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Development of Water Conducting Capacity in the Root Systems of Young Plants of Corn and Some Other C4 Grasses[1]

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ABSTRACT

Development of the primary and early nodal roots was studied in *Zea mays* L., *Zea mexicana* (Schrad.) Reeves & Mangelsd., *Sorghum bicolor* (L.) Moench., and *Sorghum sudanese* (Piper) Stapf. in relation to shoot development. In all the types studied all roots reached lengths of about 30 centimeters before the late metaxylem (LMX) was open, and young plants with total root lengths of around 100 centimeters had almost no open LMX. On average, corn seedlings with up to 36 square centimeters of leaf had no open LMX. The name "immature apices" is suggested for such long but not fully functional roots. In plants up to 50 days old a fairly constant proportion of less than half the total root length had open LMX. A pilot study of stomatal resistance on days of high evaporative demand suggested that young seedlings may show higher resistance than older plants in the afternoon. Estimates of longitudinal permeability of corn roots with only early metaxylem vessels open indicate very steep gradients of water potential would develop under such conditions.

Soil or sand sheaths encasing roots of grasses have been described as features found in desert and dry environments (13). More recently they have been described on corn (12) and mesophytic grasses in humid environments (3). Striking illustrations of such sheaths will be found in these three papers. The sheathed regions of corn roots coincide with the regions of immature xylem where LMX[2] elements are still alive (11). This region stretches much further back (up to 50 cm from the apex) than has been supposed. The present paper extends the association of soil sheaths with the immaturity of the LMX to four other C4 grasses, and explores the likely effect of the nonfunctioning xylem on water supply to the shoot.

It is widely believed that the permeability of roots to water is much greater in the axial direction (P_x) than in the radial direction (P_l). The definitions, units and measurements are set out by Newman (9), where it is clear that for a corn primary root with open LMX the belief is well founded. However, as Newman (9) shows, in the region of the root where only the EMX is open, the value of P_x is much less. The finding (11) that, in axile roots of field-grown corn, maturation of LMX is long-delayed, raised the question when in the development of the seedling the full axial permeability became operative. Each nodal root goes through a stage when it bears a coherent soil sheath for up to half a meter proximal to the bare elongating tip (2–5 mm), and has inside immature LMX (with cross walls and cytoplasm) which cannot engage in transporting water more efficiently than any other file of living cells (7). The longitudinal water permeability of such roots is thus limited to the outer ring of small (20 μm diameter) EMX elements, which are open vessels to within 10 cm from the tip (2). When the LMX elements lose their crosswalls and become open, and the soil sheath disperses leaving the root bare, the longitudinal permeability of the root will increase by a factor of at least 100 (11). If the first formed seedling roots showed a similar slow maturation of their LMX there could be a stage when the primary and early nodal roots all had only their EMX vessels open. The time at which one or more of these early roots opened their LMX would herald a dramatic change in the availability of water to the developing shoot. The sequence and numbers of developing roots in corn have been described (4) for the variety Seneca Chief. The primary root is followed closely by a tier of four roots from the coleoptilar node, and a little later by four to five roots from the second node. Roots of each tier are even-aged. Roots of successive tiers (usually seven tiers) go through similar stages of development to the earlier lower ones, from sheathed to bare. We determined to follow the development of the primary and early tiers of nodal roots, recording the presence and extent of soil sheaths, the presence or absence of crosswalls and cytoplasm in the LMX and the stage of lignification of the vessel sidewalls. These measurements would be related to the number and size of the leaves. Measurements of stomatal resistance on days of high evaporative demand might reveal whether at any stage the young seedlings were inadequately supplied with water compared with the older plants. The opportunity was taken to record also the root systems of four other C4 grasses.

Clearly, the assumption of high axial permeability becomes valid only at some distance back from the tip. The question of how far back this may be is not addressed in this paper.

MATERIALS AND METHODS

Species studied were: corn, *Zea mays* L. cvs Seneca Chief and Chapalote; Teosinte, *Zea mexicana* (Schrad.) Reeves &

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[2] Abbreviations: LMX, late metaxylem; EMX, early metaxylem.

Mangelsd; Sorghum, *Sorghum bicolor* (L.) Moench. cv Pioneer 931; and Sudan Grass, *Sorghum sudanense* (Piper) Stapf. Seeds were sown in sandy loam soil in plots at the Central Experimental Farm, Agriculture Canada, Ottawa, in May 1986, and at weekly intervals thereafter to provide a continuing supply of young plants. For Seneca Chief only, additional young seedling material was supplied from two other culture methods: grown in 12-inch pots in the greenhouse, and in a nutrient mist culture system (following Zobel, personal communication). Plants from all three sources were collected at the selected stages with their roots intact and unwashed and were taken to the laboratory for measurement.

For selected plants an estimate of their leaf area was made by separating their leaves, photocopying the leaf array, and weighing the cut-out images. The numbers and lengths of all roots and the nodes from which they came were recorded, along with the presence and extent of soil sheaths. For each root a series of hand-cut transverse sections was made at measured distances from tip to base. The sections were stained with toluidine blue O (10) and viewed with bright field and phase contrast optics. At each distance the presence/absence of crosswalls and cytoplasm in the LMX elements was noted, and the extent of lignification of their sidewalls assessed by the transition in colour from purple (pectin) to green (lignin) (10). Tests of the capacity of the various zones of the roots to conduct the toluidine blue dye solution were made using a small vacuum assembly (11) when the roots were sufficiently robust to fit in the connecting cone (stele 0.7 mm diameter).

Measurements of stomatal resistance of Seneca Chief were made with a LiCor porometer on several days when the temperature was around 33°C and the relative humidity about 30%. Resistances were recorded on the large leaf of five plants of both the smallest and largest seedlings included in the morphological measurements, from mid morning until late afternoon. All plants were growing in well-watered soil so that any mid-day closure might be attributed to inadequate conductance rather than insufficient supply.

Presentation of Data

A scheme for presenting the data is outlined in Figure 1. The base of the stem (or crown) is attached to the mesocotyl (M) which becomes the primary root (P) where the relic of the seed (Z) is still attached. The first five nodes are shown bearing progressively younger roots; each node (i) has a particular number of roots n_i. In the case illustrated, the youngest roots (originating from nodes 5 and 4) have complete soil sheaths (except at the growing tip) shown by the extent of dotting on Figure 1, and so are of the type "sheathed" and denoted S. The roots from nodes 3 and 2 are older, have lost the soil sheath in the proximal region, and are classified as "partially sheathed" (PS). The oldest nodal roots (from node 1) and the primary root have lost their sheaths except near the apex and are classed as "bare" (B). For each root there was a record of its total length (r), and the length (at its proximal end) where the LMX was open, fully mature, without crosswalls and cytoplasm (r_0). The zone of closed living LMX (r_c) is shown black in Fig. 1. The results of the measurements are presented as a series of terms of the form

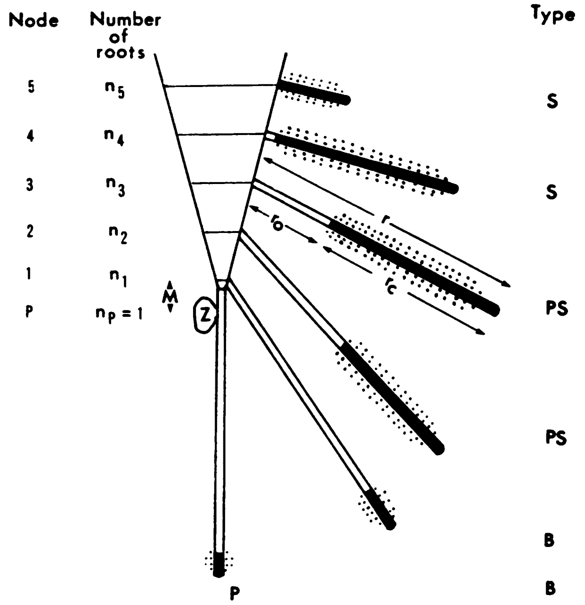

Figure 1. Scheme of measurement and description. The seed (Z) bears the primary root (P) and mesocotyl (M), from which arises the base of the stem. Nodal roots arise from five successive stem nodes. The number of roots at each node (i) is given as n_i. The presences of soil sheaths are indicated by dots; a small zone at the apex is always free of soil. The extent of the sheath determines the root type: sheathed roots (S) have sheaths throughout their length (except the apex); bare roots (B) have no sheath except for a short zone near the apex; partially sheathed roots (PS) are bare in the proximal region. If more than one type occurs at a node, both are recorded (*e.g.* B, PS). The part of the root with closed, living LMX is shown in black. Total lengths of each root (r), and of the root portion with open LMX (r_0) go to make up the terms describing the roots at each node, *viz.* Type (S, B or PS) n_i $\Sigma r_0/\Sigma r$. These terms are recorded in the tables. $(r - r_0) = r_c$ is the length of root containing closed, living LMX.

$$\text{Type (S, PS or B) } n_i \frac{\Sigma r_o}{\Sigma r}$$

for each node. For example, a seedling with only the primary root, which is partially sheathed, would have such a term as

$$\text{PS1}\,\frac{15}{35}.$$

But since n_p is always one for the primary root, this will be omitted. The term records that the root had a partial sheath and open LMX for 15 of its total 35 cm length. A plant at the stage of Figure 1, for example, would be described by six terms such as:

$$\begin{array}{lcccccc} \text{Node} & \text{P} & 1 & 2 & 3 & 4 & 5 \\ & \text{B}\,\frac{35}{40} & \text{B4}\,\frac{110}{160} & \text{PS5}\,\frac{100}{225} & \text{PS5}\,\frac{50}{125} & \text{S5}\,\frac{20}{75} & \text{S6}\,\frac{0}{35} \end{array}$$

This indicates that at node 1 there are four bare roots with a total length of 160 cm and open LMX in a total of 110 cm, and so on. In the tabulated results, the total length of roots per plant (sum of all the denominators) and total length of

Table I. *Xylem Development in Roots of Corn, cv. Seneca Chief, Grown in Nutrient Mist*

Lengths of open LMX relative to root length and leaf area. Primary roots only

Plant No.	Age	Leaf Area	Primary Root[a]	%LMX
	d	*cm²*		
1	14	46	0/12	0
2	14	25	0/20	0
3	14	32	0/21	0
4	16	11	0/22	0
5	14	21	0/24	0
6	10		0/25	0
7	14		6/29	21
8	15		12/42	29
9	21	102	15/45	33
10	21	140	16/46	35
11	21	170	24/54	44

[a] The fraction expresses:

$$\frac{\text{total cm root with open LMX}}{\text{total cm root}}$$

and the final column gives this as percentages.

open LMX per plant (sum of all numerators) are shown, and also given as a percentage. In the corn cv Chapalote, roots were found initiated on the mesocotyl. They develop after the primary root and before roots from node 1 and are recorded by a term in this position.

RESULTS

Corn cv Seneca Chief

Data from a set of seedlings grown for up to three weeks with their roots hanging free in the nutrient mist culture are shown in Table I. Nodal roots were late developing and insignificant. Primary roots only were recorded. The longest root measured was 54 cm. Up to 25 cm length the primary roots had only living LMX elements, but as they grew to 30 cm and more the proximal LMX opened, so that r_0 increased while r_c remained at 30 cm (for terminology see legend Fig. 1). In the largest plant rather less than half the root length had open LMX. There was of course no opportunity for these roots to develop soil sheaths which would have formed around the r_c lengths in the field.

Data from plants grown in pots in the greenhouse and in the field are recorded in Table II. Some seedlings formed their first tier of nodal roots between one and two weeks, while the primary root was as short as 17 cm; and by four to five weeks roots were elongating from as high as node 3. Roots of each tier started by being sheathed and remained so while the LMX was closed. As xylem maturation proceeded distally, they lost the soil sheath first at the proximal end, and later completely, becoming bare except for a short distance just proximal to the tip.

The roots did not continue to elongate at a constant rate. The primary roots of the oldest plants were little longer than those of the youngest, and the nodal roots from nodes 1 and 2 had similar lengths. Each root seemed to grow quickly to a length of 20 to 40 cm, and then grew slowly while roots of higher nodes were elongating. The opening up of LMX vessels proceeded acropetally in each root (as shown by the increasing ratio of numerator to denominator in each column of terms), but the production of new roots with closed LMX kept the ratio r_0/r well below one-half (final column).

Corn cv Chapalote (Table III)

This primitive variety of corn grew very vigorously and finally very tall (3 m). Its root systems matured faster than those of Seneca Chief (Table II). By three to four weeks the roots of the first two and sometimes three tiers, primary, mesocotyl and node 1 (2), had passed to the bare type and had developed high proportions of open LMX. Again, the production of new roots at the higher nodes kept pace with the maturation of LMX in the lower nodes so that r_0/r remained (except for plant 1) between 33 and 46%. Again, the mature roots have all reached maximum lengths of *ca.* 30 cm.

Sorghums (Tables IV and V)

The two sorghums had very small or no primary roots. The pace of development of their nodal roots is little different from that of Seneca Chief, with the node 3 roots just appearing by 4 weeks. The now familiar features of arrested elongation, acropetal maturation of LMX, and the maintenance of r_0/r around one-half to one-third were repeated.

Teosinte (Table VI)

Samples of teosinte were taken when the plants were older than any of the other varieties. Like the sorghums, it had insignificant primary roots. All the trends already stressed for root and LMX development were again clear. Even though the plants were up to 7 weeks old and had leaf areas up to 800 cm², extension of the older roots had not proceeded beyond 30 to 40 cm, nor had the proportion of open LMX (r_0/r) risen above one half (except for plant 2, 57%). Beyond this age and size the detailed analyses made in this study become inappropriately cumbersome.

Leaf Area

The relation between leaf area and length of root with open LMX (as a measure of balance between water requirement and supply) is explored for Seneca Chief in Figure 2. This is the variety for which most measurements are available, and all the plants whose leaf areas were measured, from the three

Table II. *Xylem Development in Roots of Corn, cv Seneca Chief, Grown in Soil in Pots (Plants 1-10) and in the Field (Plants 11-15)*
Lengths of root with open LMX relative to total root length by node of origin.

Plant No.	Age	Leaf Area	Roots[a]				Σ[b]	%LMX[c]
			Primary	Node 1	Node 2	Node 3		
	d	*cm*^{2}						
Pot plants								
1	14		S$\frac{0}{16}$	S4$\frac{0^{d}}{\,}$			$\frac{0}{16}$	0
2	11		S$\frac{0}{19}$	S4$\frac{0}{\,}$			$\frac{0}{19}$	0
3	11		S$\frac{5}{24}$	S4$\frac{0}{\,}$			$\frac{5}{24}$	21
4	11		S$\frac{6}{29}$	S4$\frac{0}{\,}$			$\frac{6}{29}$	21
5	14		S$\frac{0}{42}$	S4$\frac{0}{\,}$			$\frac{0}{42}$	0
6	11		S$\frac{0}{42}$	S4$\frac{0}{\,}$			$\frac{0}{42}$	0
7	11		S$\frac{19}{44}$	S4$\frac{0}{\,}$			$\frac{19}{44}$	43
8	8	29	PS$\frac{0}{22}$	S4$\frac{0}{9}$			$\frac{0}{31}$	0
9	11		S$\frac{26}{41}$	S4$\frac{0}{24}$			$\frac{26}{65}$	40
10	8	77	PS$\frac{5}{17}$	PS4$\frac{0}{74}$			$\frac{5}{91}$	5
Field plants								
11	33		PS$\frac{15}{20}$	S5$\frac{0}{52}$	S4$\frac{0}{12}$		$\frac{15}{84}$	18
12	33		B$\frac{17}{22}$	S4$\frac{0}{40}$	S4$\frac{0}{56}$		$\frac{17}{118}$	14
13	29	288	PS$\frac{18}{22}$	PS5$\frac{24}{150}$	PS3$\frac{0}{61}$	S3$\frac{0}{14}$	$\frac{42}{247}$	17
14	28	377	B$\frac{17}{23}$	B3$\frac{15}{101}$	PS4$\frac{10}{97}$	S4$\frac{0}{37}$	$\frac{42}{258}$	16
15	29	376	PS$\frac{20}{25}$	PS5$\frac{20}{151}$	PS4$\frac{22}{95}$	S4$\frac{0}{22}$	$\frac{62}{293}$	21

[a] For each node the term expresses: Root type, root number $\frac{\text{total cm root with open LMX}}{\text{total cm root}}$, where the type is bare (B), sheathed (S) or partially sheathed (PS). [b] For each plant the term expresses: $\frac{\text{total cm root with open LMX}}{\text{total cm root}}$. [c] The previous column expressed as percentages. [d] The nodal roots of tier 1 for plants 1 to 7 were short and not recorded.

culture systems, are included. The fitted line intercepts the area axis at 36 cm^2 and has a slope of 6 cm^2 cm^{-1} LMX (R^2 = 0.87).

Stomatal Resistance

On days of moderate evaporative demand no differences could be detected between the average stomatal resistance of small and large plants, or between morning and afternoon for either. For example on 2 July with the temperature 25 to 26°C and RH around 36% values of stomatal resistance in the range 1.4 to 4.3, mean 2.4 s cm^{-1}, were found for both sets of plants.

On a day of higher evaporative demand (Table VII) there is a suggestion that the smaller plants may be maintaining a higher stomatal resistance into the afternoon than the larger ones. While both sets of plants had resistances around 7 s cm^{-1} in the morning, by mid-afternoon the larger plants had reduced this to 3.9 s cm^{-1}, while the small plants maintained their morning level.

DISCUSSION

This study establishes for all five of the grasses examined the fact of long-delayed maturation of LMX vessels in the axile roots, and the correlation of this internal state (under field conditions) with a stable soil sheath on the root surface. It strongly suggests that the phenomenon is widespread in the grasses, probably very general. The recognition of a new structural and physiological complex requires the allocation

Table III. *Xylem Development in Roots of Field-Grown Corn, cv Chapalote*

Lengths of root with open LMX relative to total root length by node of origin

Plant No.	Age	Leaf Area	Roots[a]					Σ[b]	%LMX[c]
			Primary	Mesocotyl	Node 1	Node 2	Node 3		
	d	*cm²*							
1	22	230	$B\frac{25}{30}$	$B6\frac{112}{140}$	$B5\frac{134}{159}$	$S4\frac{0}{44}$		$\frac{271}{373}$	73
2	22	192	$B\frac{20}{23}$	$B5\frac{27}{95}$	$B5\frac{59}{108}$	$S5\frac{0}{33}$		$\frac{106}{259}$	41
3	23	257	$B\frac{20}{36}$	$B5\frac{62}{102}$	$B5\frac{66}{159}$	$S4\frac{0}{37}$		$\frac{148}{334}$	44
4	26	168	$B\frac{34}{41}$	$B1\frac{2}{4.6}$	$B4\frac{46}{105}$	$PS4\frac{17}{65}$		$\frac{99}{216}$	46
5	26	183	A[d]	$B6\frac{13}{82}$	$B7\frac{80}{191}$	$PS3\frac{11}{42}$		$\frac{104}{315}$	33
6	27	323	$B\frac{39}{46}$	$B5\frac{22}{92}$	$B5\frac{108}{168}$	$B4\frac{23}{90}$	$S4\frac{0}{23}$	$\frac{192}{419}$	46
7	27	284	$B\frac{13}{18}$	$B4\frac{60}{140}$	$B4\frac{69}{139}$	$B3\frac{12}{88}$	$S4\frac{0}{7}$	$\frac{154}{392}$	39

[a] For each node the term expresses: root type, root number, $\frac{\text{total cm root with open LMX}}{\text{total cm root}}$, where the type is bare (B), sheathed (S), or partially sheathed (PS). [b] For each plant the term expresses: $\frac{\text{total cm root with open LMX}}{\text{total cm root}}$. [c] The preceding column expressed as percentages. [d] A indicates absence of primary root.

Table IV. *Xylem Development in Roots of Field-Grown Sudan Grass*

Lengths of root with open LMX relative to total root length by node of origin.

Plant No.	Age	Leaf Area	Roots[a]				Σ[b]	%LMX[c]
			Primary	Node 1	Node 2	Node 3		
	d	*cm²*						
1	28	150	$B\frac{5}{6}$	$PS4\frac{8}{94}$	$S3\frac{4}{40}$	$S3\frac{0}{5}$	$\frac{17}{145}$	12
2	28	109	A[d]	$B4\frac{41}{87}$	$S3\frac{8}{49}$	$S2\frac{0}{3}$	$\frac{49}{139}$	35
3	28	109	A	$B5\frac{32}{106}$	$S3\frac{0}{41}$		$\frac{32}{147}$	22
4	29	190	$B\frac{6}{10}$	$B4\frac{34}{116}$	$PS4\frac{15}{89}$	$S3\frac{0}{10}$	$\frac{55}{225}$	24
5	29	122	$B\frac{8}{10}$	$B,S3\frac{10}{36}$	$S5\frac{7}{79}$	$S1\frac{0}{10}$	$\frac{25}{135}$	19

[a] For each node the term expresses: Root type, root number $\frac{\text{total cm root with open LMX}}{\text{total cm root}}$, where the type is bare (B), sheathed (S) or partially sheathed (PS). [b] For each plant the term expresses: $\frac{\text{total cm root with open LMX}}{\text{total cm root}}$. [c] The previous column expressed as percentages. [d] A indicates absence of primary root.

of a new name. We will use the term "immature apex" for this apical region of a root (which may extend up to 50 cm from the meristem) where the LMX elements are not yet differentiated into open vessels. Such immature apices have been demonstrated also in dicotyledons (6) but they are there not usually associated with soil sheaths.

The developmental study of the corn cv Seneca Chief (Table II) shows that all the roots of the young plant consist of these immature apices, with a very small proportion of open LMX, until the plant is about 4 weeks old, and has five to 12 roots in up to three tiers with a total length of about 2.5 m. Furthermore, it may be inferred from Figure 2 that until the leaf area reaches about 36 cm^2 the young plant is likely to have no open LMX at all. The measurements of the other four varieties, though taken from older plants, are consistent with a similar pattern of development, and suggest that they too would have roots consisting of only immature apices for several weeks.

The longitudinal permeability of a primary root like those in Table I may be calculated using Newman's formula (9):

Table V. *Xylem Development in Roots of Field-Grown Sorghum*

Lengths of root with open LMX relative to total root length by node of origin

Plant No.	Age	Leaf Area	Roots[a]					Σ[b]	%LMX[c]
			Primary	Node 1	Node 2	Node 3	Node 4		
	d	*cm²*							
1	28		$\text{B}\frac{11}{11}$	$\text{B4}\frac{58}{70}$	$\text{S5}\frac{0}{69}$	$\text{S4}\frac{0}{3}$		$\frac{69}{153}$	45
2	29		A[d]	$\text{B4}\frac{24}{77}$	$\text{S5}\frac{0}{54}$	$\text{S3}\frac{0}{2}$		$\frac{24}{133}$	18
3	29	236	$\text{B}\frac{15}{17}$	$\text{B,S4}\frac{49}{57}$	$\text{S5}\frac{0}{87}$	$\text{S5}\frac{0}{32}$		$\frac{64}{193}$	33
4	35	345	$\text{B}\frac{14}{14}$	$\text{B5}\frac{76}{124}$	$\text{PS7}\frac{94}{188}$	$\text{S4}\frac{0}{43}$		$\frac{184}{369}$	50
5	34	568	A	$\text{B,S4}\frac{75}{79}$	$\text{B,S4}\frac{70}{79}$	$\text{S4}\frac{0}{72}$	$\text{S4}\frac{0}{64}$	$\frac{145}{294}$	49
6	35	594	$\text{B}\frac{5}{5}$	$\text{PS4}\frac{40}{45}$	$\text{PS6}\frac{68}{130}$	$\text{S5}\frac{19}{108}$	$\text{S5}\frac{0}{68}$	$\frac{132}{356}$	37
7	36	700	$\text{B}\frac{6}{6}$	$\text{B,PS4}\frac{53}{61}$	$\text{PS5}\frac{82}{128}$	$\text{S4}\frac{0}{85}$	$\text{S4}\frac{0}{52}$	$\frac{141}{332}$	42

[a] For each node the term expresses: root type, root number $\frac{\text{total cm root with open LMX}}{\text{total cm root}}$, where the type is bare (B), sheathed (S) or partially sheathed (PS). [b] For each plant the term expresses: $\frac{\text{total cm root with open LMX}}{\text{total cm root}}$. [c] The previous column expressed as percentages. [d] A indicates absence of primary root.

Table VI. *Xylem Development in Roots of Field-Grown Teosinte*

Lengths of root with open LMX relative to total root length by node of origin

Plant	Age	Leaf Area	Roots[a]						Σ[b]	%LMX[c]
			Primary	Node 1	Node 2	Node 3	Node 4	Node 5		
	d	*cm²*								
1	41	418	$\text{B}\frac{6}{6}$	$\text{B4}\frac{80}{83}$	$\text{B,S5}\frac{81}{118}$	$\text{S8}\frac{56}{209}$	$\text{S4}\frac{0}{40}$	$\text{S2}\frac{0}{11}$	$\frac{223}{467}$	48
2	48		A[d]	$\text{B3}\frac{48}{52}$	$\text{PS9}\frac{169}{268}$	$\text{PS4}\frac{30}{92}$	$\text{S4}\frac{3}{24}$		$\frac{250}{436}$	57
3	48		$\text{B}\frac{10}{10}$	$\text{B6}\frac{140}{152}$	$\text{PS4}\frac{44}{127}$	$\text{S6}\frac{0}{93}$			$\frac{194}{382}$	51
4	49	343	$\text{B}\frac{6}{6}$	$\text{B6}\frac{141}{150}$	$\text{B4}\frac{103}{142}$	$\text{PS7}\frac{66}{214}$	$\text{S6}\frac{0}{113}$	$\text{S6}\frac{0}{33}$	$\frac{316}{658}$	48
5	51	821	$\text{B}\frac{7}{7}$	$\text{B4}\frac{121}{136}$	$\text{B4}\frac{29}{130}$	$\text{PS6}\frac{103}{290}$	$\text{S4}\frac{11}{86}$	$\text{S6}\frac{0}{42}$	$\frac{271}{691}$	39

[a] For each node the term expresses: root type, root number $\frac{\text{total cm root with open LMX}}{\text{total cm root}}$, where the type is bare (B), sheathed (S) or partially sheathed (PS). [b] For each plant the term expresses: $\frac{\text{total cm root with open LMX}}{\text{total cm root}}$. [c] The previous column expressed as percentages. [d] A indicates absence of primary root.

$$P_x = 12.5 \times 10^7 \pi \sum r^4$$

where r(cm) is the radius of the vessels and P_x is in units (10^{-2} cm^4 s^{-1} MPa^{-1}) = (mm^{3}s^{-1}/bar cm^{-1}). There are usually 6 LMX vessels ($r = 50$ μm) and 12 EMX vessels ($r = 12.5$ μm) (4, 7). Hence, in the zone where only EMX is open, $P_{x_E} = 1.15 \times 10^{-2}$, and where the LMX is open, $P_{x_L} = 1.47$ mm^3 s^{-1}/bar cm^{-1}.

These values may be used to make estimates of the pressure gradients which would be required to sustain transpiration under various conditions. Taking the critical case of a young seedling with 36 cm^2 leaf and only the EMX open, transpiring at a rate of 1 μg cm^{-2}s^{-1}, flow through the primary root would be necessary at 36 μg s^{-1} = 0.036 mm^3 s^{-1}. This would require a pressure gradient of $0.036/1.15 \times 10^{-2} = 3.13$ bar cm^{-1} = 313 kP$_a$ cm^{-1}. This is seen to be a considerable limitation.

The question raised at the initiation of this study, how long young plants may be thus limited in their axial water conductance, can now be answered with some precision for Seneca Chief as up to a leaf area 30 to 40 cm^2. Or, considering

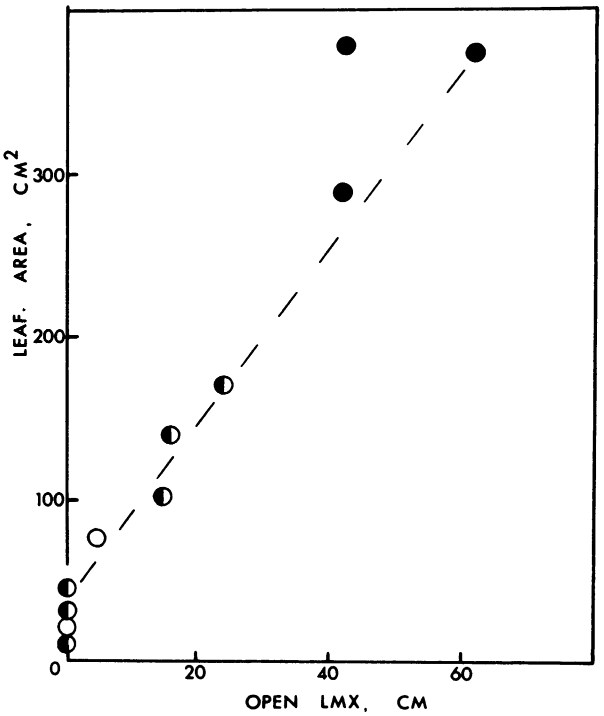

Figure 2. Plot of total leaf area *versus* total length of root with open LMX for each plant of Seneca Chief in which area measurements were made. Plants grown in the field (●), in pots in the greenhouse (◐), and in nutrient mist culture (○) are included. The regression of leaf area on length of root with open LMX is shown (a = 6 cm^2 cm^{-1} LMX, b = 36 cm^2, $R^2 = 0.87$).

Table VII. *Stomatal Resistance of Young Corn Plants of Two Sizes on a Day of High Evaporative Demand (June 23)*

Plant Height	Stomatal Resistance	
	Morning 29°C, 26–35% RH	Afternoon 33°C, 23–24% RH
cm	*s* cm^{-1}*, mean* ± *SD (n)*	
11–18	7.0 ± 2.8 (12)	7.1 ± 1.9 (12)
35–68	6.5 ± 3.0 (8)	3.9[a] ± 1.1 (8)

[a] Significantly different at 1%.

the gradient of negative water potential conducted downwards from the leaves, up to this time it will be steeply attenuated in the roots. With the maturation of the LMX vessels there is a very large change in root conductance, and in the slope of the water potential gradient. As the leaves expand they are drawing upon roots which have increasing lengths of high conductance tissue, at the rate of about 1 cm for each 6 cm^2 of leaf (Fig. 2). A similar discontinuity in development was found also in the leaf area/open LMX relation of soybean (6). The consequences of this for the paths of entry of water into roots have been discussed elsewhere (7), predicting that the main water entry will be found in old bare roots, very likely through the numerous small first and second order branch roots which invest them. The present question was whether leaves of young plants with only the EMX conducting in their roots might suffer from inadequate water supply. The pilot study reported here, while by no means conclusive, suggests that they may well do so. The data are meagre, but sufficiently encouraging to initiate a more detailed study of water limitation in young seedlings.

The comparison with four other grasses brought into prominence two surprising features common to all, the pause in elongation of older roots until younger ones reached the same length, and the constant proportion of r_0/r, the percentage of root with open LMX, at rather less than one half. The second of these features is a direct consequence of the first, since if all the roots continued to elongate, the proportion of r_0/r must constantly rise, as the length of r_c in each root is limited and falls with time. The pause in elongation cannot persist to later stages of plant growth since mature plants have many roots over a meter long. As the older roots resume their elongation the proportion of the root system with open LMX must rise to quite high values, even allowing for the large numbers of fresh immature apices produced at the higher nodes (4).

The functional importance of the immature apex as a site of nutrient accumulation and forwarding has been stressed by (8). Accumulation of K^+ was shown to levels as high as 400 mM in the vacuoles of the living LMX elements, giving new life to the hypothesis of Anderson and House (1) that the nutrients are released to the xylem sap by the breakdown of the crosswalls in vessel formation. Strong confirmation of this mechanism of accumulation and release has been provided for potassium and chloride in barley roots (5). Viewed in this way, the immature apices which are the sheathed roots of a young corn plant comprise five to 12 nutrient-accumulating reservoirs storing ions in the large vacuoles of their LMX elements, and releasing them upwards as the vessels mature, to be carried to the shoot with the transpiration water. As the plant grows larger, the relative importance of this supply of nutrients seems to dwindle. Calculations (7) balancing the potassium requirement of mature plants against the supply from immature apices suggest that only about 10% can be ascribed to this source. In old long roots considerable quantities of potassium must enter the mature zones. This again focuses attention on the activities of the branch roots, this time as sites of entry for K^+ and other nutrients. The structure and physiological capacities of these branch roots, long neglected, demand investigation with increasing insistence.

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LITERATURE CITED

1. **Anderson WP, House CR** (1967) A correlation between structure and function in the root of *Zea mays*. J Exp Bot **18:** 544–555
2. **Burley JWA, Nwoke FIO, Leister GL, Popham RA** (1970) The relationship of xylem maturation to the absorption and translocation of P^{32}. Am J Bot **57:** 504–511
3. **Duell RW, Peacock GR** (1985) Rhizosheaths on mesophytic grasses. Crop Sci **25:** 880–883
4. **Hoppe D, McCully ME, Wenzel CL** (1986) The nodal roots of *Zea*: their development in relation to structural features of the stem. Can J Bot **64:** 2524–2537

5. **Huang CX, Van Steveninck RFM** (1988) Effect of moderate salinity on patterns of potassium, sodium and chloride accumulation in cells near the root tip of barley: role of differentiating metaxylem vessels. Physiol Plant **73**: 525–533
6. **Kevekordes K, McCully ME, Canny MJ** (1988) Late maturation of large metaxylem vessels in soybean roots: significance for water and nutrient supply to the shoot. Ann Bot **62**: 105–117
7. **McCully ME, Canny MJ** (1988) Pathways and processes of water and nutrient uptake in roots. Plant Soil **111**: 159–170
8. **McCully ME, Canny MJ, Van Steveninck RFM** (1987) Accumulation of potassium by differentiating metaxylem elements of maize roots. Physiol Plant **69**: 73–80
9. **Newman EI** (1976) Water movement through root systems. Phil Trans R Soc Lond B **273**: 463–478
10. **O'Brien TP, McCully ME** (1981) The Study of Plant Structure: Principles and Selected Methods. Termarcarphi Pty, Melbourne, Australia
11. **St Aubin G, Canny MJ, McCully ME** (1986) Living vessel elements in the late metaxylem of maize roots. Ann Bot **58**: 577–586
12. **Vermeer J, McCully ME** (1982) The rhizosphere in *Zea*: new insights into its structure and development. Planta **156**: 45–61
13. **Wullstein LH, Bruening ML, Bollen WB** (1979) Nitrogen fixation associated with sand grain root sheaths (rhizosheaths) of certain xeric grasses. Physiol Plant **46**: 1–4