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INITIATION OF PROCAMBIAL STRANDS IN THE PRIMORDIA OF STAMENS AND CARPEL OF TRITICUM AESTIVUM L.

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Abstract. The procambial strands in the primordia of carpel and the stamens of *Triticum aestivum* L. originate independently and in isolation from the vascular system of the axis. The median strand of the carpel is initiated earlier than the two laterals. Once started, the procambial strands continue their initiation from their point of origin both acropetally and basipetally, the latter extension eventually linking them upto the strands lower down.

Introduction

The study of vascularisation of young flowers is becoming an important tool in solving the phylogenetic and taxonomic problems. Most of the studies so far made in this field deal with only mature flowers and not through the developmental sequences of flower. Furthermore, there are certain important topics of vascular ontogeny, such as, the position of origin, and the differentiation of procambia through successive stages of development that still need clarification.

The vascular differentiation of floral appendages has been a controvertial topic for long. Gregoire [8] recognised two types of apices development of procambium through elongation of cells, on the basis of origin and differentiation of procambia (i) vegetative and (ii) floral apices. He held that the procambium of vegetative apices was of foliar origin and their differentiation was bidirectional, whereas of floral apices, the differentiation was acropetal and of receptaculr origin. He also held that the vascular system of the receptacle was simply a 'reticulate mass' and not in any way comparable to the axial system of vegetative shoots. He, therefore, has suggested that receptacle must not be interpreted as an axis.

The above views of Gregoire were not universally accepted even at that time and since have been challenged by many workers. Brooks [4] studied *Amygdalus communis* in detail and observed the formation of procambium in the central region of the developing carpel primordium on the abaxial side, which later differentiated acropetally and basipetally until it connected up with the vascular system of the torus lower down. Arnal and Lawalree [10] while working on certain members of families voilaceae and compositeae have made similar observation. Acropetal differentiation of the procambium in floral parts has been observed by many atuhors like Phillipson [14] in *Bellis*, by Miller and Wetmore [12] in *Phlox drumondii Hook*, Tepfer [20] in *Aquilegia* and *Renunculus*; by Engard [5] in *Rubus*. Popham and Chan [15] observed similar course of procambial differentiation in floral parts of *Chrysanthemum* and Satina and Blakesle [16] in *Datura*. Boke[2] working on *Vinca rosea* found convincingly acropetal differentiation of Procambium in speals and petals but could not be certain for stamens and carpels. Barnard [1] in flower of *Triticum aestivum* and Bonnet [3] in flowers of *Avena* observed acropetal differentiation of procambium in the carpel.

Lanessan [11] reported acropetal differentiation of procambium in floral organs of *Dipsacus*, *Bryonia* and members of family umbelliferae, basipetal differentiationin in all floral organs of *Primula*, *Petasites* and members of family Rubiaceae. Instances where both types of differentiation occur in the same flower have also been recroded by Lanessan in *Rivina*.

In order to resolve the above controversy the position of inception and early longitudinal course of of differentiation of the procambium in the primordia of stamens and carpel of a grass floret is investigated, using *Triticum aestivum* L. as a type.

Materials and Methods

A spring cultivar (Sveno) of *Triticum aestivum* L. was used in this study. After the origin of inflorescence, the apices were disected out on moist paper at 4-day intervals. The appropriate material was selected trimmed and preserved in F.A.A. (for 24 hr). After washing the material in 70% ethanol, it was dehydrated in an ethanol series and taken into paraffin via chloroform. The blocks were cut at various thicknesses of from 5–10 μ and stained according to Sharman's [18] method. More details have been given previously [13].

Observations

(*a*) *Stamens*

Since early ontogeny of procambial strands can only be interpreted in the light of final form, the observations are preceded by a brief description of the course of vascular bundles in more mature stamens and the carpel.

An adult floret of *Triticum* has three stamens, one is anterior in position and the two antero-lateral. Each stamen at maturity consists of a large quadrilocular anther born upon a short filament which becomes very much eleongated just before anthesis.

A signle collateral vascular bundle extends through out the length of the filament and connective of anther. This is composed of few xylary element, more phloem elements and mostly of vascular paranchyma.

Though the series of both longitudinal and transverse sections of young florets were examined for the present study, but later were found more useful than former and are only ones described here.

In the series of transverse sections of all the stamens examined, the earliest detectable indication for the initiation of a procambial strand is the appearance of the isolated group of elongated and narrow cells at bout the middle region of the primordium. Each strand is usually formed by the longitudinal divisions of centrally located two to three cells, accompanied by their growth in length but limited transverse expnasions. The resultant procambial cells could be distinguished from neighbouring cells by their relative length, narrow transverse diameters and by having larger nuclei and differential staining of the protoplast in microscopic preparations.

The earliest stage in the development of the procambial strand was observed in the transection of a young lateral stamens, which measured 105μ in length and was almost sessile at that time. The strand initiated as isolated group of few cells and extended for almost 45μ in length and remained uniform in thickness.

It was observed that the procambial strands, which have earlier been originated as short and slender strands of elongated cells in all the three stamens, differentiate from their point of origin both acropetally in the free portion of the primordia and basipetally towards the point of insertion of the stamens mostly by periclinal divisions of the adjacent cells. This is illustrated in Figs. 1A to 1C at Ls and 3A—3D which are taken from the serial transection of two young florets. Figures 1A and 3A depict the upper regions of two lateral stamens, approximately 30 and 35 μ below the tips respectivley, wherein the young procambial strand is represented by the periclinal division of a single cell, "indicated as pest", while a very well-outlined strand comprising 9–10 cells, is present at the level shown in Figs. 1B and 3B at pest which are approximately 25μ lower down from the first ones. The procambial strand is not detectable again at the point of insertion of the stamens on the floret axis as indicated in Figs 1C and 3C which are made from the sections taken 45μ still further down. Figures 3D depicts the base of the same lateral stamen at LS, where there is no suggestion of the presence of a procambial strand.

Figures 1B to 1D illustrate similar stages for the initiation of the procambial strand in the primordium

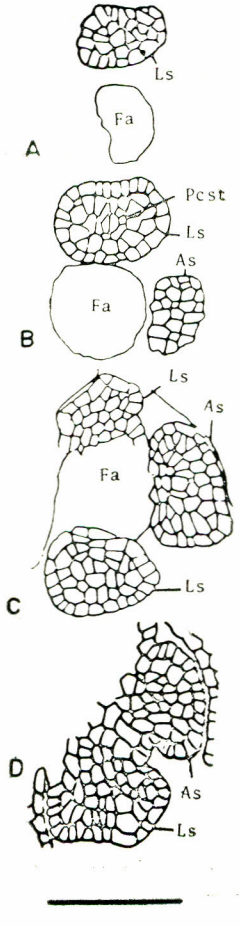

Fig. 1. Drawn from serial transections of a developing floret illustrating the position of origin and early differentiation of the procambial strand (Pcst) in the lateral stamen (A–C) and anterior stamen (C–D).

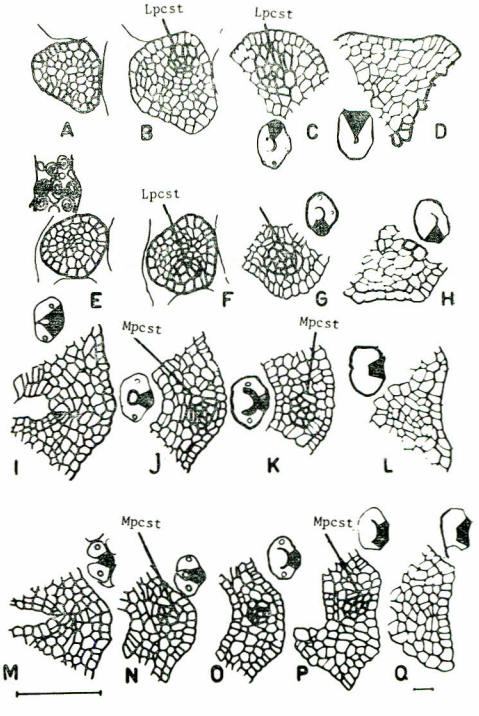

Fig. 2. Drawn from transections of developing florets, showing the position of origin and early differentiation of median (MPcst) in Figs. 2I–2L and 2M–2Q and the lateral procambial strands (LPcst) in the carpel (Fig. 2A–2D and 2E–2H).

of anterior stamen of the same floret. The illustrations are taken form three sections, which are 48 and 25μ apart respectivley.

The observation on the origin of procambial strands in the primordia of stamens suggest that in each stamen primordium, the procambial strand initiates as an isolated strand of narrow and elongated cells at about the middle region. Once initiated it differentiates both acropetally and basipetally and it is not the mere upward continuation of a more mature strand in the axis.

The early divisions initiating a procambial strand appears to spread from the centre of the future strand, as may be noted in Fig. 3A, later the cells around the central group of cells (formed by earlier divisions) have tendency to divide and elongate tangentially with respect to this group (Figs. 1B and 3B). Since these early divisions are followed by only little cell enlargement the newly formed procambial cells are relatively narrower than the neighbouring cells.

(*b*) *Carpel*

In a developing carpel three provascular or procambial strands were observed, a median and two laterals. Each lateral supplies the stigma which is on that side. The median one ends in the carpel wall just below the top.

An attempt was made to determine whether the three strands seen in the young carpel are merely the upwardly propagating ends of more mature strands in the axis, or if they originate independently of the axial supply and connect up with this later on.

Careful examination of serial transections of a number of developing carpels (Figs. 2A to 2Q, 4A to 4B and 5A to 5C) left not doubt that all three carpellary procambial strands originate in the carpel itself. The median procambial strand appears earlier than the two laterals.

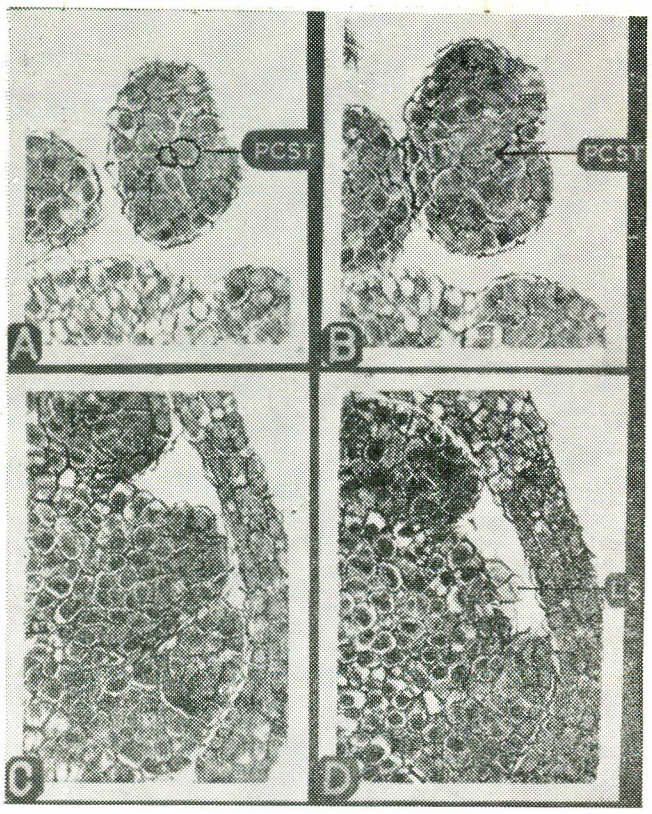

Fig. 3. Photomicrograph of serial transections of a developing floret showing the position of origin of a procambial strand (PCST) in the lateral stamen (Fig. 3A–D).

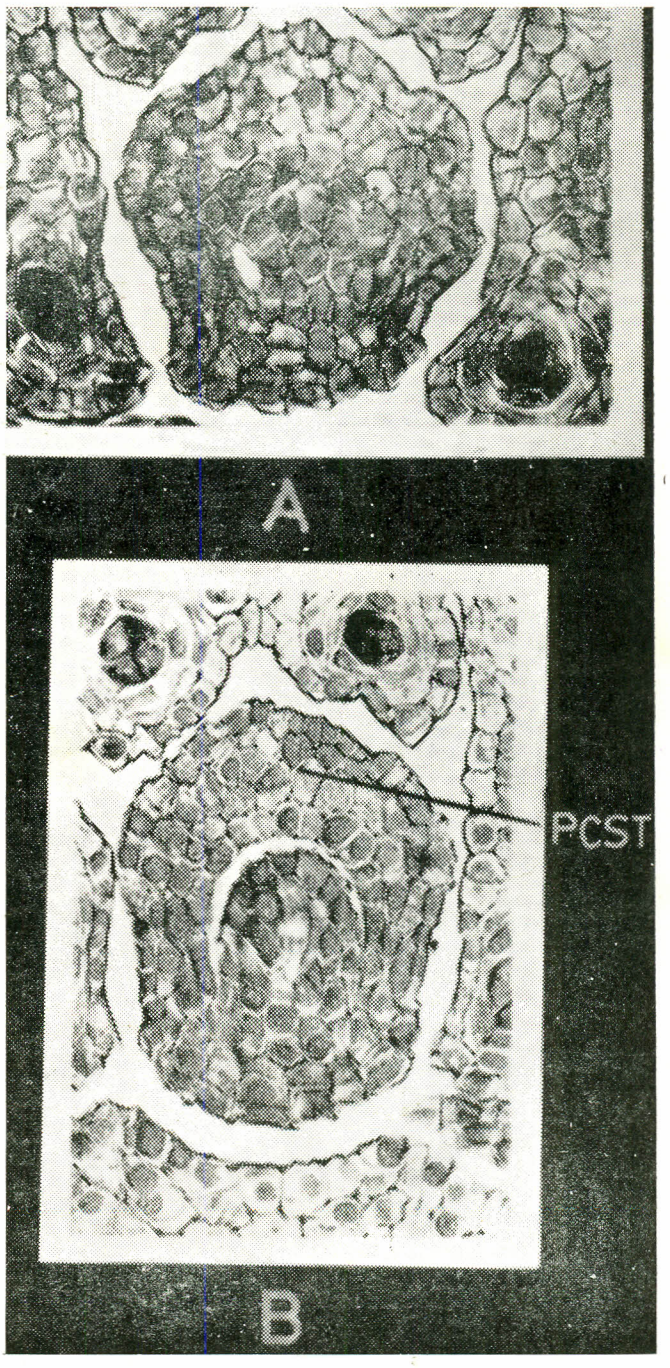

Fig. 4. Photomicrograph of serial transections of a young carpel, illustrating the position of origin of the median procambial strand in the carpel (Fig. 4A–B).

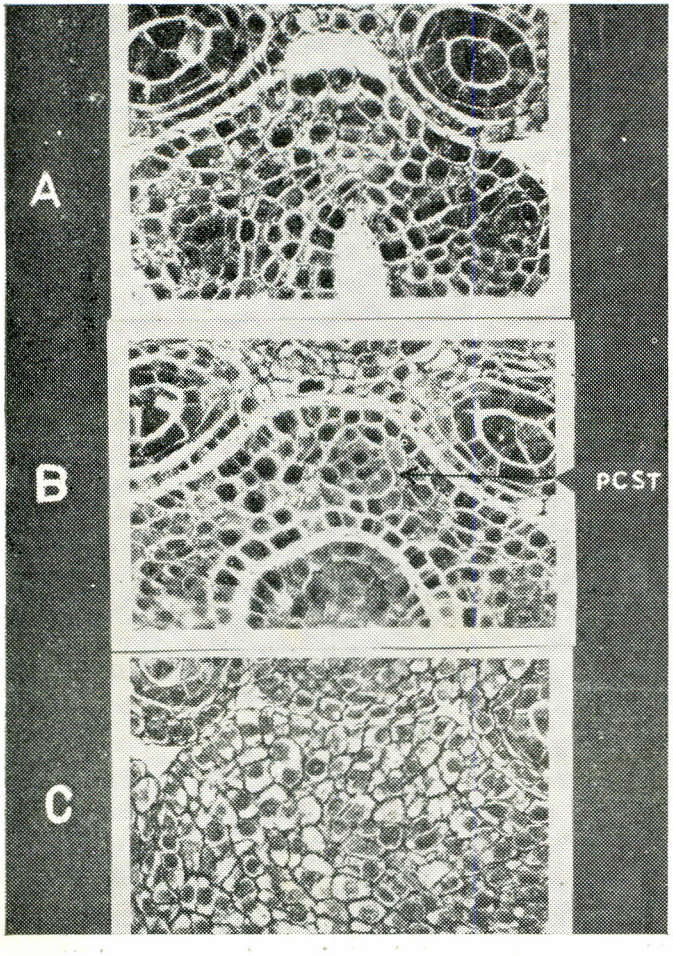

Fig. 5. Photomicrograph of serial transection of a slightly older carpel (Fig. 5A–C) showing the position of origin of the median procambial strand in the carpel.

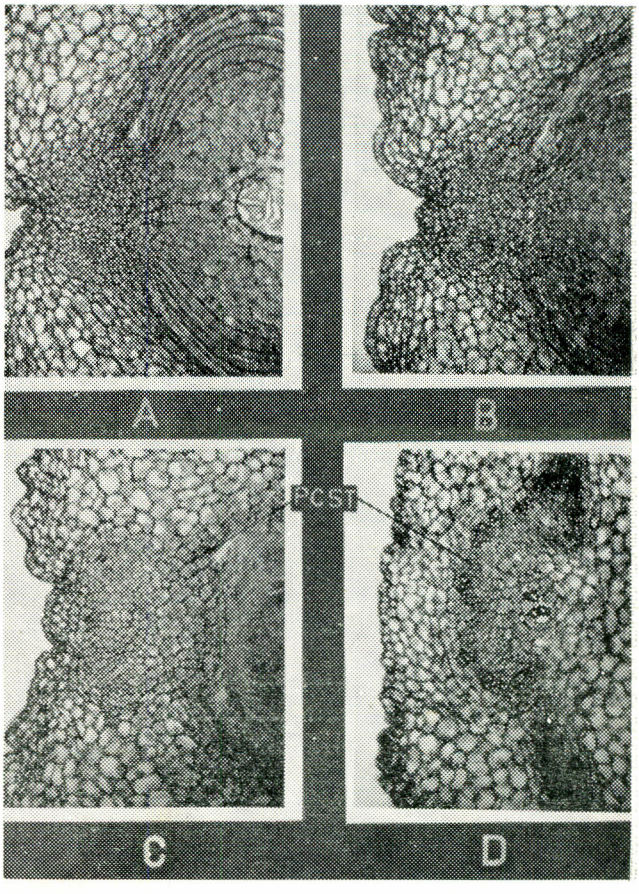

Fig. 6. Photomicrograph of serial transection of the posterier wall of the carpel illustrating the development of funicular procambial strand.

The earliest detectable stages in the initiation of median procambial strand are observed in an open, crescent-shaped developing carpel, with its median portion measuring about 160μ. No definite procambial strand is found in the upper portion of the carpel, primordium for about 100μ (Fig. 4A). However, in a section cut about 105μ below the top of the carpel, the strand is easily distinguishable comprising 6–8 cells, as shown in Fig. 4B. There is again no trace of a procambial strand lower down.

A slightly later stage is recroded from a developing carpel measruing 210μ in length. A transection of the anterior wall of the carpel, cut about 30μ below in top, is shown in Fig 5A with no suggestion of the presence of median procambial strand in it. A section taken 15 μ lower down shows a distinct strand at Mpcst in Fig. 5B. The procambial strand is composed of narrow and elongated cells and extended for about 145μ in length. However, the anterior wall of the carpel seems to be composed of homogenous cells at about the level (70μ still lower down) shown in Fig. 5C.

Figures 2I to 2L and 2M to 2Q are drawn from series of transection of two still older carpels. The upper portion of anterior wall is shown in Figs. 2I and 2M, where there is no indication of the formation of procambial strand, while very well-outlined strands are visible in Figs. 2J and 2N. Each strand could be traced about 40μ still lower down in the carpel wall (Figs 2K and 2O). However, there is no trace of procambial strand at the level shown in Figs. 2L and 2Q.

The erlier stages of intitation of the lateral procambial strands are recroded from a carpel that measures about 295μ in length. No strand s detectable in the section in the section used for Fig. 2A but a strand is quite distinguishable only 15μ lower down (Fig. 2B). This strand could be traced in the carpel wall down to the level shown in Fig. 2C, which is taken 90μ below the previous one. However, no trace of it could be found at the level 100μ below this, as may be noted in Fig. 2D.

Figures 2E to 2H illustrate a similar series of transections of a carpel from another floret.

By comparing the observation on the origin of the median procambial strand in a younger (Figs. 4A–B) and slightly more mature carpels (Figs. 5A–C and 2I–L and 2M – 2Q) it is tentatively concluded that this strand initiates as an isolated group of cells

at about the middle region of the carpel and then differentiates both acropetally in the organ itself and basipetally to join the mature strand below, in the axis.

In the light of observations made on the position of initiation of lateral procambial strands and their isolation from the mature strands of the axis at the early stages, it may be concluded that their differentiation is also bipolar.

Early Growth of Procambium

After the narrow elongated cells of the procambium have organised into an isolated slender strand, the strand propagates in length by the longitudinal division of cells at both ends. Thus the early longitudinal growth of the procambium occurs at the expense of the cells adjacent to those that began dividing first. The transverse growth occurs gradually through addition of cells on the periphery and the division of cells within the procambial strand. Since these additions occur at increasing distances from the point of origin of procambial strand, the cells that become procambial at far ends are somewhat larger and more conspicuously vacuolated than the first cells that initiated the procambium.

Funicular Strand

The funicular strand appear in the posterior wall of the carpel. The procabium of this strand differentiates much later than that of the median and laterals. The initiating cells of funicular procambium are narrower and denser than that of median and lateral bundles of the carpel (Fig 6A–D). The funicular strand, like the others, increased in its diameter by further cell divisions within the strand and also by addition of cells on its periphery. The divisions within the strand are not always periclincally orientated they may be oblique or sometimes irregular.

Discussion

In the light of observation made in the present investigations, it is logical to conclude that the procambial strand originates as a small isolated group of elongated and narrow cells in the median and lateral bundles of the carpel and the single bundle of each stamen. Each strand extends longitudinally by the periclinal divisions of cells at both ends. This results in a bidirectional differentiation of young procambium, that is, it differentiates basipetally in the floret axis and acropetally in the free portions of the carpel and stamens primordia. The transverse increase occurs through addition of cells on the periphery which overlaps with the increase in the number of cells within the procambium.

The information of the procambial initiation and its early differentiation for the monocotylednous flowers particularly for grases are meagre. Through acropetal, basipetal and bidirectional differentiation has already been reported for their leaves by Sharman [17]; Knmazwa and Masayuki.

Sharman and Hitch [19, 9] made a comprehensive study of the development of procambial strands of *Triticum Dactylis*, *Brumus*, *Cynosursus*, *Loliums* and *Poa*. They observed that procambial strand first initiated at the base of young leaf primordium, independently of the preexisting vascular system of the plant. It is only later, partially by extending downwards from their point of origin and partially by upward differentiation of the parent axis, that the link between them is established. Simultaneously the procambial strand differentiate acropetally in the free portion of leaf primordium.

Clowes (1960) supported the bipolar differentiation of procambium in *Zea mavs* leaves. According to him the order of appearance of smaller bundles is related to the basipetal maturation of leaves, a characterisitic very common among angiosperms. Esua [6] has also supported this generalisation, Bernard [1] and Bonnet [3], however, held that there is an acropetal differentiation of procambia in primordia of stamens and carpel. Their study, however, is open to doubt as they used rather old material of *Triticum* and *Avena*.

From the above survey of literature it is evident that mostly in the leaves of temperate cereals and herbage grasses the procambial initiation is the same as described for the floral parts of *Triticum*. Thus it is tentatively concluded that procambium initiation is quite independent at various locality and that bipolar differentitation at early stages is not only seen in vegetative shoots but it is also prevalent in floral parts.

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