Doctoral Thesis

Interactive effects of N-, P-, K-nutrition and water stress on the development of young maize plants (Zea mays L.)

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INTERACTIVE EFFECTS OF N-, P-, K-NUTRITION AND WATER STRESS ON THE DEVELOPMENT OF YOUNG MAIZE PLANTS (ZEA MAYS L.)

A dissertation submitted to the
SWISS FEDERAL INSTITUTE OF TECHNOLOGY ZÜRICH for the degree of
Doctor of Natural Sciences

presented by

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ZUSAMMENFASSUNG

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**Summary**

On a global scale, water deficiency is the major factor limiting agricultural production. Maize, one of the most important crops worldwide, is grown on large areas of the tropics and subtropics where droughts can occur and restrict yields. Also in temperate zones, maize yields are often confined due to suboptimal water supply.

Water availability, water use and nutrient supply to the plants are closely interacting factors influencing plant growth. However, the interactive effects of water deficiency and nutrient supply on plant physiological processes and yield production have only been little studied and are still not well understood. The objective of this study was to describe interactive effects of N-, P- and K-nutrition on the development of young maize plants grown under conditions of limited water supply, and to determine physiological reasons for differential effects of water stress on root and shoot growth under different nutrient regimes.

Maize seedlings (*Zea mays* L. cv Issa) were grown in a growth chamber up to the 5- to 7-leaf stage in pots containing a silty soil with different levels of N, P and K. Half of the pots were watered regularly, while water was withheld from the other half of the pots after day 10 or day 12 after planting. Plants were harvested at specific days after planting or when a specific soil matric potential ($\psi_s$) was reached. Shoot and root growth parameters were examined and water relations were analyzed.

Adequate N- and P-nutrition significantly improved shoot and (particularly) root growth under both water regimes, whereas no significant effects of differential K-nutrition on growth parameters were observed. Enhancement of root growth relative to shoot growth under conditions of water stress required adequate N- and P-nutrition and was particularly distinct in small plants. P-fertilization reduced the adverse effects of water stress on plant development, whereas N-fertilized plants experienced large reductions in shoot growth when water stress was imposed. Combined N- and P-fertilization resulted in optimal root and shoot development under both water regimes.

Root turgor of maize seedlings was maintained at levels > 0.5 MPa due to osmotic adjustment of up to 0.56 MPa even if soil water potential dropped below -0.5 MPa. Leaf turgor, however, decreased with increasing intensity of water stress, since no sufficient osmotic adjustment occurred (< 0.18 MPa). Evaluation of osmotic adjustment by comparing predawn osmotic potentials of well watered versus water stressed plants and calculated as the difference in osmotic potentials at full turgor between well watered and water stressed plants (from pressure-volume curves) gave comparable results.
N-fertilization increased the ability of water stressed plants for solute accumulation and thus for osmotic adjustment, particularly when combined with P-fertilization. These beneficial effects of adequate N-nutrition and combined N- and P-fertilization on osmotic adjustment may be mainly attributed to the positive effects of N- and P-fertilization on photosynthate production and translocation. Even if the extent of osmotic adjustment is not sufficient to maintain turgor pressure at low soil water potentials, solute accumulation can enhance resumption of growth upon stress relief.

Under conditions of adequate P-nutrition, the differences in water potentials both between soil and roots and between roots and shoots were reduced as compared to conditions of P-deficiency. Thus, P-fertilized plants showed higher turgor pressures at a given intensity of water stress than P-deficient plants. In N-fertilized plants, the difference between root and leaf water potentials was significantly greater than in N-deficient plants. Therefore, the sensitivity of shoot growth to low soil moisture availability was significantly increased in N-fertilized as compared to N-deficient plants.

Cell wall elasticity in leaves of water stressed plants was significantly higher as compared to well watered plants. Bulk modulus of elasticity was decreased between 1.8 and 5.3 MPa in water stressed plants ($\psi_r$ approximately -0.4 MPa) as compared to well watered plants ($\psi_r > -0.06$ MPa). Capacitance was significantly higher in water stressed than in well watered plants (+15 to +60 %). Different nutrient treatments affected elasticity and capacitance to a lesser extent than different water regimes. Moreover, the effects of different nutrient treatments on elasticity and capacitance depended on the water regime.

The positive effects of N- and P-fertilization on shoot and root growth could not be explained by their effects on plant water relations solely. Other 'specific' effects of N- and P-nutrition additionally influenced plant growth. The results of the present study suggest that the supply of (growing) tissues with specific nutrients might become a growth limiting step, particularly under conditions of water stress. This might be due to the fact that cell enlargement and particularly growth of a whole organ cannot be explained as a purely hydraulic/mechanical process. Growth is coupled with numerous metabolic processes needing carbon substrates, energy and specific nutrients, e.g. for the synthesis of new cellular material or for enzyme regulation. Cell metabolism, however, is probably optimized to a narrow range of osmotic and ionic composition and concentration; changes in solute concentration and composition (e.g. water stress-induced changes in anorganic nutrient composition) may therefore restrict cell expansion and growth.

It is therefore concluded that both quantitative and qualitative aspects of nutrient supply are important for sustained plant growth under conditions of drought stress. Positive effects of N- and P-fertilization on shoot and root development of
water stressed maize seedlings may be attributed a) to direct and particularly indirect effects of N- and P-nutrition on plant water relations (e.g. on the difference between root and leaf water potentials or on the degree of osmotic adjustment, respectively) and b) to specific effects of N- and P-nutrition on metabolic processes, as e.g. changes in cell wall rheological properties, the synthesis of new cellular material, enzyme regulation, or changes in the hormonal status of the plant.

The study presented here demonstrates that adequate N- and P-nutrition are very important for the establishment of maize seedlings, particularly under conditions of limited water supply. Since surface soils are primarily susceptible to drying, a vigorous root growth is of particular importance for seedling establishment. Adequate N- and P-nutrition clearly enhanced root (and shoot) growth of maize seedlings, particularly under conditions of limited soil moisture supply.
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ZUSAMMENFASSUNG

Interaktive Auswirkungen von N-, P-, K-Ernährung und Wasserstress auf die Jugendentwicklung von Mais (Zea mays L.)


Der Wurzelturgor der Maispflänzchen konnte dank osmotischer Anpassung auch bei einer Saugspannung > 0.5 MPa noch aufrechterhalten werden. Der Turgor der Blätter hingegen sank deutlich mit steigender Intensität des Wasserstresses, weil keine genügende osmotische Anpassung erfolgte. Die Bestimmung des Ausmasses der osmotischen Anpassung aufgrund vergleichender Messungen der osmotischen Potentiale des Zellsaftes unbewässerter und bewässerter Pflanzen bzw. basierend auf dem Vergleich der osmotischen Potentiale bei vollem Turgor (abgeleitet aus Druck-Volumen Kurven) ergab vergleichbare Resultate.


Die Zellwandelastizität in Blättern wassergestresster Pflanzen war im Vergleich zu derjenigen bewässerter Pflanzen stark erhöht. Der Elastizitätsmodulus war in wassergestressten Pflanzen (Saugspannung ca. 0.4 MPa) um 1.8 bis 5.3 MPa tiefer als in ausreichend bewässernten Pflanzen (Saugspannung < 0.06 MPa). Daher war auch die ’Capacitance’ (Wasser-Kapazität) gestresster Pflanzen gegenüber bewässerten Pflanzen signifikant erhöht (+15 bis +60 %). Die unterschiedliche Nährstoffversorgung der Pflanzen hatte einen deutlich geringeren Einfluss auf Zellwandelastizität und ’Capacitance’ als die unterschiedliche Wasserverfügbarkeit. Zudem waren die Auswirkungen der unterschiedlichen Nährstoffversorgung auf diese Parameter von der Wasserverfügbarkeit abhängig.

Aus der vorliegenden Arbeit kann daher der Schluss gezogen werden, dass sowohl quantitative wie auch insbesondere qualitative Aspekte der Nährstoffversorgung einen wichtigen Einfluss auf das Pflanzenwachstum bei unzureichender Wasserverfügbarkeit ausüben. Positive Auswirkungen einer angemessenen N- und P-Versorgung junger Maispflanzen auf das Spross- und Wurzelwachstum können zurückgeführt werden auf

a) direkte und indirekte Auswirkungen der N- und P-Versorgung auf den Wasserstatus der Pflanzen (z.B. auf den Unterschied im Wasserpotential zwischen Wurzeln und Spross bzw. auf das Vermögen zur osmotischen Anpassung) und

b) auf spezifische Auswirkungen der N- und P-Versorgung auf metabolische Prozesse, wie z.B. auf Veränderungen der Zellwandrheologie, auf die Synthese von Zellsubstanzen, auf Enzymregulierung oder auf hormonale Veränderungen innerhalb der Pflanzen.

Die vorliegende Arbeit zeigt auf, dass eine ausreichende N- und P-Versorgung eine wichtige Voraussetzung für die Etablierung junger Maispflanzen darstellt. Da die obersten Bodenschichten besonders stark der Gefahr der Austrocknung ausgesetzt sind, ist ein kräftiges Wurzelwachstum für junge Pflanzen von besonderer Wichtigkeit. Eine ausreichende N- und P-Versorgung förderte nicht nur das Spross-, sondern speziell auch das Wurzelwachstum junger Maispflanzen signifikant, insbesondere unter Bedingungen unzureichender Wasserverfügbarkeit.
1. General Introduction

On a global scale, water deficiency is the major factor limiting agricultural production. Agriculture on the other hand is the most important consumer of water in the world. The increasing demand for food and water calls for a more efficient water use in agriculture. Therefore, a better understanding of how water deficiency affects plant growth and yield production and of how water use in agriculture can be optimized is of great importance.

Maize (Zea mays L.) is one of the most important crops worldwide. Maize is widely cultivated as a food as well as a fodder crop. In 1991, maize grain yields accounted for 26% of the global cereal production. Over 130 million hectares were cultivated with maize; cultivation of maize in developing countries accounted for two-thirds of this area (FAO 1992).

On a great part of the area cultivated with maize, water deficiency is responsible for suboptimal yields. Therefore, irrigation is widely used in the cultivation of maize; positive effects of irrigation on maize yields have been documented extensively (e.g. Braunworth and Mack 1987). However, irrigation is not always possible; particularly in developing countries, limited water resources, lacking infrastructure or simply the lack of money impede additional irrigation of crops. The 1992 drought in Southern Africa, where maize represents the staple food for the inhabitants, has demonstrated these problems.

Water availability, water use and nutrient supply to the plants are closely interacting factors influencing plant growth and yield production (Shimshi 1969; Viets 1972): Limited soil moisture influences nutrient availability for plants (Olsen et al. 1961; Viets 1972; Begg and Turner 1976; Kuchenbuch et al. 1986), adequately fertilized plants may show higher drought tolerance (Lahiri 1980), water use of fertilized plants is known to be increased (Lahiri 1980; Barraclough 1989), but on the other hand water use efficiency is reported to be improved by adequate fertilization (Goudriaan and van Keulen 1979; Decau and Pujol 1984; Heitholt 1989; Schmidhalter and Oertli 1990a; Andersen et al. 1992a). Thus, the effects of nutrient supply on plant growth and yield production under conditions of drought stress are very complex.

Generally, plant growth is decreased by both limited soil water and limited nutrient supply. Water stress induced changes in plant growth resemble those of nutrient deficiencies in many cases (Hsiao 1973; Jones et al. 1986). Water stress as well as nutrient deficiencies affect shoot growth differently than root growth: N-, P-, K- and soil moisture deficiencies impair shoot growth to a greater extent than root growth, leading to higher root/shoot ratios in stressed plants (Gates 1955; Brouwer 1962; Westgate and Boyer 1985; Jones et al. 1986; Setter 1990).
An increased root/shoot ratio could represent a beneficial adaptation for drought stressed plants: Reductions in shoot growth lead to a smaller transpiring leaf area, thus decreasing water use by the plant. Enhanced root growth enables the plant to explore more soil volume for water and nutrient supply. On the other hand, maintenance of shoot growth under conditions of water stress increases leaf area, hereby increasing photosynthesis and providing photosynthates usable for osmotic adjustment and expansive growth of shoots and roots. Vigorous root growth is of particular importance for seedling establishment, because surface soils are primarily susceptible to drying (Sharp et al. 1988).

The primary events inhibiting plant growth under conditions of limited water supply are still controversial. Maintenance of turgor pressure is generally looked at as an ultimate prerequisite for cell expansion and growth. Many scientists consider osmotic adjustment (solute accumulation in cells in order to maintain turgor pressure) under conditions of water stress to represent the principal limiting factor for the maintenance of growth; transport of nutrients and other solutes into growing tissues requires much more time than transport of water (Oertli 1991a). Therefore, the nutrient status of a plant might be very important for maintenance of growth under conditions of drought stress. Several studies, however, demonstrated that cell enlargement and growth were inhibited even if turgor pressure in the growing tissues was completely maintained (Michelena and Boyer 1982; van Volkenburgh and Boyer 1985; Westgate and Boyer 1985). It was suggested that changes in cell wall yielding properties due to water stress restricted cell expansion and thus growth (Hsiao et al. 1985; Barlow 1986; Hsiao and Jing 1987; Pritchard et al. 1987; Boyer 1988; Spollen and Sharp 1991). The differential sensitivity of root and shoot expansive growth to low water availability was attributed primarily to differences in the reaction of cell wall properties to water deficits (Hsiao and Jing 1987; Spollen and Sharp 1991).

However, there are other factors besides turgor pressure and cell wall yielding properties that can restrict plant growth under conditions of drought stress: Stomatal closure due to low water availability might be the most important factor reducing photosynthesis under conditions of low water availability (Hsiao 1973). Accumulation of unused photosynthates might further restrict photosynthesis in water stressed plants (Setter 1990). Ion uptake and transport are reduced under conditions of water stress (Hsiao 1973). Protein synthesis can be decreased in drought stressed plants (Hsiao 1973). Hormonal changes in plants growing under conditions of limited water supply have been documented extensively (for references see Bradford and Hsiao 1982; Davies et al. 1986; Davies 1987). All of these processes could be influenced by the availability of (specific) nutrients to the plants.
The studies presented here explain interactive effects of N-, P- and K-nutrition on the development of maize seedlings (up to the 5- to 7-leaf stage) grown under conditions of limited water supply. In a first part, root and shoot growth of maize seedlings grown under different nutrient and soil moisture regimes are characterized (chapter 3). The results are discussed in context with recent studies on the differential sensitivity of root and shoot growth to water stress conditions. In a second part, interactive effects of N-, P- and K-nutrition on water relations of maize seedlings grown under conditions of limited water supply are described (chapter 4). Since chapters 3 and 4 refer to the same experiments, the integrated results of both parts will be discussed in chapter 4. An attempt is made to determine physiological reasons for the differential effects of water stress on root and shoot growth of maize seedlings grown under different nutrient regimes.
2. MATERIALS AND METHODS

The results presented in this study originate from mainly two experiments (A and B) described below. To verify these results and to explain some of the phenomena observed, results of similar preliminary experiments conducted earlier are referred to.

2.1 Experiment A: Harvests at specific days after planting

Four maize seeds (Zea mays L. cv Issa; pregerminated for 1 day in distilled water) were sown in pots (10.5 cm in diameter, 20 cm high) containing 1.5 l of a silty soil (Aquic Ustifluvent) with different levels of N, P and K. Some characteristics of the soil used are shown in table 1 (from Schmidhalter and Oertli 1991a). Before the soil was filled into the pots, modified Hoagland nutrient solution was added to the dry soil to obtain a) a gravimetric soil water content of 27 % and b) the desired nutrient levels for the eight nutrient treatments. The wetted soil was mixed thoroughly and allowed to equilibrate for at least two days before it was filled into the pots. Table 2 (p. 6) summarizes NO₃⁻, P-, K- and Mg-contents and nutrient supply levels of the soil in different nutrient treatments at the beginning of experiments A and B. NO₃⁻, P-, K- and Mg-contents of the soil were determined in NH₄-acetate-EDTA extracts (extraction according to Lonza-Data 1985; soil/extractant = 1:10).

<table>
<thead>
<tr>
<th>Soil Characteristics</th>
<th>Clay</th>
<th>Silt</th>
<th>Sand</th>
<th>Organic Matter</th>
<th>pH (H₂O)</th>
<th>CEC (mmol kg⁻¹)</th>
<th>Ca (mg kg⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>9.1 %</td>
<td>59.5 %</td>
<td>31.4 %</td>
<td>0.85 %</td>
<td>8.2</td>
<td>48</td>
<td>30716</td>
</tr>
</tbody>
</table>

Table 1: Soil characteristics of the soil used in experiments A and B. (CEC: Cation Exchange Capacity)

A 2 cm layer of 2-3 mm quartz sand covered the soil in the pots to minimize evaporation. During 9 days after planting (DAP), all the pots were watered regularly to a gravimetric soil water content of 27 %. On DAP 4, the number of plants was reduced to 3 uniform plants per pot representing 3 replications for each treatment at every harvest. From DAP 10 on, half of the pots were allowed to dry while the other pots were watered every day; in that way, two water regimes ('well watered' and 'water stressed') were established.

During the experiment, bulk soil water content was determined from gravimetric measurements of the pots (plant weight was estimated and considered in the calculations). Soil matric potential was calculated using a previously established
soil water retention curve (Fig. 1). At harvests, soil water content was determined gravimetrically using soil samples (mixed samples from the whole soil volume). Evapotranspiration was estimated from gravimetric measurements of the pots. The experiment was conducted in a growth chamber (day/night: 12/12 h, 20/18°C; relative humidity: 50 to 65%; photon flux density at plant height approximately 450 µmol m⁻² s⁻¹). The pots were rotated regularly.

Fig. 1:
Soil water retention curve (desorption) of the soil used in all experiments. The curve was established using a pressure plate apparatus.

On days 12, 14, 16, 18, 19 and 20 after planting (6 harvest dates), one well watered as well as one water stressed pot of each nutrient treatment were harvested. Soil matric potential $\psi_I$ at harvests ranged from -0.03 to -0.05 MPa in well watered treatments. Soil matric potentials at harvests of water stressed treatments are summarized in table 3 (p. 12). Leaf area, fresh and dry weight of shoots and roots of single plants were measured. Predawn leaf water potentials ($\psi_L$) were determined from the apical half of the youngest fully expanded leaf (mature tissue) of every plant using a pressure chamber (PMS Instrument Co. Model 1002; cf. Scholander 1964, 1965; Passioura 1982, 1991; Turner 1987). Thereafter, the same samples were sealed into small plastic bags, bathed in liquid nitrogen, pressed thoroughly, and the sap was analyzed for its osmotic potential ($\psi_w$) using a Wescor 5100 C vapor pressure osmometer. Leaf turgor ($\psi_L$) was calculated as the difference between $\psi_I$ and $\psi_w$ ($\psi_L = \psi_I - \psi_w$).

Water potentials of whole root systems ($\psi_r$) were determined at the hypocotyl of the plants: the shoots of young maize plants were cut at the hypocotyl just above the seed, and the whole shoot was sealed into the pressure chamber, the cut end of the hypocotyl being analyzed for its water potential. Preliminary investigations showed that measurements of root water potentials of intact roots as described by Schmidhalter et al. (1992b) yielded results that were closely correlated to the
results using the method described here. The method described here has the advantage that possible errors in the measurements, that may arise from damages of the roots, can be avoided.

Statistical analysis of the data was performed using SAS\textsuperscript{TM} (SAS Institute Inc., Cary, NC, USA). The experiment consisted of eight nutrient treatments and two water regimes, and harvests were performed at six harvest dates → 96 pots with three plants as replications for each pot. If not mentioned otherwise, significant effects and differences were calculated at the 5 % level.

<table>
<thead>
<tr>
<th>Nutrient Treatment</th>
<th>NO\textsubscript{3}</th>
<th>P</th>
<th>K</th>
<th>Mg</th>
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</thead>
<tbody>
<tr>
<td>NPK</td>
<td>295</td>
<td>403</td>
<td>98</td>
<td>118</td>
</tr>
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<td>NP</td>
<td>288</td>
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<td>K</td>
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<td>40</td>
<td>74</td>
<td>63</td>
</tr>
<tr>
<td>0</td>
<td>51</td>
<td>47</td>
<td>69</td>
<td>61</td>
</tr>
</tbody>
</table>

Table 2: NO\textsubscript{3}-, P-, K- and Mg-contents (mg kg\textsuperscript{-1}) of the soil at planting in different nutrient treatments of experiments A and B. Nutrient treatment 0 was not fertilized at all.

Nutrient supply levels: (according to Lonza-Data 1985)
N-fertilized ('high N') treatments: adequate N-supply.
Treatments without N-fertilization ('low N'): poor N-supply.
P-fertilized ('high P') treatments: surplus P-supply.
Treatments without P-fertilization ('low P'): adequate P-supply.
K-fertilized ('high K') treatments: moderate K-supply.
Treatments without K-fertilization ('low K'): poor K-supply.

2.2 Experiment B: Harvests at specific soil matric potentials

The design of experiment B was similar to that of experiment A. In contrast to experiment A, watering of water stressed treatments was stopped on day 12 instead of day 10 after planting. Well watered and water stressed plants were not harvested at a certain number of days after planting as in experiment A, but when the soil matric potential in the respective water stressed treatments approximated
-0.2 to -0.3 MPa (harvest 1), -0.3 to -0.4 MPa (harvest 2) and -0.4 to -0.6 MPa (harvest 3), respectively. Soil matric potential $\psi_s$ was determined from gravimetric measurements as described for experiment A. In well watered treatments, $\psi_s$ at harvest ranged from -0.04 to -0.07 MPa.

At harvests 1 to 3, all the plant parameters determined in experiment A were measured in experiment B as well. In addition, seminal root systems were dug from the soil, fixed between two sieves and cleaned using compressed air in a nearly saturated environment (Schmidhalter et al. 1992b). Osmotic potentials ($\psi_{or}$) of these root samples were determined after freezing them in liquid nitrogen using the same method as described for leaf samples in experiment A. Root turgor potential ($\psi_{rt}$) was calculated as the difference between root water potential $\psi_r$ and the osmotic potential $\psi_{or}$ of the root samples ($\psi_{rt} = \psi_r - \psi_{or}$). Root dry weight was determined using all the roots of three plants of a pot.

In addition to the measurements conducted in experiment A, pressure-volume curves (PV curves) of leaves and roots of well watered ($\psi_s$ approximately -0.05 MPa) and stressed plants ($\psi_s$ approximately -0.4 MPa) were established. Shoots were cut at the stem base at predawn, and the cut end was immediately immersed in distilled water allowing rehydration for at least 2 hours in the dark in a nearly saturated environment. Whole root systems were dug from the soil and washed with water, then dried with compressed air. To allow rehydration, seminal roots were placed into a nearly saturated environment in the dark for at least 2 hours, the cut end of the hypocotyl being immersed in distilled water. PV curves were generated using the apical half of the youngest fully expanded leaf (mature tissue) and the seminal root system, respectively. The samples were weighed, water potential was determined in the pressure chamber, the samples were weighed again and then allowed to dehydrate on the lab bench. These steps were repeated for each sample between 12 and 30 times.

Calculation of fresh weight at full turgor (FW100) was performed according to Kubiske and Abrams (1990) to avoid mistakes by misleading rehydration effects (method described in appendix A). Plots of inverse applied pressure (1/$\psi$) versus 1-RWC (RWC: relative water content) were used to determine osmotic potential at full turgor (OP100) and at zero turgor (OP0), relative water content at zero turgor and apoplastic water content. This transformation of the water potential isotherm provides better estimations of OP100 than other plots (Tyree and Richter 1981). The point of turgor loss (relative water content at zero turgor: RWC0) was determined graphically; various ways of determining RWC0 using computer algorithms (according to Sinclair and Venables 1983, Schulte and Hinckley 1985 and programs developed at our institute) failed to provide satisfactory results. Bulk modulus of elasticity ($\varepsilon$) was calculated for values of applied pressure ($\psi$) between 0.05 and 0.25 MPa according to Tyree 1981 (method described in appendix B): in this range (99.5% > RWC > 97.5%), $\varepsilon$ is constant,
because RWC versus $\psi$ shows a linear relationship. Capacitance was determined for the same range of $\psi$ according to Nobel and Jordan 1983 (method described in appendix C). All the parameters were determined using the combined results of 3 replications (measurements of samples of 3 plants) per treatment. Osmotic adjustment was calculated as the difference in OP100 between well watered and water stressed plants at a certain harvest (Turner and Jones 1980).

The experiment consisted of the same eight nutrient treatments and two water regimes as experiment A, and harvests were performed on four harvest dates (harvests 1-3 and harvest for PV curves) → 64 pots with three plants as replications for each pot. Statistical analysis of the data was performed using SAS™. If not mentioned otherwise, significant effects and differences were calculated at the 5 % level.
3. DEVELOPMENT OF SHOOTS AND ROOTS

3.1 INTRODUCTION

Nutrient deficiencies can alter the morphological and physiological responses of crop plants to water deficits. However, reports about the benefit of N-, P- and K-fertilization on plant growth under conditions of drought stress are controversial (Bennett et al. 1986; Bennett et al. 1989). This might be due to the fact that plant nutrition affects plant growth by various mechanisms, i.e. many plant parameters may be affected by changing the nutrient supply of a plant. The effects of plant nutrition on plant growth may increase or decrease a plant's susceptibility to water stress, and it is often difficult to determine whether the integrated effects of changing the nutrient supply for a water stressed plant are beneficial or not. An example shall explain this difficulty in assessing the effects of differential nutrient supply to plants growing under conditions of drought stress:

Under conditions of nutrient deficiency, root growth is generally enhanced relative to shoot growth (Brouwer 1962; Viets 1965; Maizlish et al. 1980; Huber et al. 1989). Enhanced root growth relative to shoot growth might be beneficial for plants growing under conditions of limited water supply: An increase in root growth enables a plant to explore more soil volume for water and nutrient supply, and a reduced leaf area may lead to a decrease in transpirational water loss. Maintenance of shoot growth even under conditions of water stress, however, increases leaf area, hereby increasing photosynthesis and providing photosynthates usable for osmotic adjustment and expansive growth of shoots and roots. Therefore, fertilization (resulting in enhanced shoot growth) might also be advantageous for plants growing under conditions of water stress.

The effects of N-nutrition on plant growth under conditions of water stress have been investigated in several studies. The results of these studies, however, were controversial: Radin and Parker (1979b) and Bennett et al. (1986) reported a greater sensitivity to water deficits of low-N as compared to high-N plants. Radin and Parker (1979b), Radin and Ackerson (1981), Radin et al. (1982) and Radin et al. (1985) demonstrated that greater stomatal sensitivity in low-N than in high-N plants was responsible for the higher sensitivity of N-deficient plants to water deficits. They concluded that N-deficiency could improve the tolerance of plants to water deficits. On the other hand, Morgan (1984a), Morgan (1986) and Nnoham and Odurukwe (1987) reported that high-N plants were affected to a greater extent by water stress than N-deficient plants. Morgan (1986) found a greater sensitivity of gas exchange to water deficits in high-N than in low-N plants. Bennett et al. (1989) concluded that N-deficiency does not improve plant tolerance to water stress.
P-fertilization generally enhances plant growth under conditions of water stress. Several studies have demonstrated that the supply of extra P to plants can be of considerable benefit during water stress by increasing both growth rate and yield (Nelson and Safr 1982; Sharpley and Reed 1982; Bonetti et al. 1984; Ackerson 1985; Premachandra et al. 1990b; Saneoka et al. 1990). The positive effects of P-fertilization on plant growth under conditions of limited water supply have been attributed to increases in stomatal conductance (Radin 1984) and photosynthesis (Ackerson 1985), to higher cell membrane stability, and to effects on water relations (Premachandra et al. 1990b).

K-fertilization can increase a plant's tolerance and resistance to stress due to the function of K in osmoregulation, in energy status and in the synthesis of high molecular compounds (Beringer and Trolldenier 1978). K-fertilization seems to play an important role in the adaptation of plants to water stress (Oertli 1991a). However, it is very difficult to specify the causal effects of K on drought resistance and tolerance (Beringer and Trolldenier 1978). The function of potassium in stomatal regulation is well established (Oertli 1991a). The substantial effects of K on the water status of plants (Mengel and Arneke 1982) might represent another important role of K for plant growth under conditions of drought stress. Because K-ions make a major contribution to the cell sap osmotic potential (Andersen et al. 1992b), it was suggested that K-fertilization could increase the plant's ability for osmotic adjustment under conditions of drought stress (Beringer and Trolldenier 1978). However, Andersen et al. (1992a) illustrated that no clear conclusion can yet be drawn about the possibility of stabilizing yield under drought conditions by increasing K-application.

The study presented here explains integrated effects of differential N-, P- and K-nutrition on shoot and root development of young maize plants grown under conditions of limited water supply. The results are discussed in context with recent studies on the differential sensitivity of root and shoot growth to water stress.
3.2 RESULTS

3.2.1 Experiment A: Harvests at specific days after planting

Under well watered conditions, different nutrient levels showed significant effects on the DEVELOPMENT OF THE PLANTS at all harvests: The importance of the nutritional effects on leaf area, fresh and dry weight of roots and shoots and shoot water content increased with plant age. Water stressed treatments showed less significant differences among nutrient treatments (Fig. 2): The relative differences among treatments were smaller and the variability among plants (replications) was slightly higher than in well watered treatments.

![Graph showing shoot fresh weight of different nutrient treatments](image)

Fig. 2: Development of shoot fresh weight of different nutrient treatments in experiment A. The plots show smoothed lines through the means of 3 replications at each harvest.

During plant growth, the importance of the nutritional effects in water stressed treatments decreased due to a different development of the water stress in different nutrient treatments.
The variations in plant development led to a completely different development of the **SOIL MATRIC POTENTIAL** in different nutrient treatments under the drought stress water regime (example in Fig. 3). Fast growing plants experienced higher degrees of water stress more quickly than plants with retarded growth. This fact has to be considered, when the influence of water stress on the parameters observed in different nutrient treatments are to be compared in this experiment, since \( \Psi \) of the different treatments at a certain DAP differed greatly (see table 3).

![Fig. 3: Example of different development of plant fresh weight and consequently \( \Psi \) in experiment A: Nutrient treatments a) P and b) NP. Bars represent the total shoot fresh weight of 3 plants of one pot.](image)

<table>
<thead>
<tr>
<th>Nutrient Treatment</th>
<th>12</th>
<th>14</th>
<th>16</th>
<th>18</th>
<th>19</th>
<th>20</th>
</tr>
</thead>
<tbody>
<tr>
<td>NPK</td>
<td>-0.055</td>
<td>-0.072</td>
<td>-0.134</td>
<td>-0.207</td>
<td>-0.350</td>
<td>-0.637</td>
</tr>
<tr>
<td>NP</td>
<td>-0.058</td>
<td>-0.080</td>
<td>-0.126</td>
<td>-0.138</td>
<td>-0.363</td>
<td>-0.503</td>
</tr>
<tr>
<td>NK</td>
<td>-0.056</td>
<td>-0.078</td>
<td>-0.095</td>
<td>-0.116</td>
<td>-0.124</td>
<td>-0.162</td>
</tr>
<tr>
<td>PK</td>
<td>-0.052</td>
<td>-0.071</td>
<td>-0.084</td>
<td>-0.097</td>
<td>-0.100</td>
<td>-0.135</td>
</tr>
<tr>
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<td>-0.135</td>
<td>-0.135</td>
<td>-0.278</td>
</tr>
<tr>
<td>P</td>
<td>-0.051</td>
<td>-0.079</td>
<td>-0.099</td>
<td>-0.129</td>
<td>-0.158</td>
<td>-0.189</td>
</tr>
<tr>
<td>K</td>
<td>-0.054</td>
<td>-0.066</td>
<td>-0.088</td>
<td>-0.094</td>
<td>-0.122</td>
<td>-0.127</td>
</tr>
<tr>
<td>O</td>
<td>-0.055</td>
<td>-0.074</td>
<td>-0.091</td>
<td>-0.113</td>
<td>-0.125</td>
<td>-0.166</td>
</tr>
</tbody>
</table>

Table 3: Bulk soil matric potentials in pots of the different nutrient treatments at different harvests in experiment A (water stressed treatments).
Different nutrient levels affected **ABOVE GROUND BIOMASS PRODUCTION** (leaf area, shoot fresh weight [SFW] and shoot dry weight [SDW]) and water content of shoots [SWC] of both water regimes stronger and at earlier growth stages than root growth and total dry weight production. N-fertilization enhanced (and accelerated) shoot growth (leaf area, fresh and dry weight) in well watered as well as water stressed treatments. The positive effects of N-fertilization on shoot growth were significant at all harvests. Plant leaves of treatments without N-fertilization showed N-deficiency symptoms and had low N-contents (less than 30 g kg\(^{-1}\); see table 4 p. 14) from DAP 12 on. P-fertilization affected shoot development in a similar way as N-fertilization. However, significant effects of P-fertilization were seen from DAP 16-18 on only, although leaf P-contents of P-deficient plants were already low (< 2.33 g kg\(^{-1}\); table 4 p. 14) from DAP 12 on. Significant synergistic effects (interactions) of N- and P-fertilization on shoot growth could be observed, particularly in well watered treatments. Fig. 4 illustrates these interactive effects of N- and P-fertilization on shoot growth using leaf area production of well watered plants as an example.

![Fig. 4: Effects of different nutrient treatments on leaf area production of well watered plants in experiment A (harvest at day 18 after planting).](image)

No significant effects of K-fertilization on shoot development could be detected during the 20-day experiment, neither in well watered nor water stressed treatments. Tissue analysis revealed that leaf K-contents (25 to 30 g kg\(^{-1}\); table 4 p. 14) of plants growing under K-deficient conditions were only slightly below sufficient levels as described by Bergmann (1988).

Table 4 summarizes N-, P- and K-contents of leaves at different harvests in experiment A.

Water stress tended to reduce leaf area and shoot fresh weight in all treatments. However, significant reductions were observed in treatments with N-fertilization only, i.e. in treatments with high growth rates and only when more than 5 g shoot fresh weight per plant had been produced. The effects of different nutrient treatments on leaf area and shoot fresh weight production were similar under both water regimes (Fig. 2): Treatments NPK and NP achieved the highest, treatment PK the lowest yields under both well watered and water stressed conditions.

No significant effects of water stress on shoot N- and P-contents could be observed in this experiment. In K-deficient treatments, shoot K-contents were lower in water stressed than in well watered treatments at \( \psi_s < -0.13 \) MPa. In K-fertilized treatments, no significant effects of water stress on shoot K-contents were observed.

No significant reductions in shoot dry matter production under water stress could be observed in this experiment. Shoot dry weight of water stressed treatments tended to be lower than in well watered treatments, but the relative reductions were smaller than in leaf area or shoot fresh weight (Fig. 6). The effects of drought stress, N-, P- and K-nutrition on shoot and root dry matter production in experiment A are summarized in Fig. 5 a-c.
Fig. 5: Shoot and root dry weights with and without a) N-, b) P- and c) K- fertilization of well watered and water stressed treatments in experiment A. Error bars indicate least significant differences at the 5% level between high- and low- N, P and K plants. Low N, P, K: treatments not fertilized with N, P, K, respectively. High N, P, K: treatments fertilized with N, P, K, respectively.
Fig. 6: Effect of water stress on shoot fresh and dry weight production in different nutrient treatments of experiment A. The plots show relative yields at the harvest 20 days after planting. Well watered adequately fertilized treatments (NPK) are assumed to yield 100%.

**SHOOT WATER CONTENT** (SWC=(1-SDW/SFW)*100) of well watered and adequately fertilized young maize plants decreased only slightly during early plant growth. Significant effects of different nutrient levels on water content could be observed at all 6 harvests. N-deficiency provoked an important decrease of SWC in well watered plants (down to 88%); the extent of this decrease depended on the P- and K-status of the plants. P-fertilization seemed to promote this reduction in SWC. K-fertilization on the other hand increased SWC significantly (except in treatment PK). Different nutrient levels were the dominant factors affecting SWC in well watered plants (Fig. 7).

Fig. 7:

Development of shoot water content of well watered plants during plant growth in experiment A. The plot shows smoothed lines through the means of 3 replications at each harvest.
Shoot water content was the first parameter observed to be affected by water stress conditions. Even in well watered plants, differences in soil matric potential of less than 0.02 MPa showed significant effects on SWC. Significant decreases of SWC of water stressed compared to well watered plants could be observed in all nutrient treatments, mostly at $\psi_s > -0.1$ MPa already. In N-deficient treatments, differences in SWC between well watered and stressed plants became evident at later growth stages (and consequently lower $\psi_s$) than in other treatments.

Different nutrient levels affected SWC of water stressed plants significantly at all harvests. The effects of different nutrient treatments on SWC were less evident at later harvests. This observation can be explained by the varying development of the water stress in different nutrient treatments. Under conditions of water stress, changes in shoot water content due to P-fertilization (decreased SWC) and K-fertilization (increased SWC) were more distinct than in well watered treatments. In contrast, reductions in SWC due to N-deficiency were less evident in water stressed than in well watered treatments. Shoot water contents of well watered and water stressed plants of the different nutrient treatments at similar $\psi_s$ are shown in Fig. 8.

![Fig. 8: Shoot water content of well watered and water stressed plants of the different nutrient treatments in experiment A. Comparison of data of harvests at which plants experienced similar soil matric potentials $\psi_s$.](image-url)
ROOT GROWTH was highly correlated with shoot growth in all well watered treatments ($r > 0.95$). The bigger the plants, the better differences in root growth could be explained by different nutrient treatments. N-deficient plants showed higher root dry weights than high-N plants at the first 3 harvests (DAP 12, 14, 16). As a result of the high correlation of shoot and root growth and the slower development of N-deficient plants, however, root dry weight of adequately N-fertilized plants at DAP 20 was significantly higher than in N-deficient treatments (Fig. 9). This effect of N-nutrition was consistent in both well watered and water stressed treatments.

In well watered treatments, no consistent effect of P-nutrition on root growth was observed. In water stressed treatments, however, adequate P-nutrition tended to increase root dry weights. No significant effects of K-nutrition on root growth could be observed. However, K-fertilized plants tended to have lower root dry weights than plants of K-deficient treatments (see Fig. 5 a-c).

In all nutrient treatments, absolute root growth tended to increase under water stressed compared to well watered conditions. With adequate P-fertilization, this trend was more pronounced than in P-deficient treatments. K-fertilization seemed to reduce this enhancement of root growth at low $\psi_r$. The effects of N-, P- and K-fertilization on root growth under both water regimes are shown in Fig. 10 (harvest 20 days after planting).
Fig. 10: Effects of N-, P- and K-nutrition on root growth of well watered and water stressed plants in experiment A (final harvest at day 20 after planting).


ROOT/SHOOT RATIO (RSR) of all well watered treatments decreased with plant growth (see Fig. 25 p. 42). This dependency of RSR on the growth stage of a plant has to be considered when comparing RSRs among different treatments, that affect the growth rate of plants: Under water and/or nutrient stress conditions, plants tend to grow slower. Therefore, their RSR at a certain day after planting will be higher than in well watered or adequately fertilized plants.

Different nutrient levels affected root/shoot ratio at all harvests under both water regimes. Taking into consideration the growth stage of the plants, N-, P- and K-deficiencies generally resulted in higher RSRs: At the first five harvests, N-deficient plants of both water regimes showed higher root/shoot ratios than N-fertilized plants. At harvest 6 (20 days after planting), no significant difference in RSR between high-N and N-deficient plants could be observed. P-nutrition exerted similar effects on RSR as N-nutrition, but the effects became significant after DAP 14-16 only. K-nutrition did not affect RSR in well watered treatments. In water stressed treatments, however, RSR of K-deficient plants was significantly higher than RSR of K-fertilized plants (harvests 4 to 6). The effects of N-, P- and K-fertilization on RSR under both water regimes are shown in Fig. 11.
Fig. 11: Effects of N-, P- and K-nutrition on root/shoot ratio of well watered (WW) and water stressed (WS) plants in experiment A (harvest at day 18 after planting). Computation of means included shoot growth (SDW) as a co-variate. Low N, P, K: treatments not fertilized with N, P, K, respectively. High N, P, K: treatments fertilized with N, P, K, respectively.

Water stress tended to increase RSR in all treatments. In most nutrient treatments (except NK and NP), RSR was increased by water stress before any reductions in leaf area or shoot fresh and dry weight could be observed. In N-deficient treatments, this increase in RSR could be observed at \( \psi_s > -0.1 \text{ MPa} \), in high-N treatments slightly below -0.1 MPa. Significant increases in RSR due to water stress (considering growth stage) could be observed in treatments 0, N, NP, NPK and PK at soil matric potentials < -0.1 to -0.2 MPa. Adequate P-nutrition clearly enhanced this shift in RSR in favor of the roots at low \( \psi_s \) (DAP 14-20). In contrast, K-fertilization seemed to reduce this water stress induced enhancement of root growth relative to shoot growth. Adequate N-nutrition enhanced the shift of RSR (in favor of the roots) under water stress at later harvests only (Fig. 12). In summary, N-, P- and K-deficiencies generally increased root/shoot ratios under both water regimes. Water stress induced enhancement of root growth relative to shoot growth, however, required adequate N- and P-nutrition. K-fertilization on the other hand seemed to reduce carbon partitioning from shoots to roots under water stress. It has to be considered, however, that the degree of water stress on a certain harvest day varied considerably among different nutrient treatments.
Fig. 12:
Relative increases of root/shoot ratio as an effect of low soil water supply in different nutrient treatments of experiment A (harvest on day 18 after planting). RSR of well watered plants was assumed to be 100%.
Computation of means included shoot growth (SDW) as a covariate.

Significant differences in **TOTAL BIOMASS PRODUCTION** (TBP) on a dry weight basis among different nutrient treatments were observed after DAP 19 only. N- and P-fertilization increased biomass production, and significant synergistic interactions of N- and P-fertilization were observed. No significant influence of K-nutrition on TBP could be observed. Water stress showed no significant influence on total dry matter production at different harvests during the 20 day experiment (Fig. 13).

Fig. 13: Total dry weight production (of roots and shoots) at high and low levels of N, P and K respectively under conditions of adequate (WW) and limited (WS) soil water supply in experiment A (harvest on day 18 after planting). Low N, P, K: treatments not fertilized with N, P, K, respectively. High N, P, K: treatments fertilized with N, P, K, respectively. Bars 'N*P' represent dry weight production of plants which received combined N- and P-fertilization.
A consistent tendency though could be observed: At the first harvests, water stressed treatments showed higher TBP than well watered treatments, but when the stress reached a \( \psi \) of -0.1 to -0.2 MPa, well watered treatments yielded higher TBP (example in Fig. 14).

Fig. 14: Example of root, shoot and total dry weight development in experiment A: Nutrient treatment NK; total production of 3 plants per pot. Root dry weight of a) well watered and b) water stressed treatments. Shoot dry weight of c) well watered and d) water stressed treatments. Root dry weight development of e) well watered and f) water stressed plants. Development of total biomass production of g) well watered and h) water stressed plants. Soil matric potential of water stressed treatments on the respective day of harvest.
3.2.2 Experiment B: Harvests at specific soil matric potentials

Different nutrient levels affected PLANT DEVELOPMENT significantly. Therefore, depending on the nutrient treatment, harvests took place on days 18 to 37 after planting, when the soil matric potential $\psi_s$ of water stressed treatments reached approximately -0.2 to -0.3 MPa (harvest 1), -0.3 to -0.4 MPa (harvest 2) and -0.4 to -0.6 MPa (harvest 3), respectively. Days of harvests and $\psi_s$ at harvests are reported in Table 5. N- and P-fertilization enhanced plant development significantly, K seemed to retard growth.

Shoot dry weights of water stressed plants at a certain harvest did not show significant differences among nutrient treatments; this may be explained by the different growth time of plants growing at different nutrient levels. However, leaf area, shoot fresh weight and shoot water content of water stressed plants differed significantly, as all plant parameters measured in well watered treatments did.

Since the plants of different nutrient treatments were harvested at different days after planting, comparisons of growth parameters between nutrient treatments are not reported for this experiment. The evaluation of experiment B will concentrate on the effects of water stress on plant growth under different nutrient regimes.

<table>
<thead>
<tr>
<th>Nutrient Treatment</th>
<th>Harvest 1 DAP</th>
<th>$\psi_s$</th>
<th>Harvest 2 DAP</th>
<th>$\psi_s$</th>
<th>Harvest 3 DAP</th>
<th>$\psi_s$</th>
<th>Harvest PV-Curve DAP</th>
<th>$\psi_s$</th>
</tr>
</thead>
<tbody>
<tr>
<td>NPK</td>
<td>18</td>
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<td>20</td>
<td>-0.331</td>
<td>20</td>
<td>-0.573</td>
<td>19</td>
<td>-0.423</td>
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<tr>
<td>NP</td>
<td>18</td>
<td>-0.240</td>
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<td>-0.327</td>
<td>20</td>
<td>-0.512</td>
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<td>-0.533</td>
</tr>
<tr>
<td>NK</td>
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<td>-0.409</td>
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<td>-0.484</td>
<td>31</td>
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<tr>
<td>PK</td>
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</tbody>
</table>

Table 5: Days of harvest (DAP = days after planting) and bulk $\psi_s$ (in MPa) at harvests of the different nutrient treatments in experiment B.

Considering the results of all harvests, water stress reduced SHOOT GROWTH in all nutrient treatments significantly. Large reductions (absolute and relative) in leaf area and shoot fresh weight at relatively high $\psi_s$ could be observed in all N-fertilized treatments, which showed high growth rates (Fig. 15).
Fig. 15:
Comparison of shoot fresh weights of well watered versus water stressed plants of the different nutrient treatments in experiment B (harvest 2). Reductions in shoot fresh weight due to water stress were much larger in N-fertilized than in N-deficient treatments.

Shoot dry weight (and thus photosynthesis) was less sensitive to water stress: significant reductions were seen in the nutrient treatments 0, N, NK and NP only (see Fig. 17 p. 25). Relative decreases in shoot dry weight due to water stress were considerably lower than reductions in leaf area or shoot fresh weight. P-fertilization tended to reduce the relative decreases in shoot growth due to water stress. Shoot dry weights of water stressed P-fertilized plants at harvest 1 (-0.2 > \( \psi_s > -0.3 \) MPa) were even higher than in well watered treatments (Fig. 16).

Fig. 16:
Effects of water stress on shoot dry weight production in the different nutrient treatments of experiment B (harvest 1). Shoot dry weight of well watered plants was assumed to represent 100%.

The extent of the reductions in shoot dry weight was not always correlated to the extent of the reductions in leaf area and shoot fresh weight, e.g. adequately N- and P-fertilized plants showed large decreases in shoot fresh weight, but only small reductions in shoot dry weight under conditions of drought stress. Fig. 17 a-c show water stress effects on shoot and root growth in experiment B.
Fig. 17: Shoot fresh and dry weight, root dry weight and root/shoot dry weight ratio of well watered and water stressed plants in different nutrient treatments of experiment B at harvests a) 1 (-0.2 > \( \psi_s \) > -0.3 MPa), b) 2 (-0.3 > \( \psi_s \) > -0.4 MPa) and c) 3 (-0.4 > \( \psi_s \) > -0.6 MPa). Error bars indicate least significant differences at the 5% level between water stressed and well watered treatments.
In well watered treatments, **Shoot Water Content (SWC)** was influenced by nutrient levels solely. In water stressed treatments, however, soil matric potential \((\psi_s)\) at harvest showed additional effects on SWC. N-fertilization increased shoot water content significantly at all harvests in well watered and water stressed treatments. Adequate P- and K-nutrition tended to increase SWC at later growth stages only; this effect was more pronounced in well watered than water stressed treatments (Fig. 18).

![Graph showing effects of N-, P- and K-nutrition on shoot water content](image)

**Fig. 18:** Effects of N-, P- and K-nutrition on shoot water content of well watered (WW) and water stressed (WS) plants in experiment B (harvest 3).


Water stress reduced shoot water content at all harvests in all nutrient treatments. This reduction in SWC with decreasing \(\psi_s\), however, varied with nutrient treatments: N-fertilized plants showed steeper decreases in SWC with decreasing \(\psi_s\), and relative decreases were higher than in N-deficient plants. Nevertheless, water stressed high-N plants showed higher shoot water contents than N-deficient plants (see Fig. 23 p. 34).

Water stress affected **Root Growth** of plants of different nutrient treatments in different ways: Higher absolute root dry weights under water stressed than under well watered conditions could be observed in plants with combined N- and P-fertilization. In water stressed P-deficient treatments, large reductions in root dry weight due to water stress could be observed at all harvests. P-fertilization clearly enhanced root growth under conditions of limited water supply (Fig. 19).
Fig. 19:
Effects of water stress on production of root dry weight in the different nutrient treatments of experiment B (harvest 1). Root dry weight of well watered plants was assumed to represent 100%.

In the nutrient treatments N, NP and NPK, ROOT TO SHOOT RATIOS of water stressed plants were always higher than those of well watered plants, even if plant growth stage was considered (see Fig. 17). In the other treatments, RSR tended to be lower under water stress than under well watered conditions. RSRs of well watered plants tended to be higher under N-, P- and K-deficiencies. Under water stress, however, fertilization of either nutrient (especially N) showed promoting effects on RSR: At the first harvest, RSR of N- and P-fertilized plants was increased under conditions of water stress (Fig. 20). At later harvests, reductions in RSR due to water stress were smaller in fertilized than in nutrient deficient plants. In this experiment (with bigger plants than in experiment A), the correlation between RSR and growth stage was not as high as in experiment A.

Fig. 20:
Effects of N-, P- and K-fertilization on root/shoot ratio of well watered (WW) and water stressed (WS) plants in experiment B (harvest 1).
In nutrient treatments without P-fertilization, total biomass production (TBP) was reduced at all harvests under water stress conditions. In the P-fertilized treatments NP, NPK, P and PK, however, TBP was higher in water stressed than in well watered treatments at the first harvest. At harvests 2 and 3, small decreases in TBP due to water stress could be observed in P-fertilized treatments. In general, N-fertilization increased, P-fertilization on the other hand decreased reductions in TBP due to water stress (Fig. 21).

Fig. 21: Effects of water stress on relative root and shoot dry weight and total biomass production in different nutrient treatments of experiment B (harvest 1). Total dry weight production of well watered plants was assumed to represent 100%. 

WS: water stressed treatments / WW: well watered treatments
3.3 DISCUSSION

3.3.1 Development of well watered plants

**SHOOT GROWTH** of young maize plants (up to the 5- to 7-leaf stage) was highly dependent on N-nutrition. The N-supply level of the plants was 'adequate' for N-fertilized (high-N) plants and 'poor' for N-deficient (low-N) plants respectively (table 2). Twelve days after planting, N-deficient plants showed significant reductions in leaf area and shoot fresh and dry weight (Fig. 1, Fig. 5 a). Similar results have been found in several other studies; the growth rate of N-stressed plants generally adjusts very quickly to suboptimal N-supply (Clarkson and Hanson 1980). Huber et al. (1989) explain these reductions in shoot growth of N-deficient plants by a reduced capacity for photosynthesis, decreased export of assimilates from mature to growing tissues, and a reduced biochemical capacity of growing zones in leaves to utilize sucrose.

P-deficiency also reduced shoot growth, but significant reductions could be observed after DAP 16 only (Fig. 5 b). These findings are consistent with the results of Barry and Miller (1989) and Barry et al. (1989), who point out the importance of an adequate P-nutrition of young maize plants (6-leaf stage) to obtain maximum kernel yield. P-supply levels were relatively high in my experiments: P-fertilized (high-P) plants grew on soil containing 'surplus' P, plants of low-P treatments grew at 'adequate' P-levels (table 2). It has to be noted however that leaf P-contents of all plants were relatively low in my experiments (table 4).

K-nutrition was less important for the development of shoots of young maize plants in the experiments presented here (Fig. 5 c): This may be due to the fact that K-contents of plants are usually highest at early growth stages (Beringer and Trolldenier 1978). Further, the effect of K-deficiency on photosynthesis is not as important as that of other macroelements as N or P (Catsky et al. 1987). In addition, C₄-plants are known to have higher K-efficiencies than C₃-plants (Bergmann 1988), and high Ca-levels (as in the soil used) can improve K-uptake of plants ('Viets-effect'; Viets 1944). Although K-concentrations of the soil even in K-fertilized treatments in my experiments were not very high ('moderate' versus 'poor' according to Lonza-Data 1985; extraction with NH₄-acetate-EDTA), K-contents of plants growing in K-deficient soil were only little below sufficient contents as described by Bergmann (1988) (see table 3). It is also possible that during the experiments K-ions fixed at clay particles were released and therefore contributed to the K-nutrition of the maize seedlings.

**SHOOT WATER CONTENT** of well watered plants was reduced under conditions of N- and K-deficiency. Numerous studies have shown that N-deficient plants have lower shoot water contents than N-fertilized plants, and that N-deficient plants show xeromorphic traits. These effects of N-deficiency have been attribut-
ed to accumulation of sugars and starch (Brouwer 1962; Radin and Parker 1979a) and increases of the proportion of cell wall material (Shimshi 1970; Radin and Parker 1979a). It is well established that K-ions play an important role as osmotica in plant cells, thus increasing the water content of plant tissues (Beringer 1978; Arneke 1981; Mengel and Arneke 1982; Leigh and Jones 1984; Maurya and Gupta 1984; Andersen et al. 1992b).

ROOT GROWTH of N-, P- and K-deficient plants was generally enhanced as compared to fertilized plants. Similar effects have been reported by many other workers (e.g. Brouwer 1962; Viets 1965; Maizlish et al. 1980; Huber et al. 1989). Because of the better development of N-fertilized plants though, N-deficient plants showed significantly smaller roots from DAP 19-20 on. Thus, in the long term, the enhancement of root growth under N-deficient conditions is merely relative. The promoting effect of K-deficiency on root growth on the other hand seemed to persist.

ROOT/SHOOT Ratio (RSR) of well watered plants of all nutrient treatments decreased during plant development as described by Brouwer (1962) (see Fig. 25 p. 42). RSR of young maize plants seemed to stabilize at a value of about 0.2 by the time when approximately 1.5 to 2 g shoot dry weight were produced. Long (1959) and Chevalier and Schrader (1977) reported RSR-values of 0.15-0.3 in different maize cultivars. The decrease in RSR along with the growth of a plant during early growth stages has to be considered when comparing RSRs of plants exposed to different treatments that affect plant growth, e.g. different nutrient treatments or water stressed versus well watered treatments: Plants with a slower development show higher RSRs at a certain DAP than faster growing plants, even if no causal effect of the treatment on RSR might exist (Andersen et al. 1989). This problem of misleading RSR-values can be avoided, if RSR is plotted against shoot or plant fresh or dry weight rather than against DAPs or days after imposing stress. Also in statistical analysis, plant development stage has to be considered, e.g. by including it in models as a covariate.

Fig. 22 a and b present RSR data of 5 comparable experiments (including experiments A and B) plotted against DAP and against shoot dry weight, respectively, for the nutrient treatment PK. The experiments differed somewhat in the initial nutrient status of the soil and in the day after planting, on which water stress was imposed (DAP 0 - 20). The plots positively demonstrate, how considering the growth stage of the plants can eliminate interfering factors as mentioned above. Unfortunately, in most of the numerous studies performed on RSRs, this change of RSR along with plant development has not been taken into consideration.

Root/shoot ratios of nutrient deficient plants were higher than in adequately fertilized plants, even if the growth stage of the plants was considered in the analysis of the data (Fig. 10). Numerous studies have described enhanced root
growth relative to shoot growth in plants growing under conditions of N- and P-
deficiencies (Brouwer 1962; Clarkson and Hanson 1980; Radin and Eidenbock
1984; Anderson and Schomburg 1986; Andersen et al. 1989; Huber et al. 1989).

Fig. 22: Example of how growth affecting differences among experiments can veil
root/shoot ratio patterns of developing maize seedlings. Fig. a) and b) present
the same RSR data of 5 comparable experiments plotted against days after
planting (DAP) and shoot dry weight, respectively, of the nutrient treat¬
ment PK. The experiments differed in the initial nutrient status of the soil and
in the DAP, at which water stress was imposed (DAP 0 to 20).

3.3.2 Development of water stressed plants
Conditions of water stress reduced LEAF AREA and SHOOT FRESH WEIGHT in
all nutrient treatments (Fig. 14). Fast growing N-fertilized plants encountered
more significant reductions at higher \( \psi_r \)-values than N-deficient plants; similar
results have been reported by several other authors (Tesha and Eck 1983; Morgan
1986; Nnoham and Odurukwe 1987; Bennett et al. 1989). However, absolute
shoot growth was increased in high-N as compared to N-deficient treatments. P-
fertilization seemed to reduce relative decreases in shoot development due to
water stress. Positive effects of P-fertilization on plant growth under drought
conditions have also been observed in other studies (Lahiri 1980; Sharples and
Reed 1982; Bonetti et al. 1984; Ackerson 1985; Premachandra et al. 1990b;
Saneoka et al. 1990). VAM-infections enhancing P-uptake exerted positive effects
on the growth of water stressed onion plants (Nelson and Safir 1982). As in well watered treatments, different K-nutrition showed no significant effects on shoot development of young maize plants under drought conditions. Some reasons for the lack of effects of K-fertilization in my experiments have been mentioned above (see p. 29). In addition, Tanguilig et al. (1987) found no differences in K-uptake between well watered and water stressed treatments. In the present study, K-contents of plants growing under conditions of water stress were only slightly reduced as compared to K-contents of plants growing under conditions of adequate water supply, particularly in K-fertilized treatments (see table 4).

**SHOOT DRY MATTER** production was significantly less affected by water stress than leaf area and shoot fresh weight (Fig. 4). This indicates that photosynthesis is less susceptible to low soil water potentials than cell expansion and the maintenance of a high water content (Hsiao 1973; Begg and Turner 1976; Boyer 1976; Sharp and Davies 1979; Sharp and Davies 1985; Barlow 1986). Especially growing regions require more assimilates under water stress conditions to achieve osmotic adjustment; this increased sink demand could enhance assimilate export of assimilating cells and thus compensate for eventual decreases in photosynthetic performance due to mild water stress.

N-fertilized plants experienced large reductions in shoot growth due to water stress conditions. Nevertheless, shoot development (leaf area, fresh and dry weight) of N-fertilized drought stressed plants, especially in combination with adequate P-nutrition, was significantly better than in N-deficient plants grown under conditions of drought stress (Fig. 5). Similar observations have been reported in other studies (Tesha and Eck 1983; Bennett et al. 1989; Frederick et al. 1990). The increase in leaf area, shoot fresh and dry weight even after the beginning of the water stress period was significantly higher in N- and P-fertilized as compared to N- and P-deficient treatments (data not shown), although N- and P-fertilized plants generally experienced lower $\psi$ than other plants. Thus, the positive effects of adequate N- and P-nutrition on shoot growth of maize seedlings persisted under water stress conditions. Several possible reasons for enhanced plant growth under water stress conditions at adequate or high levels of N and P have been proposed: Plants with high levels of N and P generally close their stomata at lower $\psi$ than N- and P-deficient plants (Ishihara et al. 1979; Radin and Parker 1979b; Radin and Ackerson 1981; Radin et al. 1982; Sharpley and Reed 1982; Radin 1984; Bataglia et al. 1985; Radin et al. 1985; Bennett et al. 1986; Jones et al. 1986). Plants growing at high N-levels revealed a higher photosynthetic capacity than N-deficient plants (Wong et al. 1979; Huber et al. 1989). Starch accumulation normally associated with (water) stress is suppressed in plants growing at high levels of P (Ackerson 1985; Lawlor and Leach 1985). Premachandra et al. (1990a, 1990b) reported higher cell membrane stabilities associated with high N- and P-levels in water stressed maize.
It has to be pointed out, however, that the development of a big shoot biomass not necessarily favors plant survival under drought conditions. An increase in water use during the early vegetative period may have adverse effects by increasing water stress at critical stages (Begg and Turner 1976; Lahiri 1980). On the other hand, adequate nutrition increases water use efficiency of plants significantly (Goudriaan and van Keulen 1979; Heinze and Fiedler 1980; Decau and Pujol 1984; Maurya and Gupta 1984; Olson 1984; Saikia and Dey 1984; Ackerson 1985; Bataglia et al. 1985; Power 1985; Dionne et al. 1987; Heitholt 1989; Schmidhalter and Oertli 1990a; Oertli 1991a; Schmidhalter and Oertli 1991b; Andersen et al. 1992a; Studer et al. 1992). Fast growing plants cover the soil surface more rapidly, and therefore water use efficiency is further increased. In addition, any expansion of leaf area leads to increased photosynthesis and thus more assimilates are produced usable for osmotic adjustment and for expansive growth of roots and shoots (Kriedemann 1986; Hsiao and Jing 1987). Selection for drought tolerance in maize at CIMMYT is therefore heading for plants with a fast development and high productivity (Edmeades, personal communication).

Shoot Water Content (SWC) was the first parameter observed to be changed in water stressed as compared to well watered plants. Since harvests in my experiments took place at predawn, comparisons of SWC of water stressed and well watered plants provide a valuable estimation of the relative water content (RWC) of water stressed plants (RWC being the ratio between actual water content and water content at full hydration).

Plants grown under conditions of adequate N- and K-nutrition revealed higher shoot water contents than N- and K-deficient plants under both water regimes (Fig. 16). Similar observations have been described by Shimshi (1970). Reductions in relative water content due to drought stress were less evident in N-deficient than in high-N plants. Radin and Parker (1979a), Morgan (1986) and other workers similarly reported smaller reductions of RWC under limited water supply in N-deficient plants. Morgan (1986) concluded that greater water retention at lowered leaf water potentials in N-deficient plants is related to greater drought tolerance. However, comparisons of water stress-induced reductions in relative water content alone cannot sufficiently characterize water retention in plant tissues; as shown below, shoot water content (which is definitively altered by different nutrition) has to be considered as well. Fig. 23 illustrates these relations using data of treatments NP and P of experiment A: As water stress develops, the amount of water retained in high-N plants is greater than in N-deficient plants, i.e. high-N plants show higher water retention, in spite of larger reductions in RWC during water stress development. Thus, shoot water content rather than relative water content may indicate the extent of water retention in plant tissues.
Water retention in plant tissues at low water potentials requires solute accumulation. Higher shoot water contents of adequately N- and K-fertilized plants at lowered $\psi$, consequently indicate more significant solute accumulation. Therefore maintenance of a high shoot water content may be looked at as a valuable indicator of osmotic adjustment of drought stressed plants. No correlation between shoot water content at predawn and shoot growth of young maize plants could be observed in my experiments. This might confirm suggestions that osmotic adjustment and maintenance of turgor are not alone responsible for continued plant growth and leaf expansion under water stress (Westgate and Boyer 1985; Munns 1988; Spollen and Sharp 1991). Adequate N- and P-nutrition were required for optimal plant growth under water stress conditions. These results suggest that specific solutes as well as the amount of solutes and thus $\psi$, play an important role in tissue growth and cell expansion.
As mentioned above, comparisons of root growth and root/shoot ratios among different treatments have to consider the growth stage of the plants. Different effects of water stress on root growth have been observed in the present study and described by other authors:

a) 'Mild' water stress can lead to an absolute increase in root dry weight compared to well watered treatments (Hsiao and Acevedo 1974; Sharp and Davies 1979; Aggarwal and Sinha 1983; Tanguilig et al. 1987; Schmidhalter and Oertli 1990b; Schmidhalter and Oertli 1991a). This phenomenon has been mostly observed in experiments with young plants. In the present study, adequate N- and P-nutrition enhanced such an absolute increase in root growth, particularly if plants were small (Fig. 17). However, the possibility of better root growth due to better aeration (especially in the case of increases in total biomass production) cannot be denied, since even short term anoxia can affect root growth considerably (Pearson 1966). Root growth is more negatively affected by poor aeration of the soil than shoot growth (Schmidhalter and Oertli 1991a). In addition, suberization of the endodermis and blocking of plasmodesmatal channels with callose and other structural carbohydrate material in roots of dry topsoil layers in order to prevent water loss during upward water transport may contribute to an absolute increase in root dry weight (Sharp and Davies 1985).

b) Relative increases of root growth (increases in root/shoot dry weight ratios) are commonly observed in plants growing under conditions of limited soil moisture supply (Brouwer 1962; Sharp and Davies 1985; Westgate and Boyer 1985; Schulze 1986). Such effects on dry matter partitioning in water stressed plants have been observed both with and without concurrent decreases in absolute biomass production, depending on whether water stress had affected photosynthesis or not. In the study presented here, RSR of plants growing under conditions of limited soil water supply was increased compared to RSR of well watered plants before any reductions in leaf area, shoot fresh weight or shoot dry weight due to water stress could be observed. All investigations examined reporting enhanced root growth relative to shoot growth under conditions of drought stress have been working with young plants, mostly at the seedling stage. In my experiments, adequate N- and P-nutrition seemed to be required for significant increases of RSR under water stress conditions (Fig. 19). Barraclough et al. (1989) similarly reported N-fertilization being necessary for compensatory root growth in subsoil under drought conditions.

c) In experiment B, where plants grew for a longer period than in experiment A, relative decreases in root growth (smaller RSRs, if growth stage was considered) due to water stress have been observed (Fig. 17, Fig. 19). However, relative reductions in root growth under drought as compared to well watered conditions were observed in N- and/or P-deficient plants only; N- and P-fertilization seemed to prevent relative reductions in root growth under conditions of water stress.
Tendencies of declining RSRs with plant development in water stressed maize seedlings (without considering growth stage) could also be observed in previous studies (Sharp and Davies 1979). However, declining RSRs do not necessarily imply a reduction in root elongation: They can be due to the development of thinner roots as photosynthesis is impaired as a consequence of water deficits. In such a way, additional soil volume can be explored more efficiently for nutrient and water uptake (Sharp et al. 1988).

Photosynthesize (and consequently dry matter) partitioning in plants occurs down hydrostatic pressure gradients from sources to sinks by mass flow of solutes in the sieve tubes of the phloem ('Druckstromtheorie', Münch 1930; see Fig. 24). Phloem flux is therefore largely regulated in the source and sink tissues, the former providing photosynthesize accessible for phloem loading, the latter avoiding accumulation and thus high concentrations of sugars either through dilution (water uptake and cell expansion) or through synthesis of macromolecules with minimal osmotic activity (Setter 1990). Reductions in photosynthetic activity in source tissues require relatively high intensities of water stress. Soluble sugar accumulation in photosynthetically active leaves of water stressed plants has been observed in several investigations (Ackerson 1981; Morgan 1984b; Fox and Geiger 1986). In addition, many studies have indicated that the mechanism of photosynthesize translocation itself is even less sensitive to water stress conditions than photosynthesis (for references see Setter 1990). Therefore, properties of sink tissues can be assumed to regulate photosynthesize partitioning to a great extent, particularly under conditions of water stress (Krieg 1983; Marschner 1986; Eschrich 1989; Setter 1990).

Osmotic adjustment and resulting maintenance of turgor in growing regions of leaves and roots have been observed in numerous recent studies (Sharp and Davies 1979; Westgate and Boyer 1985; Hsiao and Jing 1987; Sharp et al. 1990). They have been attributed primarily to accumulation of recent photosynthesize and/or decomposition of organic compounds in growing cells (Acevedo et al. 1979; Meyer and Boyer 1981; Sionit et al. 1981; Michelena and Boyer 1982; Boyer 1988). Munns and Weir (1981) emphasized that photosynthetic products can accumulate under drought stress when utilization is impaired to a greater extent than formation and distribution (Kriedemann 1986). Hydrolysis of sucrose, e.g., can lead to a stronger osmotic consequence for a given supply of assimilates (Rees 1974).

In spite of turgor maintenance due to osmotic adjustment, cell elongation has been observed to decrease in numerous studies (Michelena and Boyer 1982; van Volkenburgh and Boyer 1985; Westgate and Boyer 1985). The theory of 'growth induced water potentials' in growing zones (Molz and Boyer 1978; Boyer 1988) might be a possible explanation for this rapid decrease in growth associated with declines in water potentials of mature tissues in spite of turgor maintenance in
Fig. 24: Photosynthate partitioning between source and sink tissues (example: sucrose partitioning):

Phloem loading in source tissue:
1. Phloem parenchyma cells release sucrose into the apoplast close to the phloem
2. Companion cells and sieve cells having a high affinity for sucrose actively import sucrose from the apoplast against a steep concentration gradient
3. Very low osmotic potentials in phloem cells induce water influx into the phloem; this results in a high positive hydrostatic pressure in the phloem
4. The high hydrostatic pressure induces mass flow of solutes in the direction of sites with lower hydrostatic pressure (along the hydrostatic pressure gradient)

Phloem unloading in sink tissue:
5. (Passive) leakage of sucrose along a concentration gradient from the phloem into the apoplast decreases sucrose concentration in the phloem
6. Hydrolysis of sucrose by acid invertase in the apoplast leads to hexoses and low concentration of sucrose
7. (Active) uptake of hexoses by phloem parenchyma cells maintains low concentration of hexoses and thus sucrose in the apoplast

Sucrose partitioning depends mostly on the amount ('sink capacity') and velocity of sucrose consumption at sink sites. Decreased consumption increases hexose and sucrose concentration in the apoplast, leading to a similar situation as at source sites. The hydrostatic pressure gradient is hereby decreased, and mass flow along the gradient is restricted.
growing regions. The water potential in enlarging cells can be considered to consist of the sum of the osmotic and the turgor potential in these cells. Since cell wall relaxation and irreversible wall extension prevent turgor from increasing to its maximum despite water influx, the water potential in enlarging cells is kept low by the inability of the turgor to rise. Because the hydraulic conductivity between the vascular supply and the enlarging tissues is very low, a steep gradient between the water potential in growing and supplying tissues is maintained ('growth induced water potential'), and water influx from the vascular supply tissues can be maintained (Westgate and Boyer 1984). Nonami and Boyer (1990) postulated that a decrease in this gradient between the water potential in enlarging tissues and the water potential of the vascular supply caused mostly by a decreased water potential of the xylem was the primary event during growth inhibition by limited water supply.

Westgate and Boyer (1985) found similar \( \psi_s \) in elongating regions of leaves and roots of young maize plants under water stress conditions, but root growth continued at \( \psi_s \) that completely inhibited shoot growth (see also Sharp et al. 1988; Sharp 1990; Spollen and Sharp 1991). These findings indicate that the differential sensitivity of shoot and root growth to water stress conditions is not only attributable to higher solute accumulations and maintenance of turgor in roots. Other factors governing cell expansion might be equally involved in the maintenance of (root) growth at low \( \psi_s \). This conclusion is further supported by the fact that increasing solute concentrations in growing regions might diminish the hydrostatic pressure gradient between source and sink (growing) tissues; photosynthate import into growing tissues might therefore be hampered by water stress induced increases in solute concentrations (Setter 1990). In addition, cell metabolism is probably optimized to a narrow range of osmotic and ionic composition and concentration; changes in solute concentration and composition may therefore slow cell expansion and growth (Lawlor and Leach 1985).

Recent publications (Hsiao et al. 1985; Barlow 1986; Hsiao and Jing 1987; Pritchard et al. 1987; Boyer 1988; Spollen and Sharp 1991) attributed the differential sensitivity of root and shoot expansive growth to low \( \psi_s \) primarily to differences in the reaction of cell wall properties to water deficits between leaf and root elongating regions. In leaves, the cell wall is thought to harden, in roots on the contrary to become more plastic and extensible under water stress conditions (Hsiao and Jing 1987; Spollen and Sharp 1991). However, the metabolic basis for these opposite changes in cell wall yielding properties are not known. Under conditions of limited water supply, contents of abscisic acid (ABA) in plants are generally increased. Creelman et al. (1990) and Saab et al. (1990) proposed that ABA accumulation might maintain root elongation whereas shoot growth is inhibited by high levels of ABA. The authors therefore contributed differential sensitivity of root and shoot growth to low water availability to a differing
sensibility of roots and shoots to elevated ABA concentrations.

The results of the present study in context with the findings mentioned above suggest that an additional aspect should be considered to explain continuation of growth at low $\psi_s$ and differential sensitivity of root and shoot growth to water stress. Low soil water contents reduce plant availability and uptake of inorganic nutrients (Viaets 1972; Begg and Turner 1976). My experiments demonstrated that adequate N- and P-nutrition improved both shoot and root growth under conditions of limited water supply. Shifts in RSR due to continued root growth while shoot growth was restricted under conditions of water stress also required adequate N- and P-nutrition. Altered dry matter partitioning (in favor of the roots) as a result of water stress may mainly be observed in small plants as demonstrated in the present study as well as in other studies (e.g. Sharp and Davies 1979; Aggarwal and Sinha 1983; Sharp and Davies 1985; Westgate and Boyer 1985; Tanguilig et al. 1987). The total amount of nutrients required for a small plant to grow is much smaller than for a big plant, and seedlings are still capable to use readily available nutrients stored in the seed. In addition, Hsiao and Jing (1987) reported that plants undergoing a slow development of water stress were still growing at soil matric potentials at which plants experiencing a fast developing water stress completely had ceased growth. In most experiments, small plants experience a slower development of water stress than bigger plants. This may enable small plants to continue nutrient uptake and accumulation for a longer period, what might be important, since transport of nutrients is a far slower process than water exchange between cells and tissues (Schulze et al. 1988; Oertli 1991a).

Summarizing these results together with the finding that in spite of turgor maintenance (due to osmotic adjustment) growth can be inhibited at low $\psi_s$ leads to the conclusion that both specific solutes (as N- and/or P-compounds) and the sum of solutes can limit plant growth. Provided cell enlargement occurs and assimilates are diluted and/or used for metabolic processes, carbon partitioning from assimilating tissues to sinks can take place (Setter 1990). In other words, Justus von Liebig's theory of 'the minimum factor' might be a very important key to reduced cell enlargement and growth under water stress as well as to differential sensitivity of shoot and root growth to water deficits. Both qualitative and quantitative solute accumulation in water stressed tissues might restrict these processes.

Several facts support this conclusion: The experiments presented here demonstrate that shoot as well as root growth under water stress may be enhanced by adequate N- and P-nutrition (Fig. 5). Nutrient deficiencies affect shoot growth earlier and to a greater extent than root growth (Brouwer 1962). Water stress as well as nutrient deficiencies can lead to altered distributions of nutrients between
shoots and roots, e.g. N-deficiency reduces K-transport from roots to shoots (data not shown). Such effects could explain the continuation of root growth (and therefore carbon partitioning from shoots to roots) at low ψs, even when shoot growth is impaired. Enhanced carbon partitioning from shoots to roots under conditions of limited soil water supply seems to take place only as long as the (absolute) demand for nutrients is not too high, i.e. in small plants. It is generally more distinct if water stress development is slow and hence nutrient uptake and accumulation can continue for a longer period than under fast developing stress. Differential sensitivity of plant growth to low ψs induced by osmotica (e.g. in solution culture) and low water content in soils respectively (Schmidhalter and Oertli 1990b; Schmidhalter and Oertli 1991a) could be due to different effects of the stresses on nutrient availability: Low matric ψs affect nutrient uptake of plants to a great extent by limiting nutrient transport to the root surface (Viets 1972). In solution cultures, however, where low ψs are induced by osmotica, this effect is negligible. K-fertilization did not improve shoot and root growth at the seedling stage in my experiments. This might be due to the fact that K-contents in plants growing in treatments without K-fertilization were only little below sufficient levels. K-contents in young plants are generally very high and usually exceed those necessary for optimal plant growth (luxury consumption; Leigh and Jones 1984). It has to be considered, however, that at later growth stages, K might also be a limiting nutrient for cell enlargement (especially under water stress conditions): K-deposition into growing tissues under water stress parallels the decrease in water deposition, and the contribution of potassium ions to osmotic adjustment is negligible (Schildwacht 1989; Sharp et al. 1990). Negative effects of K-fertilization on growth as observed in my experiments (see Fig. 10, 13) might be due to interactions of K-nutrition with the uptake of other nutrients as Mg (data not shown), that might become limiting for cell elongation and thus growth (Bouma et al. 1979).

The conclusions presented in this study do not necessarily conflict with the above mentioned assumptions that cell expansion and differential sensitivity of shoots and roots to water stress can be attributed to differences in reactions of cell wall yielding properties to stress. It has to be pointed out, however, that cell enlargement and especially growth of a whole organ cannot be explained as a purely hydraulic/mechanical process (Hsiao et al. 1985; Lawlor and Leach 1985; Steudle 1985; Boyer 1988; Schulze et al. 1988) as in the theory of Lockhart (1965) (more recently discussed by Cosgrove 1981). Lockhart's equation though is the basis for the conclusion that, because cell enlargement can be impaired even at full turgor, cell growth might be limited by cell wall yielding properties. However, growth is coupled with numerous metabolic processes needing carbon substrates, energy and specific nutrients, e.g. for the synthesis of new cellular material. Even cell wall extension itself and changes in wall yielding properties imply the presence
of specific solutes in a cell or the uptake of specific nutrients into a cell, e.g. in order to balance proton efflux necessary to acidify the cell wall ('acid growth hypothesis') (Lawlor and Leach 1985; Lindhauer 1989). Regulation of metabolic processes (e.g. enzyme regulation) depends to a great extent on specific control ions (Lawlor and Leach 1985). Whereas carbon substrates and energy may be readily available from (local) photosynthesis, inorganic nutrients as N, P, K and Mg have to be imported. This import of inorganic nutrients, however, is a slow process, which is definitively impaired under drought conditions (Kriedemann 1986).

Although turgor maintenance may not solely be limiting plant growth under drought stress, osmotic adjustment by accumulation and/or hydrolysis of photosynthates and other organic compounds still plays a metabolically effective and energy efficient role in the alleviation of drought stress (Kriedemann 1986). Maintenance of turgor is an ultimate prerequisite for cell enlargement and growth (Steudle 1985). In addition, solute accumulation enhances resumption of growth upon stress relieve as reported in several studies (Rawson and Turner 1982; Palta 1984; Hsiao et al. 1985; Kriedemann 1986). Under severe stress, osmotic adjustment may represent an adaptation for surviving: Solutes increase to very high levels in meristematic tissues even when mature tissues die, thus maintaining cell volume, turgor and metabolic concentrations in growing regions (Munns 1988).

Summarizing it can be noted that not only biophysical (e.g. hydraulic), but also biochemical (metabolic) factors impair plant growth under drought stress conditions. Since many hydraulic effects of water stress are interrelated with biochemical and ionic events (Lawlor and Leach 1985; Schulze et al. 1988), both quantitative and qualitative changes in inorganic nutrient supply may play a major role in growth inhibition at low ψr.

Another question arises from my experiments: How important is the effect of the often described shift in root/shoot ratio under water stress conditions? Fig. 25 summarizing RSR data derived from five similar experiments suggests that root/shoot ratios of all nutrient treatments at various water regimes tend to attain similar values at a certain plant growth stage. Differences in RSR between different treatments commonly observed seem to be due to a great extent to differences in the development or growth rate of plants. Thus, direct effects of nutrients and/or water stress on RSR are often overestimated.

Nevertheless, the present study demonstrates that adequate nutrient supply can lead to a faster development of root growth under water stress in young maize plants. This is very important for seedling establishment under conditions of limited water supply, since surface soils are primarily susceptible to drying. Fig. 25 demonstrates that at the seedling stage considerable differences in RSR among
plants of different treatments may exist, even if the growth stage of the plants is taken in consideration. However, at later growth stages (SDW > 1.5 to 2 g), root/shoot ratios of different treatments tend to stabilize at very similar values.

Fig. 25: RSR data of five comparable experiments including different nutrient treatments at different water regimes. Hollow symbols represent well watered, filled symbols water stressed treatments. Experiments x and y were preliminary experiments.
3.4 SUMMARY

Shoot and root growth of maize (Zea mays L. cv Issa) seedlings grown in soil at different levels of N, P and K under well watered and water stressed conditions were examined. Adequate N- and P-nutrition enhanced shoot growth under both water regimes. Root/shoot dry weight ratios (RSR) were generally increased under conditions of N-, P- and K-deficiency. Absolute root growth, however, was increased at high N- and P-levels because root and shoot growth were highly correlated. Enhanced root growth relative to shoot growth under conditions of limited soil water supply seemed to require adequate N- and P-nutrition. Combined N- and P-fertilization exerted synergistic effects on root and shoot growth of young maize plants. No significant effects of different soil-K levels on root or shoot development of maize seedlings could be observed. Because RSR changes considerably during early plant development, plant growth stage has to be considered in studies that compare RSR among growth affecting treatments, particularly at early growth stages.

It is concluded that adequate N- and P-nutrition are of great importance for the establishment of maize seedlings, particularly under conditions of limited water supply. Since surface soils are primarily susceptible to drying, a vigorous root growth is of particular importance for seedling establishment. Adequate N- and P-nutrition clearly enhanced root growth of maize seedlings, particularly under conditions of limited soil moisture supply.

Since water stress can impair shoot and root growth even in organs at full turgor, it is suggested that both quantitative and qualitative aspects of nutrient supply are important for sustained plant growth under drought stress. The supply of (growing) tissues with specific nutrients might represent a growth limiting step, particularly under conditions of water stress.
4. WATER RELATIONS OF LEAVES AND ROOTS

4.1 INTRODUCTION

Cell enlargement and thus plant growth is the result of many complex metabolic events in combination with physical processes (Ortega 1990). Biochemical loosening of the cell wall under the mechanical stress caused by turgor pressure is generally considered as the initial step of the process of expansive growth. This stress relaxation, which lowers cell water potential, is followed by water uptake and cell enlargement. For sustained growth, turgor must be maintained at an adequate level to allow continuous wall loosening. Since solutes are diluted by the water taken up for growth, the maintenance of turgor requires a continuous accumulation of solutes. Otherwise the turgor would fall with growth until it is too low to effect stress relaxation (see Fig. 26 p. 45). Thus, expansive growth depends on the biochemical processes of wall loosening and wall formation, solute transport and generation, as well as the physical parameters of turgor pressure and water transport (Hsiao and Jing 1987).

The physical theory of plant growth indicates that the rate of cell expansion is determined predominantly by the rate of two interrelated and simultaneous physical processes: The net rate of water uptake and the rate of cell wall extension (Ortega 1990). Either one of these processes may limit growth. The physical theory of plant growth was first put into explicit analytical form by Lockhart (1965) who derived an expression relating the steady-state growth rate to the physical parameters that control water transport and wall expansion (Cosgrove 1981). Lockhart's original 'growth equations' have been augmented by several authors with additional terms to extend their utility (e.g. Cosgrove 1981; Tomos 1985; Ortega 1990). Oertli (1971; 1976; 1991b) describes the volume flow $J_v$ into a cell by the equation: $J_v = \frac{dV}{dt} = -L_p^*\Delta P - \sigma\Delta \pi$, where $V$ is the volume of the cell contents (mostly water), $t$ is the time, $L_p^*$ is the relative hydraulic conductance, $\Delta P$ is the pressure difference between the cell interior and the external medium, $\sigma$ is the reflection coefficient, and $\Delta \pi$ is the difference in osmotic pressure between the cell sap and the external medium.

The second governing 'growth equation', which describes the rate of cell wall extension, may be formulated to account for both irreversible (plastic) and reversible (elastic) wall extension (Ortega 1990): $\nu_e = \frac{dV_c}{dt}/V_c = \varphi*(P-Y)+(dP/dt)/\varepsilon$, where $\nu_e$ is the relative rate of change in volume of the cell wall chamber, $V_c$ is the volume of the cell wall chamber, $t$ is the time, $\varphi$ is the relative irreversible wall extensibility, $P$ is the turgor pressure, $Y$ is the yield threshold (a magnitude of turgor pressure that must be exceeded before plastic wall extension occurs), and $\varepsilon$ is the volumetric elastic modulus. The term $\varphi*(P-Y)$ represents the relative
Fig. 26: Conceptual diagram of the interrelations of wall relaxation, water uptake, turgor pressure, and solute accumulation in expansive growth.

Beginning at the upper right, growth is initiated by wall loosening (A) which lowers $\psi_p$ and creates a $\psi$ gradient for water uptake (B). Turgor expands the wall as water enters the cell, but cellular contents are diluted (C). Solute accumulation restores the initial $\psi_\pi$, and water enters until $\psi_p$ reaches the original value (D). The steps repeat in the next cycle (B', C', D'). The sequential presentation is artificial and is depicted for ease of understanding. In steady-state growth, wall loosening, water uptake, expansion, and solute accumulation are occurring simultaneously and continuously.

($\psi$: Water potential / $\psi_\pi$: Osmotic potential / $\psi_p$: Turgor potential)

rate of plastic, or permanent, wall extension. The term \( \frac{dP}{dt} / e \) represents the relative rate of elastic wall extension.

It is well established that plant expansive growth (cell elongation) represents the physiological process most sensitive to drought-induced changes in plant water status (Barlow 1986; Sharp 1990). Traditionally, reduced cell elongation under conditions of water stress has been attributed primarily to a reduction in cell turgor due to a reduced water potential (Boyer 1968). Even a relatively small decrease in turgor pressure can reduce or prevent growth by reducing or eliminating the effective driving force for growth (P-Y) (Hsiao et al. 1985).

According to the ‘growth equations’ as described above, maintenance of turgor at low water potentials could be mainly achieved by two different mechanisms: a) accumulation of solutes (decrease in the osmotic potential) in cells and b) changes in cell wall rheology (decrease of \( e \), decrease of \( Y \) and/or increase of \( \phi \)) (Radin 1983; Wyn Jones and Pritchard 1989).

Solute accumulation has long been known as a tolerance mechanism for moisture stress in plants growing under saline or drought stress conditions (Radin 1983). A lowering of the osmotic potential in response to water deficits can arise from the concentration of osmotic solutes as water is withdrawn from the vacuole and the cell volume decreases, or additionally from the accumulation of additional solutes in the cell. The term ‘osmotic adjustment’ generally refers to the lowering of osmotic potential arising from the net accumulation of solutes in response to water deficits or salinity. It refers to the net solute increase and should be used to distinguish the active accumulation of solutes from the passive concentration of solutes (Turner and Jones 1980). Determination of the extent of ‘osmotic adjustment’ by comparing the osmotic potentials of expressed cell sap of well watered and water stressed plants may therefore overestimate the degree of ‘osmotic adjustment’: Passive accumulation of solutes by dehydration of a cell cannot be separated from active accumulation of solutes. Additionally, the solute content in the apoplast could cause substantial errors in the determination of the osmotic potential of the cell sap (Oerthi 1971). Conversely, water of the apoplast can dilute the expressed cell sap and hereby lead to errors in the determination of the osmotic potential of the cell sap (Tyree 1976). Turner and Jones (1980) therefore suggested determining the extent of osmotic adjustment at a standardized water content at either full or zero turgor (difference in the osmotic potential at full or zero turgor between well watered and water stressed plants).

Based on the pressure-chamber technique developed by Scholander et al. (1964, 1965), Tyree and Hammel (1972) presented a theory relating changes in balance pressure (water potential) to changes in cell, tissue or organ water content. The graphical display and analysis of these relations between balance pressure and water content has become known as the pressure-volume (PV) curve technique.
The PV curve technique allows to determine a variety of meaningful parameters of plant water relations, namely osmotic potential at full and zero turgor, relative water content at zero turgor, apoplastic water content, bulk modulus of elasticity $\varepsilon$ and capacitance.

However, data derived from the analysis of PV curves have to be interpreted cautiously: The theory of the PV curve technique is based on the assumption that the volume of the cell always equals the volume of the wall chamber, i.e. it is assumed that turgor pressure is always $\geq 0$. The occurrence of negative turgor pressures in water stressed plants, however, is still highly controversial (Tyree 1976; Oerli 1983; Oerli et al. 1990). Oerli and Jenka (1985) have demonstrated that determination of osmotic adjustment at neither standardized water content gives quantitative information as to the extent of osmotic adjustment at ambient water content. Tyree and Richter (1981, 1982) and Turner (1987) concluded that the estimation of the apoplastic water content cannot be made with a high degree of accuracy from PV curve analysis. Some possible sources of errors in determining $\varepsilon$ from PV curves have been discussed by Cheung et al. (1976); they recommended comparing $\varepsilon$'s of different plants at comparable 'volume averaged turgor pressures', possibly near or at full turgor. In spite of possible errors in the determination of parameters of plant water relations from PV curves, this technique is widely used in experiments relating water stress to biophysical processes in plants.

As stated above, maintenance of cell turgor in water stressed plants may be achieved by both solute accumulation and changes in cell wall rheology. The ecological importance of changes in $\varepsilon$ is still not clear (Tyree and Karamanos 1981). Bulk modulus of elasticity is defined as $\varepsilon = V(dP/dV)$, where $dP$ is the change in turgor pressure for a given change in the water content $dV$ of a cell (Tyree and Hammel 1972; Tyree 1981). A decrease in $\varepsilon$ could enable water stressed plants to endure higher degrees of dehydration before their turgor drops to zero. Low values of $\varepsilon$ could increase the plants' ability to passively 'accumulate' solutes under conditions of water stress. Tyree and Karamanos (1981) and Tomos (1985) however concluded that changes in $\varepsilon$ are less effective in preventing turgor from falling to zero in water stressed plants as compared to osmotic adjustment.

Values of the yield threshold $Y$ have been reported to be very high in some plants (for references see Wyn Jones and Pritchard 1989), i.e. the effective driving force for cell elongation $(P-Y)$ may be quite small. Therefore, decreases in $Y$ and/or increases in wall extensibility $\phi$ might allow water stressed plants, to a certain extent, the maintenance of growth without any turgor adjustment (Wyn Jones and Pritchard 1989). However, the limited data on changes of $Y$ and/or $\phi$ due to water stress indicate that in leaves, cell walls harden under conditions of water deficits (increase in $Y$ and decrease in $\phi$), leading to growth reductions.
(Hsiao and Jing 1987). Indeed, recent publications suggest that changes in cell wall rheology might represent the initial step in the reduction of cell elongation and growth under conditions of water stress (Hsiao et al. 1985; Barlow 1986; Hsiao and Jing 1987; Pritchard et al. 1987; Boyer 1988; Spollen and Sharp 1991). However, without detailed knowledge about changes in cell and wall geometry, data on $Y$ and $\phi$ based on turgor measurements might not be qualified to prove whether water stress affects the intrinsic yielding characteristics of the cell wall (Hsiao et al. 1985).

It has further to be noted that the explanations given here only consider the biophysical aspects of plant cell growth. Cell enlargement and especially growth of a whole organ, however, cannot be explained as a purely hydraulic/mechanical process (Hsiao et al. 1985; Steudle 1985; Boyer 1988; Schulze et al. 1988): Growth is coupled with numerous metabolic processes needing carbon substrates, energy and specific nutrients, e.g. for the synthesis of new cellular material. Cell wall extension and changes in cell wall rheology imply the presence of specific solutes in a cell or the uptake of specific nutrients into a cell. However, very little is known about changes in metabolic processes under conditions of water stress and particularly about the effects of such changes on biophysical processes governing cell expansion and growth.

The study presented here (for materials and methods see chapter 2) describes the interactive effects of N-, P- and K-nutrition on water relations of maize seedlings grown under conditions of limited water supply. An attempt is made to determine physiological reasons for the different effects of water stress on root and shoot growth of maize seedlings grown under different nutrient regimes.
4.2 RESULTS

No consistent effects of plant growth stage on predawn plant water potentials of well watered plants measured at different harvests could be observed in experiments A and B. Therefore, the results of experiments A and B were analyzed simultaneously in order to obtain a better resolution of the development of plant water potentials with decreasing soil matric potentials.

To analyze the effects of different nutrient treatments on water relations of plants grown under conditions of adequate and limited soil water supply, classes of plants harvested at similar \( \psi_s \)-ranges were created ('\( \psi_s \)-classes'). Care was taken to consider at least one harvest of each nutrient treatment in each \( \psi_s \)-class and nevertheless to obtain a reasonable resolution on the range of \( \psi_s \) examined. These considerations led to a division of the harvests into five \( \psi_s \)-classes:

- \( \psi_s \)-class 1: harvests at \( 0 > \psi_s > -0.08 \) MPa
- \( \psi_s \)-class 2: harvests at \( -0.08 > \psi_s > -0.16 \) MPa
- \( \psi_s \)-class 3: harvests at \( -0.16 > \psi_s > -0.3 \) MPa
- \( \psi_s \)-class 4: harvests at \( -0.3 > \psi_s > -0.45 \) MPa
- \( \psi_s \)-class 5: harvests at \( -0.45 > \psi_s \) MPa

Thus, the effects of different nutrient treatments and of the N-, P- and K-status of the soil on plant water relations could be compared within and among \( \psi_s \)-classes.

4.2.1 Relation between plant water potential and soil matric potential

Fig. 27 displays water potentials of roots (\( \psi_r \)) and leaves (\( \psi_l \)) in relation to declining soil matric potentials (\( \psi_s \)). It can be seen that in all nutrient treatments (except treatments N, K and NK) predawn water potentials of roots were higher than average soil matric potentials, i.e. there seemed to exist a positive water potential gradient between the soil and the roots in all P-fertilized treatments and treatment 0. The water potential gradient between roots and leaves, however, was always negative in all treatments.

Statistical analysis of the data revealed that water potentials of leaves and roots were affected by different nutrient treatments at all \( \psi_s \)-ranges. N- and K-fertilized plants had significantly lower \( \psi_{\text{plant}} \)-values (of leaves and roots) at all given ranges of \( \psi_s \) than N- and K-deficient plants. P-fertilization on the other hand exerted the opposite effect on \( \psi_{\text{plant}} \) in all \( \psi_s \)-classes.

Root water potentials \( \psi_r \) decreased more or less steadily with declining \( \psi_s \) in all nutrient treatments; some oscillations of \( \psi_r \) along with declining \( \psi_s \), however, were observed, particularly in N-fertilized treatments and treatment 0.
Fig. 27: Development of water potentials of roots (diamonds, dashed lines) and leaves (squares, solid lines) along with declining soil matric potential (dotted lines) in different nutrient treatments in experiments A and B. Error bars denote standard deviations of measurements of 3 samples, each from a different plant. (Curves were fitted by eye.)
The development of leaf water potentials ($\psi_l$) along with declining $\psi_s$ showed significant differences between N-fertilized and N-deficient plants, particularly at $\psi_s > -0.3$ MPa. Leaf water potentials of well watered plants ($\psi_l > -0.08$ MPa) varied to a great extent in all nutrient treatments: In N-deficient plants, $\psi_l$ varied between -0.02 and -0.2 MPa. In N-fertilized plants, $\psi_l$-values between -0.03 and -0.55 MPa were observed at $\psi_s > -0.08$ MPa.

In treatments without N-fertilization, the decrease in $\psi_l$ paralleled the decrease in $\psi_s$ to a great extent at $\psi_s < -0.1$ MPa. In N-fertilized treatments, however, significant differences in the development of $\psi_l$ and $\psi_s$ were observed when $\psi_s$ declined from -0.08 to -0.2 to -0.3 MPa: As water stress developed, $\psi_l$ decreased to a much greater extent than $\psi_s$ in N-fertilized plants. After this steep decrease in $\psi_l$ with $\psi_s$ declining to -0.1 to -0.2 MPa, a 'recovery' or at least a stabilization of $\psi_l$ was observed in N-fertilized plants. At $\psi_s < -0.3$ MPa, the decrease in $\psi_l$ paralleled the decrease in $\psi_s$ in N-fertilized plants as it was observed in N-deficient plants.

In N-deficient treatments, only a vague cycle of a decrease and subsequent recovery of $\psi_l$ with declining $\psi_s$ could be observed at the onset of water stress. This cycle was much smaller than in N-fertilized treatments ($< 0.1$ MPa) and was restricted to $\psi_s$-values > -0.1 MPa.

Fig. 28 shows the differences in the development of $\psi_l$ along with declining $\psi_s$ between plants of a N-fertilized and a N-deficient treatment.

![Fig. 28: Development of water potentials of leaves (solid lines, squares) and roots (dashed lines, diamonds) in plants of nutrient treatments NP (N-fertilized) and P (N-deficient). Error bars denote standard deviations of measurements of 3 samples, each from a different plant.](image)
4.2.2 Comparison of leaf and root water potentials

Fig. 29 shows the development of the difference between root and leaf water potentials ($\Delta(\psi_r - \psi_l)$) with decreasing $\psi_s$ for the different nutrient treatments. It can be seen that a water potential gradient between roots and leaves had been maintained at all harvests, i.e. even during the dark period (closed stomata), no complete equilibration of water potentials between roots and leaves had occurred. The extent of the difference between $\psi_r$ and $\psi_l$, however, varied greatly both within and among the different nutrient treatments.

In N-deficient treatments, declining $\psi_s$ exerted no significant effects on the difference between root and leaf water potentials. The difference between $\psi_r$ and $\psi_l$ was quite constant (0.05 to 0.1 MPa) over the whole $\psi_s$-range examined, although at $\psi_s > -0.08$ MPa, a great variability in $\Delta(\psi_r - \psi_l)$ was observed. It seemed that $\Delta(\psi_r - \psi_l)$ increased slightly at the onset of water stress, but then decreased to the same values as in well watered plants at $\psi_s < -0.1$ MPa.

In N-fertilized plants, however, marked changes in the difference between root and leaf water potentials with declining $\psi_s$ occurred: At $\psi_s > -0.1$ MPa, a great variability in $\Delta(\psi_r - \psi_l)$ was observed as in N-deficient plants. Since $\psi_l$ of N-fertilized plants decreased to a much greater extent when $\psi_s$ declined to -0.1 to -0.2 MPa, a big difference of up to > 0.4 MPa between root and leaf water potentials developed in N-fertilized plants. Because $\psi_l$ 'recovered' to some extent when $\psi_s$ declined further, and because $\psi_r$ decreased quite steadily, the difference between root and leaf water potentials in N-fertilized plants decreased to similar values as observed in N-deficient plants at $\psi_s < -0.2$ to -0.3 MPa (Fig. 30).

Thus, the difference between root and leaf water potentials was significantly higher in N-fertilized than in N-deficient plants, particularly at $\psi_s > -0.3$ MPa (Fig. 30). P-fertilization on the other hand tended to decrease the difference between $\psi_r$ and $\psi_l$ (see Fig. 46 p. 71). No consistent effects of K-fertilization on the difference between root and leaf water potentials could be observed.
Fig. 29: Development of the difference between root and leaf water potentials ($\psi_r - \psi_l$) along with declining soil matric potential in plants of different nutrient treatments in experiments A and B. Error bars denote standard deviations of measurements of 3 samples, each from a different plant. (Curves were fitted by eye.)
4.2.3 Osmotic and turgor potentials of roots and leaves

Osmotic potentials of roots ($\psi_{\text{r}}$) of well watered plants were not affected by plant age. Root osmotic potentials of water stressed plants in all nutrient treatments in experiment B were clearly reduced compared to those of well watered plants (Fig. 31). Nevertheless, significant effects of different nutrient treatments on $\psi_{\text{r}}$ could be observed at all $\psi_{\text{s}}$-ranges. Root osmotic potentials were significantly lower in N-fertilized than in N-deficient plants at $\psi_{\text{s}} < -0.16$ MPa (Fig. 32). Lower values of $\psi_{\text{r}}$ in P-fertilized than in P-deficient plants could be observed at $\psi_{\text{s}} < -0.45$ MPa only. K-fertilization decreased $\psi_{\text{r}}$-values in the $\psi_{\text{s}}$-range between -0.16 and -0.30 MPa significantly.

In treatments NP and NPK, the decline in root osmotic potential ($\psi_{\text{r}}$) with falling $\psi_{\text{s}}$ was more evident than in other treatments: $\psi_{\text{r}}$ was decreased to a greater extent (> 0.55 MPa) in treatments NP and NPK as compared to the other nutrient treatments (0.3 to 0.4 MPa) in $\psi_{\text{s}}$-range 5 ($\psi_{\text{s}} < -0.45$ MPa).

Root turgor ($\psi_{\text{tr}}$) reflected the observed responses of $\psi_{\text{r}}$ to declining $\psi_{\text{s}}$: In treatments NP and NPK, a marked increase in $\psi_{\text{tr}}$ with falling $\psi_{\text{s}}$ (between 0 > $\psi_{\text{s}} > -0.25$ MPa) could be observed. Thus, these two treatments showed the
Fig. 31: Development of water potential components of roots along with declining soil matric potential in different nutrient treatments in experiments A and B. Root water potential: triangles, solid lines / Root osmotic potential: squares, short dashed lines / Root turgor potential: diamonds, dashed lines. Water potentials of well watered plants (\(\psi_r < -0.08\) MPa) are included in the graphs. Error bars denote standard deviations of measurements of 3 samples, each from a different plant.
highest $\psi_r$ at soil water potentials $<-0.16$ MPa, and no indication of declining $\psi_r$ even at $\psi_s < -0.5$ MPa could be observed. In treatments PK and K, $\psi_r$ decreased slightly at $\psi_s < -0.2$ MPa. In plants of the nutrient treatments N, NK and 0, marked decreases of $\psi_r$ at soil matric potentials $\psi_s < -0.4$ MPa were observed.

Root turgor ($\psi_r$) of P-deficient plants at $\psi_s < -0.16$ MPa was significantly lower than in P-fertilized plants (Fig. 32). N-fertilization similarly increased $\psi_r$ under conditions of limited soil water supply; significant effects, however, could only be observed in the $\psi_r$-range between -0.16 and -0.45 MPa. K-fertilization on the other hand reduced $\psi_r$ at low soil water potentials ($\psi_s < -0.16$ MPa). Fig. 32 summarizes the effects of N-, P- and K-fertilization on water potential components of roots of well watered and water stressed plants.

Leaf osmotic potentials ($\psi_m$) declined much less with falling $\psi_s$ than $\psi_m$ (Fig. 33): Comparisons of $\psi_m$ of well watered ($\psi_s > -0.08$ MPa) and water stressed ($\psi_s < -0.38$ MPa) plants revealed significant reductions in $\psi_m$ due to water stress.
Fig. 33: Development of water potential components of leaves along with declining soil matric potential in different nutrient treatments in experiments A and B. Leaf water potential: triangles, solid lines / Leaf osmotic potential: squares, short dashed lines / Leaf turgor potential: diamonds, dashed lines. Water potentials of well watered plants ($\psi_w < -0.08$ MPa) are included in the graphs. Error bars denote standard deviations of measurements of 3 samples, each from a different plant.
These reductions, however, were very small compared to those of $\psi_{sl}$: In treatments NK, NP and NPK, they were in the range of 0.1 to 0.12 MPa, and in the other treatments below 0.06 MPa ("osmotic adjustment"; see Fig. 47 p. 74). Significant effects of different nutrient treatments on the reduction in osmotic potentials could only be observed at low $\psi_{s}$: N- and K-fertilization increased the extent of the reduction in $\psi_{sl}$ due to water stress (see Fig. 48 p. 75), whereas no significant effect of P-nutrition could be observed.

N-fertilized plants revealed significantly lower $\psi_{sl}$-values than N-deficient plants at all $\psi_{s}$-ranges, but particularly at low $\psi_{s}$ (Fig. 34). Adequate K-nutrition seemed to exert similar effects on $\psi_{sl}$ as N-fertilization, but to a lesser extent than N-fertilization.

### Fig. 34: Effects of N-, P- and K-fertilization on water potential components of leaves of well watered plants (WW; $\psi_{s} > -0.08$ MPa) and water stressed plants (WS; $\psi_{s} < -0.3$ MPa).

The lack of (sufficient) reductions in $\psi_{sl}$ with declining $\psi_{s}$ was reflected in the leaf turgor-values ($\psi_{pl}$). Since the degree of 'osmotic adjustment' was very small in all nutrient treatments, $\psi_{pl}$-values were mainly affected by the development of
ψi along with declining ψf (Fig. 33). In N-deficient plants, a small cycle of a
decrease and subsequent recovery of ψpl could be observed at the onset of water
stress. At soil matric potentials ψs < -0.16 MPa, ψpl of N-deficient plants declined
gradually with declining ψs. In N-fertilized plants, the steep decrease in ψi at the
onset of water stress and the recovery of ψi at ψi < -0.2 to -0.3 MPa were clearly
reflected in the development of ψpl along with declining ψi: After a relatively
steep decrease in ψpl at the onset of water stress, ψpl recovered to some extent
until ψi dropped below -0.3 to -0.4 MPa. This recovery of ψpl was most distinct
in the nutrient treatments NP and NPK. At ψs < -0.3 to -0.4 MPa, ψpl of N-
fertilized plants decreased steadily with declining ψs.

Leaf turgor (ψpl) was affected by different nutrient regimes in all ψs-ranges (Fig.
34). P-fertilized plants showed significantly higher ψpl-values than P-deficient
plants over the whole range of ψs examined. This was mostly due to elevated ψi-
values at a certain ψs in P-fertilized treatments. K-fertilization on the other hand
exerted negative effects on ψpl at all ψs-ranges: K-fertilized plants showed lower
ψpl-values at a certain ψs than K-deficient plants, because ψi-values of K-fertil-
ized plants were lower at a certain ψs than in K-deficient plants. Adequate N-
nutrition exerted similar effects as K-fertilization: Although high-N plants showed
lower ψpl than N-deficient plants, decreased ψi-values at high N-levels were more
important for the development of ψpl when the soil was drying. However, signifi-
cant effects of N-fertilization on ψpl could be observed at ψs > -0.3 MPa only.
Highest ψpl-values at all ψs were attained in the nutrient treatments 0 and P. At
low soil matric potentials, treatments NP and NPK achieved similar high ψpl-
values. This was mostly due to the recovery of ψpl at -0.1 > ψs > -0.3 MPa in
these treatments.

Fig. 35 illustrates the different reactions of water potential components of roots
and leaves to declining soil water potentials. Root turgor was maintained or even
increased when water stress developed. This was obviously due to significant
reductions in root osmotic potentials. Osmotic potentials of leaves on the other
hand did not decline to a sufficient extent when water stress was imposed; thus,
leaf turgor was always lower than root turgor and declined with increasing
intensity of water stress.
Fig. 35: Development of water potential components of roots (solid lines, filled symbols) and leaves (dashed lines, hollow symbols) along with declining soil matric potential in different nutrient treatments in experiments A and B. Water potentials: triangles, solid lines / Osmotic potentials: squares, short dashed lines / Turgor potentials: diamonds, dashed lines.
4.2.4 Analysis of pressure-volume curves

Pressure volume curves (PV curves) of roots were very difficult to establish: It was impossible to determine root fresh weight exactly, and thus RWC-calculations of roots were not satisfactory. It is possible that these difficulties arose from adherent water and/or water that had entered the intercellular space when the roots were washed prior to the measurements. Fig. 36 demonstrates these problems using the results of a water stressed plant of nutrient treatment NPK as an example: Calculation of fresh weight at full turgor (FW100) of root samples was performed considering different numbers of weight/pressure-pairs (method described in appendix A). Inset b demonstrates that calculated FW100 of the root samples varied to a great extent depending on which points were considered for the regression. These differences in calculated FW100 affected the respective PV curves substantially. Because the selection of the points which were used for the regression could not be performed in a satisfactory way, no analysis of parameters derived from PV curves of root samples was performed.

Pressure volume curves of leaf samples on the other hand could be established without the problems described for root samples (Fig. 36, inset a and solid PV curve). Fig. 37 shows water potential isotherms of well watered and water stressed leaf samples of nutrient treatment NPK as examples.

In leaves, water stress exerted a major influence on all parameters derived from PV curves. The effects of water stress seemed to be dependent on the nutritional status of the plants. In all nutrient treatments except treatments P and PK, osmotic potentials at full and zero turgor were significantly lower in water stressed than in well watered plants (Fig. 38 and 39). The difference between OP100 of well watered and water stressed plants is usually looked at as the degree of osmotic adjustment in water stressed plants (Turner and Jones 1980). Leaves of nutrient treatments P and PK showed no osmotic adjustment at all (Fig. 40). The degree of osmotic adjustment of N-fertilized treatments except treatment N was considerably higher than in N-deficient treatments and reached values of 0.1 to 0.17 MPa. The values of osmotic adjustment in treatments 0, K and N were in the range of 0.04 to 0.05 MPa. These results correspond with the measurements of osmotic potentials at different harvests performed with a vapor pressure osmometer: The comparison of $\psi_{st}$ between well watered and water stressed plants of respective nutrient treatments resulted in similar degrees of 'osmotic adjustment' as determined from PV curve analysis (see Fig. 47, 48 p. 74, 75).

Relative water content at zero turgor (RWC0) was decreased under conditions of drought stress in all N- and K-fertilized treatments except treatment PK (Fig. 41). In treatments K, NK and NPK, water stress decreased the values of RWC0 to a greater extent than in the other nutrient treatments. Plants of these three treatments showed lowest RWC0-values under conditions of limited soil water supply.
Fig. 36: Pressure-volume curves of leaf (solid line) and root (dashed lines 1, 2 and 3) samples of a water stressed plant of nutrient treatment NPK. Calculation of FW100 was performed according to Kubiske and Abrams (1990).
Inset a: Calculation of FW100 for the leaf sample using the first 10 points measured for regression.
Inset b: Calculation of FW100 for the root sample using the first 6 points measured (1), the first 10 points measured (2) and points 5 to 10 measured (3) for regression, respectively.
Fig. 37: Pressure-volume curves of leaf samples of well watered (WW, dashed lines, hollow circles) and water stressed (WS, solid lines, filled triangles) plants of nutrient treatment NPK. Measurements of 3 samples of 3 different plants were used to establish each PV curve. OP100: Osmotic potential at full turgor / OP0: Osmotic potential at zero turgor
Fig. 38:
Osmotic potential at full turgor (OP100) in leaves of well watered and water stressed plants of different nutrient treatments in experiment B.

Fig. 39:
Osmotic potential at zero turgor (OP0) in leaves of well watered and water stressed plants of different nutrient treatments in experiment B.

Fig. 40:
Osmotic adjustment (calculated as the difference in OP100 between well watered plants (ψs > -0.08 MPa) and water stressed plants (ψs < -0.38 MPa)) in leaves of water stressed plants of different nutrient treatments in experiment B.

Fig. 41:
Relative water content at zero turgor (RWC0) in leaves of well watered and water stressed plants of different nutrient treatments in experiment B.
Water stress decreased the bulk modulus of elasticity ($e$) in all nutrient treatments significantly (Fig. 42). Treatments with high values of $e$ in well watered plants showed more important decreases in $e$ under conditions of water stress; at low $\psi_r$, $e$-values of different nutrient treatments were more similar than at adequate water supply.

Fig. 42:
Bulk modulus of elasticity in leaves of well watered and water stressed plants of different nutrient treatments in experiment B.

Capacitance was higher under conditions of limited water supply in all nutrient treatments (Fig. 43). Increases in capacitance due to water stress were less distinct in treatments 0, N and NP than in other treatments.

Fig. 43:
Capacitance in leaves of well watered and water stressed plants of different nutrient treatments in experiment B.

The determination of apoplastic water content was not satisfactory due to a very high variability within replications. Calculated values for apoplastic water content ranged from 10 to 27 % (mean: 17.0 %; SD: 5.8 %) in well watered plants and from 5 to 32 % (mean: 20.9 %; SD: 10.4 %) in water stressed plants. In the nutrient treatments NPK, K and 0, apoplastic water content was lower in water stressed than in well watered plants. In the other nutrient treatments, apoplastic water content of water stressed plants was higher as compared to well watered plants. Problems in evaluating apoplastic water content have been described by Tyree and Richter (1982) and Turner (1987): They concluded that the estimation of the apoplastic water content cannot be made with a high degree of accuracy from PV curve analysis.
Differences in the parameters derived from PV curves among nutrient treatments were smaller than between well watered and water stressed treatments and depended on the water regime. Nevertheless, clear effects of N-, P- and K-fertilization could be observed. In well watered treatments, OP100 and OP0 were higher in N-fertilized than in N-deficient plants, whereas under conditions of drought stress, OP100 and OP0 were lower in N-fertilized than in N-deficient plants. This can explain, to some extent, the big differences in OP100 and OP0 between well watered and water stressed plants of N-fertilized treatments. The higher degree of osmotic adjustment in N-fertilized plants is linked (to a certain extent) with this phenomenon as well. Under conditions of limited water supply, relative water content at zero turgor was significantly lower in N- and K-fertilized than in N- and K-deficient plants. In well watered treatments, no consistent influence of N-, P- or K-fertilization on RWC0 could be observed. Under conditions of water stress, the values of the bulk modulus of elasticity were significantly lower in K-fertilized than in K-deficient plants. In well watered treatments, plants with adequate N-fertilization showed lowest values of bulk modulus of elasticity. Capacitance was increased by K-fertilization at low soil water potentials. With adequate water supply, however, N-fertilization tended to increase the values of capacitance. However, all effects of different nutrient treatments on the parameters derived from PV curves were of modest importance as compared to the effects of different water regimes.
4.3 DISCUSSION

4.3.1. Relation between plant water potential and soil matric potential

Predawn water potentials of roots (and partly of shoots) were higher than soil matric potentials in all nutrient treatments except treatments K, N and NK (Fig. 27). There are mainly two reasons that could explain this positive water potential gradient between the soil and the plant:

1) During the night, when stomata are closed, the tension in the xylem can be very small. In fact, the hydrostatic pressure in the xylem can even become positive, reflecting water movement into the root xylem in response to the osmotic water potential component of the xylem sap (Nobel 1983; see Fig. 44). This positive hydrostatic pressure (termed 'root pressure') is responsible for guttation. The positive hydrostatic pressure in the xylem may cause mass flow of water and solutes in the direction of least resistance, i.e. upwards in the xylem. During the upward flow, solutes are removed from the xylem sap by cells adjacent to the xylem. This process increases the osmotic potential $\psi_x$ of the xylem sap. The gain in $\psi_x$ can exceed the loss in pressure potential during the hydraulic flow, resulting in a net gain of water potential in such a situation (Oertli 1971; Fig. 44). The gain in water potential associated with the phenomenon of root pressure might therefore explain (at least partly) plant water potentials higher than soil matric potentials.

It has to be noted, however, that in drying soils, water movement (to the roots) can be greatly restricted. Schmidhalter (1986) determined the hydraulic conductivity (k) of the soil used in my experiments for $\psi_s$-values $0 > \psi_s > -0.1$ MPa as $k(\psi_s) = 1208/(229+\psi_s^{1.355})$. At $\psi_s = 0.1$ MPa, the hydraulic conductivity approximated 1 mm day$^{-1}$. Because water movement to the roots is greatly restricted in drying soils, strong consequences of the phenomenon of root pressure on the difference between $\psi_s$ and $\psi_{plan}$ are only to be expected under conditions of adequate water supply (Salisbury and Ross 1985). Therefore, a second explanation for the phenomenon of plant water potentials higher than soil matric potentials might be of importance:

2) Gravimetric determination of soil matric potential by weighing pots or bulk soil samples provides an average $\psi_s$ throughout the whole soil volume. However, the soil in a pot does not dry uniformly: Soil layers close to the surface and soil close to roots exhibit lower $\psi_s$ than other sections. Roots on the other hand can actively penetrate into still moist regions in the soil. Such roots are very efficient in taking up water from drying soils (Sharp 1985; Barraclough et al. 1989; Schmidhalter et al. 1992a). Water potential of roots (and to a lesser extent of leaves) can approximate to $\psi_s$ during the dark period, since stomata are closed.
Active uptake of nutrients and release of nutrients into the apoplast of the stele decreases the osmotic potential $\psi_\pi$ in the apoplast of the stele.

2. Low osmotic potential in the apoplast of the stele induces water influx into the stele, hereby increasing the hydraulic pressure $\psi_p$ in the stele.

3. Positive hydraulic pressure in the xylem induces mass flow of solutes and water in the direction of least resistance (upwards the xylem).

4. Active solute uptake by cells adjacent to the xylem increases the osmotic potential of the xylem sap. If this increase in $\psi_\pi$ exceeds the decrease in $(\psi_p - \psi_\pi)$, a net gain in water potential of the xylem sap is achieved.

$\psi_\pi$: osmotic potential

$\psi_p$: pressure potential

$\psi_\eta$: gravimetric potential

$\psi$: total water potential

$\psi = \psi_\pi + \psi_p + \psi_\eta$
The results presented suggest that water potentials of roots approximate to the highest $\psi_r$ of soil accessible to the roots. Schmidhalter et al. (1992a) reported similar results from experiments with young maize plants growing at spatially variable soil matric potentials. They also concluded that during the night, roots tend to equilibrate with the zones in the soil having the highest $\psi_r$.

Root growth and $\psi_s \leftrightarrow \psi_{plan}$-relations corresponded quite well in the two experiments (see Fig. 6, 9 and 27): Plants of nutrient deficient treatments generally showed enhanced root growth at early growth stages as compared to fertilized plants; these nutrient deficient plants revealed higher $\psi_r$ than $\psi_s$ at all harvests, indicating that roots of nutrient deficient plants probably penetrated more into still wet zones of the soil than roots of adequately fertilized plants. Water stressed plants, that showed enhanced root growth at later growth stages (e.g. plants of treatments N and NP), exhibited clearly higher $\psi_r$ than $\psi_s$ at later harvests only. Plants with poor root growth (e.g. treatment NK) showed lower $\psi_r$ than $\psi_s$ at all harvests. It can be assumed that differences in the dynamics of roots in exploring the soil volume were responsible for the differences in the relation between soil matric potentials and plant water potentials among different nutrient treatments.

These results suggest that the water status of a plant at predawn (water potentials, osmotic and turgor potential components as well as osmotic adjustment of roots and leaves) might not be related directly to values of soil matric potentials determined from the bulk soil volume. When analyzing predawn plant water potentials, the water potential of roots might reflect the soil matric potential, that is actually decisive for predawn plant water relations, more accurately than measurements of bulk $\psi_s$. During the dark period, the water potential of the roots will tend to equilibrate with the soil zones accessible for the roots that have the highest $\psi_r$. Therefore, it might be preferable to relate predawn plant water relations to $\psi_r$ rather than to measurements of bulk $\psi_s$.

Fig. 45 a and b demonstrate how the interpretation of plant water potential measurements can be affected depending on whether plant water relations are related to bulk $\psi_s$ or to $\psi_r$. Root water potential components of treatments NK (difference $\Delta(\psi_r-\psi_s)$ always $> 0$) and NPK (difference $\Delta(\psi_r-\psi_s)$ always $< 0$) are shown in relation to $\psi_s$ (Fig. 45 a) and $\psi_r$ (Fig. 45 b). It can be seen that the effect of a certain intensity of 'water stress' (referred to the actually decisive $\psi_s$ for predawn water relations) on plant water potential components ($\psi_{sw}$ and $\psi_{sr}$) may be veiled, if plant water relations are related to measurements of bulk $\psi_s$. Plants of treatment NK seemed to have lower $\psi_{sr}$ than plants of treatment NPK over the whole stress range examined, if plant water potential components were related to bulk $\psi_s$. However, if plant water potential components ($\psi_{sw}$ and $\psi_{sr}$) were related to $\psi_r$, plants of treatment NPK revealed lower $\psi_{sr}$ at a particular stress intensity than plants of treatment NK. Thus, the decrease in $\psi_{sr}$ and the
resulting effects on turgor pressure at a certain intensity of water stress were overestimated in treatment NK, but underestimated in treatment NPK when plant water potential components were related to bulk $\psi_t$.

![Diagram](image)

Fig. 45a and b: Water potential (triangles), osmotic potential (squares) and turgor potential (diamonds) of roots in relation to a) soil matric potential and b) root water potential. Nutrient treatments NPK (filled symbols, solid lines) and NK (hollow symbols, dashed lines).

It can be assumed that relating plant water relations to measurements of bulk $\psi_s$ and to $\psi_t$ respectively would lead to different conclusions on how plant water relations are affected by water stress. Therefore, analysis of the effects of water stress on plant water relations was not only performed based on $\psi_s$, but also in relation to $\psi_t$. For this purpose, classes of plants harvested at similar $\psi_t$-ranges were created ("$\psi_t$-classes") according to the creation of $\psi_s$-classes.

If plant water relations were related to $\psi_t$, the effects of different nutrient treatments on plant water relations of plants subjected to water stress showed the same tendencies as if plant water relations were related to $\psi_t$. Certain differences in the results, however, could be observed depending on whether plant water relations were related to measurements of bulk $\psi_s$ or to $\psi_t$. These differences mainly concerned the stress ranges at which different nutrient treatments affected water stress induced changes in plant water relations: Relating plant water relations to $\psi_s$ resulted in lower values of $\psi_s$ and $\psi_{ps}$ in K-fertilized than in K-deficient plants at all $\psi_t$-ranges (Fig. 34); if plant water relations were related to $\psi_t$, however, these effects of K-fertilization on $\psi_t$ and $\psi_{ps}$ were only significant at $\psi_t$-values $> -0.16 \text{ MPa}$. In contrast, the effects of N-fertilization on $\psi_{st}$, on $\psi_{sr}$ and on $\psi_{pr}$ (see Fig. 32 and 34) were clearly more distinct at high intensities of water stress ($\psi_t < -0.16 \text{ MPa}$), if plant water potential components were related to $\psi_t$ instead of $\psi_s$. These findings that N-fertilization affected $\psi_{st}$, $\psi_{sr}$ and $\psi_{pr}$ mainly
under conditions of water stress, correspond with the results of the analysis of PV curves: N-fertilization decreased OP100 and OP0 in water stressed plants only (Fig. 38, 39). If plant water relations were related to \( \psi_r \), the difference between \( \psi_r \) and \( \psi_l \) was significantly lower in P-fertilized than in P-deficient plants (Fig. 46); if plant water potentials were related to \( \psi_r \) only a tendency of lower differences between \( \psi_r \) and \( \psi_l \) in P-fertilized than in P-deficient plants was observed.

![Graph](image)

The phenomenon of 'root pressure' mainly occurs in plants growing under adequate water supply (Salisbury and Ross 1985). Under conditions of water stress, limited water availability might restrict 'root pressure' to a great extent. Additionally, Schmidhalter et al. (1992a) demonstrated that even during the day leaf water potentials may be higher than average \( \psi_r \) in the rooting volume; under conditions of high transpiration, however, 'root pressure' will be of negligible importance. Therefore, under conditions of limited water supply, higher plant water potentials than soil matric potentials are probably mainly caused by water uptake of roots in still wet zones of the rooting volume. If water uptake in still moist zones of the soil occurs, 'root pressure' could additionally contribute to higher plant water potentials than soil matric potentials.

### 4.3.2 Effects of N-, P- and K-fertilization on plant water potentials

Roots of all nutrient treatments clearly revealed 'osmotic adjustment' (Fig. 31, 32). Root turgor could be maintained at values > 0.5 MPa over the whole range of \( \psi_r \) examined in all treatments (Fig. 31, 32). This was due to a significant decrease in \( \psi_r \) with declining \( \psi_r \) (or \( \psi_l \)). In treatments with combined N- and P-fertilization, a distinct increase in root turgor at the onset of water stress could be observed (Fig. 31). N- as well as P-fertilization exerted positive effects on root
turgor in plants growing under conditions of limited water supply: N-fertilization significantly increased the plants' ability to 'adjust' osmotically (Fig. 32). P-fertilized plants showed higher $\psi_r$-values at all $\psi_r$-ranges (Fig. 32). Thus, a combined N- and P-fertilization clearly increased root turgor at low $\psi_r$.

The comparison of root water potential components with root growth showed a high correlation in experiments A and B: Under conditions of water stress, both N- and P-fertilization increased root growth, whereas K-fertilized plants revealed reduced root growth as compared to K-deficient plants (Fig. 10); root turgor of N- and P-fertilized plants was significantly increased as compared to N- and P-deficient plants, whereas K-fertilized plants had lower $\psi_r$ than K-deficient plants under conditions of drought stress (Fig. 32). Root growth of P-deficient plants was reduced by water stress to a much greater extent than in high-P plants (Fig. 19); P-fertilized plants showed higher root turgor potentials than P-deficient plants under conditions of water stress (Fig. 32). Plants with combined N- and P-fertilization had higher absolute root dry weights in water stressed than in well watered treatments (Fig. 19); in treatments NP and NPK, significant increases in root turgor at the onset of water stress could be observed (Fig. 31).

In contrast to osmotic potentials of roots, osmotic potentials of leaves did not decrease sufficiently to maintain turgor ($\psi_{pl}$) (Fig. 33). Leaf osmotic potentials of N- (and to a lesser extent K-) fertilized plants were significantly lower than in N- and K-deficient plants over the whole $\psi_r$-range examined (Fig. 33, 34). The ability for osmotic adjustment was significantly increased by N-fertilization (see Fig. 48 p. 75). In N- and K-fertilized plants, however, $\psi_r$ was significantly lower at a certain $\psi_r$ than in N- and K-deficient plants (Fig. 34). Similar results have been found in several other studies (Arneke 1981; Mengel and Arneke 1982; Tesha and Eck 1983; Bennett et al. 1986; Premachandra et al. 1990a). This reduction of $\psi_r$ at high N- and K-levels was not only due to lower $\psi_r$ in all $\psi_r$-ranges (Fig. 35), but also to higher differences between $\psi_r$ and $\psi_{pl}$, particularly in N-fertilized plants (Fig. 30). Because the degree of 'osmotic adjustment' even in N- and K-fertilized leaves was very small, only the strong effects of N- and K-fertilization on $\psi_r$ were reflected in $\psi_{pl}$. Thus, leaf turgor-values were significantly lower in N- and K-fertilized than in N- and K-deficient plants at all $\psi_r$-ranges (Fig. 35). If leaf water potential components were related to $\psi_r$, these negative effects of N- and K-fertilization on $\psi_r$ were less significant; significant differences in $\psi_{pl}$ between K-fertilized and K-deficient plants could only be observed at $\psi_r$-values $> -0.16$ MPa.

In contrast to N- and K-fertilization, adequate P-nutrition led to higher $\psi_r$ at all $\psi_r$-ranges than in P-deficient plants (Fig. 33, 34). Since no significant effects of P-fertilization on $\psi_{pl}$ could be observed (Fig. 34), this effect was clearly reflected in the values of $\psi_{pl}$, which were significantly higher in P-fertilized than in P-
deficient plants at all $\psi_r$-ranges (Fig. 33, 34). This effect of P-fertilization persisted, even if leaf water potential components were related to $\psi_r$. Premachandra et al. (1990b) similarly reported higher $\psi_{pl}$ in plants growing at increased P-levels. Nevertheless, $\psi_{pl}$ of P-fertilized plants decreased steadily with increasing intensity of water stress, because no sufficient osmotic adjustment took place (Fig. 33).

The comparison of shoot growth and development (particularly in terms of leaf area) with the observed effects of water stress on leaf water potential components showed good correspondence: N-fertilized plants encountered high reductions in shoot growth when water stress was imposed (Fig. 15); $\psi_{pl}$ of N-fertilized plants was lower than in N-deficient plants at all $\psi_r$-ranges (Fig. 34). In P-fertilized treatments, water stressed plants experienced no or significantly smaller (relative) reductions in shoot growth than in low-P treatments (Fig. 16); $\psi_{pl}$ of P-fertilized plants was always higher than in low-P plants (Fig. 34). These results suggest a high dependency of growth on turgor pressure, which is generally looked at as an ultimate prerequisite for cell enlargement and growth.

It has to be noted, however, that shoot growth under conditions of limited water supply was increased by N- as well as by P-fertilization as compared to N- and P-deficient treatments (Fig. 6). Highest productivity under both water regimes was observed in treatments NP and NPK (Fig. 2, 5). Additional N was the most important factor increasing shoot growth under conditions of sufficient water supply (Fig. 2). However, $\psi_{pl}$ of N-fertilized plants was significantly lower than $\psi_{pl}$ of N-deficient plants in both well watered and in water stressed treatments (Fig. 34). These results suggest that other factors besides turgor pressure affected cell expansion and shoot growth.

In chapter 3, the thesis was postulated that both quantitative and qualitative nutrient supply might constrain cell enlargement and plant growth. 'Specific' effects of nutrients in metabolic processes might cause the supply of such nutrients to be a limiting factor for growth. The positive effects of N-fertilization on shoot growth in spite of its negative effect on $\psi_{pl}$ might confirm this hypothesis.

The comparison of root turgor with root growth in my experiments further supports this thesis: Although root turgor was maintained at values > 0.5 MPa in all nutrient treatments even at low $\psi_r$ (Fig. 31), root growth was affected differently by water stress in the different nutrient treatments (Fig. 17, 19). Both N- and particularly P-fertilization increased root growth at low $\psi_r$ significantly (Fig. 10). Enhanced root growth relative to shoot growth under conditions of limited soil water supply required adequate N- and P-nutrition (Fig. 20). These differences in root growth among different nutrient treatments in spite of full turgor maintenance in all nutrient treatments lead to the conclusion that other ('specific') effects of N and P were additionally responsible for increased root growth under conditions of drought stress.
4.3.3 Osmotic adjustment

The extent of 'osmotic adjustment' in leaves of plants growing at different nutrient regimes was similar whether calculated from $\psi_e$-measurements at the different harvests (difference in $\psi_{st}$ between well watered and water stressed plants) or whether derived from the analysis of PV curves (difference in OP100 between well watered and water stressed plants)(Fig. 47, 48). Values of osmotic adjustment calculated using the two different methods differed by less than 0.03 MPa (0.06 MPa in treatment NPK). Predawn measurements of osmotic potentials may therefore provide a good basis for comparisons of the degree of osmotic adjustment in water stressed plants. This method is much less complicated than the establishment of PV-curves and therefore represents a simple technique to compare the degree of osmotic adjustment in water stressed plants.

Fig. 47: Osmotic adjustment in leaves of plants grown at different nutrient regimes
a) calculated from $\psi_e$-measurements at different harvests as the difference in $\psi_{st}$ between well watered plants ($\psi_s > -0.08$ MPa) and water stressed plants ($\psi_s < -0.38$ MPa): $\psi_{\text{ww}} - \psi_{\text{ws}}$

and

b) derived from the analysis of PV curves as the difference in OP100 between well watered plants ($\psi_s > -0.08$ MPa) and water stressed plants ($\psi_s < -0.38$ MPa): $\text{OP100}_{\text{ww}} - \text{OP100}_{\text{ws}}$
N-fertilization increased the ability for osmotic adjustment of leaves (and roots). This could be observed both in measurements of osmotic potentials at different harvests as well as in the analysis of PV curves. N-fertilized plants showed lower \( \psi_m \) at all \( \psi_r \)-ranges than N-deficient plants, particularly at low \( \psi_r \) (Fig. 34). Osmotic adjustment of water stressed plants was increased at adequate N-levels (Fig. 48). Lower osmotic potentials and enhanced osmotic adjustment at high N-levels have been reported in several other studies (Yambao and O'Toole 1984; Bataglia et al. 1985; Bennett et al. 1986; Morgan 1986; Premachandra et al. 1990a). The increased solute content in high-N compared to N-deficient plants can be mainly attributed to the positive effects of N-fertilization on photosynthetic production rather than to direct osmotic effects of N-compounds. Several studies have demonstrated that soluble sugars are the major contributors to osmotic adjustment (Munns et al. 1979; Michelena and Boyer 1982; Morgan 1984a; Morgan 1984b; Barlow 1986; Kriedemann 1986). Sugar accumulation accounted for 70-100 % of osmotic adjustment in water stressed wheat seedlings (Munns and Weir 1981). In maize (cv Issa) seedlings, almost 100 % of the osmotic adjustment both in mature and growing tissues could be attributed to soluble sugar accumulation (Evéquoz 1993). Even K, the inorganic nutrient thought to be most effective in osmotic relations of plant tissues, contributed little or nothing to osmotic adjustment in water stressed plants (Wilson and Ludlow 1983; Barlow 1986; Sharp et al. 1990; Evéquoz 1993; Fig. 48). However, elevated CO\(_2\)-concentrations and increased photosynthetically active radiation (both enhancing photosynthesis) can increase the ability of water stressed plants to adjust osmotically (Morgan 1984b).

Adequate N-nutrition generally exerts positive effects on photosynthate production even under conditions of limited water supply. N-fertilization increases photosynthetic capacity (Wong et al. 1979; Huber et al. 1989) and may increase cell membrane stability in water stressed plants (Premachandra et al. 1990a). In addition, high-N plants might close their stomata at lower (soil) water potentials than N-deficient plants (Ishihara et al. 1979; Radin and Parker 1979b; Radin and Ackerson 1981; Radin et al. 1982; Sharpley and Reed 1982; Radin 1984; Bataglia et al. 1985; Radin et al. 1985; Bennett et al. 1986; Jones et al. 1986). Radin et al. (1985) reported 'source limited conditions' with regard to photosynthate supply in water stressed cotton leaves being reflected in osmotic potentials under conditions of N-deficiency: In N-deficient plants, the osmotic potential did not decrease during the day as in N-fertilized plants, because sink demands exceeded the ability of the sources to supply them and therefore drained the sources of available solutes. It has been demonstrated that N-fertilization and soluble sugar contents in plant tissues are positively correlated (Bataglia et al. 1985; Premachandra et al. 1990a). Thus, N-fertilization can improve the supply of photosynthates (for solute accumulation and growth processes) under conditions of limited water supply, all the more so because photosynthesis is less susceptible to low water availability than other processes as e.g. cell expansion (Hsiao 1973; Begg and Turner 1976; Boyer 1976; Sharp and Davies 1979; Sharp and Davies 1985; Barlow 1986; see chapter 3).

In plants growing at low $\psi_s$, P-fertilization decreased osmotic potentials of roots (Fig. 32). Root growth under conditions of water stress was significantly enhanced by adequate P-nutrition (Fig. 10, 19). Premachandra et al. (1990b) reported that leaf osmotic potentials were decreased and osmotic adjustment was increased in P-fertilized as compared to P-deficient maize plants. P plays an important role in the regulation of sugar metabolism (see e.g. Marschner 1986). At high P-levels, photosynthate translocation into active sink tissues is increased, because P plays an important role in the process of phloem loading in source tissues (Setter 1990). In addition, adequate P-nutrition can suppress starch accumulation and thus inhibition of photosynthesis usually associated with water stress (Ackerson 1985; Lawlor and Leach 1985). Ackerson (1985) showed that P-fertilization increased the concentration of soluble sugars in water stressed cotton plants.

Roots of water stressed plants represent possible sink tissues for photosynthates, since root turgor can be maintained even at low soil water potentials (Fig. 31, 32). Provided that enough photosynthates are available, P-fertilization can increase the transport of soluble sugars into these sink tissues. Therefore, adequate P-nutrition might be an important prerequisite for continued root growth under conditions of limited water supply.
K-fertilization tended to reduce osmotic potentials of roots and shoots under conditions of mild water stress. Similar results have been reported by several other authors (Beringer and Troudenier 1978; Arneke 1981; Mengel and Arneke 1982). It has to be pointed out, however, that important decreases in osmotic potentials due to K-fertilization were mostly reported from experiments using hydroponic cultures rather than from experiments using soil as a growth substrate. Authors working with soil as a substrate reported only small or no effects of K-fertilization on plant water potentials, particularly at low $\psi_s$ (Catsky et al. 1987; references ibidem). In my experiments, the influence of K-fertilization on osmotic potentials was more obvious under conditions of mild water stress than at very low $\psi_s$. This lack of influence of K-fertilization on osmotic adjustment in plants grown in soils under conditions of (severe) water stress might be caused by the fact that K-uptake can be considerably restricted at low $\psi_s$ (Viets 1972; Kuchenbuch et al. 1986; Dionne et al. 1987).

Although N- (and to a lesser extent K-) fertilization decreased osmotic potentials of leaves (Fig. 34), this reduction was not sufficient to maintain turgor under conditions of water stress (Fig. 33). It has to be noted, however, that the measurements of osmotic potentials in my experiments were restricted to mature tissues. Numerous studies have demonstrated that osmotic adjustment of growing tissues may be much higher than in fully expanded tissues (Westgate and Boyer 1985; Barlow 1986; Turner 1986; Hsiao and Jing 1987; Munns 1988; Sharp et al. 1990). Osmotic adjustment in mature leaf blades of maize (cv Issa) was found to be in the order of 0.2 MPa, whereas in growing regions of the same leaf adjustments of up to 0.6 MPa could be observed (Evéquoz 1993).

Nevertheless, even a small extent of solute accumulation may have positive effects on plant growth under conditions of limited water supply. Munns (1988) stated that the importance of solute increases in tissues of plants undergoing water stress may be in maintaining cell volume and metabolite concentrations above a critical value (cf. Kaiser 1982; Flower and Ludlow 1986). McCree (1986) found no evidence for additional metabolic costs (in terms of whole-plant carbon balance) despite active accumulation of organic osmotica; thus, this solute accumulation could represent a very energy-efficient device for alleviation of drought stress (Kriedemann 1986). Furthermore, solute accumulation at low water potentials may enhance resumption of growth upon stress relief (Kriedemann 1986). Fig. 49 a and b demonstrate this effect of solute accumulation using treatments NPK (little 'osmotic adjustment') and PK (no osmotic adjustment) as examples. The diagrams combine data measured at the different harvests in experiments A and B ($\psi_s$, $\psi_{sl}$ and $\psi_{ps}$) with results of the analysis of PV curves from experiment B. Hollow arrows demonstrate how water potentials changed when plants were subjected to increasing water stress. Solid arrows display the development of water potentials upon stress relief (increase in $\psi_s$). Fig. 49 a
Fig. 49 (a, b): Development of leaf water potentials in nutrient treatments NPK (a; little osmotic adjustment) and PK (b; no osmotic adjustment) with increasing intensity of water stress (hollow arrows) and upon stress relief (solid arrows). Dashed lines represent water potential isotherms (derived from PV curves) of well watered, solid lines those of water stressed plants, respectively. Points denote leaf water potentials of plants measured at different harvests with declining $\psi$, in experiments A and B.
shows that even a relatively small decrease in $\psi_x$ (< -0.2 MPa), which is not sufficient to maintain turgor, will increase turgor upon stress relief to levels higher than in not 'adjusted' plants. Solutes accumulated during a stress period are not fully dissipated immediately after rewatering: Depending on the rate and intensity of the water stress, even 15 days after rewatering only incomplete dissipation of accumulated solutes has been observed (Morgan 1984b). Enhanced resumption of leaf growth following stress relief has been reported by several authors (Jones and Turner 1978, 1980; Rawson and Turner 1982; Palta 1984). In addition, increased solute accumulation could enhance growth not only after rewatering, but also during the recovery of plant water potentials within diurnal cycles. However, if no decrease in $\psi_{ml}$ occurs (as in treatment PK, Fig. 49 b), no increase in turgor and thus no enhanced resumption of growth upon stress relief will occur.

4.3.4 Difference between root and leaf water potentials

The difference between root and leaf water potentials ($\Delta(\psi_r-\psi_l)$) was smaller in P-fertilized than in P-deficient plants (Fig. 46). Because of the smaller $\Delta(\psi_r-\psi_l)$ in P-fertilized plants, $\psi_l$ and thus $\psi_{pl}$ were higher in P-fertilized than in P-deficient plants at a certain value of $\psi_s$ (or $\psi_r$) (Fig. 34). Thus, P-fertilization could enable leaf growth at $\psi_s$ (or $\psi_r$), at which leaf expansion in P-deficient plants was restricted to a great extent (Fig. 6). P-fertilization additionally enhanced root growth of water stressed plants (Fig. 10), hereby facilitating water uptake and thus maintenance of high $\psi_r$-values (Fig. 32). It is therefore concluded that adequate P-nutrition is very important for the maintenance of plant growth under conditions of water stress.

On the other hand, $\Delta(\psi_r-\psi_l)$ was higher in N-fertilized than N-deficient plants, particularly at low intensities of water stress (Fig. 30). Thus, $\psi_l$ (and consequently $\psi_{pl}$) of N-fertilized plants was lower at a certain $\psi_s$ (or $\psi_r$) than in N-deficient plants (Fig. 34); water stress therefore restricted shoot growth of N-fertilized plants to a greater extent than in N-deficient plants (Fig. 15). Similar results have been reported in several other studies (Tesha and Eck 1983; Morgan 1986; Nnoham and Odurukwe 1987; Bennett et al. 1989). Root turgor, however, could be maintained even at low $\psi_s$ (Fig. 31, 32); thus, the roots represented a sink tissue for carbohydrates. Provided that photosynthesis and phloem loading could be maintained (by adequate N- and P-nutrition), photosynthate partitioning from shoots to roots could occur (Turner 1986). This could explain that continued root growth at low $\psi_s$ as well as the enhancement of root growth relative to shoot growth under conditions of water stress required both adequate N- and P-nutrition.
(see chapter 3). 'Osmotic adjustment' of roots was highest in treatments NP and NPK, and root turgor pressure even increased in these two treatments when water stress was imposed (Fig. 31).

The reasons for the differences in $\Delta(\psi_r - \psi_l)$ among different nutrient treatments are not clear. Radin and Eidenbock (1984) and Andersen et al. (1989) have demonstrated that the hydraulic conductivity in tissues of P-fertilized plants was higher than in P-deficient plants. Higher hydraulic conductivity in P-fertilized than in P-deficient plants could therefore be a possible reason for the observed differences in $\Delta(\psi_r - \psi_l)$ between P-fertilized and P-deficient plants.

Water flux from roots to shoots during the dark period of the day could explain the observed differences in $\Delta(\psi_r - \psi_l)$ among different nutrient treatments in an additional way: The extent of the water flux ($J_v$) from roots to shoots in the xylem depends on the hydraulic conductivity ($L_p\star$) and on the gradient in the pressure- and gravitational components of the water potential between roots and shoots ($((\Delta\psi_f + \Delta\psi_g)/\Delta x)$ according to $J_v = -L_p\star(\Delta\psi_f + \Delta\psi_g)/\Delta x$ (Oertli 1971). Since $\psi_r$ and $\psi_l$ were determined using a pressure chamber, $\Delta(\psi_r - \psi_l)$ is equal to $\Delta\psi_p$ between roots and shoots (Scholander et al. 1965). The gravitational water potential component can be neglected in the calculation of the water flow between roots and shoots in my experiments ($\Delta\psi_g = 0.003$ MPa). Therefore, we can approximate the water flux from roots to shoots as $J_v = -L_p\star\Delta(\psi_r - \psi_l)/\Delta x$. Consequently, $\Delta(\psi_r - \psi_l)$ might be affected by both changes in the hydraulic conductivity and changes in the water flux, since $\Delta(\psi_r - \psi_l)/\Delta x = J_v/L_p\star$.

In N-fertilized plants, the decrease in relative water content (RWC) due to water stress is generally more important than in N-deficient plants (Radin and Parker 1979a; Morgan 1986; Fig. 22). Additionally, N-fertilization significantly increased elasticity and capacitance in well watered plants (Fig. 42, 43). High water deficits in leaves (important reductions in RWC), high elasticity of leaf cells, and a high capacitance in N-fertilized plants could therefore lead to a greater water flux from roots to shoots in N-fertilized than in N-deficient plants: When stomata are closed, plants with high elasticity and capacitance will tend to 'refill' the leaf cells experiencing a water deficit. Low osmotic potentials in N-fertilized as compared to N-deficient plants might further enhance water flux into leaf cells of N-fertilized plants. These factors could explain an increased water flux and therefore a bigger $\Delta(\psi_r - \psi_l)$ in N-fertilized than in N-deficient plants. To verify this hypothesis, additional data on elasticity and capacitance of N-fertilized and N-deficient plants with declining $\psi_s$ would be needed.

It is possible that the observed oscillating response of $\psi_r$ to declining $\psi_s$ (Fig. 27) and the 'recovery' of $\psi_l$ and $\psi_{pl}$ in N-fertilized plants at $-0.1 > \psi_s > -0.4$ MPa (Fig. 33) were related to the roots' dynamics in exploring soil volume: A decrease in $\psi_s$ followed by a steep fall in $\psi_{pl\star}$ (particularly in $\psi_l$) might have in-
duced an increase in root growth, enabling the plants to penetrate into still wet zones in the soil. Thus, water uptake was facilitated and plant water potentials recovered to some extent. In N-fertilized plants, the recovery of $\psi_t$ was clearly more distinct than in N-deficient plants. As stated above, leaf growth was inhibited by smaller decreases in $\psi_t$ in N-fertilized as compared to N-deficient plants. Therefore, photosynthate partitioning from shoots to roots and thus enhanced root growth could have been more pronounced in N-fertilized than in N-deficient plants, thus leading to a more distinct 'recovery' of $\psi_t$ and $\psi_{p}$ in N-fertilized than in N-deficient plants. The data for root growth seemed to confirm this hypothesis (Fig. 6a): At the first harvests ($\psi_t > -0.1$ MPa), root dry weight of N-deficient plants was higher than in N-fertilized plants. However, when water stress developed ($\psi_t < -0.1$ MPa, from DAP 16 on), root dry weight of N-fertilized plants was higher than in N-deficient plants. Additionally, root to shoot dry weight ratios of plants growing under conditions of water stress were higher in N-fertilized than in N-deficient treatments (Fig. 20).

4.3.5 Water content and water potentials

Bulk modulus of elasticity ($e$) was significantly lower in water stressed than in well watered plants of all nutrient treatments (Fig. 42). Decreases in $e$ were in the range of 1.8 to 5.3 MPa (-17 to -40 %) in water stressed plants as compared to well watered plants. With adequate K-nutrition, these decreases in $e$ due to water stress were higher than under conditions of K-deficiency. Reports on the effects of water stress on $e$ are controversial: Several authors demonstrated that water stress increased $e$-values of various plants (Brown et al. 1976; Jones and Turner 1978; Karamanos 1984). However, Farah (1979) found lower $e$-values in leaves of water stressed than well watered bean plants. Leaf cells of water stressed plants are usually smaller than in well watered plants. Steudle et al. 1977 demonstrated that small cells may be more elastic than large cells. Ortega (1990) confirmed these findings. This could explain the marked decrease in $e$ in water stressed plants, as it was observed in all nutrient treatments in this study. Low values of $e$ and thus higher elasticity of cell walls in water stressed plants mean that turgor loss with decreasing (relative) water content is lower in stressed than in well watered plants. Therefore, plants with low values of $e$ can endure higher water deficits until their turgor falls to zero (buffering of $\psi_p$ against decreases in RWC). However, the ecological importance of changes in $e$ is still not clear (Tyree and Karamanos 1981). Tyree and Karamanos (1981) and Tomos (1985) concluded that changes in $e$ are less effective in preventing turgor from falling to zero in water stressed plants as compared to osmotic adjustment. Ortega
(1990) stated that although ε plays an important role in plant water relations, the irreversible wall extensibility ϕ and the yield threshold Y play major roles in plant cell growth and the regulation of growth. However, Morgan (1984b) suggested that in cases where turgor maintenance by osmotic adjustment is small (as in the case of maize (cv Issa) leaves), the effects of ε should be accounted for in estimating the contribution of 'osmoregulation' to turgor maintenance.

Capacitance was significantly increased in all nutrient treatments under conditions of water stress (Fig. 43). K-fertilization additionally increased capacitance under conditions of limited soil water supply. In situations, when water uptake from the soil does not balance transpiration of the shoot (e.g. under conditions of high transpiration and limited soil moisture supply), tissues adjacent to the transpirational path ('capacitors') can contribute water to transpiration (Koide et al. 1989). In some cases, 'capacitors' can make significant contributions to transpiration (Nobel 1983; Nobel and Jordan 1983). The loss of water caused by this process decreases RWC (and thus the water potential) of the 'capacitors'. Plant tissues with a high capacitance, however, experience smaller decreases in water potential for a certain loss in RWC than tissues with low capacitance (buffering of \( \psi_{\text{plant}} \) against decreases in RWC). High values of capacitance therefore facilitate maintenance of high water potentials and thus growth processes under conditions of low \( \psi_{\text{p}} \) and high transpiration.

Increases in capacitance and thus decreases in ε in leaves of maize seedlings subjected to water stress represent an adaptation of the plants to conditions of drought stress: Tissues with a high capacitance tolerate a higher degree of dehydration without important decreases in water potential than tissues with low capacitance. Turgor is therefore maintained at higher values for a certain decrease in RWC in adapted (decreased ε) than in not adapted (higher ε) plants. Thus, plants with high capacitance and low ε can maintain growth processes under conditions of water stress when growth of plants with lower capacitance and higher ε is already restricted. Adequate K-fertilization seemed to increase this ability to adjust elastic properties and capacitance to conditions of limited soil water supply.

In well watered treatments, N-fertilized plants manifested lower values of ε and higher capacitance than N-deficient plants (Fig. 42, 43). Similar results from experiments with wheat have been reported by Morgan (1986). Plants with high cell wall elasticity and capacitance are less susceptible to (e.g.) diurnal changes in water potentials. Furthermore, N-fertilization significantly decreased RWC0 in water stressed plants. Additionally, shoot water content was higher in N-fertilized than N-deficient plants in both well watered and water stressed treatments (Fig. 18). Several authors have presented similar results; the low shoot water contents in leaves of N-deficient plants were attributed to an increase of the proportion of cell wall material (Shimshi 1970; Radin and Parker 1979a). More rigid cell walls,
however, could decrease the extensibility of the cell walls. If adequate N-nutrition increases cell wall extensibility, less turgor pressure is required to maintain cell expansion in N-fertilized compared to N-deficient plants.

The positive effects of N-fertilization on $e$, capacitance, and possibly on cell wall extensibility might be a conceivable explanation for the phenomenon that N-fertilization exerted positive effects on shoot and root growth in spite of lower turgor potentials in N-fertilized than N-deficient plants (Fig. 34). In addition, the positive effects of N-fertilization on cell wall rheology ($e$ and extensibility) could considerably facilitate resumption of growth upon relief of water stress or during the night, when water potentials in water stressed plants can recover to some extent.
4.4 SUMMARY

Shoot and root water relations of young maize plants (*Zea mays* L. cv Issa) grown in soil at different levels of N, P and K under well watered and water stressed conditions were examined. Root turgor was maintained at levels > 0.5 MPa due to osmotic adjustment of up to 0.56 MPa even if soil water potential dropped below -0.5 MPa. Leaf turgor, however, decreased with increasing intensity of water stress, since no sufficient osmotic adjustment occurred (< 0.18 MPa). Evaluation of osmotic adjustment by comparing predawn osmotic potentials of well watered versus water stressed plants and calculated as the difference in osmotic potentials at full turgor between well watered and water stressed plants (from pressure-volume curves) gave comparable results.

N-fertilization increased the ability of water stressed plants for solute accumulation and thus for osmotic adjustment, particularly when combined with P-fertilization. These beneficial effects of adequate N-nutrition and combined N- and P-fertilization on osmotic adjustment may be mainly attributed to the positive effects of N- and P-fertilization on photosynthate production and translocation. Even if the extent of osmotic adjustment is not sufficient to maintain turgor pressure at low soil water potentials, solute accumulation can enhance resumption of growth upon stress relief and/or during the recovery of plant water potentials within diurnal cycles.

Under conditions of adequate P-nutrition, the differences in water potentials both between soil and roots and between roots and shoots were reduced as compared to conditions of P-deficiency. Thus, P-fertilized plants showed higher turgor pressures at a given intensity of water stress than P-deficient plants. In N-fertilized plants, the difference between root and leaf water potentials was significantly greater than in N-deficient plants. Therefore, the sensitivity of shoot growth to low soil moisture availability was significantly higher in N-fertilized than in N-deficient plants.

Cell wall elasticity in leaves of water stressed plants was significantly higher as compared to well watered plants. Bulk modulus of elasticity was decreased between 1.8 and 5.3 MPa in water stressed plants ($\psi_s$, approximately -0.4 MPa) as compared to well watered plants ($\psi_s > -0.06$ MPa). Capacitance was significantly higher in water stressed than in well watered plants (+15 to +60 %). Different nutrient treatments affected elasticity and capacitance to a lesser extent than different water regimes. Moreover, the effects of different nutrient treatments on elasticity and capacitance depended on the water regime.
The positive effects of N- and P-fertilization on shoot and root growth could not be explained by their effects on plant water relations solely. Other 'specific' effects of N- and P-nutrition additionally influenced plant growth. The results of my experiments suggest that the supply of (growing) tissues with specific nutrients might become a growth limiting step, particularly under conditions of water stress. This might be due to the fact that cell enlargement and particularly growth of a whole organ cannot be explained as a purely hydraulic/mechanical process. Growth is coupled with numerous metabolic processes needing carbon substrates, energy and specific nutrients, e.g. for the synthesis of new cellular material or for enzyme regulation. Cell metabolism, however, is probably optimized to a narrow range of osmotic and ionic composition and concentration; changes in solute concentration and composition (e.g. water stress-induced changes in anorganic nutrient composition) may therefore restrict cell expansion and growth.

It is therefore concluded that both quantitative and qualitative aspects of nutrient supply are of important influence for sustained plant growth under conditions of drought stress. Positive effects of N- and P-fertilization on shoot and root development of water stressed maize seedlings can be attributed a) to direct and particularly indirect effects of N- and P-nutrition on plant water relations (e.g. on the difference between \( \psi_r \) and \( \psi_i \) or on the degree of osmotic adjustment, respectively) and b) to specific effects of N- and P-nutrition on metabolic processes, as e.g. changes in cell wall rheology, the synthesis of new cellular material, enzyme regulation, or changes in the hormonal status of the plant.
5. CONCLUSIONS

5.1 Interactive Effects of N-, P-, K-Nutrition and Water Stress on the Development of Young Maize Plants

The study presented here describes interactive effects of N-, P- and K-nutrition on the development of young maize plants (5- to 7-leaf stage) grown under conditions of adequate and limited water supply. Shoot and root growth of maize seedlings grown under different nutrient and soil moisture regimes were examined. Water relations of the plants were analyzed and discussed in context with plant growth parameters. It was attempted to determine physiological reasons for the different effects of water stress on root and shoot growth of maize seedlings grown under different nutrient regimes.

The effects of water stress on root and shoot growth of young maize plants were highly dependent on the nutrient supply. N-fertilized plants (adequate N-supply) experienced large reductions in shoot growth under water stress as compared to well watered conditions (Fig. 15). However, shoot growth of water stressed N-fertilized plants was increased as compared to respective N-deficient plants (poor N-supply), particularly under conditions of combined N- and P-fertilization (Fig. 2, 5). In P-fertilized plants (surplus P-supply), the reductions in shoot growth due to water stress were smaller than in low-P plants (adequate P-supply) (Fig. 16), and P-fertilization increased shoot growth under both water regimes (Fig. 5). No significant effects of K-nutrition (K-fertilized treatments: moderate K-supply; low-K treatments: poor K-supply) on shoot growth of maize seedlings could be observed in these experiments (Fig. 5).

The effects of drought stress on root growth mainly depended on the nutrient supply and on plant growth stage. In small plants, (absolute) root growth was increased under conditions of water stress as compared to well watered conditions (Fig. 5, 10). This led to higher root/shoot ratios in water stressed than in well watered plants at all nutrient levels (Fig. 11). Since root growth was strongly correlated with shoot growth, and because N- and P-fertilization enhanced shoot growth under both water regimes, root mass of N- and P-fertilized plants was bigger than in N- and P-deficient plants, particularly under conditions of drought stress (Fig. 5, 10). Roots of K-fertilized plants tended to be smaller than roots of K-deficient plants under both water regimes (Fig. 10). P-fertilization (and to a lesser extent N-fertilization) clearly favored the enhancement of root growth relative to shoot growth under conditions of water stress (Fig. 11).

The positive effects of P-fertilization on root growth under drought stress were more evident in older plants: Root growth of water stressed P-deficient plants
was significantly reduced as compared to respective well watered plants (Fig. 19). In P-fertilized plants, these reductions were much smaller than in P-deficient plants, and root growth of plants growing under combined N- and P-fertilization was increased under water stress as compared to well watered conditions (Fig. 19). In older plants (shoot dry weight > 0.6 g), increases in root/shoot ratios under drought stress required adequate N- and P-nutrition (Fig. 20).

Some of the positive effects of N- and P-fertilization on root and shoot growth of maize seedlings could be attributed to direct and indirect effects on plant water relations. The difference in water potentials between roots and leaves was significantly greater in N-fertilized than in N-deficient plants (Fig. 28, 30). Possibly, shoot growth of high-N plants was hereby reduced at higher soil water potentials than in N-deficient plants. Increased sensitivity of shoot growth to limited soil moisture conditions at high N-levels has been reported in several other studies and was also observed in these experiments (Fig. 15). Root growth on the other hand might be favored by an increase in the difference between root and leaf water potentials. If shoot growth is restricted, but root turgor is maintained (> 0.5 MPa; Fig. 31), roots might represent sinks drawing available photosynthates from the shoot. This could lead to an enhanced carbon partitioning from shoots to roots under conditions of drought stress (Fig. 24).

In P-fertilized plants on the other hand, the differences in water potentials both between the soil and roots and between roots and leaves were smaller than in P-deficient plants (Fig. 46). Therefore, P-fertilized plants showed higher turgor pressures at a certain intensity of water stress than P-deficient plants (Fig. 32, 34). Thus root and shoot growth could be maintained at lower \( \psi_s \) in P-fertilized than in P-deficient plants (Fig. 21). Since root growth is highly correlated with shoot growth, maintenance of shoot growth under conditions of water stress can also favor root growth. Thus, these \( (\text{direct}) \) effects of N- and P-nutrition on plant water relations can partly explain the positive effects of N- and P-fertilization on growth of water stressed maize seedlings.

N-fertilization enhanced the ability for osmotic adjustment of water stressed plants (Fig. 48). This effect of N-fertilization was particularly pronounced in treatments with combined N- and P-fertilization (Fig. 47). The beneficial effects of adequate N-nutrition and combined N- and P-fertilization on osmotic adjustment may be mainly attributed to the positive effects of N and P on photosynthetic production and translocation, because soluble sugars have been shown to contribute almost solely to osmotic adjustment in water stressed plants. Even if the degree of osmotic adjustment in leaves was not sufficient to maintain turgor pressure at low \( \psi_s \), solute accumulation might enhance resumption of growth upon stress relief and/or during the recovery of plant water potentials within
diurnal cycles (Fig. 49). The increased ability for osmotic adjustment of N- and P-fertilized plants may be attributed to the positive effects of N- and P-fertilization on photosynthesis and photosynthate translocation; it therefore represents an indirect effect of N and P-nutrition on plant water relations.

However, the positive effects of N- and P-fertilization on shoot and root growth could not be explained by effects on plant water relations solely. Under water stress, shoot growth was increased by N- as well as by P-fertilization as compared to N- and P-deficient treatments (Fig. 5), and additional N was the most important factor observed to increase shoot growth of well watered plants (Fig. 2). However, $\psi_{pl}$ of N-fertilized plants was significantly lower than $\psi_{pl}$ of N-deficient plants in both well watered and in water stressed treatments (Fig. 34). Although root turgor was maintained at values > 0.5 MPa in all nutrient treatments even at low $\psi_s$ (Fig. 31), root growth was differently affected by water stress in the different nutrient treatments (Fig. 17, 19). These results suggest that other than the effects of N- and P-nutrition on plant water relations (turgor pressure) additionally affected shoot and root growth of maize seedlings.

Many recent studies suggested that other factors than water relations can impair plant growth under conditions of drought stress. My experiments demonstrated that, e.g., adequate N-nutrition increased cell wall elasticity and capacitance in well watered plants. K-fertilization had the same effects under conditions of limited water supply. Significantly elevated shoot water contents under both water regimes in N-fertilized plants might suggest higher extensibility of cell walls in high-N than in N-deficient plants; low shoot water contents have often been attributed to an increased proportion of cell wall material and thus more rigid cell walls. Such effects of different nutrient treatments on $e$, capacitance and cell wall yielding properties confirm the conclusion that 'specific' effects of nutrients on cell metabolism probably affect plant growth under both well watered and water stressed conditions in addition to effects on plant water relations. The supply of (growing) tissues with specific nutrients might therefore become a growth limiting step, particularly under conditions of water stress.

This conclusion is confirmed by the fact that cell enlargement and especially growth of a whole organ cannot be explained as a purely hydraulic/mechanical process. Growth is coupled with numerous metabolic processes needing carbon substrates, energy and specific nutrients, e.g. for the synthesis of new cellular material or for enzyme regulation. Whereas carbon substrates and energy might be readily available, inorganic nutrients as N, P, K or Mg have to be imported. This import of inorganic nutrients is a slow process, which is definitively restricted under conditions of drought stress. However, regulation of metabolic processes (e.g. enzyme regulation) depends largely on specific control ions, and cell meta-
holism is probably optimized to a narrow range of osmotic and ionic composition and concentration; changes in solute concentration and composition (e.g. water stress-induced changes in anorganic nutrient composition) may therefore restrict cell expansion and growth.

It is concluded that both quantitative and qualitative aspects of nutrient supply are important for sustained plant growth under drought stress. Positive effects of N- and P-fertilization on shoot and root development of water stressed maize seedlings can be attributed

a) to direct and indirect effects of N- and P-nutrition on water relations of the plants (e.g. on the difference between \( \psi_r \) and \( \psi_l \) or on the degree of osmotic adjustment, respectively) and

b) to specific effects of N- and P-nutrition in metabolic processes, as e.g. changes in cell wall rheological properties, the synthesis of new cellular material, enzyme regulation, or changes in the hormonal status of the plant.

The study presented here has demonstrated that adequate N- and P-nutrition are of great importance for the establishment of maize seedlings, particularly under conditions of limited water supply. Since surface soils are primarily susceptible to drying, a vigorous root growth is of particular importance for seedling establishment. Adequate N- and P-nutrition clearly enhanced root growth of maize seedlings, particularly under conditions of limited soil moisture supply.

A fast and vigorous establishment of seedlings may be very important for optimal maize yields. Enhanced seedling growth enables the plant to produce a large leaf area in a short time; a big leaf area is important for the supply of kernels with assimilates, and short vegetation periods limit maize yields namely in Switzerland. In addition, flower differentiation occurs during the period of vegetative plant growth; any restriction of vegetative growth leads to a slow down of flower differentiation, possibly leading to longer anthesis-silking intervals.

5.2 Adaptation of Maize (cv Issa) Seedlings to Water Stress

Roots of maize (cv Issa) seedlings clearly revealed osmotic adjustment. Root turgor could be maintained at values > 0.5 MPa even at low \( \psi_l \) (Fig. 31, 32). On the other hand, the degree of osmotic adjustment in leaves was not sufficient to maintain turgor pressure (Fig. 33, 34).

However, the bulk modulus of elasticity \( e \) was decreased by about 30 % in water stressed as compared to well watered plants (Fig. 42), and capacitance was
significantly higher (+15 to +60 %) in water stressed than in well watered plants (Fig. 43). These changes in \( \varepsilon \) and capacitance in leaves of maize seedlings subjected to water stress represent an adaptation of the plants to conditions of drought stress. Tissues with a high capacitance tolerate a higher degree of dehydration without important decreases in water potential than tissues with low capacitance. Turgor is therefore maintained at higher values for a certain decrease in RWC in adapted (decreased \( \varepsilon \)) than in not adapted (higher \( \varepsilon \)) plants. Thus, plants with high capacitance and low \( \varepsilon \) can maintain growth processes under conditions of water stress, at which growth of plants with lower capacitance and higher \( \varepsilon \) is already restricted.

5.3 Comparisons of Root/Shoot Ratios

Root/shoot ratio (RSR) of maize seedlings changed considerably during plant development (Fig. 25). In small plants, RSRs > 1.5 were observed in my experiments. During plant growth, RSR of young maize plants decreased continuously and seemed to stabilize at a value of about 0.2 by the time when approximately 1.5 to 2 g shoot dry weight were produced. The decrease in RSR along with the growth of a plant during early growth stages has to be considered when comparing RSRs of plants exposed to different treatments that affect plant growth, e.g. among different nutrient treatments or between water stress and well watered treatments: Plants with a slower development show higher RSRs at a certain time after planting than faster growing plants, even if no causal effect of the treatment on RSR might exist. The problem of misleading RSR-values can be avoided, if RSR is plotted against plant fresh or dry weight rather than against days after planting or days after imposing stress. Also in statistical analysis, plant development stage has to be considered, e.g. by including it in models as a covariate. However, in most of the numerous studies that compared RSRs among different treatments, this change of RSR along with plant development has not been taken into consideration.
5.4 Determination of the Degree of Osmotic adjustment

The extent of 'osmotic adjustment' in leaves of plants growing at different nutrient regimes was similar whether calculated from $\psi_\text{sat}$-measurements at the different harvests (difference in $\psi_\text{sat}$ between well watered and water stressed plants) or whether derived from the analysis of PV curves (difference in OP100 between well watered and water stressed plants)(Fig. 47, 48). Values of osmotic adjustment calculated using the two different methods differed by less than 0.03 MPa (0.06 MPa in treatment NPK). Predawn measurements of osmotic potentials may therefore provide a good basis for comparisons of the degree of osmotic adjustment in water stressed plants. This method is much less complicated than the establishment of PV-curves and therefore represents a simple technique to compare the degree of osmotic adjustment in water stressed plants.
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APPENDIX

APPENDIX A

Calculation of fresh weight at full turgor

Artificial rehydration of plant samples used for the generation of PV curves may significantly alter the PV relationships, leading to erroneous determinations of osmotic potentials, relative water content at zero turgor and bulk modulus of elasticity. Kubiske and Abrams (1990) therefore suggested that linear regression of PV data above the turgor loss point may be used to extrapolate fresh weight at full turgor (FW100) from non-rehydrated (or not fully rehydrated) samples: PV data were plotted with the balancing pressure on the y-axis and the sample fresh weight on the x-axis. Linear regression of data above the turgor loss point yielded the equation of a line with the x-intercept equal to FW100. Because non-rehydrated samples of water stressed plants may not yield interpretable PV curves (no data above the turgor loss point), Kubiske and Abrams (1991) suggested rehydrating such samples for only a short period (1-2 h), and then to calculate FW100 according to the method described above.

APPENDIX B

Determination of the bulk modulus of elasticity ($\epsilon$)

Bulk modulus of elasticity is defined as $\epsilon = V(dP/dV)$, where $dP$ is the change in turgor pressure for a given change in the water content $dV$ of a cell (Tyree and Hammel 1972; Tyree 1981). Some possible sources of errors in determining $\epsilon$ from PV curves have been discussed by Cheung et al. (1976); they recommended comparing $\epsilon$s of different plants at comparable 'volume averaged turgor pressures', possibly near or at full turgor.

Osmotic potentials of the samples were calculated for values of applied pressure $\psi$ of 0.05, 0.15 and 0.25 MPa by $\psi_{ni} = (\psi_{100}(100-H2OAP0))/(RWC_i-H2OAP0)$, where $\psi_{ni}$ is the osmotic potential at the relative water content $i$ (RWC$_i$), OP100 is the osmotic potential at full turgor, and H2OAP0 is the apoplastic water content.

Turgor potentials of the samples were then calculated as $\psi_{pi} = \psi_i - \psi_{ni}$, where $\psi_{pi}$ is the turgor potential, $\psi_i$ is the total water potential and $\psi_{ni}$ is the osmotic potential at the relative water content $i$.

Regression of $\psi_p$ versus RWC through the data at $\psi = 0.05$, 0.15 and 0.25 MPa yielded the slope $dP/dV$. All data points with $0.05 < \psi < 0.25$ MPa corresponded to RWC-values between 97.2 and 99.8 %; bulk modulus of elasticity was therefore determined for an average RWC of 98.5 %.
APPENDIX C

Determination of capacitance

Capacitance (CAP) was determined as $\text{CAP} = \Delta \text{RWC}/\Delta \psi_{\text{plant}}$, where $\Delta \text{RWC}$ is the change in relative water content (RWC) and $\Delta \psi_{\text{plant}}$ is the change in the plant water potential ($\psi_{\text{plant}}$) (Nobel and Jordan 1983).

Regression of RWC versus $\psi_{\text{plant}}$ through the data at balance pressures ($=-\psi_{\text{plant}}$) of 0.05, 0.15 and 0.25 MPa yielded the slope $\Delta \text{RWC}/\Delta \psi_{\text{plant}}$ and thus the value of capacitance.
ABBREVIATIONS AND SYMBOLS

DAP  days after planting
FW100 fresh weight at full turgor
OP0  osmotic potential at zero turgor
OP100 osmotic potential at full turgor
PV curves pressure-volume curves
RSR  root/shoot dry weight ratio
RWC  relative water content
RWCO relative water content at zero turgor
SDW  shoot dry weight
SFW  shoot fresh weight
SWC  shoot water content
TBP  total biomass production
WS  water stressed
WW  well watered

\( \psi \)  applied pressure in the pressure chamber
\( \psi_s \)  soil matric potential
\( \psi_{\text{plant}} \)  plant water potential
\( \psi_o \)  osmotic potential
\( \psi_p \)  pressure (turgor) potential
\( \psi_g \)  gravitational potential
\( \psi_l \)  leaf water potential
\( \psi_r \)  root water potential
\( \psi_{\text{sol}} \)  leaf osmotic potential
\( \psi_{\text{root}} \)  root osmotic potential
\( \psi_{\text{pl}} \)  leaf turgor potential
\( \psi_{\text{pr}} \)  root turgor potential

\( \Delta \)  difference
\( \Delta(\psi_r-\psi_l) \)  difference between root and leaf water potentials
\( \varepsilon \)  bulk modulus of elasticity
\( \varphi \)  irreversible wall extensibility
\( Y \)  yield threshold
\( J_v \)  volume flow
\( L_p^* \)  relative hydraulic conductance
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