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PATTERNS OF DILATATION GROWTH IN *FICUS PUMILA* AND *FICUS SYCOMORUS*

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ABSTRACT

Dilatation growth occurs in the secondary phloem rays, in the axial secondary phloem parenchyma, and in the parenchyma of the cortex of *Ficus pumila* (a liana) and *Ficus sycomorus* (a tree). Dilatation growth in *Ficus pumila* is mostly the result of meristematic activity, but in *Ficus sycomorus* it is the result of both meristematic activity and increase in cell size. Dilatation meristem is formed in the rays in various patterns: in the center of the ray, at one or two of the ray's margins, in horizontal or diagonal strips (relative to the axis) in the ray, or in more than one pattern in a single ray.

Key words: Bark, cortex, dilatation, *Ficus pumila*, *Ficus sycomorus*, meristem, phloem rays.

INTRODUCTION

Dilatation growth is the way in which the bark achieves the increase in the circumference of the axis resulting from secondary growth. Dilatation growth is the result of two processes, which may appear separately or in combination: enlargement of cell size, and meristematic activity (Esau 1965). The meristematic activity appears in the secondary phloem axial parenchyma, the secondary phloem rays, and the cortex (Esau 1969; Roth 1981). Roth (1981, p. 149) distinguished among four types of dilatation meristems in rays: (1) a central ray meristem, (2) a marginal ray meristem, which may shift from side to side, (3) a multiple dilatation meristem, which develops in a large dilatation zone composed of several to many rays, and (4) a common central dilatation meristem. The fourth type is actually a combination of the first and the third types. Dilatation may be very irregular, resulting in the formation of whirled tissues and various shapes of phloem rays (Roth 1981). Dilatation has been known to occur in the genus *Ficus* (Roth and Cova 1969; Roth 1981), but has not been described in detail.

Dilatation is regulated by hormones. Both wounding and hormonal applications (Lev-Yadun and Aloni 1992) have been used to test previous hypotheses on such regulation. Whitmore (1962a,b, 1963) suggested that tangential stress caused by growth induces dilatation. Huber (1961) proposed that microscopic ruptures of cell walls through tangential tension resulted in the formation of wound hormones that induced dilatation growth. Lev-Yadun and Aloni (1992) found that ethylene promotes dilatation, and proposed that auxin in physiological concentrations (without external application) inhibits dilatation, partially supporting the hypothesis suggested by Huber (1961).

The objective of this study was to examine the fate of the phloem rays of two species of the same genus

(*Ficus*) differing in habit, a liana (*Ficus pumila* L.) and a tree (*Ficus sycomorus* L.), as part of an effort to understand the regulation of ray differentiation (see Lev-Yadun and Aloni 1995 and citations therein).

MATERIALS AND METHODS

Thirty-five branches 5–50 mm in diameter from two large clones of *Ficus pumila*, and ten trunks 200–500 mm in diameter from ten different trees and ten branches 10–30 mm in diameter from five different trees (two from each tree) of *Ficus sycomorus*, were examined in the study. All specimens were growing in the coastal plain of Israel in the vicinity of Tel Aviv. Both species are cultivated in Israel: *F. sycomorus* for several thousand years and *F. pumila* in the last century. The branches and trunks of both *Ficus* species had only their first thin phellem. The branches and trunks of *F. sycomorus* were still green at the points of sampling, indicating that only a thin layer of the bark was cut off by cork formation and most photosynthetic parts of cortex were still intact. Rhytidome formation in *F. sycomorus* had started in some spots by the time the branches or trunks reached about 150 mm in diameter, but usually a cover of rhytidome was still incomplete when the trunks were 500 mm in diameter (Lev-Yadun, unpublished data). The bark samples of the main branches of *F. pumila* were taken 0.2–1.5 m from the leaves, and in *F. sycomorus*, 5.0–7.0 m from the leaves. Transverse and tangential sections 20–60 μm thick were prepared from fresh material with a Reichert sliding microtome. The tangential sections of five of the thickest branches of *F. pumila* (bark width 4.5–7.0 mm) and of five of the thickest trunks of *F. sycomorus* (bark width 12.5–21.5 mm) were made at mm intervals to follow the changes in bark structure from the last-formed phloem to the cortex.

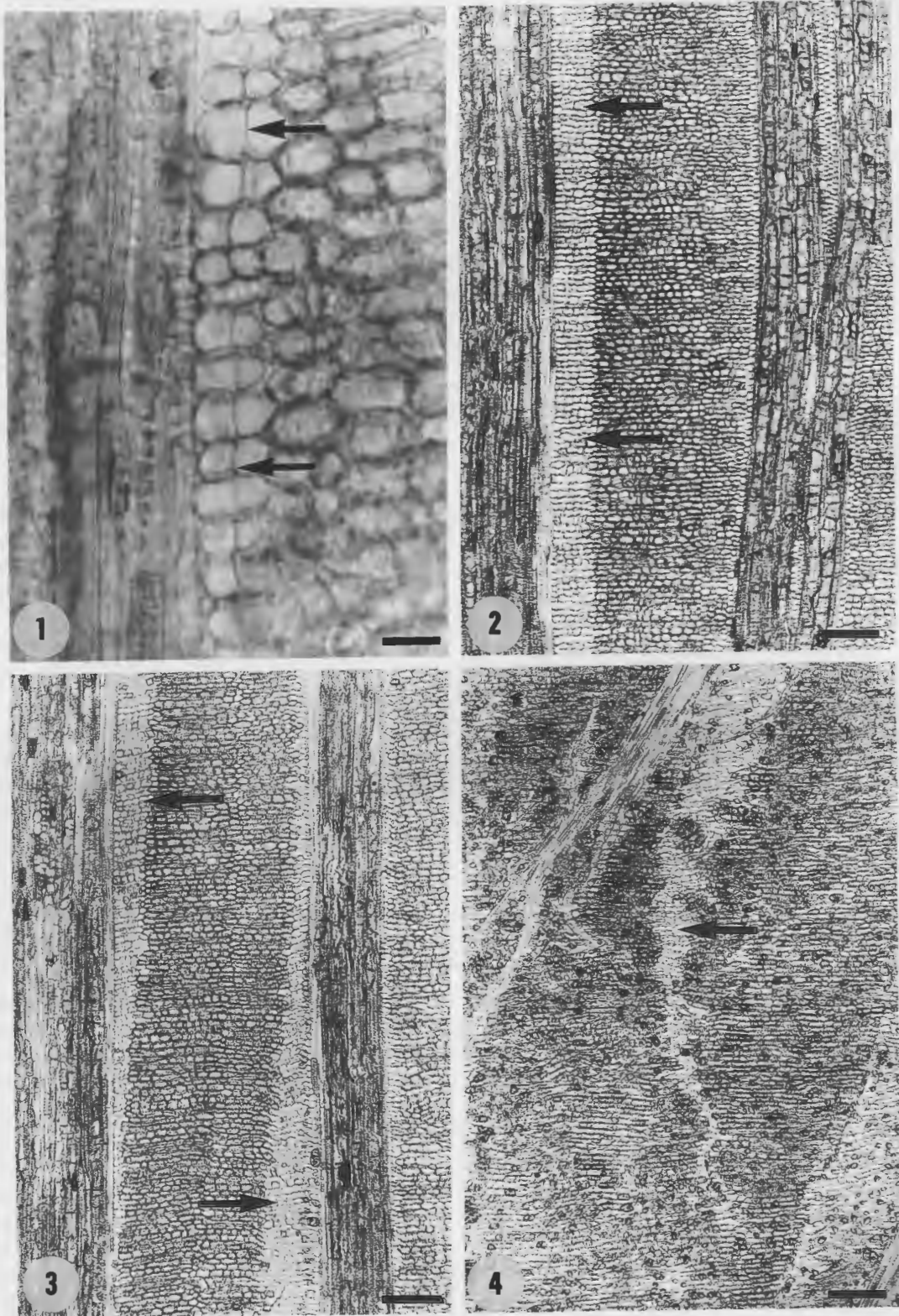


Fig. 1-4. *Ficus pumila*. Tangential section of secondary phloem rays.—1. Margin of a ray showing a narrow dilatation meristem (arrows).—2. Ray showing a wide dilatation meristem (arrows).—3. Ray showing two dilatation meristems (arrows), one on each side.—4. Ray showing an oblique dilatation meristem (arrow). (Fig. 1, bar = 22.5 μm ; Fig. 2-4, bars = 144 μm .)

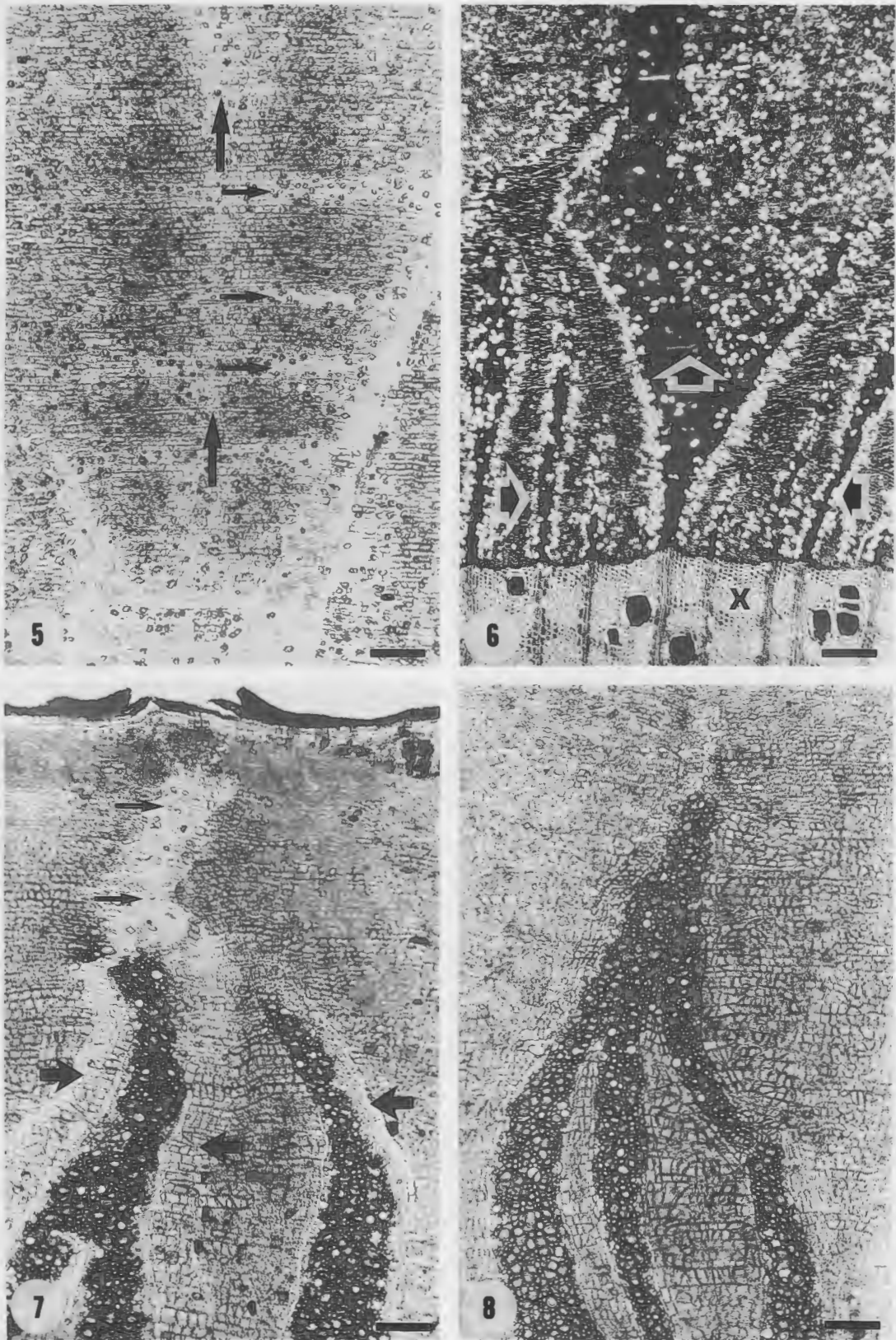


Fig. 5-8. *Ficus pumila*.—5. Tangential section of a secondary phloem ray showing both axial (large arrows) and lateral (small arrows) dilatation meristems.—6-8. Transverse sections of secondary phloem rays.—6. Rays that have strong (large arrows) or no or limited dilatation (small arrows). Xylem (X) is at the bottom. Polarized light.—7. Shows dilatation both in the rays (large arrows) and in the cortex (small arrows).—8. Shows triangles of phloem (dark area) within the rays. (Bars = 144 μ m).

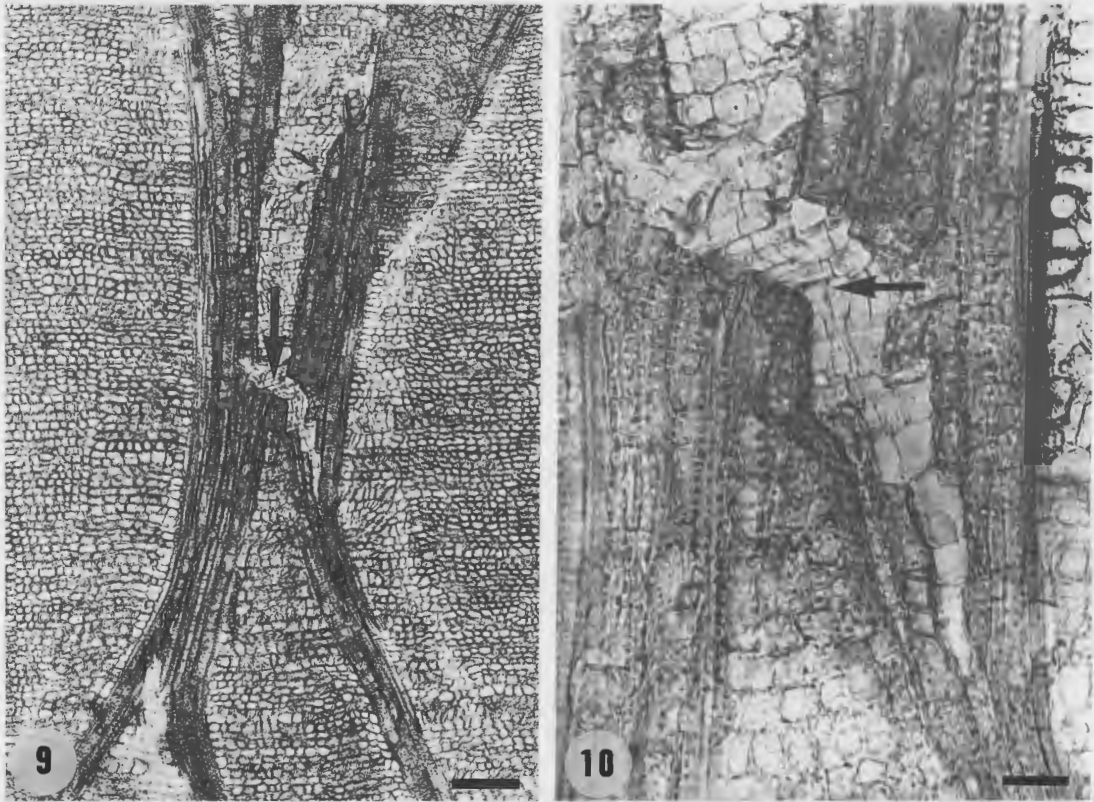


Fig. 9–10. *Ficus pumila*. Tangential section of axial system showing limited dilatation (arrow). (Fig. 9, bar = 144 μm ; Fig. 10, bar = 37 μm .)

The sections were stained with safranin and fast-green, and mounted in Canada balsam (Johansen 1940).

RESULTS

Dilatation growth in *Ficus pumila* originates mainly from phloem rays, but also from axial secondary phloem parenchyma and cortex. In all cases, a dilatation meristem is formed, and the cells of the new tissue remain almost the same size. The dilatation of the rays was found in a narrow band along the ray's edge (Fig. 1), in a wide band along the ray's edge (Fig. 2), or on both sides of the ray (Fig. 3). In some phloem rays the dilatation occurred in the middle of the ray. The dilatation meristem in the middle of the ray was formed either in an axial direction, in an oblique direction (Fig. 4), or it was formed as one longitudinal strip crossed by several lateral ones (Fig. 5). The phloem rays differed very much in the amount of dilatation. Some phloem rays did not dilate at all, whereas others dilated so much that they became fan shaped in transverse section (Fig. 6), and all intermediate patterns were regularly found. Dilatation of the cortex was sometimes continuous with the dilatation meristem of the phloem rays (Fig. 7). The axial parenchyma showed only limited dilatation, and thus remained as typical narrow tissue triangles in between the dilated zones (Fig. 8–10).

In *Ficus sycomorus*, prior to initiation of dilatation, the secondary phloem showed a regular pattern of ray distribution (Fig. 11). Dilatation started at different times in different zones (Fig. 12). It occurred mainly in the phloem rays, and was the result of both meristematic activity (Fig. 13, 14) and cell enlargement (Fig. 15). The axis of dilatation was not always parallel to the trunk axis (Fig. 16). The axial phloem parenchyma showed only limited dilatation, and when this occurred, the remains of the previous axial orientation could be seen to some extent both in cross sections (Fig. 17) and in tangential sections (Fig. 18). Like that found in *F. pumila*, dilatation of the cortex was sometimes continuous with the dilatation of the rays.

As was described above, the dilatation tissues of the two species studied share many general aspects, and the main difference is that in the tree (*F. sycomorus*) cell expansion contributed significantly to the dilatation, while in the vine (*F. pumila*) cell divisions were the main component of dilatation.

DISCUSSION

In this study, I compare naturally occurring dilatation patterns in two *Ficus* species, a liana (*F. pumila*) and a tree (*F. sycomorus*), and show both similar and different types of dilatation in their rays, axial phloem parenchyma, and primary cortex.

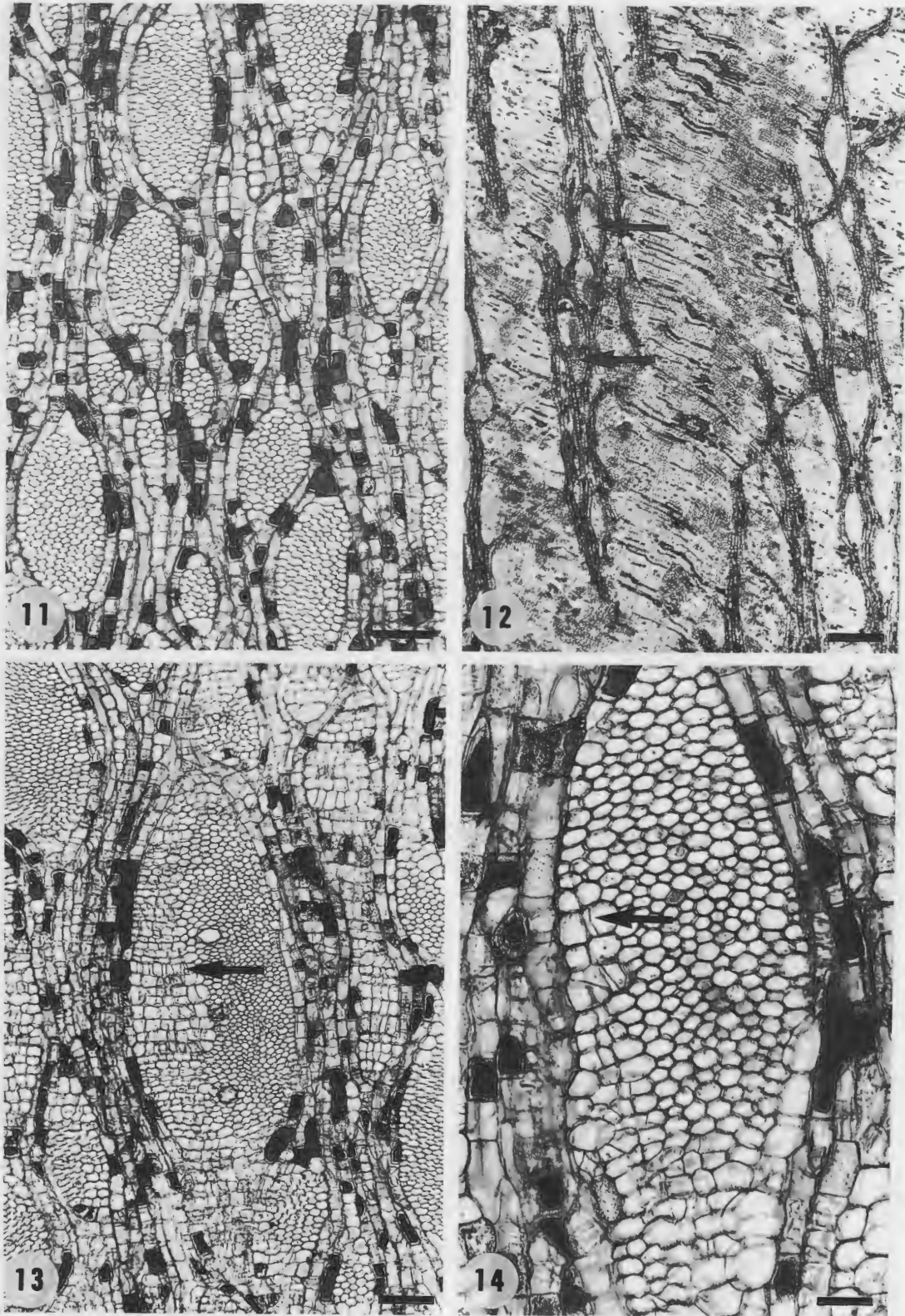


Fig. 11-14. *Ficus sycomorus*. Tangential sections.—11. Shows regular ray pattern before dilatation—12. Shows large zones with and small zones without (arrows) dilatation.—13-14. Two rays showing dilatation meristems (arrow) in parts of each ray. (Fig. 11, 13, bars = 144 μm ; Fig. 12, bar = 580 μm ; Fig. 14, bar = 58 μm .)

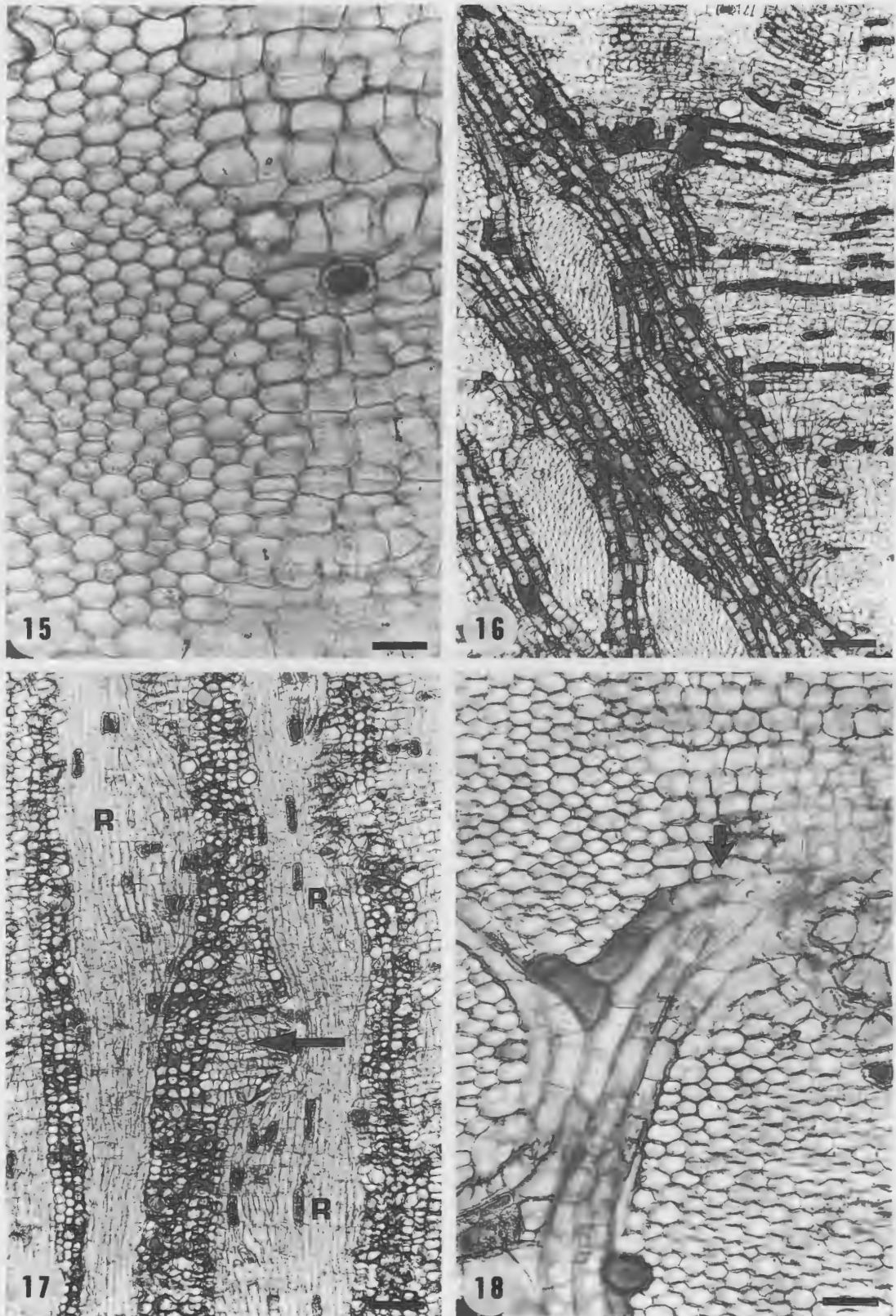


Fig. 15–18. *Ficus sycomorus*.—15–16. Tangential sections.—15. Shows dilatation formed by cell enlargement. The ray cells that remained their original size are on the left.—16. Shows that dilatation was not parallel to the axial system.—17. Transverse section showing limited dilatation in the axial phloem parenchyma (arrow). R = ray.—18. Tangential section showing dilatation of the axial system. The dilatation left “blind” branches of the remaining axial system (arrow). (Fig. 15, bar = 37 μm ; Fig. 16, 17, bars = 144 μm ; Fig. 18, bar = 58 μm .)

The major contribution of the phloem rays to dilatation growth, as found in *Ficus pumila* and *Ficus sycomorus*, is a common phenomenon (Holdheide 1951; Roth 1981). This was also found in *Citrus sinensis* (L.) Osbeck (Schneider 1955), *Tilia* sp. (Esau 1969) and in other species (Fisher and Stevenson 1981; Fisher and Mueller 1983). The axial parenchyma participates in dilatation growth in many species (Chattaway 1953, 1955; Roth 1981), but in these two *Ficus* species the contribution of the axial parenchyma to dilatation is minor. More dilatation was found in the axial parenchyma of *F. sycomorus* than in *F. pumila*. I suggest that the differences in size between these two species determine this quantitative, but not qualitative aspect. I also suggest that the differences in size and the continuously increasing distance from the main hormonal sources (leaves, buds and roots) (the leaves and buds were usually about 1 m away from the sampling point on the main branches in *F. pumila*, and at least 5 m away in *F. sycomorus*) may be involved in the difference between the two species in regard to meristematic activity and cell expansion. The fact that at a greater distance from leaves and in older trunks more dilatation occurred agrees with the results and hypothesis of Lev-Yadun and Aloni (1992) that auxin in physiological concentrations inhibits dilatation.

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