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DEVELOPMENT OF THE SUCCESSIVE CAMBIA IN ATRIPLEX HALIMUS (CHENOPODIACEAE)

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Serial sections of young and old woody stems of *Atriplex halimus* L. (Chenopodiaceae) were studied with the light microscope and analyzed cinematographically to search for possible connections between the cambia occurring in the primary vascular bundles and the successive cambia. The first extrafascicular cambia initiated from cambial bands which develop continuous with the still active intrafascicular cambia of the primary vascular bundles. The additional successive cambia also appear to start developing continuous with preceding still active cambia. The primary vascular bundles and the vascular strands of the secondary increments are all interconnected.

Introduction

In the Chenopodiaceae, Amaranthaceae, Nyctaginaceae, and in species of some other dicotyledonous families, secondary thickening deviates from that typical of most dicotyledons and is referred to as anomalous secondary thickening. This type of thickening was regarded as being derived from numerous successive cambia (SANIO 1863; DEBARY 1884; ARTSCHWAGER 1920; MAHESHWARI 1930; METCALFE and CHALK 1950; PHILIPSON, WARD, and BUTTERFIELD 1971; STEVENSON and POPHAM 1973; MIKESSELL and POPHAM 1976; WHEAT 1977; YARROW and POPHAM 1981; and others). Much attention has been paid to the question of whether each growth increment of secondary vascular tissue arises from a separate cambium layer or from a residuum of a previous cambium (BALFOUR 1965; PHILIPSON and WARD 1965; STUDHOLME and PHILIPSON 1966; ESAU and CHEADLE 1969; BAIRD and BLACKWELL 1980).

The important question, concerning the origin of the stimulus that initiates the development of each successive cambium, remained unanswered. It is well known that cambial activity can be triggered by signals originating from developing leaves (SACHS 1981). In dicotyledons with the usual secondary thickening, the cambium is continuous with the procambium (FAHN, BEN-SASSON, and SACHS 1972) and is thus in contact with the developing leaves. In monocotyledons with secondary thickening, the secondary vascular bundles are continuous with the primary ones (ZIMMERMANN and TOMLINSON 1970). The vascular strands of the secondary body of some species of the Chenopodiaceae (FAHN and SHCHORI 1968), of *Bougain-*

villea (ZAMSKI 1980), and of sugarbeet (ZAMSKI and AZENKOT 1981) anastomosed both tangentially and radially. We found no reports, however, about the existence of connections between the primary vascular bundles and the vascular strands of the secondary body.

For a more complete picture of the developmental pattern of the secondary vascular tissue of a plant with anomalous secondary thickening, we studied stems of various ages of *Atriplex halimus* both with conventional anatomical methods and with cinematographic analysis.

Material and methods

Stems of various ages were collected from *Atriplex halimus* L., a shrub growing on the Givat Ram campus of the Hebrew University, Jerusalem, and fixed in FAA. Young, terminal stem portions, about 10 cm long, were divided into smaller segments, embedded in paraffin, and sectioned with a sliding microtome. Woody stems were sectioned directly, without embedding. Serial sections were stained with a mixture of safranin and alcian green (TRACHTENBERG and FAHN 1981). In addition to the usual way of examining sections with a light microscope, the section series were photographed in sequence with a 16-mm ciné camera, and the resulting films were analyzed with a Vanguard 16-mm analyzer (ZIMMERMANN 1975).

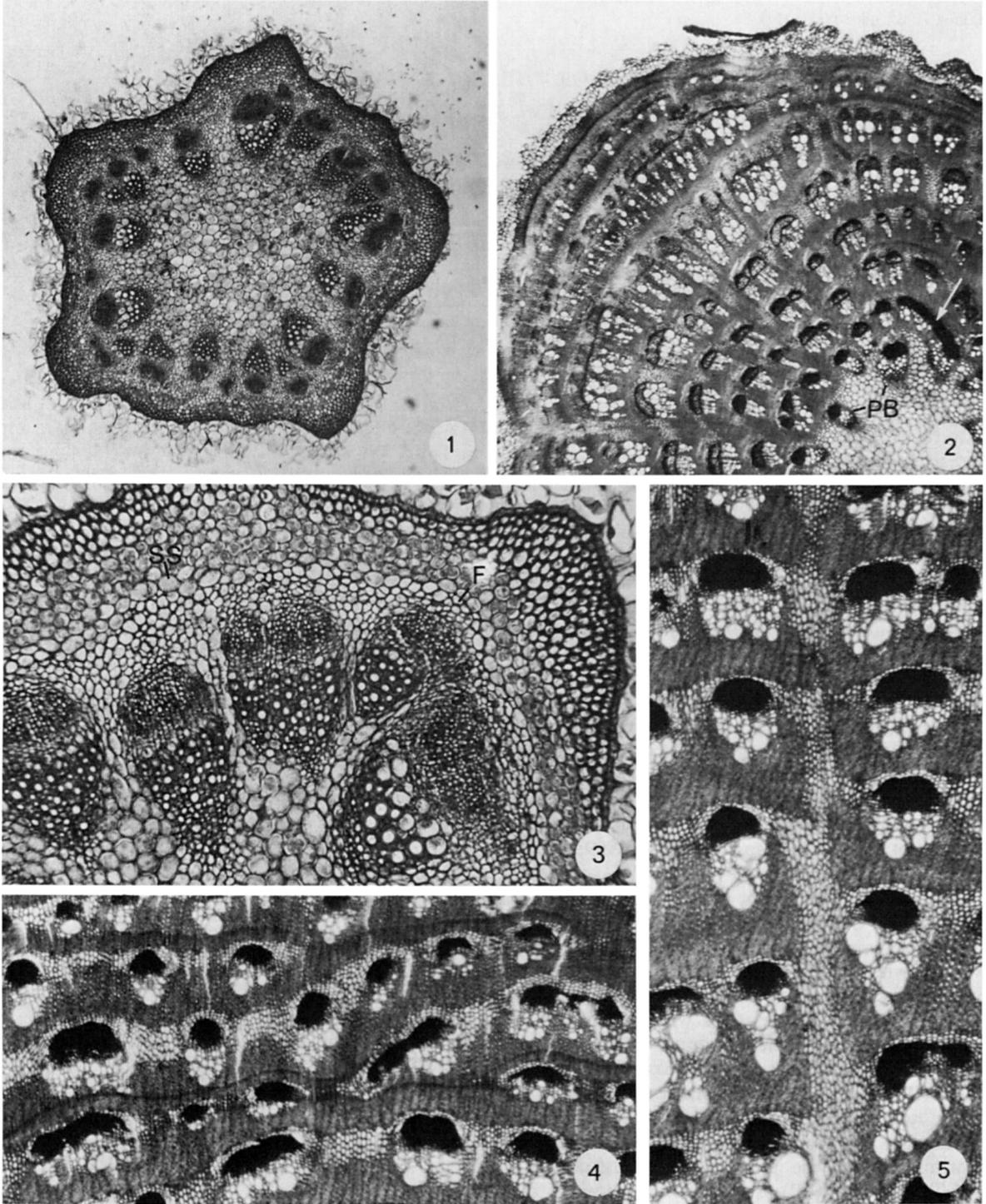
Observations

ANATOMY OF THE STEM

The structure of the primary body is, in general, similar to that of dicotyledons with the usual type of secondary thickening (figs. 1, 3). The one-layered epidermis of the young branch is covered with salt glands similar to those of the leaves. The cortex has an outer region of collenchyma, which is especially well developed at the stem angles, and an inner region of relatively large parenchyma cells. The

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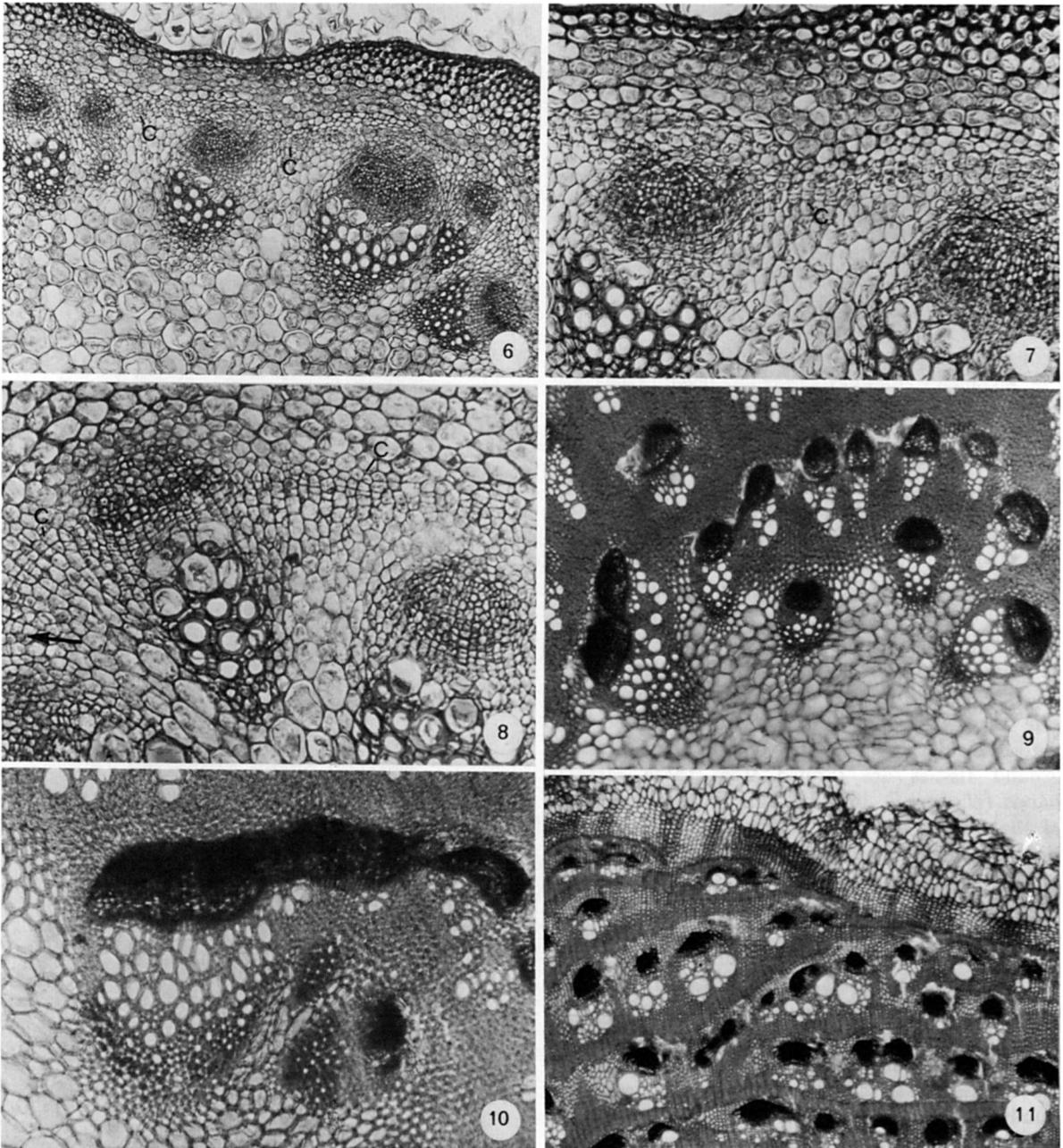


FIGS. 1-5.—Cross sections of stems of various ages. Fig. 1, Young stem in the region about 3 mm below the apex; $\times 38$. Fig. 2, Old stem with secondary thickening. A connection between a primary and two secondary bundles is indicated by an arrow; $\times 19$. *PB* = primary vascular bundles. Fig. 3, Young stem in the region about 2 mm from the apex; accessory cambia have not yet developed; $\times 118$. *SS* = starch sheath, *F* = fibers. Fig. 4, Portion of an old stem; merging of rings of vascular strands is seen; $\times 56$. Fig. 5, As in fig. 4, but showing conjunctive parenchyma in the form of a ray; $\times 56$.

cortex is delimited internally by a starch sheath. The outermost cells of the pericycle differentiate into fibers and form an almost complete cylinder (fig. 3). The primary collateral vascular bundles surround a relatively wide pith.

The secondary body (figs. 2, 4, 5) has a fibrous ground tissue in which vascular strands are embedded. Each strand consists of xylem toward the inside and phloem toward the outside. Bands of

lignified parenchyma, here referred to as conjunctive tissue, occur in association with the phloem strands. In many places the conjunctive tissue extends radially among the vascular strands. The extensions may sometimes occur in radial rows, reminiscent of rays (fig. 5). The vascular strands are arranged in more or less concentric rings. In many places, merging of rings can be observed (fig. 4).



FIGS. 6-11.—Cross sections of stems of various ages. Figs. 6-8, Stem in the region about 3 mm below the apex, showing cambial bands (C) extending from the intrafascicular cambia of primary vascular bundles into the pericycle outside neighboring bundles. On the left side in fig. 8 such a band is continuous with the intrafascicular cambium of a neighboring bundle (arrow); $\times 188$. Fig. 9, Old stem, showing arrangement of secondary vascular strands in continuation with primary bundles; $\times 94$. Fig. 10, Old stem; connection between a primary and secondary vascular bundle; $\times 150$. Fig. 11, Outer portion of an old stem; $\times 45$.

DEVELOPMENT OF THE FIRST
EXTRAFASCICULAR CAMBIUM

The three-dimensional vascular construction of the plant was studied with analytical films of cross sections (cf. fig. 1). When projected with the analyzer, the cross section appears to move. This is not real motion but the view of cross sections at successively different levels in the stem.

The stem has a $2/5$ phyllotaxis; leaf traces come off between the ridges of the stem. In the reconstruction of a sector of the stem from a film (fig. 12), the black vertical bands are the anastomosing primary vascular bundles. A leaf insertion is seen in the center near the top at *L*. Part of another one is at the lower left edge (*L*). The diagram shows the level of the stem where the first extrafascicular bundles (shown in grey), usually consisting merely of a single immature vessel and some phloem, branch off the edges of the primary vascular bundles of the inner ring (arrows). They anastomose with each other like the primary bundles.

As one follows the film in basipetal direction, more and more vascular traces branch from the primary bundles and "move" to the outer ring of the secondary bundles. Further down, they are larger and contain several vessels, some of them mature. The leaves are thus in direct contact with all of the primary and secondary bundles below them.

At about 3 mm from the shoot apex, the intrafascicular cambium of the primary vascular bundles is still active, and vessels at various stages of differentiation are present (figs. 6-8). In several places, cambial bands differentiate in interfascicular regions in continuation with the intrafascicular cambia. These cambial bands extend centrifugally into the pericycle (figs. 6-8) and tangentially outside the neighboring vascular bundles. The first extrafascicular vascular strands and the secondary ground tissues are formed from these cambial bands (cf. figs. 7, 10, 12). The deviating portions of the cambial bands appear to form the connections between the primary bundles and the first-formed vascular strands of the secondary body (figs. 9, 10). Such anastomosing connections are seen further down in the stem when the pattern of vascularization is followed in a film. In older parts of the stem with a well-developed secondary body, anastomoses occur between vascular strands of the same ring, as well as between those of neighboring rings. Occasionally a cambial band deviating from an intrafascicular cambium of a primary vascular bundle joins the cambium of a neighboring vascular bundle and does not enter the pericycle (fig. 8).

At the periphery of an older branch, various stages of cambial development can be seen (fig. 11). In places where a successive cambium is at its very early stage of development, it is initiated as an extension of a still active cambium of a previously formed vascular strand.

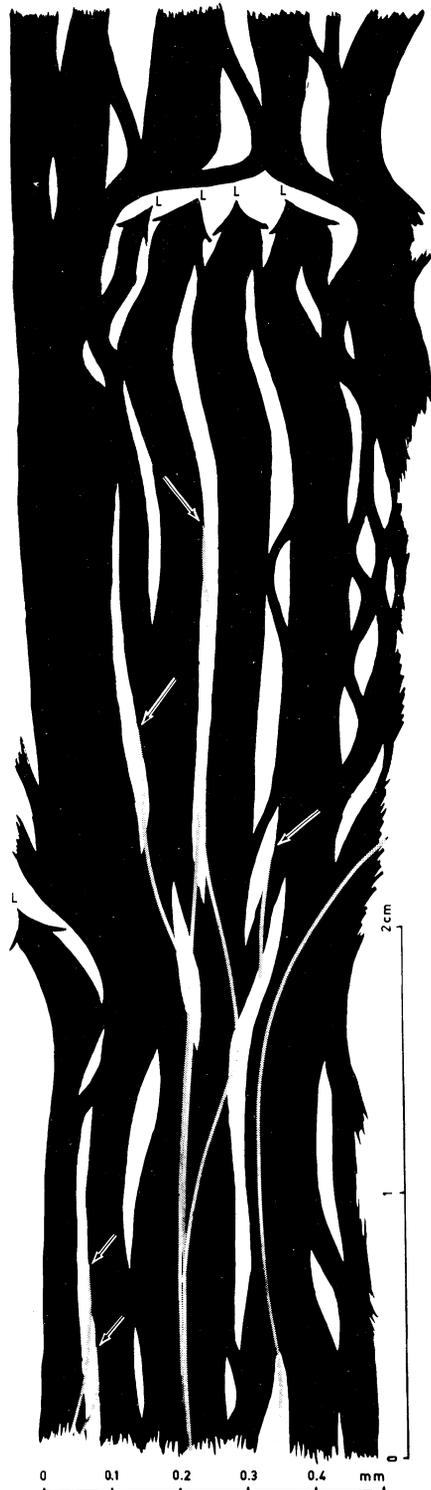


FIG. 12.—The vascular system of a sector of the stem reconstructed from a film in tangential view. The black vertical bands show the anastomosing primary bundles of the inner ring (those shown in cross section in fig. 1). Arrows indicate the points where small portions of the primary vascular bundles branch off and form the first ring of secondary strands. These extrafascicular (outer) strands are shown in gray. Note that the axial scale is foreshortened about 20 times. *L* = leaf traces.

Discussion

A major problem of the anomalous secondary growth in the Chenopodiaceae, Nyctaginaceae, and Amaranthaceae is the determination of the place of origin of the secondary increments. According to BALFOUR (1965), PHILIPSON and WARD (1965), and STUDHOLME and PHILIPSON (1966), these increments arise from one perpetually active cambium, whereas in the view of ARTSCHWAGER (1920), ESAU and CHEADLE (1969), and BAIRD and BLACKWELL (1980), each additional increment develops from a successively differentiating new cambium.

On the basis of our investigation of *Atriplex halimus*, we conclude that the first additional cambium, outside the primary vascular bundles, develops in the pericycle. It is initiated in continuation with the still active primary intrafascicular cambia, in the form of cambial bands which deviate into the pericycle. Additional successive cambia appear to start developing similarly, continuous with preceding still active cambia.

Connections among cambial segments, newly formed outside the phloem groups, and still active portions of previously formed cambia (cf. figs. 6–8) have been observed before (FAHN 1974, fig. 187, no. 1; BAIRD and BLACKWELL 1980). However,

these connections were interpreted as being formed after the separate initiation of a new cambium outside the phloem, whereas according to our present observations in *Atriplex*, the new cambia appear to be initiated in continuation with the previously formed cambia.

Our results also indicate that at later stages of development the cambial connections provide derivations which differentiate into vascular strands that connect the primary vascular bundles with the secondary bundles. The vascular connections among the secondary vascular strands of successive rings appear to develop similarly. Anastomoses of the vascular strands within the secondary body of *A. halimus* were observed by FAHN and SHCHORI (1968). The continuous initiation of the successive cambia at the periphery of the stem might well be triggered by signals received from developing leaves (SACHS 1981) via the vascular connections.

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