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Anatomy of Seedling Roots of Tropical Maize (*Zea mays* L.) Cultivars at Low Water Supply

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ABSTRACT

Establishment of maize seedlings can be difficult at low soil moisture content. Anatomy of root metaxylem vessels may influence the capacity for water transport and respective genotypic differences might be useful for selection purposes. To test this, six tropical maize (*Zea mays* L.) cultivars were grown in large PVC tubes containing a sandy substrate at 5% (M5) and 10% (M10) moisture contents for 2 weeks. The percentage changes in root diameters due to M5 was similar for most cultivars but differed for main root types. Root diameters were not consistently related to metaxylem structure, but in a few cases, thin roots had smaller diameter metaxylem vessels. The M5 treatment reduced the number of late metaxylem vessels of primary roots by about 0 to 20%, while effects on nodal roots were slight. Generally, the ratio of cross-sectional areas between late and early metaxylem vessels increased from primary to seminal and nodal roots. Within the cultivar Tuxpeño this ratio was much reduced by M5. A few cultivars maintained the combined cross-sectional areas of metaxylem vessels at M5 in some main root types, but only one cultivar could achieve this for the total of cross-sectional areas of metaxylem vessels, calculated over all root axes, by increasing the number of seminal and nodal roots. These anatomical traits seemed to be mostly constitutive with limited response to an actual environment, but they could be decisive for the suitability of a cultivar to an environment with frequent water shortages during seedling establishment.

Key words: Metaxylem vessels, water stress, tropical maize.

INTRODUCTION

Provided that there is sufficient water in deeper soil layers, an increase in root length or depth can help to avoid dehydration stress (Jordan, Douglas, and Shouse, 1983). Genotypic differences in avoidance of dehydration have led to increasing interest in root morphology of crops like soybean (Boyer, Johnson, and Saupe, 1980) and sorghum (Blum and Arkin, 1984; Jordan and Miller, 1980). While genotypic variation of root traits has been reported in many crops (O'Toole and Bland, 1987), suitable strategies to exploit this variation must be further investigated because it is often small in adapted breeding stock compared with exotic germplasm of the same species (Jordan and Miller, 1980). For maize seedlings, three main root types have to be discriminated: the primary root, the seminal or mesocotyledon roots which are similar in morphology, and the first tiers of nodal roots (Stamp, 1984). Seedlings of tropical lowland maize cultivars exhibited considerable differences in traits of these

main root types under low and high water supply but these could not fully account for most of the differences in the yield components of mature plants (Weerathaworn, Siri, Geisler, and Stamp, 1989). Less attention has been paid to the anatomy of maize roots. A few detailed descriptions of the development of xylem vessels on successive tiers of nodal roots can be found (Hoppe, McCully, and Wenzel, 1986). According to O'Toole and Bland (1987), xylem resistance to water flow is of a physical nature and is dependent on the number and diameter of vessels. However, St. Aubin, Canny, and McCully (1986) and McCully and Canny (1988) could show that the transport capacity of xylem vessels is influenced by the stage of differentiation. Large, late metaxylem vessels mature at a distance of about 20 to 30 cm from the root tip. Small, early metaxylem vessels, however, usually developed in the zone where lateral root growth is visible (Danilova, 1988). For this reason, geno-

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typic differences in the anatomy of metaxylem vessels of cotton, for example (McMichael, Burke, Berlin, Hatfield, and Quisenberry, 1985; Oosterhuis and Wullschleger, 1987; Oosterhuis, Wullschleger, and Stewart, 1988) may be related indirectly to water transport only at appropriate physiological stages of root development.

Little is known about genotypic differences in the root anatomy of maize seedlings. Investigations of central European maize cultivars revealed considerable differences in the number and diameter of early and late metaxylem vessels (Kiel, 1990). The main focus of the present study was on the root anatomy of tropical lowland maize cultivars which had been selected under drought conditions of rain-fed agriculture. Special attention was paid to possible mechanisms of adaptation to a reduced water supply.

MATERIALS AND METHODS

Plant materials

Three open-pollinated cultivars (Suwan 3, Caripeño, Tuxpeño) and three hybrids (KTX.2602, KTX.2904, KSX.2301) from the maize breeding programme of the National Corn and Sorghum Research Centre, Kasetsart University, in Thailand, were used.

Soil moisture conditions

PVC tubes, 400 mm in length and 100 mm in diameter, contained 3.1 dm³ of sand with a particle size of 0.5–0.75 mm. The oven-dried sand was moistened to either 5% (M5) or 10% (M10) of the dry weight with a solution containing the basic nutrients: 0.492 MgSO₄, 0.330 CaCl₂, 0.088 K₂SO₄, 0.136 KH₂PO₄ g dm⁻³ distilled water (Stamp, 1984). Nutritive substances were sufficient for the early growth stage. Because of large kernel reserves nitrogen was omitted, for during the early seedling stage additional nitrogen supply retards main root growth in favour of prolific growth of lateral roots in maize (Stamp, 1984).

General procedures

The maize seeds were soaked in distilled water for 24 h at 22 °C and allowed to germinate on filter paper moistened with distilled water. Pregermination occurred in a growth chamber, in darkness, at a temperature of 24 °C. Uniform 2-d-old seedlings were planted at a depth of 2 cm in PVC tubes, one seedling per tube.

All tubes were covered with plastic sheets to minimize water

evaporation from the sand. When the coleoptiles were visible, the plastic sheets were cut in order to allow seedlings to grow through them.

The experiment was conducted in a growth chamber (Heræus Vephl, 5/2000) under a 12 h photoperiod, an irradiance of 350 µmol m⁻² s⁻¹ provided by fluorescent lamps, 70–80% relative humidity and 24/22 °C (day/night) temperatures.

Harvest

Fourteen days after transplanting, roots were removed from the sand substrate by gently washing with water. Thereafter, roots were stored in 5% glutaraldehyde until needed for anatomical investigations.

Sampling procedures

Anatomical characteristics were examined on the primary root and the longest seminal and nodal roots. Cross-sections were cut by hand at a distance of 5 cm from the root base, studied under a light microscope and the following parameters recorded: root and stele diameter, cortex thickness, late and early metaxylem diameter. Assuming that the root is circular, the root cross-section, the stele, and late and early metaxylem surface areas were calculated from the respective diameters. A factorial completely randomized design with a split-plot for main root type was used with six maize cultivars, three main root types, two water regimes and five replications. Analysis of variance was carried out (SAS Institute, 1988). For all data, standard errors of the means are shown as ± values in tables.

RESULTS

Diameter of main roots

The diameter of seedling roots varied considerably among genotypes as shown for the primary root. Genotypic variation was especially high when water supply was low (Table 1). KSX.2301 generally exhibited a small diameter of the primary root which held true for the seminal and nodal roots as well. The response to low water supply was moderate, in most genotypes, root diameter was reduced by a few per cent in primary roots. Seminal and nodal roots were about 20% thinner than primary roots. The relative reduction in root diameter due to low water supply was similar for most genotypes.

TABLE 1. Diameters of main roots (µm) of six tropical maize cultivars at two soil moisture regimes, 5% (M5) and 10% (M10)

Cultivar		Tuxpeño	s.e.	Caripeño	s.e.	Suwan 3	s.e.	KSX.2301	s.e.	KTX.2602	s.e.	KTX.2904	s.e.
Primary root	M5	1049	±39	1015	±19	980	±54	864	±30	1125	±65	939	±50
	M10	1075	±62	1075	±65	1017	±23	881	±44	1067	±38	977	±53
M5, % of M10		98		95		96		98		105		96	
Seminal root	M5	771	±46	800	±43	774	±62	629	±28	762	±11	667	±32
	M10	815	±68	774	±51	817	±37	684	±47	806	±54	780	±51
M5, % of M10		95		103		95		92		95		86	
Nodal root	M5	748	±55	736	±26	774	±62	719	±31	719	±36	649	±34
	M10	786	±33	728	±76	757	±30	719	±62	788	±51	675	±43
M5, % of M10		95		101		102		100		91		96	

sectional areas from the two vessel types increased slightly from primary to seminal roots and almost doubled from primary to nodal roots (Table 5). Some differences were observed between cultivars, especially for seminal roots of Tuxpeño at low water supply.

The percentage of late metaxylem circumferences from the total sum of metaxylem circumferences

When the sums of circumferences for each metaxylem type were calculated within each root type, the percentage of late metaxylem vessels from this sum was mostly identical for a given cultivar and root type disregarding the water regime (Table 6). It would appear that the total amount of cell walls for late and early metaxylem vessels is seemingly spent within a cultivar in a fixed relationship, while numbers and diameters of specific metaxylem vessels are somewhat more sensitive to water supply. A definite explanation is not possible at the moment.

Number of seminal and nodal roots

Maize seedlings at the four-leaf stage already possess many seminal as well as first nodal roots. Although the latter have not usually penetrated deeply into the soil at this stage, the actual number of main roots available for the water supply of a seedling should be taken into account. Genotypic variability in the number of seminal roots was high under both water regimes (Table 7). While most cultivars showed an increase of 1–2 seminal roots from M10 to M5, the drought sensitive Caripeño showed a decrease. While numbers of seminal roots were already fixed at the harvest date, new nodal roots were still being

formed. This might explain the generally lower number of nodal roots at M5.

Total cross-sectional area of metaxylem vessels for all root types

When the total available cross-sectional area of metaxylem vessels was multiplied by the respective number of main roots, the result was very different from that of single roots (Table 8). Under full water supply, Tuxpeño, Caripeño and KTX.2602 had extremely high cross-sectional areas. This ranking order changed remarkably under low water supply. While values of Caripeño declined severely, mainly because of a reduced number of roots, Suwan 3 improved its position mainly because of an increased number of main roots. Tuxpeño, too, overcompensated for a reduced cross-sectional area of single roots by an increase in total root number.

DISCUSSION

If enough water is available in the deeper soil profile, plant roots generally penetrate the upper layers rapidly so as to continue water uptake. This is one mechanism to avoid drought effects (Blum, 1988; Gregory, 1989). Little is known about the possible control of water flow by root anatomy. Richards and Passioura (1989) began a wheat breeding programme with the objective of reducing the diameter of the one major xylem vessel in order to regulate the utilization of limited soil water reserves. In our study, the diameters of main roots from maize gave few conclusive indications of the root anatomy. Thin roots had, in extreme cases, slightly reduced numbers of

TABLE 6. *The percentage of late metaxylem circumferences from the total sum of metaxylem circumferences of six tropical maize cultivars at two soil moisture regimes, 5% (M5) and 10% (M10)*

Cultivar		Tuxpeño	Caripeño	Suwan 3	KSX.2301	KTX.2602	KTX.2904
Primary root	M5	57	60	57	55	56	60
	M10	58	59	61	55	58	62
M5, % of M10		98	102	93	100	97	97
Seminal root	M5	52	61	61	58	64	60
	M10	62	63	56	58	61	54
M5, % of M10		84	97	109	100	105	111
Nodal root	M5	64	69	66	62	65	65
	M10	68	67	68	65	64	65
M5, % of M10		94	103	97	95	102	100

TABLE 7. *Numbers of seminal and nodal roots of six tropical maize cultivars at two soil moisture regimes, 5% (M5) and 10% (M10)*

Cultivar		Tuxpeño	s.e.	Caripeño	s.e.	Suwan 3	s.e.	KSX.2301	s.e.	KTX.2602	s.e.	KTX.2904	s.e.
Seminal roots	M5	7.8	±1.0	5.4	±0.7	6.6	±1.7	4.6	±0.2	7.8	±2.0	7.0	±1.0
	M10	5.8	±0.6	7.0	±1.2	4.8	±0.5	5.0	±0.8	6.2	±1.5	5.8	±0.9
M5, % of M10		134		77		138		92		126		121	
Nodal roots	M5	4.2	±0.2	4.4	±0.2	4.4	±0.2	3.6	±0.4	4.8	±0.5	5.0	±0.4
	M10	3.6	±0.4	5.4	±1.0	4.8	±0.5	4.0	±0.8	5.4	±0.5	5.4	±0.5
M5, % of M10		117		81		92		90		89		93	

TABLE 8. Total cross-sectional areas of late and early metaxylem vessels ($\mu\text{m}^2 \times 10$) for all root types of six tropical maize cultivars at two soil moisture regimes, 5% (M5) and 10% (M10)

Cultivar	Tuxpeño	Caripeño	Suwan 3	KSX.2301	KTX.2602	KTX.2904
M5	3328	2668	3115	1453	3091	2373
M10	3560	3464	2973	1718	3230	2722
M5, % of M10	93	77	104	84	95	87

metaxylem vessels although the effect seemed to be greater on the diameters of metaxylem vessels. Thin main roots with lateral roots can enable a maize seedling to maintain a high ratio of root surface area to leaf area and a low expenditure of dry matter for the root system (Kiel, 1990). Furthermore, osmotic adjustment is possible in thin roots without osmoticum accumulation per unit length (Sharp, Silk, and Hsiao, 1990).

It has still to be shown that thin roots are an advantage in drought-prone environments which often possess layers of compact soil within the profile. KSX.2301, the cultivar with small root diameters, was very slow in developing roots under low water supply. Even in nodal roots, which started to develop after some exposure to low water supply, varietal differences were appreciably larger than those caused by water supply. These findings minimize the possibility that cultivars might, in some way, adapt to water stress by a flexible response of root diameter.

Resistance to water flow can be increased in wheat either by reducing the number of root axes or the number and diameter of metaxylem vessels (Belford, Klepper, and Rickman, 1987). In maize, the number of metaxylem vessels within a root may provide an additional component for consideration in drought tolerance. Kiel (1990) found significant genotypic variability in numbers of early and late metaxylem vessels in seedling roots of north-western European maize cultivars. In the local tropical lowland maize cultivars in the present study, the genotypic variability was of a similar magnitude. Obviously, however, the ranking order of cultivars was organ-specific. Similar ranking orders of genotypes at primary and seminal roots differed from that of nodal roots. It still remains to be determined if this has consequences for an early, predetermined response to low water supply followed by a more flexible response. With regard to the few genotypes with thin roots and small metaxylem vessels the hypothesis of Passioura (1972) could be considered. Small metaxylem vessels might be useful for an increased efficiency of water use under limited soil water supplies. The situation is more complex, however, in the maize seedling root system because several large late and many medium-sized early metaxylem vessels are found within one main root. Although diameters of early metaxylem vessels are smaller and their resistance to water flow consequently higher than that of late metaxylem vessels (although the latter are not always fully differentiated, Danilova, 1988; McCully and Canny, 1988), their cross-

sectional area takes up a considerable proportion of the sum of cross-sectional areas of all metaxylem vessels within a root. In older plants the proportion of cross-sectional area from early metaxylem vessels becomes almost insignificant in nodal roots on higher tiers (Stamp and Kiel, 1992). The almost negligible effect of water stress on the percentage of late metaxylem circumferences from the total sum of metaxylem circumferences limits the extent of a flexible response based on different water flow resistances of the two metaxylem vessel types. The question arises why the available amount of metaxylem cell walls of each vessel type is such a fixed parameter. This could possibly indicate specific functions for each vessel type.

Considering the system of main roots as a whole, several other, seemingly independent, patterns of adaptation exist for the total of cross-sectional areas of metaxylem vessels. Thus, a large area may be achieved by high numbers of metaxylem vessels per single root as well as by high numbers of seminal and nodal roots. Some cultivars had remarkably stable sums of cross-sectional areas of metaxylem vessels within a specific root type at low as compared to high water supply. No cultivar, however, achieved stable or even increased total cross-sectional areas without developing more main roots.

Conclusive correlations with yield components under drought conditions were not observed for the anatomical root traits as they were for the morphological root traits (Weerathaworn *et al.* 1989). Possibly, anatomical traits of seedling roots have to be regarded as constitutive for a cultivar because an adaptation to changing water availability is low. In this case the value of differences in anatomical traits must be re-evaluated with regard to seedling establishment at low levels of water supply in the soil.

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