Structural characteristics of a giant tropical liana and its mode of canopy spread in an alien environment

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To circumvent the practical difficulties in research on tropical rainforest lianas in their natural habitat due to prevailing weather conditions, dense camouflaging vegetation and problems in transporting equipment for experimental investigations, *Entada pursaetha* DC (syn. *Entada scandens* Benth., Leguminosae) was grown inside a research campus in a dry subtropical environment. A solitary genet has attained a gigantic size in 17 years, infesting crowns of semi-evergreen trees growing in an area roughly equivalent to 1.6 ha. It has used aerially formed, cable-like stolons for navigating and spreading its canopy across tree gaps. Some of its parts which had remained unseen in its natural habitat due to dense vegetation are described. The attained size of this liana in a climatically different environment raises the question as to why it is restricted to evergreen rainforests. Some research problems for which this liana will be useful are pointed out.

Keywords: *Entada*, lianas, natural habitat, plant growth, rainforest.

A LIANA is a woody plant which is rooted in the ground, but needs the physical support of a nearby tree for its weak stem and branches to lean and ascend for exposing its canopy to sunlight. Based on transect sampling in rainforests, it has been estimated that climbers or lianas comprise about one-fifth of all plant types[1] (trees, shrubs, herbs, epiphytes, climbers, lianas and stragglers). Investigations on lianas in tropical rainforests are hindered by dense vegetation; even their gross morphology has neither been adequately described nor illustrated. Therefore, if a rainforest liana can be successfully grown in a research campus, this can be considered a breakthrough as opportunities can be opened up for various types of research – such as biomechanical characteristics of its specific parts, tropic responses, host preference, climbing mechanism, nitrogen fixation, type of photosynthesis (C3 or C4), root pressure, reproductive biology, mechanism in invasive growth and morphological response upon contact with support trees. With these objectives, seeds of *Entada pursaetha* (Mimosoideae, Leguminosae) were sown in a research campus in Bangalore – a city in Deccan Plateau – with an average elevation of 918 msl and mean annual precipitation of 950 mm, chiefly during the monsoon period from July to October. A single plant has unexpectedly attained a gigantic size in less than 17 years, with its canopy infesting the crowns of nearby trees. Although data on the ontogenetic changes of this genet are unavailable because of the passage of time, we attempt an interpretation of its growth characteristics and reconstruct the events in *Entada* development from its extant morphological organization. We point out some questions vital to understanding the evolution of the lianoid forms.

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Materials and methods

Entada pursaetha DC has been reported from Silhet (now Bangladesh), Manipur, the Andamans and Nicobar Islands and the Eastern and the Western Ghats in peninsular India[2–4]. Seeds of *Entada* were collected from the Western Ghats (lat. 13°55′–15°31′N, long. 74°9′–75°10′E) about 55 km from the Arabian Sea, at an elevation of 700–800 msl. The region receives 450 cm or more annual rainfall, and during post-monsoon period the wind speed is 8–10 m/s. Following mechanical cracking of the hard testa, the seeds were kept in a coarse cloth bag and floated in pond water for about 20 days before sowing at various places in the campus. Of the seven seeds sown, one buried in the soil close to a tree of *Bauhinia purpurea* (Caesalpinioideae, Leguminosae) has grown into a liana, spreading its canopy on a miniforest of the semi-evergreen tropical trees, in an area roughly equivalent to 1.6 ha. Since its climbing parts are mostly hidden among the crowns of support trees, locating their interconnections and estimating the spread area of this liana required observations over a period of time, especially when the identity could be confirmed by examination of its flowers and fruits. Here we focus on some features of *E. pursaetha* (hereafter referred to as *Entada*) of value to liana biology.

Figure 1. The tree-form of *Entada pursaetha*. ***a***, Self-supporting trunk (thick arrow) in proximity to *Bauhinia purpurea* (Leguminosae). The pleats comprising upright trunk uncoil at or above breast height (thin arrow) and diverge as separate branches (thin arrows) that lean on the surrounding support trees. ***b***, Festoons of secondary branches suspended from support trees. *Entada* has overtaken and oversized *B. purpurea*.

Results and discussion

The superstructure of *Entada* is comprised of a mix of structures of a tree and a woody climber, and some unique structures. Its erect trunk is comprised of anticlockwise-twisted pleats. Its climber part comprises of hammock-like, twisted, woody stems. The structure that has spread its canopy from one support tree to another are long, leafless, cable-like stems (stolons) that navigated aerially approximately 15 m above the ground, differentiating foliage upon accessing a living tree.

Freestanding trunk

The *Entada* trunk has a girth of 2.1 m at the base and 1.7 m at breast height and is organized as helically twisted pleats (Figure 1 *a*). Although we missed out the ontogenic changes, the self-supporting trunk may have resulted from orthotropic vegetative offshoots that developed from the base of the sapling. This is plausible because according to the noted researcher of rainforests, P. W. Richards[5], 'tropical rain-forest trees often produce coppice-shoots very readily when the main trunk has fallen or decayed ... a new formation of coppice-shoots grows up round the secondary main trunk'. We assume that in its juvenile phase *Entada* formed circumnutating offshoots from the base, allowing mutual contacts and eventually fusing to form a mechanically-independent trunk. Circumnutation is a common property in climbers that enables contacting a potential support in the vicinity[6–8]. Sectioning of this solitary specimen for wood anatomy was not possible. However, a reason for considering the *Entada* trunk as comprised of basally formed conjoined, offshoots is because the pleats unwind at 1.5–3 m above the ground and diverge as branches either in vertical or horizontal directions. No other liana is known with a trunk constructed similarly, although the Neotropical liana *Croton nuntians* (Euphorbiaceae) in French Guyana is freestanding and resembles a young tree, but becomes unstable and leans on surrounding vegetation for support[9].

Anticlockwise twists in climbing parts

The uncoiled trunk pleats have branched out into hammock-like, highly twisted, woody branches (Figure 1 *b*). Yet, no above-ground part has twined around a support tree or its branches; hence *Entada* is not a twiner. Rather, its branches mostly lie on the host branches for support and are occasionally entangled into them. A striking feature of *Entada* are the climbing branches shaped into an 'Archimedes screw' (Figure 2) with pronounced tangential thickening. The significance of this patterning is unknown. Recently, a theory has been put forward for the formation of twists in stems subjected to bending stress[10].

The predominantly anticlockwise helices in *Entada* prompted us to examine the direction of coiling in climbers growing in a nearby miniforest in the campus. Anticlockwise ascend was observed in all climbers. Edwards *et al.*[11] reported anticlockwise twining in plants at 17 sites in nine countries in both the northern and southern hemisphere. An exception is the yam *Dioscorea*, where species have been classified on the basis of stems twining to the left or to the right[12]. The handedness of growth depends on the orientation in which cortical microfibrils are organized under the control of *spiral* gene[13]. However, it is not known whether helical microtubule arrays are the cause or the consequence of organ twisting.

We have not observed any thorns, hooks, spines or stem tendrils that could facilitate anchoring of *Entada* to the supporting tree. Rather, physical support is gained by occasional placing of its branches on those of support trees. At best, *Entada* may be classified as a straggler.

Figure 2. The climber-form of *E. pursaetha*. ***a***, Hammock-like branches with twists (arrow). ***b***, Major types (arrows) of branches, numbered 1 to 4. Note Archimedes screw patterning in branch # 3.

Figure 3. ***a***, *Entada* in a decumbent orientation against a wall is distinguished from other species of woody climbers by white and yellow inflorescence. ***b***, A 2 ft long pod.

Some of its overhanging leafy branches that were exposed to full sunlight during March–April (before monsoon rains begin) produced inflorescence (Figure 3).

Invasion and spreading strategy

Thus far, all previously reported lianas spread their canopy by means of ground stolons which then climb on available support. *Entada* is unique: it has formed specialized, cable-like, aerial stolons (Figure 4) that have extended near-horizontally into air, crossing gaps and spreading canopy from the primary support tree onto the crowns of other support trees (Figure 5). The length of these aerial stolons exceeds 15 m; and there is no evidence of a support tree being present between the inter-support distances, because of a dividing tarred road. Hence investigations are required as to how *Entada* sensed the availability of support trees across tree gaps, the time and rate of elongation of stolons and the chemical cues directing their aerial trajectory towards the available crown. Indeed, it was the aerial stolons traversing a road junction over a lamp post which attracted the attention of two authors to an unusual plant type growing in the campus. Following contact with the crown of support trees, the stolons have branched and much of their twisted woody branches appear to support each other (self-support), with this being augmented by the branches that have infiltrated into the trees. A stand of bamboo culms accessed across a gap due to a road is bent down to a greater degree than the uninfested culms, either because of the weight of *Entada* or because *Entada* exerted a force to pull them down. Structural adjustments that are required to counter stress and strain as a consequence of tension due to pull need investigation.

Figure 4. Mode of spread in *E. pursaetha*. ***a***, Leafless aerial shoots navigating across a gap towards tree canopy. ***b***, Horizontally extending shoots traversing a gap between trees and bypassing an inanimate support (lamp post) in a road junction in their trajectory towards living trees. Since this photograph was taken, the aerial stolons (cable-like stems) have been cut as these were posing a hazard to vehicular traffic.

Figure 5. Invasive growth. Aerial stolon (arrow) crossing tree gap to spread on crown of tree canopy.

Since the aerial stolons are oriented towards a vegetated tract across a tarred road without crisscrossing (Figure 4), a possibility is that other than phototropism, some volatile chemicals produced by the 'host' trees not only provided a cue for the development of cables, but also directed their extension towards trellises. This speculation is supported by a recent finding that volatile compounds, α-pinene, β-myrcene, 2-carene, *p*-cymene, β-phellandrene, limonene, (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene and an unidentified monoterpene released by tomato plant guide the dodder vine, *Cuscuta pentagona*[14]. Rowe and Speck[15] have illustrated 'searcher branches' in a woody liana *Strychnos* sp. (Loganiaceae), having a cable-like appearance and extending horizontally 3–4 m across the canopy gap to locate new support. Upon contact with a neighbouring tree, the *Entada* cables (stolons) differentiated normal foliage, viz. compound leaves with thick leaflets. The branches of *Entada* have infiltrated and entangled with that of *Bauhinia purpurea*, *Cassia spectabilis*, *Broussonetia papyrifera*, *Tebebuia rosea*, *Eucalyptus tereticornis*, *Tectona grandis* and *Bambusa* sp. However, we have not observed *Entada* on dead branches of standing trees, raising the possibility of requirement of living support trees for infestation. Since coiling, bending or flexing and differentiating into morphologically distinct parts occur in response to contact, the phenomenon of thigmomorphogenesis appears to be important in the infiltration and spread of *Entada* on living trees.

We have not observed new cables (aerial stolons) being formed in the four years since regular observation of *Entada*, suggesting that there could be periodicity of years in triggering its development. Some bamboos behave similarly[16]. A contentious explanation is that the aerial stolons were formed in response to some unusual weather trigger. Perhaps, more likely is periodicity in their development. Possibly these were stiff as the culms of bamboo, and extended rapidly across tree gaps. Based on an estimate of its spread size and the timescale, it appears that *Entada* could be amongst the fastest growing plants; rivalling the bamboos in which the culms grow almost 4 ft in a 24 h period (www.lewisbamboo.com/habits.html). The fast growth rate of stolons against gravity will enable them to take mechanical risk[17].

Cable-like stolon along the ground surface with ascending apex was illustrated in a palm *Desmoncus orthacanthus*, growing in the rainforests in South America[18] and in rhizomatous shrub *Xanthorhiza simplicissima*, growing in the Botanical Garden in Freiburg, Germany[19]. However, data on its rate of extension was not given. Penalosa[7] reported a liana *Ipomoea phillomega* in the rainforest of Mexico, with leafless, creeping stems (stolons) on the ground that extend up to 30 m at a mean rate of 13.6 cm/day, and turning upwards in a *S*-shaped manner upon contact with a potential support and twining around a support host in sunny clearings. The climber *Clematis* *maritima* changes its morphology when growing on aboveground areas and on sand[17]. We have not observed surface-growing stems in adult *Entada*. Its aerial stolons changed morphology upon accessing a support tree, suggesting that in addition to light and circumnavigational movement, contact-induced differentiation of foliage is important in mechanistic explanation of *Entada* spread on crowns of support trees as a straggler. Trellis availability is a major factor determining the success of canopy-bound lianas[20].

Hydraulic supply

The parent and the interconnected daughter canopies of *Entada* are founded on a single germinated seed and hence on a single root system. Since the aerial stolons ultimately connect to the rooted trunk, these must constitute the hydraulic system for the entire canopy.

When aerial stolons (cables) extending across a road junction, posing hazard to motorists were cut, colourless, watery sap trickled from the cut cables. This suggests that water is translocated by root pressure, requiring development of non-destructive methods for investigation of its underground parts. Apparently, the twists in plant structure do not resist the movement of water, making *Entada* a good material for investigations of pressure-generating capability for water movement, compared to a tree. Following severing, the daughter canopies differentiated by aerial stolons and distributed on surrounding trees dried, confirming that the aerial cables constitute the hydraulic supply system and the structural form for the spread of the canopy on support trees.

Ecophysiology

Occasionally, a terminal leaflet in the pinnate compound leaves of *Entada* is modified into a forked tendril (Figure 6 *b*). Tendril development may be influenced by the amount of light filtering through the canopy, and its function may only be to orient the leaf for maximal absorption of sunlight by the canopy in natural habitat under cloudy conditions. A visual comparison of the density of *Entada* foliage with that of the surrounding trees suggests that this liana invests more of photosynthetically fixed carbon in woody branches, which have a capacity to resprout after breakage.

The first sighting of a single 12 inches long, green pod was in May 2003, and again in 2005 and 2008. It therefore appears that fruiting in the alien environment is a rare phenomenon, for unknown reasons. Although being a leguminous plant, *Entada* is assumed to be self-pollinated, the lack of a pollinator species could account for its rare fruiting. Further observations are required to determine if flowering and fruiting in the daughter canopies is synchronized with that of the interconnected parent canopy. Brandis[2] described fruits of *E. pursaetha* as 2–4 ft long and 3–4 inches broad. An *Entada* pod in the Phansad Wildlife Sanctuary (about 152 km from Mumbai) was found to be nearly 6 ft long. *Entada* pods are therefore among the largest legumes.

The ability to produce large pods with rather large seeds[2,3] suggests a high photosynthetic rate. It is believed that lianas have a fast growth rate because of their high photosynthetic rate due to elevated CO_2 in the canopy[21]. Contrary to popular belief, liana density and growth are unrelated to the mean annual precipitation[19,21,22]. Schnitzer[22] reported that lianas grow nearly twice as much as trees during the wet season, but more than seven times that of trees during the dry season. This observation was corroborated by Swaine and Grace[23]. In view of the requirement of seedling material for experimental investigations in the laboratory, the reproductive biology of *Entada* assumes special importance.

Regeneration

Aerial stolons (diameter approximately <10 cm) that had begun to cause obstruction to vehicular traffic were cut. Two to four metre long cut pieces of woody stems (diameter 20–30 cm) were gathered and left in the open. In about 4 weeks the cut stems sprouted one to 1½ m tall shoots with stiff, erect stems producing foliage (Figure 6). Since sprouting occurred during the dry season, this observation signifies that *Entada* stores considerable water inside the stem tissue. However, the cut stems did not root, and the sprouts dried after the rains ceased. However, the ability of cut stems to resprout has implication in its natural habitat where strong wind and rain prevail: The branches that are unable to resist wind-induced breakage or those that are unstable under their own weight may fall on the ground and function as ramets (vegetatively produced, independent plants). This raises the question of the specific contribution of the ramets (broken and fallen branches that resprout and form roots) versus the genets (single individual plants from sexually formed seeds) in the composition of *Entada* thickets in its natural habitat. In Panama, Putz[20] noted the propensity for lianas to sprout vigorously from fallen stems. Based

Figure 6. Regeneration in *E. pursaetha*. ***a***, Sprouting of shoots in cut, aerial stolons and attached branch. ***b***, Forked leaf tendril (arrow) showing anticlockwise twining.

Table 1. Summary of salient characters of *Entada pursaetha*

Observation	Phenomenon implied
Seeds required scarification and incubation in pond water for germination	Mechanical dormancy
Free-standing, upright trunk formed by conjoining of basally sprouted branches	Circumnutation of coppices and thigmomorphogenesis
Anticlockwise twists throughout mature plant body	Morphological plasticity
Branches lean on support trees	Discrimination of living support?
Navigation towards canopy of support trees across large gaps by leafless aerial stolons (remote sensing)	Perception of chemical cues
Time taken by genet to spread canopy on neighbouring trees <17 yrs	Rapid growth
Aerial stolons produce foliage following contact and infiltration into support trees	Thigmomorphogenesis
Infrequent fruiting despite profuse flowering	Dependency on a pollinator?
Pod >2 ft, seeds large	High photosynthetic rate, large maternal investment
Terminal leaflet modifies into tendril	Interception of light filtering through canopy and response to quantity and quality of light
Maintained greenness and spread over 1.6 ha despite seasonal drought	Deep root system, high root pressure

Table 2. Research problems for which an introduced *Entada* can be especially valuable

Research area	Description
Biological species invasion	Tracking the timetable, speed for navigation of aerial stolons towards support trees. Navigation of aerial stolons – evidence for chemical cues.
Plant biomechanics	Measurement and comparison of root pressure, transpiration rate, ascent of water to canopy, causes of anticlockwise twists and helical geometry and flexural rigidity of stems, xylem architecture and water transport, and correlation of anatomical parameters of different stem types with structural bending modulus. Reasons for the formation of 'screw' type reaction wood (Figure 2).
Plant morphogenesis	Mechanoperception of support trees and differentiation of foliage, germination of seeds, seedling morphology, and role of circumnutation behaviour in seedling for construction of self-supporting trunk.
Plant physiology, horticulture	Rooting of ramets, growth rate and response to light, estimation of compensation point.
Plant population genetics	DNA analysis for differentiation of ramets versus genets
Plant microbiology	Benefit from nitrogen-fixing ability. Possible benefit to trellises from symbiotic nitrogen-fixing ability of leguminous liana
Plant reproductive biology	Causes of irregular fruit set, quantitization of viable seeds produced/individual
Ecophysiology	Mechanisms in photosynthetic acclimation to light changes in canopy because of density of foliage, determination of compensation point
Plant ecology	Periodicity in formation of navigating aerial stolons, timetable of their development and speed of extension, the estimation of life-span, comparative analyses of inorganic nutrients (N, P, K, Ca, Mg) in soils in the campus and the wetlands (natural habitat).

on seedling excavations, Putz found that 90% liana species in the understorey were ramets.

Paradox of growth in alien environment

The factors that may explain an alien liana thriving in a place which receives only about 95 cm annual rainfall and where the soil surface (red earth) is generally dry, except for the monsoon months (May–September) are:

(1) Foremost, a safe mode of infiltration on available support trees by means of aerially formed stolons, thereby avoiding risk of injury from trampling by grazing animals.

(2) Nutrient-rich soil in the campus (the soils in rainforests is generally nutrient-poor because of the leaching of nutrients by rains through the millennia[5,24]).

(3) Presumed deep root system of *Entada* allowing access to water table, or water which seeped down from a

nearby stream. This is in keeping with a report[25] that root systems in excavated liana seedlings of *Davilla kunthii* (Dilleniaceae) in eastern Amazonia were more than eight times longer than the aboveground stem.

(4) Higher solar illumination[26].

(5) Absence of herbivores or pathogens and less competition for resources as more area is available for aerial spread, root growth and nutrient absorption, unlike in dense vegetated tropical forests.

Finally, what explains the distribution of *Entada* in coastal sea areas and river banks? Water may play a key role for dispersal as well as for breaking of dormancy of big, heavy *Entada* seeds. The presence of aquatic microorganisms and the lytic enzymes leached from them would soften the testa.

Despite the extensive spread of *Entada* genet in an alien environment, we are hesitant in attributing this as 'success', since ecologically 'success' is a measure of reproductive efficiency, namely the number of individual genets or ramets per unit area and density of liana growth[26]. Success of introduced *Entada* can only be assessed if it becomes naturalized by production of new genets or ramets.

Conclusion

A solitary *Entada* genet introduced in a research campus has provided an opportunity to observe new morphological features in a giant liana (Table 1), raising questions and ideas on the ecology of the lianas and the biomechanics of lianoid forms (Table 2). Some of the lead questions that have arisen from its regular observations are: (1) How did the liana construct the self-supporting trunk? (2) How does the liana sense availability of support tree from distance? (3) How do the aerial, cable-like stolons navigate precisely for infiltrating into the tree canopy? (4) How does the liana apply force to pull down a support (bamboo)? (5) What mechanisms liana uses to perceive and avoid an inadequate support in its trajectory? (6) How might have the liana growth habit evolved? (7) What is the lifespan of liana? (The general belief being that lianas have a long life-span). (8) Does *Entada* require a living tree for support?

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