

Evaluation of the differential osmotic adjustments between roots and leaves of maize seedlings with single or combined NPK-nutrient supply

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Abstract. Many physiological mechanisms associated with nutrient supply have been implicated as improving plant growth under drought conditions. However, benefits to plant growth under drought might derive from an increased recovery of soil water through osmotic adjustment in the shoots and especially in the roots. Thus, experiments were carried out to investigate the effects of the nutrients N, P and K applied singly or in combination, on the osmotic adjustment and turgor maintenance in the roots and leaves of maize seedlings. The seedlings were harvested between 18 and 37 days after sowing according to the soil matric threshold potentials. Soil matric potentials and shoot and root biomass were determined at harvest. Turgor pressure and osmotic adjustment of the leaves and roots were estimated by measurements of their water and osmotic potentials. Results showed that plants with either of the combined fertilisation treatments NPK or NP grew faster at a given level of drought stress than those with no fertilisation, N, P or K applied individually or the combined nutrient treatments PK and NK. Among the fertiliser applications with either a single or two combined nutrients, plants treated with any of N, P or NP grew faster than those with either K or NK. The association between the interactive effects of nutrients and drought stress on the osmotic adjustment and turgor maintenance in roots may partially explain the role of nutrients in drought tolerance of maize seedlings. In particular, the roots exhibited a higher osmotic adjustment than the leaves for all nutrient treatments, suggesting that shoot growth shows a higher sensitivity to water deficit compared to root growth. We conclude that the maintained turgor of roots under drought stress obtained with an optimal nutrient supply results in better root growth and apparently promotes overall plant growth, suggesting that osmotic adjustment is an adaptation not only for surviving stress, but also for growth under such conditions.

Additional keywords: maize, nitrogen, osmotic adjustment, phosphorus, potassium, turgor maintenance, water stress.

Introduction

Drought stress is the main factor limiting crop production in rain-fed farm systems as a result of increasing frequency of dry periods in many regions of the world. The great challenge in the future will be to increase food production with reduced water supplies, particularly in countries with limited water and land resources (Debaeke and Aboudrare 2004). Drought tolerance in plants is a complex occurrence. Among those characteristics that apparently confer drought tolerance, osmotic adjustment has received increasing interest during recent years. In particular, it has been hypothesised that osmotic adjustment can increase water extraction from soil by stimulating root growth (Greacen and Oh 1972; Morgan and Condon 1986; Morgan 1992). In a report by Sharp *et al.* (2004), they showed that the primary root for several crop species maintains substantial elongation rates at water potentials lower than -1.5 MPa, whereas shoot growth is already inhibited completely at much higher water potentials. Evidence is pointing increasingly to the root as a sensor of plant water deficits and moving the emphasis from the leaf to the

root in this area (Sharp and Davies 1979; Hsiao and Xu 2000; Serraj and Sinclair 2002). However, the changes in root osmotic adjustment or turgor maintenance with soil drying remain poorly understood.

Nutrient supply can strongly affect crop productivity under drought conditions through a variety of complex mechanisms (Turner and Jones 1980; Turner *et al.* 1987; Hu and Schmidhalter 2005). The positive effects of N and P on plant growth under drought conditions have been attributed to an increase in water-use efficiency, stomatal conductance and cell membrane stability photosynthesis, as well as to improved osmotic adjustment (Ackerson 1985; Brueck *et al.* 2000; Sawwan *et al.* 2000). By contrast, K increases drought tolerance through its functions in stomatal regulation, energy status, charge balance, protein synthesis and homeostasis (Beringer and Trolldenier 1978; Marschner 1995). Although many physiological mechanisms associated with nutrient supply have been implicated in improving plant growth under drought, we hypothesise that the complicated interaction of drought and nutrients for plant

growth may derive fundamentally from an increased recovery of soil water through osmotic adjustment in either the shoots or the roots, especially in the roots. As such, the objective of this study was to investigate the effect and role of N, P and K nutrients applied either singly or in combination on the osmotic adjustment and turgor maintenance in either the roots or leaves of maize seedlings.

Materials and methods

Plant materials and growth conditions

Maize seeds (*Zea mays* L. cv Issa) that were pre-germinated for a day in distilled water were sown four to a pot. Each of the 96 pots (10.5 cm in diameter and 20 cm high) contained 1.5 L of silty soil with different levels of NPK. The properties of the soil are shown in Table 1 (Schmidhalter and Oertli 1991). Nitrate, P, K and Mg contents of the soil were determined in NH_4 -acetate-EDTA extracts before the experiment started (Lonza-Data 1985) and are presented in Table 2. Modified Hoagland nutrient solution was added to the dry soil to obtain a gravimetric soil water content of 27% under eight different nutrient treatments (including a control). The wetted soil was mixed thoroughly and allowed to equilibrate for more than 2 days. Thereafter, the soil was sieved and placed into pots. To minimise water loss through evaporation, a 2-cm layer of quartz sand ($\phi = 2$ mm) covered the soil surface. Four days after sowing, the seedlings were thinned to three plants per pot. The experiment was conducted in a growth chamber with a 12-h photoperiod. The light intensity was $\sim 450 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ (PPFD). The day/night air temperature was 20/18°C and the relative humidity was maintained at 50–65%. All treatments were replicated three times.

Plants were harvested at specific soil matric potentials rather than at specific days after sowing, given that different nutrient levels affect plant development differentially and so result in variable soil matric potentials at any given day after withholding water.

Table 1. Soil characteristics of the investigated soil

Clay (%)	Silt (%)	Sand (%)	Organic matter (%)	pH	Cation exchange capacity (mmol kg^{-1})	Ca (g kg^{-1})
9.1	59.5	31.4	0.85	8.2	48	3.07

Table 2. The compositions of the different NPK nutrient treatments according to Lonza-Data (1985) for both the well-watered and drought treatments

Nutrient levels A, C, E according to Lonza-Data (1985). A, deficient; C, adequate; E, excessive

Nutrient treatments	NO_3^-	Levels	Composition of nutrients (mg kg^{-1} soil)					
			P	Levels	K	Levels	Mg	Levels
0	47	A	61	A	32	C	1734	C
K	40	A	63	A	79	E	1715	C
P	37	A	116	C	30	C	1783	C
N	486	C	61	A	30	C	1731	C
PK	35	A	116	C	81	E	1731	C
NK	506	C	59	A	81	E	1890	C
NP	381	C	112	C	32	C	1769	C
NPK	403	C	118	C	69	E	1794	C

Determination of soil matric potentials

Pots were weighed daily before watering. Bulk soil water content was determined from gravimetric measurements of the pots (plant weight was estimated and considered in the calculations). For harvesting, soil water content was determined gravimetrically using soil samples (mixed samples from the whole soil volume) and the soil matric potential was calculated using a soil retention curve that was established previously (Schmidhalter 1997).

Soil moisture content in all treatments was maintained at the initial levels by adding tap water until day 12 after sowing. Thereafter, drought conditions were simulated by withholding further watering. The plants in the drought treatments were harvested when the soil matric potentials reached approximately -0.22 to -0.60 MPa, with -0.22 to -0.35 MPa being considered as moderate drought stress and -0.35 to -0.60 MPa as severe drought stress. The soil matric potential in the well-watered treatments at each harvest ranged from -0.04 to -0.07 MPa. The times of the different harvests is shown in Table 3.

Determination of plant biomass, turgor pressure and osmotic adjustment of the leaves and roots

At harvest, the fresh and dry weight of the shoots and the dry weight of the roots were measured for each plant. The calculation of the growth rate ($\text{mg per plant per day}$) during the period of drought stress was based on the corresponding values for these variables at day 12 for all fertiliser treatments, which were taken from the parallel study of Studer (1993).

The turgor pressure was estimated as the difference between the water and osmotic potentials for both leaves and roots. According to Studer (1993), osmotic adjustments, as calculated from the difference in the pre-dawn osmotic potential (Ψ_π) between the well-watered and droughted plants, are almost the same as those calculated from the analysis of pressure–volume curve regardless of the nutrient treatments. As such, the osmotic adjustments of leaves and roots were all calculated by the simpler pre-dawn measurements method.

For leaves, pre-dawn water potentials were measured from the apical half of the youngest fully expanded leaf with a pressure chamber (PMS Instrument Co. Model 1002, CA, USA) according to Scholander *et al.* (1965), Passioura (1991) and Turner (1988, 2004). Thereafter, the samples were sealed into small plastic bags, bathed in liquid nitrogen, then thawed at room

Table 3. The soil matric potentials (Ψ_s) for both the well-watered (WW) and drought (D) treatments as measured at harvest after a given number of days after sowing (DAS)

Nutrient treatments	DAS	Ψ_s (MPa)		DAS	Ψ_s (MPa)		DAS	Ψ_s (MPa)	
		WW	D		WW	D		WW	D
0	29	-0.04 to -0.07	-0.30	30	-0.04 to -0.07	-0.48	33	-0.04 to -0.07	-0.59
K	31	-0.04 to -0.07	-0.24	37	-0.04 to -0.07	-0.39	37	-0.04 to -0.07	-0.54
P	23	-0.04 to -0.07	-0.23	25	-0.04 to -0.07	-0.37	28	-0.04 to -0.07	-0.60
N	24	-0.04 to -0.07	-0.22	27	-0.04 to -0.07	-0.39	27	-0.04 to -0.07	-0.47
PK	25	-0.04 to -0.07	-0.28	29	-0.04 to -0.07	-0.40	30	-0.04 to -0.07	-0.54
NK	26	-0.04 to -0.07	-0.25	26	-0.04 to -0.07	-0.41	32	-0.04 to -0.07	-0.48
NP	18	-0.04 to -0.07	-0.24	20	-0.04 to -0.07	-0.33	20	-0.04 to -0.07	-0.51
NPK	18	-0.04 to -0.07	-0.25	20	-0.04 to -0.07	-0.33	20	-0.04 to -0.07	-0.57

temperature and placed in a syringe. The leaf sap was expressed under pressure and osmotic potential (Ψ_π) was then determined with a vapour pressure osmometer (Wescor 5100C, Wescor Inc., Logan, UT, USA).

For roots, the same measurements of the pre-dawn water status were made for whole seminal root systems with a pressure chamber/osmometer technique as adapted by Schmidhalter *et al.* (1992). Only the intact root system cut above the root–shoot junction, and with the bulk of the soil shaken gently away from the root–shoot system, was used for the pressure chamber measurements (for further details, see Schmidhalter *et al.* 1998a). Pressure chamber measurements were not corrected for the Ψ_π of the xylem sap: previous investigations showed that values of the latter are higher than -0.05 MPa in leaves and markedly higher than -0.16 MPa for roots (Schmidhalter *et al.* 1998b). Therefore, whereas leaf Ψ_w in these experiments were approximated closely by the measured balancing pressures, root Ψ_w may have been underestimated. McCully (1999) suggests that osmotic potentials of root xylem sap are rather high (< -0.08 MPa) and pre-dawn values were only slightly decreased, but still within this range. Enns *et al.* (2000) contend that a rational examination of the published work, in the light of what is known about xylem maturation in maize roots, supports that the solutes of the xylem sap are maintained by the intact plant at a level which keeps root xylem osmotic potential more positive than -0.1 MPa, over a wide range of osmotic values of the medium.

After the pressure chamber reading was taken, roots fixed by two nets, were cleaned more thoroughly in less than 30 s using a stream of compressed air in a humidified chamber. After the measurements, all root tissues were immediately sealed in plastic bags and kept on ice before being transferred to a -80°C freezer. For Ψ_π determinations, the tissues were immersed in liquid nitrogen. Samples were then equilibrated at room temperature, placed in a syringe and the root sap was expressed under pressure. Osmotic potentials of the root samples were measured with a vapour pressure osmometer (Wescor) and were not corrected for apoplastic dilution.

Statistical analysis of data

A randomised complete block design was used. Data were analysed by an analysis of variance (ANOVA) using SAS (SAS, Institute Inc., Cary, NC, USA) to test the significance of the main effects. Factors were considered to be significant at a nominal $P < 0.05$.

Results

Interactive effects of NPK nutrients and drought on shoot and root growth

Under well-watered conditions, the shoot growth rate on a dry weight (DW) basis for all nutrient treatments ranged from 23 to 115 mg DW plant⁻¹ day⁻¹ as compared to 19–110 mg DW plant⁻¹ day⁻¹ under drought conditions (Fig. 1A). In general, the shoot growth rate was higher with N fertilisation than without, under well-watered conditions; under drought conditions, the rate was higher with each of P, NP and NPK fertilisations regardless of the level of drought stress. Compared with the well-watered treatments, all possible relative changes in growth rate (increased, reduced or unchanged) under drought conditions were observed depending on the nutrient treatment and the level of drought stress. For example, DW per day was increased with NPK fertilisation under mild drought stress, whereas there was no difference under more severe drought conditions. A reduction in the growth rate under drought was observed in the N, NP and NK fertilisation treatments at all levels of drought stress.

The growth rate of roots for all nutrient treatments ranged from 4 to 30 mg DW plant⁻¹ day⁻¹ and from 4 to 40 mg DW plant⁻¹ day⁻¹ under well-watered and drought conditions, respectively (Fig. 1B). The lowest rate in both well-watered and drought treatments occurred with K fertilisation, whereas the highest rate was achieved with NPK fertilisation for the droughted plants. Similar to the results for shoot growth rate on a DW basis, drought increased, reduced or did not change the root growth rate depending on the nutrient treatment and level of drought stress compared with the well-watered treatments.

Values of the root–shoot ratio depended on both the levels of fertilisation and water status. In particular, drought increased root–shoot ratios under optimal fertilisation treatments compared to well-watered treatments (Fig. 2). However, for nutrient deficient treatments, drought either decreased the root–shoot ratios or left them unchanged.

Changes in turgor pressure of leaves and root

The changes in leaf and root turgor pressure with changes in the soil matric potential under the different NPK fertilisation treatments are shown in Fig. 3. A higher turgor pressure in the roots relative to that in the leaves was observed, especially in drought conditions. On average, the turgor pressure in well-

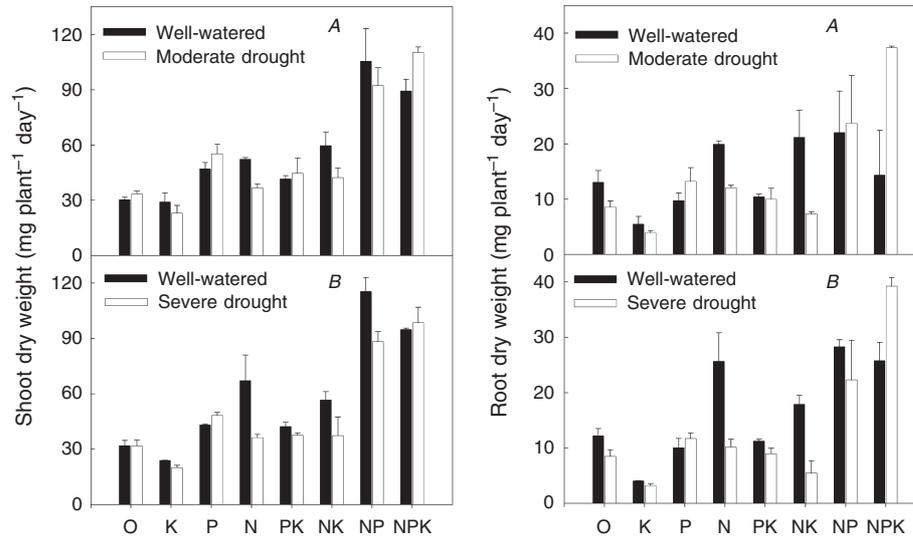


Fig. 1. Effects of N, P and K nutrients applied singly or in combination, or no nutrient application (0) under (A) moderate (soil matric potentials between -0.22 to -0.35 MPa) and (B) severe drought conditions (between -0.35 to -0.60 MPa) on the growth rate of shoots and roots [mg dry weight (DW) per plant per day] in maize seedlings. Error bars represent standard errors ($n = 2$) and fit within the plot symbol if not visible.

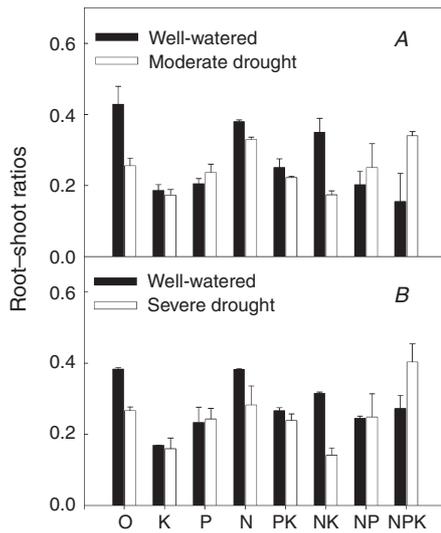


Fig. 2. Effects of N, P and K nutrients applied singly or in combination or no nutrient application (0) under (A) moderate (soil matric potentials between -0.22 to -0.35 MPa) and (B) severe drought conditions (-0.35 to -0.60 MPa) on the root–shoot ratios in maize seedlings. Error bars represent standard errors ($n = 2$) and fit within the plot symbol if not visible.

watered plants was ~ 1.5 times higher in the roots than in the leaves, whereas it was ~ 2.5 times higher in droughted plants.

The turgor pressure in the leaves always decreased with decreasing soil matric potential in all the nutrient treatments. By contrast, the response in the roots depended on the nutrient treatment. For example, the turgor pressure in roots with any of P, NP and NPK fertilisation increased with decreasing soil matric potential, whereas it decreased slightly with K fertilisation. Finally, the turgor pressure first increased or

remained unchanged, and then decreased with a decrease in the soil matric potential in the control treatment and with each of N, PK and NK fertilisation. Although a difference in plant growth among the nutrient treatments under well-watered conditions was observed (Fig. 1), the turgor pressure remained similar for the leaves and roots. However, under drought conditions, there was a clear difference in the turgor pressure of both the leaves and roots among the nutrient treatments. Under the severest drought stresses, the highest and lowest leaf turgor pressures (0.3 to 0.38 MPa and 0.04 to 0.10 MPa, respectively) were found for plants fertilised with P, NP and NPK and with N and NK, respectively. Similarly, the highest and lowest root turgor pressures (0.90 to 0.96 MPa and 0.55 to 0.62 MPa, respectively) were also obtained under the same respective treatment sets.

Changes in osmotic adjustment of leaves and roots

The osmotic adjustment, as calculated from the difference in the pre-dawn osmotic potentials between the well-watered and drought treatments at a given NPK fertilisation, is presented in Fig. 4. The osmotic adjustment in both the leaves and roots tended to increase or remain unchanged with decreasing soil matric potential. Similar to the observed differences in turgor pressure between the leaves and roots, the osmotic adjustment was higher in the roots than in the leaves regardless of the nutrient treatment and level of drought stress.

The form of the nutrient fertilisation affected the degree of osmotic adjustment in the leaves and roots at a given level of drought stress. In leaves, the osmotic adjustment for the control treatment and with K, P, PK or NP fertilisation was similar for all three levels of drought stress, while it increased with decreasing soil matric potentials with N, NK and NPK fertilisation. The averaged osmotic adjustment from the three drought-stress levels in the leaves was ~ 0.01 MPa with

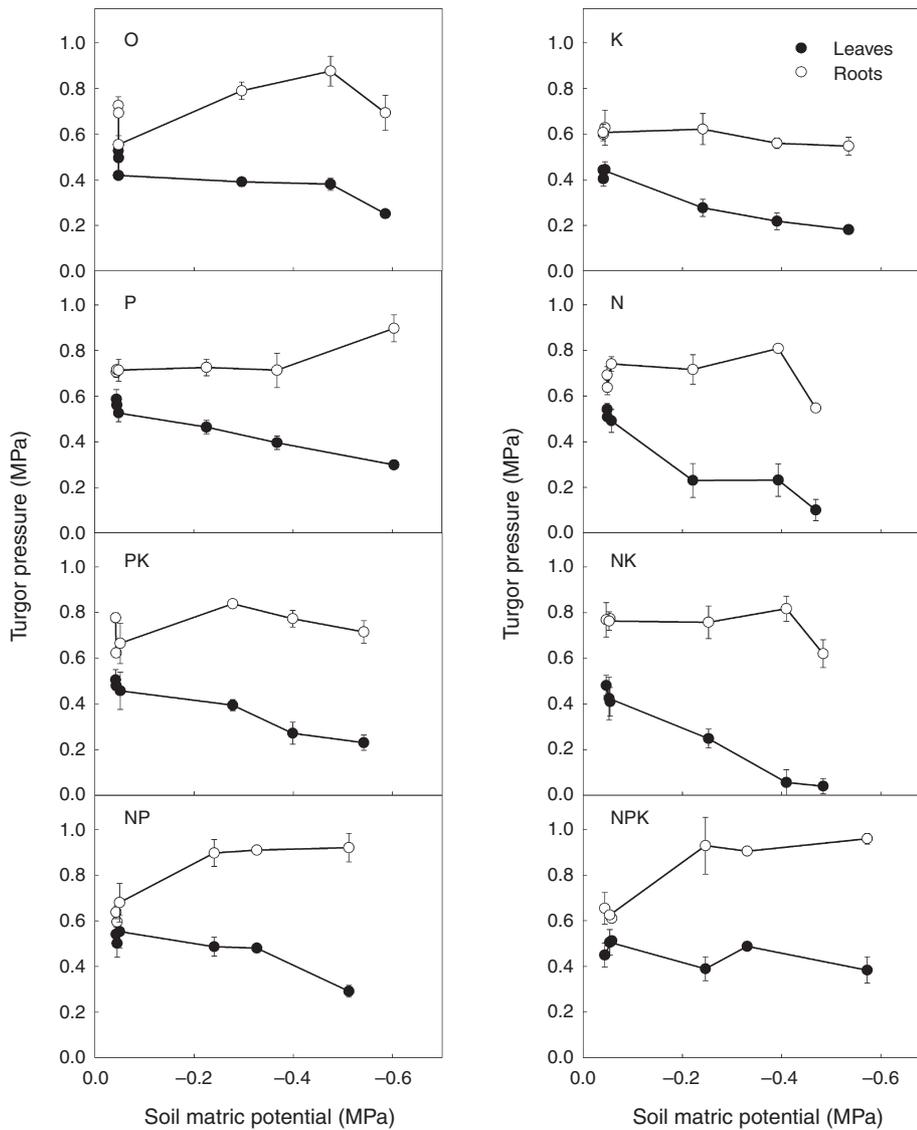


Fig. 3. Change in turgor pressure in shoots and roots of maize seedlings with the soil matric potentials with no nutrient application (0) or with N, P, and K nutrients applied singly or in combination. Error bars represent standard errors ($n = 3$) and fit within the plot symbol if not visible.

P fertilisation, 0.04 MPa with PK fertilisation, 0.05 MPa with no fertilisation, 0.06 MPa with K or N fertilisation, 0.09 MPa with NPK fertilisation, 0.10 MPa with NP fertilisation and 0.13 MPa with NK fertilisation. Similarly, the highest osmotic adjustment in the roots was also found with NPK, NP or NK fertilisation. For example, the averaged osmotic adjustment in roots was ~ 0.25 MPa with N fertilisation, 0.29 MPa with K or P fertilisation, 0.31 MPa with PK fertilisation, 0.32 MPa with no fertilisation, 0.33 MPa with NPK fertilisation, 0.45 MPa with NP fertilisation and 0.58 MPa with NK fertilisation.

Discussion

The present study showed that plants with the combined NPK or NP fertilisation treatments grew faster at a given level of drought

stress than those with no fertilisation or those with the single N, P or K nutrient or combined PK or NK nutrient treatments (Fig. 1). This result suggests that an optimised fertilisation treatment can increase plant tolerance to drought stress compared with nutrient-deficient treatments, and this finding is in agreement with reports in the literature (e.g. Smika *et al.* 1965; Turner and Jones 1980; Turner *et al.* 1987; Hu and Schmidhalter 2005). We also observed that plants with N, P or NP fertilisation grew faster than those with K or NK fertilisation among the treatments using only one or two nutrients. Although many physiological mechanisms associated with all three nutrients have been implicated in the improvement of plant growth under drought conditions (see Introduction), our results suggest that the positive benefit to plant growth may derive, at least in part, from an increased recovery of soil water through osmotic

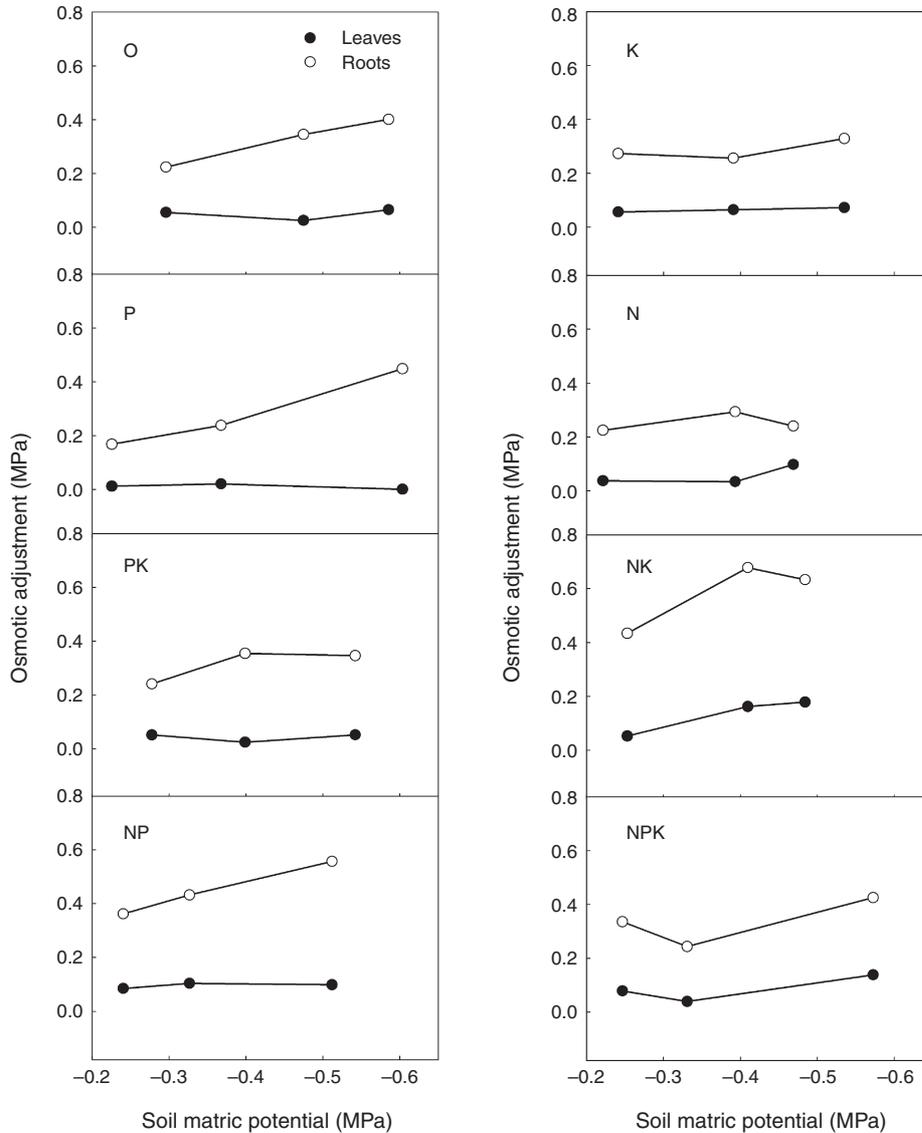


Fig. 4. Change in osmotic adjustment in shoots and roots of maize seedlings with the soil matric potentials with no nutrient application (0) or with N, P, and K nutrients applied singly or in combination.

adjustment and turgor maintenance either in the shoots or in roots (Figs 5, 6). To our knowledge, this is the first report relating NPK nutrients to osmotic adjustment in both the leaves and roots of maize seedlings.

Osmotic adjustment and turgor maintenance

Osmotic adjustment has been reported to be an important mechanism for drought adaptation in many crop plants (Turner and Jones 1980; Turner *et al.* 1987; Ludlow and Muchow 1990; Morgan 1992; Subbarao *et al.* 1995; Hare *et al.* 1998), with enhanced osmotic adjustment as a result of increasing the optimal NPK nutrient application also having been widely reported (e.g. Yambao and O'Toole 1984; Bataglia *et al.* 1985; Bennett *et al.* 1986; Morgan 1986; Premachandra *et al.* 1990). Under drought conditions, soluble sugars are the major contributors to osmotic adjustment mechanisms (Munns *et al.*

1979; Michelena and Boyer 1982; Morgan 1984; Barlow 1986; Kriedemann 1986). For example, sugar accumulation accounted for 70–100% of the osmotic adjustment in water-stressed wheat seedlings (Munns and Weir 1981). Further, almost 100% of the osmotic adjustment in both mature and growing tissues in maize (cv. Issa) seedlings could be attributed to soluble sugar accumulation (Evequoz 1993). This can be further supported by the lower concentration of the inorganic ions found in the sap of leaves and roots of maize seedlings under drought (A. Schneider and U. Schmidhalter, unpublished data). Thus, the increased solute content in NPK-supplied plants compared to nutrient-deficient plants can be attributed mainly to the positive effects of optimal fertilisation on photosynthate production rather than to direct osmotic effects on the accumulation of N and P compounds and K accumulation in plants. Although K nutrition does play an important role in osmoticum-mediated cell expansion

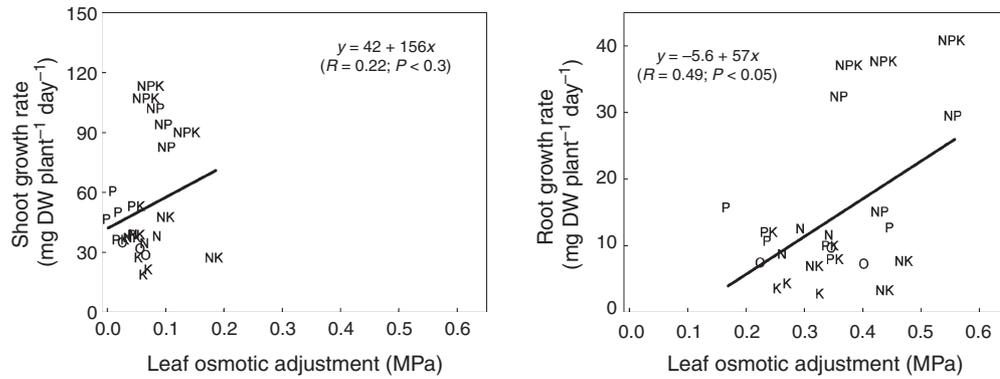


Fig. 5. The relationship between the leaf osmotic adjustment and the growth rate of shoots (mg DW per plant per day), and between the root osmotic adjustment and the growth rate of roots (mg DW per plant per day) of maize seedlings under all NPK nutrient treatments and drought conditions.

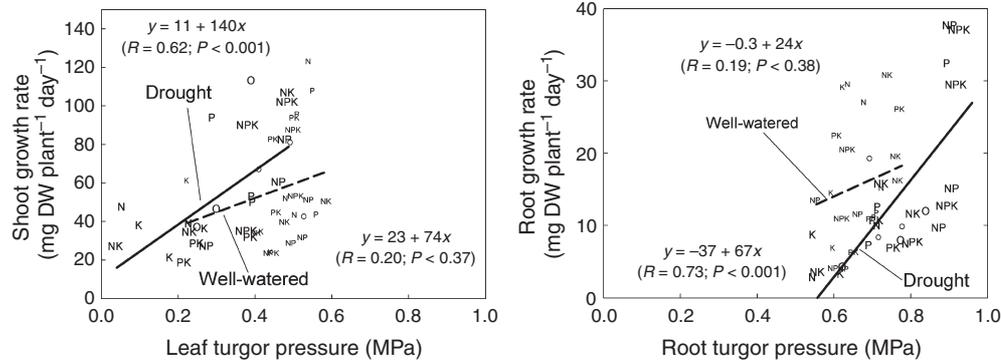


Fig. 6. The relationship between the leaf turgor pressure and the growth rate of shoots (mg DW per plant per day) and between the root turgor pressure and the growth rate of roots (mg DW per plant per day) of maize seedlings under all NPK nutrient treatments and under both well-watered and drought conditions.

(Marschner 1995), this study shows that K fertilisation by itself contributed less to osmotic adjustment in drought stressed maize seedlings than did N or P fertilisation (Fig. 3). This result may be due to both the sufficient K in soil used in this experiment and the smaller positive effect of K^+ on photosynthesis compared with that of N or P (Catsky *et al.* 1987). In contrast, it has been reported by Wolf *et al.* (2006) that, for maize plants compared with dicots and other monocots lacking subsidiary cells, K^+ ion is more efficient in maize plants, because it can be shuttling in K^+ channel between the guard cells and subsidiary cell during stomatal movement.

Differences in osmotic adjustment and turgor maintenance between the leaves and roots

Despite the positive correlation between osmotic adjustment and the net increase in DW for both the shoots and the roots during the drought period (Fig. 5), the roots clearly obtained a higher osmotic adjustment than the leaves under all nutrient treatments, albeit with a greater range in values. Furthermore, the correlation between growth rate and osmotic adjustment were significant in the roots only. This suggests that a higher sensitivity to water deficit exists in the growth of the shoots than in that of the roots, which is in agreement with previous studies conducted with optimum nutrient supplies (Schmidhalter *et al.* 1998b).

As a result, the turgor in the roots was maintained better than that in the leaves for any given nutrient treatment (Fig. 6). In a recent review, Hsiao and Xu (2000) suggested that this result might be explained by the fact that the growth zone of roots adjusts osmotically to sudden reductions in water potential, whereas that of the leaf adjusts slowly or not at all. A better maintenance of root turgor as compared to leaf turgor was also shown for maize seedlings under a mild drought stress in drying soil (Schmidhalter *et al.* 1998a). Furthermore, Sharp and Davies (1979) showed that root turgor was maintained longer into a drying cycle in maize than was leaf turgor. Matyssek *et al.* (1991) suggested that the high osmotic adjustment in the root tips could divert water from the other plant organs into the root tips, resulting in sustained root growth in dry soils. If true, this mechanism has the important consequence that root growth can be sustained at the onset of soil drying so that the roots can penetrate deeper into the soil and into new water reserves. Although the determination of osmotic adjustment in this study was conducted for the whole root system, the results may reflect those of only the root tips given that the root tips have at least the same degree of osmotic adjustment as the whole root system (Schmidhalter *et al.* 1998a, 1998b).

Many reports (e.g. Munns 1988; Serraj and Sinclair 2002) have debated whether or not osmotic adjustment benefits

growth in droughted plants. Munns (1988) stated that osmotic adjustment might be an adaptation for simply surviving the stress rather than for growing during the stress. By contrast, our study shows that osmotic adjustment benefits root growth of maize seedlings under drought, especially for plants treated with combined NP or NPK nutrients (Fig. 5). Furthermore, the osmotic adjustment that occurs in roots does have an effect on root elongation (Voetberg and Sharp 1991). Data obtained in wheat (Morgan and Condon 1986; Morgan 1995) clearly showed a greater depth of water extraction in high v. low osmotic adjustment lines. Thus, our study suggests that osmotic adjustment in roots may prove to be an important physiological mechanism or criteria to assess the response of plant growth to drought.

The maintenance of turgor in roots results in better root growth during water deficits and is also important in maintaining an adequate water supply to the plant (O'Toole and Bland 1987; Sponchiado *et al.* 1989; Serraj and Sinclair 2002; Sharp *et al.* 2004). Therefore, in plants growing in drier conditions the development of the root system is usually less inhibited, if not more enhanced, than shoot growth, resulting in the higher root–shoot ratios typically observed under drought conditions (Schmidhalter and Oertli 1991; Schmidhalter 1997). However, our results show that the root–shoot ratios under drought conditions were higher compared with the well-watered conditions only under the optimal fertilisation treatments (NP or NPK; Fig. 4) due to a higher turgor maintenance (Fig. 6), suggesting that some caution must be taken when interpreting a change in root–shoot ratios under drought conditions. Previous studies with optimum nutrient supply support the notion of increased root–shoot ratios, although the increases are more marked in some species than in others (Schmidhalter 1997). Overall, the effect of the different nutrients on the root–shoot ratios may be a result of the competition of the roots with the shoots for minerals and water and for assimilates produced by the mature leaves.

In conclusion, the interactive effects of the nutrients and drought on the osmotic adjustment and turgor maintenance in the roots may partially explain the role of the nutrients in increasing the drought tolerance of maize seedlings. A higher osmotic adjustment under all nutrient treatments was observed in the roots than in the leaves, suggesting that there exists a higher sensitivity to growth in shoots under water deficits than in roots. This results in higher turgor maintenance in the roots for a given nutrient treatment, resulting in improved root growth under the optimal nutrient supply during water deficits that in turn helps to maintain an adequate plant water supply.

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