

INDUCED RING-FASCIATION IN TOMATO PLANTS

BY G. P. MAJUMDAR

(*Biological Laboratories, University of Dacca, Dacca*)

Received June 23, 1954

THE phenomenon of Fasciation has been described under two main types: Band-fasciation and ring-fasciation. Band-fasciation is of wide-spread occurrence in the vascular plants (halophytes and hydrophytes are excepted), and it affects almost all their parts (Masters, 1869; Worsdell, 1915; White, 1948).

Ring fasciation is, on the other hand, rare in nature. Instead of becoming flattened as in band-fasciation the cylindrical main axis becomes enlarged and hollow "with the inner cavity somewhat freely exposed to the atmosphere" (White, pp. 326-27). White in his forty pages review of the phenomenon devoted only one small paragraph to ring-fasciation.*

Gorter (1951) and Wardlaw (1953) could induce ring-fasciation in tomato plants by the application of TIBA to their vegetative shoot apices. Their reports are illustrated with excellent sketches and photomicrographs. As this short paper has been prepared on the data provided by these illustrations I consider it necessary to give a short description of the latter.

DATA

Gorter's Fig. 13 D (Pl. I) and photo. 4 A show the development of a ring-like out-growth (meristem) below the organic apex of the shoot after the application of TIBA. Figs. 5, 3 and 4 (Pl. II) show successive stages in the development of this outgrowth into a tubular ring-fasciated axis, and its resolution into a number of growth centres (when compared with the photo. 4 C they are flower primordia). Photos. 3 A and 3 B clearly show the changing over of the vegetative into flowering shoot apex on TIBA treatment. Photos. 4 B, 5, 6 and 7 show the internal structures of the treated axes in transverse (*t.s.*) and longitudinal (*l.s.*) sections. 4 B shows two treated seedlings in *l.s.*; 5, *t.s.* of ring-fasciated axis showing two rings of vascular tissues, the inner with inverse orientation with fairly advanced stage of tissue differentiation (*cp.* Worsdell, Fig. 26; and Wardlaw, Fig. 1). Photos. 6 is a *l.s.* of ring-fasciated axis with somewhat well-developed central bud,

* *Bot. Rev.*, 14, 319-58.

and 7, a *l.s.* through young ring-fasciated axis resolved into separate growth centres (*cp.* Fig. 4, Pl. II).

Wardlaw's figures are all photomicrographs. Fig. 1 is a *t.s.* of the ring-fasciated axis at the level of the tip of the organic apex (central bud). It shows the hollow stem, two concentric rings of vascular tissues, the inner with inverse orientation, and the free tip of the apical dome; Fig. 2 is a *t.s.* of the same axis taken just below the organic apex; it shows three concentric rings of vascular tissues with normal orientation in the outer and inner rings, but inverted in the middle one. The inner ring is still in the provascular stage with xylem and phloem elements just differentiating. Wardlaw described the inner ring as belonging to the central bud. Fig. 3 is a *t.s.* of the same axis below the so-called ring-fasciated region showing the normal stem structure (herbaceous woody type).

A close examination of the figures and photographs described above bring out the following points: When TIBA is applied to the vegetative shoot apices of tomato plants (i) the growth and elongation of the apical dome is considerably slowed down, (ii) a ring-like lateral outgrowth takes place from the subapical region of the dome, (iii) the ring-like outgrowth then develops into a tubular axis enclosing the organic apex (Wardlaw), and resolved into a number of growth centres which ultimately develop into a ring-fasciated inflorescence (Gorter), (iv) the ring-fasciated axis shows two concentric rings of vascular tissues, the outer with normal and the inner with inverse orientation of xylem and phloem, (v) at the level of the origin of the tubular axis there occur three rings of vascular-tissues, the outer and inner with normal and the middle one with inverse orientation, and (iv) as a result of TIBA application the vegetative apex is changed into a flowering shoot apex (Gorter).

DISCUSSION

The whole problem may be discussed under the following two heads: (1) the method of origin of the ring-fasciated shoots in tomato plants under TIBA treatment, and (2) the origin and nature of the two and three concentric rings of vascular tissues in the ring-fasciated region and their absence lower down in the axis (Wardlaw).

1. *The method of origin.*—Since the days of Linnaeus those who made special studies of the phenomenon tried to explain the true morphology of the ring- and band-fasciated shoots. Linnaeus (1751) thought that fasciation of the axis was the result of an increase and fusion (congenital) of a large number of growth points or buds. Masters (1869) and Reed (1912) supported Linnaeus. Moquin-Tandon (1841) on the other hand considered

fasciation as the result of the flattening or enlargement of a single growing point. This was supported by Compton (1911) on anatomical grounds. Worsdell (1905) however, gave altogether a different explanation. According to him fasciation is the result of "a congenital fusion of an unusual number of branches fusing in one plane because of reversion to the ancestral form." With regard to ring-fasciation Worsdell thinks that it is an attempt on the part of the cylindrical organ to effect a multiple dichotomy (p. 90).

Nestler (1897) who made a special study of ring-fasciation suggested three possible ways of its formation, namely, (i) by the united growth of a large number of buds (growth points) as suggested by Linnaeus, (ii) by the formation of a ring of cells derived from the distal apical cell of the terminal bud, and (iii) as a result of the arrest of the growth of the distal region of the shoot apex followed by the continued enhanced growth of the embryonic tissue below (Wardlaw, p. 213). In the last two methods only a single growing point is involved (*cp.*, Moquin-Tandon).

Wardlaw supports Moquin-Tandon but figures and photographs of Gorter appear to support Linnaeus.

Schoute (1936) envisaged three superposed zones in the apical meristem each behaving biochemically differently but in correlation with one another. Wardlaw agrees with him and regards the formation of ring-fasciation in his material as due to the increased growth of the third zone and the arrested or very slow growth of the upper two zones of the shoot apex.

Cup-like limited outgrowth of the thalamus or torus is a common feature in the *Discifloreae* (Bentham and Hooker). One school of floral morphologists think that the carpel is formed by the outgrowth of the torus in the form of a rim-meristem, and particularly so in the case where the organic apex is converted into a basal placenta bearing the ovule (*cp.*, also the proliferation of the apex within the ovary). Wardlaw has cited a large number of workers who have reported increased growth of the subapical region of the apical dome under chemical treatment. Gorter's figures and photomicrographs are very convincing in this regard.

The development of a ring-like outgrowth (meristem) enclosing and outgrowing the organic apex under chemical treatment, and its final development into a tubular axis (Wardlaw) or into a ring-fasciated inflorescence (Gorter) may be regarded as quite an established fact [*see* Gorter's Figs. 5, 3, 4 (Pl. II) and photo. 4 C].

2. *Presence of two and three concentric vascular rings, one with inverse orientation of tissues* (Photos. Gorter's 5 and 6; Wardlaw's 1 and 2).—

Professor Wardlaw is a skilled Plant Surgeon, and whatever structural differentiation he notices in his surgical cases he regards them as prototypes of normal happenings in normally developing plants. He, therefore, believes only in the detached origin and basipetal differentiation of the provascular tissues in the shoot apices of vascular plants though there are many who have reported a continuous acropetal differentiation in their materials (Esau, 1954). The occurrence of double rings of vascular tissues, one with normal and the other with inverse orientation, he explains by saying that "pre-vascular tissue will be differentiated in relation to both the outer and inner flanks of the (same) ring meristem, and two vascular cylinders with their phloem oriented to the outer and inner surfaces respectively, will be formed" (p. 214). It is not supported by facts. In a recent review on the Primary Vascular Differentiation in Plants Esau (1954) has observed that "these deductions (drawn from surgical studies) are for the most part hypothetical because they are not based on critical histogenetic evidence" (p. 80).

The presence of the third vascular ring with normal orientation of tissues in Fig. 2 is explained by Wardlaw as originated from the apical meristem (*i.e.*, independent origin with basipetal differentiation). The absence of the inner and middle rings in Fig. 3 is explained by him (p. 212) as due to their fading out lower down in the axis without having made any connection with the stelar ring of the main axis, or in other words, their origin is detached and function perhaps undecided.

Gorter also holds similar views with Wardlaw on the origin of the outer and inner rings of vascular tissues in the ring-fasciated axis. She says that the prevascular tissue has its inception below the outer and inner flanks of the ring meristem, and collateral vascular tissue is differentiated in relation to both the outer and inner sides of the tube-like axis, *i.e.*, two separate vascular rings are seen in cross-section connected by only parenchymatous tissue (Photos. 5 and 7). Neither Gorter nor Wardlaw appears to have studied their ring-fasciated shoots in serial transverse and longitudinal sections and that alone would have shown the continuity or otherwise of the three concentric rings of vascular tissues.

Gorter and Wardlaw would not accept the presence of three concentric rings of vascular tissues as due to the invagination of the same stelar ring. Gorter's sketch 7 (Pl. II) and Photo. 4 B, as far as I can see, clearly show invagination of the axial stele. She writes to me (private communication) "I cannot see that in Photograph 7, which is a longitudinal section of the tubular axis, the inner and outer rings are continuous. These photographs have to give the final answer." That is very true. But when this photograph

is critically examined its very nature and structure show that it is an oblique section of the type of treated apex depicted in her sketches 3 and 4 (Pl. II). Moreover, a scrutiny of this figure under magnification indicates a continuity of the outer and inner vascular tissues through a provascular meristem over the central parenchyma in the right half of the photograph.

Neither Gorter nor Wardlaw referred to Worsdell (1915). Worsdell regarded ring-fasciation as "primarily induced by an apical invagination of the organ comparable to the turning inside out of a glove-finger" (pp. 90-91). He has illustrated his contention with two figures, one *t.s.* and the other *l.s.* (Fig. 26, p. 89). The *t.s.* shows two concentric rings of vascular tissues, the inner with inverse orientation, and the *l.s.* showing their origin by invagination of the original stelar tissues.

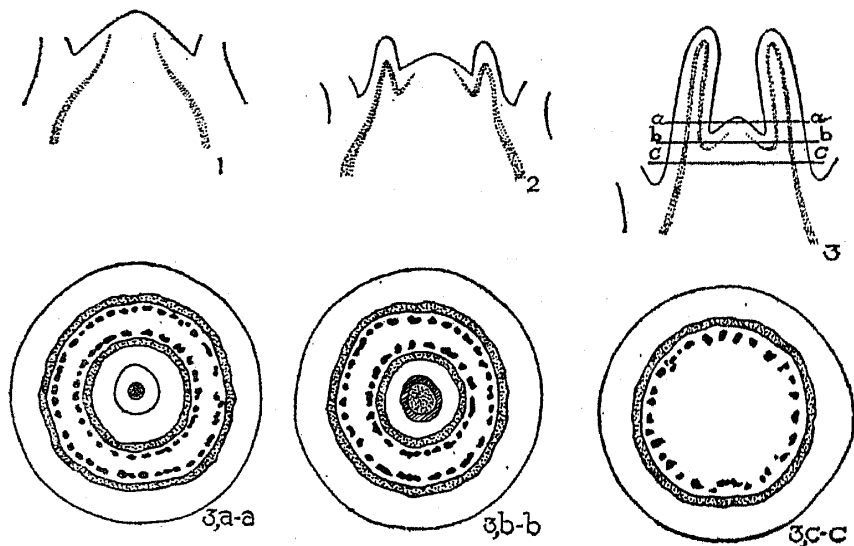
Both the authors also failed to take into their consideration the occurrence of similar structures showing double rings of vascular tissues with normal and inverse orientation of their elements in the receptacular 'floral cup' of the inferior ovary reported in certain species of the Rosaceæ, Santalaceæ, Cactaceæ, and Calycanthaceæ (Puri, p. 512, 1951). These are cited as examples of the "Sinking of the gynoeceium in the receptacle involving the invagination of the top of the stele" (Eames and MacDaniels, 1947, Figs. 167, K, L, pp. 352-53). Puri has given the following account of the manner in which the development of the cup and the invagination of the stele take place: The growing apex having become inactive growth is continued laterally in the region below the apex and vertically in the peripheral region round the apex. As a result the receptacle rises to a greater or less extent in the form of a hollow cup, carries the peripheral organs on its edge and leaves the carpels in the bottom. This intercalary growth also involves the procambial cylinder which as a result bulges out in the wall of the receptacular cup as a pouch. Obviously, therefore, the stelar bundles which have to supply carpellary traces appear to descend along the inner wall of the receptacular cup and have their xylem on the outside (p. 512). The receptacular cup with its double rings of vascular tissues, the inner with inverse orientation (*cp.*, Fig. 2 of Wardlaw and Photos. 5 and 6 of Gorter) is not considered as ring-fasciated axis.

The above comparison, however, does not account for the presence of a third ring of vascular tissue in the ring-fasciated axis of Gorter (Photo. 6) and of Wardlaw (Fig. 3). So far as the writer is aware only one case of ring-fasciation with three vascular cylinders was reported by Reichardt in a scape of the Dandelion (Worsdell, p. 90). Reichardt reported that the innermost ring ended blindly *passing from below upwards* in the solid core just below

the narrowed termination of the cavity, *i.e.*, in the organic apex (Gorter, Photo. 6)

On the evidence presented above the following explanation for the presence of all the three (never more than three in the reported cases) rings of vascular tissues in the ring-fasciated axes of Gorter and Wardlaw is suggested:

At the time when TIBA was applied to the shoot apices of tomato plants the provascular tissue had already reached the base of the apical meristem (continuous acropetal differentiation). It is on evidence that provascular differentiation extends to the flank meristem very close to, within 3 or 4 cell layers of, the extreme tip even before the visible emergence of a leaf primordium (Esau, 1951, 1954). The application of the chemical caused enhanced growth of the subapical region with the corresponding arrest of active growth or elongation of the apical dome. The growth of the subapical region initially took the form of a ring around the base of the free dome, which finally developed into a hollow axis with the slowly growing organic apex at its floor. This vertical growth also raised the provascular cylinder (main stele) in the form of a loop, its continuity with the apical meristem remaining unbroken (Figs. 1, 2 and 3). Gorter's Photos. 4B and 6 clearly show the continuity respectively of the outer and inner and the middle and the inner rings of the vascular tissues.



TEXT-FIGS. 1-3 are median longitudinal sections respectively of the shoot apices of tomato plants before and after the application of TIBA (all diagrammatic). Fig. 1. Shows the provascular tissues reaching the flank meristem before the application of TIBA. Fig. 2. Shows the sub-apical outgrowth and the raising of the provascular tissue along with it. Fig. 3. Shows the final position of the provascular meristem in the tubular axis. Figs. 3 a-a, b-b and c-c are *t.s.* through the last apex at different levels. These figures are the exact replica of Wardlaw's photomicrographs 1-3.

If the above interpretation is correct the nature and the fact of orientation of xylem and phloem in the three rings are easily explained, and the same prevascular tissue will appear in the three rings as reported by Gorter and Wardlaw in their materials (Figs. 3 *a-a*, 3 *b-b* and 3 *c-c*; *cp.*, also Eames and MacDaniels, Fig. 167, K, L). The growth of the apical dome is slowed down but never completely arrested (*see* Gorter, Photo. 6). The continuity of the provascular tissue is also never broken, but a portion of it may be left behind to mark its original position in the apical bud (Gorter, Photo. 6), and one is not to assume the origin of the three rings as independent of one another. This also explains the absence of the middle and inner rings in Wardlaw's Fig. 3.

Wardlaw concludes that "the vascular arrangements in these leafless ring-fasciation provide further evidence, of a rather novel kind, that the tissue pattern in the axis is determined by the shoot meristem" (p. 215). But the writer thinks on the other hand that it provides evidence for the continuous acropetal differentiation of the provascular tissue from the axial stele to the base of the apical meristem, as has been reported by Esau, Wetmore, Majumdar and others. Esau (1954) remarks that Wardlaw's conclusions are based on "weak foundation and the consequent hypothetical character of the guiding assumptions upon which the recent experimental work has been based" (p. 79).

The writer is of the opinion that Gorter's material is a real case of induced ring-fasciation of inflorescence axes (Photo. 4 C) like Reichardt's fasciated scape of the Dandelion. Gorter has further shown that application of TIBA causes a change of the vegetative shoot apex of tomato plants into flowering shoot apex (Photo. 3 A, B). The apical meristem of the flowering shoot resolves into a large number of flower primordia after the hollow tube has grown for some time [Figs. 5, 3, 4 (Pl. II) and Photo. 7]. Wardlaw's material on Gorter's more fuller evidence represents the lower portions of the ring-fasciated inflorescence axes before the flower primordia were formed. The anatomical evidence does not support any other conclusion.

LITERATURE

1. Compton, R. H. .. "The anatomy of Mummy Pea," *New Phyt.*, 1911, 10, 249-55.
2. Gorter, C. J. .. "The influence of 2, 3, 5-tri-iodobenzoic acids in the growing points of tomatoes, II. The initiation of ring-fasciation," *Proc. Akad. Sci. Amst.*, 1951, 54, 181-90.
3. Eames and MacDaniels .. *An Introduction to Plant Anatomy*, N.Y., 1917.
4. Esau, K. .. *Plant Anatomy*, N.Y., 1953.
5. ——— .. "Primary Vascular Differentiation in Plants," *Biol. Rev.*, 1954, 29, 46-86.

6. Linnaeus, C. .. *Philosophia Botanica* (in White), 1751.
7. Masters, M. T. .. *Vegetable Teratology*, Lond., 1869.
8. Morquin-Tandon, A. .. *Elements de teratologie Vegetale* (in White), 1849.
9. Nestler, A. .. *Uber Ringfasciation*, S. S. Gess, wiss, 1897, 103, 1 (in Gorter).
10. Penzig, O. .. *Pflanzen Teratologie*, 1890-94, 2.
11. Puri, V. .. "The rôle of floral anatomy in the solution of morphological problems," *Bot. Rev.*, 1951, 17, 471-553.
12. Reed, T. .. "On morphology and physiology of fasciated seedlings," *Ann. Bot.*, 1912, 26, 388-402.
13. Schoute, J. C. .. "Fasciation and Dichotomy," *Rec. Trav. bot. neerl.*, 1936, 33, 649.
14. Wardlaw, C. W. .. "Action of tri-iodobenzoic acid, etc.," *New Phyt.*, 1953, 52, 210-17.
15. White, O. E. .. "Fasciation," *Bot. Rev.*, 1948, 14, 319-58.
16. Worsdell, W. C. .. "Fasciation—Its Meaning and Origin," *New Phyt.*, 1905, 4, 55-74.
17. ——— .. *The Principles of Plant Teratology*, 1915, 1.