

Construction and Economy of Plant Stems as Revealed by Use of the *Bic*-method

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Accepted: 29 October 1991

The *Bic*-method, developed by F. Otto for the investigation and classification of light-weight structures in architecture and then also applied to constructions in nature, can be used for mechanical analysis of plants. It allows statements on tension and pressure stability of plant stems and a direct comparison of stems with different anatomy. The multiplication of the *Bic*-value by an energy value (construction cost or energy content of the plant organ) results in a dimensionless constructive expenditure value, which is comparable to the value of the construction economy in architecture. This value may then be related to the average lifespan of the plant organ.

Stems of *Ephedra foeminea*, *Pachysandra terminalis*, and *Taxus baccata* as well as flower stalks of *Cyclamen persicum* and *Taraxacum officinale* are investigated to show the applicability of the method. The lowest *Bic*-values (highest mechanical stability) are found for the lignified stems of *Ephedra* and *Taxus*. The constructive expenditure values are higher in herbaceous than in woody axes; in relation to the average life span the long-living lignified tissues show by far the lowest values. The very high values of the flower-stalks are attributed to the fact that short-lived organs also need a minimum expenditure of materials and energy for their construction.

Key words: Stem, *Bic*-value, construction cost, energy expenditure value, stress-strain graph, *Cyclamen persicum*, *Ephedra foeminea*, *Pachysandra terminalis*, *Taraxacum officinale* (dandelion), *Taxus baccata* (yew), flower stalk.

INTRODUCTION

Mechanical properties of plant stems have been investigated since the 19th century. Many of the data, especially those reported by Schwendener (1874) and Rasdorsky (1928, 1937), are found in textbooks; a short historical survey can be found in Mosbrugger (1990). During the last two decades there has been increasing interest in the mechanics of structural biomaterials (for review see Wainwright *et al.*, 1976; Vincent, 1982). However, living intact plant stems have seldom been investigated quantitatively. This is mainly attributed to their anisotropy. Stems consist of tissues of very different elastic moduli and therefore form a composite material. So it is not possible to determine by stress-strain experiments the elastic moduli of whole stems accurately. However, an idealized elastic modulus for the linear part of the stress-strain curve may be calculated; another method for the calculation of an (idealized) elastic modulus from bending data was described by Nachtigall, Wisser and Wisser (1986) who applied it to grasses. Alternatively, it is possible to make separate measurements on the different tissues and then calculate the mechanical efficiency from their relative proportions in the stem. Useful theoretical considerations regarding this method and its applicability in the mechanics of plant axes and in palaeobotany were published by Speck and Vogellehner (1988), Spatz, Speck and Vogellehner (1990) and Speck, Spatz and Vogellehner (1990). One main problem is the measurement of the cross-section of the different tissues. Without a clear definition of

this area the measurement of strain seems problematic. Since the area is used for the calculations one has to decide whether to consider the whole cross section of stem tissues or only the area of the cell walls.

Size, shape and structure of plant stems underlie mechanical constraints (Mosbrugger, 1990; Speck *et al.*, 1990). A direct comparison of stems of various species with different stem architecture and load capacities would be desirable not only from an evolutionary, but also from an ecological point of view.

This problem may be solved by using the rather simple *Bic*-method of Otto (Schaur, 1979; Otto, 1985*b*) which was invented for the description of light weight structures in general. Using this method, it is not necessary to determine any area of a cross-section, but to weigh the axes being investigated which is simpler and rather unequivocal. Here we describe the principles of the *Bic*-method applied to plant axes and show its applicability as a good approximation based on the results obtained from selected species.

The *Bic*-value is a measure of the mechanical stability of a piece of matter or a construction related to its mass. A construction of high mechanical effectiveness but low mass (low energetic expenses) in engineering is called a light-weight structure, which is characterized by a low *Bic*-value. When the *Bic*-value of a plant organ is multiplied by the energy content of the organ or by the energy expenditure for constructing this organ (measured as an energy content value), a dimensionless value is obtained, which is a constructive expenditure value. When it is low, the expenditure of the plant to reach its load capacity is small and

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the construction may be considered as mechanically effective.

However, because the different tissues are not examined separately, it is not possible to determine which tissue is most responsible for the effectiveness of the construction and also why any construction is more effective than another one.

THEORETICAL BASIS

The Bic-method

The method was used first by Otto (1954) and the term 'Bic' coined later (Otto, 1968). It has since been used in many publications regarding structures especially in architecture. The *Bic*-value is defined as the ratio of the mass, m , of an object to its maximum capability to transmit forces of a given load condition. The *Bic* therefore refers to the case of ultimate load, at which the object is destroyed or permanently deformed. If an object is loaded to failure, the *Bic* can be determined from the ultimate load, F , the transmission distance, s , and the mass of the object, m :

$$Bic = \frac{m}{Fs} \text{ (g N}^{-1} \text{ m}^{-1}\text{)}.$$

The *Bic* depends not only on the mass of the object, but also on its form, its material, and the type and nature of loading.

A given object has different *Bic*-values for different states of loading, therefore each *Bic*-value has to be related to a definite load type. Two objects of the same form but of different materials usually show different *Bic*-values even when the type and nature of loading are the same. The *Bic*-value may also be considered as the mass (in g) required in a given load condition to transmit 1 N over a distance of 1 m. The *Bic*-value relates only to the failure of the material, not to failure by local buckling and by global (Euler) buckling. This must be taken into consideration especially in the pressure experiments.

In the case of an object whose form, and thereby its ability to transmit forces, are specific to a certain task, we can refer to the 'expenditure' of material. Expenditure is the mass required to fulfill a certain task. The *Bic*-value then is a measure of the expenditure (in g) needed to perform the structural task. Objects with low *Bic*-values are more effective than those with high *Bic*-values. Their effectiveness is then the reciprocal of the *Bic*.

The *Bic* is largely independent of the absolute size of the object. For a given load, the *Bic*-value is a function of form and material, but usually not of the scale. Geometrically similar objects consisting of the same material(s) have, at least theoretically, the same *Bic*-values for the same nature of load.

To compare different constructions, the *Bic*-values are often presented in relation to the relative structural slenderness of the object (Schaur, 1979) which in this case is given by

$$\lambda = \frac{s}{\sqrt{F}} \text{ (m N}^{-0.5}\text{)},$$

where s is transmission distance of the load (m), and F the ultimate load (N). In plant mechanics, the relative slenderness according to Mosbrugger (1990) is defined by

$$\Gamma_r = \frac{l^{\frac{3}{2}}}{d}, \text{ (m}^{0.5}\text{)}$$

where l is the length, and d the diameter of the plant stem (as a column). For our purpose, this value may be used as well.

If objects show similar relative structural slenderness, they can be compared directly, independent of their form and material, by using the *Bic*-value. The *Bic*-value increases as the relative structural slenderness of objects stressed by bending or compression increases. In tension the *Bic*-value is less dependent on the structural slenderness.

Economy

The economy of a construction is the relation of its expenditure to its effectiveness. Expenditure here means the total energy expenditure which is necessary for the synthesis of the bearing mass.

As an energy value, the total calorific energy or the calorific energy of the ash-free plant substance may be used. Perhaps a more accurate value is the construction cost of the organs as defined by Williams *et al.* (1987), which can be calculated from calorific energy, N-content, and ash content. Also, construction costs of non-storage compounds, maintenance costs (Merino, Field and Mooney, 1984) and energy expenditure values (Diamantoglou, Rhizopoulou and Kull, 1989b) may be calculated (see Material and Methods) and could be used as energy quantity for the calculation of the economy of the construction.

The *Bic*-value multiplied by an energy value, E , (referred to 1 g of dry matter) results in a dimensionless value, which we call the expenditure value of the construction, or the constructive expenditure value, K :

$$K = Bic E.$$

K is comparable to the value of the constructional economy in architecture. The smaller this value, the less the expenditure to obtain the measured load-capacity of the construction.

In a final step, the very different lifespans of plant species or plant organs can be taken into consideration. Some plant stems have a short lifetime (e.g. axes of ephemeral or annual species, stalks of flowers and fruits) and others, such as stems of woody plants, show durability. Therefore it makes sense to relate the expenditure value, K , to the average life span of the construction.

MATERIALS AND METHODS

Plant material

Stems of three different species were used:

1. *Ephedra foeminea* Forsskal (*Ephedra fragilis* Desf. ssp. *campylopoda* (C.A. Mey.) Asch u. Gräbner). A long lived evergreen, stemmed shrub without leaves, and an average

stem lifespan (according to observations by Diamantoglou in Greece) of 3–6 years (Diamantoglou *et al.*, 1989a, b). The species was erroneously determined as *E. distachya*; an inspection by H. Freitag, Kassel demonstrated it to be *E. foeminea*.

2. *Taxus baccata* L. A woody plant; 1 and 2 year old twigs were used. Average twig lifespan of 5–10 years.

3. *Pachysandra terminalis* Sieb et Zucc. An evergreen non-woody chamaephyte; 1–3 year old stems were used. Average stem lifespan (in pots) of 4 years (compare with Yoshie *et al.*, 1990).

For reasons of comparison, scapes of *Taraxacum officinale* Web. and pedicels of a hybrid of *Cyclamen persicum* Mill. were also investigated.

Methods

Mechanical investigations. Internodal lengths from the stems of herbaceous plants, and twigs of young woody plants, were cut for use. Nodes in some preliminary experiments led to mechanical weakness and therefore were omitted in all experiments. If possible, pieces of 3, 5 and 7 cm lengths were used for the tension experiments. The transmission distance is the length of the free part of the axes, the fixed part has to be disregarded. Theoretically, the *Bic*-value in the tension experiments should be independent of the length of the stem used. On the other hand, the probability of a failure rises with the length of the piece. Therefore using *Pachysandra* we tested whether the failure and the length of the piece are correlated, but it was found that the variance in experiments with stems from different plants was greater than the supposed effect of the length.

All *Bic*-values were calculated using the dry mass of the axes. The introduction of the forces must be performed carefully and, most of all, gently.

Tension. For measuring the ultimate tensile load, the fixing of the plant must be firmer than the stem itself; on the other hand, the stem should not be hurt by fastening or be allowed to dry out. The best method to avoid damage was to glue the axes with cyanoacrylate glue (Epple bond 4202) mixed with sawdust, into covers of gelatine (halves of medical gelatine capsules). During the drying period of about 20 min, the pieces were kept in a damp box. The gelatine covers at both ends of the stem were then fixed and hung up in a construction where they were loaded with increasing masses, and the ultimate load was measured as quickly as possible. Experiments in which the axes broke away from the fixation and those with fractures in the fixed part or near its boundary were omitted.

Pressure. Short pieces of the stems investigated were fastened to a pressure frame apparatus constructed as described by Otto (1985b). It is not necessary to fix the ends in a special way. The mass was raised to failure by pressure. All experiments, in which failure by buckling occurred, were omitted. When elastic bending was observed, shorter pieces were used.

Cone-shaped axes. When plant axes show a distinct cone-shape, a marked influence on the tension stability is observed. The *Bic*-values of tension load then become

dependent on the length of the piece used for experiments, because the share of ineffective mass is smaller in shorter pieces. Since fixation is necessary in tension experiments it is not possible to use very short pieces of the stalks. Hence, conic stems have to be converted by calculation into cylindrical axes. In our experiments, this calculation was always necessary for *Taxus*. The conic shape may be characterized by the value:

$$\frac{\text{lower area} - \text{upper area}}{\text{length}}$$

which is in the range 0.8–1.6% (mean value 1.16%; s.d. ± 0.22). From the volume and the dry mass of the truncated cone the specific gravity is calculated as follows:

$$\rho = \frac{m_K}{V_K} = \frac{m_K}{\frac{\pi s}{3} \left(\left(\frac{d_0}{2} \right)^2 + \frac{(d_0 + d_u)}{4} + \left(\frac{d_u}{2} \right)^2 \right)} \quad (\text{gm}^{-3})$$

where V_K is the volume of the truncated cone, m_K the dry mass of the truncated cone, d_0 the upper diameter, d_u the lower diameter and s is the transmission distance.

Using this value, the mass of the bearing cylinder is determined, which is then used to calculate the *Bic*-value:

$$m_{\text{cylinder}} = \rho V_{\text{cylinder}} = \rho \pi d_0^2 \frac{s}{4}$$

Because the failure usually occurred near the upper end, the upper diameter was used for the calculation.

Stress-strain graph. In some experiments using scapes of *Taraxacum* and stems of *Pachysandra* (1 year old) stress-strain graphs for tension were determined. For *Pachysandra*, a continuously recording apparatus was used to investigate the tension strength; the values for *Taraxacum* were obtained by individual measurements. For *Taraxacum*, not only pieces (2 cm long) of intact scapes, but also pieces of separated tissues (epidermis plus collenchyma; parenchyma plus bundles) were investigated. We succeeded in the separation of the tissues by carefully incising the scape longitudinally after bending and then pulling apart the separated ends. The stress was calculated using the total area of the cross section and also using only the area of epidermis plus collenchyma, which primarily sustains the load.

Statistical methods. First, the Gaussian distribution of the *Bic*-values measured for *Pachysandra* was checked, which is a pre-requisite for the application of the statistical methods employed.

For the calculated *Bic*-values, the standard deviations (s) and the coefficients of variation (V_c):

$$V_c = 100 \times \frac{s}{\bar{x}} (\%)$$

were calculated. They are included in Table 1.

Energy values. The calorific total energy content was measured by adiabatic calorimetry as described by Diamantoglou *et al.* (1989a, b). The ash content was determined gravimetrically after combustion of the plant material in a

muffle furnace for 1.5 h at 500 °C. Based on the values obtained, the calculation of the energy equivalents was corrected and designated as the energy of ash-free material.

The total N-content was measured by the Kjeldahl-method as described by Diamantoglou and Kull (1988). The construction cost was calculated according to the method of Williams *et al.* (1987) using a value for growth efficiency $E_0 = 0.87$ (Diamantoglou *et al.*, 1989b) and considering nitrate as the nitrogen source.

From the estimation of the contents of the storage substances (soluble sugars, starch, lipids), according to the methods described by Diamantoglou and Kull (1982), their energy contents were calculated and summed. This leads to the energy content of the storage products. The construction cost of the storage compounds was calculated as described by Diamantoglou *et al.* (1989b). The difference between the total construction cost and the construction cost of the storage substances may be considered as the construction cost of the non-storage substances which mainly comprise the load-bearing components of a tissue. In this calculation the secondary plant substances are disregarded and this is a major source of inaccuracy.

For *Ephedra*, the total energy content, the energy of ash-free materials, total construction cost and construction-cost of non-storage substances had been measured throughout the year (Diamantoglou *et al.*, 1989a, b). For *Taxus*, the contents of storage compounds and their variation throughout a year's course had been investigated earlier (Distelbarth, Kull and Jeremias, 1984) and corresponding data on *Pachysandra* are available from unpublished results of Distelbarth.

RESULTS AND DISCUSSION

Stress-strain diagrams

In Fig. 1 stress-strain curves for tension in 1-year-old stems of *Pachysandra* are shown and Fig. 2 presents the same graphs for the scapes of *Taraxacum*. From these diagrams

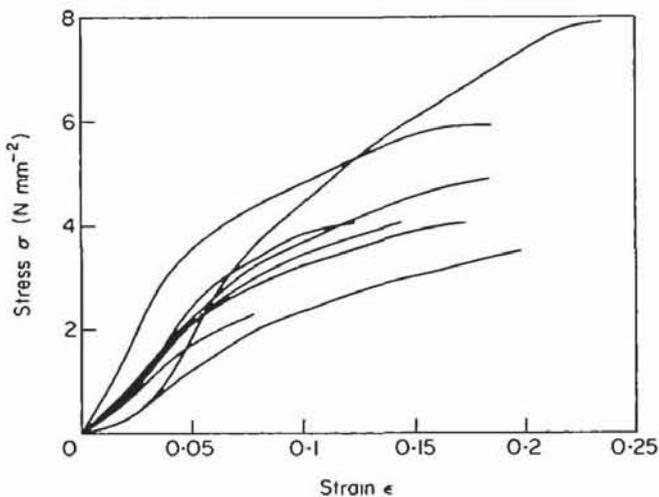


FIG. 1. Stress-strain diagrams for tension of 1-year-old *Pachysandra terminalis* stems.

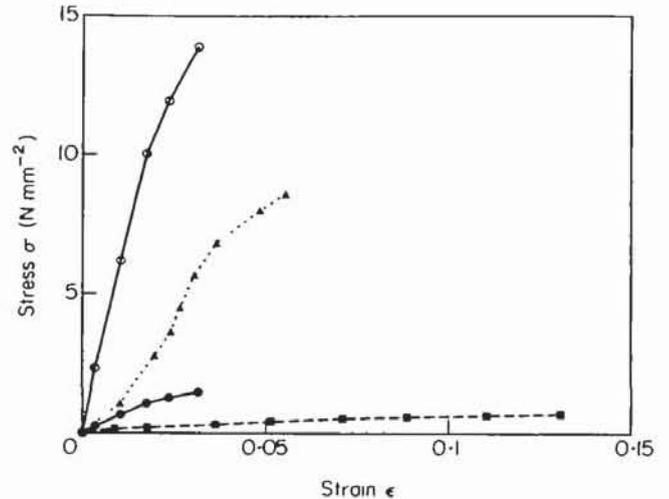


FIG. 2. Stress-strain diagrams for tension of whole axes and separated tissues of *Taraxacum officinale* scapes. For whole scapes, the stress was calculated using the area of only epidermis and collenchyma (○—○) and using the whole area of the cross-section (●—●). (▲····▲) Epidermis plus collenchyma; (■—■) parenchyma plus vascular bundles.

it may be seen that it is not possible to get clear values of Young's (elastic) moduli. The behaviour of the internodes by approximation may be described as elastic-plastic deformation; however, the sigmoidal shape of the curves does not really fit this description. Disregarding the deformation by very small loads, there is an approximately elastic behaviour connected with small deformations and a plastic behaviour for large ones. It is well known that in living, and especially in the herbaceous plants, turgor pressure and the ability to avoid big forces by elasticity are of major importance for their mechanical stability (Ulrich, 1951; Nachtigall *et al.*, 1986; Dierks and Hafner, 1987; Speck and Vogellehner, 1988; Speck *et al.*, 1990). The problems of an unequivocal measurement of the strain, which is a prerequisite for the calculation of Young's modulus, may be seen from Fig. 2, which shows that the elastic behaviour is not linear over a large range of stresses.

Bic-values

The *Bic*-values for compression and tension loads are shown in Table 1. The values for compression are always higher than those for tension; plants have to expend a greater mass to achieve their compression stability than to reach their tension stability. Therefore, failure by compression should be more frequent in plant axes than failure by tension. In woody plants, pre-stressing represents an energy saving device to reduce the peripheral compressive stress (Mosbrugger, 1990). The *Bic*-values of compression and tension together allow an estimation of the mechanical efficiency of the axes as a whole, because bending may be regarded as a composite effect which is separable into a tension load on one side of a stem and a compression load on the other side.

From many investigations on bending stress of woody

TABLE 1. *Bic*-values for compression and tension load

| Species | Compression | | | | | Tension | | | | |
|-------------------------------|---------------------|---|-----------------|----------|---------------------------|---|-----------------|----------|---------------------------|--|
| | Age of axes (years) | <i>Bic</i> 10 ⁻⁴ (gN ⁻¹ m ⁻¹) | No. experiments | <i>s</i> | <i>V</i> _c (%) | <i>Bic</i> 10 ⁻⁴ (gN ⁻¹ m ⁻¹) | No. experiments | <i>s</i> | <i>V</i> _c (%) | |
| <i>Ephedra foeminea</i> | 2 | 617 | 8 | 90 | 14.5 | 168 | 26 | 57 | 34.0 | |
| <i>Pachysandra terminalis</i> | 1 | 1250 | 9 | 306 | 24.4 | 667 | 47 | 151 | 22.6 | |
| | 2 | 1706 | 12 | 197 | 11.6 | 465 | 31 | 126 | 27.6 | |
| | 3 | 1640 | 13 | 260 | 15.7 | 431 | 10 | 68 | 15.6 | |
| <i>Taxus baccata</i> | 1 | 1270 | 4 | 348 | 27.3 | 419 | 10 | 96 | 22.8 | |
| | 2 | 617 | 9 | 100 | 16.2 | 375 | 10 | 101 | 27.3 | |
| <i>Taraxacum officinale</i> | Scapes | 1467 | 6 | 390 | 26.7 | 998 | 15 | 304 | 30.5 | |
| <i>Cyclamen persicum</i> | Pedicels | 1118 | 6 | 447 | 40.4 | 807 | 3 | 194 | 24.1 | |

s, Standard deviations; *V*_c, coefficient of variation.

TABLE 2. *Energy contents and construction costs*

| Species | Age of axes (years) | Calorific energy content (kJ g ⁻¹) | Ash content (% dry mass) | N content (% dry mass) | Energy content of ash-free substance (kJ g ⁻¹) | Energy content of non-storage substances (kJ g ⁻¹) | Construction cost (kJ g ⁻¹) |
|-------------------------------|---------------------|--|--------------------------|------------------------|--|--|---|
| <i>Ephedra foeminea</i> | 2 | 18.13 | 7.5 | 1.35 | 19.60 | 16.14 | 22.01 |
| <i>Pachysandra terminalis</i> | 1 | 17.33 | 6.3 | 1.32 | 18.49 | 13.05 | 21.08 |
| | 2 | 16.86 | 6.7 | 1.31 | 18.06 | 11.82 | 20.46 |
| | 3 | 16.71 | 6.8 | 0.94 | 17.93 | 12.28 | 20.15 |
| <i>Taxus baccata</i> | 1 | 19.35 | 5.9 | 1.29 | 20.49 | 16.30 | 23.41 |
| | 2 | 19.00 | 5.2 | 0.85 | 20.19 | 16.65 | 23.10 |
| <i>Taraxacum officinale</i> | Scapes | 15.56 | 9.6 | 1.18 | 17.22 | 9.54 | 18.92 |
| <i>Cyclamen persicum</i> | Pedicels | 14.59 | 8.3 | 1.60 | 15.91 | 10.77 | 17.83 |

stems it is known that the destruction in most cases starts with a compression failure, often as a shear (Archer, 1987; Wessolly, 1988). Dierks and Hafner (1987) obtained similar results for the herbaceous stalks of *Cyclamen*. Therefore, the ultimate compression load is of particular importance. We made some bending experiments with *Ephedra* and *Pachysandra* stems and surveyed the fracture area by SEM. Also, our findings point to a failure by compression, which in most cases was attributed to a separation of the inner and outer tissues of the stem, probably because the cortex is less compressible than the pith.

The lowest *Bic*-values are found for the lignified tissues (2 year old) of axes of *Ephedra* and *Taxus*. In the latter species, the *Bic*-values of twigs in the first year (weak lignification before secondary thickening starts) are comparable to those of herbaceous *Pachysandra* stems. With ongoing lignification of the twigs the *Bic*-values for compression decline by about one-half. In the stems of *Pachysandra*, which do not form wood, no such effect is observed. In woody stems, where the fraction of wood rises during secondary thick-

ening, the *Bic*-values as a threshold will reach eventually the values measured for the living wood of the respective species.

High *Bic*-values for tension are found in the short-lived stalks of *Taraxacum* and *Cyclamen*; however, the *Bic*-values for compression are in the usual range for herbaceous stems.

Energy values

The energy values, which we then used for the calculation of the constructive expenditure values, are shown in Table 2. The calorific energy contents are in the usual range, as described by Pipp and Larcher (1987*a, b*); they are higher for lignified than for herbaceous tissues. The same is true for the energy content of the ash-free substance. In *Taxus* twigs, a high calorific energy value is found even in the first year, at least partly due to a high content of storage substances. The variation of the calorific energy contents throughout a year in *Ephedra* and *Taxus* (2 years old) as well as in *Pachysandra* (1 year old) is always less than 0.5 kJ g⁻¹. These

TABLE 3. Constructive expenditure values K (calculated using construction costs and using energy contents of non-storage substances) and relation of K to the average lifespan

| Species | Age of axes (years) | <i>Bic</i> -values for compression \times construction cost K_p | <i>Bic</i> -value for compression \times energy content of non-storage substances | <i>Bic</i> -value for tension \times construction cost K_t | <i>Bic</i> -value for tension \times energy content of non-storage substances | Average lifespan (days) | $\frac{K_p}{\text{lifespan}}$ (d^{-1}) | $\frac{K_t}{\text{lifespan}}$ (d^{-1}) |
|-------------------------------|---------------------|---|---|--|---|-------------------------|--|--|
| <i>Ephedra foeminea</i> | 2 | 1360 | 1000 | 370 | 270 | > 900 | < 1.5 | < 0.4 |
| <i>Pachysandra terminalis</i> | 1 | 2635 | 1630 | 1405 | 870 | > 1000 | < 2.65 | < 1.4 |
| | 2 | 3490 | 2015 | 950 | 550 | 700 | 5.0 | 1.4 |
| | 3 | 3305 | 2015 | 870 | 530 | 350 | 9.4 | 2.5 |
| <i>Taxus baccata</i> | 1 | 2970 | 2070 | 980 | 685 | > 2000 | < 1.5 | < 0.5 |
| | 2 | 1425 | 1030 | 865 | 625 | > 1600 | < 0.9 | < 0.55 |
| <i>Taraxacum officinale</i> | Scapes | 2775 | 1400 | 1890 | 950 | < 40 | > 69 | > 47 |
| <i>Cyclamen persicum</i> | Pedicels | 1990 | 1205 | 1440 | 870 | < 80 | > 25 | > 18 |

variations are much smaller than the degree of accuracy which can be reached in measuring the *Bic*-values.

The construction cost is also much higher in lignified tissues and lower in herbaceous ones, especially in short-lived stems. Since the construction cost for perennial axes does not vary much throughout the year (Diamantoglou *et al.*, 1989b) it seems particularly appropriate to consider it as an energy-value for the calculation of the constructive expenditure values.

The energy content of the non-storage substances, which can be assumed to be mainly the energy value of the bearing tissues, is also relatively constant throughout a year (Diamantoglou *et al.*, 1989b), but to obtain the values one has to acquire more experimental data. Therefore, we prefer to use the construction cost as an energy value; however, for preliminary descriptions the calorific energy values may be used for the calculations.

For the lignified tissues of *Ephedra* we had found that the energy of the ash-free substance is rather well correlated to the crude fibre content (Diamantoglou *et al.*, 1989a). The latter, on the other hand, is related to the energy content of the bearing tissues. Therefore, the energy content of the ash-free substance may also be a good measure to get approximate values of the construction expenditure.

Constructive expenditure values

Low values of the constructive expenditure mean a high efficiency/cost ratio. Generally, herbaceous axes show higher values than woody stems, especially regarding compression (Table 3). In *Taxus*, the constructive expenditure value declines with lignification. This may be expected, because the construction cost is relatively high, but after the construction no further expenditure is necessary for wood. The constructive expenditure for compression in lignified *Taxus* is similar to that of *Ephedra*, which shows the lowest of the measured values. The mechanical efficiency of the different tissues (measured as *Bic*-values) has a

greater influence on the constructive expenditure values than the energy values have. This results mainly from the fact that the energy values are determined predominantly by the chemical composition of the plant material and therefore may only fluctuate in a limited range (Pipp and Larcher, 1987a).

When the energy contents of non-storage substances, instead of the construction costs, are used for the calculation of the constructive expenditure values, such values also show the same trend with the exception of the scapes of *Taraxacum*, where a major difference is observed. This is mainly caused by the high sugar content of the scape-tissues (25% of dry weight). Therefore, the constructive expenditures calculated using the construction costs are higher for *Taraxacum* than for *Cyclamen*; however, when the energy content of non-storage substances is used instead, the expenditure values are rather similar. The high amount of sugars in *Taraxacum* is probably used in fruit development. This points to the fact that in flower and fruit stalks functions other than those requiring mechanical stability are essential. In *Pachysandra*, a similar but less marked effect is recognizable. This is not surprising because in all green stems photosynthesis is a more or less important additional function.

Constructive expenditure values in relation to lifespan

Table 3 also shows the constructive expenditure values (calculated using the construction costs) related to the average lifespan. Predation by animals and other processes leading to a premature death of a plant or a plant organ have to be ignored for these calculations. Low values are found for lignified tissues, which are effective long-term constructions. With an increasing amount of wood in the stems, the values are declining further, as can be seen from the data for compression in *Taxus*. In *Pachysandra*, where lignification is very weak, there is no decline but a rise occurs because the stems have a rather limited lifespan.

Naturally, the short-lived stalks of the flowers show high values, which are somewhat lower in *Cyclamen* than in *Taraxacum*. The pedicels of *Cyclamen* during fruit-ripening gradually become prostrate, the fruits are laid down and the pedicels then have no further significant bearing-power. The values for *Cyclamen* would also be lower than those for *Taraxacum*, if the life spans used for calculation were considered to be identical. Probably the very high values for *Taraxacum* are caused by the storage function of the scapes, whereas the *Cyclamen* pedicels primarily have bearing and transport functions. Because of the transport functions, which are very important for flower and fruit stalks, these axes generally need a minimum area of vascular bundles. According to the *Bic*-values and the constructive expenditure, this area—at least in the species investigated—seems to be distinctly larger than is necessary for mechanical reasons.

Conclusions

From our results it may be seen that the *Bic*-method can successfully be used to obtain knowledge of the mechanical properties of anisotropic plant axes, where stress-strain curves do not lead to unequivocal results. Furthermore, the constructive expenditure values, which are calculated using energy contents, perhaps may be a useful quantitative value in ecological investigations. We are now analysing other species of different anatomical and ecological qualities as well as of different systematic positions. Furthermore, the influence of the water content of tissues and of turgor pressure on the mechanical properties in the herbaceous species can be investigated by the methods described. Some preliminary results were published earlier (Kull and Herbig, 1989) and some reflections on possible ecological applications of the method are discussed by Kull (1990). Furthermore, the *Bic*-values of plant axes may be included in general *Bic*/ λ -diagrams (for example Otto, 1985a) and in this way compared directly with other constructions in nature and engineering.

ACKNOWLEDGEMENTS

Thanks are due to Dr R. Blum for stress-strain measurements, to Dr Martin Schliephacke and Dipl.-Biol. Ulrike Vallon for experimental help, to Dr L. Wessolly for valuable discussions, and to Mrs B. Solis-Schreiter for correction of the English. This work was supported by the Deutsche Forschungsgemeinschaft (SFB 230: Natürliche Konstruktionen).

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