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Research Article

Stem anatomy and ontogeny of vascular variants in *Ipomoea asarifolia* (Desr.) Roem. & Schult. (Convolvulaceae)

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An increase in stem thickness and ontogeny of successive cambia, intraxylary cambium, and inter-and intraxylary phloem is elaborated for the first time in *Ipomoea asarifolia* (Desr.) Roem. & Schult. (Convolvulaceae). As the plants grew older, several small segments of cambium were initiated simultaneously external to the phloem formed by regular vascular cambium. Ontogenetically, these cambial segments were initiated from two different tissues, i.e. from the pericyclic parenchyma and dilating ray parenchyma cells. Products of both cambial segments showed unique orientation, and they may be identified based on the orientation of the xylem and phloem elements produced by them. Cambial segments initiating from the pericyclic parenchyma began with repeated divisions in one to a few cells to form oval to circular patches of the meristematic cells. This resulted in the formation of oval to elliptic vascular cylinders. The vascular cylinders were later interconnected by forming cambial segments that exclusively formed thin-walled parenchyma on either side. In the second type, dilating ray cells underwent swelling followed by repeated anticlinal divisions and produced xylem on one side and phloem on the other side of the cambium; thus, these vascular cylinders were oriented tangentially. The secondary xylem consisted of dimorphic vessels, fibres, axial and ray parenchyma, and interxylary phloem. In the thick stems, intraxylary cambium was initiated from the marginal pith cells situated on the inner face of the protoxylem. Initially, this cambium was unifacial and deposited only intraxylary phloem, but subsequently, it became bidirectional and began to deposit secondary xylem centrifugally. The presence of variant secondary growth is correlated with climbing habits and family characteristics of the Convolvulaceae.

Keywords: cambial variant, intraxylary cambium, successive cambia

Introduction

In the early stage of the life cycle, climbing plants are self-supporting; therefore, the stem stiffness is higher, but as they start climbing in most of the species, their architecture changes drastically (Carlquist 2001, Isnard and Silk 2009, Rajput et al.

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2023, 2024a, 2024b). These structural alterations include development of cambial variants, parenchyma abundance, formation of wide and narrow vessels (i.e. vessel dimorphism), large and tall rays to increase stem flexibility (Carlquist 2001, Rowe et al. 2004, Pace et al. 2009, Rajput et al. 2023, 2024a, 2024b), collectively referred to as anomalous secondary growth (Eames and MacDaniels 1947), cambial variants (Carlquist 1988), lianescent vascular syndrome (Angyalossy et al. 2015), or vascular variants (Cunha Neto 2023). Climbing growth forms are important constituents of forest ecosystems, contributing to the many vital aspects of forest dynamics, structure, and composition (Isnard and Silk 2009). It may represent 10–45% of woody stems in some tropical forests (Schnitzern et al. 2005). Moreover, they respond strongly to increasing CO_2 concentration and/or benefit from anthropogenic perturbation and increasing forest fragmentation (Londré and Schnitze 2006, Mohan et al. 2006). Despite their pivotal role in forest ecosystems, growth trajectories in several climbing species are yet to be investigated. Studies on such groups have been neglected because of their relatively less economic importance than timber trees (Carlquist 2009). Members of the family Convolvulaceae are cultivated globally due to aesthetic (ornamentals) and food (like sweet potato) values (Staples and Brummitt 2007) and ethnomedicinal properties. The family is dominated by herbaceous to woody climbers, while herbs, shrubs, and trees are rare (Simpson 2010).

Hallier (1893) provided the first detailed anatomical descriptions of different members of the Convolvulaceae and documented various types of vascular variants. Pfeiffer (1926) extended Hallier's work by characterizing and classifying additional and known types of vascular variants in *Ipomoea.* Stem anatomy of various species of *Ipomoea*, including other genera of the Convolvulaceae, has been studied by Carlquist and Hanson (1991). Besides these, the differentiation of cambium (Lujan 1974), evolutionary implications of typical and variant secondary growth (McDonald 1992) and development of the cambium and formation of successive cambia in different species of Convolvulaceae have been examined by various researchers (Scott and Brebner 1891, Solereder 1908, Artschwager 1918, Kennedy and Crafts 1931, Metcalfe and Chalk 1950, Lowell and Lucansky 1990, McDonald 1992, Rajput et al. 2008, 2014a, 2014b, 2024a, 2024b Terrazas et al. 2011, 2021, Ramoliya et al. 2022, Lawand et al. 2023, Kapadane et al. 2023).

The present study on *Ipomoea asarifolia* documents additional features that differ from the earlier reports on this genus that may contribute to a better understanding of the genus *Ipomoea* and its closely related species in the Convolvulaceae. Therefore, the main aim of the present investigation was to elucidate the structure and development of vascular variants, the structure of the secondary xylem, and the formation of interxylary cambium in *I. asarifolia* and the possible significance of the vascular variants with the climbing habit.

Material and methods

The samples of various stem diameters, starting from the shoot apex to fifteen mm in diameter, were collected from the main stems of five individuals of *Ipomoea asarifolia* (Desr.) Roem. & Schult. (Convolvulaceae). All these individuals were growing naturally along the roadside at Attangudi (Shivganga Dist.), Tamil Nadu state (India). Stem pieces about 5–7 cm long were cut at different heights (10–15 cm above the ground, middle part, and apical portion of the stem) and fixed in FAA (Berlyn and Miksche 1976) immediately after collection. After 12 h of fixation, these samples were transferred to 70% alcohol for further processing and storage. Suitably trimmed blocks along with bark were sectioned at 12–15 µm thickness in transverse, radial, and tangential longitudinal planes using a sliding microtome. Sections were stained with 1% aqueous solution of Safranin-Astra blue (1:9) combination (Srebotnik and Messner 1994), and slides were mounted permanently in Dibutyl Phthalate Xylene (DPX) after dehydrating through the ethanol xylene series.

The length of the wide vessel elements and the length and width of fibriform vessels and fibres were obtained from the macerated xylem. For maceration, the small pieces of secondary xylem adjacent to the outermost cambium ring were scraped with a razor blade and treated with Jeffrey's fluid (Johansen 1940) at 60°C for 36–48 h. Subsequently, macerated xylem samples were washed thoroughly with tap water and stained with 1% aqueous safranin. The tangential width (i.e. lumen diameter) of wide vessel elements was measured directly from the transverse sections. The length and width of the sieve tube elements, ray height, and width were measured directly from the tangential longitudinal sections. Thirty measurements were taken arbitrarily to obtain the mean and standard deviation for each cell type. Important results were micro-photographed with a Leica (DM 2000) trinocular research microscope. Wood descriptions follow the IAWA Committee (1989) and Carlquist (2001), while terms related to climbing plant anatomy are adopted from Angyalossy et al. (2015), and inverse cambium is adopted from earlier work (Rajput et al. 2008).

Results

Anatomy of the young stem

The young (2–3 mm thick) stems were oval to elliptic (Fig. 1A), in which an outermost layer, i.e. epidermis, was made up of a single layer of oval to polygonal cells. It was followed by several cells with a wide cortex that was composed of compactly arranged oval to polygonal cells (Fig. 1B–D). An endodermis formed a continuous ring beneath the cortex (Fig. 1B, C) while pericyclic fibres were yet to differentiate at this stage. Endodermis enclosed several vascular bundles composed of external protophloem, procambium, and protoxylem and intraxylary protophloem on the inner margin of it (Fig. 1B, C). A central portion of the stem was occupied by

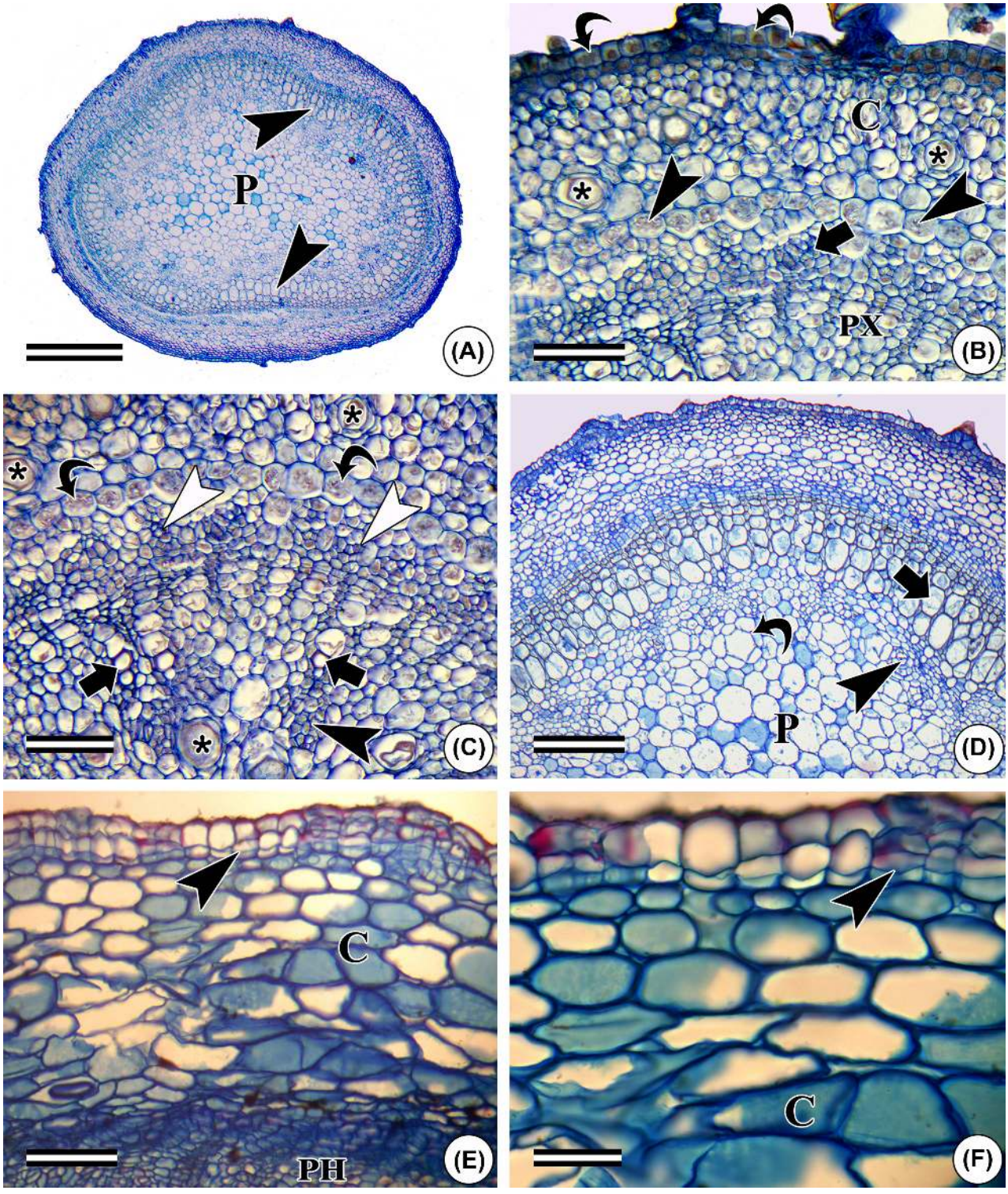


Figure 1. Transverse view (A–F) of the young stem of *Ipomoea asarifolia* showing its structure and composition. (A) Young stem showing a complete ring of the metaxylem (arrowheads) and establishment of vascular cambium. (B) Young stem showing epidermis (curved arrow), cortex (=C), laticifers (asterisks), endodermis (arrowheads), external protophloem (arrow), and differentiating protoxylem (PX). (C) Simultaneous differentiation of regular and internal phloem (black arrowhead) and protoxylem (arrows). Note the endodermis (curved arrow) and laticifers in the cortex and pith (P) region (asterisks). (D) Recently formed a complete ring of vascular cambium and initiation of the secondary xylem development. The arrow shows metaxylem, while the arrowhead indicates intraxylary phloem. Curved arrow shows laticifers in the pith (P) region. (E) Periclinal divisions in the sub-epidermal cells showing initiation of phellogen (arrowhead). (F) Enlarged view of (E) showing initiation of phellogen (arrowhead). Scale bars: (A) = 500 µm; (B), (C), (F) = 50 µm; (D) = 200 µm; (E) = 100 µm.

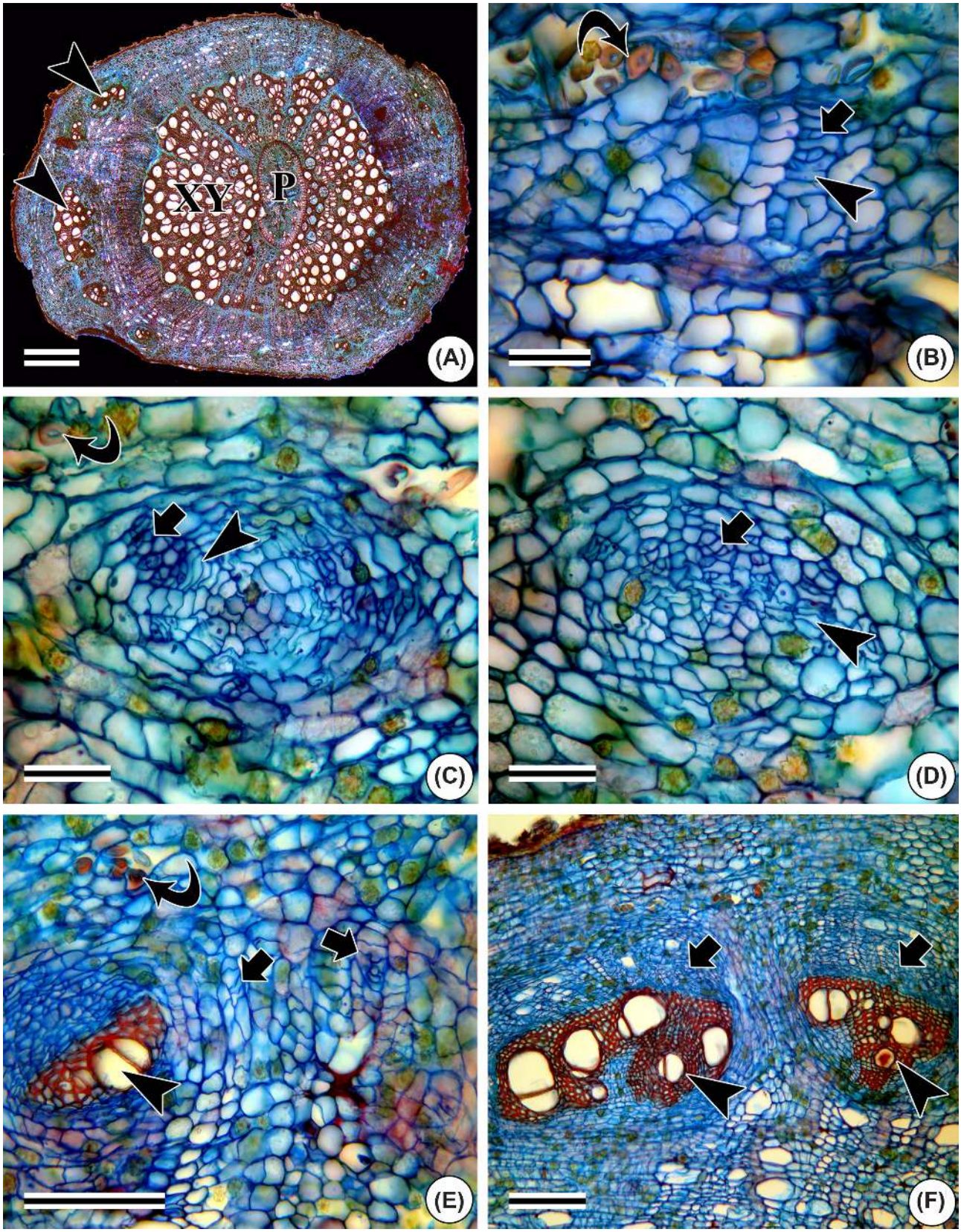


Figure 2. Transverse (A–F) view of mature stem *Ipomoea asarifolia* and initiation of successive cambium/vascular cylinders. (A) A thick stem showing vascular cylinders (arrowheads) and the structure of secondary xylem (XY) formed by the regular vascular cambium. Abbreviation:

Figure 2. Continued.

P = pith. (B) Initiation of successive cambium (arrowhead) and differentiating sieve tube elements (arrow). The curved arrow indicates pericyclic fibres. (C), (D) Development of a circular patch of cambium (arrowheads) and formation of sieve elements (arrow). The curved arrow indicates pericyclic fibres. (E) Newly formed vascular cylinder (arrowhead) with secondary xylem and phloem. Arrows showing cell divisions to develop the adjacent vascular cylinder. Note the pericyclic fibres (curved arrow). (F) Well-developed vascular cylinders showing xylem (arrowheads) and phloem (arrows). Note the orientation of vascular cylinders. Scale bars: (A) = 1 mm; (B)–(D) = 50 µm; (E), (F) = 200 µm.

unlignified, polygonal pith cells and differentiating laticifers (Fig. 1B, C). Subsequently, all these vascular bundles were interconnected by initiating interfascicular cambium and establishing a complete ring of vascular cambium (Fig. 1D). As the stem diameter increased, the epidermis was replaced by several cell layers of periderm. The sub-epidermal cells underwent periclinal divisions and gave rise to phellogen (Fig. 1E, F). At this stage, cortical cells underwent tangential elongation due to an increase in stem diameter by exerting pressure from the differentiating xylem. Thus, they became oval to elliptic and compressed while the complete ring of fibres became fragmented (Fig. 1E, F).

Development of successive cambia

As the plants grew further, initiation of additional cambial segments external to the regular vascular cambium were observed in 6-8 mm thick stems (Fig. 2A). However, these small segments of the cambium failed to form a complete ring of the successive cambium; therefore, newly formed vascular cylinders were separated from each other by the conjunctive tissues. Initiation of these small segments of the successive cambia/vascular cylinders was observed from the pericyclic parenchyma and dilating ray cells. Some of the parenchyma cells on the inner side of the pericyclic fibres underwent tangential divisions (Fig. 2B) and formed circular/concentric patches of meristematic cells (Fig. 2C, D). Subsequently, these cells began to differentiate into phloem elements, followed by lignified elements of the secondary xylem (Fig. 2E, F). Bidirectional activity of these circular/semi-circular cambial segments formed secondary phloem on the outer face and thick-walled xylem elements on the inner side (Fig. 2A, E, F). Gradually, these circular/semi-circular patches of cambium extended tangentially and formed oval to elliptic or triangular vascular bundles (Fig. 3A, B).

Development of vascular cylinders was also observed from the dilating phloem ray cells (Fig. 3C, D). The present species is characterised by the presence of uni-biseriate rays, while triseriate rays were observed occasionally. The ray cells from the non-conducting phloem (towards the periphery) underwent anticlinal divisions and formed several cells wide funnel-shaped dilating ray (Fig. 3C). Soon after, some of the newly formed cells began to differentiate into sieve elements (Fig. 3D) followed by differentiation of lignified xylem elements (Fig. 4A, B). Since this meristem was initiated by tangential divisions, the newly differentiated vascular cylinder most often showed diagonal orientation of the secondary xylem and phloem elements (Fig. 4B). In thick stems, the ray parenchyma between successive cambia showed delayed dilation of phloem rays (i.e. after the formation well-differentiated vascular cylinder from pericyclic parenchyma). The phloem ray cells between successive cambia showed anticlinal divisions and showed differentiation of sieve elements (Fig. 4D). The formation of circular, small cambial segments (Fig. 4C, D).

Anatomy of secondary xylem

The secondary xylem was diffuse porous and composed of both wider as well as narrow vessels (fibriform vessels), fibres, interxylary phloem, axial and ray parenchyma cells (Fig. 5A–D). Wide vessels were mostly solitary with a simple perforation plate on slightly oblique to transverse end walls. Their length and width were measured from 132–371 µm and 141–215 µm, respectively, in regular secondary xylem, while the length of the vessel elements was shorter and the diameter was larger as compared to the xylem formed by the successive cambia (Table 1). On the other hand, narrow vessels differ from imperforated tracheary elements in having small, simple perforations at the terminal ends of each cell (Fig. 5D, E). It is difficult to distinguish them in transverse view due to their narrow diameter and similarity with the adjacent fibres, but they may be discriminated by their relatively thick walls. These narrow/fibriform vessels were always found to be associated with the wide vessels. As compared to the xylem formed by the successive cambia, their length and width (548–862 µm and 26–41 µm) were more in regular secondary xylem (Table 1). The alternate bordered pits on their lateral walls were oval to elliptic, and oblong with 7–10 µm in diameter. Occasionally, formation of perforated ray cells was also observed in the xylem rays (Fig. 6A). These cells were more or less similar to the ray cells, except in having a small perforation on both ends.

The occurrence of tyloses was common in the wider vessels in all the successive rings (Fig. 6B). Protoplasm of the contact cells protrudes through the pit cavities into the vessel lumina by forming a balloon-like protrusion into the lumen and blocks it partially or completely. Tyloses were not only observed in the wider vessels of secondary xylem, but they were also observed in the protoxylem and metaxylem vessels (Fig. 6C). They were characterised by the presence of a distinct nucleus and heavy deposition of starch. These protrusions frequently showed cell division in them, and perform the function of starch storage. Thick-walled, lignified axial parenchyma cells were vasicentric and formed a sheath around the vessels, while thin-walled parenchyma formed patches of irregular shape and size (Fig. 5A, B). These patches of parenchyma were differentiated due to the differential activity of the vascular cambium. Small segments of the cambium differentiate thin-walled parenchyma instead of lignified derivatives towards the xylem side for a short period,

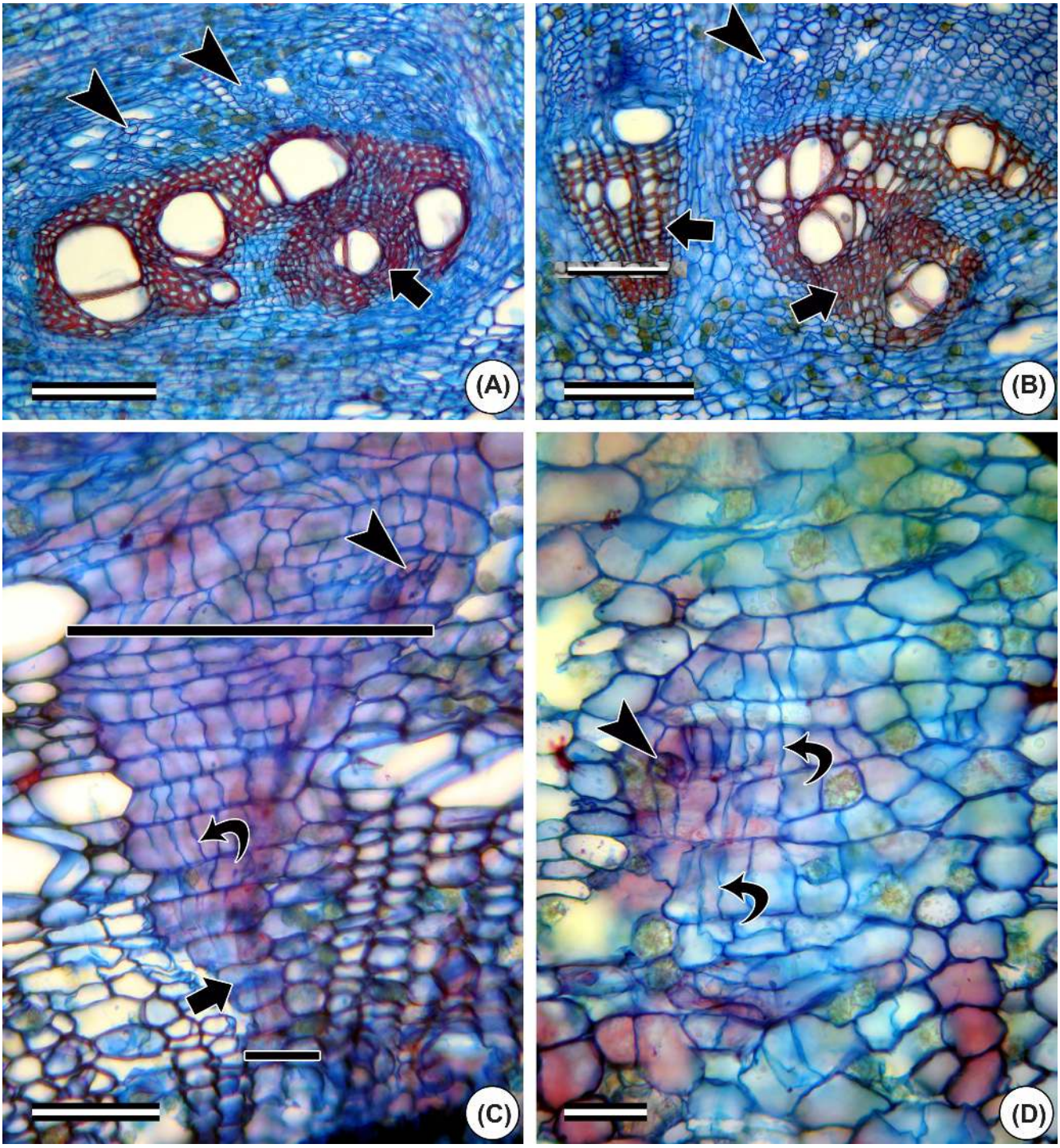


Figure 3. Transverse view of *Ipomoea asarifolia* stem. (A), (B) Orientation of the secondary xylem (arrow/s) and phloem (arrowhead/s) developed from the pericyclic parenchyma. (C) Dilating phloem ray showing anticlinal divisions (curved arrow). Note the increasing size of the ray from the cambium towards the periphery (bar lines). The arrowhead shows differentiating sieve elements, while the arrow indicates initiation of ray dilation. (D) Enlarged view of one of the dilating rays showing tangential divisions in rays (curved arrows) and differentiating sieve elements (arrowhead) from the dividing ray cell. Scale bars: (A), (B) = 200 µm; (C), (D) = 100 µm.

which subsequently revert back and begin to deposit lignified derivatives. Xylem fibres were non-septate with simple pits on their lateral walls. They were measured from 846–973 µm in regular secondary xylem and 778–935 µm in variant secondary xylem. The xylem rays were most often uni-biseriate, while tall, large (Table 1), and multiseriate rays were observed occasionally. They were measured 79–356 µm in height and 18–43 µm in width.

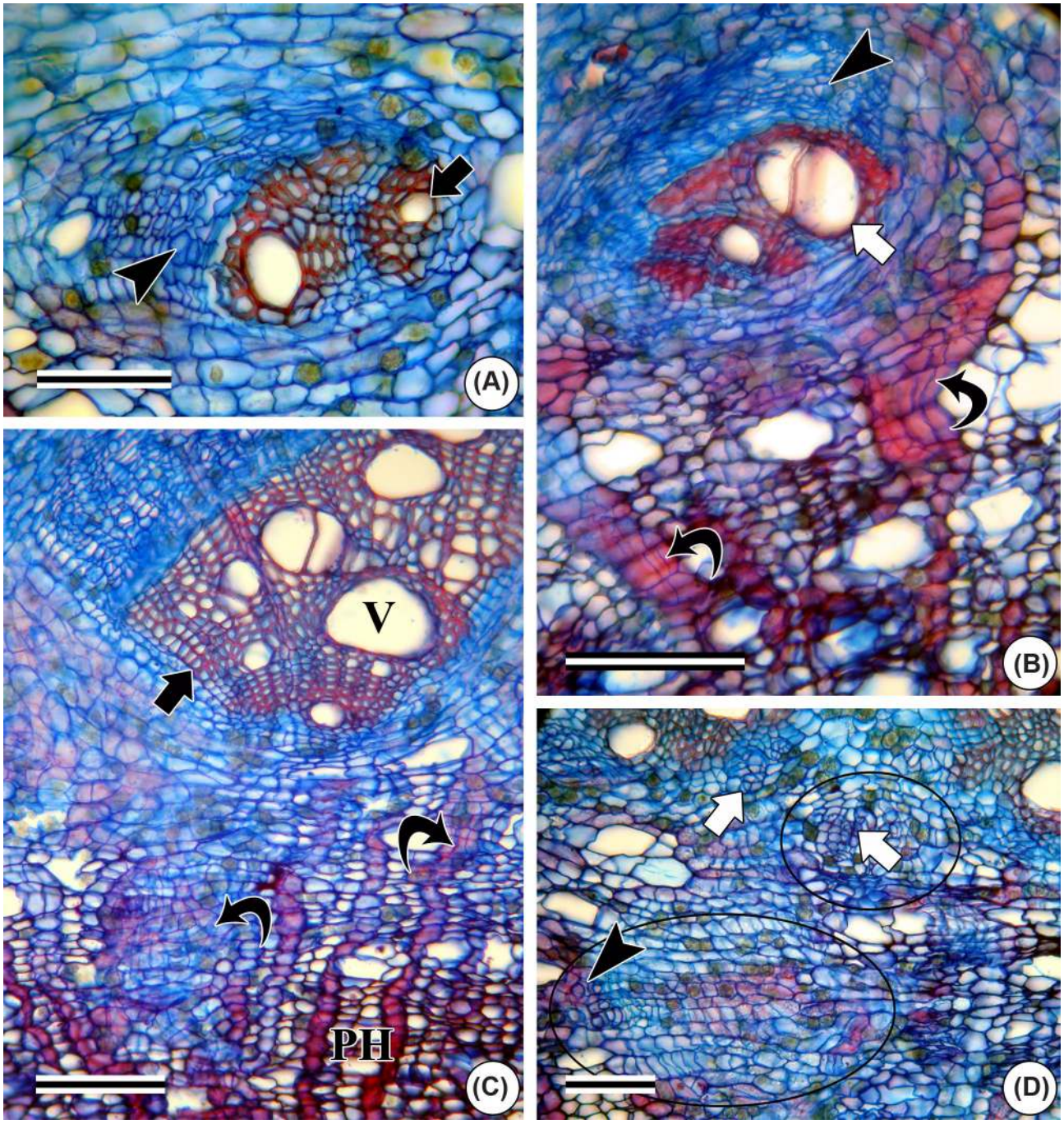


Figure 4. (A)–(D) Transverse view of *Ipomoea asarifolia* stems showing development of vascular cylinder in dilating phloem rays and meristematic activity in conjunctive tissues. (A) A recently formed vascular cylinder in the dilating phloem ray. Note the orientation of the secondary xylem (arrow) and phloem (arrowhead). (B) A complete view of dilating phloem ray showing vascular cylinder and its secondary xylem (arrow) and phloem (arrowhead). The curved arrows indicate divisions in ray cells. (C) Phloem ray located between successive cambia showing anticlinal divisions (curved arrow) in dilating ray. The arrow indicates a vascular cylinder formed outside the regular phloem (PH). Abbreviation: V = vessel. (D) Stem portion between successive cambia showing dilating ray (lower elliptic circle) while the upper circle indicates meristematic activity in conjunctive tissue. Note the sieve elements (arrowhead) formed in a ray, while the arrow shows sieve elements in the conjunctive tissue. Scale bars: (A) = 100 μm, (B)–(D) = 200 μm.

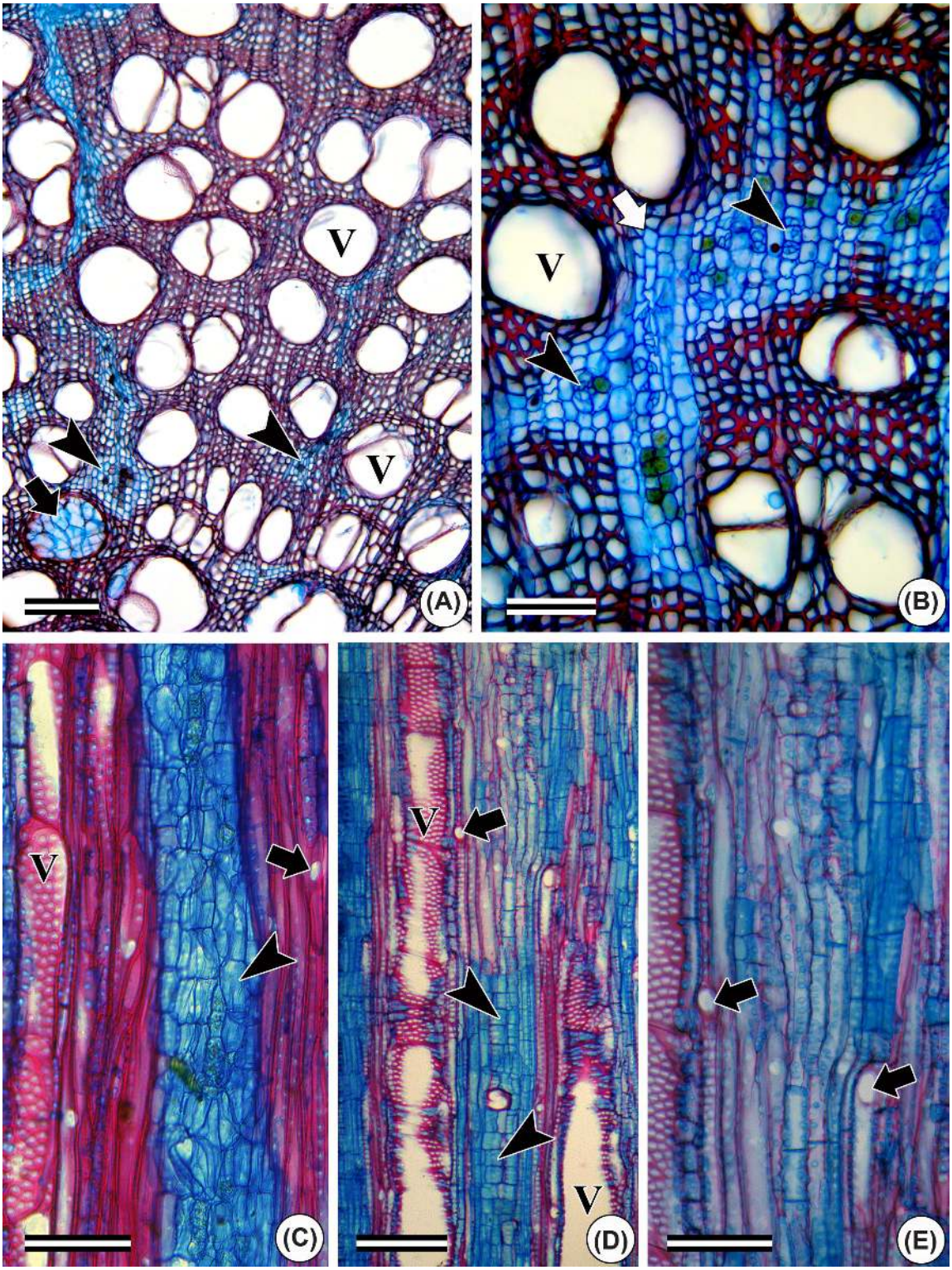


Figure 5. Transverse (A, B) and longitudinal (C–E) view of the secondary xylem in the mature stem of *Ipomoea asarifolia. (*A) Structure of secondary xylem showing distribution of vessels, thin-walled parenchyma patches (arrowheads), and tyloses (arrow). Abbreviation: V = vessels. (B) Enlarged view of the secondary xylem showing interxylary phloem (arrowheads) in one of the thin-walled parenchyma patches (arrow). Abbreviation: V = vessel. (C) Structure of the secondary xylem in tangential longitudinal view. Arrowhead indicates multiseriate rays, while the arrow shows a fibriform vessel. Abbreviation: V = vessels. (D) Radial longitudinal view of the secondary xylem showing ray (arrowhead) and fibriform vessel (arrow). Abbreviation: V = vessels. (E) Enlarged view of the secondary xylem showing fibriform vessels (arrows). Scale bars: (A), (D) = 200 µm; (B), (C), (E) = 100 µm.

Table 1. Dimensional details (in µm) of the regular and variant secondary xylem elements in *Ipomoea asarifolia* (Desr.) Roem. & Schult. (Convolvulaceae).

	Wide vessel elements		Narrow vessel elements		Xylem fibres		Uni-biseriate rays	
Cell type	Length	Diameter	Length	Diameter	Length	Width	Height	Width
Regular secondary xylem	132–371	141–215	548–862	26–41	846–973	18–32	79–356	18–43
Variant xylem (formed by successive cambia)	126–312	156–402	604–724	14–35	778–935	14–27	56–289	18–35

The secondary phloem was composed of sieve tube elements, companion cells, associated parenchyma cells, and ray cells. The length (214–267 µm) and width (20–26 µm) of the sieve tube elements were greater in the variant phloem as compared to the regular phloem (Table 2). Similar to the xylem, phloem rays were mostly uni-biseriate, while tall and large rays were observed occasionally.

Development of interxylary phloem and interxylary cambium

With the passage of time, in thick (8–10 mm) stems, individual or group of the xylem parenchyma underwent dedifferentiation and produce isolated or group of sieve elements (Fig. 6D). However, the parenchyma cells situated deep inside the secondary xylem underwent repeated divisions, and redifferentiated into interxylary phloem islands (Fig. 6E, F). During the differentiation of interxylary sieve elements, the xylem parenchyma (i.e. sieve tube mother cell) underwent recurrent divisions and formed a group of 2–6 narrow sieve tube elements. Therefore, all these sieve tube elements were accommodated within the area having equal size and shape to that of adjacent/neighbouring parenchyma cells (Fig. 6D–F). The cellular composition of these islands remained similar to the regular phloem. It was composed of narrow sieve tubes, companion cells, and associated phloem parenchyma cells. Most of these axial parenchyma cells adjacent to or within the phloem islands showed accumulation of druses (Fig. 6D, F). Formation of interxylary sieve elements began from the innermost parenchyma patches, and it gradually extended towards the cortex. Therefore, the phloem islands were more frequently towards the pith as compared to recently formed parenchyma islands located towards the periphery. In fully grown mature plants, repeated divisions in these parenchyma cells led to the formation of tangentially flattened radial files of 2–3 cells, giving an appearance like cambium, referred to as interxylary cambium. These cambial cells exclusively produced narrow sieve elements, while the development of xylem from these interxylary cambia was not observed.

Development of internal (intraxylary) phloem and internal (intraxylary) cambium

In the young stems, differentiation of internal primary phloem initiated simultaneously with the regular protophloem and protoxylem from the procambial derivatives (Fig. 1C, D). Subsequently, additional intraxylary secondary phloem was dedifferentiated from the adjacent pith cells (Fig. 7A), and a considerable amount of internal phloem was accumulated prior to the development of the internal cambium (Fig. 7B, C). In the relatively thick (3–4 mm) stems, marginal pith cells located on the inner margin of protoxylem underwent radial and tangential expansion followed by periclinal divisions (Fig. 7B). Repeated divisions in these cells consequently led to the formation of radially arranged meristematic cells (Fig. 7B, E). Henceforth, these meristematic cells are referred to as internal cambium. Initially, these segments were formed between the protoxylem and intraxylary phloem (Fig. 7B, C). These segments gradually spread tangentially and formed almost a continuous ring of internal cambium (Fig. 7D). Initially, this cambium was functionally unidirectional and produced only phloem derivatives (Fig. 7B, C). The internal sieve elements were 173–254 µm in length and 14–22 µm in width (Table 2). Later on, it became functionally bidirectional and deposited secondary xylem and phloem (Fig. 7E, F). Formation of tyloses was also observed in the vessels formed by the internal cambium (Fig. 7E). With the advancement of the secondary growth, the continuous ring of initially formed xylem became ruptured due to the proliferation of the pith cells and formation of intraxylary phloem and xylem elements (Fig. 7D). The rupture of the xylem ring interconnected the pith with the axial parenchyma of the regular secondary xylem (Fig. 7D).

Discussion

The genus *Ipomoea* is characterized by the presence of intraxylary phloem during the young stage, and as the plants grow in age, formation of successive cambia, functionally inverse cambia, and interxylary phloem in the majority of species occurs (Metcalfe and Chalk 1950, Lowell and Lucansky 1990, Carlquist and Hanson 1991, Rajput et al. 2008, Terrazas et al. 2011, Thacker et al. 2024). Besides these features, the presence of median bicollateral arcs with two adjoining collateral vascular bundles in leaf and secretory structures in leaves, stem, and roots (Metcalfe and Chalk 1950, Lowell and Lucansky 1986). In the present study, *Ipomoea asarifolia* is characterized by the presence of all these features.

The occurrence of internal phloem is universal in the Convolvulaceae (Hallier 1893, Pfeiffer 1926, Fukuda 1967, Lowell and Lucansky 1986, 1990, Carlquist and Hanson 1991, Rajput et al. 2008, 2024a, 2024b, Terrazas et al. 2011, Lawand et al. 2023, Ramoliya et al. 2022). There is a difference of opinion regarding the origin of internal phloem, i.e. from the procambial derivatives or from the marginal pith cells located on the inner margin of the protoxylem (Fukuda 1967, Patil et al. 2009, Terrazas et al. 2011, pp. 772, Rajput et al. 2014b, 2014c, 2024a, 2024b, Lekhak et al. 2018, Ramoliya et al. 2022, Thacker et al. 2024). *Argyreia*

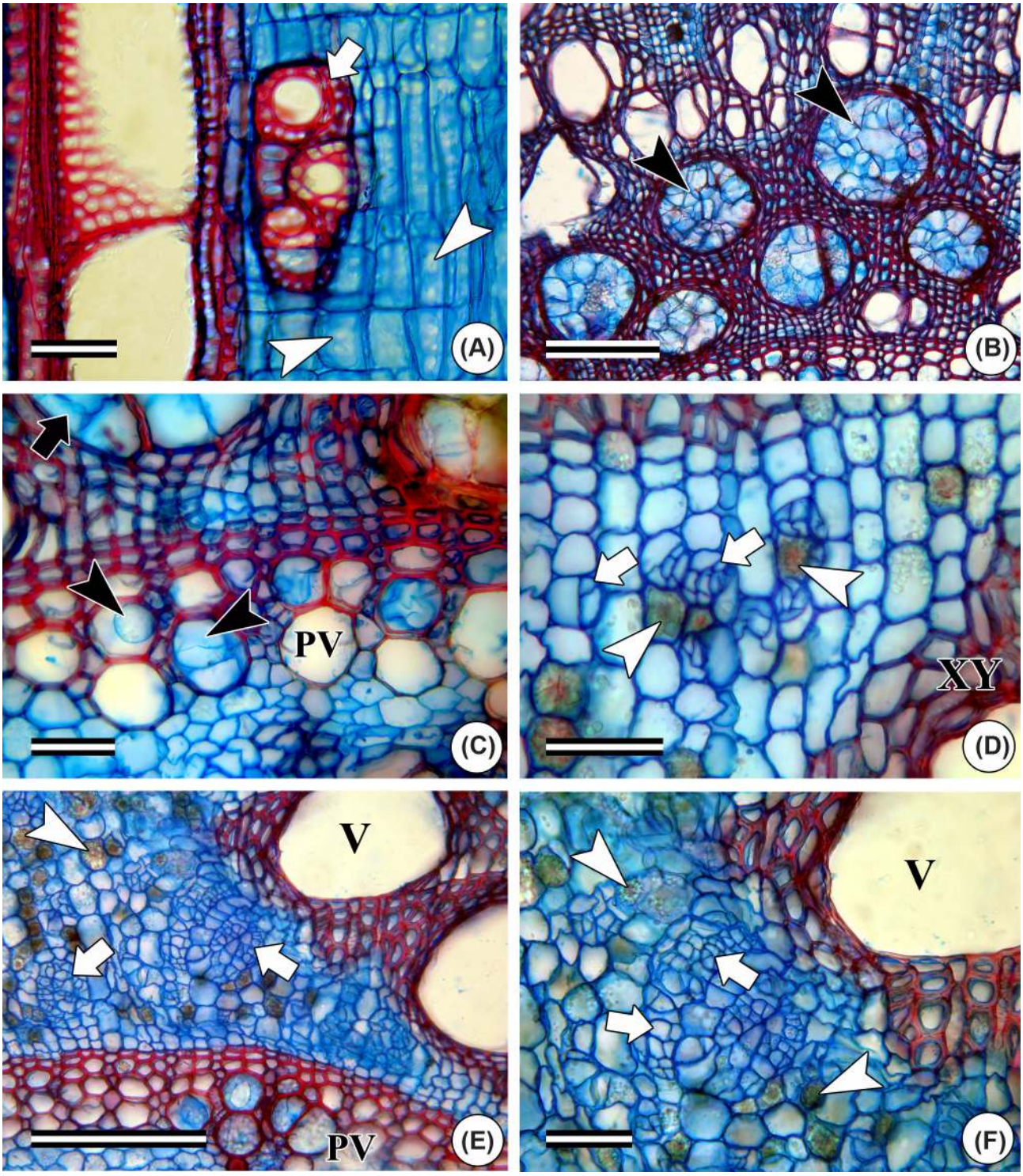


Figure 6. Structure of the secondary xylem in radial longitudinal (A) and transverse view (B–F) of the mature stem of *Ipomoea asarifolia*. (A) Perforated ray cells (arrow) and structure of ray cells (arrowheads). (B) Vessels in the secondary xylem occluded with thin-walled tyloses (arrowheads). (C) Protoxylem vessels showing tyloses (arrowheads). The arrow indicates a part of the vessel with tyloses in secondary xylem. *Abbreviation*: PV = protoxylem vessel. (D) Interxylary phloem (arrows) in one of the parenchyma patches. Arrowheads indicate druses in parenchyma cells adjacent to the interxylary sieve elements. (E) Interxylary phloem (arrows) in a deeply situated parenchyma patch. Note the number of sieve elements. Abbreviations: PV = protoxylem vessel, V = vessel. (F) Enlarged view of (E) showing interxylary phloem (arrows) while arrowheads indicate druses containing thin-walled parenchyma cells. Abbreviation: V = vessel. Scale bars: (A), (C), (D), (F) = 50 µm, (B), (E) = 200 µm.

Table 2. Dimensional details (in µm) of the regular and variant secondary phloem elements in *Ipomoea asarifolia* (Desr.) Roem. & Schult. (Convolvulaceae).

	Sieve tube elements		Uni-biseriate rays	
Cell type	Length	Diameter	Height	Width
Regular secondary phloem	115–156	17–24	96–249	20–36
Variant phloem (formed by successive cambia)	214–267	20–26	108–324	20–46
Internal (intraxylary) phloem	173–254	14–22	-	-

nervosa (Convolvulaceae) showed the absence of primary internal phloem, while secondary internal phloem develops after the initiation of secondary xylem (Kapadane et al. 2019). Similarly, in *Beaumontia jerordiana*, the primary intraxylary phloem develops deep inside the pith cells (Gondaliya et al. 2018), indicating their origin from the pith cells, while in species of *Ipomoea* it develops from the procambial derivatives (De Bary 1884, Scott and Brebner 1891, Pfeiffer 1926, Kennedy and Crafts 1931, Fukuda 1967, Lowell and Lucansky, 1986, Rajput et al. 2008).

At the primary growth stage in *I. asarifolia*, each developing vascular bundle was associated with primary internal phloem on the inner margin of the protoxylem. Internal protophloem develops concomitant to the regular (external) protophloem in *I. asarifolia*. In Convolvulaceae, it may develop after or concomitant to the regular external protophloem (Kennedy and Crafts 1931, Hayward 1932, Fukuda 1967, Mikesell and Schroeder 1984, Lowell and Lucansky 1986, 1990, Patil et al. 2009). In some cases, it may develop after the complete establishment of the vascular bundles or after the establishment of the regular vascular cambium, as reported in *Ipomoea arborescens* (Terrazas et al. 2011), *Cressa cretica* (Rajput et al. 2014c), and after the initiation of the secondary growth as observed in *Argyreia nervosa* (Kapadane et al. 2019, Rajput et al. 2024a). Its development has also been reported from the marginal pith cells (Carlquist and Hanson 1991, Terrazas et al. 2011, Carlquist 2013). Later, the bulk of additional secondary internal phloem may develop from the adjacent pith cells or by the action of the internal cambium that initiates between the primary xylem and primary internal phloem (Carlquist and Hanson 1991, Rajput et al. 2008, 2013, 2017). A similar mode of development is reported in our earlier studies (Rajput and Gondaliya 2017, Lekhak et al. 2018, Ramoliya et al. 2022, Lawand et al. 2023, Thacker et al. 2024).

Besides procambial derivatives, additional internal phloem develops from the internal cambium. With the advancement of the secondary growth, the intraxylary cambium is initiated by the differentiation of the parenchyma cells located between protoxylem and intraxylary phloem (Carlquist and Hanson 1991, Rajput et al. 2013, 2014a, 2014b, 2014c, Kapadane et al. 2019, Ramoliya et al. 2022, Lawand et al. 2023). It is a rare feature and is reported in the members of the families like Apocynaceae (including Asclepiadaceae), Bignoniaceae, Convolvulaceae, Loganiaceae, Solanaceae, etc. (Fukuda 1967, Gondaliya et al. 2018, Moya et al. 2017, Rajput et al. 2018, Lawand et al. 2023, Thacker et al. 2024). Perusal of the literature indicates that 19 families of eudicots are characterized by the presence of internal phloem (Carlquist 2001, 2013). However, there is no information that from these 19 families, how many of them are characterized by the presence of internal cambium.

In the majority of the reported cases, internal cambium initiates as a small segment, which remains functionally unidirectional in the beginning and may become bidirectional and produce xylem centrifugally and phloem centripetally as the plants grow in age (Patil and Rajput 2008, Patil et al. 2009, 2014, Terrazas et al. 2011, Rajput and Gondaliya 2017, Rajput et al. 2021, Lawand et al. 2023, Thacker et al. 2024). In all these species, it does not form a complete cylinder of the cambium. In the present study, initially, the internal cambium was unidirectional and produced only phloem derivatives. However, later it became bidirectional and deposited xylem externally and phloem internally (Carlquist and Hanson 1991). It seems to be the regular feature of the genus *Ipomoea*, in which the majority of species showed such a bidirectional nature of the internal phloem (Carlquist and Hanson 1991, Rajput et al. 2013, 2014a, 2014b, 2014c, Thacker et al. 2024). Formation of xylem and phloem by the internal cambium seems to be an adaptive feature as a safe path for the rapid conduction of photosynthate during the reproductive phase (Rajput et al. 2018, 2021) and protection against sap sucking, bark-damaging, and stem-boring insects, as this phloem is located in the pith region (Rajput et al. 2024a, 2024b).

After a certain period of regular secondary growth, the stem diameter of *Ipomoea asarifolia* increases by forming successive cambia. Earlier studies reported its initiation from the inner cortical cells and phloematic parenchyma (Lowell and Lucansky 1986, 1990) or from the derivatives of the pericycle (Rajput et al. 2008, Terrazas et al. 2011, Thacker et al. 2024). In the present study, the origin of successive cambia is observed from the derivatives of the pericyclic parenchyma as well as from the phloematic ray parenchyma cells. These cambial segments fail to form a complete ring; therefore, vascular cylinders formed by these segments were widely separated from each other by thin-walled parenchyma cells. Thus, the stem appears as a cable and may provide flexibility to the twining stems. As shown in Fig. 3A, B, and 4A, B, products of both cambial origins can be easily discriminated based on the orientation of the vascular elements/cylinders. The vascular cylinders originating from the pericycle derivatives produced secondary phloem externally and xylem internally, while those originating from the dilating phloem ray parenchyma were diagonally oriented.

Though initiation of vascular cylinders from the dilating ray cells is reported for the first time in *Ipomoea*, a similar

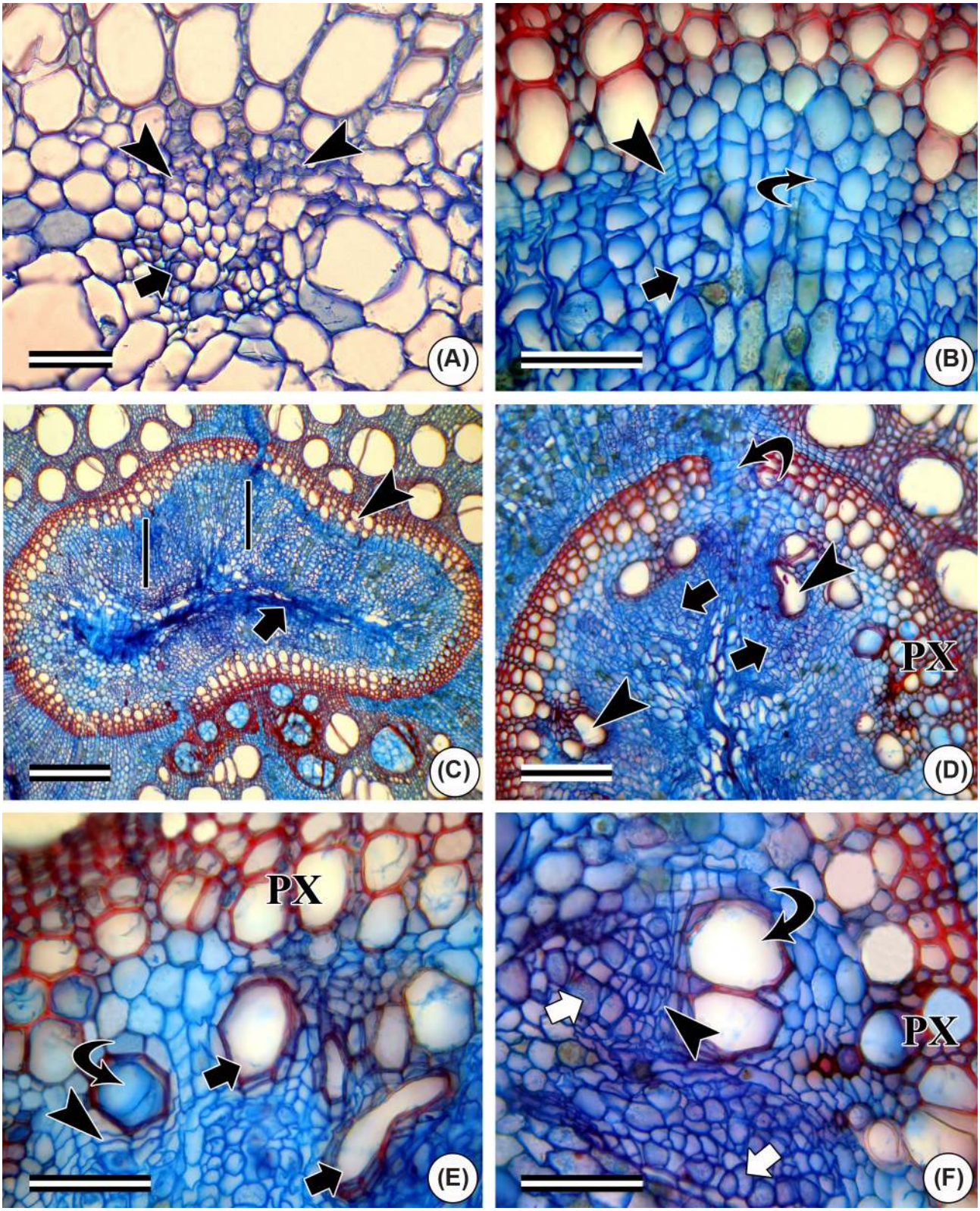


Figure 7. Transverse view of the young and mature stem of *Ipomoea asarifolia* showing the pith portion. (A) Internal phloem developed from procambial derivatives (arrowheads) and from the marginal pith cells (arrow) in young stems. Note the pith cells between both types of phloem. (B) Internal cambium (arrowhead) showing radial arrangement of cells. The curved arrow indicates dividing the pith cell, while the arrow indicates the internal sieve elements. Note the unifacial nature of the cambium. (C) Pith portion of relatively thick stem showing internal phloem. Note the quantity of phloem (vertical bars) developed by the cambium. The arrowhead shows protoxylem, while the arrow

Figure 7. Continued.

indicates crushed pith cells. (D) Bifacial cell division activity of internal cambium showing phloem (arrows), recently formed vessels (arrowheads). The curved arrow indicates rupture of the secondary xylem cylinder. Abbreviation: PX = protoxylem. (E) Vessels (arrows) formed from the internal cambium (arrowhead). Note the tyloses (curved arrow) in the vessel formed from the internal cambium. Abbreviation: PX = protoxylem. (F) Enlarged view of D showing internal cambium (arrowhead), xylem (curved arrow), and phloem (arrow) formed from it. Abbreviation: PX = protoxylem. Scale bars: (A) = 50 µm; (B), (E), (F) = 100 µm; (C) = 500 µm; (D) = 200 µm.

origin has been reported in the members like *Phaseolus lunatus* and *Mucuna pruriens* of the Fabaceae (Rajput et al. 2023, Rami et al. 2025), in *Distimake vitifolius*, *D. quinquefolius*, and *Camonea umbellata* of the Convolvulaceae (Rajput et al. 2024a, 2024b). An interesting observation, i.e. dilation of phloem rays in the inner successive cambia, is observed for the first time in the present study. The dilating phloem rays frequently formed sieve elements in all the samples investigated. In earlier studies, Kapadane et al. (2023) documented that the formation of lignified elements (without phloem) between adjacent successive rings is reported in *Argyreia elliptica* of Convolvulaceae.

The secondary xylem of the Convolvulaceae is characterized by the presence of thick-walled, lignified vasicentric parenchyma and randomly distributed patches of thin-walled axial parenchyma (Carlquist and Hanson 1991, Rajput et al. 2008, 2024a, 2024b). *Ipomoea asarifolia* showed the presence of both thin-walled parenchyma patches that were embedded within thick-walled xylem, while vasicentric parenchyma formed a sheath around the vessels. The presence of scanty vasicentric parenchyma is a common feature of the family, but they are not readily seen in the transverse view due to its thick walls and is more or less similar in diameter to the adjacent xylem fibres. However, they are slightly thinner than the fibres (Lowell and Lucansky 1986, 1990, Carlquist and Hanson 1991, Rajput et al. 2008, 2024a, 2024b, Lawand et al. 2023, Thacker et al. 2024). Formation of a sheath by thick-walled parenchyma around the vessels may be associated with the starch hypothesis as proposed by Carlquist (2001). This statement may also be supported by the presence of fibriform vessels in association with the wide vessels and may be playing an important role in the safeguard of the water column by hydrolyzing the starch and altering the osmotic potential (Carlquist 2001, pp. 293) when the wide vessels are facing the problem of air embolism. Available literature indicates that the narrow vessels are more resistant to air embolism as compared to the wide vessels (Ellmore and Ewers 1985, Carlquist 1991, Carlquist and Hanson 1991, Lens et al. 2022). Therefore, it appears that the presence of fibriform vessels may act as an alternative route for the translocation if the plants are facing the problem of vulnerability towards air embolism. The occurrence of wide vessels in the stem of lianas is very well exemplified by the lianoid Convolvulaceae (Carlquist and Hanson 1991). The co-occurrence of both wide plus narrow vessels has been reported in several lianoid genera of the Convolvulaceae (Carlquist and Hanson 1991, Rajput et al. 2008, Lekhak et al. 2018, Kapadane et al. 2023, Lawand et al. 2023). Therefore, the incidence of narrow plus wider vessels appears to be an adaptive feature towards greater potential for conductive efficiency and safety towards air embolism in climbing members.

In the secondary xylem, the protoplasts of axial and the ray parenchyma cells located next to the vessel may protrude into the vessel lumina through the pit cavities (Evert 2006). As shown in cross-section, several protrusion balloons out as tyloses into the vessel lumen. These outgrowths either enlarged gradually or underwent division activity and consequently blocked the vessels completely. The presence of nuclei and divisions in the developing tyloses indicates that formation of tyloses is hormonally controlled (VanderMolen et al. 1987, Evert 2006). Available literature indicates that tyloses store a variety of substances like organic and phenolic compounds, minerals, starch, gums, resins, druses, and prismatic crystals (De Micco et al. 2016), and they may develop secondary walls and may differentiate into sclereids (Chattaway 1949, Evert 2006, Rajput 2016, Moya et al. 2019). In *I. asarifolia*, the development of tyloses was common in the wide vessels of the secondary xylem, while they were also observed in protoxylem and metaxylem vessel elements. Available literature indicates that the occurrence of tyloses in the wide vessels of climbing members is a common feature, while they were observed rarely in protoxylem as well as in metaxylem vessel elements (Zimmermann 1979, De Micco et al. 2016, Rajput et al. 2017). Their occurrence in wide and narrow vessels is reported in climbing members of the Convolvulaceae is reported earlier (Tamaio et al. 2021). In contrast, their presence in the vessels formed by the internal cambium is reported for the first time in the literature. Various hypotheses have been proposed by earlier researchers that explain the reason for the development of tyloses (De Micco et al. 2016). Their development in prematurely developed vessels is correlated with a defense mechanism by inhibiting the spread of the pathogens throughout the plant via xylem vessels (Beckman and Talboys 1981, VanderMolen et al. 1987). They are also said to develop in response to stressful situations. Both the reasons appear to be true in the present case, as *I. asarifolia* is a climbing member that is vulnerable to internal injury due to stem torsion. Development of tyloses in response to pruning injury is documented in the grapevine climber by Sun et al. (2006, 2007). Further, the study by these authors also discusses wound repair and pathogen movement. In the present study, most often these plants were found to be attacked by the sap-feeding and stem-boring insects (personal observations not mentioned in the results). Thus, there is a possibility of pathogen invasion through the injured portion of the stems. In another study, Sun et al. (2007) reported an increase in ethylene concentration in pruning cut stems of grapevines and further documented an increase in the

number of tyloses in these stems. There is a similar possibility of tyloses development in *I. asarifolia* in response to insect injury and formation of tyloses.

Besides the presence of multiple cambia, formation of interxylary phloem from the thin-walled parenchyma in the later part of the secondary growth is characteristic of most of the members of the Convolvulaceae and is reported by earlier researchers (Lowell and Lucansky 1986, 1990, Carlquist and Hanson 1991, McDonald 1992, Rajput et al. 2008, 2014b, 2024a, 2024b, Lekhak et al. 2018, Ramoliya et al. 2022, Lawand et al. 2023). Absence of interxylary phloem in the early stage of the secondary growth and its development only after a certain stage of secondary growth, and the highest number of interxylary phloem islands was observed in the older stem (Rajput et al. 2008, Ramoliya et al. 2022, Lawand et al. 2023, Thacker et al. 2024). As shown in Fig. 6E and F of the current study, phloem islands were more common in the deeply situated parenchyma patches of the thick stems as compared to parenchyma patches close to the cambial zone. As observed in the present study, the formation of interxylary phloem in the druses containing parenchyma patches has not been reported so far. Therefore, Carlquist and Hanson (1991) has also suspected the occurrence of interxylary phloem in such patches of thin walled parenchyma in other species of the Convolvulaceae and stated that '*….. although, sieve elements are not observed in species that have druses containing patches of thin walled parenchyma, one cannot categorically state that sieve tube elements are always absent in these patches: study of liquid preserved samples are recommended*'. It is true in the case of *I. asarifolia* that liquid-preserved samples showed the presence of interxylary phloem, where the adjacent cell containing druses are shown in Fig. 6D. These druse-containing cell was surrounded by the interxylary phloem.

Conclusion

Stems of *Ipomoea asarifolia* are characterized by the presence of interxylary and internal phloem, successive cambia, formation of vascular cylinders from the dilation of phloem rays, and the presence of internal cambium. The occurrence of tyloses in the wide vessels is a common feature, while their presence in the protoxylem elements is a rare feature. Its occurrence in the present study may be associated with the internal injury in response to climbing and twisting of the stem around the supporting object. Successive cambia initiate from the pericyclic parenchyma. Formation of interxylary phloem took place by the dedifferentiation of the thin-walled axial parenchyma located in the parenchyma patches. Its formation may be associated with the rapid translocation of photosynthate from leaves towards the roots to meet the demand versus supply of photosynthate to the developing organs. Initiation of internal cambium and differentiation of both xylem and phloem from it seems to provide a safe path for the conducting elements from the sap-sucking and bark-damaging insects. An abundance of thin-walled, non-lignified axial parenchyma and the formation of successive cambia in the form of individual vascular cylinders may be associated with the climbing habit to provide the stem flexibility. Moreover, the main xylem ring surrounded by individual vascular cylinders external to the regular phloem may be functioning like a cable to provide strength as well as flexibility.

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Author contributions

Khyati D. Thacker: Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal). **Kailas K. Kapadane**: Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal). **Vinay M. Raole**: Conceptualization (supporting); Data curation (equal); Funding acquisition (supporting); Investigation (supporting); Project administration (equal); Resources (equal); Validation (equal); Writing – review and editing (equal). **Kishore S. Rajput**: Conceptualization (lead); Funding acquisition (lead); Investigation (lead); Project administration (lead); Supervision (lead); Validation (equal); Writing – review and editing (equal).

Data availability statement

This article has no additional data.

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