The concept of a ‘factor of safety’ is used by biologists and engineers who generally agree that structures must be mechanically reliable, i.e. that structures must be capable of coping with unprecedented loads without failing. These factors can be calculated for individual structures or for a population of otherwise equivalent mechanical structures differing in their load capabilities. Objective methods for quantifying factors of safety for biological structures are nevertheless difficult to devise because (1) actual (working) loads are defined by environmental conditions that can vary widely, (2) breaking loads (capability) of otherwise mechanically equivalent structures can likewise vary as a result of developmental variation, and (3) specific criteria for failure must be determined a priori.

In this paper, we illustrate and discuss two methods for computing factors of safety for plants. One method works well for individual stems or entire plants, the other is useful when dealing with a population of conspecifics exhibiting a norm of reaction. Both methods require estimates of the actual and breaking bending (or torsional) moments experienced by stems, and both are amenable to dealing with any biologically reasonable criterion for failure. However, the two methods differ in terms of the assumptions made and the types of data that need to be gathered. The advantage of the first method is that it estimates the potential for survival of an individual stem or plant. The disadvantage is that it neglects natural variation among otherwise mechanically homologous individuals. The advantage of the second (statistical) approach is that it estimates the probability of survival of a population in a particular habitat. The disadvantage of this approach is that it sheds little light on the probability of an individual’s survival.

Key words: biomechanics, safety factor, plant, stem, computation.

Introduction

Biologists and engineers agree that load-supporting structures must be mechanically reliable, i.e. that structures must be able to tolerate loads larger than those they normally experience (Volk, 1958; Spotts, 1959; Cannell and Coutts, 1988; Gibson and Ashby, 1988; Mattheck, 1992). Evidence for this perspective is that most structures are over-built, i.e. the load capability of most structures is larger than the working load. The extent to which the load capability exceeds the actual load is called the factor of safety, the de minimus value of which is 1, since this permits no margin for error in terms of the ability to cope with the normal environment (Wainwright et al., 1976). No intrinsic upper limit exists for the factor of safety. However, a practical trade-off exists between the probability of mechanical failure and the costs required to reduce this probability to an acceptable level (see Niklas, 1998).

The concept of a factor of safety is useful, but attempts to provide an objective numerical index expressing mechanical reliability have met with mixed results, especially when applied to organic structures. The traditional approach is either to use the dimensionless quotient of the load capability and the working load as the measure of the factor of safety (e.g. Tateno and Bae, 1990) or the quotient of surrogate measures of these two kinds of loads, such as breaking and actual bending stresses (e.g. Keller and Spengler, 1989). This method assumes that the two kinds of load (or their surrogate measures) are dependent variables, such that a well-defined relationship exists between the two. When this condition is met, the loads of a few randomly sampled representative structures from a population are sufficient to determine the factor of safety for the population. However, in many cases, actual loads and load capabilities are not correlated with one another. Load capabilities are dictated by the intrinsic properties of structures (e.g. their shape, geometry, absolute size and material properties), whereas actual loads depend on the external environment in which these structures function mechanically (e.g. duration, direction, magnitude and type of externally applied forces). This is especially true for organic structures. The load capability of plant stems is clearly predetermined developmentally, whereas the actual loads experienced by stems can vary, often dramatically, as a function of ambient wind speed, snow or ice accumulation, etc. Under these circumstances, it is biologically realistic to adopt a statistically based perspective when calculating factors of safety, one that uses the means and variances of the actual loads and load capabilities observed for a population. This
approach requires extensive sampling of populations, but it has the advantage of taking manufacturing imperfections, which are as relevant to engineered structures as they are to biological entities (Ang and Tang, 1975), into account.

Another practical concern when calculating factors of safety is that mechanical reliability can be expressed numerically only in terms of a predetermined criterion for failure. Shafts are designed to experience torsion, and columns are designed to sustain compressive forces. Each of these kinds of support member is expected to fail as a consequence of its actual load exceeding its load capability. Consequently, a factor of safety can be calculated for each kind of simple member on the basis of a well-defined a priori failure criterion (Volk, 1958; Spotts, 1959). In contrast, biological as well as complex engineered structures rarely experience simple loading conditions – stems typically bend as they twist – and so each structure can have as many different factors of safety as it has criteria for failure (Niklas, 1998). The challenge is to determine the most likely (or most serious) mode of failure before calculating a factor of safety.

Factors of safety also have little meaning unless they are ascribed to mechanically equivalent structures. Despite their similar general appearance, the columns supporting the lower and upper stories of a building are not equivalent mechanical structures – they bear different loads and operate under different working environments. By the same token, stems differing in size and location within the infrastructure of a tree canopy are not equivalent structures because they operate in different physical and biological environments. Thus, it is just as misleading and inappropriate to calculate a factor of safety for all the columns in a building as it is to ascribe a single factor of safety to all the stems in a tree canopy (Ang and Tang, 1975; Niklas, 1998, 1999). It is far more reasonable to expect the factor of safety to vary spatially within the infrastructure of a building or an organism. Any attempt to calculate a factor of safety, therefore, must determine the extent to which superficially similar structures are mechanically homologous, establish the appropriate criterion for failure and only then seek an objective numerical expression for the factors of safety of otherwise equivalent (homologous) structures.

**The individual approach**

The individual organism must be mechanically reliable if it is to survive and reproduce, and thus it is reasonable to assume that the growth and development of each individual must establish a factor of safety against mechanical failure. As noted, the accepted approach to calculating this factor, here denoted by $S$, is to take the dimensionless quotient of the load capability $\omega$ and the actual load $\chi$ (i.e. $S=\omega/\chi$). Nevertheless, the sporophyte of most vascular plant species consists of a population of stems differing in their bulk elastic modulus, density, size, shape and location (Esau, 1936; Bierhorst, 1971). The magnitude of $S$ will therefore vary among the elements of the individual plant because the values of $\omega$ and $\chi$ of stems will vary. These variations must be cast in the context of both static and dynamic mechanical forces, since all terrestrial plants must deal with the effect of gravity (self-loading) and that of the wind (drag forces) (Mattheck, 1992; Vogel, 1994). Consequently, we cannot speak of a single factor of safety for an individual plant nor for an individual stem.

The greatest challenge to calculating $S$ lies in estimating the actual load a stem experiences, because this load can vary dramatically as a consequence of dynamic mechanical forces, such as wind-induced pressure (Wainwright et al., 1976; Vogel, 1994, 1996). In contrast, the load capability of a stem is reasonably easy to measure; it is the load that causes a structure either to fail or to become permanently impaired in function, either of which can be tested directly in the laboratory. Thus, our focus here is on estimating the actual dynamic loads an individual stem experiences.

Under most circumstances, the dynamic load exerted on a plant stem is the drag force $D_t$ incurred by wind. The magnitude of this force is given by the formula:

$$D_t = 0.5 \rho u^2 S_p C_D,$$

(1)

where $\rho$ is the density of air, $u$ is the local wind speed, $S_p$ is the projected area of the stem, and $C_D$ is the drag coefficient (see Nobel, 1983; Vogel, 1994). This formula can be used to estimate the bending moments and stresses experienced by the individual stems in a tree because most plant stems are mechanically analogous to a tapered beam, which can be approximated as a series of cylindrical elements differing in diameter $d$ in accordance with the accumulation of secondary tissues in the basipetal direction (Fig. 1). Using the subscript $j$ to denote the cylindrical elements distal to any element $i$, the bending moment induced by $D_t$ measured at the base of element $i$ is the sum of all the moments applied by the cylindrical elements distal to it. Assuming low wind speeds such that $D_t$ is exerted perpendicular to the length of each stem element, this cumulative bending moment $M_i$ is given by the formula:

$$M_i = \sum_{j=1}^{i} 0.5 \rho u^2 [d_i(x_i-x_j)] C_D x_j,$$

(2)

where $x_j$ is the effective length of the element [i.e. $S_p = d_j(x_i-x_j)$], and $x_i$ designates the location of each stem element with respect to the top ($x=0$) of the tree (Fig. 1). Since the tensile or compressive bending stresses resulting from any bending moment invariably reach their maximum intensity at the surface of any element (Timoshenko and Gere, 1961; Wainwright et al., 1976; Niklas, 1992), the magnitude of the maximum stress $\sigma_i$ is given by the formula:

$$\sigma_i = \frac{d_i M_i}{2 I_i} = 10 \frac{M_i}{d_i^2},$$

(3)

where $I_i$ is the axial second moment of area, which for a terete cylinder equals $\pi d_i^4/4$ (Wainwright et al., 1976; Niklas, 1992).

Neglecting the stresses resulting from static loads, we adopt the maximum stress created by drag $\sigma_d$ as a surrogate measure of the actual (dynamic) load. Similarly, we use the breaking stress $\sigma_b$ of stem tissues as a surrogate measure of the load capability.
Calculating factors of safety for plant stems

of a stem. The factor of safety anywhere along the length of a stem can be thus calculated on the basis of the formula:

\[ S_i = \frac{\sigma_u}{\sigma_y}. \]  

**An illustration of the individual method**

Since \( u, d \) and \( x \) vary as functions of stem location in the infrastructure of a branched sporophyte, the practical application of equation 4 or any similar formula requires knowledge of the vertical wind profile and the morphometry of the individual plant. This information is not difficult to acquire, as is illustrated for a wild cherry tree (Prunus serotina Ehrh.) measuring 13.11 m in overall height \( h \) and 0.401 m in diameter at its base.

Ambient wind speeds were measured (by K.J.N.) along the length of the trunk at 13 different elevations differing by 1 m over a period of 30 days. The local wind speeds \( u \) recorded for each location were then normalized with respect to the maximum wind speed \( U \) measured at the top of the tree and plotted as a function of normalized distance \( x/h \) from the top of the tree \((x=0)\) to determine a representative normalized wind profile (Fig. 2). This profile was used to estimate the magnitudes of local wind speeds within the tree for each of three specified maximum wind speed \((U=10, 20\) and \(50\) m s\(^{-1}\)) on the basis of a third-order polynomial regression formula that best fits the data \((r^2=0.964, P>0.005)\). Values for \( u \) are means ± s.e.m. See text for further details.

The tree based on the breaking stress of wild cherry wood \( (i.e. \sigma_y=186\) MN m\(^{-2}\), \(N=53\) wood samples) were calculated.

As expected from equation 2, the bending moments produced by each of the three maximum wind speeds increased from the top to the base of the tree (Fig. 4A). The bending stresses resulting from these moments were best described by a third-order polynomial regression formula, which indicated that stresses were highest for stems located approximately 30 cm and 5 m from the top of the tree (Fig. 4B). The relationship

\[ uU=1.05-3.62(x/h)+9.93(x/h)^2-7.27(x/h)^3. \]
between the factor of safety and stem location with respect to the top of the tree was also best approximated by a third-order polynomial regression formula (Fig. 5). This formula indicated that safety factors were lowest for stems located 30 cm from the top of the tree and near the base of the tree \((x \approx 13.11 \text{ m})\). The factor of safety calculated for comparatively high wind speeds (i.e. \(U \geq 20 \text{ m s}^{-1}\)) fell below unity at these two locations. Our calculations thus suggest that this tree will respond to excessively high wind either by the failure of a constellation of peripheral branches or by failure at the base of the trunk. Obviously, the first of these two predicted responses is preferable, since the removal of peripheral branches will reduce the bending moments and stresses experienced by older subtending portions of the tree, which arguably represent comparatively larger metabolic investments and have the potential to regenerate missing portions of the plant body.

Our calculations neglect the bending moments imposed on stems by wind exerting pressure on leaves. Similarly, the static loadings of the tree were neglected in our calculations. However, the leaves of many species can streamline their shape when subjected to high winds and are typically borne on very flexible branches that deflect and further reduce drag forces (Vogel, 1996, and see references therein), whereas many tree species lack leaves during the winter yet have branches that can generate substantial drag. In terms of static loadings, the S-shaped trend in the factor of safety calculated on the basis of dynamic wind loading (Fig. 5) agrees with that reported for factors of safety calculated on the basis of static (self-weight) loads (see Niklas, 1999). Consequently, we believe that trees will generally respond to high wind speeds either by losing young branches or by failing at the base of their trunk (provided the root system remains intact).

The population approach

For this method, the factor of safety \(S\) is once again expressed numerically in terms of the quotient of the load capability \(\omega\) and the actual load \(\chi\) (or in terms of surrogate measures of these loads). However, this method assumes (1) that it is either impossible or impractical precisely to predict \(\chi\) or \(\omega\) (or their respective surrogate measures) for each load-bearing structure in a large population, (2) that both kinds of loads have a frequency distribution that conforms to some mathematically well-defined probability distribution (e.g. Gaussian or Weibull), (3) that the mean values of these loads (\(\bar{\chi}\) and \(\bar{\omega}\), respectively) are accompanied by mechanically acceptable tolerance bands (i.e. the ranges of \(\chi\) and \(\omega\) preclude
Probability density, \( z \) for the difference between load capability and actual load portion of the two frequency distributions. (B) Frequency distribution bands ± \( D_c \) (A) Frequency distributions of \( w \) (taken from Niklas, 1998, with permission) percentage of mechanically unreliable structures in the population dimensionless variable normally distributed variable structures in the population. (C) Frequency distribution curve for the area under the frequency distribution curve for which \( w - c \) equals the percentage of mechanically unreliable reliable; structures for which \( w - c \) (shown as a shaded region) equals the percentage of mechanically unreliable structures in the population. (A) Frequency distributions of actual loads \( \chi \) and load capabilities \( \omega \) for a hypothetical population of mechanically equivalent structures. (A) Frequency distributions of \( \chi \) and \( \omega \) with different mean actual load \( \bar{\chi} \) and mean load capability \( \bar{\omega} \) but with overlapping tolerance bands \( \pm \Delta \chi \) and \( \pm \Delta \omega \). The shaded region denotes the overlapping portion of the two frequency distributions. (B) Frequency distribution for the difference between load capability and actual load \( \omega - \chi \). All structures in the population for which \( \omega - \chi \geq 0 \) are mechanically reliable; structures for which \( \omega - \chi < 0 \) are mechanically unreliable. The area under the frequency distribution curve for which \( \omega - \chi < 0 \) (shown as a shaded region) equals the percentage of mechanically unreliable structures in the population. (C) Frequency distribution curve for the normally distributed variable \( \omega - \chi \) expressed in terms of the standard dimensionless variable \( t \). The shaded region corresponds to the percentage of mechanically unreliable structures in the population (taken from Niklas, 1998, with permission)

\[
A_f = \int_{-t_f}^{t_f} e^{-t^2/2} dt,
\]

where \( t_f \) is the critical value corresponding to the area under the \( \omega - \chi \) normal distribution curve that lies between \( -t_f \) and \( t_f \); see Fig. 6C. This relationship can be found because \( A_f \) is given in standard statistical tables for different values of \( t_f \) based on the formula:

\[
A_{\omega = 0} = A_f = \int_{-t_f}^{t_f} e^{-t^2/2} dt,
\]

where \( z \) denotes the probability density of \( t \) and \( A_f \) equals the percentage of all points with values of \( z \leq t \). Regression of the values of \( A_f \) against the corresponding values of \( -t_f \) provided in

Calculating factors of safety for plant stems 3277

- \( \omega \) and \( \chi \) have a Gaussian frequency distribution, then \( A_f \) is computed by taking the difference between \( \chi \) and \( \omega \) and evaluating the frequency distribution of \( \omega - \chi \) (Fig. 6B). When mechanical failure is intolerable, all values of \( \omega - \chi \) must be greater than zero such that \( A_f = 0 \). The area under the \( \omega - \chi \) distribution curve for which \( \omega - \chi < 0 \) is a function of the standard deviations of \( \omega - \chi \), \( \chi \), and \( \omega \). This area is determined by using the dimensionless variable \( t \) (the familiar statistical relationship between the standard deviation of any variable, here arbitrarily designated as \( y \)) and the difference between its values. Noting, that:

\[
t_y = (y - \bar{y}) / \text{S.D.} y,
\]

where \( y \) here denotes \( \omega - \chi \), it then follows that:

\[
t_{\omega - \chi} = (\omega - \chi) / \text{S.D.}_{\omega - \chi},
\]

where the standard deviation term is given by:

\[
\text{S.D.}_{\omega - \chi} = (\text{S.D.}_{\omega}^2 + \text{S.D.}_\chi^2)^{1/2},
\]

which assumes that \( \chi \) and \( \omega \) are independent variables (see Niklas, 1998). Since mechanical failure will occur only when \( \omega - \chi < 0 \), the point of interest on the frequency distribution curve is where \( \omega - \chi = 0 \), from which it follows that:

\[
t_{\omega - \chi} = t_f = \frac{(\bar{\omega} - \bar{\chi})}{\text{S.D.}_{\omega - \chi}},
\]

From equation 7, it is clear that:

\[
-t_f = \frac{(\bar{\omega} - \bar{\chi})}{\text{S.D.}_{\omega - \chi}^2 + \text{S.D.}_\chi^2}.
\]

The derivation of \( S \) requires a numerical relationship between the value of \( t_f \) and \( A_f \) (i.e. the area under the \( \omega - \chi \) normal distribution curve that lies between \( -t_f \) and \( t_f \); see Fig. 6C). This relationship can be found because \( A_f \) is given in standard statistical tables for different values of \( t_f \) based on the formula:

\[
A_{\omega = 0} = A_f = \int_{-t_f}^{t_f} e^{-t^2/2} dt,
\]
these tables gives approximate solutions of equation 9 that have the form of log–linear equations. For example, within the range 0.001 ≤ \( A_t \) ≤ 0.015 (i.e. 0.1–1.5% tolerable failure), regression analysis gives \( -a_t = 1.2922A_t^{-0.1284} \) \(( r^2 = 0.992 \)). Inserting this regression formula into equation 9 gives the formula:

\[
-a_t = \frac{1.2922}{A_t^{0.1284}} = \frac{\bar{\omega} - \bar{X}}{(\text{s.d.}^2 + \text{s.d.}^2 \cdot 1)^{1/2}}.
\]  

(10)

from which it follows that the factor of safety \( S \) is:

\[
S = \frac{\bar{\omega}}{\bar{X}} = 1 + \frac{1.2922 \cdot (\text{s.d.}^2 + \text{s.d.}^2)^{1/2}}{A_t^{0.1284}}.
\]

Within the slightly less stringent range of tolerable mechanical failure 0.001 ≤ \( A_t \) ≤ 0.023 (i.e. 0.1–2.3% tolerable failure), regression analysis gives \( -a_t = 1.1846A_t^{-0.1430} \) \(( r^2 = 0.985 \)), and thus:

\[
S = \frac{\bar{\omega}}{\bar{X}} = 1 + \frac{1.1846 \cdot (\text{s.d.}^2 + \text{s.d.}^2)^{1/2}}{A_t^{0.1430}}.
\]

(12)

When mechanical failure never occurs, it is clear that \( A_t = 0 \) such that formulae such as equations 11 and 12 give absurd results. However, when failure is highly improbable, \( \bar{X} + \Delta X \ll \bar{\omega} - \Delta \omega \), and so \( \bar{\omega} \geq \bar{X} + \Delta X + \Delta \omega \), from which it follows that:

\[
S = \frac{\bar{\omega}}{\bar{X}} \geq 1 + \frac{\Delta X + \Delta \omega}{\bar{X}} = 1 + \frac{(\Delta \omega/\bar{\omega})}{1 - (\Delta_{\omega}/\bar{\omega})}.
\]

(13)

Since \( \bar{X} \) and \( \omega \) are assumed to have Gaussian distributions, 99.73% of all loads fall within ± 3 s.d., and so equation 13 takes the form:

\[
S \geq \frac{\bar{\omega}}{\bar{X}} \left( \frac{\bar{X} + 3\text{s.d.}}{\bar{\omega} + 3\text{s.d.}} \right). \quad (14)

The statistical approach to compute \( S \) is easily extended to deal with situations in which both kinds of loads have Weibull frequency distributions. Under these circumstances, the safety factor can be computed on the basis of the formula (Niklas et al., 1999):

\[
S = \frac{\bar{\omega}}{\bar{X}} = \frac{\beta \gamma \left[ 1 + \frac{1}{\alpha \omega} \right]}{\beta \gamma \left[ 1 + \frac{1}{\alpha X} \right]}.
\]

(15)

where the gamma function \( \Gamma(1+x) = \int e^{-t}t^{x-1}dt \) is provided in tabulated form in standard statistical references (e.g. Korn and Korn, 1968), and where the standard deviations s.d.\( \omega \) and s.d.\( X \) can be calculated from the Weibull shape and scaling parameters as:

\[
\text{s.d.} = \beta \Gamma(1 + \frac{2}{\alpha}) - \Gamma^2(1 + \frac{1}{\alpha}). \quad (16)
\]

Equation 15 is a mathematical analog to equations 11 and 12 because it renders (in terms of statistical parameters) the quotient of the means of load capabilities and actual loads of otherwise equivalent mechanical structures that have Weibull frequency distributions in a population. And just as equations 11 and 12 stipulate that loads have normal frequency distributions, standard statistical analyses must be used to determine whether loads have Weibull frequency distributions when equation 15 is used to compute a factor of safety. This assumption is easily tested because the probability of survival \( P_s \) for any variable with a Weibull frequency distribution is given by the formula:

\[
P_s(X) = \exp \left[ -\left( \frac{X}{B} \right)^\alpha \right]. \quad (17)
\]

where \( X \) denotes the numerical value of \( y \) assumed to have a Weibull frequency distribution, and \( \alpha \) and \( \beta \) are the respective shape and the scaling parameters of the frequency distribution of \( y \) (Weibull, 1939). In general, \( \beta \) is expected to lie very near the mean value of \( y \). Values of \( \alpha \) can be evaluated by trial and error to determine the equation providing the best fit for the observed probability of survival of \( y \). Importantly, sensitivity analyses of the effects of the numerical values of \( \alpha \), \( \beta \) and \( A_t \) on the numerical value of \( S \) indicate that equation 15 is comparatively insensitive to substantial error estimates (see Niklas et al., 1999).

Illustrations of the population approach

Niklas (1998) applied this method to the sporophyte of the taxonomically enigmatic pteridophyte *Psilotum nudum*. The aerial portions of this plant consist of repeatedly bifurcate trusses composed of cylindrical axial elements differing in tissue stiffness, length and cross-sectional shape and size. Each of 186 individual elements from the five most proximal levels of branching among 52 aerial trusses was tested in bending and torsion to determine its load capabilities. Similarly, the actual loads of each of these 186 elements were determined on the basis of morphometric analyses to determine their weight, size, shape and orientation. Statistical tests were subsequently used to determine the frequency distributions of the mechanical and morphometric properties of axes removed from each level of branching. These tests demonstrated that the properties of the axial elements had Gaussian distributions for each level of branching such that equations 11 and 12 or 14 could be legitimately applied to the data. It is significant that non-Gaussian frequency distributions would have been determined for each of these mechanical and morphometric properties had all the elements removed from the 52 *P. nudum* trusses been treated as a single population. This emphasizes the desirability of identifying and analyzing statistically each class of mechanically homologous structure as a separate population.

Factors of safety were computed for the axial elements from each of the most proximal five levels of branching on the basis of two criteria of failure (i.e. failure in bending and in torsion). Each of these two factors decreased linearly in a basalpetal
Calculating factors of safety for plant stems

Regardless of which among contending methods a biologist uses to express factors of safety numerically, every method requires some knowledge of the actual (working) loads that structures experience during their functional lifetime. In the engineering sciences, these loads are comparatively easily measured or, indeed, specified and thus known *a priori* (Volk, 1958; Spotts, 1959; Ang and Tang, 1975). In contrast, the biologist must either infer or fastidiously measure actual loads with certain knowledge that dynamic loads, such as wind-induced drag, can vary spatially around a large organism and temporally over many orders of magnitude over short periods (Mayhead, 1973; Grace, 1978; Raupach and Thom, 1981; Vogel, 1996). Unlike the engineer, the biologist must also contend with norms of reaction, phenotypic variations in the physical and mechanical properties of individuals drawn from the same population but experiencing perhaps even slight differences in local environmental conditions.

In this paper, we have tried to underscore the uncertainty in estimating or precisely knowing actual loads as well as the need to appreciate the intrinsic variation in the physical and mechanical properties of otherwise structurally similar portions of the plant body. We have also tried to emphasize that any numerical expression of the factor of safety rests on assumptions about a structure’s most likely mode of mechanical failure. Clearly, different criteria of failure produce different factors of safety even for the same structure. Experience shows that structures subjected to complex loading conditions (e.g. bending and torsion) fail at their first opportunity, i.e. that their mechanical reliability depends on the magnitude and kind of stress that structures are least able to sustain (Timoshenko and Gere, 1961; Cannell and Coutts, 1988). Thus, even though many different factors of safety can be computed for the same structure, some are irrelevant because they have no bearing on the loading conditions that will incur mechanical failure. It is desirable, therefore, to explore all potential modes of failure and to determine the one most likely to occur before factors of safety are ascribed to a particular organic structure.

Each of the two approaches reviewed here has its merits and distractions. What we call the ‘individual approach’ is well established in the engineering and biological literature, and is essential whenever the concern is with the reliability of a particular (individual) structure rather than with a class of mechanically homologous structures. Objective quantification of the survival probability of the individual plant or animal is as important to the biologist as it is to the engineer concerned with a particular bridge or building. The approach also has the

direction from the top to the base of each truss (Fig. 7). Axial elements belonging to the most distal of the five levels of branching had higher factors of safety for bending than for torsion. The reverse was true for the axes removed from the lowest level of branching (Fig. 7). These results illustrate that different factors of safety can be computed for mechanically homologous structures depending on which criterion of failure is selected and that, for any criterion of failure, the factor of safety can vary as a function of the location of a stem in the branching infrastructure of a plant.

Niklas et al. (1999) also used the population approach to compute the factors of safety for the flower stalks (peduncles) of isogenic garlic (*Allium sativum*) populations grown under windy field and protected glasshouse conditions. Because meteorological data needed to estimate drag forces (and thus actual dynamic loads) were not available and because failure in bending was used as the criterion for mechanical reliability, these authors used the actual lengths and critical buckling lengths \((L_i \text{ and } L_{cr}, \text{ respectively})\) of peduncles as surrogate measures of the actual loads and load capabilities. These surrogates were found to have Weibull frequency distributions, and so equation 15 was used to compute the factor of safety. The factors of safety for the populations of field- and glasshouse-grown peduncles were 1.782 and 1.029, respectively. These factors of safety are also numerically similar to those that would have been computed on the basis of the assumption that the mechanical and physical properties of *Allium* peduncles had Gaussian frequency distributions (i.e. an assumption that yields \(S=1.76\) and 1.18 for field- and glasshouse-grown peduncles). Thus, different measures of reliability indicate that the factor of safety for *Allium* flower stalks subjected during their growth and development to chronic mechanical disturbance is higher than that of mechanically unperturbed flower stalks and that peduncles protected from the wind have, on average, safety factors very near the threshold beyond which mechanical failure under self-loading will occur.

**Discussion**

Fig. 7. Factors of safety in bending \((F_s; \text{open circles})\) and torsion \((F_t, \text{open squares})\) plotted against branch level number \(N\) for *Psilotum nudum* (the relative positions of branch levels are shown in the stick-figure). Regression lines are based on reduced major axis regression analysis (model Type II). For further details, see text (taken from Niklas, 1988, with permission).
merit of being direct and simple. The actual loads and load capabilities of a particular structure can be predicted or directly measured, and so estimates of the factor of safety assume an unambiguous significance. The principal disadvantage of this approach is that it fails to account for variation across otherwise mechanically equivalent structures.

Variation exists among individuals drawn from a population of organisms as a result of differences in development, growth and local environment, just as variation among engineered artifacts results from fabrication or production defects. In biology, this variation provides the raw materials for evolution, and the survival of species typically depends on it. A severe storm or flood may eliminate a large percentage of the individuals in a population, but only a few individuals need survive after a catastrophic event to perpetuate the species locally. Natural variation in the factor of safety among individuals in a population is advantageous, and the quantification of this variation is essential to our understanding of biomechanics and evolution. For this reason, the approach we have called the ‘population’ approach has merit. Its principal disadvantage is that it is labor-intensive, requiring extensive sampling and testing of numerous individuals.

Clearly, the two approaches are not mutually exclusive. Indeed, the ‘population’ approach requires knowledge of the physical and mechanical properties of individuals, and so it rests on the ‘individual’ approach. The issue here is not exclusivity, but rather the objectives of a particular research agenda – if knowledge of the individual’s factor of safety is sufficient for this agenda, then the ‘population’ approach is unnecessary. It cannot escape attention, however, that most vascular plant sporophytes are branched structures and that, in this sense, the individual plant consists of a population of stems, the failure of one or many of which can lead to the death of the plant. Thus, the two approaches outlined in this paper invariably become juxtaposed in the majority of botanical research agendas concerned with factors of safety.

Organisms do not choose their factors of safety in the same sense that engineers do. With the exception of humans, there can be no conscious effort to anticipate or accommodate normal or unprecedented loading conditions. However, the factor of safety of every load-bearing structure reflects some degree of experience with the probability that fabrication defects or unprecedented environmental conditions will result in structural failure. This experience determines the lowest acceptable factor of safety below which structures will fail. Similarly, construction costs define an upper limit to the safety factor because it is unreasonable to demand unconditional mechanical reliability. Since any organic structure too weak for service or too expensive to build will have a high probability of being eliminated from a population by natural selection, organic factors of safety reflect to some degree the historical legacy of the trade-off between construction costs and the probability of failure, just as the factors of safety of engineered structures reflect past experiences in the engineering sciences. Consequently, the concept of factors of safety can be as legitimately applied to biological structures as it is applied to engineered artifacts. Our task as biologists is to continue to seek objective, precise and accurate methods to quantify as well as appreciate the significance of these factors to ecology and evolution.

References