

## THE IMPORTANCE OF FRICTIONAL INTERACTIONS IN MAINTAINING THE STABILITY OF THE TWINING HABIT<sup>1</sup>

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The stability of twining vines under gravitational loads suggests an important role for friction. The coefficient of friction,  $\mu$ , between vine stems and wood is high, often five times greater than between leather and wood, as determined by slip tests on an inclined plane. Stem trichomes function like ratchets to facilitate climbing upward (or to facilitate slipping if the stem is inverted). A mathematical model predicts large masses (kg) must be applied to the base of a twining vine to cause slipping. Vines slip as predicted when  $\mu$  is low and arc length on the pole is short, and they break before slipping when  $\mu$  is large or arc length is long. In contrast, twining vines are unstable in compression, collapsing when small masses (<10 g) are hung from the top of the vine. However, if the loads are applied below the uppermost gyre, the stabilizing tensional effect dominates. Therefore, in nature vines twining on a cylindrical support are stable under gravitational loads, unless these loads occur near the apex. A corollary is that a short apical coil can hold up large masses of maturing shoot.

**Key words:** biomechanics; curvature; friction; helix; *Ipomoea purpurea*; structural stability; twining; vines.

Curved and twisted structures are common in nature, yet there are few biomechanical studies involving large curvature or torsion. Twining vines are curved and twisted and have physical features similar to both mechanical springs and ropes. Like springs, twining vines have helical shapes. Like ropes, vines fall over when removed from rigid supports. The mechanical properties of vines are reminiscent of the novelties known as “finger trap” puzzles (Fig. 1). These toys, cylindrical shells made from helically woven straps, tighten to pinch inserted fingers when pulled apart, but loosen when compressed, widening the diameter of the trap. This paper explores the tightening and consequent stability of a helical coil in tension.

We analyze the stability of the twining habit, including the nature of the forces maintaining the helical form of vines twining around cylindrical supports. Plant habit is the positioning—the location and configuration—of stems, roots, and leaves. The habit of an organ influences its access to light and its structural stability. The habit of a plant axis, like the geometry of a space curve (DoCarmo, 1979), can be specified by the values of  $s$ , the arc length along the axis;  $\kappa$ , the associated curvature; and  $\tau$ , the torsion. Thus an understanding of plant habit requires an understanding of the manner in which curvature and torsion are produced and maintained. Furthermore,  $\kappa$  and  $\tau$  enter into force and moment balances of curved and twisted structures (Love, 1944; Costello 1978).

To understand axial curvature and torsion, we need some definitions based on the Frenet vectors, the unit tangent, normal and binormal to a curve in space (Fig. 2). The curvature vector,  $\boldsymbol{\kappa}$ , lies along the direction of the unit normal ( $\mathbf{n}$ ) to the curve and is the rate of change of the unit tangent ( $\mathbf{t}$ ) as we

move along the curve,  $\boldsymbol{\kappa} = \kappa \mathbf{n} = (\partial \mathbf{t} / \partial s)$ . A more intuitive measure is the radius  $R$  of the circle that just fits the curve locally. An arc has large curvature if it is fit by a small circle, and the converse is true. It can be shown that  $\kappa$  is the reciprocal of  $R$ . For a plant stem the spatial distribution of curvature can be characterized by plots of  $\kappa$  or  $R$  vs.  $s$ , where  $s$  is the distance along the edge or a computed midline of a photographic projection of a stem (Silk and Erickson, 1978; Whippo and Hangartner, 2003). Since stems are often straight, having zero  $\kappa$  but infinite  $R$ , it is convenient to plot curvature rather than the radius of curvature as a function of position. A planar curve given by a set of values ( $s$ ,  $\kappa$ ) retains its shape even if it is rotated and translated in space. If the curve lies in more than one plane, as is the case for twining vines, it is specified by  $s$ ,  $\kappa$ ,  $\tau$ . The torsion  $\tau$  is a measure of the rate at which the curve is twisting out of the local plane and is given by  $\boldsymbol{\tau} = \tau \mathbf{n} = -(\partial \mathbf{b} / \partial s)$ , where  $\mathbf{b}$  is the binormal, i.e., the unit vector perpendicular to the plane of the curve.

Twining stems have uniform curvature and torsion (Fig. 3) and provide an instructive model system for studying growth rate patterns that produce plant habit (Silk and Abou Haidar, 1986; Silk, 1989). Ascending a smooth vertical pole, a twining vine forms a helical tube of tissue (Fig. 2). The helix  $\boldsymbol{\alpha}$  through the center of the vine is

$$\boldsymbol{\alpha}(s) = a \cos(s/d) \mathbf{i} + a \sin(s/d) \mathbf{j} + c(s/d) \mathbf{k}$$

where the variable  $s$  is distance along  $\boldsymbol{\alpha}$ ; the parameter  $a$  is the radius of the helix;  $c$  is the pitch, i.e., the gyre wavelength divided by  $2\pi$ ; and  $\mathbf{i}$ ,  $\mathbf{j}$ , and  $\mathbf{k}$  are the unit vectors of the cartesian reference frame. The curvature and torsion at all locations on the helix are

$$\kappa = a/d^2 \quad \tau = c/d^2,$$

where  $d^2 = a^2 + c^2$ . As will be described in our model, the biomechanical analysis of twining involves curvature, tensile forces along  $\mathbf{t}$ , and normal loads (forces per unit length) along  $\mathbf{n}$ .

Climbing vines are a prominent feature of tropical forests where light is limiting (Putz and Holbrook, 1991; Rowe and Speck, 1996). The twining mode of growth has evolved in many plant families and enables vines to ascend vertical sup-

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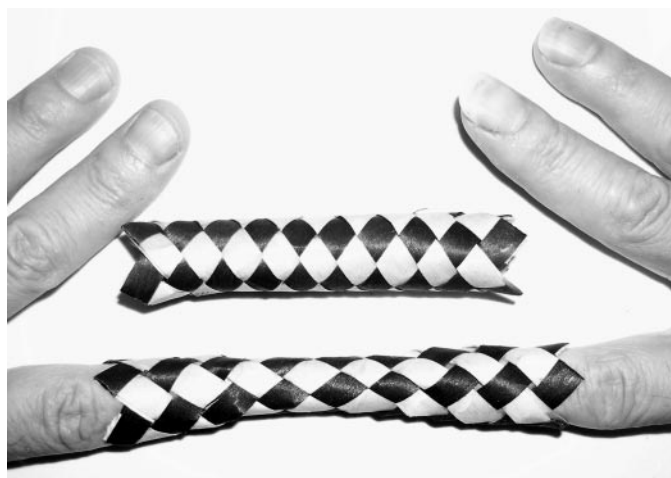


Fig. 1. "Finger trap" toy. The finger trap, made of helically woven straps, contracts radially as it is pulled longitudinally and loosens as the coils widen in compression.

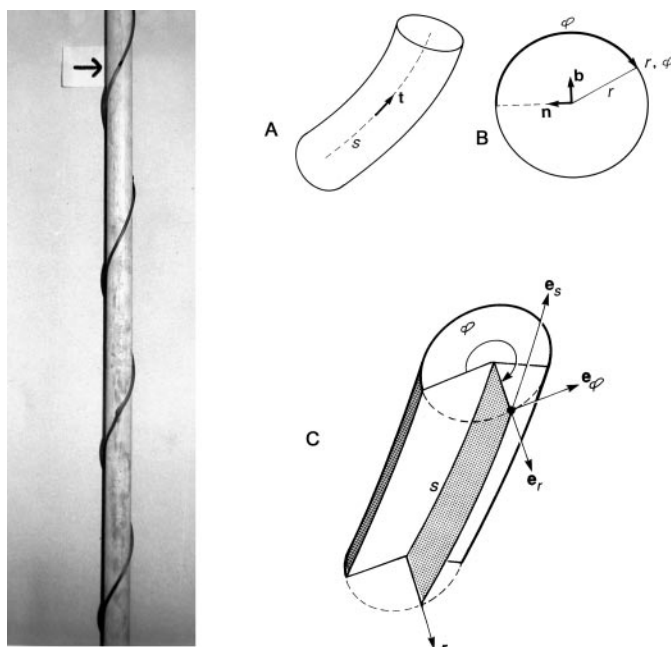
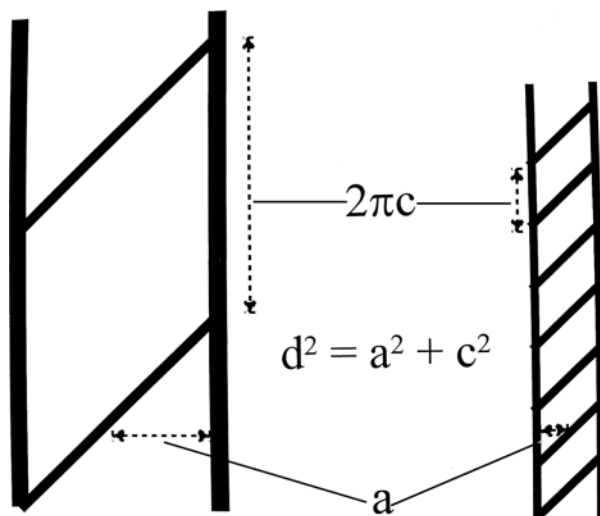


Fig. 2. Natural coordinate system for the analysis of twining mechanics. On a cylindrical support, a vine stem grows into a helical form (photograph, left). The Frenet vectors  $\mathbf{t}$ ,  $\mathbf{n}$ , and  $\mathbf{b}$  vary with position on the helix that runs through the center of the vine stem (diagrams A and B, right). The unit tangent  $\mathbf{t}$  lies along the helix; the unit normal  $\mathbf{n}$  is horizontal and points toward the center of the vertical supporting pole; and the unit binormal  $\mathbf{b}$  rotates so that it remains perpendicular to  $\mathbf{t}$  and  $\mathbf{n}$ . The plane containing  $\mathbf{n}$  and  $\mathbf{b}$  cuts a cross-section through the vine stem. The natural coordinates  $s$  (arc length along the helix),  $r$  (distance along the radius of the helical tissue tube), and  $\varphi$  (angle, measured from the normal) are defined in terms of the Frenet vectors. The unit vectors  $\mathbf{e}$  can be drawn tangent to the natural coordinate curves; and surfaces can be visualized corresponding to constant values of the natural coordinates (diagram C, lower right). The forces generated by the twining habit are dominated by axial tensions (tensile forces in the  $\mathbf{t}$  direction) balanced by normal loads (forces per unit length in the  $\mathbf{n}$  direction).



$$\kappa = \frac{\partial \mathbf{t}}{\partial s} = \frac{a}{d^2} \quad \tau = -\frac{\partial \mathbf{b}}{\partial s} = \frac{c}{d^2}$$

Fig. 3. Geometry of the twining habit. The helix is characterized by parameters  $a$ ,  $c$ , and  $d$  and has uniform curvature,  $\kappa$  and torsion,  $\tau$  related to the helical parameters. The helical parameters are found empirically to vary with the diameter of the support. See legend to Fig. 2 for the definition of the arc length  $s$  and the Frenet vectors  $\mathbf{t}$  and  $\mathbf{b}$ .

ports with a minimum expenditure of biomass. The evolutionary success of the twining habit suggests that good mechanical stability should be associated with the helical structure. Silk and Hubbard (1991) showed that the mechanics of the twining habit involves an innate tendency for the vine to grow into a coil of smaller radius than the cylindrical supporting structure. This causes the stem to hug the support. Putz and Holbrook (1991) explored the model of loosely coiled springs to show that friction must also play an important role. In this paper we extend the earlier analyses to quantify the role of frictional interactions in maintaining the stability of the twining habit.

## MATERIALS AND METHODS

**Cultivation of vines**—Morning glory vines were grown from seeds of *Ipomoea purpurea* (L.) Roth (Convolvulaceae) cv. Heavenly Blue. Plants were maintained in a growth chamber as described previously (Silk and Hubbard, 1991). After eight leaves had emerged, stems were allowed to twine around a wooden dowel or the TWIFOR force measuring apparatus (Matista and Silk, 1997).

**Coefficients of friction**—To determine the coefficient of friction between vine stems and differently textured surfaces, stem segments were placed on a flat piece of wood ("plane surface") either left bare, covered in contact paper (smoothest texture), or covered with wool fabric (roughest texture). The plane surface was then elevated at one side using a micromanipulator (Olympus America, San Diego, California, USA). Measured from the horizontal, the angle of inclination at which the stem segment slid down the plane was recorded. Two types of placement were used in the measurements. First the segments were firmly placed, so that the entire surface of the stem was in good contact with the plane. This placement was intended to mimic the stem experiencing a twining force so that it is in close contact with its support. In a second set of determinations, termed "gentle placement," the same stem

segments were placed on the plane surface with as little pressure as possible. The slip test was also performed for two orientations: an “upright” configuration in which the apical end of the stem segment was at the higher end of the inclined plane and an “inverted” configuration in which the basal end of the segment was placed on the higher end of the inclined plane. An aluminum plate was used to determine frictional coefficients of the nylon string. Uncoiled vine stems were used for the slip tests on an aluminum pole. The coefficient of static friction,  $\mu$ , was calculated as the tangent of the angle at which the stem or string first slips on the inclined plane. The coefficient of kinetic friction could be estimated as 0.75  $\mu$  (e.g., Beer and Johnston, 1977).

**Measurements of the loads produced by the twining stems**—A load-measuring apparatus, the TWIFOR, was used to record the normal load exerted by the helical vine stem (Matista and Silk, 1997; Scher et al., 2001). The apparatus has a vertical support pole that is cut in half longitudinally to make two poles with semicircular cross sections. The half-poles are mounted in close proximity so that the twining vine acts to pull the halves together. One half-pole is mounted rigidly in a fixed platform, and the other is anchored in a swinging bar suspended at each end from the fixed platform. Suspending elements are thin plastic strips and a thin beam load cell, supplied with balancing, compensating, and conductive elements and a rated capacity for 113 g (Omega Engineering Inc., Stamford, Connecticut, USA). The normal load exerted by the plant on the pole is sensed as a slight horizontal movement of the bar and recorded with a datalogger (Campbell Scientific, Logan, Utah, USA) connected to the load cell. Calibration of the TWIFOR involves an analog to the twining stem: a helically wrapped nylon string of 1 mm diameter. The TWIFOR gives stable output for the calibrating string, with mV output constant in time (Silk and Matista, 1997). The force produced by the calibrating string rapidly drops to zero when the masses are removed from the string. For the experiments shown in Fig. 4, the vine stem was tied to pieces of string at each end and wrapped in a helical form around the TWIFOR. The ends of the string were draped over pulleys, and a mass of 12 g was attached to one end. Progressively greater masses were added at the other end of the system, and millivolt output was recorded as a function of the applied mass.

**Stability of the vine in tension**—To test the validity of eq. 9 (predicting weights required for slipping of string and vine stems), nylon string or a vine segment with pieces of string slip knotted to each end were wrapped in a helical form around an aluminum pole. The ends of the nylon string were draped over pulleys, with the pulleys positioned to establish the pitch of the helix. A mass of 12 g was attached with a clothes hook to one end of the string, and an empty weighing bottle was attached to the other end. Water was poured into the weighing bottle until the string or vine began to slip on the pole or until the vine tore or broke. The mass required for slippage or breakage was measured on a standard precision balance (Mettler-Toledo Inc., Columbus, Ohio, USA).

**Instability of the vine in compression**—Small masses (2.5 g) were hung from a leaf axil near the top of the uppermost gyre of a twining vine of *Ipomoea purpurea*. Masses were added to the leaf axil until the helix collapsed. During the collapse of the helix, the coiled stem fell to the bottom of the support pole.

**Statistics**—Differences in sliding angle due to substrate, placement method, stem orientation, and presence of epidermal trichomes were analyzed with a general linear model from Minitab Statistical Software (Release 13 for Windows; Minitab Inc., State College, Pennsylvania, USA). Factors were assumed to be fixed and crossed. Analysis of variance was performed with an *F* test ( $P < 0.005$ ). Tabular data are shown as means  $\pm$  SD.

## RESULTS

**The stem of the twining vine has a high coefficient of friction**—Frictional interactions between stems and surfaces were characterized by determining the angle at which stem

TABLE 1. (A) Angle of slide in degrees and (B) coefficient of static friction ( $\mu$ ) for hairless and hairy stems of *Ipomoea purpurea* placed on surfaces with different textures. Four replicates were used in the hairy slide tests, six replicates for hairless stem segments sliding on wool and contact paper-covered surfaces, and 21 replicates for hairless stems sliding on wood. “Firmly placed” segments were pressed onto the plane to simulate effects of twining forces in situ; “gently placed” segments were placed lightly onto the plane.

	Hairless		Hairy	
	Firmly placed	Gently placed	Firmly placed	Gently placed
(A) Angle of slide				
Inverted				
Wood	53.1 $\pm$ 17.0	22.5 $\pm$ 6.7	34.0 $\pm$ 5.8	23.0 $\pm$ 0.7
Paper	57.7 $\pm$ 9.5	25.7 $\pm$ 3.6	28.2 $\pm$ 3.3	20.5 $\pm$ 2.1
Wool	75.8 $\pm$ 15.6	37.2 $\pm$ 4.4	>90	44.7 $\pm$ 0.8
Upright				
Wood	56.2 $\pm$ 19.9	22.1 $\pm$ 4.9	72.2 $\pm$ 19.7	33.8 $\pm$ 6.9
Paper	48.3 $\pm$ 10.0	24.7 $\pm$ 4.8	31.0 $\pm$ 4.2	23.2 $\pm$ 1.8
Wool	68.8 $\pm$ 20.8	36.5 $\pm$ 5.1	>90	>90
(B) Coefficient of static friction				
Inverted				
Wood	1.33	0.41	0.67	0.42
Paper	1.58	0.48	0.54	0.37
Wool	3.96	0.76	—	0.99
Upright				
Wood	1.50	0.41	3.12	0.67
Paper	1.12	0.42	0.60	0.43
Wool	2.58	0.59	—	—

segments began to slide off an inclined plane. The coefficient of static friction was calculated as the tangent of the angle of slip. Once the vine begins to move on its support, a continuing slide is related to the coefficient of kinetic friction, generally about 25% lower than the coefficient of static friction (e.g., Beer and Johnston, 1977).

Two *I. purpurea* phenotypes, having hairless stems and hairy stems, were found in plants grown from a single seed packet. The frictional properties of these two stem types were compared. The effects of smooth and rough surfaces and the effect of placing segments upside down were also determined. In both stem phenotypes, the angle of slip was highest on the rough (wool covered) surface (Silk et al., 2000; Table 1). In fact, for the hairy phenotype most segments did not slide at all on the woolen surface; rather, when the plane surface was inclined substantially past the vertical, the segments would fall off the plane (“undefined” coefficient of friction in Table 1). This suggests that the stem trichomes grip the wool fibers in some way. In the upright configuration, the angle of slip of the hairy phenotype was least on smooth paper, highest on wool, and intermediate for the bare wood surface. For the hairless phenotype, there was no significant difference between frictional interactions on the wood and paper surfaces.

An interesting difference in frictional properties was apparent between upright and inverted stem segments for the hairy stem phenotype. In general, the upright hairy segments had larger frictional interactions than the inverted hairy segments. Furthermore, the frictional interaction was greater for hairy than for hairless stems upright on the wood surface, but less for hairy stems than for hairless stems sliding upside down. This suggested that the stem trichomes act like miniature ratchets or the hairs on climbing skins of mountaineering skis.



In the “uphill” direction the trichomes engage the surface and facilitate climbing, while in the “downhill” direction the trichomes facilitate slipping.

In general, Table 1 shows that the gently placed vine stem has a coefficient of friction in the range reported for other materials on dry surfaces: metal on wood has  $\mu$  between 0.15 and 0.60, while wood on leather has  $\mu$  between 0.25 and 0.50 (Beer and Johnston, 1977). In contrast, the firmly placed upright vine stem, with  $\mu$  in the range 0.61–3.12, has an unusually high coefficient of friction. This shows that in nature a twining vine segment will have large frictional interactions with supporting structures.

**Relevance of the problem of a rope wrapped around a pole and generalization to helical forms**—Analysis of the mechanical interaction between the vine and its supporting pole indicates that the vine puts itself into tension as it “grabs” the pole (Silk and Hubbard, 1991). That is, the tendency of the stem to tighten its coil (make a helix of smaller radius and larger torsion than the helix on the supporting pole) produces a normal load (a force per unit length), acting toward the center of the pole, balanced by an axial tension in the vine (Fig. 2). Compressive loads tend to open the helix so that frictional interactions with the pole are eliminated (see Fig. 1 for another example). In contrast, added axial tension causes the vine to push harder on the pole, so that frictional interactions are facilitated. Thus twining stems should be stable in tension but weak in compression. Putz and Holbrook (1991) showed that the problem of a rope wrapped around a pole was relevant to tendrill twining. Here we extend their approach to assess the stability of the twining stem. We ask, what is the axial force that must be added to the vine to cause it to slip on its supporting pole?

To analyze the situation of a helically wrapped vine experiencing an additional axial load, a frictional term can be added to the basic equations of the force balance of a thin, elastic rod (Love, 1944). We assume a frictional load acts along the tangent. As is conventionally assumed, the frictional load is proportional to the normal load with the proportionality constant set by the coefficient of friction. The complete balance of forces is given by

$$F'_t - \kappa F_n + p_t = 0 \quad (1)$$

$$F'_n + \kappa F_t - \tau F_b + p_n = 0 \quad (2)$$

$$F'_b + \tau F_n + p_b = 0, \quad (3)$$

where  $F$  represents forces and  $p$  represents applied loads (force per unit length) along the unit vectors  $\mathbf{t}$ ,  $\mathbf{n}$ , and  $\mathbf{b}$  directed respectively along the tangent, normal, and binormal to the central helix; and the prime represents differentiation with respect to arc length along the helix (Fig. 2; Love, 1944; Silk and Hubbard, 1991).

As is conventional in the study of wire ropes (Costello, 1978), we will ignore the resultant normal and binormal forces. The frictional load acts along the tangent and thus helps prevent the vine from slipping.

$$p_t = \mu p_n. \quad (4)$$

From eq. 2, since  $F_b$  and  $F'_n$  are negligible

$$p_t = -\mu \kappa F_t. \quad (5)$$

Note that eqs. 4 and 5 imply that

$$p_n = -\kappa F_t, \quad (6)$$

which is the force balance in the frictionless analysis of Silk and Hubbard (1991). Equation 6 is in great contrast to the conventional force balances for either beams or helical springs. In cantilevers, for instance, curvature and torsion are assumed negligible; the normal load is integrated along the beam to give the shear force  $F_n$ ; the shear force is integrated along the beam to give the bending moment  $M_b$ ; and the axial force  $F_t$  sums to zero through the cross-section because the upper surface of the beam is in tension, while the lower surface is in compression (e.g., Beer and Johnston, 1977). For helical springs  $F_t$  and  $M_b$  are important, and  $p_n$  is usually neglected (Lin and Pisano, 1988). In contrast, eq. 6 states that the twining stem has a normal distributed load, acting along the line of contact between the stem and the pole, balanced by an internal, axial tensile force.

Substituting in eq. 1 we see

$$F'_t - \mu \kappa F_t = 0. \quad (7)$$

Integrating along  $s$ , the arc length following the central helix

$$\int F'_t/F_t ds = \int \mu \kappa ds. \quad (8)$$

Integrating, collecting terms, and rearranging we find

$$F_t = A e^{\mu \kappa \Delta s} \quad (9)$$

where  $A$ , the constant of integration, is the tension (an axial force) at the top of the vine.

Note that when the vine is wrapped in a circle, the curvature is  $1/r$ , where  $r$  is the radius of the pole; and the arc length  $\Delta s$  can be written  $r\Delta\theta$ . Equation 9 then is seen as a generalization of Euler's familiar formula for the force  $F_t$  that can be held by a smaller initial force  $F_i$  at one end of a rope wrapped around a pole

$$F_t = F_i e^{\mu \Delta\theta}, \quad (10)$$

where  $\Delta\theta$  is the total angle of wrap of the rope around the pole (Hibbeler, 1983; Putz and Holbrook, 1991). The contrast between eq. 9 and eq. 10 illuminates the difference between the botanical system and a rope. In a rope wrapped helically around a pole,  $A$  of eq. 9 would be the same as  $F_i$  of eq. 10.  $F_i$  is a force applied to one end of the helically wrapped rope, and  $F_t$  would be the force that would need to be added to the other end of the rope to make it slip. In a twining stem, initial contact with a vertical pole induces the growth gradients that cause the plant to cling to the pole. By developing growth gradients within the stem (and with form change impeded by the pole), the vine generates its own twining force., thus  $A$  is the twining force, an axial tension measurable with the calibrated TWIFOR in contact with a gyre near the top of the vine and without added masses (see Silk and Matista, 1997). In contrast, the rope can only remain in place with an externally applied force  $F_i$ . In both helical systems, the force at the apical end can support a larger mass (applied load or maturing vine stem with leaves) below the coiled region.

Equation 9 can be used as a model to find the importance of various factors in maintaining the stability of the twining habit. Let us use eq. 9 and consider the case of a vine wrapped around a wooden pole of 1.91 cm diameter (Fig. 2). Silk and Hubbard (1991) have tabulated values for  $\kappa$ ,  $\tau$ , and gyre arc lengths in *I. purpurea*. Typical values of  $\mu = 1.5$  (this paper),

TABLE 2. Predicted and actual masses required for slipping of nylon string or vine stem on supporting pole. Numbers in the last column represent mean values for ten vines  $\pm 1$  SD.  $A$  (initial twining force),  $\mu$  (coefficient of friction),  $\kappa$  (curvature), and  $\Delta s$  (arc length of helix on pole) are as explained in Results (in Empirical tests of equation for slipping).

Type of loading	$A$ (g)	$\mu$	$\kappa$ (cm <sup>-1</sup> )	$\Delta s$ (cm)	Predicted mass for slip (g)	Actual mass for slip (g)
Vine with twining force	30	1.5	0.25	12	2700	
Vine with twining force and large friction	30	3	0.25	12	243 092	
Vine with twining force and two gyres	30	1.5	0.25	24	243 092	
Vine with small friction and small twining force	10	0.41	0.25	12	34	
Nylon string with 12 g on Al pole	12	0.49	0.33	7.8	42	45 $\pm$ 4
String with 12 g on Al pole, two gyres	12	0.49	0.33	15.6	149	142 $\pm$ 15
Vine with 12 g on Al pole	12	0.93	0.27	8.6	96	165 $\pm$ 40
Vine with 12 g on Al pole, two gyres	12	0.93	0.27	17.2	701	638 $\pm$ 238

and  $\kappa = 0.25 \text{ cm}^{-1}$  can be used with the arc length of the vine around the pole  $s = 12 \text{ cm}$ . If we assume a twining force produced by the vine in the typical range, equivalent to 30 g of tension (Scher et al., 2001), then eq. 9 predicts that more than 2700 g would need to be applied before the vine would begin to slip down the pole (Table 2). Note that the value of  $F_i$  from eq. 9 is very sensitive to both the coefficient of friction and the length of the vine in contact with the pole. If hairy stems with  $\mu = 3$  are used, or if the vine has two full gyres wrapped around the pole ( $s = 24 \text{ cm}$ ), then the mass needed to make the vine slip would be greater than 243 kg! At the other extreme, a vine lightly resting on a smooth pole (corresponding to our gentle placement,  $\mu = 0.41$ ), and before the development of a large twining force ( $A = 10 \text{ g}$ ,  $s = 12 \text{ cm}$ ) might slip downward if only 34 g were applied to the bottom of the vine.

**Empirical test of the assumption that the normal load is proportional to applied axial tension**—The model assumes that the normal load exerted by a vine on the pole is proportional to applied axial tension, eq. 6. This assumption was tested with our device to measure twining loads, the TWIFOR (see Material and Methods). The vine was wrapped helically

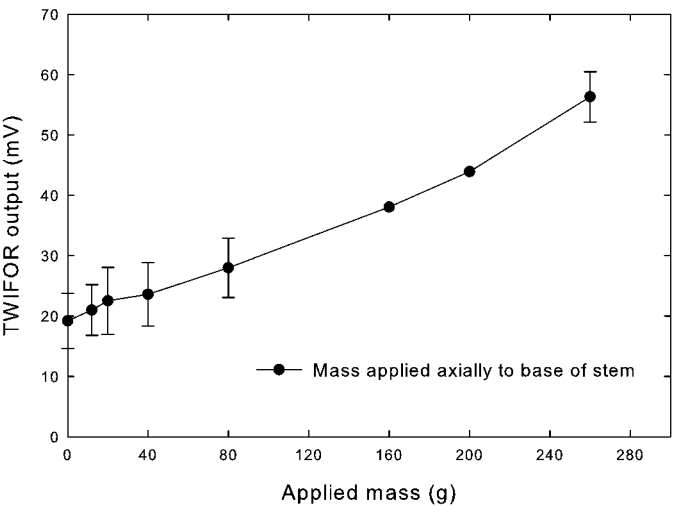


Fig. 4. Normal load vs. applied tension. Stems were wrapped around the TWIFOR load-measuring device and put into axial tension by adding nylon strings at each end, draping the strings over pulleys and adding masses to the strings. Stems in tension exerted progressively greater normal loads with greater applied tension. The force curve represents the mean of 10 vines. Bars indicate 1 SD.

around the split pole, and masses were added to provide increasing amounts of axial tension. The normal load was seen to increase with added mass (Fig. 4). The best regression of load with mass is linear with  $r^2 = 0.98$ . The model also predicts that the vine will not slip on a rough surface until hundreds of grams are pulling axially on the vine. On the TWIFOR, vines tore or broke when more than 800 g were applied, and slipping was never observed. This supported the hypothesis that the vine would not be likely to slip in tension. However, because the force required for slipping could not be measured, this approach fails to test the major prediction of eq. 9.

**Empirical tests of equation for stem slipping**—To test eq. 9 we used a smooth aluminum pole to reduce the coefficient of friction. We measured slipping first in nylon string and then in uncoiled lengths of *I. purpurea* vine so that  $A = F_i$  would be only the applied load of 12 g. Slip tests gave  $\mu = 0.91$  for the vine and  $\mu = 0.48$  for the string sliding on an aluminum plate. Observed values of the mass required to cause slipping were similar to the predicted values for masses in the range between 30–700 g (Table 2; Fig. 5). Larger masses tore the vine before causing any slippage. This supports the hypothesis that in situ the vine twining on a rough support would usually break before it slips in tension. The twining force that develops as the top of the vine hugs the pole is amplified exponentially with the coefficient of friction and the length of the helical contact.

**The mechanics of the twining habit includes an irreversible component of tension in response to an applied load**—The mechanical behavior of the axially loaded vine was similar in some ways to that of the nylon string. The greater stability of the vine in tension is explainable by the higher friction of the vine (compared to the nylon string) on the pole. A less explicable difference between vine and calibrating string is the irreversibility of the normal load exerted by the vine. As the masses were added to the vine, the output of the TWIFOR increased (Fig. 4). This was similar to the response for a calibrating string. However, for nylon string, the output from the TWIFOR falls immediately to zero loading when the mass is removed from the string. In contrast, for the vine much of the force remains after the load is removed. Typically 80% of the force output from a 260-g load remained after the load was removed from the base of the plant. Only when the vine was snapped against the pole so that the geometry of the vine/pole interaction was disturbed did the TWIFOR return to the output for zero loading. This suggests a viscous or plastic component to the force exerted by the vine loaded in tension. It also means

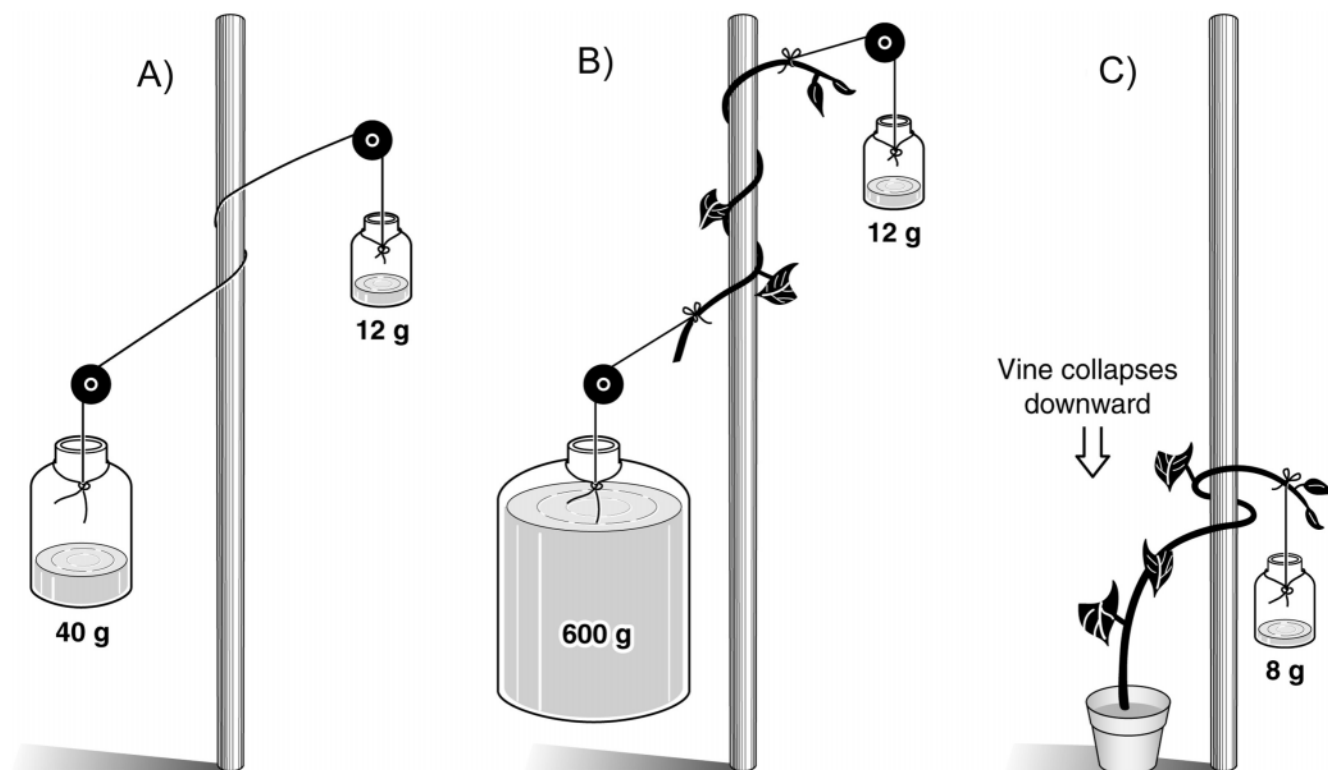


Fig. 5. Tests of eq. 9 to predict axial force required for slippage on a pole. A nylon string, or a noncoiled vine stem attached to two lengths of nylon string, was wrapped in a helical form on an aluminum pole and draped over pulleys (black circles). A mass of 12 g was applied at one end of the system, and water was poured into a weighing bottle until the string or vine slipped on the supporting pole. Predicted and actual masses causing slipping are shown in Table 2. (A) Nylon string wrapped in a single helical gyre. (B) *Ipomoea purpurea* vine wrapped in two helical gyres. (C) Vine subjected to a force with a large compressive component applied near the apex.

that the twining force oscillations observed during growth of vines in situ (Matista and Silk, 1997; Scher et al., 2001) must involve repeated, active opening and closing of the helix over time.

**The twining vine is weak in compression**—To demonstrate the weakness of the twining habit in compression, we hung progressively heavier masses, in increments of 2.5 g, from the leaf axil located at the apical end of the uppermost gyre (Fig. 5, right). The helical form of the vine remained stable until a sudden collapse occurred as the helical gyres were compressed. Of the sample of 10 vines, one collapsed when 2.5 g was applied and two remained stable until 15 g had been applied. The average mass producing compressive failure was  $8.25 \pm 4.25$  g. However, when the masses were applied below the uppermost gyre, the helix did not collapse. This is because the upper gyres were put into tension by the mass hanging below them, and the tendency to slip was resisted by the mechanism described above for the vine in tension.

Once the vine grows above a supporting structure, the unsupported part of the stem exerts a force and bending moment and tends to destabilize the older helical structure on the pole. Collapse of an existing helix is not observed, however. Instead, after the shoot apex reaches the end of a supporting pole the vine uncoils: the wavelengths of the upper gyres increase; the vine no longer touches the pole; and a reversion to an erect searching habit is observed.

During twining the apical stem segment remains uncoiled and is displaced during growth in an undulating, circular path.

Unlike the searching habit that occurs in the absence of the support pole, the radius of the path is small, so the length of the unsupported portion of the stem remains short. In our *I. purpurea* stems twining on 6.2 mm poles, the unsupported stem segment is 2–4 cm in length and weighs 15–30 mg, well below the 8000 mg load required to collapse the helix; thus the twining habit appears to be engineered to avoid compressive loads.

## DISCUSSION

Helical growth has been the subject of recent interest, as molecular and cellular determinants have been discovered for handedness of twisting growth forms in roots of *Arabidopsis* (Thitamadee et al., 2002; Yuen et al., 2003). In classical literature, the growth of twining stems has fascinated scientists since the time of Darwin (1876). Twining plants grow in a searching mode characterized by sweeping circular or elliptical movement of the apex. After the stem encounters a suitable support the growth pattern changes (see Baillaud, 1962, for a review of the historical literature). A growth tensor in a natural coordinate system can be used to find the intrastem pattern of expansion and twisting that produces the well-known corkscrewlike shape of the twining vine (Silk, 1989). The shift from selfsupporting to a supported growth habit in woody vines has been shown to involve an increase in stem flexibility resulting from both a smaller stem diameter and a more flexible wood type (Gartner, 1991; Gallenmueller et al., 2004). Furthermore, an anatomical basis for the variation in material

mechanical properties has been determined (Rowe and Speck, 1996; Gallenmueller et al., 2004). Recently the twining habit has been characterized in terms of wood chemistry and microfibril angle (Hoffmann et al., 2003), thus there is historical and recent interest in the mechanical properties of vine stems. Nevertheless, the literature contains little analysis of the mechanical function of the twining habit.

In nature, some species of twining stems, including *I. purpurea*, appear to have mostly continuous contact between stem and support. Other species, such as *Phaseolus* spp., touch the support infrequently and appear to be more selfsupporting. A complete analysis of the mechanics of the twining habit would involve modeling the range of frictional interactions observed in nature, from species that twine smoothly with continuous contact to species with intermittent contact and a more self-supporting habit. Theoretical treatments of the dynamics of helical strips have identified instabilities that might be relevant to the problem of optimum mechanical design for those vines with intermittent contact (Goriely and Shipman, 2000; Goriely et al., 2001).

In this study, we put the vine into tension and thereby ensured continuous contact. The results of this manipulation demonstrate that in nature, gravitational loads (unless they are applied very near the vine apex) will stabilize the twining habit if the vine is wrapped around the pole. It is also instructive to think of the frictional interaction as a mechanism by which a small apical stem portion can hold up a large mass of older stem. This explains the observation that a loosely coiled, heavy, older vine segment can simultaneously stabilize and be held up by one or two tightly wound younger coils (Putz and Holbrook, 1991).

The twining vine, unstable in compression and stable in tension, is similar to structures made of rope or cloth, such as clotheslines, tents, and "finger traps." Indeed, many plant structures are stabilized by tensile forces (Vogel, 1988; Niklas, 1992; Moulia, 2001). For the twining habit, an underlying mystery is how a vertical pole of a particular radius induces the tendency to produce stem coils of a particular "potential" radius (observable when the stem is removed from its support). Because the potential coil radius is smaller than the pole radius, contact with the supporting pole is assured. As shown in this paper, the frictional interactions arising from the contact produce stability under tensional forces and allow a few coils near the top of the vine to support a large mass of maturing stem against the pull of gravity.

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