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On the Strength of Herbaceous Vascular Plant Stems

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During the past 120 years researchers have tried to provide an understanding of the relationship between the arrangement of stiffening tissue in the cross-section of plant stems and their mechanical integrity. The mechanical analysis of vertical stems of self-supporting plants has traditionally been concerned with issues involving global and local stability of the stem, and with stresses developed due to wind loads. Plant stem tissue, considered as a material, is both heterogeneous and highly anisotropic, and this must be reflected in any characterization of its mechanical behaviour. This fact strongly influences the type of failure criterion which should be applied for compressive failure of the stem subjected to loads causing bending. It is shown, here, that applying modern ideas as to the appropriate criteria for compressive failure of fibre-reinforced composite materials can influence how we assess the efficacy of various stelar arrangements concerning their ability to fulfill their mechanical function. Specifically, it is demonstrated that peripheral arrangements of supporting tissue are, in some circumstances, less advantageous than more uniform distributions of this tissue.

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Key words: Plant stems, stem bending, compressive strength, stelar types.

INTRODUCTION

Mechanical analysis of the strength, stiffness and stability of plant stems has its foundations in the seminal work of Schwendener (1874). He modelled plant stems as vertical beams subjected to side loads (mainly wind). The basic ideas of Schwendener were developed and put on a firm analytical basis by Rasdorsky (1926, 1928). The only stem tissue taken into account in these analyses was that of the vascular bundles and other relatively stiff cellulosic material in the stem. Soft (e.g. parenchymatous) tissue, in which the fibrous stiff tissue is embedded, was considered to make a negligible contribution to the mechanical integrity of the stem, except insofar as it serves to fix the supporting tissue in its proper place. When considering stem strength, it was assumed that there is some maximum limiting stress, σ_{f-fail} , that the *stiff tissue* can tolerate. Strength of materials theory was used to calculate the bending moment, M_{max} , which the stem could bear, according to the relationship

$$\sigma_{f-fail} = \frac{M_{max}c}{I_f} \quad (1)$$

Here c is the distance from the centre of the stem to the outermost radius at which stiff tissue is extant, and I_f is the second moment of area of the stiff tissue areas which occur in the stem cross-section. Since we will be considering only overall stem cross-sections, for which second moments of area are equal with respect to all axes passing through the centre of the stem, it is convenient to define I_f mathematically as

$$I_f = \frac{1}{2} \int \rho^2 dA, \quad (2)$$

where ρ is the radial distance from the stem axis, and the integration is over all areas of stiff tissue, i.e. the contribution of an element of stiff tissue area to I_f is weighted by the square of its distance from the axis. (The word 'axis' used throughout this paper is not meant in the botanical sense, but rather refers to a theoretical longitudinal centreline passing through the cross-section of a rod-like element.) It is common to denote a section modulus by $S = I_f/c$; thus this section modulus S , is a measure of the relative merit in resisting stress of a particular stelar arrangement. For example, consider the arrangements shown in Fig. 1; each arrangement has 24 identical 'vascular bundles'. One can easily calculate that the second moment of area of (A) is very nearly twice that of (B)—because more of the bundles are further from the stem axis; and since the distance to the *outermost* stiff tissue in the two arrangements shown is the same, it is concluded from eqn (1) that arrangement (A) is twice as good as (B). The very simple, and appealing, conclusion is that it is always preferable to have stiff tissue placed as far from the stem axis as possible. The tradition begun by Schwendener (1874) has been carried through to

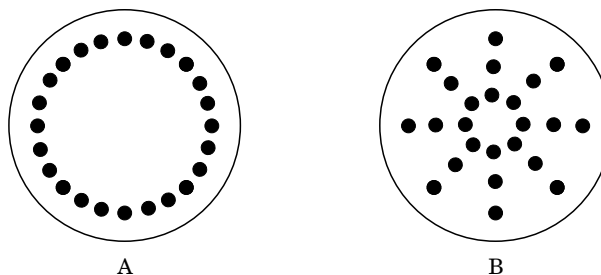


FIG. 1. Archetypal stelar arrangements. A, Peripheral bundles; B, disperse bundles.

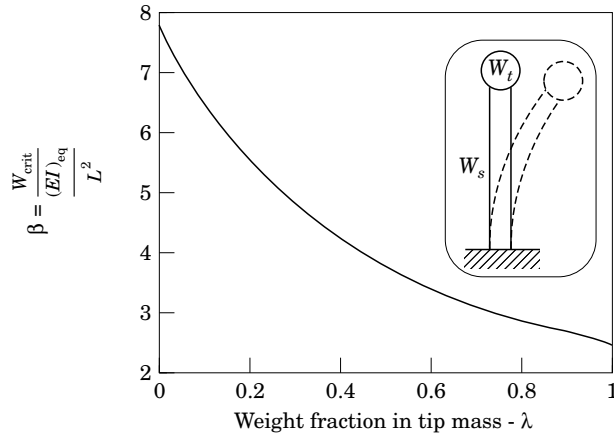


FIG. 2. Nondimensionalized total critical weight as a function of weight fraction, λ , at the tip. W_s , weight uniformly distributed in 'stem'; W_t ,

$$\text{weight at tip; } \lambda = \frac{W_t}{W_t + W_s}.$$

this day (see, for example, Haberlandt, 1914; Rasdorsky, 1928; Strasburger, 1965; Speck and Vogellehner, 1988; Speck, Spatz and Vogellehner, 1990). In this paper we argue that it is necessary to reconsider the above line of thought. We will show that, from the viewpoint of the mechanical integrity of the stem when subjected to bending, a disperse arrangement of stiff tissue (as shown schematically in Fig. 1B) may be advantageous. In order to test this hypothesis, it is sufficient to idealize a stem cross-section as being composed of two tissue types only: one stiff in fibrous form, and a second constituting a homogeneous matrix of soft material. It is known that failure of herbaceous plant stems in bending is precipitated by damage on the compression (concave) side of the stem (Niklas, 1992). We will have recourse to current understanding of the compressive failure mechanisms in highly anisotropic materials. Such compressive failure is characterized by material instability: if the high anisotropy is due to the presence of reinforcing fibres, it is known that the soft matrix in which the fibre is embedded is dominant in determining compressive strength; fibre strength in compression is not relevant, and indeed even the precise elastic properties of the fibre are of only secondary importance. It is possible to adjust the basic philosophy pioneered by Schwendener (1874), by simply taking the matrix into account in the calculation; but this would not be sufficient to reflect the influence of the matrix as described above. Such an approach would only result in eqn (1) being replaced by

$$\sigma_{t-fail} = \frac{M_{max}c}{I_f + \frac{E_m}{E_f}I_m} \quad (3)$$

where I_m is the total second moment of soft tissue, and E_m and E_f are the Young's moduli in the direction of the stem axis of the matrix and fibres, respectively. It is known that the elastic modulus of stiff tissue in herbaceous plant stems is at least two orders of magnitude greater than that of the

soft tissue (Niklas, 1993). Thus, it is clear from eqn (3) that, even for quite small volume fractions of fibres, no qualitative change in the value of M_{max} is to be expected.

However, it must be emphasized that the situation is not as simple as would appear from the above discussion. Failure of plant stems is clearly not only precipitated by strength criteria in compression as the result of a bending moment. Another extremely important consideration is the overall stability of the plant considered as a columnar structure (Niklas, 1992, 1995). If we idealize a plant as a column of uniform cross-section surmounted by a tip mass (Fig. 2, inset), then it is known that such a structure will become elastically unstable (buckle) at some critical total weight. Denote the total weight of the plant by W , and the fraction of this total weight contained in the tip mass by λ . Then, $W_t = \lambda W$ is the tip weight, and $W_s = (1 - \lambda)W$ is the weight of the stem, which is assumed to be equally distributed along its length. The total critical weight of the plant at which buckling will occur is given by

$$W_{crit} = \beta \frac{(EI)_{eq}}{L^2} \quad (4)$$

(Timoshenko and Gere, 1961). Here L is the length of the stem, $(EI)_{eq}$ is the effective flexural rigidity of the stem given by

$$(EI)_{eq} = E_m I_m + E_f I_f, \quad (5)$$

and β is a constant varying between 2.47, when the weight of the stem can be considered negligible compared to the weight of the tip mass ($\lambda = 1$), and 7.84, when the weight of the tip mass is negligible compared to the weight of the stem ($\lambda = 0$). The case for all the mass being uniformly distributed along the stem ($\lambda = 0$) was solved and applied to the stability of trees by Greenhill (1881); the other extreme ($\lambda = 1$) is the classical result found more than a century earlier by Euler. In Fig. 2 we show the values of β as a function of the fraction of the plant weight contained in the tip. The flexural rigidity [eqn (5)] is generally perceived as a measure of the self-supporting ability of a stem (e.g. Rowe, Speck and Galtier, 1993). Now considering eqn (5), and taking into account that $E_f \gg E_m$, it is immediately clear that in order to maximize the total critical weight of the plant it is always better to place the stiff tissue as far from the stem centre as possible, i.e. the arrangement in Fig. 1A is preferable to that in Fig. 1B. Note that maximizing $(EI)_{eq}$ is tantamount to maximizing the section modulus for the stiff tissue alone, since we are holding constant the maximum distance from stem centre to a stiff fibre. So as far as *overall plant stability* is concerned, the conclusion based on the traditional analysis is valid. One is led to the conclusion that if stability is the limiting factor, then the traditional line of thinking is valid. If stem strength (i.e. resistance to side loads) is the limiting factor then the considerations which we will outline in the next section dominate: a disperse arrangement of fibrous material is advantageous. Thus depending on plant architecture, environmental conditions, etc. the arrangement in Fig. 1A or the arrangement in Fig. 1B could be preferable.

Up to now we have neglected considerations of turgor pressure in plant cells, which is known to contribute

considerably to the structural integrity for many plants. The simplest approach to taking into account turgor pressure is that of Dierks and Hafner (1987). Here the entire stem is simply envisioned as a single thin-walled cylindrical pressure vessel. The inner stem tissue is seen as producing some 'pressure', p , equal to the cellular turgor pressure, which bears on the 'thin walls' (epidermis and collenchyma) of the pressurized container. This pressure produces a longitudinal tensile stress in the cylinder walls before any bending moment is applied. It is then assumed that the tube walls can tolerate no compressive stress whatsoever, and one calculates the moment exactly required to negate the initial tensile stress. Denote by t and r the wall thickness and radius of the tube to the midpoint of the wall. Then if $t \ll r$ it is found that this moment is

$$M_{\max} = \frac{\pi}{2} r^3 p. \quad (6)$$

Such a theory sees the precise stellar geometry, the thickness of the thin walls and, indeed, the material properties, as not influencing the capability of the stem to withstand the moment in any way. On the other hand, the generally-accepted view is that one must perceive the individual cells as small pressure vessels which themselves contain the turgor pressure (Falk, Hertz and Virgin, 1958; Hettiaratchi and O'Callaghan, 1978; Niklas, 1989). The tissue is then seen as a *material* whose *dimensions* and *stiffness* are influenced by the turgor pressure. In other words, the turgor pressure in individual cells, which causes stress and strain in the *cell wall*, does not result in any stress in a tissue sample composed of a large number of statistically similar cells arranged in a statistically homogeneous or periodic fashion. This is so since the term 'stress', as used here, is defined based on averaging over a representative volume, elements whose dimensions are large compared to that of a single cell. Several investigators have proposed models to explain how turgor pressure influences the dilatation and stiffness of the soft tissue (Falk, Hertz and Virgin, 1958; Niklas, 1989; Vincent and Jeronimidis, 1991), and have performed experiments to determine turgor pressure–property relationships (Parrish, Leopold and Hanna, 1982; Niklas and O'Rourke, 1987; Niklas, 1991; Vincent and Jeronimidis, 1991). This generally-accepted viewpoint, which we will accept here, does imply that the outer tissue of a plant stem can be advantageously pre-stressed due to the turgor pressure, but this pre-stressing is due to the expansion of the turgid soft tissue *behaving as a material*. Indeed it is well known that turgor pressure results in pre-stress. This is simply demonstrated by slicing a fresh stem longitudinally into quarters; each quarter will curve outward (Bower, 1956). The implication is that the outermost tissue was in tension; then, since under bending it is the compressive stress on the concave side of the stem which precipitates failure, the pre-stressing of the stem serves as a 'reserve' of strength. Such behaviour is not explained by the model represented by eqn (6); but pre-stressing in plant stems also results from growth stresses (Kutschera, 1989, 1995). Indeed, it is not clear that for a given turgor pressure one can distinguish semantically between pre-stress due to growth

stresses as opposed to that due to turgor pressure; clearly the two are inextricably intertwined.

The 'turgor pressure-growth-residual stress' triangle has a long history (see Peters and Tomos (1996) for a review). For our purposes, the situation is best capsulized in the following quotation from Sachs (1882): 'Growth itself must cause states of tension in the layers of a cell-wall or of the tissue of which an organ is composed, if the layers, although firmly united to one another, grow unequally ... Since the growth of every organized structure, such as a cell-wall, can only proceed so long as it is permeated with water, and since moreover the growth of the entire cell requires it to be in a turgid condition, and this condition itself has an influence on growth, it is extremely difficult to decide how far each of these phenomena is the cause of the other.' We make no attempt to distinguish 'cause and effect'. For our purposes, all we need is the recognition that for a given turgor pressure some given distribution of tissue stress exists in a stem. Now, considering the beneficial residual stresses that may exist in a stem at a given turgor pressure, whatever might cause them, we will be able to argue that stellar arrangements as in Fig. 1B are less sensitive in terms of stem strength to changes in turgor pressure than are arrangements in Fig. 1A. We will conclude that the strength of a plant stem with dispersed stiff tissue (Fig. 1B) is apparently greater than when the stiff tissue is concentrated near the periphery (Fig. 1A), although global stability is improved in the latter case.

Before we consider the nature of compressive failure of stems in bending we must consider one more class of failure mechanisms which further complicates the situation. Our analysis will be based on the classical theory of beam bending. This is also the basis of the traditional analyses; it is only the material failure criterion which we will reconsider. The classical theory assumes that the beam cross-section does not change shape during the bending process. This assumption can break down within either of two basic scenarios. The first is called local bifurcation buckling—here the behaviour of a tube in bending is linear until at some value of bending moment there is a sudden shape change of the tube wall (Seide and Weingarten, 1961). The second scenario is non-linear. It is known that when a thin-walled tube is bent its cross-section ovalizes. The result is that the relationship between the applied bending moment and the resulting longitudinal radius of curvature of the tube is not linear. At some critical moment the tube cross-section suddenly collapses inward. Historically, this latter type of local buckling has been the one considered for botanical structures. The relevance of the phenomenon to the integrity of hollow plant stems was already noted by Schwendener (1874). The basic theory for this type of failure was developed by Brazier (1927) and generalized for the type of tissue properties which are encountered in hollow plant stems by Schulgasser and Witztum (1992). Recently, this phenomenon has also been extensively studied numerically (Spatz, Speck and Vogellehner, 1990; Spatz and Speck, 1994). However, even in a non-hollow element ovalization can occur if the constituting tissue is highly anisotropic. Such possible ovalization is considered by Haberlandt (1914) and was observed by Mergenthaler-Pauler (1952) for *Cyclamen persicum* and *Primula officinalis*.

Niklas (1992) has discussed the possible importance of this failure mode. Schulgasser and Witzum (1992) found the critical Brazier buckling moment for bending of a tube with a soft core [the core-rind construction of many stems (Niklas, 1992)]. Gibson *et al.* (1995) and Karam and Gibson (1995) considered this case for both Brazier and bifurcation buckling. We will not take this possible instability at the *structural* level of the stem into account here; rather we consider the instability under compressive stress at the *material* (microstructural) level.

MATERIAL COMPRESSIVE FAILURE

With the advent of modern composite materials composed of aligned, strong, stiff, parallel fibres in a relatively soft matrix (generally glass, graphite or boron fibres in epoxy or polyester matrices) in the early 1960s, it was quickly realized that the inherent weakness of these materials under compression applied in the direction parallel to the fibres was a serious problem in some applications. It was observed that the dominant compressive failure mode was localized compressive buckling, or kinking. In early papers by Rosen (1965) and Schuerch (1966), two possible elastic fibre buckling modes were identified and considered. These were denoted as the shear (or antisymmetric) and the extension (or symmetric or transverse) modes, and are illustrated in Fig. 3A and B, respectively. The analyses of both Rosen and Schuerch indicated that for the shear mode the critical compressive stress is given by

$$\sigma_{\text{comp}}|_{\text{crit}} = G_{\text{eff}}, \quad (7)$$

where G_{eff} is the effective axial shear modulus of the composite. The solutions of the two authors for the extension mode differ slightly, but both involve roughly similar relationships involving the Young's moduli of both the fibres and the matrix. For a given volume fraction of fibres, both analyses indicated that the shear (antisymmetric) mode becomes dominant as the ratio of fibre to matrix stiffness increases.

In the intervening years, a great volume of experimental and theoretical work has appeared, which has generally

indicated that while the critical compressive stress is not exactly predicted by eqn (7), it is nevertheless *directly proportional* to the effective shear modulus of the composite material. Much of this work is referenced in Guynn, Ochoa and Bradley (1992), and in Schultheisz and Waas (1996). In reality, it was found in experiments that failure in real materials usually shows itself by single or multiple kink bands which progress across the width of a material sample subjected to uniform compression (Kyriakides *et al.*, 1995). The failure pattern observed in the compression of wood in the longitudinal direction is similar (Kollmann and Cote, 1968).

Now let us consider eqn (7) more closely. It has been found experimentally that this equation generally overestimates the actual compressive strength by a factor of between 2 and 5 (Budiansky and Fleck, 1993). When only the matrix properties were varied in a series of tests it was found that critical compressive stress is proportional—but not equal—to the effective shear modulus (Piggot and Harris, 1980; Piggot, 1981; Budiansky and Fleck, 1993). Another early set of experiments which strikingly illustrates the situation was performed by Lager and June (1969). They tested the longitudinal compressive behaviour for various volume fractions of aligned boron fibres in an epoxy matrix. It was found that when fibre volume fraction is changed from 10 to 50%, the *compressive strength* is approximately only doubled; this corresponds to the increase in the axial shear modulus. The *tensile strength*, on the other hand, would increase by almost a factor of five over this range, since the tensile strength is dominated by the quantity of very stiff and strong fibres. Thus we conclude that, for this type of material, the compressive strength does not lie principally in the *strength of the fibres*; it lies in the *axial shear modulus of the composite* which, for other than very high volume fractions of fibres is mainly controlled by the shear properties of the matrix material and only secondarily by the elastic (but not strength) properties of the fibre itself.

For practical applications, eqn (7) should be modified by adding a constant of proportionality

$$\sigma_{\text{comp}}|_{\text{crit}} = C G_{\text{eff}}. \quad (8)$$

Many theoretical models have been invoked to explain the discrepancy inherent in the constant of proportionality being other than one; usually these involve considering initial pre-existing imperfections in the alignment of the fibres, partial debonding of the fibres, and/or non-linearities, including plastic deformation, in the behaviour of the matrix. Analyses have also been performed attacking the problem of predicting critical compressive stress of highly anisotropic materials without considering the microstructure of the material. Christensen (1994) provided an asymptotic solution for the limit of large ratios between the longitudinal Young's modulus and the other elastic moduli; again the critical compressive stress was found to equal the shear modulus. A more general analysis was carried out for the case of instabilities originating at a free surface by deBotton and Schulgasser (1996) which also revealed that as the anisotropy becomes large the critical compressive stress approaches the shear modulus. A similar conclusion is

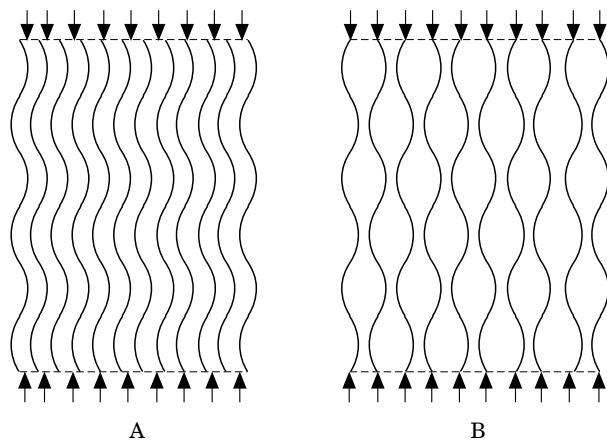


FIG. 3. Buckling modes of a fibre reinforced composite subjected to longitudinal compression. A, Shear (antisymmetric) mode; B, extension (symmetric, transverse) mode.

arrived at for the limit of high anisotropy by Geynomat, Müller and Triantafyllidis (1993), who considered very general cases including material non-linearity. We are inevitably led to the conclusion that a reasonable criterion for material failure in compression is given by eqn (8).

ANALYSIS AND RESULTS

We now wish to examine various stelar types (arrangements of stiff tissue) in order to show that since compressive failure is due to an instability at a compressive stress proportional to the shear modulus for a highly anisotropic material, a dispersed arrangement of stiff tissue is advantageous. Many different arrangements of stiff tissue distribution are possible. The wide spectrum of known configurations is apparent when we consider the range of stelar classes and subclasses defined by Schmid (1982). Since our purpose is only to challenge the determination, based on a traditional type of analysis, that it is necessarily preferable to place stiff tissue as far from the stem axis as possible, it is sufficient for us to choose one family of counter-examples which can be handled analytically. We choose as our benchmark system that shown in Fig. 4.

Fig. 4A shows stiff tissue homogeneously dispersed in a soft matrix throughout the stem cross-section; in Fig. 4B the concentration of tissue is greater in an annular region between the outer diameter d_o and the intermediate diameter d_i than in the central 'core' of diameter d_i . The volume fraction of stiff material when distributed as in Fig. 4A will be denoted by v_f ; we denote by v_i and v_o the volume fractions in the inner core and outer region, respectively, for the distribution shown in Fig. 4B. The total stiff tissue in the two cases will be kept equal. Only the case $v_o > v_i$ is of interest. Thus, the fraction of the total stiff tissue in the core, f_i , satisfies the relationships

$$f_i = \frac{v_i d_i^2}{v_f d_o^2}, \quad 1 - f_i = \frac{v_o}{v_f} \left(1 - \frac{d_i^2}{d_o^2}\right). \quad (9)$$

We will first consider the case when there are no fibres

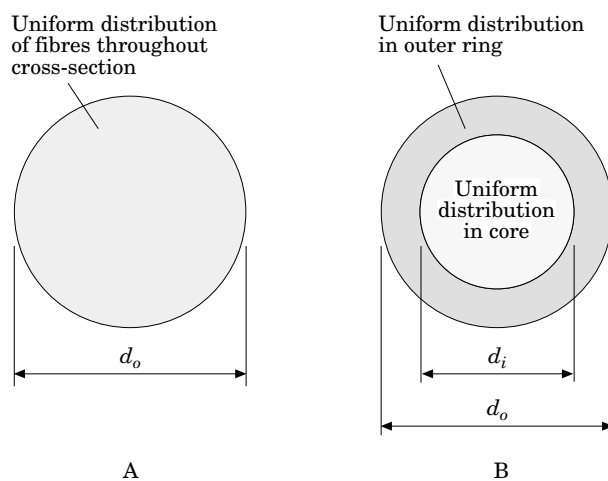


FIG. 4. Benchmark system of distribution of stiff tissue in cross-section. A, Homogeneous distribution; B, stiff tissue concentration is greater in an annular region (ring) than in the core.

whatsoever in the core region (i.e. $f_i = 0$ and $v_i = 0$), and examine the performance of Fig. 4B with respect to Fig. 4A for various ratios of d_i/d_o ; as this ratio increases the concentration of stiff material in the outer ring increases. Note that Fig. 4A is really only the degenerate case of Fig. 4B when d_i is taken as 0. Clearly, according to a traditional analysis the arrangement shown in Fig. 4B is always preferable to Fig. 4A. Afterwards we will consider the case when the total stiff tissue volume fraction v_f and the intermediate diameter d_i are held constant but the relative ratio $v_o:v_i$ is changed.

The benchmark system could model quite well stelar types of the sort designated 'eustele *sensu stricto*' by Schmid (1982). In some stems with this classification, the stiff tissue is more or less uniformly dispersed in the stem cross-section (e.g. *Cyperus alternifolius* (umbrella sedge), *Ferula communis*). In others there is a more or less continuous gradation of stiff tissue concentration [e.g. *Zea mays* (corn), *Saccharum officinarum* (sugar cane)] with the stiff tissue being relatively sparse near the stem axis and more crowded towards the periphery; the steepness of this gradation varies from species to species. This latter distribution of vascular bundles is also evident in palm tree stems (Waterhouse and Quinn, 1978; Rich, 1987). We do not deny the fact that whatever the stelar category, there is always a layer of stiff tissue at the outer circumference of the stem, which may include the epidermis and other stiff tissue. This layer sometimes constitutes only a small fraction of the total stiff tissue in the stem cross-section but, on the other hand, it is often quite thick and thus of great significance. But we emphasize that since our main purpose is to test the general validity of the traditional hypothesis in assessing the contribution of stele organization to the stem strength, we will neglect this stiff layer. The benchmark system of Fig. 4 can reasonably suggest how merit values can be attached to the various gradations. In order to make quantitative comparisons, we have chosen the following parameters for our benchmark system in all graphical/numerical presentations of the results: (1) the volume fraction of stiff fibrous material is 0.05 (i.e. 5%); (2) the ratio of the axial Young's modulus of the stiff material to that of the soft matricial material is 200:1. The stiffness ratio is a median number based on Niklas (1993). We also assume that each material is itself isotropic. For the matrix material this is probably a reasonable approximation as far as mechanical behaviour; for the stiff material less so. However, the stiff fibrous material itself is most certainly anisotropic in the sense that its axial shear modulus is less than that which it would be were it isotropic; thus the effect we wish to illustrate will be magnified even further, especially when considering high volume fractions of fibres in which case the fibre shear modulus appreciably influences the effective shear modulus of the material. Finally we will choose the Poisson's ratios of both materials as 0.3; but the results to be presented are insensitive to the precise choice of this parameter. The material system which we have chosen can be shown to produce a ratio of longitudinal Young's modulus to axial shear modulus equal to about 25:1 for tissue in which the stiff phase is uniformly distributed in the cross-section (see equations below). This is about the ratio to be expected

globally in a herbaceous stem (Ennos, 1993; O'Dogherty *et al.*, 1995).

We now calculate the ability of the arrangement in Fig. 4B to withstand bending stress as a function of d_i for a given volume fraction of stiff fibres v_f , if they were distributed uniformly as in Fig. 4A. We will be interested in the axial normal stress in the annular region. Therefore the equivalent second moment for the section is given by

$$I_{eq} = \frac{\pi}{64} \left(d_o^4 - d_i^4 + \frac{E_i}{E_o} d_i^4 \right), \quad (10)$$

where E_i and E_o are the effective axial Young's moduli in the core and annular regions, respectively. We can calculate E_i and E_o from the expressions (Hashin, 1983)

$$E_i = v_i E_f + (1 - v_i) E_m, \quad E_o = v_o E_f + (1 - v_o) E_m. \quad (11)$$

According to the arguments in the previous section, the critical compressive stress in the annular region is given by [eqn (8)]

$$\sigma_o|_{crit} = C G_o, \quad (12)$$

where G_o is the effective axial shear modulus in the annular region. G_o is well approximated by

$$G_o = G_m + \frac{2v_o(G_f - G_m)G_m}{2G_m + (1 - v_o)(G_f - G_m)}, \quad (13)$$

and since the fibres and matrix are both taken to be individually isotropic, the shear moduli are given by

$$G_m = \frac{E_m}{2(1 + \nu)}, \quad G_f = \frac{E_f}{2(1 + \nu)}, \quad (14)$$

where ν is the common Poisson's ratio. Equation (13) is the lower bound for the effective modulus as given by the Hashin bounds (Hashin, 1965) and is known to be a very accurate representation of the effective axial shear modulus when the fibre cross-section is convex and the fibres are uniformly dispersed in a region (Hashin, 1983). At very high concentrations of fibres this formula may appreciably underestimate the effective axial shear modulus.

Since at failure

$$\sigma_o|_{crit} = \frac{M_{max} \frac{d_o}{2}}{I_{eq}} \quad (15)$$

we can find M_{max} explicitly from eqns (10) to (15). For comparison purposes it is convenient to normalize the maximum permitted moment with respect to that for a uniform dispersion throughout the entire cross-section. Thus we will consider the permitted moment, non-dimensionalized, in the form

$$\frac{M_{max}}{M_{max}|_{d_i=0}}.$$

This result is plotted in Fig. 5 for the benchmark values of the parameters, when no stiff tissue is found in the core. Also shown there is the normalized effective flexural modulus

$$\frac{(EI)_{eq}}{(EI)_{eq}|_{d_i=0}}$$

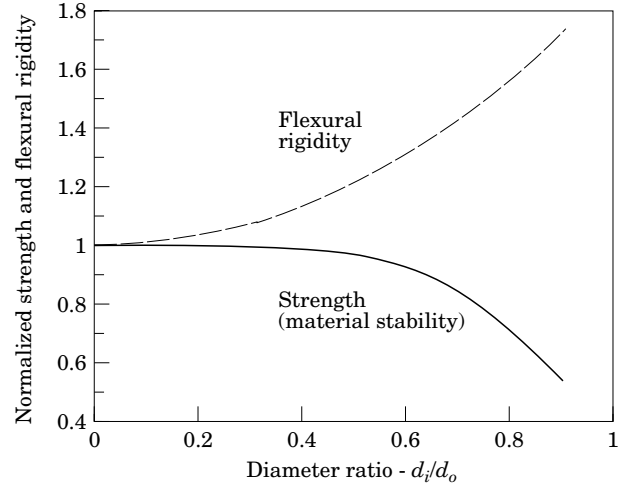


FIG. 5. Normalized strength and flexural rigidity of an idealized stem with no stiff tissue in core as a function of the ratio of core to outer diameter.

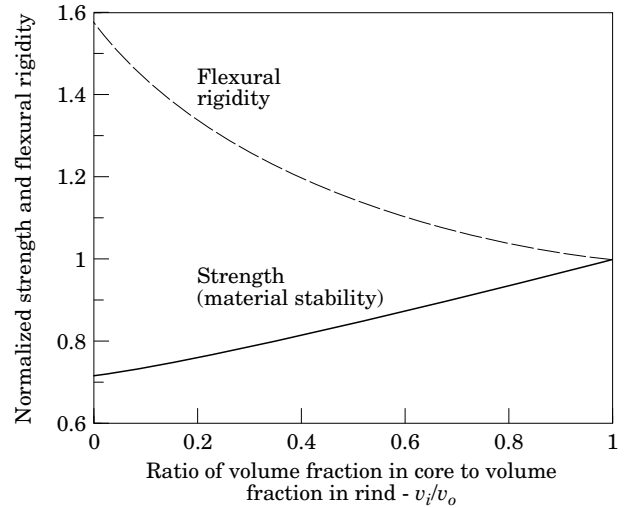


FIG. 6. Normalized strength and flexural rigidity of an idealized stem with the core to outer diameter ratio held at 0.8 as a function of the ratio of stiff tissue volume fractions in the core and rind.

found by using eqn (5); this is a measure of merit in terms of buckling stability. We have also calculated the maximum permitted moments based on the traditional strength criteria [eqns (1) and (2)]; when these are normalized with respect to the case of uniform dispersion throughout the entire cross-section, as is expected, are only very slightly different from those for the normalized flexural modulus, and therefore are not shown. The curves are plotted only until $d_i/d_o = 0.9$. At this point the volume fraction of fibres in the outer annular ring is already 26%, and it is questionable how valid the calculation for M_{max} is much beyond this point, both because the approximation in eqn (13) becomes less accurate and also because equating $\sigma_o|_{crit}$ to a multiple of G_o [eqn (12)] becomes less reliable.

Figure 5 is very instructive. Until $d_i/d_o = 0.5$ the loss of strength due to removing the stiff tissue from the centre of the stem is negligible, while the increase in flexural modulus

(proportional to overall stability) is more than 25%. However, as the stiff tissue is moved further outward, the strength begins to fall appreciably. Thus our main contention is confirmed, i.e. since compressive failure is related to an instability involving not only the fibres themselves, but also the matrix in which they are embedded, a stelar arrangement with fibres more distant from the stem centre is not necessarily advantageous if the limiting factor is bending strength. We can further elucidate the nature of the compromise between bending strength and flexural rigidity, if we consider, for a given intermediate diameter d_i , the more realistic possibility that $f_i \neq 0$. This is shown in Fig. 6 for the case of $d_i/d_o = 0.8$. As the volume fraction of stiff tissue in the core decreases relative to that in the rind, flexural rigidity increases, but on the other hand the strength decreases.

The above results clearly prove our contention.

TURGOR PRESSURE

The analysis in the previous section validates our basic hypothesis; it is our present purpose to demonstrate that considerations of turgor pressure will not introduce factors which essentially alter the conclusion. In trying to assess the possible influence of stelar arrangement on the ability of a plant to utilize turgor pressure in order to maintain its mechanical integrity, it is very important to view a plant

stem starting from the situation when it is fully turgid and in some state of pre-stress, rather than considering the situation from the opposite point of view, i.e. as if we had non-turgid tissue which we then pressurized and subsequently asked how this pressurization would contribute to structural integrity. This is so because, as was pointed out, we cannot hope to separate growth stresses from stresses caused by turgor; the former develop while the tissue is turgid. The 'normal' state of pre-stress, known to be advantageous to the plant, is for the turgid state; we will not question the developmental history which led to this state. We postulate that the stem could somehow achieve any state of pre-stress which would be beneficial to its mechanical performance. We ask the question: if a plant in its 'normal' state is subjected to water stress so that turgor pressure is reduced, then by what relative factor would the structural integrity of the stem be reduced for the various stelar arrangements? It is crucial to our argument to clarify this point, and to this end we describe the intuitive approach to the problem.

Consider the longitudinal section of the 'stem' shown in Fig. 7A; we have 'soft' tissue enclosed by a relatively stiff tube; there is no turgor pressure. We now 'pressurize' the soft tissue; the simplistic picture for understanding the situation is shown in Fig. 7B. Clearly the outer shell is now in a state of axial tension, and any bending moment applied to the stem which results in failure on the compression side must first overcome this residual pre-existing 'good' stress (in the sense that it is tensile and thus must be overcome before the stress turns compressive), so now the moment which can be applied is greater than that had there been no turgor pressure. We negate this approach; the system must be taken to contain residual stresses before we begin to analyse the problem.

Consider Fig. 7C which represents a longitudinal section of a stelar arrangement as idealized in Fig. 4A, i.e. a uniform distribution of stiff tissue throughout a soft matrix. We offer the following (admittedly artificial) scenario for constructing a plant stem with useful residual stress: again we start with no turgor pressure. Now pressurize the soft tissue, and let this tissue pressure be maintained throughout the process to be described. There is no stress in any representative volume element of the composite. (Such a representative element includes many 'fibres' and many parenchymatous cells.) Now cut out the 'core' of material indicated in Fig. 7C, and maintain the turgor pressure in the tissue both in this core and in the outer tube. Apply axial tension to the outer tube and, while the tension is applied, reglue the core to the tube so that they again form an integral structure. Release the tension. The resulting structure has built-in compression in the central portion, and built-in tension in the outer portion. Any level of pre-stress can be achieved as long as the stresses are not destructive to the material. When a bending moment is now applied, the resulting compressive stresses (on the concave side) are additive in the core region, while in the outer region the compressive stresses are reduced by the pre-existing tensile stress. Since the stress due to bending at any point in the cross-section is a linear function of distance from the stem axis, we can increase the moment until compressive

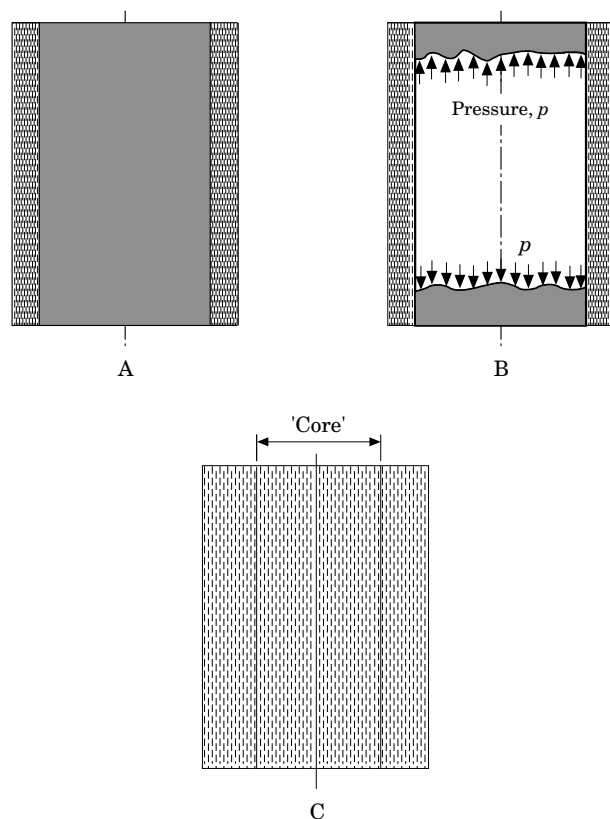


FIG. 7. Possible idealization of longitudinal stem section for considering the influence of turgor on strength. A, 'Soft' tissue enclosed by a relatively stiff tube; B, simplistic modelling to show the influence of turgor pressure; C, uniform distribution of stiff tissue.

failure occurs at the outer periphery of the stem or at the outer radius of the core; which will occur first would depend on the level of pre-stress. Our stem is artificial, and our process is artificial; it is not intended to mimic nature. But the important point is that nature could have achieved this end, i.e. pre-stressing during cell expansion in the growth stage, by some other scenario. Our scenario is intended only to demonstrate that the existence of pre-stress need not be related to specific tissue distribution. It may be counter-intuitive, but we must conclude that there is no *a priori* reason to consider the idealization of Fig. 7C to be less advantageous than that of Fig. 7A.

We now consider again Fig. 4 and start with the assumption that at full turgor pressure both (A) and (B) could conceivably achieve any state of pre-stress which might be beneficial to the plant; this is possible based on growth stress during development. Now we consider how changes in turgor pressure influence parenchymatous tissue. Both from theoretical models and from experiments, it has been concluded that reducing turgor pressure has two effects: reducing tissue stiffness, and concomitantly causing tissue contraction. (We consider only immediate responses to turgor change; obviously, in the long term, cell wall properties themselves will be affected.) We will consider these two effects separately.

From Fig. 4 it is clear that if turgor pressure reduction results in reducing rigidity of the soft (parenchymatous) tissue, then the value of G_o , and hence of $\sigma_o|_{crit}$, for the composite material is reduced. But reduction of the elastic rigidity of the soft tissue will not essentially change the stress in the composite for a given applied bending moment as long as the geometry of stiff tissue distribution is not changed; this is so since the ratio E_i/E_o which appears in eqn (10) will be very weakly influenced by changes in the ratio E_i/E_m , since in any event this latter ratio is very high (≥ 200). Thus we conclude that rigidity changes of the soft tissue will reduce the strength by about the same percentage, in terms of compressive failure, for any stelar arrangement. We reach the same conclusion as far as reduction of flexural rigidity, based on similar arguments.

Now we consider the other effect—contraction of the tissue. Consider Fig. 4A; since the entire cross-section is at least statistically homogeneous, at the level of a composite material, contraction of parenchymatous tissue results in no stress whatsoever. It may, however, reduce the compressive strength of the materials, and this possibility will be considered below. Considering Fig. 4B; the volume fraction of stiff tissue in the core is less than that in the outer ring; thus, since the stiff tissue itself does not contract, the core tissue would contract more than the outer tissue if these were not constrained by being joined together. This will result in tensile stresses in the core tissue and *compressive stresses in the outer tissue*. If the stem is now bent, such a member is at a disadvantage since it starts with compressive stress at the periphery, which will be added to the compressive stress due to the bending on the concave side. So the distribution of Fig. 4B is seemingly more sensitive in terms of strength reduction, than a uniform distribution of stiff tissue.

Now we address the question posed above: does reduction

of turgor pressure and the consequent shrinkage of parenchymatous tissue—thus inducing prior compression in the stiff reinforcing fibres—reduce the compressive strength and, if so, is such a strength reduction, in terms of percentages, dependent on the volume fraction of stiff reinforcement? We have no clear answer; the question must be left open. But this effect, if it is negative, is in addition to the other conditions discussed above which indicate that a uniform distribution is seemingly preferable, so there is no reason to decide that, as far as the contribution of turgor pressure to mechanical integrity is concerned, a peripheral arrangement of stiff material is advantageous.

DISCUSSION

We have shown that from the point of view of mechanical integrity of a plant stem subjected to bending, it is not necessarily true that optimal construction implies that stiff tissue should be concentrated at, or near, the periphery. Historically, optimality has been associated with such a peripheral arrangement of stiff tissue. But since the earliest work in plant biomechanics it was recognized that many plant stems do in fact deviate from this 'optimal' arrangement [see Nachtigall (1994)] and that some explanation should be found. Thus Schwendener (1874) refers to 'not very rational reinforcing systems', and Haberlandt (1914) to 'irrational constructional peculiarities'. We have argued here that this apparent deviation from the optimal may simply be because what was generally considered optimal in terms of strength is simply not optimal. However, historically, explanations for this situation are based on the recognition that as more of the stiff tissue is located further from the periphery (closer to the stem axis) flexibility increases, i.e. $(EI)_{eq}$ decreases. Thus the rationale which has seemingly been accepted for these 'irrationalities' is that proposed by Rasdorsky (1930), i.e. that flexibility of the plant stem in and of itself serves to reduce those stresses experienced by that plant stem which might result in failure by a process of 'passive withdrawal from the influence of the wind'. This mechanism, which has recently been referred to as 'passive automatic adjustment' by Nachtigall (1994), may operate in some plants. The explanation for the simplest possible case is illustrated in Fig. 8. Stem flexibility may reduce drag force in the leaf crown by reorienting its

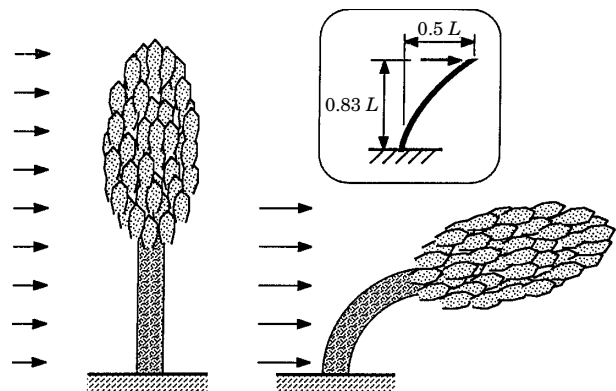


FIG. 8. Simple model for considering passive automatic adjustment.

presentation to the wind while reducing the moment arm of this drag force. The 'compromise' involves sacrificing strength and vertical stability in order to attain sufficient flexibility to reduce the bending moment. The idea is appealing, but to our knowledge no quantitative analytical or experimental evidence has been brought in its support. It would be difficult to reconcile this approach using the classical criterion for failure as expressed in eqns (1) or (3) for the case of an element which is vertical, or nearly vertical, in quiescent air.

Consider a very simplistic example as illustrated in the inset of Fig. 8. Suppose that a vertical beam (stem) made flexible by having a stelar arrangement such as in Fig. 1B, is subjected to a horizontal tip load so that the horizontal deflection of the tip is 50% of the beam (stem) length L . From large deflection theory (Bisshop and Drucker, 1945) we find that the tip of the beam, due to the load, will descend only by about $0.17 L$; thus the bending moment is reduced by only 17%. But if the stelar arrangement was as in Fig. 1A then, as we have noted, the value of $(EI)_{eq}$ would be approximately double, the horizontal deflection of the tip would be reduced to about $0.3 L$ and the tip would descend only about $0.07 L$ —thus the bending stress would indeed be about 15% greater—but according to the classical theory the relevant stress in the fibres would be halved. So, clearly, within the classical approach to failure stress in stems, it is untenable to claim that the arrangement in Fig. 1B could be an improvement on that in Fig. 1A because of 'passive automatic adjustment'. However, if the failure criterion is as has been suggested here, then any bending moment reduction due to the 'passive automatic adjustment' is additive to the advantages already gained by using the arrangement in Fig. 1B rather than that in Fig. 1A. It is not our purpose to negate the idea of passive automatic adjustment entirely; we only wish to point out that demonstrating its validity in self-supporting vertical stems is problematic.

For elements which are very flexible, the concept of passive automatic adjustment is certainly reasonable; but these situations are not really appropriate to the present discussion. Thus Rasdorsky (1937) gives the example of grass blades; but these are not designed essentially to resist bending, except to the extent required to bring about solar presentation when not otherwise stressed. Indeed, Vincent (1982) has shown that the grass leaf is an excellent *tensile* structure, referring especially to its fracture properties in this mode; such tensile performance may have importance in protecting it against predation by small grazing animals. Similarly, Vogel (1994) discussed reconfiguration of various algae subjected to strong water flow; again it would be hard to argue that there is, in the design of the alga stipe, a major requirement for bending resistance. We note also the suggestion of Ennos (1993), that a mechanism of the above sort might be operative for the sedge *Carex acutiformis*. He points out that the free standing stem of this plant generally sags laterally; under the influence of wind and, due to the low torsional stiffness of the stem, the plant rotates about the lower portions of the stem thus presenting less frontal area to the wind, reducing the bending moment in the stem, and at the same time, limiting the torsional moment

imposed on the lower portion of the stem had the torsional rigidity been greater.

The idea of passive automatic adjustment is related to, but really quite different from and not to be confused with, the reconfiguration concept as applied in another context by Vogel (1989, 1994). The difference is best illustrated by considering the situation for trees. Vogel points out that the elements upon which the wind bears—leaves and clusters of leaves—are 'reconfigured' in strong wind, so that the drag coefficient on the crown, when computed based on a fixed cross-section, is non-constant—decreasing significantly. The ability to reconfigure radically is apparently related to leaf geometry and structure, and additionally to the elastic properties of the petioles (Vogel, 1992). Thus, the bending moment experienced by the trunk, and the overturning moment imposed on the root system is much less than if the elements loaded by the wind were rigid. In other words the 'reconfiguration' is not of the plant element which is subject to failure, but of some other element which imposes the load.

Land plants, in their quest for gaining height advantage, have evolved highly anisotropic tissue arrangements in order to achieve the bending stiffness which will ensure stability. But a consequence of the highly anisotropic material is a sensitivity to compressive failure due to local material instability. This 'Achilles' heel' cannot be ignored when trying to understand the optimality of observed stelar arrangements in plants.

LITERATURE CITED

- Bisshop KE, Drucker DC. 1945. Large deflection of cantilever beams. *Quarterly of Applied Mathematics* **3**: 272–275.
- deBotton G, Schulgasser K. 1996. Bifurcation of orthotropic solids. *Journal of Applied Mechanics* **63**: 317–320.
- Bower FO. 1956. *Botany of the living plant*. London: Macmillan.
- Brazier LG. 1927. On the flexure of thin cylindrical shells and other 'thin' sections. *Proceedings of the Royal Society of London A* **116**: 104–114.
- Budiansky B, Fleck NA. 1993. Compressive failure of fibre composites. *Journal of the Mechanics and Physics of Solids* **41**: 183–211.
- Christensen RM. 1994. Material instability for fiber composites. *Journal of Applied Mechanics* **61**: 476–477.
- Dierks K, Hafner L. 1987. Mechanical properties of the cyclamen stalk and their structural basis. In: Bereiter-Hahn J, Anderson OR, eds. *Cytomechanics*. Berlin: Springer-Verlag, 242–246.
- Ennos AR. 1993. The mechanics of the flower stem of the sedge *Carex acutiformis*. *Annals of Botany* **72**: 123–127.
- Falk S, Hertz CH, Virgin HI. 1958. On the relation between turgor pressure and tissue rigidity. I. *Physiolgia Plantarum* **11**: 802–817.
- Geynomat G, Müller S, Triantafyllidis N. 1993. Homogenization of nonlinearly elastic materials, microscopic bifurcation and macroscopic loss of rank-one convexity. *Archives of Rational Mechanics and Analysis* **121**: 231–290.
- Gibson LJ, Ashby MF, Karam GN, West U, Shercliff HR. 1995. The mechanical properties of natural materials. II. Microstructures for mechanical efficiency. *Proceedings of the Royal Society of London A* **450**: 141–162.
- Greenhill AG. 1881. Determination of the greatest height consistent with stability that a vertical pole or mast can be made, and of the greatest height to which a tree of given proportions can grow. *Proceedings of the Cambridge Philosophical Society* **4**: 65–73.
- Guyon EG, Ochoa OO, Bradley WL. 1992. A parametric study of variables that affect fibre microbuckling initiation in composite laminates: Part 1—analyses. *Journal of Composite Materials* **26**: 1594–1616.

- Haberlandt G. 1914. *Physiological plant anatomy* (translated by Drummond, M.). London: Macmillan.
- Hashin Z. 1965. On elastic behaviour of fibre reinforced materials of arbitrary transverse phase geometry. *Journal of the Mechanics and Physics of Solids* 10: 119–134.
- Hashin Z. 1983. Analysis of composite materials—a survey. *Journal of Applied Mechanics* 50: 481–505.
- Hettiaratchi DRP, O'Callaghan JR. 1978. Structural mechanics of plant cells. *Journal of Theoretical Biology* 74: 235–257.
- Karam GN, Gibson LJ. 1995. Elastic buckling of cylindrical shells with elastic cores—I. Analysis. *International Journal of Solids and Structures* 32: 1259–1283.
- Kollmann FFP, Cote WA Jr. 1968. *Principles of wood science and technology*. Berlin: Springer-Verlag.
- Kryiakides S, Arseculeratne R, Perry EJ, Liechti KM. 1995. On the compressive failure of fiber reinforced composites. *International Journal of Solids and Structures* 32: 689–738.
- Kutschera U. 1989. Tissue stresses in growing plant organs. *Physiolgia Plantarum* 77: 157–163.
- Kutschera U. 1995. Tissue pressure and cell turgor in axial plant organs: Implications for the organismal theory of multicellularity. *Journal of Plant Physiology* 146: 126–132.
- Lager JR, June RR. 1969. Compressive strength of boron-epoxy composites. *Journal of Composite Materials* 3: 48–56.
- Mergenthaler-Pauler M. 1952. Die Spannungsverhältnisse in einigen aufrechten, zylindrischen Pflanzenorganen. *Zeitschrift für Botanik* 40: 363–384.
- Nachtigall W. 1994. On the research history of plant biomechanics. *Biomimetics* 2: 87–107.
- Niklas KJ. 1989. Mechanical behavior of plant tissues as inferred from the theory of pressurized cellular solids. *American Journal of Botany* 76: 929–937.
- Niklas KJ. 1991. Biomechanical responses of *Chamaedorea* and *Spathiphyllum* petioles to tissue dehydration. *Annals of Botany* 67: 67–76.
- Niklas KJ. 1992. *Plant biomechanics: an engineering approach to plant form and function*. Chicago: University of Chicago Press.
- Niklas KJ. 1993. Influence of tissue density-specific mechanical properties on the scaling of plant height. *Annals of Botany* 72: 173–179.
- Niklas KJ. 1995. Plant height and the properties of some herbaceous stems. *Annals of Botany* 75: 133–142.
- Niklas KJ, O'Rourke TD. 1987. Flexural rigidity of chive and its response to water potential. *American Journal of Botany* 74: 1033–1044.
- O'Dogherty MJ, Huber JA, Dyson J, Marshall CJ. 1995. A study of the physical and mechanical properties of wheat straw. *Journal of Agricultural Engineering Research* 62: 133–142.
- Parrish DJ, Leopold AC, Hanna MA. 1982. Turgor changes with accelerated aging of soybeans. *Crop Science* 22: 666–669.
- Peters WS, Tomos AD. 1996. The history of tissue tension. *Annals of Botany* 77: 657–665.
- Piggot MR. 1981. A theoretical framework for the compressive properties of aligned fibre composites. *Journal of Materials Science* 16: 2837–2845.
- Piggot MR, Harris B. 1980. Compression strength of carbon, glass and Kevlar-49 fibre reinforced polyester resins. *Journal of Materials Science* 15: 2523–2538.
- Rasdorsky W. 1926. Über die Dimensionsproportionen der Pflanzenachsen. *Berichte der deutschen botanischen Gesellschaft* 44: 175–200.
- Rasdorsky W. 1928. Über das baumechanische Modell der Pflanzen. *Berichte der deutschen botanischen Gesellschaft* 46: 48–104.
- Rasdorsky W. 1930. Die Lehre von Biegungsfedern im Dienste der Pflanzenmechanik. *Berichte der deutschen botanischen Gesellschaft* 48: 253–275.
- Rasdorsky W. 1937. Über die Baumechanik der Pflanzen. *Biologia Generalis* 12: 359–398.
- Rich PM. 1987. Mechanical structure of the stem of arborescent palms. *Botanical Gazette* 148: 42–50.
- Rosen BW. 1965. Mechanics of composite materials. In: *Fiber composite materials*. Metals Park, Ohio: American Society for Metals, 37–75.
- Rowe NP, Speck T, Galtier J. 1993. Biomechanical analysis of a palaeozoic gymnosperm stem. *Proceedings of the Royal Society of London B* 252: 19–28.
- Sachs J. 1882. *Textbook of botany*, 2nd edition. Oxford: Clarendon Press, 791.
- Schmid R. 1982. The terminology and classification of steles: Historical perspective and the outlines of a system. *Botanical Review* 48: 817–931.
- Schuerch H. 1966. Prediction of compressive strength in uniaxial boron fiber-metal matrix composite materials. *AIAA Journal* 4: 102–106.
- Schulgasser K, Witzum A. 1992. On the strength, stiffness and stability of tubular plant stems and leaves. *Journal of Theoretical Biology* 155: 497–515.
- Schultheisz CR, Waas AM. 1996. Compressive failure of composites, Part I: Testing and micromechanical theories. *Progress in Aerospace Science* 32: 1–42.
- Schwendener S. 1874. *Das Mechanische Prinzip im anatomischen Bau der Monokotylen*. Leipzig: Engelmann Verlag.
- Seide P, Weingarten V. 1961. On the buckling of cylindrical circular shells under pure bending. *Journal of Applied Mechanics* 28: 112–116.
- Spatz H-C, Speck T. 1994. Local buckling and other modes of failure in hollow plant stems. *Biomimetics* 2: 149–173.
- Spatz H-C, Speck T, Vogellehner D. 1990. Contributions to the biomechanics of plants. II. Stability against local buckling in hollow plant stems. *Botanica Acta* 103: 123–130.
- Speck T, Vogellehner D. 1988. Biophysical examinations of the bending stability of various stele types and the upright axes of early 'vascular' land plants. *Botanica Acta* 101: 262–268.
- Speck T, Spatz H-C, Vogellehner D. 1990. Contributions to the biomechanics of plants. I. Stabilities of plant stems with strengthening elements of different cross-sections against weight and wind forces. *Botanica Acta* 103: 111–122.
- Strasburger E. 1965. *Strasburger's textbook of botany* (rewritten by Harder R, et al., translated from 28th German edition by Bell P and Coombe D). London: Longmans.
- Timoshenko SP, Gere JM. 1961. *Theory of elastic stability*, 2nd edition. New York: McGraw-Hill.
- Vincent JFV. 1982. The mechanical design of grass. *Journal of Materials Science* 17: 856–860.
- Vincent JFV, Jeronimidis G. 1991. The mechanical design of fossil plants. In: Rayner JMV, Wootton RJ, eds. *Evolution*. Cambridge: Cambridge University Press, 21–36.
- Vogel S. 1989. Drag and reconfiguration of broad leaves in high winds. *Journal of Experimental Botany* 40: 941–948.
- Vogel S. 1992. Twist-to-bend ratios and cross-sectional shapes of petioles and stems. *Journal of Experimental Botany* 43: 1527–1532.
- Vogel S. 1994. *Life in moving fluids*, 2nd edition. Princeton: Princeton University Press.
- Waterhouse JT, Quinn CJ. 1978. Growth patterns in the stem of the palm *Archontophoenix cunninghamiana*. *Botanical Journal of the Linnean Society* 77: 73–93.