1. INTRODUCTION

Growth is by far the most complex of all physiological processes and as such is not susceptible to any precise definition. Many authors restrict the term "growth" as irreversible change in size and weight i.e. cell division and cell enlargement process which ultimately results in increase in height and size. In plants, growth is broadly divided into two classes; vegetative growth and reproductive growth. Vegetative growth is responsible for the development of vegetative organs, whereas reproductive growth gives rise to reproductive organs of plant like gynoecium, androecium and embryo. On the basis of its pattern, growth is further classified as primary and secondary growth (Meyer and Aderson 1952). Primary growth is initiated in apical portion of shoot and root meristem. It results in the construction of primary tissues of a plant which accounts for overall increase in the length of the plant axis at both stem and root tips, and in the development of the branching system of the stems and roots (Fig. I). Primary growth is also responsible for the formation of lateral appendages such as root hairs, leaves and floral parts (Esau 1965; Fahn 1967; Mauseth 1988b; Evert 2006). In many species such as pteridophytes and many monocotyledons, the primary tissues constitute the entire plant while secondary growth is not observed in them due to absence of vascular cambium (Esau 1977). However, in gymnosperms and most dicotyledons, stems and roots not only grow continuously by proliferation of the fundamental tissues of these organs but also increase in diameter as a result of the activity of the lateral meristem called as "the vascular cambium". In most of the dicotyledons and gymnosperms, vascular cambium remains functional throughout the life span. Sometimes it ceases, due to slow continuance of cell division and enlargement in some of the tissues, particularly those near the periphery. Species, in which the primary tissues constitute the entire body of the plant, is the sole mode of growth in diameter (Meyer and Anderson 1952). During growth, a part of the promeristem is gradually transformed into a procambium from which primary vascular tissues develop. Cell division in apical meristems occur both longitudinally and in various lateral planes, thus giving rise to the more or less cylindrical configuration of the typical stem (Meyer and Anderson 1952).

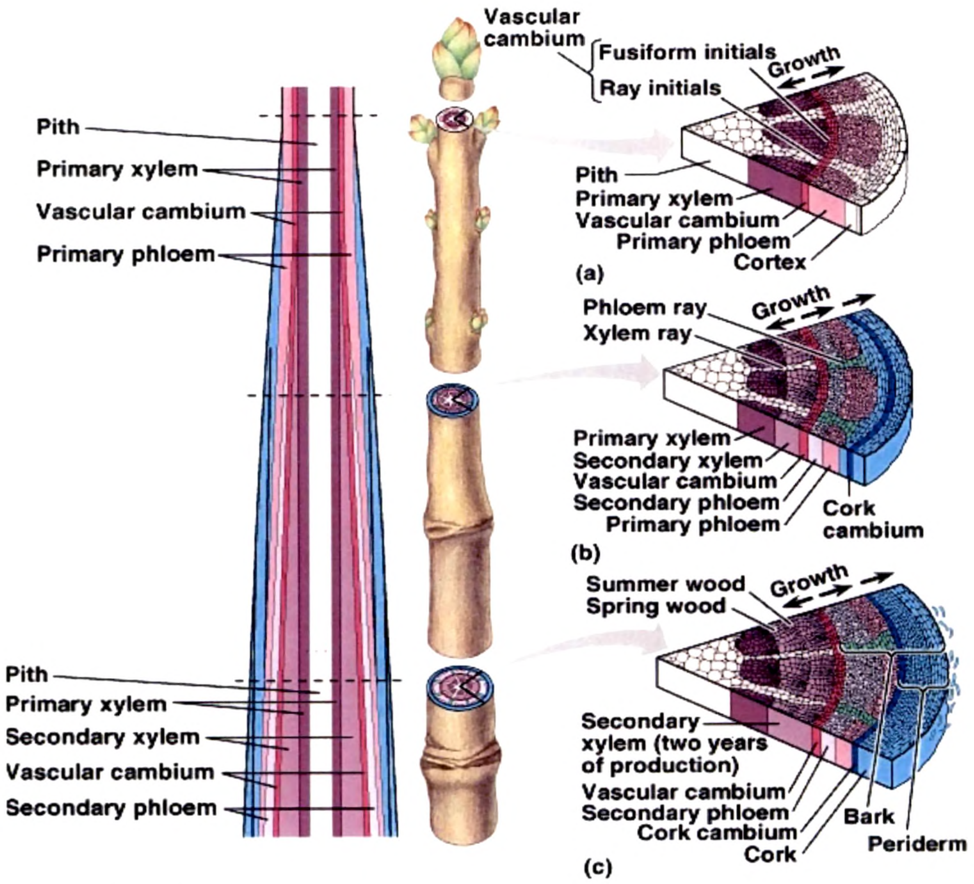
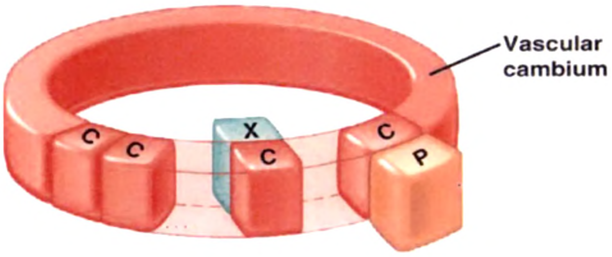


Figure I: Plant showing primary and secondary growth in stem (after Campbell and Reece 2008).

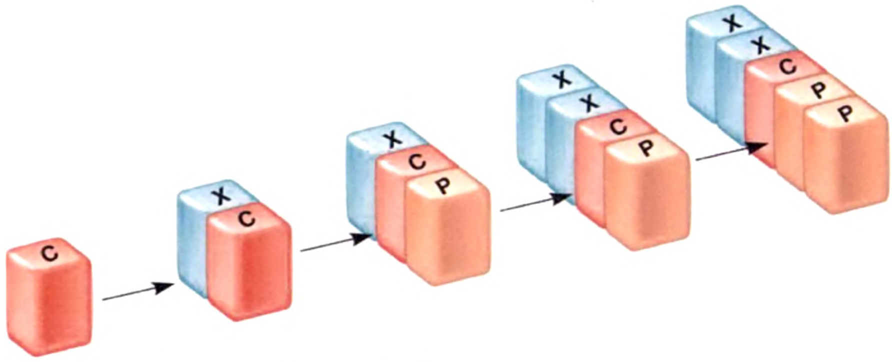
Growth in diameter of roots and stems results principally from the activity of lateral meristem (the vascular cambium), which is responsible for the secondary growth of plants (Fig. I). In any plant, secondary growth is affected by the cell division activity of the vascular cambium. These growing layers in the cambium due to cell division activity constantly provide additional and renewed conducting and supporting elements of secondary xylem and phloem (Larson 1994; Spicer and Groover 2010). Owing to its dynamic nature and growth patterns, it forms one of the important plant tissues responsible for secondary growth and for the scientific studies too. Primary growth chiefly increases the length of the axis and adds the appendages where as secondary growth increases the diameter of the axis (after initial increase) of the large body of woody plants (Esau 1965; Mauseth 1988b; Evert 2006; Wang and Li 2008; Delgado *et al.* 2010; Jardin *et al.* 2010; Spicer and Groover 2010). Only in tree ferns and a few of the monocotyledons a large body (thick stem) is present which is wholly primary in nature (Eames and McDaniels 1947; Schweingruber *et al.* 2006). Majority of the larger monocotyledons, including some species of palms, woody Yuccas and lilies, possess secondary growth of special type (Cheadle 1937; Tomlinson and Zimmermann 1969; Lu and Chiang 1976; DeMason 1984; Rudall 1991, 1995; Spicer and Groover 2010).

Various patterns of secondary growth can be observed in herbaceous species: i) In some herbaceous dicots, there is very little or almost no cambial activity which consequently results into no prominent secondary growth. ii) In some others there is limited amount of secondary growth due to the cell division and differentiation activity of cambium within each vascular bundle (Ye 2002; Spicer and Groover 2010). iii) In third category, parenchyma cells between the vascular bundles acquire meristematic character and form an interfascicular cambium that joins with the fascicular cambium to form a continuous ring (Philipson and Ward 1965). In those stems where the procambium tissue is a cylinder rather than a series of separate provascular strands, in such stems the vascular cambium develops as a continuous cylinder from the beginning itself. Differentiation of xylem mother cells results into formation of vessels, tracheids, fibres and axial parenchyma while phloem mother cells differentiate into sieve tubes, companion cells, fibres, and phloem parenchyma. The vascular rays are continuous form of xylem to phloem across the cambium. Periodically number of rays in the cambium may be increased by conversion of fusiform cambial initials into ray initials to produce vascular rays or vice versa (Meyer and Anderson 1952).

Cambium being an imperative lateral meristem is responsible for the production of wood (Esau 1965; Mauseth 1988b; Evert 2006; Wang and Li 2008; Delgado *et al.* 2010; Jardin *et al.* 2010; Spicer and Groover 2010); therefore, due attention is paid worldwide to study the same for understanding the process of wood formation. In temperate trees, seasonal behaviour of vascular cambium has been studied thoroughly, but similar studies are very few on tropical trees (Rao and Dave 1981; Sagheer and Iqbal 1987; Siddiqi 1991; Iqbal 1994, 1995; Rao *et al.* 1996a, b; Rao and Rajput 1999; Rajput and Rao 2000; Venugopal *et al.* 2007). Continuous and sustainable supply of wood to meet current demand requires thorough understanding of the cambial behaviour for the manipulation and improvement of the wood quality. Tremendous efforts have been initiated along these lines to study and understand the hormonal, biochemical, molecular and other mechanisms of the cambial activity and formation of wood throughout the world (Savidge 2000; Kyung-Hwan Han 2001; Plomion *et al.* 2001; Uggla *et al.* 2001; Jura *et al.* 2006; Begum *et al.* 2010; Delgado *et al.* 2010; Jardin *et al.* 2010; Spicer and Groover 2010). Every plant, After attaining a definite height, each plant primarily encounter the problem of gravity, and to overcome this major hurdle, trees apply a method of increasing their diameter with a dynamic lateral meristem called the "vascular cambium".



(a) Types of cell division



(b) Accumulation of secondary growth

Figure II: **(a)** Radial division of vascular cambium produces xylem (X) and phloem (P) cells. **(b)** Secondary growth showing repeated radial division of cambium which produces more xylem than phloem. (after Campbell and Reece 2008).

The vascular cambium is initially derived from procambial cells which differentiated acropetally from pre-existing promeristem strands into the apex of elongating primary shoot. Following the maturation of primary xylem and phloem, the cells located between primary xylem and phloem remains meristematic in nature called fascicular cambium. At the time of initiation of secondary growth, the cells located between the adjacent vascular bundles acquire meristematic nature and form interfascicular cambium. These fascicular and interfascicular segments of cambium join to form a complete cylinder of vascular cambium (Esau 1965; Mauseth 1988b; Evert 2006). By composition, the vascular cambium is made up of two types of initials, the fusiform initial, and the ray initial (Esau 1965; Mauseth 1988b; Evert 2006; Spicer and Groover 2010). The fusiform initials are an elongated cell with tapering ends and gives rise to axially elongated derivatives of xylem centripetally and phloem centrifugally. On the other hand, ray initials are much smaller, more or less isodiametric in shape and give rise to xylem and phloem rays. The cambium becomes active in the formation of new cells before primary growth has entirely ceased in all the tissues at the corresponding level of the stem (Meyer and Anderson 1952). Periclinal divisions in the cambium cells result in the development of secondary xylem on its inner face and secondary phloem on its outer face which cause an increase in the diameter of the axis (Fig. IIa, b). In each growing season, continuation of secondary growth results in the development of secondary xylem cells inside and secondary phloem exterior to it. The enlargement of the xylem cells originating from the cambium initials push the cambium and results in outward movement of the cambium; thus, resulting in an increase in the girth of the cambium cylinder.

Vascular cambium of different taxa varies in its structure and function depending on its derivatives, the genetic constitution, and physiological phenomenon of the plants as well as the environmental factors (Philipson *et al.* 1971; Iqbal and Ghouse 1987). Dormancy of the bud, cambium and leaf shedding are in response to environmental pulsation representing temporary level of adjustment (Halle *et al.* 1978). Developing leaves produce hormones necessary for cambial activity and attributes to the development of its derivatives (Hess and Sachs 1972; Rao and Dave 1981, 1983; Paliwal and Paliwal 1990a, b; Savidge 1996; Rajput and Rao 1998a, b, 2000; Rao and Rajput 1999, 2001). Various environmental and physiological factors have been observed by several authors as controlling the cambial activity. The effect of temperature is considered as a factor of primary importance for activating the cambium (Paliwal and Prasad 1970; Philipson *et al.* 1971; Tsuda and Shimaji 1971; Chou and Chiang 1973; Kramer and Kozlowski 1979; Rao and Dave 1983; Iqbal and Ghouse 1985; Antonova *et al.* 1988; Badola *et al.* 1989; Rao *et al.* 1996a, b; Srinivas 1996; Rajput and Rao 1998a, b, 2000; Rao and Rajput 1999, 2001). In tropical environment, onset of dry season brings about dormancy and reactivation of cambium and formation its derivatives starts after the arrival of first shower of rains (Fahn 1990). Compared to tropical species, cambial activity in temperate trees has been studied thoroughly but similar information is lacking on the tropical trees (Rao and Dave 1981; Sagheer and Iqbal 1987; Siddiqi 1991; Rao 1996a, b; Rao and Rajput 1999; Rajput and Rao 2000; Venugopal *et al.* 2007).

On the basis of habit and forms, the plants may be classified into self supporting and plants that are dependent on other object for support i.e. non-self supporting (Isnard *et al.* 2003; Lopes *et al.* 2008; Spicer and Groover 2010). Climbing plants differ from trees and shrubs in number of characteristics; most notable is the mechanical properties of the stem (Isnard *et al.* 2003; Lopes *et al.* 2008; Field *et al.* 2011). This variation in the mechanical properties of wood is mostly related with a shift from self supporting habit to climbing habit. Lianas have particularly induced several remarkable changes in anatomical and mechanical properties of the secondary xylem such as formation of successive cambia, interxylary phloem, dissected or compound xylem, furrowed xylem and so on. It is accepted universally that the shift from self supporting to climbing habit is resulted in the development of several interesting structures which differ from the more usual types, thus sometimes referred as anomalous (Cutter 1969) or cambial variant (Carlquist 1988; Sajo and Castro 2006; Spicer and Groover 2010; Patil *et al.* 2011; Rajput *et al.* 2011). Variant secondary growth is therefore widespread in lianas and it is considered to increase stem flexibility to protect the vessels from air embolism, and to phloem and increase storage parenchyma. It also limits physical disruption of vascular tissues during twisting and bending, and promotes wound healing after girdling (Dobbins and Fisher 1986; Fisher and Ewers 1992; Lopes *et al.* 2008; Patil *et al.* 2011).

Lianas (woody vines) are the important components of tropical forests, contributing approximately 25% of the species diversity of woody stems (Gentry 1991; Schnitzer and Bongers 2002; Isnard and Silk 2009; Field *et al.* 2011; Speck and Burget 2011). Though, they constitute a small proportion of the woody biomass in tropical forests (Gentry 1991; Hegarty and Caballe 1991; Gerwing and Farias 2000; DeWalt and Chave 2004), they have a dis-proportionate effect on forest dynamics (Schnitzer and Bongers 2002; Speck and Burget 2011). Lianas compete with trees both above and below ground (Schnitzer *et al.* 2005; Letcher and Chazdon 2009). They can cause considerable physical damage to their hosts (Putz and Holbrook 1991); and may alter gap-phase dynamics (Schnitzer *et al.* 2001; Letcher and Chazdon 2009) and impact tree seedling regeneration (Perez-Salicrup 2001). Despite their prevalence in tropical forests and their strong impact on forest dynamics, lianas have received relatively little attention compared to trees (Letcher and Chazdon 2009; Isnard and Silk 2009). Though they are an important constituent of forest ecosystem, histological studies on their cambial activity have always been neglected on this major component of forest ecosystem (Putz and Holbrook 1991; Isnard *et al.* 2003; Lopes *et al.* 2008; Isnard and Silk 2009; Rajput *et al.* 2010b). The underlying reason for this may be their lesser economic importance when compared to timber trees (Carlqist 2001a; Rajput *et al.* 2008; Patil *et al.* 2011). In the process of understanding the cambial behaviour, our studies on anomalous behaviour of vascular cambium may throw some light on the understanding of cambial behaviour and management of wood quantity, quality, properties etc.

Morphologically, climbing plants can be classified into different types such as vines (climbers) and lianas. By definition, vines are plants that are rooted in the ground but dependent up on external plants or object for mechanical support. Vines may thus be interpreted as mechanical parasites that are in competition with their host plant for light, water and mineral resources (Putz 1984; Stevens 1987). According to Liang *et al.* (2010), vines are herbaceous climbing plants, having weak stem that derives support by climbing, trailing, twining or creeping along a surface. A climber is general name for a vine, it is nothing but a week stem plant that readily grows up on a support or over other plants for support, while woody climbers are perennial plants which are woody in nature, and hook climbers may include any plants climbing by the aid of recurvate spines, hooks or thorns, which passively assist them in climbing (http://www.thefreedictionary.com;http://en.wikipedia.org/wiki/Climber). Lianas are woody climbing plants that rely on other plants for support (Putz 1984; Putz and Holbrook 1991; Liang *et al.* 2010). A liana can be long-stemmed, woody vines that are rooted in the soil at ground level and use trees as well as other means of vertical support to climb up to the canopy in order to get access to well-lit areas of the forest (Liana 2011, *Encyclopaedia Britannica*). Lianas are special characteristics of tropical moist deciduous forests and rainforests. They are conspicuous component of tropical forest ecosystems and represent one of the most important structural differences between tropical and temperate forest (Gentry 1991; Cambell and Newbery 1993; Perez-Salicrup and Meijere 2005).

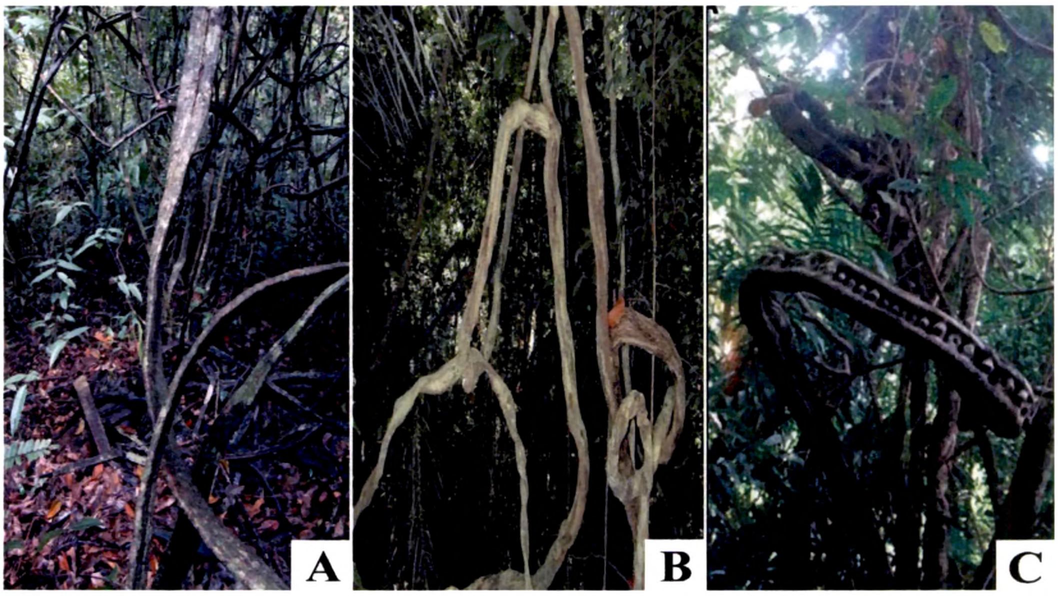


Figure III: A) Liana habit showing flattened stem of *Macherium* sp., B) Hanging and twining liana of *Camptosema isopetalum*, and C) Stem splitting and high flexibility of *Bauhinia* sp. (Caesalpiniaceae).

Flatten or twisted lianas often become tangled together to form a hanging network of vegetation (Fig. IIIA-C). Lianas belong to several different plant families and may grow up to 60 cm (about 24 inches) in diameter and 100 mt (about 330 feet) in length. They comprise a significant part, about 25% of the woody flora, of many tropical forests (Gentry 1988), and form an important structural component of the forests by "tying" the forest together (Fox 1968; Jacobs 1976; Gentry 1983; Putz 1984). They contribute in terms of flowers and fruits for animals, and form important walkways for arboreal animals (Emmons and Gentry 1983). These structural parasites exploit the trunks and limbs of tropical trees for support in order to place their own leaves into well-lit portions of the forest canopy. The presence of large lianas provides a very good indicator of older, more mature stands of forest. This successful establishment of climbers or woody lianas is possible because of the presence of attachment mechanisms and special adaptive stem structure. This allows them to survive in the forest ecosystem (Schnitzer *et al.* 2005). Anomalous stem anatomies also allow lianas to survive traumatic events after major injuries by nonfatal splitting of the stem and rapid repair of vascular disruption by wound healing in stems (Fisher and Ewers 1989, 1991).

Liana architecture develops with a "duality" between an initial self-supporting phase and a later climbing phase (Cremers 1973, 1974; Caballe 1986a, b, 1998). Liana seedlings typically achieve vertical growth before becoming unstable and climbing onto the surrounding vegetation via a large diversity of attachment modes. Later during its development, shoots of mature lianas that reach the top of the canopy can also be held erect, an advantage for finding and attaching to surrounding support. Thus, a striking ontogenetic change occurs in stems of many lianas and has great significance in terms of mechanical and hydraulic function. Schenck (1893) and Haberlandt (1928) suggested that the "anomalous" disposition of secondary tissues (cambial variants) might increase the flexibility of the stem, augmenting its resistance to mechanical damage caused by twisting.

In dicotyledons and gymnosperms, extension growth is followed by increase in girth or thickness of the stem referred as secondary growth. As mentioned earlier that in the young apical shoots, vascular bundles arranged in the form of ring became joined by interfascicular and form continuous cylinder of vascular cambium. This ring of vascular cambium remains functional throughout the life span of the plant with brief spell of dormancy alternating with the active period of cell division (Esau 1965; Fahn 1967; Larson 1994; Iqbal 1994, 1995; Evert 2006). During the cell division activity, a single ring of cambium form secondary xylem occurring centripetally and secondary phloem centrifugally, such pattern of cell division is called as normal activity of cambium. However, in certain dicotyledons and few gymnosperms, activity of the cambium deviates from its normal activity and results in formation of anomalies (Handa 1939; Stevenson 1990; Carlquist 1988, 1996a, 2001a; Rajput *et al.* 2008; Field *et al.* 2011; Patil *et al.* 2011; Rajput *et al.* 2011). This deviation in the pattern of cell division and differentiation of its derivatives by the cambium is known as anomalous secondary growth (Eames and McDaniels 1947; Esau 1965; Fahn 1967).

Anomalous secondary growth is the term under which cambial confirmations, cambial products and cambial numbers have been grouped, which differ from the most common "normal" condition namely, a single cylindrical cambium that produce phloem externally and xylem internally. The term *cambial variant* is employed now days as a way of referring to the less common types as "anomalous" may give the misleading impression of a disorderly action (Carlquist 1988, 2001a, 2004, 2007a, b). Such growth includes, features like unequal activity of the cambium on different portions of the circumference of the axis, the alteration of the relative amount and position of the xylem and phloem, and the appearance of additional cambia that result into secondary growth differing from the normal secondary growth (Fahn 1967). Obaton (1960) reported cambial variant in 108 species of woody lianas in 21 families of plants in western Africa. According to him, the first reference to anomalous structure was given by De Mirbel (1828) who drew attention to the presence of four vascular bundles arising from the main vascular system of the stem in *Calycanthus*. Another early work cited by Obaton was done by Gaudichaud, who in 1833 studied lianas from Brazil belonging to the Aristolochiaceae, Bignoniaceae, Fabaceae, Malphiaginaceae and Sapindaceae. In 1843, de Jussieu studied *Tetrapterys* (Malphighiaceae) where there are interruptions in the xylem through which structural continuity is maintained between the cortex and pith. The early investigators reported presence of various types that occur in mature or relatively mature stems but Westermaier and Ambronn (1881) made an early attempts to show how anomalous thickening began and develop ontogenetically (Metcalfe 1983).

Extensive work on liana stem anatomy by Schenck (1893) and later Obaton (1957) revealed a high frequency of anomalous/variant structure in lianas (Metcalfe and Chalk 1983; Putz and Mooney 1991; Carlquist 2001a). In such plants, not only the pattern of secondary thickening varies but sometimes it also changes the outline confirmation of the stem (Fig. IIIA, C). Stems of such species most often develop various confirmations other than the slender such as lobbed (*Dolichos lablab*, *Securidaca rivinaefolia*), flattened or winged stems (*Bauhinia surinamensis*, *Rhynchosia phaseoloides*), square (some members of Bignoniaceae), triangular (*Serjania lethalis, S. laruotiana*) or like a cross as in *Senegalia pedicillata* and so on.. However, change in the outline confirmation may be the product of single vascular cambium that is normal in position but functionally abnormal in conformation (Philipson and Ward 1965; Basson and Bierhost 1967; Philipson 1990; Carlquist 2001a) or may be due to the eccentric activity of successive cambia as in some members of Menispermaceae (Mennega 1982; Jacques and Franceschi 2007). The complexity of anatomical construction in many lianas is known to arise after the development of climbing architecture (Caballe 1998) although, some anomalous anatomical organizations are characteristic to family or genus, they cannot be used as a reliable guide to the phylogeny (Schenck 1893; Obaton 1957; Putz and Mooney 1991; Caballe 1993; Carlquist 2001a; Field *et al.* 2011). Apparently, there is no correlation between the type of anomalous structure and attachment mode.

Review of literature indicates that the cambial variants occur frequently in lianas as compared to tree species (Schenk 1893; Obaton 1960; Metcalfe and Chalk 1983; Putz and Mooney 1991; Carlquist 2001a; Letcher and Chazdon 2009; Rajput *et al.* 2010; Patil *et al.* 2011). Carlquist (1988) also reported similar findings that cambial variants represent a form of secondary growth which is especially common in lianas of various families. This is however, not a universal correlation for similar variant types occurring in plants that are not lianas and conversely there are some lianas in which secondary thickening confirm the normal type. It is also evident that the various types of cambial variants do not go hand in hand with the taxonomy of the plants concerned. Although cambial variants are known only in a small proportion of the dicot families, any one type of anomaly may occur in families, in which generally accepted criteria of taxonomy provide little or no evidence of affinity. Nevertheless, cambial variants are always of diagnostic value because of its restricted taxonomic occurrence (Metcalfe and Chalk 1983; Putz and Mooney 1991; Carlquist 2001a).

Anomalous structures may be directly influenced by external environmental conditions. The woody climbers or lianas constructed differently both from morphologically and physiologically from the normal ones. As thickness increases in lianas, it shows abnormal secondary growth and the storage organs exhibit anomalous structure. At the same time, there are some cases of anomalous condition which showed variations of the design (Eames and McDaniels 1953, Sajo and Castro 2006). Haberlandt (1914) has referred them as adaptive and non-adaptive anomalies of secondary growth respectively. Precise reason behind occurrence of cambial variants is yet not known, but it is considered that it is due to the effect of physiological or environmental stress (Joshi 1935; Dobbins and Fisher1986; Putz and Mooney 1991). Carlquist (1988) tried to explain why lianas have such structure? According to him, the function of flat stem of lianas seems related to their climbing habit, either when adpressed to stems of supporting tree trunks (*Marcgravia*) or leaning on them (*Heteropteris*). During this growth form, the cambium changes its activity in one or many aspects, leading to the production of soft-walled tissues mixed with thick-walled lignified tissues, which presumably provide higher flexibility to climbing stems (Rowe *et al.* 2004; Isnard and Silk 2009), which allow them twisting without damaging the secondary xylem (Carlquist 1988). Alternatively, these structures might also play a role in photosynthate storage (Carlquist 1988) and wound repair (Dobbins and Fisher 1986). Diverse list of ecological and functional significance may be found in the literature for the occurrence of cambial variant (Eames and McDaniels 1947; Philipson *et al.* 1971; Metcalfe and Chalk 1983; Carlquist 1988, 2001a; Fisher and Ewers 1989). According to Kerner (1895), stem flattening is the result of injuries due to lateral pressure in the conducting tissues, which are prevented in the climbing plants by forming the ribbon shaped stems. Obaton (1960) lists the cambial variant types in relation to habitable categories, and according him one can find that flattened stems are restricted to lianas and are the only stem type found in epiphytic lianas. Different plant families have independently evolved cambial variants along the course of angiosperm evolution, with different variants being so characteristic of each plant group that these plant families can be identified based only on their stems (Caballe 1993). For instance, the Menispermaceae exhibit successive cambia (Schenck 1983; Jacques and De Franceschi 2007), the Sapindaceae show multiple steles (Schenck 1983; Carlquist 1988), some Fabaceae show asymmetrical growth (Schenck 1983;

Fisher and Ewers 1992), while the Bignoniaceae exhibit a xylem that is furrowed by phloem wedges (Dobbins 1971; Schenck 1983; Carlquist 1988).

Another characteristic feature in the stems of lianas and vines is the abundance of parenchyma cells. The function of this parenchyma or conversely, the dispersed nature of xylem and phloem units within the parenchymatous background and distribution of phloem in various types of cambial variants has resulted into diverse hypotheses (Carlquist 1988, 2001a). Among those that can be offered are the following:

1. Parenchyma between wood segments provides greater flexibility for lianas and vines, permitting them to adapt to shift induced by growth in the trees on which they are supported. Furthermore, the parenchyma is held under this hypothesis to permit torsion of the stem with minimum of damage to the vessels and sieve tubes (Schenck 1893; Carlquist 1975, 1985, 1988, 2001a).
2. Parenchyma abundance in stems of lianas and vines provides a site for starch storage. This stored starch could be supplied at the time of massive flowering and fruiting when the vine or liana reaches canopy status. Additionally, the starch storage could function in the way it does in some trees such as the sugar maple, (*Acer sachorum*), in which starch in parenchyma is hydrolyzed into sugars that are transferred into vessels, where the increase in osmotic pressure generates flow of water to those sites (Sauter 1966a, b; Braun 1970, 1983, 1984; Carlquist 1985, 1988).
3. Parenchymatization represents an alternative background tissue, present instead of fibres and sclerenchyma because lianas and vines are not self-supporting (Carlquist 1988, 2001a).
4. Parenchyma permits repair of the vascular system by formation of new cambia that can replace deactivated conducting cells with new functional one. This would permit lianas that fall to the ground with collapse of their supporting trees to survive and continue functioning. A corollary of this hypothesis is that redundancy of conducting tissue, when it is scattered throughout a stem, provides a degree of safety that permit non injured xylem and phloem to continue conduction even though some parts of stem are injured (Dobbins and Fisher 1986; Fisher and Ewers 1989; Carlquist 1988, 2001a).

Few cases cited above shows anomalous structures which are not directly influenced by environmental factors. However, in most of the cases anomalies are results of ecological adaptations which influenced by environmental factors (Carlquist 1988). In attempting to correlate cambial variants with habit and ecology, one must first note that cambial variants are particularly conspicuous in lianas and vines, but there are several instances in which cambial variants occur in plants of entirely different habitats. For example, in Beet (*Beta vulgaris,* Chenopodiaceae), the rings of vascular tissue produced by successive cambia and primary thickening meristem. This mechanism may represent a successful way of providing innervations for the storage structure. On the other hand, vascular strands are scattered throughout other storage organs without successive cambia, such as potatoes or sweet potatoes (Rapoport and Loomis 1986; Carlquist 2007a; Rajput *et al.* 2008).

As already stated that occurrence of cambial variants are quite common in the climbing plants and in storage roots. They are different from the normal ones in the mechanical construction and physiological function points of view. The methods leading to the formation of these cambial variants are though quite variable; however they may be put into two main categories:

i) Cambium is of normal type in which irregular or peculiar activity of the cambium results into formation of unusual arrangement and proportion of the vascular tissues.

ii) Where the cambium itself represents oddity in deposition of vascular elements which consequently results into unusual structure and arrangement of secondary tissues; or the original cambium is replaced by other cambium layers which are unusual both in arrangement and behavior (Eames and McDaniels 1953; Cutter 1969; Gangulee *et al.* 1988; Lopes *et al.* 2008).

Due to large number of variations and diversity in origin of cambial variant, their position and functional pattern etc., posed a problem to different workers which consequently led to development of a variety of terminology and classifications (Philipson and Ward 1965; Philipson *et al.* 1971; Metcalfe and Chalk 1983; Carlquist 1988; Patil *et al.* 2009). Therefore, it is very difficult to classify them into distinct groups because of their diversity and intergrading with normal forms of cambial growth. In some families of dicots like the Amaranthaceae, Chenopodiaceae, Menispermiaceae and Nyctaginaceae and certain gymnosperms (*Gnetum* and *Welwitschia* and some members of Cycadles), there are series of multiple cambia which are functional at a time (Carlquist 2007a; Rajput *et al.* 2010). Usually, the normal cambium functions for a while and then ceases to divide. A new cambia then form in succession toward the outer face of the stem, which ultimately results in. wood that is composed of concentric rings of secondary xylem alternating with the secondary phloem. Another example of species forming successive cambia is *Avicennia resinifera.* In this species, the first ring of the supernumerary cambium arises by division of the inner cells of the cortex and subsequent cambia arise from the derivatives of the previous cambium (Studholme and Philipson 1966; Nele *et al.* 2008). Formation of successive cambia has also been reported in *Bougainvillea*, each of which originates from the derivatives of the former cambium. Functionally, each cambium is bidirectional and give rise to secondary xylem centripetally and secondary phloem centrifugally (Esau and Cheadle 1969). In some woody plants, strands of secondary phloem are found embedded within the secondary xylem; formation of such phloem is referred as included phloem or interxylary phloem (IAWA Committee 1989). Interxylary and included phloem are terms applied to the phloem produced centripetally from the cambium or externally from isolated cambial segments within the secondary xylem as in *Strychnos* and in several Bignoniaceae species (Mikesell and Popham 1976; Carlquist 1988).

Numbers of classifications on cambial variants have been proposed by earlier workers (Schenck 1893; Pfeiffer 1926; Metcalfe and Chalk 1950; Boureau 1957; Obaton 1960; Philipson and Ward 1965; de Bary 1984; Carlquist 1988, 2001a). The monographic work published by Schenk (1893) and Pfeiffer (1926) is basic study on cambial variants. In addition to extended descriptive coverage, the literature citation of that monograph is exceptionally extensive. Thereafter, detail wood histology of West African lianas (a group rich in cambial variants) is presented by Obaton (1960). A brief summary of type with useful diagrammatic illustrations has been offered by Chalk and Chattway (1937).

Metcalf and Chalk (1983) summarized different types of cambial variants by giving emphasis on the major types of cambial variants reported so far. Their description on different anomalies includes: Bicollateral vascular bundles, Intraxylary (internal) phloem, Medullary bundles, Cortical bundles, Interxylary (included) phloem, Concentric rings of xylem alternating with phloem, Stem axes elliptical, flattened, or furrowed in cross section, Lobed stems, and Furrowed or Fissured xylem. A special treatment has been given to the Sapindaceae due to its very special polystelic cambial variants. Several species of liana from this family attracted an attention of various investigators due to four very unique type of cambial variant (Radlkofer 1875; Schenk 1893; Obaton 1960; Van der Walt *et al.* 1973; Caballe 1993; Klaassen 1999; Araujo and Costa 2006; Tamaio and Angyalossy 2009; Tamaio *et al.* 2011). Anatomy of the Sapindaceae was documented for the first time by Radlkofer (1875, 1931-1934, 1932). According to him, there are three different types of cambial variants in the Sapindaceae, they are: 1) The compound xylem mass, 2) The divided xylem mass, 3) The corded xylem mass and 4) The cleft xylem mass.

Philipson and Ward (1965) classified cambial variants into two main classes, their classification is as follow:

1. Cambium normal in position but atypical:
    - i. Asymmetric activity
    - ii. Cessation of xylem formation
    - iii. Modified interfascicular cambium
    - iv. Included phloem: *Combretum* type
    - v. Included phloem: *Strychnos* type
2. Cambia in unusual position:
    - vi. Medullary cambia
    - vii. Cortical cambia

According to Carlquist (1988, 2001a), the variants reported to date may be said to fall into three main categories:

1. Successive cambia (Concentric type according to some authors).
2. A single cambium that yields interxylary phloem as well as xylem internally (Foraminate type according to some authors).
3. Cambia that begin as single (or in a few cases, multiples and simultaneous) normal cambia that produce phloem externally and xylem internally, and which have or develop a conformation other than cylindrical.

The third category is again sub divided into the following:-

- I. Stem flattened in transection
- II. Stem lobed in transection:- a) Stem lobed but not fragmented
  - b) Stem lobed and fragmented
- III. Stem with xylem furrowed
- IV. Xylem in plates
- V. Wood portion dispersed separated by parenchyma
- VI. Divided xylem cylinder
- VII. Compound secondary xylem

Though, several classifications have been proposed by earlier workers on the basis of topography of cambial variant, yet there are several new types existing in nature which do not fit in any of the categories proposed so far in the existing classifications. Therefore in the present study, an attempt is also made to incorporate these new types of cambial variants in the existing cambial variant types of proposed classifications.

The following objectives were considered to study the various types of cambial variants and pattern of secondary growth in plants showing deviation from the normal cambial activity:

1. Origin and development of procambium in the young stem of plants showing variants at primary growth.
2. Structure and development of primary vascular tissues in stem with primary growth.
3. Initiation and development of vascular cambium and formation of internal phloem in the main stem.
4. Structure and development of different types of cambial variants.
5. Rayless nature of secondary xylem.
6. Inverse orientation of vascular cambium i.e. production of secondary xylem towards the periphery and secondary phloem towards pith.
7. Ecological wood anatomy and its correlation with its habit.

Fig. V- Classification by Sherwin Carlquist (1988)

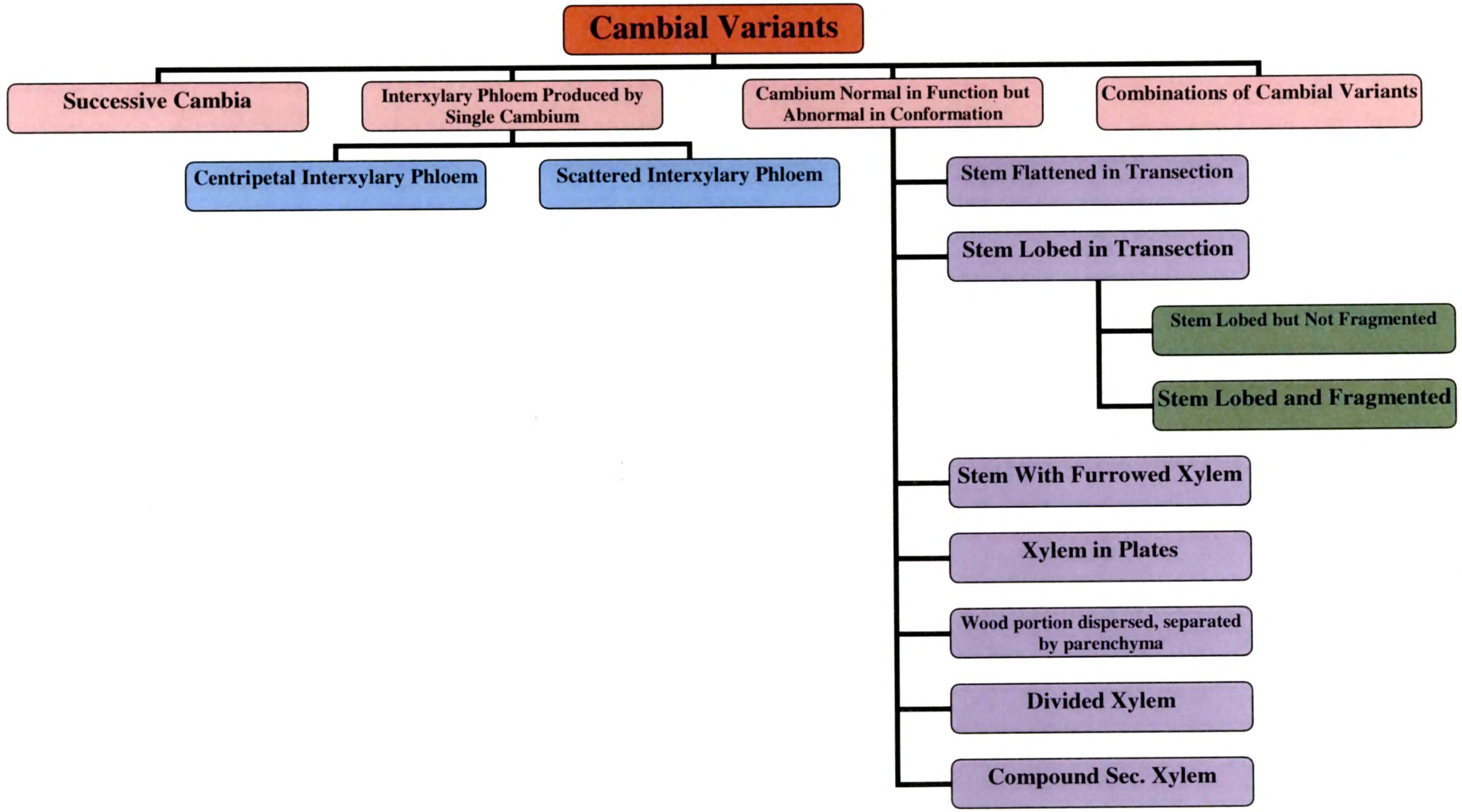


Fig. VI- Modified Classification based on Sherwin Carlquist (1988)