The mechanics of climbing and attachment in twining plants

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Twining plants achieve vertical growth by revolving around supports of different sizes on which they exert a pressure. These well-known observations raise many intriguing questions that can be addressed within the framework of elastic filamentary structures. Here, mechanical aspects of this problem are investigated by modeling the stem close to the apex as a growing elastic rod with intrinsic curvature and twist. The analysis reveals that vertical growth is achieved thanks to the presence of discrete contact points as well as regions with continuous contact. Further, the experimentally observed fact that the plant stem is under tension is shown to be directly related to the positive contact pressure. Finally, the maximal radius of the pole around which a twiner can climb is identified.

Climbing plants have developed a fascinating array of mechanical strategies to achieve vertical growth without being able to support themselves. Hookers, leaners, weavers, rooters, stickers, clingers, tendril-bearers, or twiners are just a few realizations of the 30 different ways vines manage to grow by taking advantage of their surrounding [1]. Twiners, such as garden peas, climbing jasmines, and morning-glories, are perhaps the most studied of all vines [2]. The growing tip waves around in a circular motion known as circumnutation until it finds an appropriate upright support and then start wrapping around it to extend upward. The tip of the vine keeps nutating and the vine pursue its climbing process by forming a spiral around the support. The growth process of twining plants raises many interesting mechanical questions already noted by 19th century botanists and further studied by Silk, Holbrook and co-workers [3–7].

Can a given twining plant climb around supports of different sizes? This question was first raised by Charles Darwin in his book on *The movements and habits of climbing plants*[8]. In there he comments: "Most twining plants are adapted to ascend supports of moderate though of different thicknesses. Our English twiners, as far as I have seen, never twine round trees...". As an example, Darwin noted that *Solanum dulcamara* can twine around supports of 3mm but not on supports of 5 or 6mm (see many other examples in [9]). The natural question is then to determine the critical cylinder radius above which a plant is no longer able to twine. In the process of establishing themselves on a pole, twining plants rely on friction[2, 7]. As noted by Julius von Sachs [10], the vine may slide off "...if the surface of their vertical support is too smooth to furnish a strong mutual friction". What is the effect of friction in the vine ability to grasp the pole? Similarly, what is the pressure generated by a plant on the pole? How does it change with its intrinsic properties and shape? Whereas most plants such as trees or flowers stems are in compression, a peculiar feature of twining plants is that their stem is in tension [4]. How is this tension generated? There is no applied load at the tip of the growing plant, gravity only increases compression and although the stem can build compressive and tensile domains through differential growth the net effect, once averaged over the cross-section, vanishes. Therefore, a vine in continuous contact with a pole cannot generate tension. As we will see, tension is actually produced when the plant establishes discrete points of contacts which create anchorage points. The purpose of this Letter is to identify through simple mechanical arguments how twining vines establish themselves, develop discrete and continuous contacts, and to answer Darwin's question on the critical pole radius.
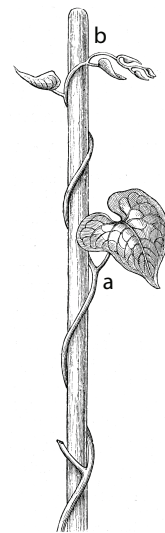

FIG. 1: Blue Bindweed (*Ipomoea purpurea*), a typical twining plant (illustration from Sachs' physiology of plants [10]). The shoot apex spans from *a* to *b*.

Most authors have studied the helical shape of the twining vine around the pole. By contrast here we focus on the formation of these helices by looking at the way the tip of the vine manages to grasp the pole. The vine before lignification is a long, thin, elastic filament subject to twisting and bending. Due to the small linear density of the vine and the large stresses developed through self-contact, the gravitational load on the vine has been found experimentally to be negligible by comparison to other forces involved in the problem (for instance the linear weight in *Pharbitis nil* is about 0.4 mN cm^{-1} but, it can exert a contact force of 300 mN cm^{-1} [4]). Therefore it will be omitted in the analysis of the grasping problem. During the circumnutation process, the vine at the apex develops intrinsic curvature and torsion. We assume these curvatures to be constant and uniform. This assumption is also consistent with the vertical and lateral oscillation of the vine tip observed during growth.

It is therefore reasonable to model the vine as a uniform inextensible and unshearable elastic rod with circular cross-section, constant intrinsic curvature and twist, in possible contact with a cylindrical support. Since growth is slow with respect to other time scales in the problem, the attachment problem consists in finding possible equilibria of the rod on the cylinder with appropriate boundary conditions. An inextensible and unshearable rod of length L may be represented by its centerline $\mathbf{r}(s)$, where s is the arclength ($0 \leq s \leq L$), and an orthonormal basis formed by the tangent vector $\mathbf{d}_3(s) = \mathbf{r}'$, and two vectors $\mathbf{d}_1(s)$, $\mathbf{d}_2(s)$ representing the orientation of material cross sections. A complete kinetic description is given by: $\mathbf{d}_i' = \mathbf{u} \times \mathbf{d}_i$, $i = 1, 2, 3$ where ( )$'$ denotes the derivative with respect to s and $\mathbf{u}$ is the strain vector. The two first components of $\mathbf{u}$ are related to the Frenet curvature $\kappa = \sqrt{\mathsf{u}_1^2 + \mathsf{u}_2^2}$ and u_3 is the twist which comprises both material twisting and Frenet torsion τ. The stresses in a cross section at s can be averaged to yield a resultant force $\mathbf{n}(s)$ and resultant moment $\mathbf{m}(s)$ acting at $\mathbf{r}(s)$. The balance of linear and angular momenta yields [11]

$$\mathbf{n}' + \mathbf{f} = \mathbf{0}, \qquad \mathbf{m}' + \mathbf{r}' \times \mathbf{n} = \mathbf{0}, \tag{1}$$

where $\mathbf{f}(s)$ is the body force per unit length applied on the cross section at s (body couples are ignored here). The body force is used to model the effect of contact with the support. To close the system, we assume the linear constitutive relations $\mathbf{m} = B\mathsf{u}_1\mathbf{d}_1 + B(\mathsf{u}_2 - \widehat{\mathsf{u}}_2)\mathbf{d}_2 + C(\mathsf{u}_3 - \widehat{\mathsf{u}}_3)\mathbf{d}_3$, where $\widehat{\mathsf{u}}_2$ and $\widehat{\mathsf{u}}_3$ are, respectively, the intrinsic curvature and twist of the rod, and B and C are the bending and twist rigidities. To gain some insight on the problem, we first consider a simple two-dimensional version where the vine, rather than twining around a pole, is restricted in the plane. In this case $\widehat{\mathsf{u}}_2 = 1/\widehat{R}$ and $\widehat{\mathsf{u}}_3 = 0$. The filament is assumed to be clamped at its base ($s = 0$), that is $\mathbf{r}(0) = (R, 0)$, $\mathbf{d}_3(0) = (0, 1)$. That is, $\widehat{R}$, the natural radius of the vine, corresponds to
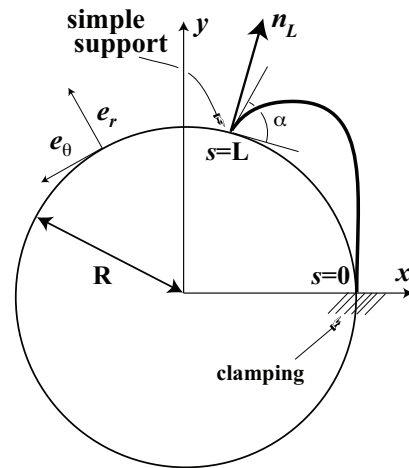

FIG. 2: Diagram of the apex region of a climbing twiner

the radius of the vine when taken away from its support (see [4] for the experimental procedure that provides the value of $\widehat{R}$). The clamp models the constraint applied by the lower part of the plant on the shoot apex. The tip at $s = L$ lies on the disc and no moment is applied to it so that its curvature is equal to the intrinsic curvature $\mathsf{u}_2(L) = \widehat{\mathsf{u}}_2$. We also require the external force at L to be radial (see Fig. 2). For each length L and ratio of radii $\rho = R/\widehat{R}$, these boundary conditions ensure the existence of a discrete set of solutions. Therefore solutions can be obtained numerically by traditional shooting methods for boundary-value problems: starting with the initial values at $s = 0$ ($\mathbf{r}(0) = (R, 0)$, $\mathbf{d}_3(0) = (0, 1)$, $\mathbf{m}(0)$, and $\mathbf{n}(0)$ to be given by an initial guess), Eq. (1) is integrated with a Runge-Kutta alogrithm, up to $s = L$ where we check the end conditions. If they are not satisfied, we adjust the values for $\mathbf{m}(0)$ and $\mathbf{n}(0)$ until the computed solution satisfies the boundary conditions. Once a solution is known, the process of growth on the disk is carried out by finding solutions with increasing length, using parameter continuation. For each solution, we track the angle α that the tip makes with the tangent to the disk (see Fig. 2). We refer to the portion of the filament off disk as the *anchor*. For small ρ, a typical bifurcation diagram with distinct equilibria branches is shown in Fig 3. On the first branch (continuous line) and for small enough L, we find stable solutions which can be continued up to a (fold) point where they first penetrate the disk. This is a bifurcation point where we identify another branch (the vertical line in Fig. 3) corresponding to solutions having a segment in continuous contact with the disk in addition to the anchor part. The length of the continuous part can be extended arbitrarily while the anchor does not change shape. The remaining upper part of the first branch (dotted curve) corresponds to unphysical configurations penetrating the disk. All solutions on the branch corresponding to large values of α (dash-dotted curve)

are either unphysical or dynamically unstable (as determined by computing the linearized dynamics around the configuration [12]). For larger values of ρ there are also two branches of equilibria. On the lower branch, there exist stable configurations for $0 < L < L_{\max}$. At $L_{\max}$ a fold point is reached with a loss of stability and a dynamical jump occurs to configurations where the filament rolls on itself and leaves the disk (see Fig. 4). This rolled-up solutions can have arbitrary length (see vertical line in Fig. 4). These solutions are not viable for a twining plants since they do not allow the vine to grow around the pole by increasing its length. The bifurcation between these two behaviors defines the maximal radius on which a vine can grow and is found to occur at the unique value $\rho_c \simeq 3.3$ where the two branches of equilibria cross. That is, in the plane a vine cannot grow on disks that are more than 3.3 times larger than its natural radius.

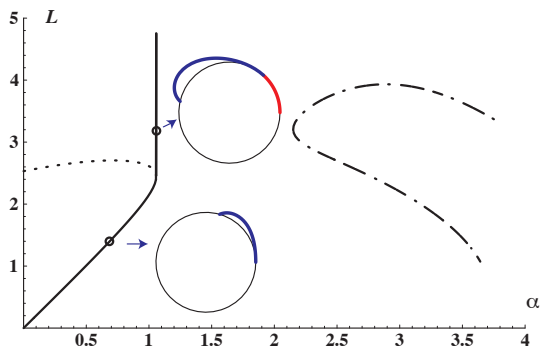In the section of the filament in continuous contact

FIG. 3: Below the critical curvature ratio, $3 = \rho < \rho_c$, filaments can grow by first changing its inclination at the tip then by adding a continuous segment (in red) of arbitrary size. Dotted and Dash-dotted curves represent curves that are either unstable (do not remain attached on the pole) or unphysical (where the vine enters the disk). They are however useful to understand the bifurcation.
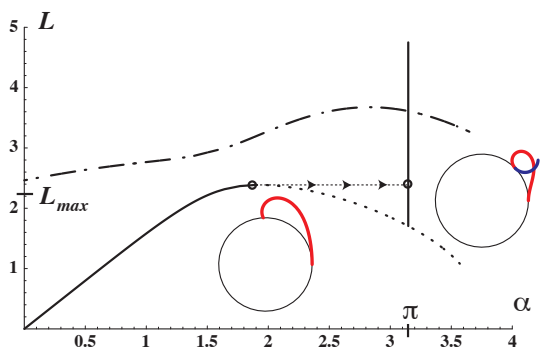

FIG. 4: Above the critical curvature ratio $3.5 = \rho > \rho_c$, filaments attachment on the disk are limited in length. Past a certain L_{max} value, the filaments rolls up on itself and does not manage further growth to keep growing around the pole.

with the disk the radial component of the force vanishes.

From Eq. (1), we see that the tension $\mathsf{n}_3 = \mathbf{n} \cdot \mathbf{d}_3$ balances the contact force $p = \mathbf{f} \cdot \mathbf{e}_r$ so that $\mathsf{n}_3 = R\,p$. Since the support can only provide repulsive contact force ($p > 0$), the previous relation implies that the filament must be in tension ($\mathsf{n}_3 > 0$). This tension is provided by the pointwise contact force at the end $s = L$ of the filament and transmitted by the anchor to the part [of the filament] in continuous contact with the disk. Further use of the moment balance and of the constitutive relation yields

$$p = \frac{B}{R^2}\left(\frac{1}{\widehat{R}} - \frac{1}{R}\right), \qquad (2)$$

from which we see that the condition $\rho > 1$ must be satisfied for p to be positive.

The analysis so far has been restricted to the frictionless case. However, it has been emphasized by different authors [2, 7] that friction plays an important role in the ability of a climbing plant to support its weight. Here friction is modeled by a tangential component of the disk reaction force on the tip of the anchor. To understand its effect, we first consider an equilibrium configuration obtained in the absence of friction. We then change the length of the filament without moving the tip. This is made possible by introducing a tangential component in the reaction force along $\mathbf{e}_\theta$ at $s = L$ due to friction. As L keeps increasing (resp. decreasing), the tangential force component reaches a critical value equal to $\mu\,p$ where $\mu < 0$ (resp. $\mu > 0$) is the friction coefficient. Past this value the tip slips incrementally on the disk to find a new nearby equilibrium configuration where the tangential component equals the critical tangential value. Therefore, to identify the equilibrium configurations with friction we increase the length and find configurations where the tangential force equals $\mu\,p$. For each friction coefficient μ we compute, as detailed above, the critcal value $\rho_c = \rho_c(\mu)$ defining the bifurcation between filaments that can grow around the disk and filaments that leave the disk. The results in Fig 5 show that friction can have a crucial effect on the ability of a plant to remain on a large disk. Note that in the case of a twining plant, once the tip is in contact with the pole, friction prevents the plant from sliding back, therefore corresponding to positive values of μ. Intuitively, one can understand Darwin's problem as follows: for thin supports the vine tip and the tangent of the support are almost parallel and the vine follows the support without curling back on itself. For thicker supports, in order to maintain its grip, the tip needs to touch the support surface at a larger angle α. If the support becomes too large, so will the angle α and the vine will curl back on itself. For increasing friction the contact angle needed for this to happen will be higher and consequently the plant can wind on thicker supports.

We now turn our attention to the three dimensional case. The main properties found in the two-dimensional case still hold, namely, discrete points of contacts exist between plant and support, tension is generated by these
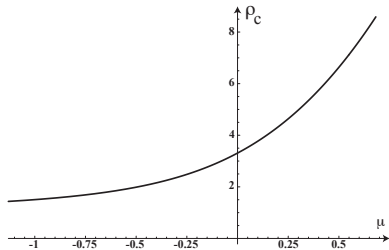
FIG. 5: Change of critical radii ratio as a function of friction. Positive friction coefficient acts when the tangential force prevents the filament from sliding back whereas negative friction coefficients correspond to situation where friction prevents the tip from slipping forward. Range of μ values are consistent with experimental data in ref [7]. The prediction of an upper bound of ρ_c around 8 is consistent with the observation of Bell [13].

contact points, and attachment is possible only by difference between intrinsic curvature and twist and geometry of support. However, there are new subtle difficulties associated with growing a filament on a cylinder. The base of the apex where the filament is clamped can now have an arbitrary orientation. In our model, this orientation is closely related to the pitch of the plant helix-like shape on the pole (it was experimentally observed that the plant adopts an almost uniform helical shape provided that the number of gyres is large enough and the support is uniform [13]). Therefore, we investigate the mechanical origin of the helical shape on the pole and find that for given intrinsic curvature $\widehat{u}_2$ and twist $\widehat{u}_3$, there exists a single helical equilibrium on a cylinder of radius R with pitch angle β. Solving Eq. (1) in cylindrical geometry yields the trigonometric equation

$$C(u_2 - \widehat{u}_2)\sin 2\beta = B(u_3 - \widehat{u}_3)\cos 2\beta \,, \qquad (3)$$

where $u_2 = \frac{\sin^2 \beta}{R}$ and $u_3 = \frac{\sin \beta \cos \beta}{R}$ are the curvature and torsion of the helix. As before, this continuous solution lying on the cylinder can only be maintained by the tensile force provided by the anchor. The problem is then to find an anchor starting with the correct pitch angle and tension. In general no such solution can be found. We then return to a three dimensional version of the boundary value problem: the filament is clamped at $s = 0$ and is simply supported by a radial force at its the tip $s = L$ where it contacts the pole. Not surprisingly, the bifurcation diagram becomes quite complex to study (with multiple solutions with discrete and continuous contacts). Rather than providing an exhaustive description, we look for helix-like solutions, with non-uniform pitch angle, in continuous contact with the cylinder. The solutions ends with an anchor (see Fig 6). We can now define a ρ_{max} as the largest value of $\rho = R/\widehat{R}$ such that the continuous part of the segment can be extended. Extensive numerical studies show that the value of ρ_{max} obtained

in the planar case provides an upper bound for the three dimensional case.
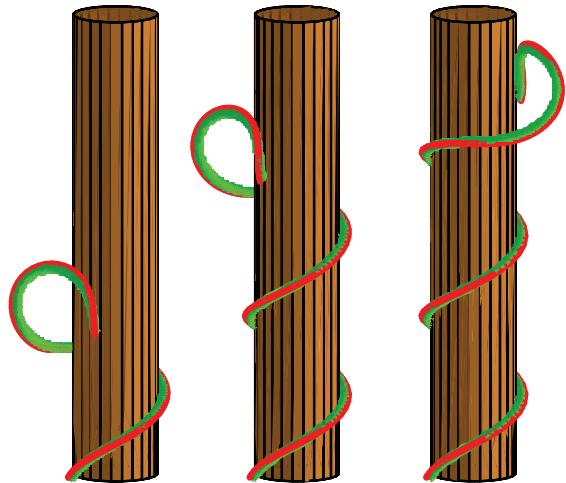

FIG. 6: A sequence of three-dimensional solutions to the attachment problem. Note the continuous, almost helical, solution, followed by the anchor that provides tension in the filament.

The present analysis shows that a mechanical model for anchoring and attachment based on rod theory can provide a simple explanation for the limitation of twining plants to wind around thick supports and for the role of friction to boost the plant ability to achieve vertical growth. The model also explains how tension is generated and shows that both continuous and discrete contact points between stem and pole exist. However, the present model does not address the fact that the stem, after it establishes itself on the pole, may adapt its intrinsic curvature due to stress and contact. We believe this remodeling might be important to obtain an accurate picture of the stem shape on the pole, but this non obvious theoritical treatment must be left for futur work.

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