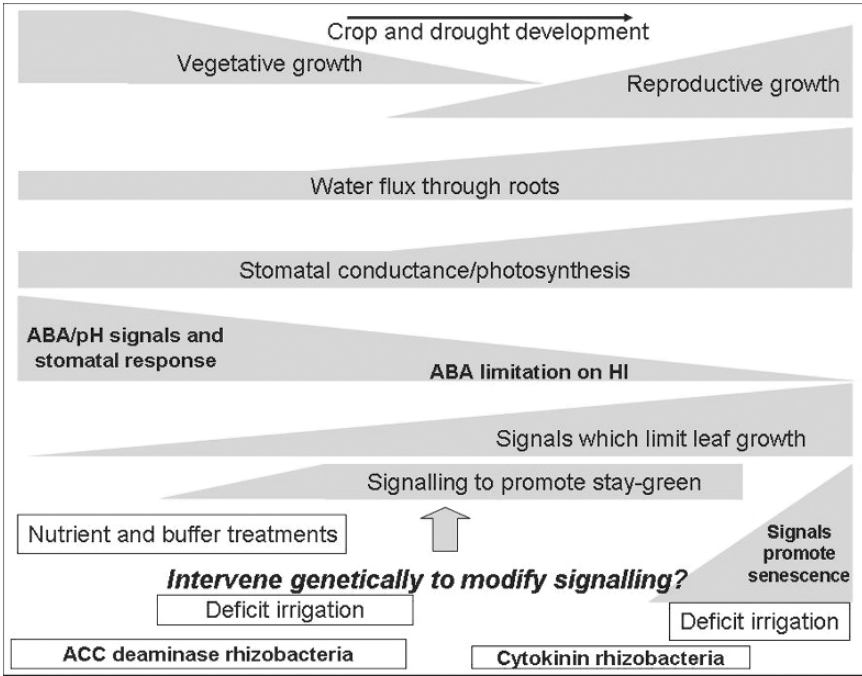


Figure 1. Proposed ideotype for a grain crop growing largely on stored water with inter-relationships shown between signaling capacities and vegetative and reproductive capacities

We also suggest application of particular management techniques and timing of possible genetic intervention (the use of a particular genotype with capacity for modified signaling capacity and response through the use of inducible promoters?). These interventions are proposed to modify signaling pathways and to enhance yield and efficiency of water use in dryland environments. The impacts on yield of the inter-relationships proposed in the diagram can be understood with reference to Figure 1.

It should be clear from Equation 1 that whatever the water availability throughout the growing season, there must be enough water available in the soil for the production and maturation of reproductive plant parts. In crops that produce grain yield towards the end of the season and are growing mainly on stored water, this can mean a requirement for judicious water use earlier in the season. This can be brought about by restricted root growth and/or restricted hydraulic conductivity of the root system. Water use can also be regulated by a sensitive system detecting soil drying, with this information passing to the shoots for effective control of water loss through stomatal regulation. Clearly the evolution of such a system (Cowan, 1988) allows water use (and plant development) to be linked to water availability with a fail-safe system operating to minimize the chances of damaging water deficits

during reproductive development or even more catastrophic hydraulic failure at any point in the development of the crop (Sperry et al., 2002).

Root proliferation and effective scavenging for water can help to ensure that more water is available for reproductive development late in the season and these properties in combination with hydraulic lift can result in increased productivity simply by ensuring that more water goes through the plant (Equation 1). Restricted root signaling or low sensitivity of shoot growth to signaling early in the season will help plants cover the ground more rapidly, reduce water loss from the soil and thereby enable more water to move through the plant, thereby increasing carbon gain and water use efficiency. Restricted canopy growth once canopy closure has been reached (increased signaling?) can make more assimilates available for reproductive development, assuming that stomata are still partly open and photosynthesis is continuing (reduced stomatal signaling or reduced sensitivity of stomata to signals?) Root signals that induce stay-green characteristics and perhaps subsequently promote redistribution of assimilate and nitrogen to developing reproductive structures (Yang et al. 2001) can enhance harvest index and yield.

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