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Considerable study has been devoted to the ontogeny of tobacco in terms of gross morphology and metabolism. In comparison with the number of such studies we have as yet but few data on the ontogenetic anatomy of this important plant. Consequently it seemed desirable to investigate certain aspects of developmental anatomy characterizing the several distinctive growth stages of tobacco. Since preliminary observations had given some indications that marked variations in stem tissue occurred during growth, an experiment was undertaken to trace these changes throughout the life cycle.

METHODS

Forty-five plants of Little Turkish tobacco were used in this study. Plants were started from locally grown seed in flats early in the spring and the final samples were taken at the end of July. The plants were grown in well fertilized greenhouse soil. Temperature during the early part of the experiment was kept at 75° F during the day and 65° F at night. During the latter part of the experiment high outside temperatures prevented such close regulation. When approximately one inch high the plants were transferred to four inch clay pots. After the first sampling at the commencement of elongation, the remaining plants were transferred to eight inch pots.

Samples were taken from the plants at each of five distinctive stages of development as follows: (1) Commencement of elongation of the main axis when plants were actively vegetative; (2) Initiation of floral buds about one month before first floral buds became visible; (3) Anthesis, opening of first flower; (4) Full bloom of the inflorescence; and (5) Mid-maturity of fruit, when the first capsules began to turn brown. At each sampling sections were taken from the lower portion of the fourth internode of the stem as counted from the base of the plant. Stem sections were cut on the freezing microtome to a thickness of 100 microns, stained in Safranin and Fast Green, and mounted in "Clarite" (a synthetic resin proprietary).

The prepared slides were enlarged with a micro-projector to fifty diameters and measurements were made directly in microns at this enlargement by means of a special scale. The measurements were made as follows: Stem diameter, Pith diameter, Cortex radius, and Xylem radius. The pith diameter was taken from the internal phloem on one side to the opposite internal phloem of the stem. Cortex radius included all the tissue outside of the starch sheath. Xylem radius was measured from the cambial region to the innermost vessels.

Measurements were made on four separate diameters (eight radii) and the results averaged. This procedure was found to give accurate results. In addition the number of cells in the pith and cortex were measured by counting cells in ½ the pith and from ¼ to ⅛ of the cortex and multiplying by the appropriate number. Number

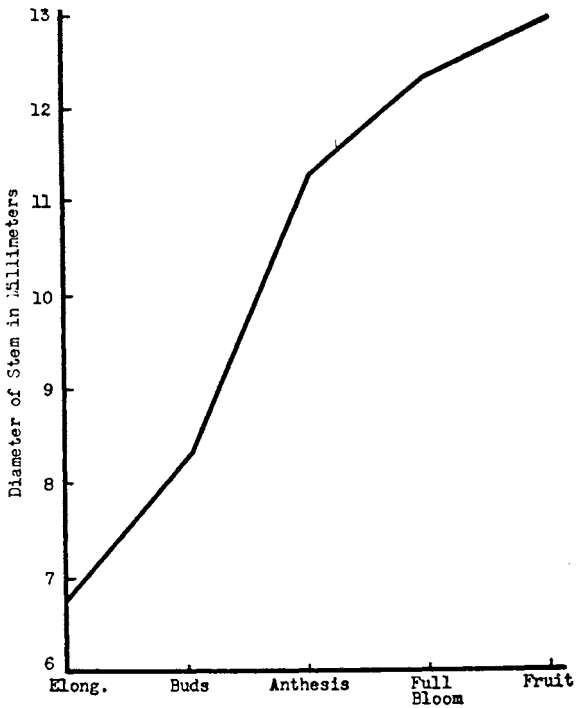

Fig. 1—The Diameter of the Basal Portion of the Stem of Little Turkish Tobacco at the Indicated Stages of Ontogeny.

of cells in thickness of the cortex was measured by averaging readings on eight different radii of each section. The average number of vessels in a field 400 microns in diameter in various regions of the xylem was also determined. Discussion is limited to generalized trends of the tissues at the various stages, but exact numerical data are given in accompanying figures and tables.

RESULTS

The total stem diameter showed its greatest increase in size concurrent with and just following the grand period of elongation but the rate declined to a great extent after anthesis. Slight enlargement of the stem continued throughout the duration of the study (Fig. 1).

The diameter of the pith, in contrast to stem diameter, showed a

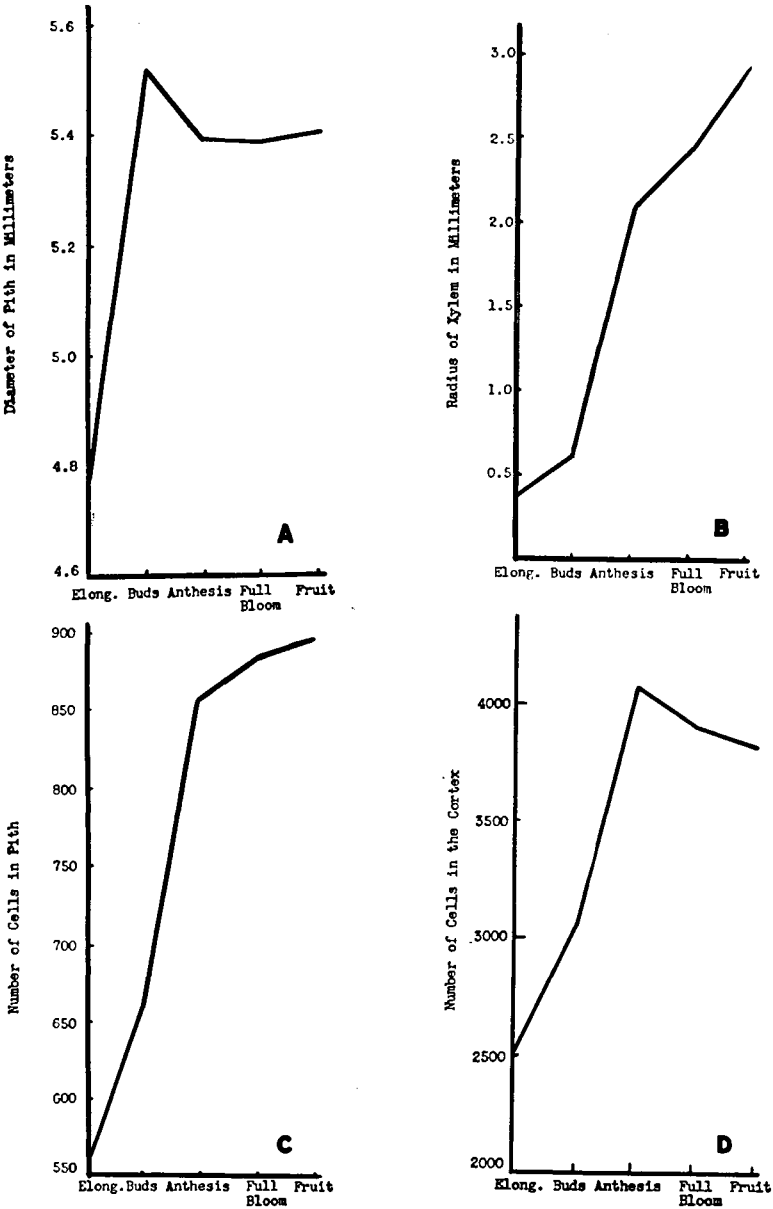

Fig. 2—Measurements made on the Basal Portion of the Stem of Little Turkish Tobacco at the Indicated Stages of Ontogeny.

A. Diameter of the Pith in Millimeter.
B. Radius of the Xylem in Microns.
C. Number of Cells in the Pith.
D. Number of Cells in the Cortex.

considerable enlargement during the elongation period but remained constant thereafter (Fig. 2). The slight difference between the pith diameter at the inception of floral buds and at the following stages did not appear to be significant. In contrast to this pattern of increase in diameter of the pith there was a slight increase in the cell number in the pith during the period of greatest elongation which was followed by a period of rapid gain in cell number after inception of floral buds when enlargement of the pith diameter had

TABLE I

Number of Vessels in each 400 Micron Field of the Xylem in the Stem of Tobacco at Various Stages of Development.

	Stages of Development				
	Elongation	Bud Primordia	Anthesis	Full Bloom	Seed
First Formed Vessels	10	10	11	11	11
Vessels in next 400 Microns	.....	7	7	7	6
Vessels in Youngest Xylem	.....	.....	4	4	3½

ceased. Subsequently the number of pith cells remained uniform (Fig. 2). The cause of this increase in cell number after the diameter of the pith had ceased to enlarge seems to be associated either with an impetus to cell division brought about by physiological changes occurring at inception of floral buds, or by a tendency of cells to divide upon exceeding a certain size. The first of these is supported to some extent at least by observations on other tissues such as xylem and cortex.

The increase in the radius of the xylem is slight during elongation, showing its greatest gain after inception of floral buds. Xylem formation declines after anthesis (Fig. 2). It is of interest to note that the xylem curve (Fig. 2) which is dependent on cell division very closely follows the curve for the number of cells in the pith, suggesting dependence of both upon a common factor. This developmental response seems to indicate a general impetus to cell division at the time of initiation of floral primordia.

On the basis of the number of xylem vessels in a standard field of 0.4 mm diameter, the rate of formation of new vessels slowly declined even though xylem radius was increasing (Table I). In the original secondary xylem there were about eleven vessels per field. This number of vessels per field was reduced to four in the youngest xylem. As can be seen in Fig. 3 the size of each vessel varies reciprocally with the number of vessels per unit area.

The radius of the cortex and the number of cells in radial thick-

ness of the cortex is essentially uniform throughout ontogeny (Table II). The uniformity of these two values is striking, being shown by no other tissue studied. The number of cells in the cortex does not show this uniformity, indicating an active division of cortical cells in a radial plane during early stages of ontogeny (Fig. 2).

TABLE II

Radius of Tobacco Stem Cortex Expressed in Microns and in Cell Thickness at Various Stages of Development.

	Stage of Development				
	Elongation	Bud Primordia	Anthesis	Full Bloom	Seed
Radius in Microns	800	810	800	800	830
Thickness in Cells	11	12	11	11	11

The cortex shows a response to an impetus for cell division during formation of the floral bud primordia similar to that shown by the pith and xylem. Cell division in the cortex stops at anthesis and all further increase in size (which actually occurs since the stem diameter and outer diameter of the xylem increases) is due to enlargement of the cells in the tangential plane.

TABLE III

The Cross-sectional Area in Square Millimeters of Various Tissues in the Basal Portion of the Stem of Tobacco at Various Stages of Ontogeny.

Stage	Pith	Xylem	Cortex	Total Stem
Elongation	17.56	3.27	14.95	35.78
Bud Primordia	23.97	11.29	18.85	54.11
Anthesis	22.90	50.24	26.26	99.40
Full Bloom	22.90	62.87	30.17	115.94
Seed	22.90	76.85	30.95	130.70

The areas occupied by the major tissues were calculated at the various stages in ontogeny (Table III). It is evident that the pith changes from the predominant element of the stem at the first sampling to the most subordinate in latter ontogeny. The xylem shows a reverse relationship to the pith, starting as the least in area and progressing to the major tissue of the stem during the reproductive stages. Thus tobacco as an "herbaceous annual" may become predominantly woody in character before the growing season is over. The cortex always maintains an intermediate position between the pith and xylem throughout ontogeny.

By comparing the rate of increase in number of cells in both pith and cortical tissue with their increase in area, it can be seen that the rate of cell division may not necessarily be the causative factor in increase in size of tissue. In the pith much of the cell division took place after enlargement had ceased whereas enlargement continued in the cortex after cell division had ceased.

The data of this study indicate that the period of stem elongation is one of rapid cell enlargement but not of rapid division of the cell in the stem. The differentiation of stem tissues and the division of the cells of the pith and cortex apparently occur in response to a stimulus supplied by the formation of floral primordia, or both formation of floral primordia and accelerated cell division are in response to some other common stimulus.

The stages of ontogeny selected for study in this paper are arbitrary to a certain extent but the data show that there is a definite change in stem tissues between each stage. With the exception of the formation of floral primordia which requires some estimation, each of the other stages is readily visible to the unaided eye by changes in gross anatomy. The anatomical data given here as well as physiological studies by other authors indicate that each of the stages chosen are important (transitional) phases in the ontogeny of tobacco.

SUMMARY

Little Turkish Tobacco was grown under normal greenhouse conditions in rich greenhouse soil. The anatomy of the basal portion of the stem was studied at five basic stages of ontogeny, viz; a. elongation of main axis, b. formation of floral primordia, c. anthesis, d. full bloom, and e. mid-maturity of fruit. The following behaviour was noted:

1. Stem diameter increased in size rapidly till anthesis after which time the increase was less rapid.
2. Pith diameter exhibited rapid enlargement till formation of floral primordia after which there was no further increase in size. In contrast to this the number of cells in the pith showed the greatest increase between initiation of floral primordia and anthesis.
3. Xylem enlargement followed a pattern similar to that of cell number in the pith, suggesting that both are dependent on a common impetus for cell division. Vessels in xylem per unit area decreased in number but increased in size during ontogeny.
4. Cortex radius and number of cells in thickness of cortex remained constant during ontogeny, but cell division took place in a radial plane, the increase in cell number following the same curve as that in the pith.

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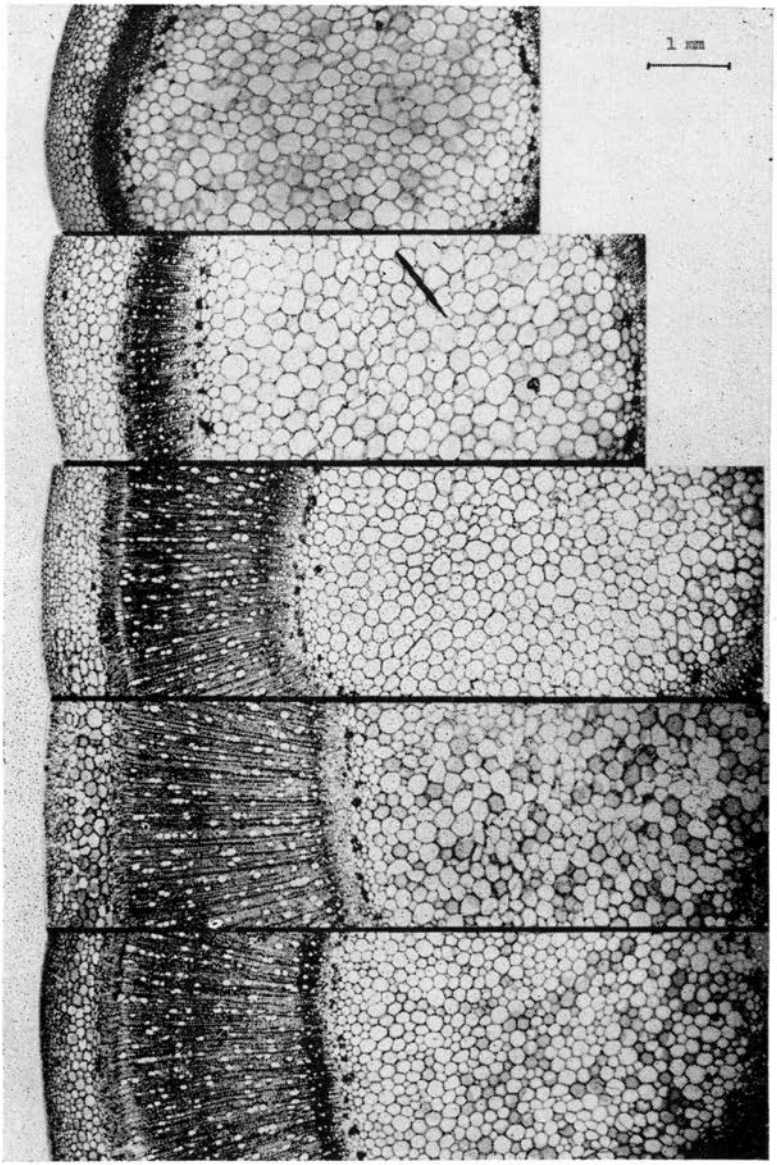

Fig. 3—Portions of the Cross Sections of the Basal Portion of the Tobacco Stem taken at various stages of Ontogeny. Reading from top to bottom: Elongation of Main Axis, Formation of Floral Primordia, Anthesis, Full Bloom, and Mid-Maturity of the Seed.