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Osmotic adjustment and the inhibition of leaf, root, stem and silk growth at low water potentials in maize

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Abstract. The expansion growth of plant organs is inhibited at low water potentials (Ψ_w), but the inhibition has not been compared in different organs of the same plant. Therefore, we determined elongation rates of the roots, stems, leaves, and styles (silks) of maize (*Zea mays* L.) as soil water was depleted. The Ψ_w was measured in the region of cell expansion of each organ. The complicating effects of transpiration were avoided by making measurements at the end of the dark period when the air had been saturated with water vapor for 10 h and transpiration was less than 1% of the rate in the light. Growth was inhibited as the Ψ_w in the region of cell expansion decreased in each organ. The Ψ_w required to stop growth was −0.50, −0.75, and −1.00 MPa, in this order, in the stem, silks, and leaves. However, the roots grew at these Ψ_w and ceased only when Ψ_w was lower than −1.4 MPa. The osmotic potential decreased in each region of cell expansion and, in leaves, roots and stems, the decrease was sufficient to maintain turgor fully. In the silks, the decrease was less and turgor fell. In the mature tissue, the Ψ_w of the stem, leaves and roots was similar to that of the soil when adequate water was supplied. This indicated that an equilibrium existed between these tissues, the vascular system, and the soil. At the same time, the Ψ_w was lower in the expanding regions than in the mature tissues, indicating that there was a Ψ_w disequilibrium between the growing tissue and the vascular system. The disequilibrium was interpreted as a Ψ_w gradient for supplying water to the enlarging cells. When water was withheld, this gradient disappeared in the leaf because Ψ_w decreased more in the xylem than in the soil, indicating that a high flow resistance had developed in the xylem. In the roots, the gradient did not decrease because vascular Ψ_w changed about the same amount as the soil Ψ_w. Therefore, the gradient in Ψ_w favored water uptake by roots but not leaves at low Ψ_w. The data show that expansion growth responds to low Ψ_w differently in different growing regions of the plant. Because growth depends on the maintenance of turgor for extending the cell walls and the presence of Ψ_w gradients for supplying water to the expanding cells, several factors could have been responsible for these differences. The decrease of turgor in the silks and the loss of the Ψ_w gradient in the leaves probably contributed to the high sensitivity of these organs. In the leaves, the gradient loss was so complete that it would have prevented growth regardless of other changes. In the roots, the maintenance of turgor and Ψ_w gradients probably allowed growth to continue. This difference in turgor and gradient maintenance could contribute to the increase in root/shoot ratios generally observed in water-limited conditions.

Key words: Cell enlargement – Osmotic adjustment – Turgor maintenance – Water potential gradients – *Zea* (osmotic adjustment).

Introduction

In this study, we compared the growth and solute accumulation of leaves, roots, stems and styles (silks) of maize at various water potentials (Ψ_w) to determine whether the growth response varies

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Symbols: Ψ_s = osmotic potential; Ψ_w = water potential

between different parts of the plant when water is in limited supply. Early work indicated that different plant regions may respond differently to an imposed water deficit (Gates 1955). Commonly observed increases in the ratio of root-to-shoot dry weights (El Nadi et al. 1969; Hoffman et al. 1971; Read and Bartlett 1972; Cutler and Rains 1977; Sharp and Davies 1979; Meyer and Boyer 1981) imply that roots grow more than the aerial parts of the plant when water is limited. Although this behavior might be caused by differences in the soil and aerial environements, Hsiao and Acevedo (1974) and Sharp and Davies (1979) suggested that continued root growth at low Ψ_W could be the result of a high capacity for solute accumulation and turgor maintenance at low Ψ_W.

According to theory, cell enlargement occurs when a demand for water is created by extension of the cell walls under the action of turgor, and water is supplied by gradients in water potential (Lockhart 1965; Boyer 1968; Ray et al. 1972; Boyer and Wu 1978; Cosgrove 1981). As water enters, solutes must enter to prevent dilution and maintain the osmotic forces necessary to drive enlargement and supply the metabolites for wall synthesis. Changes in any of these processes might affect growth at low Ψ_W.

Most commonly, the effects of low Ψ_W on cell enlargement are attributed to turgor losses because turgor can decrease rapidly as low Ψ_W develops (Boyer 1968; Hsiao and Acevedo 1974; Hsiao et al. 1976; Bunce 1977; Jones and Turner 1978; Takami et al. 1981). However, a direct relationship between enlargement and turgor is not always observed (Cutler et al. 1977, 1980; Acevedo et al. 1979), and turgor in regions of enlargement often shows little or no decrease even though enlargement is inhibited (Meyer and Boyer 1972, 1981; Matsuda and Riazi 1981; Michelena and Boyer 1982; Cavalieri and Boyer 1982).

Solute accumulation has been observed at low Ψ_W in root apices (Greacen and Oh 1972; Sharp and Davies 1979; Ayers 1981), shoot apices (Munns et al. 1979), stems (Meyer and Boyer 1972, 1981; Cavalieri and Boyer 1982), and leaves (Cutler et al. 1977; Matsuda and Riazi 1981; Munns and Wier 1981; Michelena and Boyer 1982). This process helps to maintain turgor and contributes to the maintenance of slow growth in leaves and stems, but a substantial inhibition still occurs at moderately low Ψ_W (Meyer and Boyer 1972, 1981; Matsuda and Riazi 1981; Cavalieri and Boyer 1982; Michelena and Boyer 1982). Therefore, while solute accumulation contributes to enlargement, it may not fully compensate for the effects of limited water, at least in certain tissues.

A direct comparison has not been made between growing regions of different plant organs for the capacity to grow, accumulate solute, and maintain turgor at low Ψ_W. In the comparative studies reported here, we measured the water status of the growing regions directly and found a differing capacity for growth that is regulated by factors within the plant rather than differences in the external environment.

Material and methods

Plant material and culture conditions. Maize plants (*Zea mays* L. cv. B73XMo17; Illinois Foundation Seeds, Tolono, Ill., USA) were grown from seed in soil in controlled-environment chambers (day/night temperatures: 30/20±1° C; relative humidity: 50/95±5%; lightperiod: 14 h). Fluorescent cool-white lamps provided 800±50 μmol photons m^{-2} s^{-1} (photosynthetically active radiation) at the level of the upper leaves.

For leaf and root measurements, plants were grown for three weeks in plastic pots having a 19.5 cm top diameter and containing 1.8 kg of soil (a 2:1:1 mixture, by vol., of soil:peat:perlite). For stem and silk measurements, plants were grown for six and eight weeks, respectively, in larger plastic pails containing 12.0 kg of the same mixture of soil. One week prior to sampling, the entire pot was enclosed in two opaque plastic bags to maintain a uniform soil Ψ_W. Earlier work (Blizzard and Boyer 1980) showed that this procedure maintained soil Ψ_W uniform throughout the pot to within ±0.04 MPa. The plastic bags were sealed tightly around the stem and a small tube (1 cm inner diameter) was inserted along the stem to facilitate gas exchange. All plants received Hoagland solution No. 1 (Hoagland and Arnon 1950) without micronutrients twice weekly beginning at 7 d after planting. The nitrate concentration was doubled after three weeks to meet the increased nutrient demand of the plants during internode elongation. Water was added to the soil between nutrient additions if the soil appeared slightly dry. Low water potentials were imposed by withholding water and nutrients from the soil.

Growth measurements. Rates of elongation are the average per hour for 24 h of growth under the above environmental conditions prior to sampling for Ψ_W. Leaf elongation was measured as the increase in distance between the leaf tip and the top of the pot. Root elongation was measured as the increase in distance between the root apex and a mark placed 20 mm from the apex. The elongation of stem internode 12 was measured as the increase in distance between two needle marks placed at the apical and basal ends of the internode.

Silk elongation was determined using a continuous-displacement transducer. Twenty to thirty silks were attached to a monofilament line using a hairpin clamp to which two abrasive surfaces were glued. The line was wrapped around the shaft of a mini-torque continuous potentiometer (Conrac Corp., Des Plaines, Ill., USA; Mini-torque Model 85153) and kept taut by a 5 g counterweight. A change in silk length was measured as a change in voltage across the potentiometer. The transducer was attached to the plant along the second stem internode above the ear. Therefore, the measurement of silk growth also included some earshoot elongation. Pollination was prevented by removing all tassels prior to anthesis.

The location of each zone of elongation was identified on plants treated similarly to those sampled for water status and growth. The zones of elongation of the leaves, stems, and roots were measured by marking with small needles or with ink as previously described (Westgate and Boyer 1984). The zone of elongation of the silk was determined by carefully cutting and peeling away the leaf sheaths enclosing the ear (husks), marking the silks as a group every 2 cm, replacing the husks, and enclosing the entire ear in a plastic bag lined with wet paper towels.

The growth chamber was maintained at 25° C, near 100% relative humidity, and dark for 24 h. This approach resulted in the incomplete marking of most silks but at least 90 silks, 20–25 cm in length, had two or more consecutive marks at some point along their length. Elongation rates were calculated as the increase in distance between consecutive marks using individual silks to form a composite curve by averaging the elongation rates in each 10% length interval (i.e. 0–10, 11–20, 21–30, etc.).

The zone of elongation in the silks also was determined from profiles of epidermal cell lengths. It was assumed that the length of the epidermal cells was proportional to the length of the elongating cells in the style. Seven to ten silks of equal length were chosen from the basal third of the ear when silks were 8.5, 25.6 and 41.5 cm in length. Five-millimeter sections were excised from five positions along each of the silks. Ten epidermal cells were chosen at random in each section and their lengths were measured to the nearest 5 μm.

Water-potential measurements. The Ψ_w were measured in the same plants used for growth measurements and samples were taken immediately after the growth period when the plants had been in the dark for the last 10 h. Transpiration was less than 1% of the rate in the light for the 10 h, and this assured that Ψ_w reflected water movement for growth and not transpiration. The plant organ to be sampled was excised from the plant and rapidly transferred to a humidity box for further dissection. All subsequent tissue manipulations were performed at saturating humidity within the box to minimize water loss from the tissue after excision. Tissue samples were taken from various positions along each plant organ in order to compare the water status of growing and mature tissues. The time to complete the sampling after detachment of the tissue was less than 3 min for each organ.

Axes from individual nodal roots (six to eight segments, each 10 mm long), leaf sections (2 cm long, including midveins and midrib), and stem segments (removed from the stem by making two transverse slices 1.5 to 2.0 cm apart and one tangential slice 3–4 mm from the surface) were placed at the bottom of a psychrometer chamber which was coated with melted and resolidified petrolatum (Boyer 1967). Additional petrolatum was used at the base of the cup for stem tissue, which was placed cut surface down to minimize the exposed cut surface. Sufficient tissue was sampled to cover the bottom of the psychrometer cup (≈ 2 cm^2). For the silks, the region enclosed by the ear leaves (husks) was sampled. Measurements indicated that silk Ψ_w was uniform along the length of the enclosed region. A 2 cm section of 20–30 silks was excised from the middle of this region and placed in the bottom of a psychrometer cup.

Water potential was measured using isopiestic technique (Boyer and Knipling 1965) corrected for heat of respiration (Barrs 1965). Measurements required 3–4 h at which time thermocouple output varied less than 0.01 MPa h^{-1}. To measure the osmotic potential (Ψ_s) and turgor, the psychrometer chambers were removed from the psychrometer system, sealed, frozen for 10 min at −70° C, thawed, and immediately returned to the psychrometer system. The Ψ_s was measured by isopiestic technique (required about 2 h), and turgor was calculated as $\Psi_w - \Psi_s$.

Dry weights. Roots were separated from the shoot at the surface of the stem. Roots and shoots were washed thoroughly to remove soil particles and then dried at 60° C for 48 h.

Results

In maize, elongation growth is confined to specific regions of each growing organ except in the silks (see below). For leaves, stems and roots, the zone was confined to the basal 5 cm, basal 3.5 cm, and apical 1.0 cm, in the order given. We monitored the rate of elongation of stem internode 12 (from base of plant), leaf 8 (from base of plant), nodal roots, and silks as water was withheld from the soil. Figure 1 shows that elongation of the stem, silks and leaves decreased rapidly and growth was completely inhibited in this order, at a Ψ_w of −0.50, −0.75 and −1.0 MPa in the growing regions. However, roots continued elongating at near control rates at Ψ_w that completely inhibited the growth of the other plant parts. In fact, root growth continued to a Ψ_w of −1.4 MPa while leaves on the same plant were beginning to shrink (Fig. 1). The silk and stem data were collected of necessity on plants older than those used for root and leaf measurements. However, it was unlikely that the differences in response were a consequence

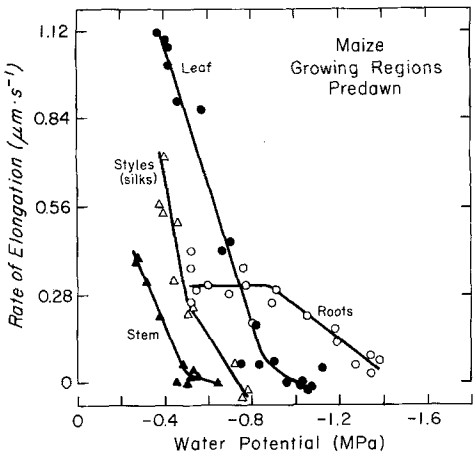

Fig. 1. Elongation of stem internode 12 (▲), silks (△), leaf 8 (●), and nodal roots (○) of maize at various water potentials. Water potentials were measured in the growing region of each plant organ at the end of the dark period (predawn). Growth was measured in the same organ of the same plants. Leaves and roots were sampled simultaneously from the same plant. Stem and silk data are from older plants. Silk elongation includes some ear-shoot growth (see Fig. 11). Each point is from a single plant

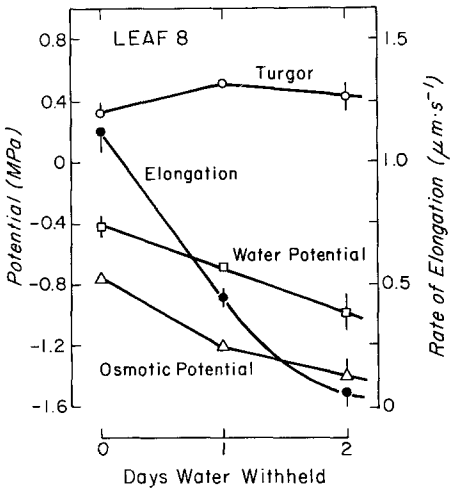

Fig. 2. Growth rate and water status of the growing region of leaf 8 of maize when water was withheld from the soil. Leaves were sampled at the end of the dark period beginning at 20 d after planting. The data are the mean ±1 SD of three to five samples

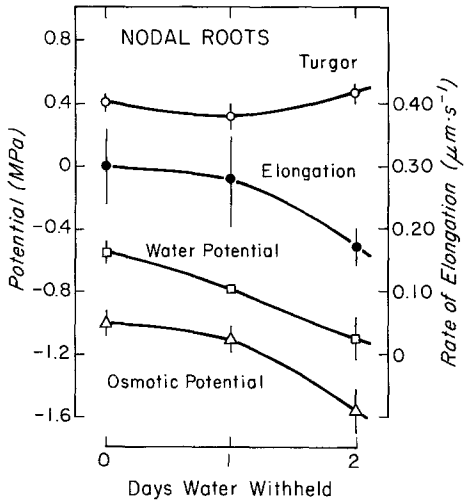

Fig. 3. Growth rate and water status of the growing region of the nodal roots of maize when water was withheld from the soil. Roots were sampled at the same time as the leaves on the same plants used for Fig. 2. The data are the mean ±1 SD of four samples

of plant age because the leaf and root comparison was made on the same plants.

We also measured the Ψ_S and turgor in the growing regions of each plant part to test whether the differences in response were a consequence of varying degrees of solute accumulation (osmotic adjustment) and turgor maintenance at low Ψ_W. Figure 2 shows that, as the rate of leaf elongation declined, leaf Ψ_S decreased from −0.76 MPa at high Ψ_W to −1.4 MPa at low Ψ_W, indicating that the solute concentration in the enlarging cells had nearly doubled. Turgor in the elongating region did not decrease even though growth approached zero (Fig. 2). Root elongation continued on these plants under the same conditions (compare Figs. 2 and 3). As in the growing region of the leaf, solutes accumulated (Ψ_S decreased) and turgor did not decrease. Also in the stems, internode elongation was inhibited almost completely at Ψ_W of −0.54 MPa in the growing region (Fig. 4), but solutes accumulated and turgor did not decrease.

The similarity in solute accumulation and turgor maintenance in the growing regions of all three vegetative organs indicated that another factor was causing the differential sensitivity of growth to low Ψ_W. We investigated one possibility, the supply of water to the growing regions, by estimating the magnitude of the gradient in Ψ_W between the growing regions and their vascular supply. If the magnitude of the gradient changed, growth could be affected. To make this measurement, advantage was taken of the absence of water movement in the mature tissue. This caused Ψ_W to equilibrate

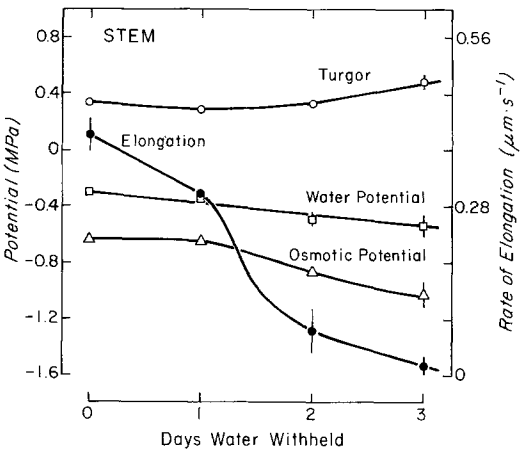

Fig. 4. Growth rate and water status of stem internode 12 of maize when water was withheld from the soil. Stems were sampled at the end of the dark period beginning at 42 d after planting. Data are the mean ±1 SD of three to five samples

with that of the local xylem and provided an estimate of Ψ_W in the xylem of the nearby growing tissue (Westgate and Boyer 1984). From a profile of Ψ_W along the length of each organ, the gradient beginning in the xylem and extending into the surrounding region of elongation could be estimated.

In the leaf, the profile showed a difference in Ψ_W between the mature blade and the growing region that was approx. 0.28 MPa (Fig. 5) when the leaf was expanding rapidly (2.0 mm h^{-1}). In the roots, the difference was 0.42 MPa (Fig. 6). The Ψ_W of the mature tissue was close to that of the soil, indicating that the entire xylem was

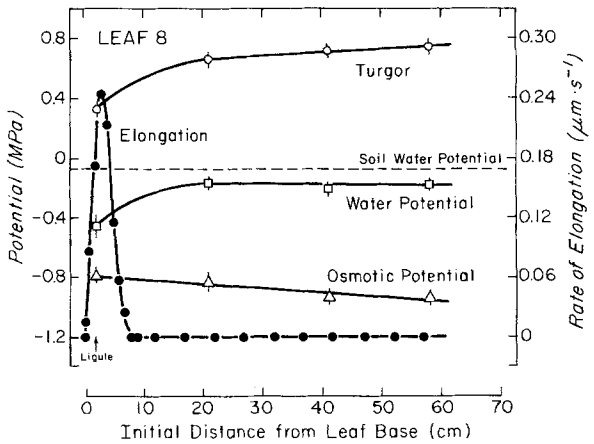

Fig. 5. Elongation and water status along maize leaf 8 at high water potential. The data are the mean ±1 SD of four samples. Soil water potential: −0.08 MPa

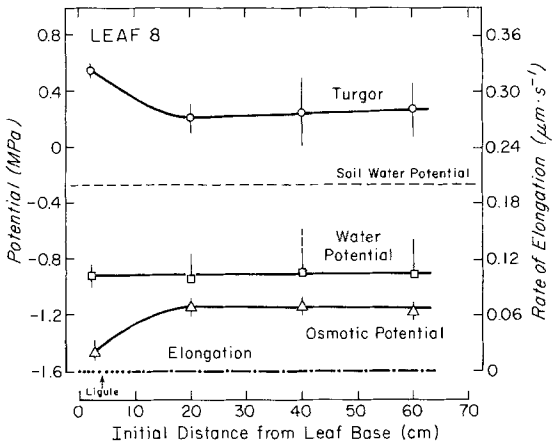

Fig. 7. Elongation and water status along maize leaf 8 at low water potential. Water was withheld from the soil for 3 d, which was sufficient to prevent leaf growth. The data are the mean ±1 SD of four samples. Soil water potential: −0.26 MPa

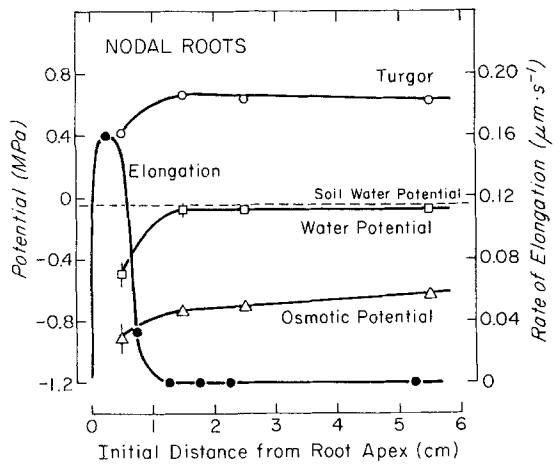

Fig. 6. Elongation and water status along the nodal roots of maize at high water potential. The data are the mean ±1 SD of four samples. Soil water potential: −0.06 MPa

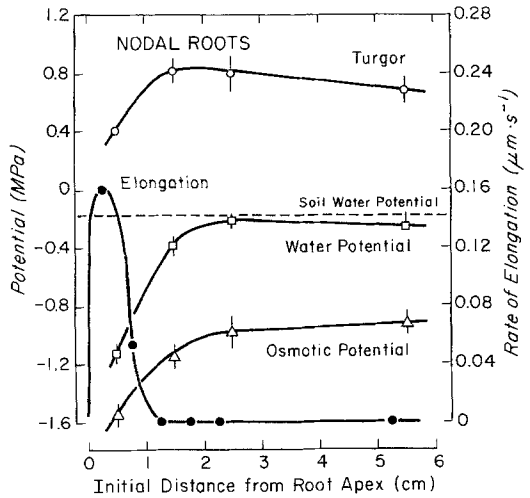

Fig. 8. Elongation and water status along nodal roots of maize at low water potential. Water was withheld from the soil for 3 d, which was sufficient to prevent the elongation of leaf 8 (Fig. 7). The data are the mean ±1 SD of four samples. Soil water potential: −0.20 MPa

in near-equilibrium with the Ψ_w of the mature tissue, and the Ψ_w difference between growing and mature regions arose outside of the xylem.

When water was withheld from the soil until leaf growth stopped (required 3 d, Fig. 7), this difference in Ψ_w had disappeared in the leaf. The Ψ_w was about −0.94 MPa regardless of position along the leaf and was not in equilibrium with the Ψ_w of the soil (−0.26 MPa), indicating that a high resistance to water movement had formed between the soil and the leaf. In contrast to the leaf, the difference in Ψ_w increased in roots encountering low Ψ_w, and growth continued (Fig. 8).

The osmotic potential decreased throughout the length of the leaf after water was withheld but mostly in the elongating region (compare Figs. 5 and 7) where it decreased to −1.45 MPa. A similar pattern was observed in the roots (compare Figs. 6 and 8). Turgor increased in the elongating region of the leaf but decreased about 0.5 MPa in the mature region (from 0.76 in the mature region in Fig. 5 to 0.26 MPa in Fig. 7). Turgor was unchanged in the elongating region of the root but increased in the mature tissue (from 0.65 MPa in the mature tissue in Fig. 6 to 0.85 MPa in Fig. 8).

The continued root growth at a Ψ_w that completely inhibited leaf growth indicated that low Ψ_w might affect dry matter accumulation less in roots

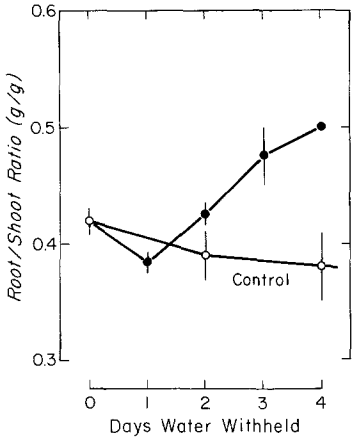

Fig. 9. Ratio of root to shoot dry weights for well-watered (o) and water-deficient (•) maize seedlings. Leaf water potentials were −0.4 MPa in the controls but decreased to −1.1 MPa in the water-deficient plants. Data are the mean ±1 SD of three plants

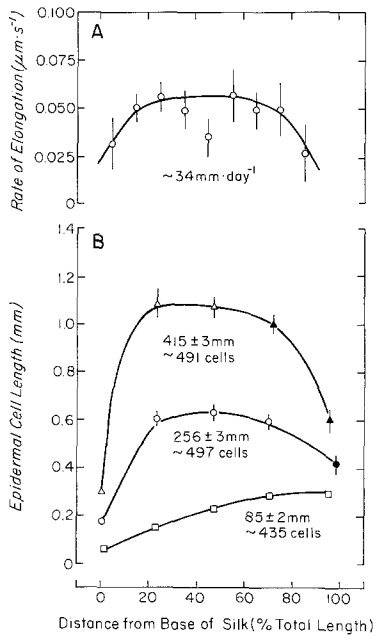

Fig. 10A, B. Profile of elongation and epidermal cell lengths along rapidly expanding styles (silks) of maize. **A** Elongation; **B** epidermal cell lengths. Each point is the mean ±95% confidence interval. The number of cells in the silks was estimated by totaling the number of cells in each length interval, calculated from the length of the interval divided by the length of the cells in the interval. *Closed symbols* indicate the exposed region of the silks

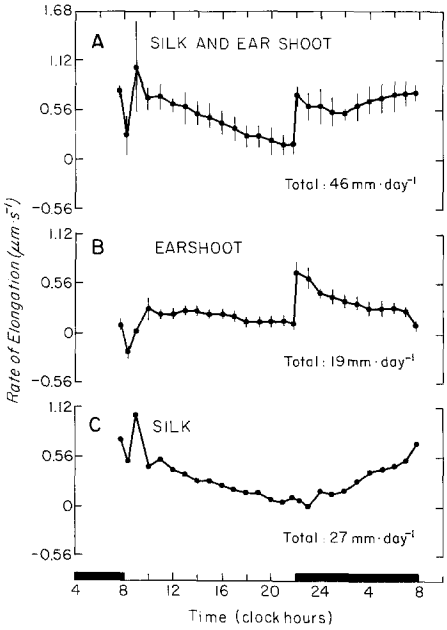

Fig. 11A–C. Diurnal elongation of unpollinated styles (silks) of maize at high water potential. **A** Silks plus earshoot; **B** earshoot only; **C** silks calculated as the difference between curves **A** and **B**. Each point is the mean ±1 SD of at least three measurements

than in shoots (which consisted mostly of leaves at this stage of growth). We measured root and shoot dry weights as Ψ_w decreased and found a rapid increase in the root/shoot ratio, confirming this effect on dry-matter accumulation (Fig. 9).

The pattern of silk growth was different from that of the vegetative organs. Cell elongation occurred throughout silks that were marked while remaining attached to the ear (Fig. 10A) or that were observed for epidermal cell lengths (Fig. 10B). The small increase in cell numbers indicates that the elongation was primarily a result of increases in cell length, as suggested by Kiesselback (1949).

The elongation of the silks plus earshoot responded rapidly to changes in environmental conditions (Fig. 11A); about 40% of it was attributable to earshoot growth (Fig. 11 B) and 60% to silk growth (Fig. 11C). The rate of silk elongation was rapid early in the photoperiod but decreased gradually during the day (Fig. 11C). Growth recovered slowly during the dark period to a maximum at predawn.

Silk plus earshoot elongation was fully inhibited when the Ψ_w of the silks decreased to −0.78 MPa (Fig. 12) but, unlike the growing regions of the leaves, stems and roots, osmotic adjustment in the silks was slight and turgor decreased from 0.52 to 0.36 MPa (Fig. 12). We attempted to determine the difference in Ψ_w between the xylem and the elongating cells but, because the entire silk was elongating (Fig. 10), there was no mature silk tissue and the behavior of xylem Ψ_w within the silks could not be measured.

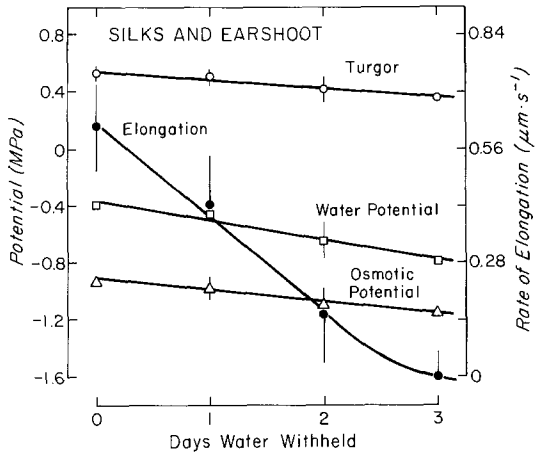

Fig. 12. Growth of styles (silks) plus earshoot and water status of styles of maize when water was withheld from the soil. Data are the mean ±1 SD of three samples of unpollinated silks

Discussion

The results show that the growth of different organs of the plant responds differently to low Ψ_w. Stems and silks did not grow at Ψ_w that allowed roots to grow rapidly. Leaves were intermediate in their response. The differences were large, such that the growing regions of roots required Ψ_w 0.7–0.8 MPa lower than in stems for the same degree of inhibition.

In these experiments, Ψ_w was measured in the growing regions to assure that Ψ_w of the expanding cells was known. However, the growing regions were enclosed by other tissues or soil and had to be excised for the measurements. Excision in air can deprive the tissue of a water supply and, because turgor extends the cell walls during growth and could continue to do so after excision, the tissue could experience a relaxation of the cell walls and a decrease in turgor, decreasing the Ψ_w (Cosgrove et al. 1984). Although this behavior could be important at high Ψ_w where rapid growth was occurring, there could be no wall relaxation at low Ψ_w when no growth was occurring. Therefore, the Ψ_w of −0.5, −0.75, −1.0 and below −1.4 MPa that completely inhibited stem, silk, leaf and root growth could not have been affected by wall relaxation. These Ψ_w must have represented the Ψ_w before excision, and the large differences in growth response must have been present in the intact plant.

This indicates that there were inherent differences in the sensitivity of growing cells depending on the part of the plant in which the cells were located. The control of this sensitivity must have resided in the plant because the Ψ_w necessary to prevent growth was a property of the growing tissue itself, not an external factor. The differences were not caused by differential dehydration of shoot and root tissues because the differences were apparent at comparable Ψ_w and turgor.

There are several cell characteristics that might account for the differential sensitivity of growing regions to low Ψ_w. Among them, we explored changes in solute concentration, turgor, and the Ψ_w gradients associated with water movement into the growing cells. In all of the vegetative tissues, solute concentrations increased substantially in the elongating cells and probably consisted mostly of photosynthate (Acevedo et al. 1979; Michelena and Boyer 1982). The likely presence of increased concentrations of photosynthate in the regions of cell expansion indicates that the differential sensitivity of growth to low Ψ_w could not be attributed to a lack of substrates. Moreover, the similarity in Ψ_s of the elongating regions of the roots and leaves indicates that the differential sensitivity could not be attributed to more solutes accumulating in roots than in leaves. This is at variance with the conclusions of Hsiao and Acevedo (1974) and Sharp and Davies (1979) who suggested that roots may have a higher capacity for osmotic adjustment than leaves. However, these investigators did not measure Ψ_s in the growing regions of leaves and would not have detected the large osmotic adjustment occurring there.

By contrast, Ψ_s decreased only slightly in the silks under the same conditions. Why the silks did not accumulate much solute is unknown, although it is noteworthy that the total sugar content of the plant was low during silk growth (Westgate and Boyer 1985), possibly indicating insufficient photosynthate was available for accumulation by the silks.

The solute concentrations form the osmotic driving force for water entry into the cells and for turgor generation. The concentrations increased sufficiently in the growing regions of the vegetative tissues so that turgor remained constant or even appeared to increase as the plants became water deficient and growth ceased. However, the apparent increase in turgor may not have occurred in the intact plant. The turgor measured in excised tissue may have been lower than in intact growing tissue because of the possibility of wall relaxation (Cosgrove et al. 1984) or other excision effects. We studied the magnitude of the changes in Ψ_w upon excision of rapidly growing tissue in sunflower leaves (Boyer 1968, 1974), soybean stems (Boyer and Wu, 1978; Cavalieri and Boyer 1982), and maize stems (Westgate and Boyer 1984). In all

cases, the changes were small, the largest being 0.14 MPa (Boyer and Wu 1978). If we assume this worst case, the turgor of the intact growing tissue could have been 0.14 MPa higher than reported here. This would increase the turgor at the left side of Figs. 2–4 (high Ψ_w) but not at the right side (low Ψ_w, where wall relaxation would not occur because of the absence of cell enlargement). Thus, turgor would have been about constant as Ψ_w decreased. Taking this correction into account, differences in turgor maintenance cannot explain the differences in inhibition of the vegetative organs at low Ψ_w. On the other hand, the decreases in silk turgor under similar conditions probably caused the high sensitivity of this tissue. Indeed, decreases in leaf turgor can be made to occur by depriving leaves of solute for osmotic adjustment (Michelena and Boyer 1982), in which case leaves respond like silks to low Ψ_w (completely inhibited at Ψ_w of -0.75 to -0.80 MPa).

The elimination of photosynthate supply and turgor as factors controlling the behavior of vegetative growth at low Ψ_w when solutes are present for osmotic adjustment, as in the present study, implies that cell-wall properties or water supply were involved (Lockhart 1965; Ray et al. 1972; Boyer and Wu 1978). Although cell-wall properties affect growth, the disappearance of the Ψ_w gradient in leaves was probably important because it would prevent water from entering the elongating region. In this situation, changes in wall properties would be inconsequential because growth would be limited by the water supply. The collapse of the Ψ_w gradient evident in the leaves did not occur in the roots. We propose that this difference could explain, at least in part, the difference in sensitivity of root and shoot growth to low Ψ_w.

It should be noted that the disappearance of the gradient in the leaves resulted from a decline in Ψ_w of the xylem, measured in mature tissue. The decline indicates a lack of Ψ_w equilibrium between the mature tissue and the soil even after 10 h in the dark. This implies that a large resistance had formed in the flow path. The resistance would effectively remove the leaf from contact with water in the soil. Because the supply of water in the leaf xylem is limited, it would be rapidly depleted by the surrounding elongating region, further lowering the Ψ_w of the xylem. As growth depends on water entry from the xylem, the decreasing xylem Ψ_w would prevent growth.

It is noteworthy that emboli form at leaf Ψ_w of -0.8 MPa and below (Milburn 1966; Boyer 1971; Blizzard and Boyer 1980). Water potentials in this range are consistent with the Ψ_w reached by the leaves in the present work and indicate that xylem emboli might have caused the observed increase in flow resistance between the leaves and the soil. Therefore, the generation of vascular emboli could be the basic reason for the disappearance of the Ψ_w gradient in the leaves.

Correlations between growth and the water status of mature leaf tissue have been noted previously in grasses (Boyer 1970; Acevedo et al. 1971; Chu and McPherson 1977; Cutler et al. 1980). However, the water status of mature tissue can be rapidly transmitted to elongating tissue via the vascular system (Westgate and Boyer 1984). This transmitted signal could control growth by lowering the Ψ_w of the vascular system, thus decreasing Ψ_w gradients in the elongating tissue. If so, the apparent correlation between turgor in mature tissue and growth in expanding regions would not reflect a direct effect of turgor on growth but rather an effect of Ψ_w gradients in the growing region.

The Ψ_w gradients associated with growth are present in intact leaves and stems (Boyer 1968, 1970, 1974; Boyer and Wu 1978; Cavalieri and Boyer 1982; Westgate and Boyer 1984). Therefore, the gradients cannot be attributed to excision effects. Boyer (1968) and Molz and Boyer (1978) suggested that they arise from extension of the cell walls rapidly enough to prevent turgor (and Ψ_w) from reaching its maximum. According to this concept, the cell Ψ_w are inherently generated by the growth process, but it is well to note that the Ψ_w gradient can also be affected by changes in xylem Ψ_w, which represents one end of the Ψ_w gradient.

Cosgrove and Cleland (1983) also propose that the low Ψ_w results from a high solute concentration in the cell walls. However, while solutes are undoubtedly present (Boyer 1967), pressures of about 0.2 MPa were required to force water from growing sunflower leaves (Boyer 1968, 1974), which is not consistent with high solute concentrations causing the low Ψ_w of elongating tissue.

Central to both hypotheses is the idea that the Ψ_w gradient originates from the activity of cell enlargement, and that the xylem is one end (the supply end) of the gradient. According to the first hypothesis, the gradient serves cell enlargement by supplying water. As long as the xylem Ψ_w changes slowly, the enlarging cells adjust (Westgate and Boyer 1984), the gradient is maintained, and water can enter. When xylem Ψ_w decreases rapidly, the enlarging cells may be unable to adjust. In the present work, the disconnection of the leaf xylem from the soil water supply (as indicated by the disequilibrium between the mature leaf and the soil)

caused the enlarging cells to deplete the xylem water – a rapid event – and the xylem Ψ_w fell until it equilibrated with the Ψ_w of the enlarging cells. In this situation, water uptake ceased, preventing enlargement. This situation would persist as long as the disconnection from the soil water supply persisted. Accordingly, leaf growth would not occur until water was resupplied and the Ψ_w gradient was reestablished. It is clear that the disappearance of the Ψ_w gradient can have long-term effects on the growth of plant organs and is controlled not only by the activity of cell enlargement but also by events affecting the Ψ_w of the xylem.

The differential sensitivity of growth to low Ψ_w may explain some of the developmental changes that occur as plants encounter limited water supplies. For example, the failure of silk elongation at low Ψ_w is often cited in the failure of reproduction under these conditions (Herrero and Johnson 1981). Also, the decrease in stem and leaf elongation relative to the roots at low Ψ_w may contribute to the commonly observed increases in root/shoot ratios (El Nadi et al. 1969; Hoffman et al. 1971; Read and Bartlett 1972; Cutler and Rains 1977; Sharp and Davies 1979; Meyer and Boyer 1981). Both these phenomena result in altered dry-matter partitioning within the plant. Thus, the factors contributing to altered dry-matter partitioning may originate in part from the differential sensitivity of cell expansion to low Ψ_w in various parts of the plant.

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