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Origin, evolution and diversification of the scandent habit in flowering plants

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Abstract

From the Darwin's time to the 21st century the climbing habit and tendril movements of plants continue to fascinate the biologists. Among flowering plants about 94 dicotyledonous families and about 10 monocotyledonous families have climbing species. The starting clades of flowering plants have families with climbing habit. Climbing habit is rare in vascular cryptogams and in gymnosperms. But climbing hooks and tendrils have been discovered in the seed ferns. Origin of the climbing habit in vascular plants initiated after the move of the plants to the land habitat. Some of the plants became climbers in order to reach the light and expose leaf surface to free air. Climbing plants are dependent on the availability of physical support to reach the canopy and in this way they prevent shading by neighbouring plants. Climbers that find a suitable support usually have a higher biomass and reproductive output than those that grow unsupported. The evolution of the biomechanical climbing architecture have triggered by basal apomorphic constraints, complexification, simplification and developmental loss. The biomechanics of the climbing stems are controlled by presence or absence of secondary growth and the number, complexity and coordination of development of primary and secondary tissues. The climbing architecture developed with a duality between an initial self-support phase and a later climbing phase. The anatomical novelty of climbing plants is surprising and the outcome of it is the frequency of anomaly in climbers that include unusual functioning of cambia, development of accessory cambia, or due to both. However, the diversity of anomaly cannot be used as a reliable guide to the phylogeny. Climbers typically have a high ratio of supported leaf weight to xylem areas, i.e., low Huber value. Vines have greater performance and fitness than those that remain prostrate. The location of a suitable support is the key process in the life history of climbing plants.

Keywords: anatomy, architecture, evolution, climbing plants, origin

1. Introduction

Climbing or scandent plants are clinging or twining to other objects (Woodland, 2009) [48]. Such plants may be annual or perennial, herbaceous or woody. Majority of the climbing flowering plants are dicotyledonous. The woody climbing plants are major components in the tree canopy layer of some tropical forests (Simpson, 2010) [43]. Charles Darwin (1865) [8] presented his findings on climbing plants in the *Journal of the Linnean Society*. Darwin (1875) [9] published a revised monograph with illustrations by his son George. Chapter V of the book, The Power of Movement in Plants (Darwin, 1881) deals with climbing plants. Since the time of Darwin, the diversity of climbing plants continued to fascinate the biologists (Isnard and Silk, 2009) [25].

Classification of Climbers

Vines are climbers with elongate, weak stems, that are generally supported by means of scrambling, twining, tendrils or roots and they may be annual or perennial, herbaceous or woody. A liana (or liane) is a woody, perennial vine. Creepers are herbaceous plants that produce small, weak horizontal branches. Creepers may colonize large areas with the development of adventitious roots. The weak branches never take support to climb. Trailers are identical to creepers but they do not develop adventitious roots. On the basis of their mode of attachment, Darwin (1865) [8] divided climbing plants into five categories. Isnard and Silk (2009) [25] adopted the same classification.

1. Twining plants
2. Leaf-climbers
3. Tendril-bearers
4. Root-climbers
5. Hook-climbers

Gentry (1985) [15] recognized four fundamental climbing strategies by ecology as well as morphology.

1. Lianas/lianes are woody, relatively thick-stemmed climbers that began life as terrestrial seedlings and are capable of growth in mature forests.
2. Vines are thin-stemmed climbers or clambearers that begin life as terrestrial seedlings and generally grow in disturbed habitats.
3. Woody hemiepiphytes, including stranglers, typically began life as epiphytic seedlings with roots later reaching the ground. Other woody hemiepiphytes start out as terrestrial climbers, later sending out a system of adventitious roots and/or losing contact with the ground.
4. Herbaceous epiphytes and hemiepiphytes include all herbaceous species that climb appressed to tree trunks and climb usually via adventitious roots.

Sometimes lianas are designated as proto-epiphytes. They may begin life rooted in the soil and as they climb they establish connections with the host or with pockets of humus and become hemiepiphytes. In the later period the contact with soil may become insignificant and at that stage they become holoepiphytes (Ingrouille and Eddie, 2006) [23].

Fig 1: Three phases in the life history of some liana.

2. Materials and Methods

The study was carried out in different areas of West Bengal to collect climbing plant specimens over a time span of about five years. Both dicotyledonous and monocotyledonous climbing species were collected. Extensive studies of their habitat, other ecological aspects and association of plant communities were taken into consideration during the study. To identify the climbing species, and for documentation, flowering twigs and fruits were collected, pressed and dried herbarium sheets were prepared. For the purpose of studying the detailed anatomical structures, small parts of stems were collected and preserved in FAA solution. Transverse sections were made manually and double stained.

3. Climbing or attachment organs

Climbing plants show a considerable range of morphological features that prevent the shoot system from falling (Bell and Bryan, 2008) [3]. Twining climbers lack a dedicated climbing organ. They coil their stem around a support for climbing. The circular/spiral movement of the twining plant was designated as circumnutation by Darwin (1865, 1880) [8, 9]. Circumnutations are a complex phenomenon and are controlled by an ultradian oscillator of a broad period range (from a few minutes to several hours) as well as by a circadian oscillator (Brown, 1993 [5]; Stolarz, 2009) [46]. The coiling of stem around the support may be clockwise (e.g., *Mikania*) or anticlockwise (e.g., *Tinospora*). Climbing organs include hooks, thorns, prickles, tendrils, clinging roots, cirri and flagellum. Hooks are produced in some lianas. Some others produce thorns or prickles and they help in the initial stages of climbing. In the genus *Smilax* the pair of stipules become modified into tendrils. Leaf petioles and leaf rachis are twining organs in *Clematis.* Tendril is the most specialized and effective climbing organ. Leaf tendrils are found in a variety of forms. In *Lathyrus aphaca* the entire leaf is modified into a tendril. The distal part of a simple leaf may be elaborated to form a twining tendril. In compound leaves of some climbers one or more leaflets are modified into tendrils. In the case of compound leaves, the proportion of leaflet tendril to ordinary leaflet may be flexible or very consistent in a given species. The genetic control of the morphogenesis in *Pisum sativum* have been studied by Gourlay *et al* (2000) [19], DeMason and Villani (2001) [11], Kumar *et al* (2010) [31]. etc. Tendrils, after establishing contact with the support, twine around due to the faster growth rate on the side away from the support. The twining may be clockwise in one part and anticlockwise in other part of the tendril. During the initial growth, the tendrils may function as grappling iron. The distal end of the tendrils may be modified into recurved hook-like structures or bear suckers for effective attachment to the support (Bell and Bryan, 2008) [3]. Gelatinous fibres are found in the reaction wood and they generate tensile growth stress and produce bending of branches. Such gelatinous fibres are present in the tendrils and with the help of these fibres tendril can squeeze a support. The distribution of such fibres is dependent on the type of tendril (Bowling and Vaughan, 2009). Tendrils also develop from the entire inflorescence or from a part of it. The leaf-axillary tendril of the Cucurbitaceae appears to be a stem tendril, but it may represent the prophyll of the leaf-axillary bud (Bell and Bryan, 2008) [3]. In the climbing bamboos like *Dinochloa*, the roughened leaf sheaths function as climbing organ (Ingrouille and Eddie, 2006) [23].

Clinging roots are adventitious in nature and they arise only on the side of the shoot toward the surface being climbed, where the humidity may be slightly higher and the light is less intense. With the help of clinging roots a climbing plant can ascend supports of any diameter and texture (Putz, 1984) [35]. Cirri are barbed whip-tip extension of leaf midrib in scandent palms of the subfamilies Arecoideae and Calamoideae. Some species of *Calamus* produce sterile inflorescence modified as a climbing organ in the form of barbed whip (Dransfield, 1986 [12]; Beentje, 2016) [2].

4. Origin and evolution of the climbing habit

Plants became climbers, in order, it may be presumed, to reach the light, and to expose a large surface of leaves to its action and to that of the free air. This is effected by climbers with wonderfully little expenditure of organized matter, in comparison with trees, which have to support a load of heavy branches by a massive trunk (Darwin, 1865) [8]. The location of a suitable support is a key process in the life history of climbing plants (Hegarty, 1991) [20]. The origin of the climbing habit in vascular plants started after the move of the plants to the land habitat. Although land surfaces must have been available for colonization soon after life evolved in the Precambrian.

This delay in colonization of terrestrial habitats has been related to oxygen levels in the palaeo-atmosphere and specifically to the lack of a sufficient ozone shield to protect terrestrial organisms from ultraviolet radiation. The evolution of the climbing habit has taken place independently many times in the course of evolution and the important families with climbing habit are not necessarily related. Climbers and lianas include members of ferns, gymnosperms, and a great variety of dicotyledonous and monocotyledonous families including climbing bamboos and palms (fig. 2).

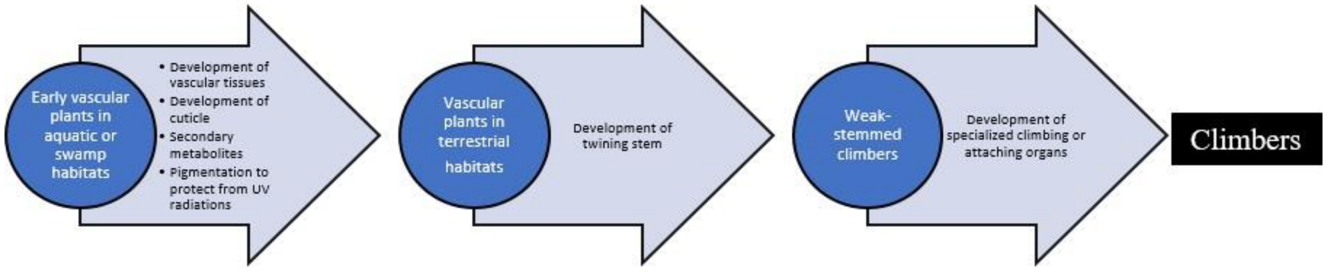

Fig 2: Steps in the origin of climbing habit.

Climbing plants depend on the availability of physical support to reach the canopy and thereby prevent shading by neighbouring plants (Gianoli, 2004) [17]. Vines that find a suitable support usually have a greater biomass and reproductive output than those that grow unsupported.

Among extant gymnosperms the scandent habit is found in some species of *Gnetum* and *Ephedra*. The climbing habit is common in the seed ferns. The prominent climbing habit is found in Lyginopteridales with geographical distribution of Carboniferos period (Taylor, Taylor and Krings, 2009) [43]. *Heterangium grievii* is a small liana with distal pinnules modified into climber hooks. The compression fossil of *Sphenopteris elegans* shows a slender stem and leaf petioles that are comparable to the twining petioles of *Clematis*. The foliage taxa *Karinopteris, Mariopteris* and *Pseudomarioteris* have distal pinnules modified into climber hooks like that of *Heterangium*.

In the late Palaeozoic seed ferns, a conspicuous feature is the presence of large number of climber hooks, some up to 4 cm long, which usually develop from apical prolongations of pinna axes and pinnule midveins. There is considerable variation among species with regard to size and morphology of the climber hooks. The climber hooks range from simple prolongations with recurved tips to complex forms with secondary hooks on the adaxial side. These variations represent adaptations of individual species to certain morphological features of their most frequently support plants (Kerp and Krings, 1998) [28]. In *Pseudomariopteris busquetii* from Lower Permian of Germany, slender stem entwined around the stump of arborescent lycopods (Cleal and Thomas, 1999) [6]. *Dicksonites pluckenetii* of late Pennsylvanian-early Permian of Europe and North America bears axillary branched tendrils. *Blanzyopteris praedentata* of the Upper Pennsylvanian strata of France produced complex climbing organs composed of a main axis or tendril that produced lateral branches. The laterals produced numerous branchlets up to 1.5 cm long that widened apically and terminated in adhesive pads (Krings and Kerp, 1999) [29]. The leaflet tendrils of *Lescuropteris genuina* are comparable to the leaflet tendrils of extant Fabaceae (Krings and Kerp, 1997).

The epidermal cells of the tendrils have large papillae, not found in any other part of the plant and these papillae function in the transmission of contact stimuli, which are important in detecting tendril growth around the support and this process is called thigmotropism (Krings *et al*, 2003) [30]. The starting clades (APG IV, 2016) [1] of flowering plants contain climbing species in the families Austrobaileyaceae, Trimeniaceae, Schisandraceae, Piperaceae, Aristolochiaceae, Annonaceae, Hernandiaceae and Lauraceae. The basal plesiomorphic constraint, complexification, simplification and developmental loss can drastically influence ways in which different plants have evolved different biomechanical climbing architectures (Rowe *et al*, 2004) [39]. The anomalous stem structure is not a good indicator of phylogeny and there is no correlation between anomalous stem structure and mode of attachment to the support.

5. Diversification of the climbing habit

The suggestion that nearly half of the families of vascular plants (excluding ferns) contain climbing species (Schenck, 1892) is contested by Gentry (1991) [40].

According to him there are at least 133 families that include at least a few climbers in contrast to 113 estimated by Schenck (1892) and the difference in the numbers can be attributed to the concept of families and identification of new members in the time gap of 99 years.

Gentry (1991) [40] identified 36 seed plant families exclusive to the old world and 97 families shared both by the new and the old world.

A screening of the families of angiosperms for climbing habit in the classification of Cronquist (1981) [7] revealed total 104 families that contain one or more climbing members, of which 94 families are dicotyledonous and 10 families are monocotyledonous (Fig.3). Highest number of families with climbing members belong to the subclass Rosidae.

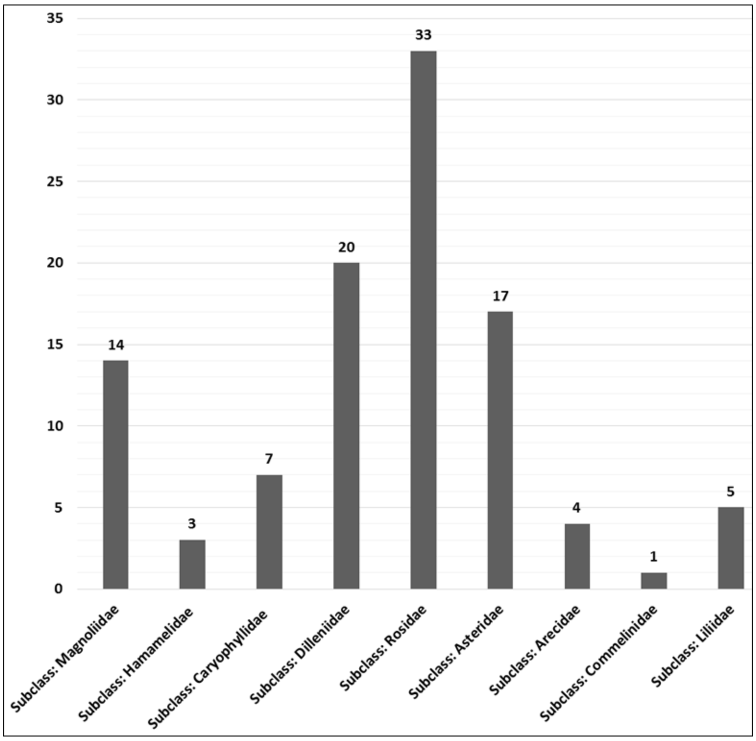

Fig 3: Distribution of climbing families among different subclasses of Magnoliophyta.

Some of the families are exclusively climbing and others contain few climbing members, or with a few scandent members. Out of total 104 families having climbing members, 37 families (35.57%) are almost exclusively scandent, 59 families (56.73%) contain few climber representatives and 8 (7.69%) families contain very few climbing members (Fig 4).

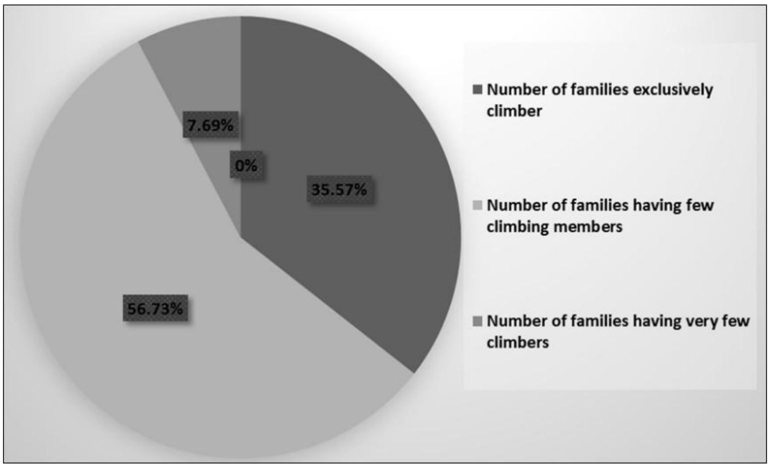

Fig 4: Families with relative proportion of scandent members.

Karthikeyan (2000) [27], estimated 1734 climbing species (herbaceous as well as shrubby) in the flora of India.

6. Ecology of the climbing habit

Climbing plants need to attach themselves to an external support in order to grow vertically to a significant extent and enhance light acquisition (Gianoli, 2015) [18]. The climber diversity in forests is influenced by the availability of trellis (Garbin *et al*, 2012) [14].

If climbers fail to get the support, they often show reduced growth and/or reproduction compared to those successfully climbing onto an external support (Putz, 1984 [35]; Stansbury *et al*, 2007) [46]. The host tree attributes that determine the probability of colonization by climbers are various (Putz, 1980; Putz, 1984 [35]; Hegarty, 1991 [20]; Putz and Holbrook, 1991) [36]. For example (i) the diameter of the support tree influences their suitability for twining plants, (ii) the relative abundance of stem twiners decreases with increasing tree diameter, (iii) for tendril climbers the upper limit of usable trunk diameter is low, (iv) root climbers are not constrained by large support diameter, and (v) bark roughness and flakiness may also influence support use by climbers.

Putz (1984) summarized the mutual interactions of lianas and the support plants. Lianas can influence tree growth and mortality rates in at least five ways: (i) by competing with trees for light and thereby slowing tree growth, (ii) by increasing tree mortality rates by weighing down tree crowns and increasing mechanical strains (torque) on the stem and roots, (iii) by increasing the number and size of trees pulled down when liana laden trees fall, (iv) by slowing the rates of tree sapling height growth in tree fall gaps through the combined effects of shading and mechanical damage and (v) by binding trees together and thereby increasing the stability of the individual trees.

7. Architecture of climbing plants

Though woody climbing plants belong to wide range of unrelated families and they show a limited range of patterns of branching (Bell and Bryan, 2008) [2]. The architectural features of lianas are identical to the tree architecture to some extent (Putz and Holbrook, 1991 [36]; Gianoli, 2004 [17]; Rowe and Speck, 2005). According to the Leeuwenberg model, each sympodial unit bears more than one similar unit at its distal end. In a free-standing tree the distal ends of the sympodial units develop inflorescence, but in the climbing habit, the inflorescences are replaced by tendrils. However, architecture of lianas is unique with the presence of a juvenile and an adult form. The juvenile form is slow growing with rhizomatous or stoloniferous shoot. The distal end of the juvenile form produces the adult form after getting the required support. Bell and Bryan (2008) [3] summarized three distinct architectural pattern in lianas that are distinct from tree architecture:

1. Juvenile form orthotropic and adult climbing form monopodial with lateral inflorescences.
2. Juvenile form orthotropic and adult climbing sympodial.
3. Juvenile form plagiotropic then climbing by means of adventitious roots.

The biomechanics of climbing habit have been studied in dicotyledonous and monocotyledonous species in great details by Silk (1989) [42], Silk and Hubbard (1991) [43], Matista and Silk (1997) [32], Isnard *et al* (2005, 2009) [25] and Hesse *et al* (2016) [22]. In lianas the Huber value is low, that is the ratio of supported leaf weight to xylem area is high (Hegarty and Caballe, 1991) [20].

8. Anatomical novelty of climbing plants

Climbing plants show distinctive anatomical features in comparison to that of the trees. Climbers usually have distinctly lower rate of secondary radial growth than the trees, lianas have more slender stems than trees and slender stems of lianas are more flexible than the trees. Due to the flexibility, lianas may hang, swing, or coil around the support (Isnard and Silk, 2009) [25]. Material stiffness of mature liana stem may ten times lower than those of trees (Niklas, 1992) [33]. The stem stiffness of liana stems is attributed to-(i) secondary xylem with thick-walled fibres, (ii) high frequency of narrow vessels and (iii) separate bundles or a ring of primary fibres near the periphery of stem. The increased flexibility of liana stem is effected by geometric adaptations, like non-circular geometry of the stem cross section and compartmentalization of xylem in a soft parenchyma (Fisher and Ewers, 1991; Speck and Rowe, 2003) [24].

Lianas usually have stem anomalies. Anomalies may result from supernumerary cambia, or irregular development of cambia, and unusual functioning of cambia with the formation of significant amount of parenchyma. The complexity of anatomical construction probably arise after the development of climbing architecture.

The adaptations leading to variable secondary growth of lianas and climbers are: (a) marked increase in both vessel diameter and proportion; (b) marked increase in the incidence of anomalous secondary growth; (c) an increase in both ray size (especially height) and proportion; and (d) an increase or decrease in the proportion of fiber. In many cases there is an increase in the development of undifferentiated non-lignified parenchyma, distributed in the ground tissue of the woody stem which is essentially weak. Wood is usually characterized by the presence of included phloem, occurrence of undifferentiated parenchyma as pockets in the normal ground tissue of xylem or as the ground mass of the stem in which xylem is present in pockets. The included phloem occurs as either irregularly distributed or regularly concentrically arranged pockets in the axial tissue or in both radial and axial tissues.

10. Results

Studies on the anatomical characteristics, ecology, architecture and evolution of climbing taxa revealed the unique nature of the climbing life form. The evolution of the climbing habit in flowering plants evolved independently in different lineages. It is not possible to correlate the families having climbing members. However, the starting clades have climbing members. The climbing habit originated in vascular plants with the change of habitat from the aquatic to the terrestrial ones. Vines exhibit higher biomass and reproductive success after getting the proper support for climbing. Anatomical specialization in the climbing dicotyledonous taxa includes secondary phloem wedges, intraxylay and interxylary phloem, splitted cambial ring and the occurrence of several cambial rings. Climbing species of monocotyledons, e.g., *Asparagus racemosus* and *Smilax ovalifolia* lack secondary growth due to the absence of cambia. A thick band of sclerenchymatous hypodermis constituted the mechanical tissue. The closed vascular bundles are scattered in the ground tissue.

11. Discussion

Out of 27 climbing species, only three plants have phloem wedges. They are *Pyrostegia venusta* (where phloem wedges are extended close to the pith), *Dolichandra unguis-cati* (major phloem wedges are four in number with several short adjacent phloem wedges), *Merremia tridentata* (phloem wedges are two in number). Intraxyllary phloem tissues are present in three species such as *Campsis grandiflora* (intraxylary phloem patches occurring in two opposite patches at the periphery of the pith), *Combretum roxburghii* (four patches of intraxylary phloem patches are present), *Hemidesmus indicus* (continuous ring of intraxylary phloem present at the periphery of the pith). One having the vascular bundles bicollateral with limited secondary growth, e.g., *Coccinia grandis*. Secondary xylem appears as separate strands due to the formation of excess secondary medullary rays in 2 species, *viz*., *Stephania japonica* (strands are seven in number) and *Tinospora sinensis* (strands are more than seven in number). Secondary xylem produced in excess in two opposite side of cambial ring in *Ipomoea obscura*. Accessory cambial strips are produced outside secondary phloem in *Antigonon leptopus*. Short secondary phloem wedges are present in *Allophylus cobbe*. Secondary phloem with radial broad fibrous strands present in *Abrus precatorius*. The cambial ring is four-ridged in *Bauhinia vahlii*. Secondary phloem with dark brown resinous cells is present in *Passiflora coccinea* but absent in *Passiflora suberosa*. Pith with brownish tanniferous cells is found in *Tiliacora racemosa*. Growth rings are distinct in *Hiptage acuminata* and such rings are not distinct in others. Several, distinct vascular cylinders with separate cambial rings are present in the stem of *Serjania rachiptera*. Such conditition is not found in others. Medullary vascular bundles and interxylary secondary phloem strands are present in *Bougainvillea spectabilis*. Secondary growth is absent and the vascular bundled are scattered in the prosenchymatous ground tissue in *Asparagus racemosus*. The subepidermal continuous ring of fibres provide mechanical support. Pericycle is occurring in the form of isolated patches in *Mikania micrantha, Cayratia pedata, Passiflora coccinea, Passiflora suberosa, Abrus precatorius* &*Tarlmounia elliptica.* The complete ring of fibres representing the pericycle is observed in *Limacia villosa, Tiliacora racemosa, Stephania japonica,* and *Tinospora sinensis.* The pith is spongy and the vascular strands are slender in *Mikania micrantha*. The pith is narrow in *Abrus precatorius* and it is wide in *Tarlmounia elliptica.*

12. Conclusion

The climbing habit represents a specialized adaptive strategy to achieve enhanced light acquisition. To reach the goal, climbing plants have developed specialized climbing and/or attaching organs with significant change in the development and orientation of mechanical tissues. As a result of which climbing plants constituting a significant component of plant evolution, diversity and abundance and play a major role in forest communities and ecosystems (Putz and Mooney, 1991) [20]. Lianas contribute many vital aspects of forest dynamics, structure and composition (Putz, 1984) [35]. Philips *et al* (2002) [34] and Wright *et al* (2004) [50], on the basis of long-term census, reported that abundance of lianas is apparently increasing in relation to that of the tree species. However, in the present scenario, climbing plants, particularly the diversity of lianas are most vulnerable.

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