

Osmolyte accumulation: can it really help increase crop yield under drought conditions?

R. SERRAJ¹ & T. R. SINCLAIR²

¹Laboratoire de Physiologie Végétale, Département de Biologie, Faculté des Sciences – Semlalia, 2390 Marrakech, Morocco and
²USDA-ARS-SAA-CMAVE-CGERU, c/o University of Florida, Agronomy Department, Agronomy, Physiology and Genetics Laboratory, IFAS Building #350, 2005 SW 23rd Street, PO Box 110965, Gainesville, FL 32611-0965 USA

ABSTRACT

Osmolyte accumulation (OA) is frequently cited as a key putative mechanism for increasing yields of crops subjected to drought conditions. The hypothesis is that OA results in a number of benefits that sustain cell and tissue activity under water-deficit conditions. It has been proposed as an effective tolerance mechanism for water deficits, which could be enhanced in crops by traditional plant breeding, marker-assisted selection or genetic engineering, to generate drought-tolerant crops. However, field studies examining the association between OA and crop yield have tended to show no consistent benefit. The few, often-cited, investigations with positive associations were obtained under severe water deficits with extremely low yields or conditions with special water-supply scenarios when much of the benefit is plant survival. Under conditions where water deficits threaten crop survival, yields are so low that even large fractional yield gains offer little practical benefit to growers. Indeed, the often-cited benefit of turgor maintenance in cells is likely to result in crop behaviour that is exactly opposite to what is beneficial to crops. The one clear mechanism identified in this review for beneficial yield responses to OA is in the maintenance of root development in order to reach water that may be available deeper in the soil profile.

Key-words: Crop growth; drought stress; osmotic adjustment.

INTRODUCTION

The accumulation of osmolyte compounds, usually called 'osmotic adjustment' or 'osmoregulation', is often proposed as a solution to overcoming the negative consequences of water deficits in crop production. It has long been proposed as an adaptative mechanism for drought and salt tolerance (Martin 1930; Bernstein 1961), but it has received increas-

ing interest during the last 20 years. Indeed, osmolyte accumulation (OA) in plant cells results in a decrease of the cell osmotic potential and thus in maintenance of water absorption and cell turgor pressure, which might contribute to sustaining physiological processes, such as stomatal opening, photosynthesis, and expansion growth (Blum, Mayer & Gozlan 1983; Morgan 1984; Ludlow & Muchow 1990; Blum 1996). OA has also been emphasized as a selection criterion in traditional crop breeding programmes to improve grain yield in dry environments (Morgan 1983; Blum *et al.* 1983; Ludlow & Muchow 1990; Tangpremsri *et al.* 1991; Belhassen, This & Monneveux 1995; Zhang, Nguyen & Blum 1999). This hypothesis is also widely offered as the justification for much of the molecular genetics research on OA with a large surge in publications on this topic. Munns (1988) indicated more than 10 years ago that there was an increasing number of papers on OA in international journals. We found that in the recent literature the annual number of papers on this topic has increased to over 250 (Table 1).

The attraction of stimulated OA in cells is the ability to readily induce over-expression in the production of non-toxic compounds resulting in a number of putative benefits for crop production in drought-stressed environments. This research was probably encouraged by the possibility that OA might be controlled by a single gene in wheat (Morgan 1991). A number of genes and cDNAs encoding osmolyte biosynthesis have now been genetically introduced into transgenic plants (Zhang *et al.* 1999). Furthermore, the apparent existence of genetic variation of OA in a number of species has recently opened the way for speculation on the potential use of OA genes and/or molecular markers in breeding via marker-assisted selection to improve crop drought tolerance (Belhassen *et al.* 1995; Nguyen, Babu & Blum 1997; Zhang *et al.* 1999). The identification of molecular markers and QTLs linked to OA capacity has already been investigated in many crops, including wheat (*Triticum aestivum* L.) (Van Deynze *et al.* 1995), rice (*Oryza sativa* L.) (Lilley *et al.* 1996; Price & Courtois 1999), barley (*Hordeum vulgare* L.) (Teulat *et al.* 1998) and sunflower (*Helianthus annuus* L.) (Jamaux, Steinmetz & Belhassen 1997).

However, the explosion of investigations on OA has taken place with little evidence that crop yield is benefitted by OA. Munns (1988) offered an early warning concerning the worth of measuring OA as a benefit to plant perfor-

Correspondence: T. R. Sinclair. Fax: +1 352 392 6139; e-mail: trsincl@gnv.ifas.ufl.edu

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Table 1. Papers found in the literature including osmotic adjustment, drought, and crop yield as keywords

	<i>Agricola</i> (1985–97)	Current contents (1997–99)
a. Osmotic Adjustment	788	258
b. Drought	8838	2338
c. Yield	126229	23188
d. a + b	287	139
e. a + c	70	49
f. a + b + c	30	36

mance. The objective of this paper is to consider again the caution about the putative benefits of OA on crop yield. The specific objectives of this paper are to review the link between water deficit and crop yield, examine the hypothesis of the influence of OA and crop physiological activity, and consider the possible influence of OA on soil water recovery.

YIELD AND CROP WATER USE

Before examining the putative benefits of OA on crop yield, it is useful to set the context of the influence of water deficit on plant growth. The response of plants to soil water deficit can be delineated into three distinct stages of soil dehydration as illustrated in Fig. 1 (Sinclair & Ludlow 1986). Stage I occurs at high soil moisture, when water is freely available from the soil and both stomatal conductance and water vapour loss are maximal. The transpiration rate during this stage is therefore determined by environmental conditions around the leaves. Stage II starts when the rate of water uptake from the soil cannot match the potential transpiration rate. Stomatal conductance declines, thereby keeping transpiration rate similar to the rate of uptake of soil water and resulting in the maintenance of plant water balance. Finally, stage III begins when the ability of stomata to compensate for a declining rate of water uptake from the soil has been exhausted, and stomatal conductance is at a minimum.

Virtually all major processes contributing to crop yield including leaf gas exchange (Ritchie, Burnett & Henderson 1972; Ritchie 1973; Sinclair & Ludlow 1986; Koppers, Koppers & Schulze 1988), leaf growth (Sinclair 1986; Rosenthal *et al.* 1987; Lecoecur & Sinclair 1996; Muchow & Sinclair 1991) are inhibited late in stage I or in stage II of soil drying. At the end of stage II, the rate of growth-supporting processes has essentially reached zero and no further growth occurs in the plants. Consequently, the amount of water extracted up to the end of stage II determines the cumulative growth by the plants on a particular soil water reservoir. Not surprisingly, research on soil water use in crop growth going back more than 100 years has consistently shown an intimate and stable relationship between plant growth and transpirational water use after correcting for variations in atmospheric humidity (Tanner & Sinclair

1983). Overall therefore increased crop yields invariably require increased amounts of water to allow stomata opening for photosynthesis, the consequent water loss, and the accumulation of crop mass.

Stage III develops when the soil water has decreased to a level where photosynthesis and carbon accumulation are no longer occurring. The focus of stage III is survival and water conservation is essential to allow the plant to endure these severe conditions (Sinclair 2000). Although plant survival is a critical trait in natural dryland ecosystems, stage III has little relevance to questions about crop yield and increasing crop productivity for most agricultural situations (Tardieu 1996). This is true because the development of a severe water deficit that threatens survival in stage III necessarily means that the total quantity of water available to the crop has been very limited. As a consequence, crops subjected to a prolonged period of stage III drought will necessarily have greatly diminished crop growth and limited yield capacity. In industrial nations, it is likely that harvesting a crop with the very low yields necessarily associated with restricted water availability leading to stage III water deficit will not be economically viable. In subsistence agriculture, a stage III water deficit also means very low yield but the grower is usually forced out of human necessity to harvest whatever can be recovered. Even in subsistence cropping, options to enhance crop survival may mean only a small or no crop yield increase and offers little solution to social progress in view of the many environmental and socio-economic limitations that ultimately constrain the productivity of these agricultural systems.

YIELD AND OSMOLYTE ACCUMULATION

In spite of the widespread suggestion that OA is beneficial for increasing crop yields under water-deficit conditions, experimental data offer little supporting evidence. Table 2 summarizes most of the published work where the link

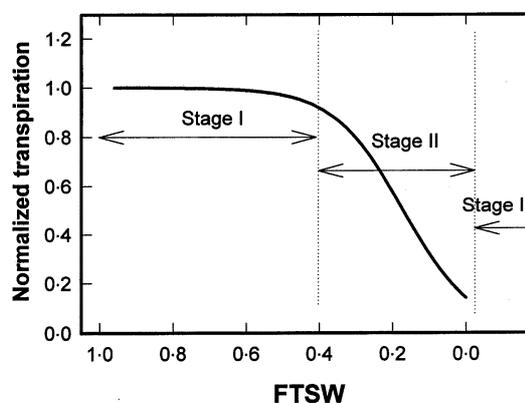


Figure 1. Typical plot of normalized leaf transpiration (NTR) against the fraction of transpirable soil water (FTSW). From the data of Sinclair & Ludlow (1986).

Table 2. Relationship between osmotic adjustment and crop yield reported in the literature

Species	Positive effect	Reference	Comments
Wheat	Yes	Morgan 1983	Very low yield. No direct measurement of OA.
	Yes	Morgan & Condon 1986	Same results as above. Difference in water extraction.
	Yes	Morgan 1995	Yield difference between low and high OA only significant in three pairs among nine compared, in case of severe drought stress. Effect of OA on soil water extraction.
	No	Blum <i>et al.</i> 1999	Non-significant results with positive regression a consequence of results from one line out of 10.
Barley	No	Grumet <i>et al.</i> 1987	Growth disadvantage of low osmotic potential population for total above-ground biomass production and grain yield under both dry and irrigated conditions.
Sorghum	Yes	Ludlow <i>et al.</i> 1990	Effect of OA on root length. No effect on DM yield, effect on harvest index
	Inconsistent	Santamaria <i>et al.</i> 1990	Among three pairs of lines, one pair showed that OA increased water extraction, one pair OA allowed better panicle exertion, one pair showed yield advantage to low OA.
Maize	No	Bolaños & Edmeades 1991	Correlations between OA and performance under drought were weak, inconsistent and non-significant.
	No	Guei & Wassom 1993	Non-significant correlations between OA and yield.
Rice	No	Fukai & Cooper 1995	No measurement of OA effect on yield. OA develops quickly.
Cotton	No	Quisenberry <i>et al.</i> 1984	Significant negative correlation between low solute potential and shoot dry matter production under drought conditions.
Soybean	No	Cortes & Sinclair 1986	Maintaining water supply to plant tissue of much greater benefit than OA.
Pea	Only under severe drought stress	Rodríguez-Maribona <i>et al.</i> 1992	Extrapolation of greenhouse OA measurements on yield data in field trials.
Chickpea	Only for low yield	Morgan <i>et al.</i> 1991	No direct measurement of OA.
Pigeonpea	Inconsistent	Subbarao <i>et al.</i> 2000	Correlations between OA and yield positive at 72 and 82 DAS, negative at 92 DAS.

between OA and crop yield has been examined. In all of these studies, OA was measured as osmotic adjustment and it was measured exclusively in the leaves. Crop yields of high osmotic-adjusting lines were typically compared with those of low osmotic-adjusting lines. The data published by Morgan on wheat (Morgan 1983; Morgan & Condon 1986; Morgan 1995) and by Ludlow on sorghum (Ludlow, Santamaria & Fukai 1990; Santamaria, Ludlow & Fukai 1990) are the ones usually cited as the critical references for the putative benefits of OA on crop yield.

Morgan (1983) worked with wheat and initiated his studies on yield and OA by evaluating various wheat lines for osmotic adjustment under greenhouse conditions using estimates of the relative water content (RWC) at a given value of water potential (-2.5 MPa) to select for high osmotic-adjusting lines. Unfortunately, there were no direct measurements of osmotic adjustment either in the greenhouse or in the field, and osmotic adjustment was inferred from indirect correlations, neglecting possible variations in the value of modulus of elasticity. Indeed, Babu *et al.* (1999) showed recently that different methods of OA measurement do not necessarily give consistent results.

Grain yields in the field of the wheat lines selected for putative differences in osmotic adjustment (Morgan 1983) were 44 g m^{-2} for lines identified with high OA and 29 g m^{-2} for lines with low OA. These results likely reflected an

advantage in this particular experimental conditions during severe stage III survival. The difficulty is that these yield levels were so low that even yield at 44 g m^{-2} would be considered a failed crop by growers. In industrial agriculture, yields of at least 150 g m^{-2} , and more probably in the range of $200\text{--}400 \text{ g m}^{-2}$, are probably needed for viable production under dryland conditions.

Morgan (1995) also reported comparisons of wheat grain yield under drought for low and high osmotic-adjusting lines from 5 years of field experiments. Among the nine comparisons presented, only three pairs had a significantly greater yield in high osmotic adjustment lines (Fig. 2), and these were limited to cases of severe water deficits and very low grain yield. Three other comparison pairs had small non-significant advantage for high osmotic-adjusting lines, and three pairs had lower although non-significant yield for the high osmotic-adjusting group.

Recently, Blum, Zhang & Nguyen (1999) reported comparisons of OA and yield among 10 spring wheat cultivars, including two of Morgan's lines. The conclusion offered from this work was support for Morgan's hypothesis of an association between high OA and plant production under drought stress. This conclusion was based only on a non-significant correlation between OA and yield, due mainly to a difference with one low-producing genotype, which also happened to have low OA. All of the nine other lines

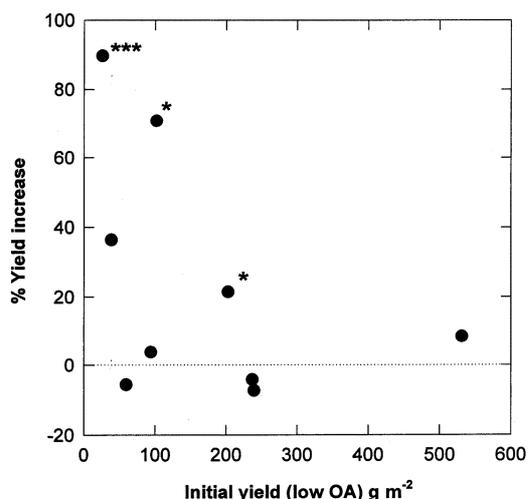


Figure 2. Plot of the percentage of yield increase due to osmotic adjustment versus initial yield in wheat cultivars. From the data of Morgan (1995).

had comparable yields, although their OA values ranged between 0.47 and 0.63 MPa.

Ludlow *et al.* (1990) reported a positive association between high osmotic adjustment capacity and grain yield under a post-anthesis water deficit in sorghum. The higher yield was apparently due to both more and larger grains, and it was associated with higher harvest index and distribution index. Interestingly, there was almost no effect of osmotic adjustment on dry matter at maturity in this study. The main physiological effect of OA was then interpreted to be turgor maintenance in the panicle, which may have resulted in continued metabolic activity during grain filling, and thus higher harvest index. This study may have reflected the special case where OA could have extended physiological activity in the panicle prior to the rescue of the crop by rainfall.

Results were also reported from the same sorghum lines as above for the contribution of osmotic adjustment to grain yield when subjected to severe pre-anthesis water deficits (Santamaria *et al.* 1990). The overall response was a higher average grain yield for high osmotic-adjusting lines, mainly due to a larger grain number and higher harvest index. However, among the three pairs of lines compared, one pair showed a non-significant yield advantage for the low osmotic-adjusting line, one pair showed that osmotic adjustment was associated with more water extraction, and the third pair showed that osmotic adjustment was associated with better panicle exertion.

Osmotic-adjustment capacity of seven pea genotypes was measured in a greenhouse test and compared to grain yield obtained in field trials (Rodríguez-Maribona *et al.* 1992). The correlation between osmotic-adjustment capacity and yield was only significant in the case of dry years, but not in a rainy year when drought was only moderate and higher yields were achieved. The same results were obtained with chickpea (Morgan, Rodríguez-Maribona & Knights 1991), in that greater yields were produced by lines

with high osmotic-adjustment capacity only when grown in environments of greatest stress where yields were low.

In addition to the above often-cited studies, usually used as references to illustrate the beneficial effect of OA on grain yield, there are numerous reports showing no effect of osmotic adjustment, or even reporting negative effects of osmotic adjustment on crop yields (Table 2). Quisenberry, Cartwright & McMichael (1984) reported significant negative correlation between cotton shoot weights and osmotic adjustment estimated by the osmotic potential where zero turgor occurred. They concluded that if selection pressure is directed towards enhancing osmotic adjustment under drought, a reduced growth potential may result. Grumet, Albrechtsen & Handon (1987) reported that barley lines selected for high osmotic adjustment had slower growth, lower dry matter production and grain yield than lines with low osmotic adjustment. No yield benefit was found with osmotic adjustment in four sorghum cultivars under severe drought (Flower, Rani & Peacock 1990). Recently, Subbarao, Chauhan & Johansen (2000) reported that OA was positively correlated with grain yields at 72 and 82 days after sowing (DAS) whereas OA at 92 DAS contributed negatively to the yield. Bolaños & Edmeades (1991) showed that correlations between osmotic adjustment and performance of tropical maize populations under drought were weak, inconsistent and non-significant. The same conclusion has been apparently made by the CIMMYT maize program (see Guei & Wassom 1993). A large research effort with rice has failed to produce evidence of a benefit of OA on crop yield (Fukai & Cooper 1995).

Overall, the exceptional results within the published literature are those showing a positive correlation between osmotic adjustment and yield, and these are usually obtained under severe drought stress when the yields are too low to be of practical value.

WEAKNESS OF OSMOLYTE ACCUMULATION HYPOTHESIS

The advantage of OA in crop plants is usually suggested to result from one or more of the following mechanisms: osmoprotection of cells, maintenance of cell and tissue turgor, tissue mortality at greater stress levels, and increased soil water uptake. The relevance of the first three hypotheses to crop production are discussed in this section and the possibility of increased soil water uptake is considered in the next section.

Osmoprotection

The osmoprotection mechanism is based on intimate associations of non-toxic compounds with various cellular components. To survive under severe osmotic stresses, certain micro-organisms, algae and plants have evolved a high capacity to synthesize and accumulate non-toxic solutes, called osmoprotectants, osmolytes or compatible solutes. The accumulation of such compounds, mostly in the cyto-

plasm can protect cell membranes, proteins and metabolic machinery, which would preserve subcellular structure from damage as a result of cell dehydration (Rhodes & Samaras 1994; Rathinasabapathi, 2000). Unfortunately, many investigations have not clearly differentiated between the osmoprotection and osmotic adjustment mechanisms and their respective roles in water-deficit response. It is often assumed that the increase in cellular osmolarity which results from the accumulation of compatible solutes is accompanied by influx or reduced efflux of water from cells, thus resulting in higher turgor and cell expansion (Rhodes & Samaras 1994; Nuccio *et al.* 1999; Zhang *et al.* 1999). The putative value of turgor enhancement is discussed in the next section.

The accumulation of compatible osmoprotectant compounds has been a target for plant genetic engineering for more than 15 years (LeRudulier *et al.* 1984) and is still in progress for many crops. Genetic engineering for enhanced synthesis of osmoprotectants, such as proline and glycine betaine, is assumed to contribute to drought tolerance improvement. Several reviews have recently discussed osmoprotection in plants and its potential application in improving drought and salt stress tolerance (Holmström *et al.* 1996; Hare & Cress 1997; Holmberg & Bülow 1998; Hare, Cress & Van Staden 1998; Nuccio *et al.* 1999; Zhang *et al.* 1999; Rathinasabapathi, 2000). For example, transgenic tobacco plants overexpressing proline synthesis genes have even been claimed to induce osmotic adjustment and increased drought stress tolerance (Kishor *et al.* 1995), but without any physiological evidence that osmotic adjustment was actually induced by proline in these plants (Blum *et al.* 1996; Sharp *et al.* 1996). Hare *et al.* (1998) recently pointed out that the hypothetical role of OA in mediating osmotic adjustment and protecting subcellular structure has become a central dogma in stress physiology, although transgenic plants engineered to accumulate proline, mannitol, fructans, trehalose, or glycine betaine show marginal improvements in osmotic-stress tolerance, with probably no link with osmotic adjustment (Blum *et al.* 1996; Nguyen *et al.* 1997; Hare *et al.* 1998; Zhang *et al.* 1999).

In regards to crop production, the osmoprotection mechanism is probably not functional until severe dehydration is threatened, i.e. the plant is well into stage III. Therefore, osmoprotection by definition could be a mechanism associated with plant survival, which could be critical in natural ecosystems, but as discussed previously, it has little relevance to crop production. Traits required to be beneficial for practical crop yield increases need to be operational at an earlier stage of soil drying and somehow cause improved physiological activity before dehydration occurs in the cells.

Turgor maintenance

A second hypothesis for the benefit of OA is the maintenance of cell and tissue water content and turgor. In this case, OA allows the osmotic potential of the cell to decrease and as a consequence, increase the gradient for water flux into the cell and maintenance of turgor. Although the tur-

gor maintenance scenario has a superficial appeal, under cropping conditions with increasing soil dehydration, the putative advantage of continued growth and use of water may be exactly the opposite of what is needed (Tardieu 1996). If turgor maintenance results in maintenance of green leaf area and delay of water-conserving mechanisms such as leaf wilting and rolling (Hsiao *et al.* 1984) and stomatal closure, then high rates of plant dehydration are sustained. As a consequence, leaf water potential would fall more rapidly as a result of OA (Morgan 1984) and cause leaf and plant death when the threshold of lethal relative water content is reached, or if the soil water is exhausted (Ludlow & Muchow 1990). Ludlow & Muchow (1990) further illustrated this case by pointing out that some high OA legume species die before other species that have low OA (Ludlow *et al.* 1983; Sinclair & Ludlow 1986). Ludlow & Muchow (1990) concluded that osmotic-adjustment traits might not be desirable for subsistence agriculture as it is associated with an increased risk of exhausting soil water.

The consequence of delayed stomatal closure as a result of OA and turgor maintenance was examined over 20 years of weather scenarios using a systems analysis approach (Sinclair and Muchow 2001). In their analysis, the initiation of the decrease in stomatal conductance, as illustrated in Fig. 1, was shifted to the right so that it occurred at a lower soil water content. There was no case in the 20 years in which delayed stomatal closure markedly increased yield. In fact, in several years the delayed stomatal closure resulted in sustained soil drying so that the crop was subjected to greater stress and yields were decreased substantially. This analysis showed that mean crop yield was, in fact, decreased by delaying stomatal closure at the beginning of stage II.

Turgor maintenance might also be hypothesized to have a specific benefit on plant recovery from stage II water deficit. At this stage, OA and turgor maintenance could be suggested to allow more rapid recovery of plants from water deficit if they are provided with water. In reality, however, leaf gas exchange and leaf area development have been observed to recover rapidly following stage II water-deficit stress (Xianshi, Sinclair & Ray 1997). There seems to be little opportunity to substantially improve plant performance by more rapid recovery from stage II water deficits.

Lethal stress levels

Osmotic adjustment has been suggested to enhance dehydration tolerance (Turner & Jones 1980; Hsiao *et al.* 1984; Morgan 1984), which extends the duration of plant survival under severe drought conditions (Ludlow & Muchow 1990; Sinclair 2000). Dehydration tolerance can be expressed as either lethal RWC or lethal leaf water potential (Ludlow & Muchow 1990). However, consistent associations between OA and dehydration tolerance have not been observed. Lilley & Ludlow (1996) reported that 50% of the genotypic variation in lethal osmotic potential was accounted for by variation in osmotic adjustment. Flower & Ludlow (1987) also showed that pigeonpea genotypes with greater osmotic

adjustment were more dehydration tolerant. Basnayake *et al.* (1993) showed, on the other hand, that maximum osmotic adjustment was inversely related to desiccation tolerance in sorghum, as lethal RWC increased linearly with osmotic adjustment increase. Sorghum lines with high osmotic adjustment died at a relatively higher RWC than those with low osmotic adjustment (Basnayake *et al.* 1993). One possible explanation of such contradictory results would be that OA is a consequence of water deficits causing decreased consumption of organic solutes, rather than a physiological mechanism involved in an adaptive plant response (Munns 1988).

In any event, a change in the stress level to which a plant can survive is again of little relevance to crop production in contrast to natural environments. This mechanism is clearly targeted to prolonging Stage III stress, which as already discussed is not relevant for most cropping situations. The total water availability and yield levels will necessarily be extremely low when the mortality of the crop is at risk.

IMPROVED SOIL WATER RECOVERY

As discussed previously, crop yield increases must be associated with increases in transpirational water losses. Therefore, any putative benefit of OA under water deficit conditions invariably requires an increased recovery of soil water. Two hypothesis have been presented for OA to allow greater soil water uptake. One is to increase the gradient in water potential between the plant and soil and the second is to enhance the volume of soil being exploited for water.

Increased water potential gradient

In principle, water movement into plants is continued if a water potential gradient between the plant and the soil water is maintained. Therefore, one possibility as the soil dries is to lower plant water potential by OA so as to maintain a water potential gradient and sustain soil water uptake by the plant. Unfortunately, once soil has dried to the transition from stage II to III, there is very little additional water to be extracted from the soil.

The limitation on OA to obtain additional water is estimated by considering the additional water that can be extracted from the soil as a result of a decrease in the water potential of the plant associated with OA. Commonly, the osmotic potential of most crop plants is between -1.5 and -2.0 MPa (Kramer 1983). It is not surprising, then, that the soil water potential at which plants reach the permanent wilting point was originally observed to be approximately -1.5 MPa (Richards & Weaver 1943). The additional water that can be extracted from the soil can be estimated as the volumetric fraction of water retained in the soil between -1.5 MPa and the adjusted osmotic potential of the plant.

Shifts in osmotic potential as a result of OA range in crop species between 0 and 2 MPa for wheat (Morgan 1977, 1983; Blum *et al.* 1999), 0.4–1.5 MPa for rice (Lilley & Ludlow 1996), 0.8–1.7 MPa for sorghum (Basnayake *et al.* 1993). However, most of the extremely high values for

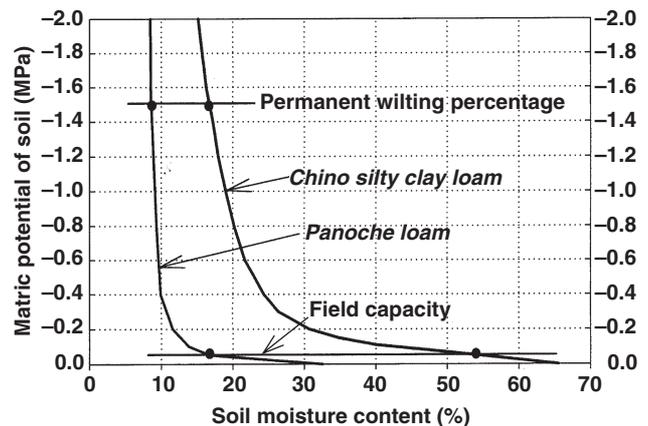


Figure 3. Relationship between soil matric potentials and water content, plotted from the data of Wadleigh, Gauch & Magistad (1946) and Richards & Weaver (1944) for sandy loam and a clay loam soils, respectively.

osmotic adjustment were obtained in plants subjected to severe conditions. Assuming an osmotic adjustment value at the end of stage III is likely to be on the order of 0.5 MPa (Turner *et al.* 1986), then the additional water made available to the plant as a result of osmotic adjustment is roughly the soil water content between -1.5 and -2.0 MPa. For most soils, however, very little moisture is released by soils in this range of water potential. This is illustrated in Fig. 3 for two soils showing very little further decrease in soil moisture content as the water potential decreases to less than -1.5 MPa. The possible benefit of OA is even less for those crops where the initial base osmotic potential is less than -1.5 MPa.

Further, the putative benefit of OA for increased water uptake is one that again develops at the beginning or during stage III stress. Such severe stress levels exist only after substantial crop yield capability has been lost and crop yields will be low. The relevance of this mechanism is likely to be very minimal for most cropping situations.

Increased soil volume

The density of roots required to extract soil water is roughly only about 1.0 – 1.5 cm cm⁻³ (Cowan 1965; Gardner 1964). Therefore, under most conditions the critical variable in determining the size of the soil water reservoir available to crops is the depth of rooting, assuming that soil at the deeper depths has been recharged and contains water. If genetic limitations of the crop or soil conditions limit rooting into deeper wet soil, the yielding capability of the crop can be severely limited. In the systems analysis of Sinclair and Muchow (2001) to assess traits for yield increases under water-limited conditions, the trait that consistently increased crop yields was an increase in rooting depth.

An important possibility for a role of osmotic adjustment may be in root tips so that root growth can be sustained at the onset of soil drying and roots penetrate deeper into the soil and into new water reserves. OA occurs in

roots and has an impact on root elongation (Voetberg & Sharp 1991). Data obtained on wheat (Morgan & Condon 1986; Morgan 1995) clearly show a greater depth of water extraction in high osmotic-adjusting lines in comparison with low osmotic-adjusting lines. Osmotic adjustment could even be greater in root tips than in leaves, as it has been shown for maize (Sharp & Davies 1979; Westgate & Boyer 1985). Hsiao & Xu (2000) suggested in a recent report that the growth zone of roots adjusts osmotically to sudden reductions in water potential, whereas the leaf adjusts slowly or not at all, which could explain the higher sensitivity of leaf growth to water deficits, compared to roots. Matyssek, Tang & Boyer (1991) suggested that high osmotic adjustment in root tips could divert water from other plant organs into the root tips, which results in sustained root growth in dry soils. However, OA in root tips has not been the focus of recent research to improve plant performance under water-deficit conditions.

CONCLUSIONS

Very little direct evidence exists showing that crop yields benefit by increased OA. In fact, most published papers indicate no effect, or a negative influence of OA on crop yield. Those few papers that have shown a positive yield response are almost invariably from experiments where yields are extremely low, and hence, irrelevant for most agricultural conditions.

The failure to obtain evidence for a strong benefit of OA on yield is likely to have resulted because most of the hypothetical benefits are expressed only when crop survival is threatened. For most agricultural conditions, crop survival is not an important issue because yields under such severe stresses are so low that any putative benefits are not beneficial to growers. Further, the hypothetical benefits of turgor maintenance in response to drying soil tend only to worsen the situation. Water conservation is the appropriate response for most cropping situations when the soil reaches the later stages of drying. Maintenance of high stomatal conductance and leaf turgor as a consequence of OA sustains water loss so that the crop rapidly enters the survival stage, and as result crop mortality is threatened.

The single advantage of OA identified in this review is that which may occur in root tips. Osmolyte accumulation in roots that allows continued, or even increased, root development into deeper, wet soil can give plants access to an increased water reservoir on which the crop can grow and/or survive. Hence, investigations that seek to improve crop performance by increasing OA need to focus on roots and root tips.

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