CHAPTER - II

Non-self-supporting plants are the important components of the terrestrial ecosystem (Isnard & Silk, 2009; Schnitzer & Bongers, 2011) and play several crucial roles in ecosystem services such as species diversity, carbon, nutrients and water sequestration (Isnard & Silk, 2009; Schnitzer & Bongers, 2011). These changes occur in the conducting elements due to the activity of the cambium. Differentiation of conducting tissues and activity of the cambium are indispensable factors in the survival and adaptation strategies of woody plants in a variety of ecosystems. In response to adaptation, structural transformation is one of the important aspects of the climbing species. Alterations in mechanical tissue probably have the highest contribution to the success of the climbing habit. In most cases, these alterations are unique and specific to certain groups, genera or species. Therefore, such a feature can be used as a diagnostic character of taxonomic value (Carlquist, 2001; Pace *et al.,* 2009; Rajput *et al.,* 2021). For example, intraxylary phloem and successive cambia in Convolvulaceae (Schenck, 1893; Metcalfe & Chalk, 1950; Fukuda, 1967; Pant & Bhatnagar, 1975; Lowell & Lucansky, 1986; Carlquist & Hanson, 1991; McDonald, 1992; Rajput *et al.*, 2008; Terrazas *et al.*, 2011; Rajput, 2017; Rajput & Gondaliya, 2017; Lekhak *et al.*, 2018; Rajput *et al.,* 2021), compound, corded, divided or fissured vascular cylinders in Sapindaceae (Radlkofer, 1875; Schenck, 1893; Tamaio & Somner, 2010; Bastos *et al.,* 2016; Lopes *et al.,* 2017; Cunha-Neto *et al.,* 2018), phloem wedges or furrowed xylem in the tribe Bignonieae (Bignoniaceae; De Barry, 1884; Schenck, 1893; Dobbins, 1971; Pace *et al.,* 2016) and other families (Angyalossy *et al.,* 2015). Similarly, most of the climbing members of the Sapindaceae show various types of cambial variants (Chery *et al.,*, 2020a) which are unique to certain tribes or may be shared by closely allied genera (Radlkofer, 1875; Schenck, 1893; Araújo & Costa, 2006, 2007; Tamaio & Angyalossy, 2009; Tamaio & Somner, 2010; Bastos *et al.,* 2016; Lopes *et al.,* 2017; Cunha-Neto *et al.,* 2018; Rajput *et al.,* 2021).

The importance of anatomical features in plant systematics was recognized long back in 1671 by Marcelo Malpighi in the form of a seminal book entitled *Anatomia Plantarum.* Bureau (1894) used anatomical features for the first time in plant classification and delimitation of taxa at various levels in Bignoniaceae. Since then, anatomical features of various organs like nodes, petiole, rachis, leaf lamina, presence of cortical and medullary bundles have been used to resolve the systematic position of cryptic species. Vegetative anatomy of various organs such as leaf and petiole anatomy, stomatal and trichome types, their distribution and frequency, and structure and development of tendrils has been studied by earlier researchers (De Candolle, 1879; Schenk, 1893; Solereder, 1908; Metcalfe & Chalk, 1950; Dehgan, 1982; Kamel & Loutfy, 2001; Kocsis & Borhidi, 2003; Agbagwa & Ndakwa, 2004; Noraini & Cutler, 2009; Mabel *et al.,* 2013; Firetti-Leggieri *et al.,* 2014).

The transport of water and the cost of plant body structure are the two properties, which mainly determine the structure of the secondary xylem. The lianas usually have a narrow and slender stem that is capable of transporting a considerable amount of water needed to fulfill the demand of a large canopy of the liana growing above the supporting host. During this growth adjustment, the stem outline of many non-self-supporting plants changes and it may be flat, triangular or square, lobbed or cruciform (Schenck, 1893; Pfeifer, 1926; Chalk & Chattaway, 1937; Metcalfe & Chalk, 1950; Obaton, 1960; Carlquist, 2001; Rajput *et al.*, 2012a, b, 2017; Lekhak *et al.*, 2018; Gama & Oskolski, 2021; Tamaio *et al.*, 2021). Though the stem outline in transverse view may vary from species to species while their roots remain circular in outline. These variations in the outline of stem and roots of the same species are an indirect indication of the role of the stem outline in mechanical support.

The root is main organ that plays a crucial role in anchoring the plant and is responsible for the supply of mineral elements and water. Lianas also have tremendously deep and resourceful root systems that allow them to cope with the demand versus supply of water and nutrients (Holbrook & Putz, 1996). Many of the lianas are also able to retain their leaves to continue the process of photosynthesis even during the drier part of the season; therefore, permitting vigorous radiation to be accessible to their leaves for extended periods (Schnitzer, 2005).

The climbing habit evolved by achieving stem elasticity and several structural modifications in the mechanical tissue (Darwin, 1865; Fisher & Ewers 1989, 1992; Rowe & Speck, 1996, 1998, 2005; Carlquist, 2001; Rowe *et al.*, 2004; Lekhak *et al.*, 2018; Rajput *et al.*, 2020). Stem flexibility is accomplished by changing growth forms and comparatively profusion of parenchyma cells and reduction in the mechanical tissue, wide rays, formation of parenchyma wedges, phloem wedges and by developing various kinds of cambial variants (Obaton, 1969; Carlquist, 1988, 2001; Pace *et al.*, 2009, 2018; Gerolamo *et al.*, 2020). Among these alterations, modification in the secondary growth is one of the behaviors to advance hydraulic capability and abundance of parenchyma to increase stem flexibility (Carlquist, 2001; Carlquist & Hanson, 1991; Ewers & Fisher, 1991; Rowe *et al.*, 2004; Rajput, *et al.*, 2008; Isnard & Silk, 2009; Schnitzer & Bongers, 2011; Angyalossy *et al.*, 2015; Rajput *et al.*, 2012, 2013; Lekhak *et al.*, 2018) for climbing or twining on the host that protects the conducting tissues from internal injury during stem torsion (Carlquist, 1988). The narrow stem diameter and altered mechanical tissue of the stems in climbing plants act like a cable and help them to protect the vessel from cavitation while an abundance of axial parenchyma helps them during external and internal injuries (Carlquist, 2001; Rowe *et al.*, 2004; Rowe & Speck, 2005; Isnard & Silk, 2009; Schnitzer & Bongers, 2011; Rajput *et al.*, 2012b, 2013; Lekhak *et al.*, 2018).

In self-supporting growth form, most of their energy is utilized in the radial growth for the formation of mechanical tissue to support the crown biomass whereas, non-self-supporting species (vines, climbers, twiners, lianas) rely on external structure (i.e., host/supporting object) for their mechanical support (Schnitzer & Bongers, 2011; Wyka *et al.*, 2013; Angyalossy *et al.*, 2015). These non-self-supporting members utilize their energy in extension growth instead of developing mechanical tissue to compete for above-ground resources, particularly sunlight (Bowling & Vaughn, 2009; Schnitzer & Bongers, 2011). These alterations in the mechanical properties and pattern of secondary growth such as the formation of the successive cambia, inter- and intraxylary phloem, vessel dimorphism, abundant parenchyma and large rays are the key adaptive features for the successful evolution of the climbing habit. All these features are reported in several climbing members belonging to different families of eudicots and gymnosperms including *Gnetum* by earlier researchers (Schenck, 1893; Pfeifer, 1926; Obaton, 1960; Carlquist, 2001; Rowe *et al.*, 2004; Rowe & Speck, 2005; Isnard & Silk, 2009; Speck & Bugert, 2011; Rajput *et al.,* 2010, 2013; Schnitzer *et al.*, 2015; Lekhak *et al.*, 2018).

Variant secondary growth comprises structures like altered activity of vascular cambium in various parts of the stem, modification of comparative extent and location of xylem and phloem, and the development of supplementary cambia that result in the variant secondary growth, which differs from that of normal or regular growth pattern (Fahn, 1967). According to Obaton (1960), the first reference to the variant structure was explained by De Mirbel (1828) who depicted the presence of four vascular bundles arising from the main vascular system of the stem in *Calycanthus*. Obaton (1960) further quoted that additional initial work was completed by Gaudichaud in 1833. Gaudichaud further studied the anatomical structure of lianas from Brazil belonging to the families Aristolochiaceae, Bignoniaceae, Fabaceae, Malpighiaceae and Sapindaceae. Subsequently, de Jussieu (1843) studied *Tetrapterys* (Malpighiaceae) showing the interruptions in the xylem through which structural continuity is maintained between the cortex and pith. Though, earlier researchers reported the presence of various types of variant structures that occur in mature or comparatively mature stems, the ontogeny of these variant structures was presented by Westermaier and Ambronn (1881).

Alterations in the pattern of secondary thickening in lianas may vary from species to species or may be unique and characteristic to certain tribes, and families or may be shared by allied genera (Rajput *et al.,* 2021). Therefore, these features may be used as diagnostic characters for the identification at a family level, for example, Bignoniaceae (Pace *et al.*, 2009) or Sapindaceae (Radlkofer, 1875; Schenck, 1893; Tamaio & Angyalossy, 2009; Tamaio & Somner, 2010; Bastos *et al.*, 2016; Lopes *et al.*, 2017; Cunha-Neto *et al.*, 2018; Chery *et al.*, 2020). These alterations in the increase in stem diameter sometimes lead to a change in the circular outline confirmation of the stem and frequently develop various types of stem outline such as lobed stem (e.g., *Dolichos lablab*, *Hewittia malabarica*, *Securidaca rivinaefolia*, *Turbina corymbosa*), flat or winged stem (e.g., *Bauhinia surinamensis*, *Machaerium multifoliatum*, *Rhynchosia phaseoloides*, *R. pyramidalis*), square (young stem of *Vitis quadrangularis* and some members of Bignoniaceae), triangular (*Serjania lethalis, S. laruotiana*) or cruciform (i.e., like a cross or "+") as observed in *Senegalia pedicillata* and *Grewia caffra*. These changes in the stem outline may be due to the irregular activity of a single ring of vascular cambium which is otherwise functionally normal in development (Philipson & Ward, 1965; Basson & Bierhost, 1967; Philipson, 1990; Carlquist, 2001a) or may be due to development of successive cambia only on a specific side of the stem (Moya *et al.*, 2018; Leme *et al.*, 2020; Rajput *et al.*, 2012) or may be due to the eccentric activity of successive cambia as in case of some members of Menispermaceae (Mennega, 1982; Jacques & Franceschi, 2007).

Such alterations in the structure and composition of the stems of non-self-supporting plants are usually known to occur only after the initiation of climbing habit (Caballe, 1998; Carlquist, 2001; Rowe *et al.*, 2004; Rowe & Speck, 2005; Isnard & Silk, 2009; Rajput *et al.*, 2012b, 2013; Angyalossy *et al.*, 2015; Lekhak *et al.*, 2018; Chery *et al.*, 2020; Tamaio *et al.*, 2021). During the early stages of secondary growth (i.e., before the development climbing habit), young plants of branches shows typical secondary growth which is characteristic of self-supporting plants (Rowe & Speck, 1996, 2005). A typical secondary growth includes uniform development of secondary xylem by vascular cambium around the stem circumference. Therefore, the young stems or shoots bear a relatively hard and stiff secondary xylem that helps them to stand erect in search of supporting objects. Thus, they are referred as '*searchers'* by Rowe and Speck (2005). However, as they start climbing, their anatomy changes which include the formation of wide vessels, wide rays, and abundant parenchyma (Rowe *et al.*, 2004; Rowe & Speck, 2005; Isnard & Silk, 2009; Terrazas *et al.*, 2011; Angyalossy *et al.*, 2015; Lekhak *et al.*, 2018). In certain climbers (e.g., *Condylocarpon* (Apocynaceae), *Strychnos* (Loganiaceae), *Schnella* (Fabaceae)

Serjania mexicana (Sapindaceae) etc.) with a woody and self-supporting growth phase, there is a sudden change in the wood structure with thick-walled fibres and narrow vessels to early compliant wood with a higher frequency of large diameter vessels leading to a significant reduction of stem stiffness (Carlquist, 1991; Rowe *et al.*, 2004, Rowe & Speck, 2005; Isnard & Silk, 2009; Angyalossy *et al.*, 2015; Lekhak *et al.*, 2018). Besides these changes, most of the non-self-supporting members show the development of various types of cambial variants that are hypothesized to result from the climbing habit (Carlquist, 1988, 2001; Isnard & Silk, 2009; Angyalossy *et al.*, 2015; Lekhak *et al.*, 2018; Rajput *et al.*, 2021), including the formation of successive cambia.

All these cambial variants have been categorized variously by earlier researchers (Schenck, 1893; Pfeiffer, 1926; Boureau, 1957; Obaton, 1960; Philipson & Ward, 1965; Metcalfe & Chalk, 1950, 1983; De Bary, 1984; Carlquist, 1988, 2001). These classifications include extensive monographs (Pfeiffer, 1926), diagrammatic illustrations (Chalk & Chattaway, 1937) or cellular details and outline diagrams of the monograph (Obaton, 1960). These classifications include, bicollateral vascular bundles, medullary bundles, cortical bundles, intraxylary (internal) phloem, interxylary (included) phloem, concentric rings of xylem alternating with phloem, stem axes elliptical, flattened, or furrowed in cross-section, stems lobed and furrowed or fissured xylem. Among them, the family Sapindaceae is of special interest and treated separately due to a unique type of cambial variant (referred to as compound xylem i.e., Polystele xylem). In Sapindaceae four different types of cambial variants have been reported; i) The compound xylem mass, ii) The divided xylem mass, iii) The corded xylem mass and iv) The cleft xylem mass (Radlkofer, 1875; Schenk 1893; Obaton, 1960; Van der Walt *et al.*, 1973; Caballe, 1993; Klaassen, 1999; Araujo & Costa, 2006; Tamaio & Angyalossy, 2009; Tamaio *et al.*, 2011).

All these variants' growth patterns reported so far have been classified under three major groups by Carlquist (1988, 2001); 1) formation of successive cambia, 2) a single cambium that produces interxylary phloem as well as xylem towards the centre, and 3) a cambium that originates as normal single cambium (or in a few cases, multiple and simultaneous) which produces phloem centrifugally and xylem centripetally but has no cylindrical conformation. The third category is further divided into seven subcategories: i) stem flattened in trans-section, ii) stem lobed in trans-section (stem lobed but not fragmented, and stem lobed and fragmented), iii) stem with xylem furrowed, iv) xylem in plates, v) wood portion dispersed separated by parenchyma, vi) divided xylem cylinder and vii) compound secondary xylem.

With this brief background, the present study attempts to understand the structural alterations in the growth patterns and structure of secondary xylem by studying their developmental stages in selected tropical lianas.

➢ Objectives of the proposed study:

1. To study the origin and development of procambium and vascular cambium.
2. To study the structure and development of primary and secondary vascular tissue prior to climbing habit.
3. To study the behaviour of meristem (pattern secondary growth) that is responsible for secondary growth after adapting the climbing habit.
4. To study the structural alterations induced in the secondary xylem and phloem in response to the shift from self-supporting to climbing habit.
5. To correlate these alterations in the secondary tissues with ecological wood anatomy.