Sahyadri Conservation Series 59

BOTANICAL WONDER AT INDIAN INSTITUTE OF SCIENCE

[*Entada pursaetha* – Wonder Climber of Western Ghats]

Ramachandra T.V. Gouri Kulkarni Akhil C. A. M.D. Subash Chandran

ENVIS Technical Report: 111

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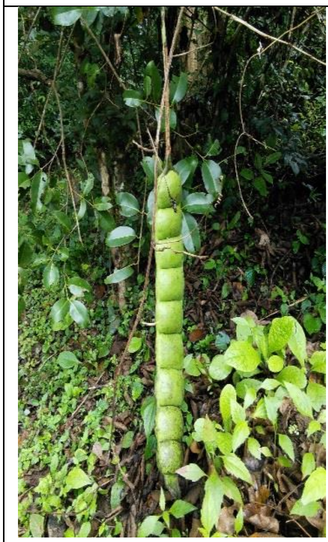
1.0 Summary

Morphological Characteristic of *Entada pursaetha*	
Synonym:	*Entada pursaetha* DC.; *Entada scandens* auct. non Benth.; *Entada monostachya* DC.
Vernacular name:	Hallekaayi-balli, Pallekaayi (Kannada)
Common name:	African Dream-nut, Elephant Creeper, Mackay Bean, Ladynut
Global distribution:	Tropical and South Africa, Sri Lanka, India to China, Malaysia to Australia
Flowering & Fruiting:	March to May
Habitat:	Common along river and stream sides of evergreen and semi-evergreen forests.
Ecosystem service:	Seeds eaten by Indian Giant Squirrel (*Ratufa indica indica*)
Uses - Food:	White kernels of seeds are edible**.**
Uses - Medicine:	Bark and seed used for ulcers, stem for skin diseases, seed used as stomach ache, anti-rheumatic, anti-inflammatory and dietary supplement. Seeds are known as African Dream-nut and used for hallucinatory effects by shamans of Africa.

Description: It is a gigantic climber with twisted angled stems. Bark brown and fibrous. Leaves dark green, bi-pinnate, leaf-rachis glabrous, grooved, ending in a bifid tendril, pinnae 2-3 pairs, leaflets 3-4 pairs, up to 9*4 cm, ovate-oblong, obtuse of emarginated at apex. Spikes up to 30 cm long, from the axils of upper leaves or from nodes on the leafless branches. Flowers in long axillary pendulous spikes, up to 30 cm long, from the axils of the

upper leaves or from the nodes on the leafless branches. Small, polygamous, pale yellow in colour. Calyx campanulate, 5-toothed. Petals 5, oblanceolate, free or slightly cohering. Stamens 10, free, shortly connate at base, exserted; anthers tipped with deciduous stalked gland. Ovary subsessile, many ovuled c. 8 or more; style filiform. Fruit a pod, huge, up to 2 m × 15 cm size, compressed, woody, 6-15 jointed; joints discoid or square. Breaking down into single-seeded segments, leaving the outer rim. Seed flat, round disc shaped, c. 5 cm in diam., smooth glabrous brown or purple in colour, testa very hard. Can survive lengthy periods of immersion in fresh water and sea water facilitating water dispersal and establishment close to streams and rivers and coastal forests.	
Source of seeds	Pod containing 14 seeds was collected from the evergreen Forest in Yellapur taluk, Uttara Kannada district, Western Ghats (latitude 13°55' to 15°31'N, longitude. 74°9' to 75°10'E) about 55 km from the Arabian Sea, at an elevation of 700-800 meters above sea level.
Climate at seed collection location	The region receives 450 cm or more annual rainfall, and during post monsoon period the wind speed is 8-10 m/s.
	 
Year of planting	1988 (planted seeds at seven locations and among these only the one planted near CES grew and spread in the vicinity of CES at Silver oak marg).
Planted by	T V Ramachandra
Pre-treatment	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 seven locations in Indian Institute of Science campus.

Germination success	Of the 7 seeds sown, one buried in soil close to a tree of *Bauhinia purpurea* (Caesalpinioideae, Leguminosae) (adjacent to CES department) has grown into a liana, spreading its canopy on a miniforest of semi-evergreen tropical trees, in an area roughly equivalent to 1.6 ha.
Climate	In a dry subtropical environment, the receives about 800 mm annual rainfall and located at 918 m asl.

2.0 Introduction:

The Western Ghats refers to the unbroken chain of hills (of which Palakkad gap is an exception) running in the North-South direction for about 1600 km parallel to the Arabian Sea from river Tapti (22˚26‟N) to Kanyakumari (about 8˚0‟ N) and extends zonally from 72˚55‟E to 78˚11‟ E covering an area of about 1, 64,280 km^2. It is one of the 35 global biodiversity hotspots and the habitat to a large number of endemic plant and animal species. These species face threat of vulnerability and extinction due to habitat loss with changes in weather and climate. Climate in the Western Ghats varies with altitudinal gradation and distance from the equator. Annual rainfall in the region with proximity to the sea averages to 3000-4000 mm.

The tropical rain forests and other humid forests are known for their exceptional richness for various species of giant climbers, the lianas, than the temperate or drier tropical forests. Liana are conspicuous structural component of tropical forests and make about one fourth of the woody plant diversity of peninsular Malaysia, rated as high as South American forests in liana richness (Appanah et al., 1993; Bhat, 2014). The dark canopies in such forests permit only scanty light into the forest interior, as diffused light and sun-flecks. In the competition for light the trees grow taller until they reach the canopy or sub-canopy levels and many those requiring full exposure to sunlight emerge above the general canopy as towering giants. The plants that keep away from this race for light are adapted to the dimness of the forest floor, which is not as rich in herbs, but may be covered with seedlings and saplings of the trees as well as of the lianas. Evolution has its own ways in such situation, as one has to look up towards the crowns of trees to see bulk of the rain forest herbs clinging on to branches and trunks as epiphytes, along with wreath of mosses and ferns. It is no exaggeration to say that in the rain forest one has to look up than on to the floor for the herb layer diversity. Although woody and having own well developed root systems the lianas need physical support to hold on and climb up to reach heights to expose their foliage to the sunlight. In the younger stages lianas are more shade tolerant, have more tender stems which coil over support, which may be the trunks and branches of trees. With the passage of time their main stems and branches turn stronger and woodier, yet the lianas cannot stand on their own. Growth is slow for these 'climbing trees' while in the deep shade. The growth happens prolifically in tree fall gaps. Coiling on any support nearby, from tree saplings to larger trees, the lianas in gaps grow in tangles, their long slender shoots linking trees like cables, turning thicker and woody and assuming diverse forms like ropes and cables, or suspended in the air in huge loops or in serpentine coils. Many trees are affected in the stranglehold of lianas, their trunks misshapen, growth stunted, the weaker collapsing in a mass unable to bear the weight of these climbing trees. The liana cutting became an established silvicultural practice especially to free the trees in forest plantations.

Lianas have certain crucial ecological role in forest ecosystems. Tree fall in the tropical forest, forming a canopy gap, allowing sunlight onto the floor, is an occasion of immense activity on the exposed ground, where the falling light stimulates a flush of fresh growth in the vegetation. Tree saplings that have been almost dormant for years get activated, gaining height rapidly. The juvenile lianas with greater vigour, overtop these saplings creating virtually a sub-canopy in the tree fall gap. This canopy rises in the air pushed up collectively by the force of numerous juvenile trees, especially short duration pioneers, activated by sunlight. Once again a damp and dark interior is created underneath the canopy of lianas and pioneer trees (light-loving, fast growing, short lived trees like *Macaranga*, *Trema*, *Ervatamia* etc.). As the 'canopy lifting' happens, the characteristic species of the rain forest or evergreen forest find suitable microclimatic conditions driving the succession process towards the climax vegetation. The lianas help to stabilise the microclimate of the forest floor by forming a mass of leafy vegetation to close canopy gaps (Schnitzer and Bongers, 2002; Parthasarthy et al., 2004). Heavy load of lianas on trees, however, can cause mechanical damage of the hosts and also reduce their growth rates (Pérez-Salicrup, 2001). Addo-Fordjour et al., (2013) found liana species richness and abundance were significantly lower in the high disturbance forest, whereas the liana biomass was higher in low disturbance forests.

Lianas are woody stem rooted in the ground and need physical support for their growth due to weak stem. Liana competes with tree for resources such as soil nutrients, sunlight and water.

Liana are prominent component of tropical forest which plays a vital role in ecosystem processes (foliage, fruit production and carbon sequestration) and species diversity. Species diversity of lianas encompasses of 25% and woody stem density accounts 10-45% mainly in tropical forests around the world. Western Ghats has higher species richness compared to Eastern Ghats and Coromandel Coast in Indian Peninsular. (Schnitzer et al., 2015, 2002, Parthasarathy et al., 2004, Muthumperumal and Parathasarathy 2010). Liana plays vital role in forest by maintaining diversity, regeneration, forest functioning includes nutrient cycling, forest transpiration, water use and carbon sequestration. Some of the liana species constitute group of non-timber forest product. Some species of Liana species has medicinal value. For instance, *E. rheedii* bark is used to cure scabies in Tanzania (Brink and Achigan-Dako, 2012). Liana also has wide range of benefits to arthropods, birds, arboreal mammals, primates by providing food resource (leaves, fruit, flowers, nectar, sap), exposure to a reduced suite of predators and also serve as fallback food i.e., abundant foods of relatively low quality that are used during periods of low overall food availability (Schnitzer et al., 2015). Seeds of *Entada rheedei* are cooked and eaten by especially forest dwelling communities. Entada is a promising candidate herb for the development of a phytomedicine against liver ailments (Gupta et al., 2011).

Liana grown successfully in a premier research campus is a breakthrough as opportunities have been 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.

3. *Entada rheedei* (Fabaceae), the lianous species, is a conspicuous liana in the Western Ghats. It has a wider distribution in the world tropical Africa, India to China, Philippines and northern Australia. In India it occurs from sub-Himalayan tracts through the states of Sikkim and Assam to Bihar and Orissa to the monsoon forests of Western and Eastern Ghats (Brink, and Achigan-Dako, 2012). It is also found in the Andaman Islands. This magnificent liana is seen along river and stream sides of humid forests. *Entada rheedei* with its angled woody stems racing up even the tallest trees, coiling anti-clockwise and clockwise on support, is a phenomenal species that one could witness in the Western Ghats. Its growth dynamics could be now noticed in the urban ecosystem of Bangalore, by observing a remarkable specimen of *Entada*, in the Indian Institute of Science, on Silver Oak marg in front of the Centre for

Ecological Sciences, introduced from the Western Ghats in late 1980's. Seeds of *Entada* were collected from the Western Ghats (13°55′–15°31′N, 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* (Fabaceae) has grown into a liana, spreading its canopy on a miniforest of the semi-evergreen tropical trees.

A single plant has unexpectedly attained a gigantic size in 25 years, with its canopy infesting the crowns of nearby trees which covers an area roughly equivalent to 1.6 ha. It has remarkable aerial stolons, of about 15 m long, even crossing over a tar road through the air, without any support, and reaching the trees in a mini-forest on the other side where it is firmly anchored to trees and clumps of bamboos, spreading rapidly (Maheshwari et al., 2009). Frightened with the profuse growth and spread of aerial stolons (with the excuse of possible threat to motorists on the road below) one of the administrator got some stolons cut or pruned. It was noticed water trickled out of stolons, showing how an efficient water conducting system is working through the entanglement of branches.

Different parts of *Entada rheedei* have been used in native medicine. The folk healers of Araku Valley in the Vishakapatanam district apply seed paste to scabies and boils (Padal and Sathyavathi, 2013). Two new tryptophan derivative compounds from the seed kernels of *E. rheedei* may offer an alternative as potential therapeutic for cancer and AIDS (Nzowa et al., 2013). In Southeast Asian countries and in India the various parts of the climber are used in different ways to cleanse fresh wounds, heal minor scrapes and burns (Bureau of Plant Industry, 2009). Seed paste of Entada is applied over the affected and the inflamed swellings by the Kanikkar tribe of Agasthyamalai in Kerala, reduce pain due to rheumatism. Its anti-inflammatory property has been proved by Kalpanadevi et al., (2012).

The seeds of Entada from India are coveted items in the Egyptian market because of the medicinal values. Seeds of Entada are rich in potassium (K) and phosphorous (P) (1264 and 1240 mg/100 g respectively), followed by calcium (Ca) and sodium (Na) (199 and 68 mg/100 g respectively). The micro element Iron (Fe) level in the seed was 3.3 mg/100 g. Richness of these elements in the seeds probably accounts for their medicinal as well as dietary values

(Okba et al., 2013). Amino acids are also an important constituent in seeds of *Entada rheedei*. According to the study of Okba et al., 2013 the total percentage of the amino acids in 100 grams of seeds was 23.499 g. Leucine is one of the essential amino acid (2.597 g/100 g seeds), followed by phenylalanine (2.116 g/100 g seeds) and lysine (1.776 g/100 g seeds). Phenyl alanine is useful in treating painful arthritic problems. Its relatively high level in Entada seed may explain its use in folk medicine specially for treating arthritis and other rheumatoid diseases. Glutamic acid (3.737 g/100 g seeds) was the main non-essential amino acid, which is important in the metabolism of sugars and fats and used in treatment of ulcers.

The *Entada* is encompassed of a mix of tree structures 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.

3.1 Anticlockwise twists in climbing parts: The uncoiled trunk pleats have branched out into hammock-like, highly twisted, woody branches (Figure 1). 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' with pronounced tangential thickening (Figure 2) (Vogel 2007).

The predominantly anticlockwise helices in *Entada* prompted 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 in 2007 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 (Gamble 1935; Punekar and Lakshminarasimhan, 2002). The handedness of growth depends on the orientation in which cortical microfibrils are organized under the control of spiral gene (Hashimoto 2002). 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. Some of its overhanging leafy branches that were exposed to full sunlight during March–April (before monsoon rains begin) produced inflorescence (Figure 1.b).

3.2 Hydraulic supply: The parent and 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.

3.3 Ecophysiology: Occasionally, a terminal leaflet in the pinnate compound leaves of *Entada* is modified into a forked tendril. 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 photo synthetically 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 2008, 2011 and 2015. 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.

The ability to produce large pods with rather large seeds (Brandis 1921, Saldanha and Nicolson 1976) 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 (Granados and Korner 2002). Contrary to popular belief, liana density and growth are unrelated to the mean annual precipitation (Rowe 2004, Granados and Korner 2002, Schnitzer 2005). Schnitzer in 2005 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 (2007). In view of the requirement of seedling material for experimental investigations in the laboratory, the reproductive biology of *Entada* assumes special importance.

3.4 Spreading strategy: Previously all 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 that have extended near-horizontally into air, crossing gaps and spreading canopy from the primary support tree onto the crowns of other support trees. 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. The aerial stolons traversing a road junction over a lamp post highlights of 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 further investigations. The aerial stolons are oriented towards a vegetated tract across a tarred road without crisscrossing, 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.

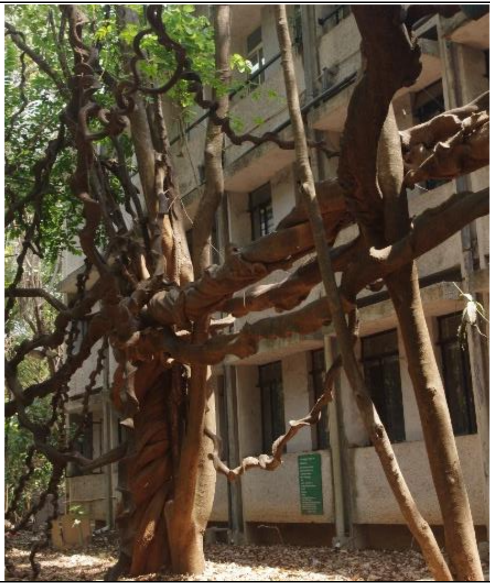
This speculation is supported by a recent finding that volatile compounds, α-pinene, β-myrcene, 2-carene, p-cymene, β-phellandrene, limonene, (E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene and an unidentified monoterpene released by tomato plant guide the dodder vine, *Cuscuta pentagona* (Runyon et al., 2007). Rowe and Speck (2005) 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, *Entada* was not observed 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. It was 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 (Putz 1724).

3.5 Regeneration: Aerial stolons (diameter approximately <10 cm) that had begun to cause obstruction to vehicular traffic were cut. Two to four meter 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. 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 re-sprout 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.

3.6 Paradox of growth in alien environment: 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:

- 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.
- Nutrient-rich soil in the campus compared to the soils in rainforests is generally nutrient-poor because of the leaching of nutrients by rains through the millennia (Richards 1972, Terborgh 1992; Van der Heijden and Phillips, 2008).
- 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 (Restom and Nepstad 2004) that root systems in excavated liana seedlings of *Davilla kunthii* (Dilleniaceae) in eastern Amazonia were more than eight times longer than the aboveground stem.
- Higher solar illumination (Heijden et al., 2008).
- 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.

Despite the extensive spread of *Entada* genet in an alien environment. However, ecologically 'success' is a measure of reproductive efficiency, namely the number of individual genets or ramets per unit area and density of liana growth (Heijden et al., 2008). Success of introduced *Entada* be assessed by production of new genets or ramets.



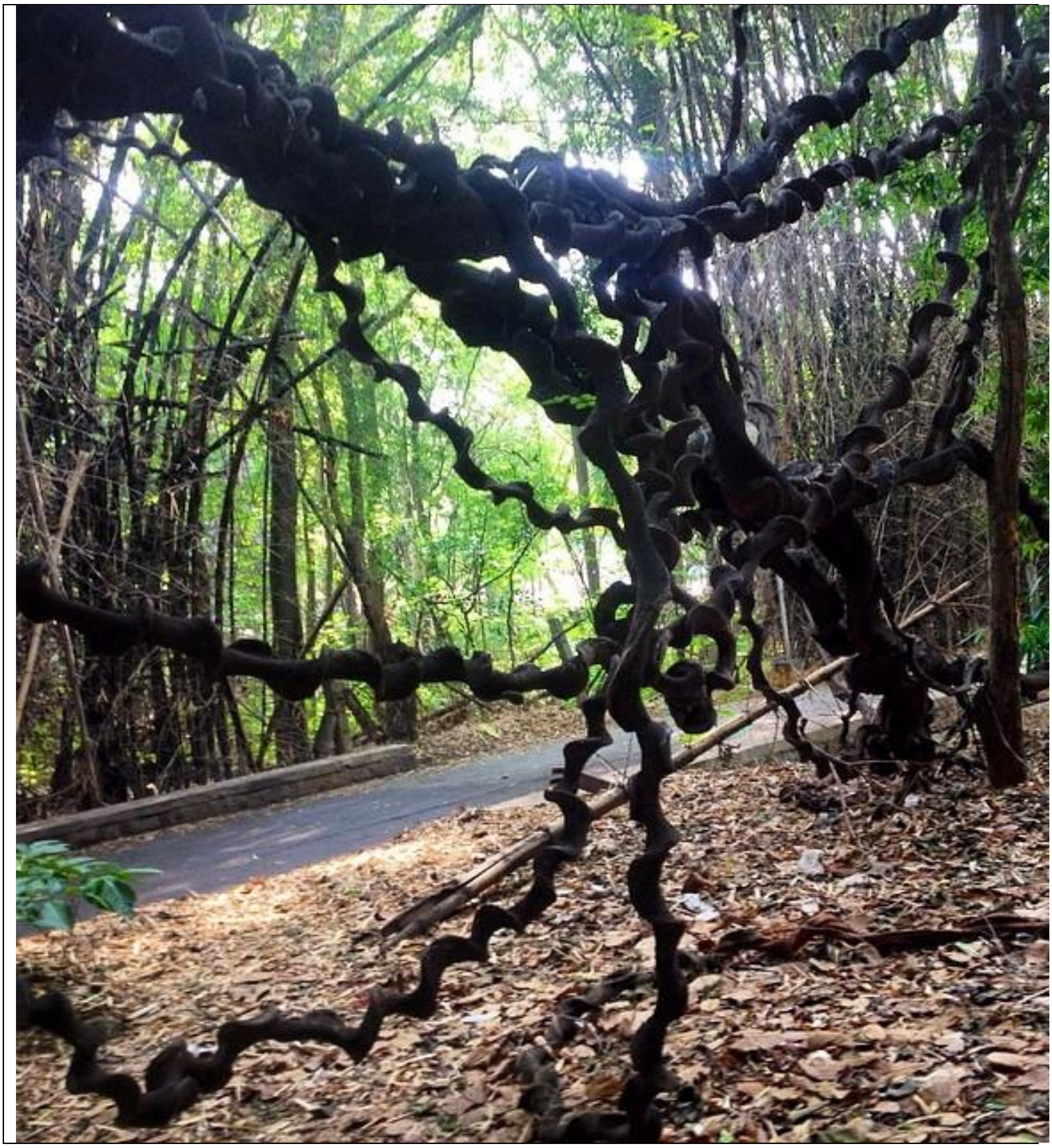


Figure 2: Hammock-like branches with twists. b. Spread of *E. pursaetha* c. The climber-form of *E. pursaetha* d. tree-form of *Entada pursaetha* self-supporting trunk in proximity to *Bauhinia purpurea*.

Reference

Addo-Fordjour, P., El Duah, P. and Agbesi, D.K.K. Factors Influencing Liana Species Richness and Structure following Anthropogenic Disturbance in a Tropical Forest, Ghana, ISRN Forestry. 2013.

Appanah, S., Gentry, A.H. and La Frankie, J.E. Liana diversity and species richness of Malaysian rain forests. Journal of Tropical Forest Science, 1993, 6 (2), 116-123.

Bhat, K.G. Flora of South Kanara (Dakshina Kannada and Udupi Districts of Karnataka). Indian Naturalist, 2014.

Brandis, D., Indian Trees, International Book Distributors, Dehradun, 1921.

Bureau of Plant Industry, *Entada phaseolides* (Linn) Merr. Republic of the Phillippines Department of Agriculture (F). 2009.

Brink, M., Achigan-Dako E.G., Plant Resources of Tropical Africa 16. Fibres. PROTA Foundation, Wageningen, Netherlands 2012, 152-154.

Edwards, W., Moles, A. T. and Franks, P., The global trend in plant twining direction. Global Ecol. Biogeogr., 2007, 16, 795– 800.

Gamble, J. S. and Fischer, C. E. C., Dioscoreaceae. In Flora of the Presidency of Madras, Vol. III, Genus Dioscorea L., Adlard & Son Ltd, London, 1935, 1053–1055.

Granados, J. and Körner, C., In deep shade, elevated CO_2 increases the vigour of tropical climbing plants. Global Change Biol., 2002, 8, 1109–1117.

Gupta, G., More, A.S., Kumari, R.R., Kumar, A., Nabi, S.U., and Tandan, S.K. Effect of *Entada pursaetha* DC. Against experimentally induced hepatotoxicity in wistar rats. Haryana Vet. 2011, 50, 64-67.

Hashimoto, T., Molecular genetic analysis of left–right handedness in plants. Philos. Trans. R. Soc. London Ser. B, 2002, 357, 799–808.

http://eol.org/pages/703396/communities

Kalpanadevi, V., Shanmugasundaram, R. and Mohan, V.R. Antiinflammatory activity of seed extract of *Entada pursaetha* DC against carrageenan induced Paw edema. Science Research Reporter 2012, 2(1), 69-71.

Maheshwari, R., Rao, K.S. and Ramachandra, T.V. Structural characteristics of a giant tropical liana and its mode of canopy spread in an alien environment. Current Science, 2009, 96 (1), 58-64.

Muthumperumal, C and Parthasarathy N, A large-scale inventory of liana diversity in tropical forests of South Eastern Ghats, India. Systematics and Biodiversity, 2010, 8, 289-300.

Nzowa, L.K., Teponno, R.B., Tapondjou, L.A., Verotta, L., Liao, Z., Graham, D., Zink, M.C. and Barboni, L. Two new tryptophan derivatives from the seed kernels of Entada rheedei: Effects on cell viability and HIV infectivity. Fitoterapia 2013, 87, 37–42.

Okba, M. M., Soliman, F. M., El Deeb, K. S., & Yousif, M. F. Botanical study, DNA fingerprinting, nutritional values and certain proximates of *Entada rheedei* Spreng. 2013.

Padal, S.B. and Sathyavathi, K. Ethnomedicinal uses of some Mimosaceae family plants of Araku-valley, Visakhapatnam district, Andhra Pradesh, India. Int J Pharm Bio Sci, 2013, 3 (2), 611-616.

Parthasarthy, N., Muthuramkumar, S. and Reddy, M.S. Pattern of liana diversity in tropical evergreen forests of peninsular India. Forest Ecology and Management, 2004, 190, 15-31.

Pérez-Salicrup, D.R. Effect of liana cutting on tree regeneration in a liana forest in Amazonian Bolivia, Ecology, 2001, 82 (2), 389-396.

Punekar, S. A., and Lakshminarasimhan, P. Flora of Anshi National Park: Western Ghats-Karnataka. Biospheres Publ. 2011.

Putz, F. E., The natural history of lianas on Barro Colorado Island, Panama. Ecology, 1984, 65, 1713–1724.

Restom, G. and Nepstad, G., Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. For. Ecol. Manage., 2004, 190, 109–118.

Richards, P. W., The Tropical Rain Forest: An Ecological Study, University Press, Cambridge, 1972.

Rowe, N. and Speck, T., Plant growth forms: an ecological and evolutionary perspective. New Phytologist, 2005, 166, 61–72.

Rowe, N., Isnard, S. and Speck, T., Diversity of mechanical architectures in climbing plants: An evolutionary perspective. Journal of Plant Growth Regulator, 2004, 23, 108–128.

Runyon, J. B., Mescher, M. C. and De Moraes, C. M., Volatile chemical cues guide host location and host selection by parasitic plants. Science, 2007, 313, 1964–1967.

Saldanha, C. J. and Nicolson, D. H., Flora of Hassan District, Karnataka, India, Amerind Publishing Co Pvt Ltd, New Delhi, 1976.

Schnitzer, S. A., A mechanistic explanation for global patterns of liana. The American Naturalist, 2005, 166, 262–266.

Schnitzer S.A. and Bongers F., The ecology of lianas and their role in forests. Trends in Ecology & Evolution, 2002, 17(5), 223-230.

Schnitzer S.A., Bongers F., Burnham R.J. and Putz F.E., Ecology of Lianas. Published by John Wiley & Sons, Ltd, UK, 2015.

Swaine, M. D. and Grace, J., Lianas may be favoured by low rainfall: evidence from Ghana. Plant Ecol., 2007, 192, 271–276.

Terborgh, J., The Diversity of Tropical Rainforests, Scientific American Books, New York, 1992.

Van der Heijden, G. M. F. and Phillips, O. L., What controls liana success in Neotropical forests? Global Ecol. Biogeogr., 2008, 17, 372–383.

Vogel, S., Living in a physical world XI. To twist or bend when stressed. Journal of Biosciences, 2007, 32, 643–655.

In this issue

A giant liana in an alien environment

A liana is a plant requiring physical support for its weak stems to climb a host tree for maximizing photosynthesis. Lianas epitomize tropical rain forests but because of the difficulty in research in conditions of high rainfall and dense vegetation, lianas have remained poorly studied. To

initiate research on various aspects of liana biology seeds of a leguminous liana *Entada pursaetha* were collected from coastal region and sown inside a research campus in a dry subtropical region. In 17 years a single seedling has grown into a giant liana, perhaps the largest recorded. Though its unchecked spread in the campus has caused problems requiring pruning, the availability of a liana inside a campus opens up several opportunities for research, including the diversity in the morphology of the liana branches, the biomechanics of the upright trunk constructed by anticlockwise coiled branches uncoiling at breast height into highly twisted spreading branches that lean on support host trees, the mechanism in hydraulic supply, and navigation by the aerially formed leafless shoots that have spread its canopy on surrounding trees. The vigour of the introduced liana in an alien environment raises the question as to why this liana is confined to the coastal areas or the river banks. The large seeds of this liana remain dormant due to hard seed coat. Water may be required for the dispersal of the seeds, and also for softening the seed coat by lytic enzymes released from the aquatic microorganisms. See **page 58**.

Large branchiopods

The special section is the outcome of the Sixth International Large Branchiopods Symposium organized by the Acharya Nagarjuna University, Nagarjuna Nagar, in September 2007 at Vijayawada (see *Curr Sci*., 2008, **94**, 164–165). As a major class of Crustacea, the branchiopods are comprised of calm shrimps, fairy and brine shrimps and tadpole shrimps. They inhabit unstable ephemeral inland and brackish waters. Describing the distribution of 35 species of clam shrimps in India, M. K. Durga Prasad and G. Simhachalam (**page 71**) indicate the endemicity of 32 species. Summarizing his 20 years of intense field studies, B. V. Timms (**page 74**) explains the unusual species richness and the amazing halophilic branchiopods of Australia. Using molecular markers, R. Tizol-Correa *et al.* (**page 81**) trace the phylogenetic relationships of the brine shrimps from tropical salt-pans of Mexico and Cuba. From an experimental interspecific hybridization study of the African fairy shrimps, H. J. Dumont and Els Adriaens (**page 88**) report that the rate of evolution in these fairy shrimps has remained unusually slow.

To tide over the unfavourable dry season, these animals adopt different patterns of reproduction; some are bisexual, while others display a wide range of sexuality and modes of reproduction. In the Mexican waters, H. Garcia-Velazco *et al.* (**page 91**) record the occurrence of parthenogenetic females and cross-fertilizing hermaphrodites in the tadpole shrimp population. From an experimental study, S. C. Weeks (Akron University, USA, **page 98**) suggests that males introduced into the population by an amphigenic hermaphrodite can be sustained for a few generations.

These creatures are also capable of generating drought-resistant cysts; for instance, the cysts of the brine shrimp alone are known to synthesize and store two unique hitherto unknown proteins called Artemin and p26. These proteins withstand the thus for unknown minimal residual water of 0.7 μg/g cyst and when hydrated (1 million times) 0.7 g water/g cyst. N. Munuswamy *et al.* (**page 103**) have recorded their presence in the cysts of the Indian fairy shrimp. Besides this, the branchiopods adopt a sort of bet-hedging strategy by hatching only a cohort of the accumulated cysts bank, when pools are filled with rainwater.

All developing countries practising aquaculture import *Artemia* cysts from USA. For instance, to feed 1000 million hatchings of shrimp cultivated for export, India imports 100 tonnes of *Artemia* cysts at the cost of Rs 560 million. Some companies fill up deliberately commercial brine shrimps cysts with different shrimp species and thereby introduce unsolicited *Artemia*, which may hybridize with native species. To identify such a 'contaminant', R. Campos-Ramos *et al.* (**page 111**) describe a bio-kinetic range of cyst-hatching temperatures for *Artemia* spp. C. Arulvasu and N. Munuswamy (**page 114**) have shown that *Artemia* nauplii can also be enriched with growth-promoting polyunsaturated fatty acid by soaking the larvae in 0.5% shrimp head oil emulsion for a period of 9 h. In an ingenious study, C. Orozco-Medina *et al.* (**page 120**) have shown that the metanauplii of *Artemia* ingested bacterial cells. Thus, the special section highlights the academically interesting and economically useful large branchiopods.

T. J. Pandian
N. Munuswamy
—*Guest Editors*

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 anti-clockwise-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?

1. Gentry, A. H. and Dodson, C., Contribution of nontrees to species richness of a tropical rainforest. *Biotropica*, 1987, **19**, 149–156.
2. Brandis, D., *Indian Trees*, International Book Distributors, Dehradun, 1921.
3. Saldanha, C. J. and Nicolson, D. H., *Flora of Hasan District, Karnataka, India*, Amerind Publishing Co Pvt Ltd, New Delhi, 1976.
4. Parthasarathy, N., Muthuramakumar, S. and Reddy, M. S., Patterns of liana diversity in tropical evergreen forests of peninsular India. *For. Ecol. Manage*., 2004, **190**, 15–31.
5. Richards, P. W., *The Tropical Rain Forest: An Ecological Study*, University Press, Cambridge, 1972.
6. Darwin, C., The movements and habits of climbing plants. *Bot. J. Linn. Soc*., 1867, **9**, 1–118.
7. Penalosa, J., Basal branching and vegetative spread in two tropical rain forest lianas. *Biotropica*, 2004, **6**, 1–9.
8. Larson, K. C., Circumnutation behavior of an exotic honeysuckle vine and its native congener: influence on clonal mobility. *Am. J. Bot*., 2000, **87**, 533–538.
9. Gallenmüller, F., Rowe, N. and Speck, T., Development and growth form of the neotropical liana *Croton nuntians*: the effect of light and mode of attachment on the biomechanics of the stem. *J. Plant Growth Regul*., 2004. **23**, 83–97.
10. Vogel, S., Living in a physical world XI. To twist or bend when stressed. *J. Biosci*., 2007, **32**, 643–655.
11. Edwards, W., Moles, A. T. and Franks, P., The global trend in plant twining direction. *Global Ecol. Biogeogr*., 2007, **16**, 795–800.
12. Gamble, J. S. and Fischer, C. E. C., Dioscoreaceae. In *Flora of the Presidency of Madras, Vol. III, Genus Dioscorea* L., Adlard & Son Ltd, London, 1935, pp. 1053–1055.
13. Hashimoto, T., Molecular genetic analysis of left–right handedness in plants. *Philos. Trans. R. Soc. London Ser. B*, 2002, **357**, 799–808.
14. Runyon, J. B., Mescher, M. C. and De Moraes, C. M., Volatile chemical cues guide host location and host selection by parasitic plants. *Science*, 2007, **313**, 1964–1967.
15. Rowe, N. and Speck, T., Plant growth forms: an ecological and evolutionary perspective. *New Phytol*., 2005, **166**, 61–72.
16. Whitmore, T. C., *Tropical Rain Forests of the Far East*, Clarendon Press, Oxford, 1984.
17. Read, J. and Stokes, A., Plant biomechanics in an ecological context. *Am. J. Bot*. 2006, **93**, 1546–1565.
18. Isnard, S., Speck, T. and Rowe, N. P., Biomechanics and development of the climbing habit in two species of the South American palm genus *Desmoncus* (Arecaceae). *Am. J. Bot*., 2005, **9**, 1444–1456.
19. Rowe, N., Isnard, S. and Speck, T., Diversity of mechanical architectures in climbing plants: An evolutionary perspective. *J. Plant Growth Regul*., 2004, **23**, 108–128.
20. Putz, F. E., The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, 1984, **65**, 1713–1724.
21. Granados, J. and Körner, C., In deep shade, elevated CO_2 increases the vigour of tropical climbing plants. *Global Change Biol*., 2002, **8**, 1109–1117.
22. Schnitzer, S. A., A mechanistic explanation for global patterns of liana. *Am. Nat*., 2005, **166**, 262–266.
23. Swaine, M. D. and Grace, J., Lianas may be favoured by low rainfall: evidence from Ghana. *Plant Ecol*., 2007, **192**, 271–276.
24. Terborgh, J., *The Diversity of Tropical Rainforests*, Scientific American Books, New York, 1992.
25. Restom, G. and Nepstad, G., Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. *For. Ecol. Manage*., 2004, **190**, 109–118.
26. van der Heijden, G. M. F. and Phillips, O. L., What controls liana success in Neotropical forests? *Global Ecol. Biogeogr*., 2008, **17**, 372–383.

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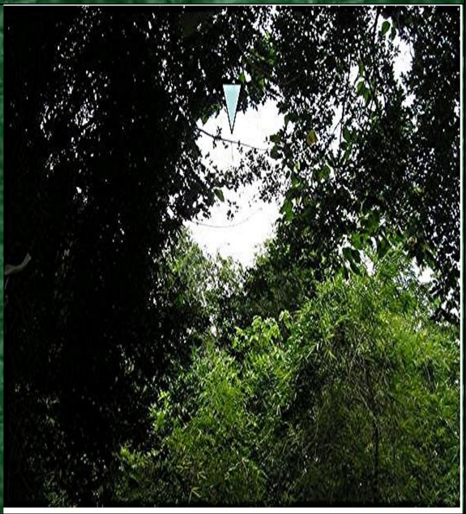

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