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Biomechanics of plant stems with square and circular cross-sections: what is the advantage of quadratic stems over cylindrical ones?

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Although plant stem cross-sections are most often circular, some are square, triangular or elliptic, but these are rare. The advantage of quadratic stems over cylindrical ones, if one exists, is unclear. Here we propose a (bio) mechanical advantage of square-stemmed plants. Our idea is based on the fact that the second moment of inertia I of a stem, depending on the shape of the cross-section, determines the plant's resistance to bending and torsion deformations induced by wind load and gravitation: a larger I results in greater mechanical resistance. When can a quadratic stem have a larger I than a cylindrical stem of comparable material? We calculated the rotation-invariant I of quadratic and cylindrical hollow stems with the same cross-section area as functions of the quotient k of the inner and outer dimensions, and the quotient Q of the outer dimensions of square and circlular stems. We determined those configurations of the geometric control parameters k and Q for which the I of a quadratic stem is larger than that of a cylindrical one; that is, the former stem is more resistant to mechanical deformations than the latter. This finding provides a clear mechanical benefit of square-stemmed over circle-stemmed plants.

1. Introduction

Plant stems connect above- and under-ground leaves and roots, and have several important functions,

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including mechanical support, material transport and storage, for example. Their anatomical variability ensures the diversity and success of plants in various ecosystems [1].

The stem of the majority of plants is cylindrical with a circular cross-section. Table 2 in appendix A lists 10 well-known circle-stemmed plant species. The dominance of circular cross-sections suggests that this rotation-invariant stem shape may have certain advantages compared to other cross-section shapes. The stem has to endure, without fracture, the bending and torsion deformations induced by wind load and gravitation. The greater the second moment of inertia I of the stem's cross-section, the more it resists against both forms of deformation. This is well known in mechanics [2–5]. As a first approximation, we could think that if the direction of wind hitting a plant of near rotation-symmetric shape is random, then owing to the nearly rotation-invariant strains, the most mechanically advantageous stem shape is cylindrical, because the I of a circular cross-section is clearly independent of the orientation of the stem's axis crossing the circle's centre.

However, several plant species have square (figures 1 and 2), triangular or elliptic stem cross-section [6–15]. Table 2 in appendix A lists the Latin and English names of 84 flower species with a square stem. Although square-stemmed plants are much rarer than circular-stemmed varieties, the former are more prevalent than plants with triangular or elliptic stems. Here we mention only five species with triangular stem [16]: *Vaccinium myrtillus* (bilberry), *Allium ursinum* (ramsons), *Leucojum aestivum* (summer snowflake), *Carex riparia* (greater pond-sedge) and *Sagittaria sagittifolia* (arrowhead). Flowers with elliptic stems are, for instance, *Cystopteris fragilis* (brittle bladder-fern), *Potamogeton crispus* (curled pondweed), *Asplenium marinum* (sea spleenwort), *Clematis vitalba* (traveller's joy), *Clematis flammula* (virgin's bower) [17]. Many species of square-stemmed plants are frequently observable in parks, gardens and meadows.

The evolutionary advantage of plant stems with square, triangle or elliptic cross-sections over cylindrical stems is not yet clarified. According to Shima *et al.* [18], the reason why certain plants have a polygonal cross-section, rather than a circular, could be that this may aid phyllotaxis formation, helping to identify the site of leaf formation. Furthermore, a polygonal shape might provide improved cross-sectional mechanical performance. Inspired by the square bamboo (*Chimonobambusa quadrangularis*), Shima *et al.* [18] proposed a mathematical description of the rounded squares observed in the cross-section of this bamboo species, possessing rounded sides and filleted corners.

The aim of this work is to reveal a possible mechanical advantage of quadratic plant stems. Here, we compare the moments of inertia I_{square} and I_{circle} of hollow quadratic and cylindrical stems having the same cross-section area F, as functions of the quotient k of the inner and outer dimensions, and the quotient Q of the outer dimensions of the square and circle stems. We determine those configurations of the geometric control parameters k and Q for which the I of a quadratic stem is larger than that of a cylindrical one [19]. We show that the former stem is more resistant to mechanical deformations than the latter, which marks an evolutionary advantage for square-stemmed plants.

2. Calculation methods

For the purpose of easier traceability of our comprehensive calculations presented here, table 1 lists a summary of the parameters, symbols, mathematical expressions, conditions and limits used in this section as well as in appendices B–D. Our goal is to determine the second moment of inertia I of quadratic and cylindrical hollow plant stems of equal cross-section area. A larger value of I ensures greater resistance of the stem to bending and torsion deformations induced by wind load and gravitation.

Figure 1. Four examples for flowers with stems of square cross-section: (*a*) Jerusalem sage, *Phlomis russeliana*, (*b*) Argentinian vervain, *Verbena bonariensis*, (*c*) catmint, *Nepeta*×*faassenii*, (*d*) balkan clary, *Salvia nemorosa* (photos taken by Gábor Horváth).

Figure 2. Flowers, stems, leaves (*a*) and the square cross-section of the cup plant, *Silphium perfoliatum* (*b*) (photos taken by Gábor Horváth).

Table 1. Definition of parameters, symbols, expressions, conditions and limits determining the second moment of inertia *I* of quadratic and cylindrical hollow plant stems with the same area *F* of their square and circular cross-sections.

parameters	symbols and expressions
inner side length of a square collar	$a_{\text{inner,square}}$
outer side length of a square collar	$a_{\text{outer,square}} \equiv a_{\text{square}}$
quotient of the inner and outer side lengths of a square collar	$k_{\text{square}} = \frac{a_{\text{inner,square}}}{a_{\text{outer,square}}} = \frac{a_{\text{inner,square}}}{a_{\text{square}}}$
inner diameter of a circular collar (annulus)	$a_{\text{inner,circle}}$
outer diameter of a circular collar (annulus)	$a_{\text{outer,circle}} \equiv a_{\text{circle}}$
quotient of the inner and outer diameters of a circular collar (annulus)	$k_{\text{circle}} = \frac{a_{\text{inner,circle}}}{a_{\text{outer,circle}}} = \frac{a_{\text{inner,circle}}}{a_{\text{circle}}}$
quotient of the outer side length of a square stem and the outer diameter of a circle stem	$Q = \frac{a_{\text{outer,square}}}{a_{\text{outer,circle}}} = \frac{a_{\text{square}}}{a_{\text{circle}}}$
area of a square collar	$F_{\text{square}}(a_{\text{square}}, k_{\text{square}}) = a_{\text{square}}^2(1 - k_{\text{square}}^2)$
area of a circle collar	$F_{\text{circle}}(a_{\text{circle}}, k_{\text{circle}}) = \frac{\pi a_{\text{circle}}^2(1 - k_{\text{circle}}^2)}{4}$
conditions	**limits of Q**
from condition $J(k_{\text{circle},Q}) \geq 0$ follows	$Q \geq g(k_{\text{circle}}) = \sqrt{\frac{\pi(1 - k_{\text{square}}^2)}{8}}$
from condition $1 - \pi(1 - k_{\text{circle}}^2)/4Q^2 \geq 0$ it follows	$Q \geq q(k_{\text{circle}}) = \sqrt{\frac{\pi(1 - k_{\text{square}}^2)}{4}}$
from condition $J(k_{\text{square}}, Q) \geq 0$ follows	$Q \geq f(k_{\text{square}}) = \sqrt{\frac{\pi}{2(1 - k_{\text{square}}^2)}}$
from condition $1 - 4Q^2(1 - k_{\text{square}}^2)/\pi \geq 0$ it follows	$Q \leq \sqrt{\frac{\pi}{4(1 - k_{\text{square}}^2)}} = h(k_{\text{square}}) = \frac{f(k_{\text{square}})}{\sqrt{2}}$
moment of inertia	**symbols and expressions**
moment of inertia of a square collar	$I_{\text{square}}(a_{\text{square}}, k_{\text{square}}) = \frac{a_{\text{square}}^4(1 - k_{\text{square}}^4)}{12}$
moment of inertia of a circle collar	$I_{\text{circle}}(a_{\text{circle}}, k_{\text{circle}}) = \frac{\pi a_{\text{circle}}^4(1 - k_{\text{circle}}^4)}{64}$
quotient of the moments of inertia of square and circle collars	$J = \frac{I_{\text{square}}}{I_{\text{circle}}}$

(a) Moment of inertia of a square rotated by angle *α*

Consider a square of side length a_{square}, one of the sides of which closes an angle α with the neutral axis NN coinciding with axis x crossing the square's geometrical centre O, shown in figure 3*a*. And let us determine the moment of inertia I_{square} of this square for NN. The moments of inertia I_{u} and I_{v} of this square for the orthogonal axes v and u shown in figure 3*a* closing an angle α with axes y and x are

$$I_u = I_v = \frac{a_{\text{square}}^4}{12}. \tag{2.1}$$

Using equation (2.1) and equation (C 3) in appendix C, we obtain

$$I_u + I_v = \frac{a^4_{square}}{6} = I_x + I_y, \tag{2.2}$$

$$I_x \cos^2\alpha + I_y \sin^2\alpha - \sin 2\alpha \int_A xy\,dA = \frac{a^4_{square}}{12}. \tag{2.3}$$

From equations (2.2) and (2.3), we get

$$I_x = I_{square}(a_{square}, \alpha) = \frac{a^4_{square}}{12} + \frac{\sin 2\alpha \iint_A xy\,dx\,dy}{\cos^2\alpha - \sin^2\alpha} = \frac{a^4_{square}}{12}, \tag{2.4}$$

because according to figure 3*b* and owing to the fourfold symmetry of the square,

$$I_{xy} = \iint_A xy\,dx\,dy = 0. \tag{2.5}$$

The explanation of this is as follows: in figure 3*b*, the uniform-shaped yellow and orange, as well as bright and dark green tetragons are each other's 90° rotations around the origin O. The product $+x \cdot +y = xy$ of the coordinates of point A($+x$,$+y$) is exactly the opposite of the coordinate product $-x \cdot +y = xy$ of point B($-x$,$+y$). The same is true for the coordinate products $-x \cdot -y = xy$ and $+x \cdot -y = -xy$ of points C($-x$, $-y$) and D($+x$, $-y$), respectively. Therefore, and owing to the fourfold symmetric form identity of these tetragons, calculating the integral of equation (2.5) for the whole square area, each pair of opposite-signed coordinate products of point pairs A and B, as well as C and D eliminate each other, resulting in the disappearance of the integral in equation (2.5).

Hence, on the basis of equation (2.4), a square with side length a_{square} has a constant moment of inertia $I_{square} = a^4_{square}/12$, independently of the orientation α of the axis crossing the square centre O.

(b) Moments of inertia of square and circlular collars

The cross-sections of plant stems studied in this work have either a square- (figure 4*a*) or a circular- (figure 4*b*) collar shape, or in special cases a full (i.e. filled) square or circular shape. Let the outer and inner side lengths of the square collar be $a_{outer,square} \equiv a_{square}$ and $a_{inner,square} = k_{square} a_{outer,square} = k_{square} a_{square}$ ($0 \le k_{square} = a_{inner,square}/a_{outer,square} < 1$), respectively. Using equation (2.4), the moment of inertia $I_{square}(a_{square}, k_{square})$ of this square collar is the difference of the moments of inertia $I_{square}(a_{square})$ and $I_{square}(k_{square} a_{square})$ of the outer and inner squares shown in figure 4*a*:

$$I_{square}(a_{square}, k_{square}) = \frac{a^4_{square}(1 - k^4_{square})}{12}, \quad 0 \le k_{square} < 1. \tag{2.6}$$

The moment of inertia $I_{circle}(a_{circle})$ of a circle with diameter a_{circle} is [2,4]

$$I_{circle}(a_{circle}) = \frac{\pi a^4_{circle}}{64}. \tag{2.7}$$

Let the outer and inner diameters of the circular collar in figure 4*b* be a_{circle} and $k_{circle} a_{circle}$ ($0 \le k_{circle} < 1$), respectively. Using equation (2.7), the moment of inertia $I_{circle}(a_{circle}, k_{circle})$ of this circular collar is the difference of the moments of inertia $I_{circle}(a_{circle})$ and $I_{circle}(k_{circle} a_{circle})$ of the outer and inner circles:

$$I_{circle}(a_{circle}, k_{circle}) = \frac{\pi a^4_{circle}(1 - k^4_{circle})}{64}, \quad 0 \le k_{circle} < 1. \tag{2.8}$$

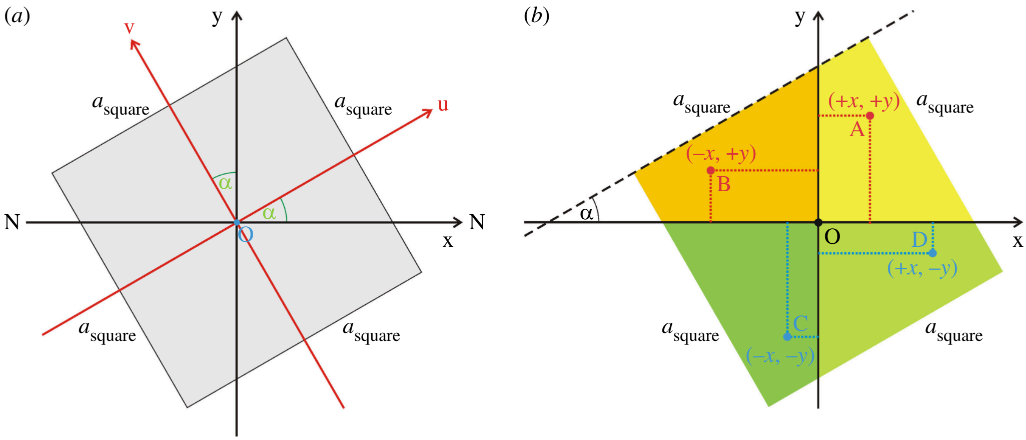

Figure 3. (*a*) Calculation of the moment of inertia I_{square} of a square (grey) for the neutral axis NN coinciding with axis x, when the side length a_{square} is rotated by angle a from axes x and y around the origin O. (*b*) For justification of the zero value of integral $I_{xy} = \iint_A xy\mathrm{d}x\mathrm{d}y = 0$ occurring in the calculation of I_{square}.

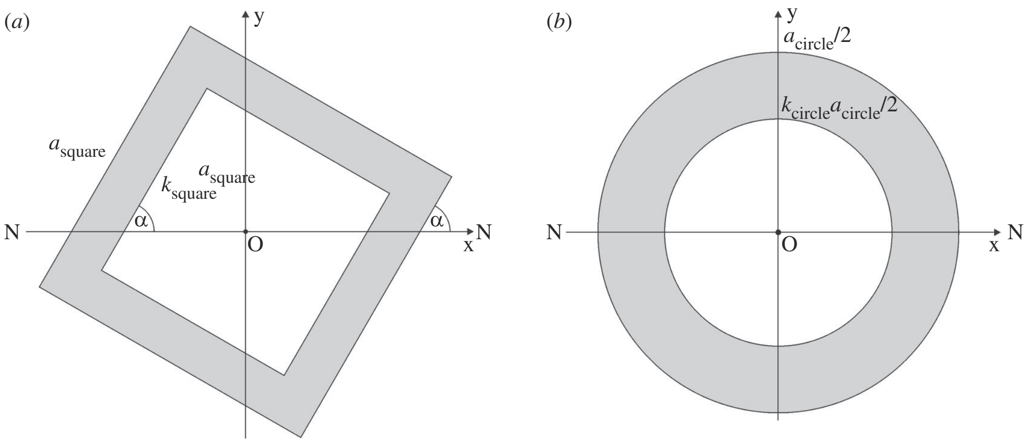

Figure 4. (*a*) A square collar, the outer side length a_{square} of which is rotated by angle a around the geometrical centre O, and its inner side length is $k_{square}a_{square}$ with $0 \le k_{square} < 1$. (*b*) A circle collar, the outer diameter of which is a_{circle} and the inner diameter is $k_{circle}a_{circle}$ with $0 \le k_{circle} < 1$. For both collars, the neutral axis NN coincides with axis x crossing O.

(c) Calculation of moments of inertia of square and circlular collars with the same area

Consider a cylindrical and a quadratic plant stem of equal length composed from the same amount of plant material, that is, having the same area F of their circlular- and square-collar cross-sections:

$$F_{circle}(a_{circle}, k_{circle}) = F_{square}(a_{square}, k_{square}), \quad 0 \le k_{circle} < 1, \quad 0 \le k_{square} < 1. \tag{2.9}$$

The areas of these collars are as follows:

$$F_{circle}(a_{circle}, k_{circle}) = \frac{\Pi a_{circle}^2(1 - k_{circle}^2)}{4}, \quad F_{square}(a_{square}, k_{square}) = a_{square}^2\left(1 - k_{square}^2\right). \tag{2.10}$$

From equations (2.9) and (2.10), we obtain

$$k_{\text{square}}(k_{\text{circle}}, Q) = \sqrt{1 - \frac{\pi(1-k_{\text{circle}}^2)}{4Q^2}}, \quad Q = \frac{a_{\text{square}}}{a_{\text{circle}}},$$

$$k_{\text{square}}(k_{\text{circle}} = 1, Q) = 1, \quad k_{\text{square}}(k_{\text{circle}} = 0, Q) = \sqrt{1 - \frac{\pi}{4Q^2}}. \tag{2.11}$$

Using equations (2.6), (2.8) and (2.11), we get

$$I_{\text{square}} = \frac{Q^4 a_{\text{circle}}^4}{12}\left\{1 - \left[1 - \frac{\pi\left(1-k_{\text{circle}}^2\right)}{4Q^2}\right]^2\right\}, \quad Q = \frac{a_{\text{square}}}{a_{\text{circle}}}. \tag{2.12}$$

Dividing equation (2.12) by equation (2.8), we obtain the quotient J of the moments of inertia I_{square} and I_{circle} of the cross-section of quadratic and cylindrical plant stems:

$$J(k_{\text{circle}}, Q) = \frac{I_{\text{square}}}{I_{\text{circle}}} = \frac{16Q^4}{3\pi\left(1-k_{\text{circle}}^4\right)}\left\{1 - \left[1 - \frac{\pi\left(1-k_{\text{circle}}^4\right)}{4Q^2}\right]^2\right\}, \quad 0 \le k_{\text{circle}} < 1, Q = \frac{a_{\text{square}}}{a_{\text{circle}}}. \tag{2.13}$$

From the criterion $J(k_{\text{circle}}, Q) = I_{\text{square}}/I_{\text{circle}} \ge 0$, it follows that

$$Q \ge \sqrt{\frac{\pi\left(1-k_{\text{circle}}^2\right)}{8}} = g(k_{\text{circle}}), \quad g_{\text{min}} = g(k_{\text{circle}=1}) = 0, \quad g_{\text{max}} = g(k_{\text{circle}=0}) = \sqrt{\frac{\pi}{8}} \approx 0.6267, \tag{2.14}$$

which means that the lower limit of $Q = a_{\text{square}}/a_{\text{circle}}$ is the function $g(k_{\text{circle}})$ decribed by [14]. From the condition that the argument under the square root in equation (2.11) describing $k_{\text{square}}(k_{\text{circle}}, Q)$ cannot be negative, that is, from the criterion $1 - \pi\left(1-k_{\text{circle}}^2\right)/4Q^2 \ge 0$, we obtain the following limit:

$$Q \ge \sqrt{\frac{\pi\left(1-k_{\text{circle}}^2\right)}{4}} = q(k_{\text{circle}}),$$

$$q_{\text{min}} = q(k_{\text{circle}} = 1) = 0, \quad q_{\text{max}} = q(k_{\text{circle}} = 0) = 0 = \sqrt{\frac{\pi}{4}} \approx 0.8862. \tag{2.15}$$

Since $q(k_{\text{circle}}) = \sqrt{\pi\left(1-k_{\text{circle}}^2\right)/4} > g(k_{\text{circle}}) = \sqrt{\pi\left(1-k_{\text{circle}}^2\right)/8}$, the condition $Q \ge q(k_{\text{circle}})$ is the stronger lower limit which determines the possible Q values. In the case of $F_{\text{circle}} = F_{\text{square}} = F$, from equation (2.10), we get

$$a_{\text{circle}}(k_{\text{circle}}, F) = \sqrt{\frac{4}{\pi}} \cdot \sqrt{\frac{F}{1-k_{\text{circle}}^2}}, \quad a_{\text{circle,min}}(k_{\text{circle}} = 0, F) = \sqrt{\frac{4}{\backslash\text{pi}}} \cdot \sqrt{F},$$

$$a_{\text{square}}(k_{\text{square}}, F) = \sqrt{\frac{F}{1-k_{\text{square}}^2}}, \quad a_{\text{square,min}}(k_{\text{square}} = 0, F) = \sqrt{F}. \tag{2.16}$$

Using equations (2.6), (2.8) and (2.11), we get

$$J\left(k_{\text{square}}, Q\right) = \frac{I_{\text{square}}}{I_{\text{circle}}} = \frac{4\pi Q^2\left(1+k_{\text{square}}^2\right)}{6\pi - 12Q^2\left(1-k_{\text{square}}^2\right)}, \quad 0 \le k_{\text{square}} < 1, \quad Q = \frac{a_{\text{square}}}{a_{\text{circle}}}. \tag{2.17}$$

From the condition $J(k_{\text{square}}, Q) = I_{\text{square}}/I_{\text{circle}} \ge 0$, it follows that

$$Q \le \sqrt{\frac{\pi}{2\left(1-k_{\text{square}}^2\right)}} = f\left(k_{\text{square}}\right),$$

$$f_{min} = f\left(k_{\text{square}} = 0\right) = \sqrt{\frac{\pi}{2}} \approx 1.2533, \quad f_{max} = f\left(k_{\text{square}} = 1\right) = \infty, \tag{2.18}$$

which means that one of the upper limits of $Q = a_{\text{square}}/a_{\text{circle}}$ is the function $f(k_{\text{square}})$ decribed by equation (2.18). On the other hand, from equation (2.11) we obtain

$$k_{\text{circle}}(k_{\text{square}}, Q) = \sqrt{1 - \frac{4Q^2(1-k_{square}^2)}{\pi}}, \quad Q = \frac{a_{\text{square}}}{a_{\text{circle}}},$$

$$k_{\text{circle}}(k_{\text{square}} = 1, Q) = 1, \quad k_{\text{circle}}(k_{\text{square}} = 0, Q) = \sqrt{1 - \frac{4Q^2}{\pi}}. \tag{2.19}$$

From the condition that the argument under the square root in equation (2.19) describing $k_{\text{circle}}(k_{\text{square}}, Q)$ cannot be negative, that is, from the criterion $1 - 4Q^2(1-k_{square}^2)/\pi \geq 0$, we obtain the following second limit:

$$Q \leq \sqrt{\frac{\pi}{4(1-k_{\text{square}}^2)}} = h(k_{\text{square}}) = \frac{f(k_{\text{square}})}{\sqrt{2}},$$

$$h_{\max} = h(k_{\text{square}} = 1) = \infty, \quad h_{\min} = h(k_{\text{square}} = 0) = \frac{\sqrt{\pi}}{2} = 0.8862. \tag{2.20}$$

Hence, there are two upper limits of Q, that is, functions $f(k_{\text{square}})$ and $h(k_{\text{square}})$ described by equations (2.18) and (2.20), respectively. Since $h(k_{\text{square}})$=$f(k_{\text{square}})/\sqrt{2}$, that is $h(k_{\text{square}}) < f(k_{\text{square}})$, therefore the smaller upper limit $h(k_{\text{square}})$ is the stronger.

3. Results

Figure 5 shows the relation $k_{\text{square}}(k_{\text{circle}}, Q)$ between variables k_{square} and k_{circle} decribed by equation (2.11) for three different Q values. The curve with $Q_1 = 0.5$ does not reach the horizontal axis of k_{circle}, because according to equation (2.15), the numerical value pairs (Q, k_{circle}) falling in the prohibited area below curve $q(k_{\text{circle}})$ cannot occur.

Figure 6 displays the diameter $a_{\text{circle}}(k_{\text{circle}}, F)$ of a cylindrical plant stem and the side length $a_{\text{square}}(k_{\text{square}}, F)$ of a quadratic plant stem versus k_{circle} and k_{square} for a given cross-section area $F = 0.1\ \text{m}^2$.

Figure 7*a* shows the values of quotient $J = I_{\text{square}}/I_{\text{circle}}$ calculated from equation (2.13) as functions of the variables $k_{\text{circle}} = a_{\text{circle,inner}}/a_{\text{circle}}$ and $Q = a_{\text{square}}/a_{\text{circle}}$. If $J = I_{\text{square}}/I_{\text{circle}} > 1$, then with the same cross-section area (i.e. with uniform plant material), the quadratic plant stem is more resistant to bending and torsion than the cylindrical stem, which means a biomechanical advantage for square-stemmed plants over circle-stemmed ones. In figure 7*a*, we can see that for all $0 \leq k_{\text{circle}} < 1$ values, $J = I_{\text{square}}/I_{\text{circle}} > 1$ in the green region of the Q–k_{circle} domain above curve $z(k_{\text{circle}})$ given by equation (D 1) (given in appendix D) and curve $q(k_{\text{circle}})$ is described by equation (2.15), while $J = I_{\text{square}}/I_{\text{circle}} < 1$ is in the red region between curves $z(k_{\text{circle}})$ and $q(k_{\text{circle}})$. Hence, in the green and red regions, the quadractic and the cylindrical stems are the stronger. Figure 7*b* presents examples for the shapes of plant stems with square- and circular-collar cross-sections of the same area versus some values of variables Q and k_{circle}.

Figure 8*a* displays the values of $J(k_{\text{square}}, Q) = I_{\text{square}}/I_{\text{circle}}$ calculated from equation (2.17) versus the variables $k_{\text{square}} = a_{\text{square,inner}}/a_{\text{square}}$ and $Q = a_{\text{square}}/a_{\text{circle}}$. Here it is true again that if $J(k_{\text{square}}, Q) = I_{\text{square}}/I_{\text{circle}} > 1$, then the quadratic plant stem is mechanically stronger than the cylindrical stem in the case equal cross-section area. According to figure 8*a*, $J(k_{\text{square}}, Q) = I_{\text{square}}/I_{\text{circle}} > 1$ in the green region of the Q-k_{square} domain between curve $h(k_{\text{square}})$ described by equation (2.20) and curve $p(k_{\text{square}})$, given by the equation (D 2) (see Appendix D), while $J(k_{\text{square}}, Q) = I_{\text{square}}/I_{\text{circle}} < 1$ is true for the red region below curve $p(k_{\text{square}})$. Hence, in the green region, quadratic plant stems are mechanically more advantageous than cylindrical stems, and vice versa in the red region. Figure 8*b* presents examples for the shapes of plant stems with square- and circlular-collar cross-sections of equal area versus some values of variables Q and k_{square}.

Hence, in the upper green region of domains Q-k_{circle} and Q-k_{square} in figures 7*a* and 8*a*, quadratic plant stems endure the strains induced by wind load and gravitation better than

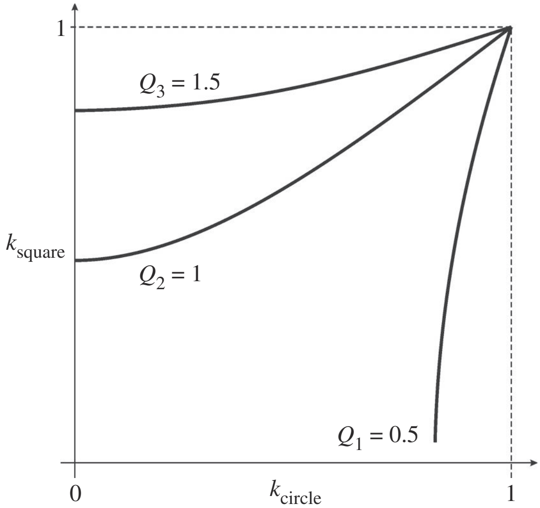

Figure 5. Curves $k_{square}(k_{circle}, Q = a_{square}/a_{circle})$ for $Q_1 = 0.5$, $Q_2 = 1$ and $Q_3 = 1.5$ calculated from equation (2.11).

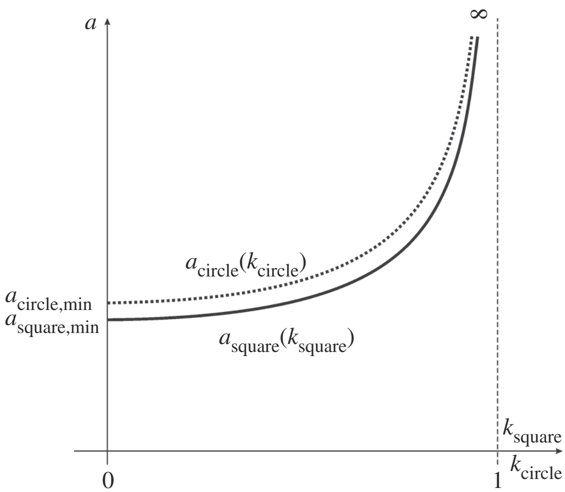

Figure 6. Diameter $a_{circle}(k_{circle}, f)$ and side length $a_{square}(k_{square}, f)$ of cylindrical and quadratic plant stems described by equation (2.16) for the same cross-section area $F = 0.1\ m^2$ as functions of $0 \leq k_{circle} \neq k_{square} < 1$, where the relation between k_{square} and k_{circle} is described by equation (2.11).

cylindrical plant stems, while in the lower red region the opposite is true. This finding serves an explanation of the mechanical advantage of quadratic plant stems against cylindrical ones.

4. Discussion

Stems function as supports for plants but also carry food and water. There are many biomechanical and physiological reasons of the enormous variation between stems from grass blades to tree trunks, how they form and work, what happens inside them, why easily bent stems and stiff stems can give plants different advantages, why stems grow sideways, etc [3,8,20–22]. This variability and adaptation of stems allow plants to survive in different habitats and conditions. Supporting mechanics is only one of the several vital roles of stems. In this work we studied

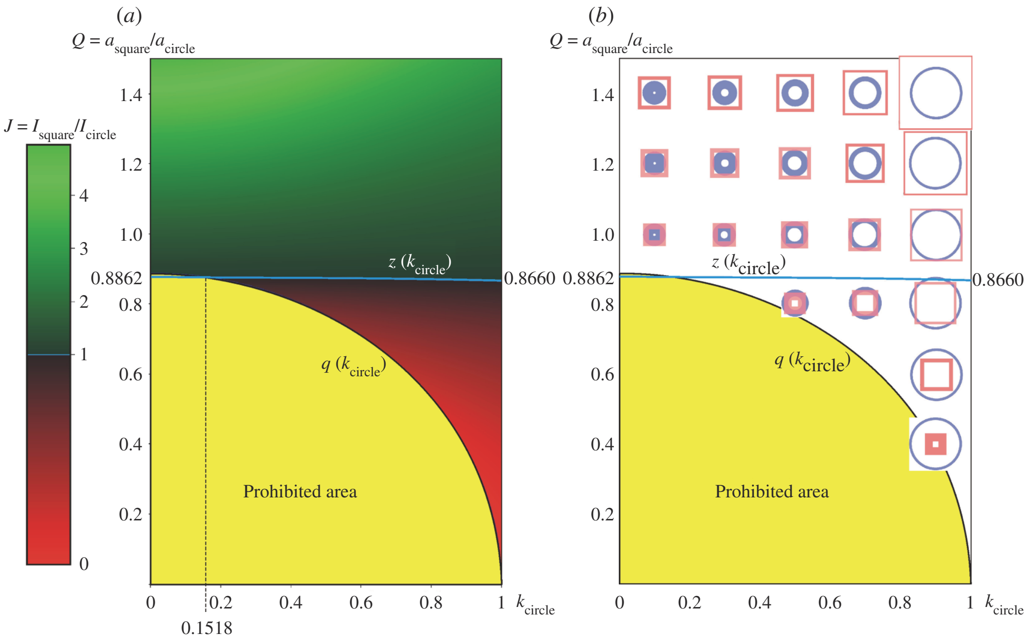

Figure 7. (*a*) Colour-coded values of $J(Q, k_{circle}) = I_{square}/I_{circle}$ calculated for the same cross-section area from equation (2.13) as functions of $Q = a_{square}/a_{circle}$ and $k_{circle} = a_{circle,inner}/a_{circle}$, where the equation of the boundary curve $q(k_{circle})$ of variable Q is given by equation (2.15), and equation (D 1) describes the curve $z(k_{circle})$ along which $J(Q, k_{circle}) = 1$. The colour shade is green or red, if $J(Q, k_{circle})>1$ or $J(Q, k_{circle}) < 1$, respectively. According to equation (2.15), numerical value pairs (Q, k_{circle}) falling in the yellow prohibited area below curve $q(k_{circle})$ cannot occur. (*b*) Cross-section shapes of quadratic (pink) and cylindrical (blue) plant stems with the same area displayed for 20 different (Q, k_{circle}) value pairs.

only one aspect of the structure and mechanics of plant stems, that is, a possible mechanical advantage of quadratic stems against cylindrical ones.

The cross-section of plant stems is most often circular, but there exist also square, triangle and elliptic cross-section shapes, although the latter are quite rare. The benefits of the most common cylindrical stems compared to other cross-section shapes is not well understood. In this work, we started from the fact that the moment of inertia I of a plant stem — depending on the shape of its cross-section—determines the resistance of the stem to the mechanical (bending and torsion) deformations induced by the wind load and gravitation. Since a larger I results in greater resistance, therefore, for the same material (i.e. cross-section area) there are certain quadratic stems which have larger I than cylindrical ones.

We have calculated and compared the moments of inertia I_{square} and I_{circle} of plant stems with square- and circular-collar cross-sections of the same area (material use) as functions of $k_{circle} = a_{circle,inner}/a_{circle}$, $k_{square} = a_{square,inner}/a_{square}$ and $Q = a_{square}/a_{circle}$ (table 1). We found that I_{square} and I_{circle} are rotation invariant, that is they are independent of the orientation of the axis crossing the geometrical centre of these collars.

We found for any $0 \le k_{circle} < 1$ value, that in the Q–k_{circle} variable domain (figure 7*a*), the region above curves $z(k_{circle})$ and $q(k_{circle})$, the quotient $J(Q, k_{circle}) = I_{square}/I_{circle}$ is larger than 1, while in the region between curves $z(k_{circle})$ and $q(k_{circle})$, this quotient is smaller than 1. Thus, in the former variable region, the quadratic stem shape is better, because it has a larger moment of inertia, and therefore is more resistant to mechanical deformations, while in the latter region the cylindrical stem shape is more resistant.

We also found for any $0 \le k_{square} < 1$ value, that in the region between curves $p(k_{square})$ and $h(k_{square})$ of the Q–k_{square} variable domain (figure 8*a*), the quotient $J(Q, k_{square}) = I_{square}/I_{circle}$ is larger than 1, while in the region below curve $p(k_{square})$ this quotient is smaller than 1.

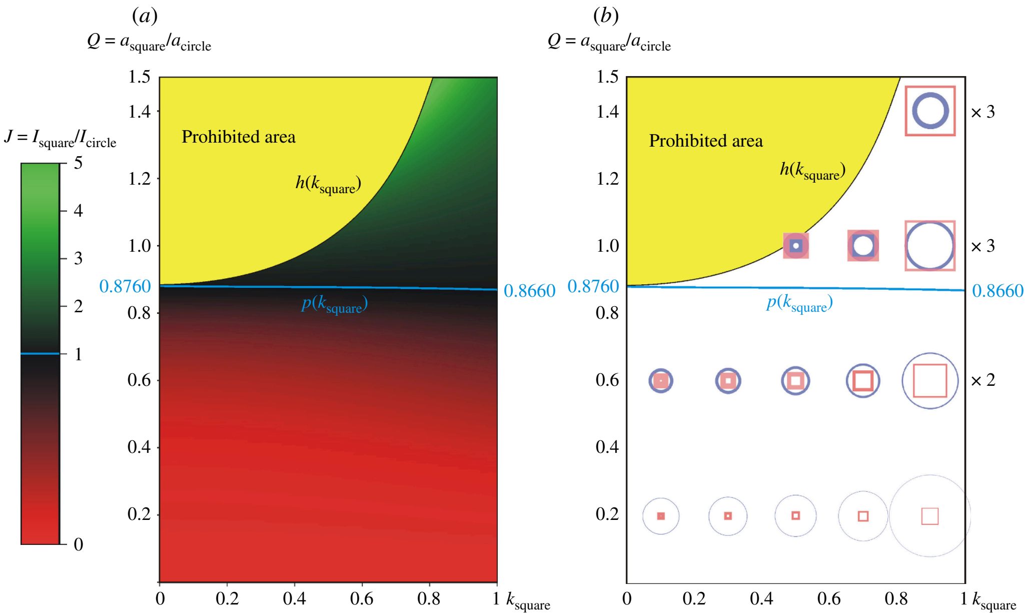

Figure 8. (*a*) Colour-coded values of $J(Q, k_{square}) = I_{square}/I_{circle}$ calculated for the same cross-section area from (2.17) as functions of $Q = a_{square}/a_{circle}$ and $k_{square} = a_{square,inner}/a_{square}$, where the equation of the upper boundary curve $h(k_{square})$ of variable Q is given by (2.20), and (D 2) in appendix D describes the curve $p(k_{square})$ along which $J(Q, k_{square}) = 1$. The colour shade is green or red, if $J(Q, k_{square}) > 1$ or $J(Q, k_{square}) < 1$, respectively, while the prohibited area of the Q–k_{circle} domain is coloured by yellow. According to (2.20), numerical value pairs (Q, k_{square}) falling in the yellow prohibited area above curve $h(k_{square})$ cannot occur. (*b*) Cross-sectional shapes of quadratic (pink) and cylindrical (blue) plant stems with the same area displayed for 18 different (Q, k_{square}) value pairs. With the aim of a better visualization, in the row with $Q = 0.6$ the shapes are enlarged by factor 2 (×2), while in rows with $Q = 1$ and $Q = 1.4$ by factor 3 (×3).

Consequently, in the former variable region, the quadratic plant stems are more resistant to bending and torsion deformations, while in the latter region, the cylindrical stems are more resistant.

The results presented here quantify the values of the relative stem width $Q = a_{square}/a_{circle}$ at which a quadratic plant stem is stronger ($J = I_{square}/I_{circle} > 1$) than a cylindrical stem for a given cross-section area F, and for a particular parameter pair k_{square} and k_{circle} being not independent of each other. However, there is still no explanation as to why the plant in question does not have such configurations of the parameter pair k_{circle} and a_{circle} for which the cylindrical stem is stronger than the quadratic one ($J = I_{square}/I_{circle} < 1$), and therefore the stem is cylindrical instead of quadratic. There may still be unknown biological (plant physiological) reasons for this that precludes the realization of the configurations of the parameter pair k_{circle} and a_{circle}, which ensures the mechanical advantage of the cylindrical stem.

Following our analytical calculations a practical question arose. To what extent do our theoretical results match the cross-sectional shapes of actual plant stems? To answer this question, it would be necessary to know the ranges of parameters $k_{circle} = a_{circle,inner}/a_{circle}$ (figure 7) and $k_{square} = a_{square,inner}/a_{square}$ (figure 8) of plant species with circular and square hollow stems (tables 2 and 3 in appendix A). However, such comprehensive plant-anatomical data are not available in the literature. Similar measurements have already been performed on human and animal gas- and marrow-filled long bones: to test the biomechanical optimality of the wall thickness of cylindrical hollow limb bones (humeri, femora, tibiotarsi) in the red fox (*Vulpes vulpes*) [23], in human mummies [24], as well as in crows (*Corvus corone cornix*) and magpies (*Pica pica*) [25]. The values of $k = a_{inner\ diameter}/a_{outer\ diameter}$ were measured along these bones from X-ray photographs. It is a task of future studies to measure the values of k_{circle} and k_{square} on cylindrical and quadratic plant stems.

In real plants, the stems are often hard near the epidermis and soft inside. In our analytical calculations, we did not take into consideration the possible change of hardness (i.e. Young's modulus E and shear modulus G) of the stem material along the cross-section. For mathematical simplicity, we considered the stem material to be uniform, that is, homogenous and anisotropic. A future improvement of our theoretical calculations should take into account such non-uniformity of hardness in cross-sectional structures of real plant stems. However, to this end, the spatial distribution of E and G should be measured along the cross-section, which is a challenging biometric task. It would be difficult to predict quantitatively the influence of such non-uniformity on the moments of inertia I_{square} and I_{circle} of quadratic and cylindrical plant stems, and thus, on the main results presented here (figures 7 and 8). Nevertheless, we assume that in case of non-uniform stems, the quotient $J = I_{\text{square}}/I_{\text{circle}}$ may have qualitatively similar characteristics (i.e. dependence on Q, k_{square} and k_{circle}) to those of uniform stems (figures 7 and 8) found in this work.

Here, we have concentrated on the comparison of the moments of inertia I_{square} and I_{circle} of quadratic and cylindrical hollow plant stems possessing concentric squares or circles, respectively, as outer and inner boundaries of the plant material, because the majority of hollow stems have such a concentric structure. We determined those values of the control parameters k and Q (table 1) of the cross-section shape of quadratic and cylindrical stems with the same area, for which $I_{\text{square}} > I_{\text{circle}}$, meaning that the former stems are more resistant to bending and torsion deformations induced by wind load and gravitation than the latter stems.

Similarly to the present work, Shima *et al*. [18] calculated the moment of inertia of a rounded square with rounded edges and fillet corners. From this they derived the so-called improvement ratio $\eta = (R_{\text{rs}} - R_{\text{a}})/R_{\text{a}}$ as a function of the cross-sectional shape, ranging from an exact circle to an exact square with sharp vertices. Here, $R_{\text{rs}} = \sqrt{I_{\text{rs}}/A}$ and I_{rs} are, respectively, the gyration radius and moment of inertia of the plant material sandwiched by two concentrically arranged rounded squares, while $R_{\text{a}} = \sqrt{I_{\text{a}}/A}$ and I_{a} are, respectively, the gyration radius and momentum of an annulus with the same cross-section area A as the rounded square. The gyration radius measures the buckling resistance of a column under axial compression. If $\eta > 0$, then $R_{\text{rs}} > R_{\text{a}}$, that is, $I_{\text{rs}} > I_{\text{a}}$, therefore the stem with a rounded square cross-section is more resistant to buckling than that of the cylindrical stem.

Indirectly, through the gyration radius, Shima *et al*. [18] compared practically the moments of inertia of an annulus and a collar between two concentric rounded squares with the same area of annulus and collar versus the following four geometric parameters: (i) radius a of a circle with the same area as the rounded square, (ii) side length ℓ of a reference square within the rounded square, (iii) angle θ between a straight line passing through the upper-right vertex of the reference square and the square's horizontal side, and (iv) distance h of the vertex from the rounded square along the straight line; a determines the same area of the annulus and the rounded square collar, ℓ and h control the dimensions of the inner reference square and the outer rounded square, while θ controls the roundness of the latter.

Shima *et al*. [18] calculated the improvement ratio η (involving the moments of inertia) versus the same aforementioned four parameters. They found that, to obtain a greater η, it is advantageous to make the outer boundary of the hollow stem more square while making the inner boundary more circular. This general result relates to the earlier special finding of Gere & Timoshenko [26], who showed that the cross-sectional performance (i.e. resistance to mechanical deformations) is highest when the outer boundary is that of a square with sharp vertices and the inner boundary is a circle. In the opinion of Shima *et al*. [18], an exact square may not be preferred as the outer boundary, because when the hollow column bends, stress concentrations occur around acute vertices, so that locally it may break. They suggested that to prevent local breaking, fillet corners represent the best solution. They demonstrated that such filleted corners do not significantly reduce the cross-sectional moment of inertia I of the hollow square column.

To summarize: although using various approaches with different geometrical parameters, Shima *et al*. [18], and we in this work, compared indirectly/directly the moments of inertia of rounded/sharp quadratic and cylindrical hollow plant stems to determine those parameter configurations at which quadratic stems are more resistant to mechanical distortions than the most widespread cylindrical stems. Both approaches provide clear results regarding the geometrical prerequisites of the mechanical advantage of quadratic or cylindrical plant stems over the other.

As discussed in §1, in addition to plants with circlular (table 2 in appendix A) and square (table 3 in appendix A) stem cross-sections, there are also plants, for which the stem cross-sections are trianglular [16] or elliptic [17]. The biomechanical study of triangular and elliptical plant stems is a future task, in which the moment of inertia I of an equilateral triangle and an ellipse is to be calculated for an axis closing angle α with the triangle's side length and the ellipse's major axis. Other future research could be to investigate the ecological implications of different stem shapes: e.g. possible correlations between stem shape and the occurrence of certain environmental mechanical stresses, for example wind load.

5. Conclusions

The moments of inertia I_{square} and I_{circle} of plant stems with square- and circlular-collar cross-sections are rotation invariant, that is they are independent of the orientation of the axis crossing the geometrical centre of these collars.

In the region above curves $z(k_{\text{circle}})$ and $q(k_{\text{circle}})$ of the Q–k_{circle} variable domain (where $0 \leq k_{\text{circle}} = a_{\text{circle,inner}}/a_{\text{circle}} < 1$, $Q = a_{\text{square}}/a_{\text{circle}}$) a quadratic stem shape (with outer side length a_{square}) is more resistant to bending and torsion deformations (figure 7) than the corresponding cylindrical stem of the same cross-section area (i.e. material use) with outer side diameter a_{circle}. On the other hand, in the region between $z(k_{\text{circle}})$ and $q(k_{\text{circle}})$, the cylindrical stem shape is more resistant mechanically.

Similarly, in the region between curves $p(k_{\text{square}})$ and $h(k_{square})$ of the Q–k_{circle} variable domain (where $0 \leq k_{\text{square}} = a_{\text{square,inner}}/a_{\text{square}} < 1$) a quadratic stem shape is more resistant to mechanical deformations (figure 8) than the corresponding cylindrical stem of the same cross-section area, while in the region below $p(k_{\text{square}})$, the cylindrical stem shape is more resistant.

Data accessibility. All data underlying the results presented are available in this paper.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. ÁB.: conceptualization, formal analysis, investigation, methodology, software, validation, visualization; G.H.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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Appendix A: tables of flower names

See tables 2 and 3.

Table 2. Latin and English names of 10 well-known flower species with a cylindrical stem [27]

latin name	english name
Taraxacum officinale	dandelion
Phragmites australis	common reed
Dendrocalamus sinicus	dragon bamboo
Triticum aestivum	common wheat
Reynoutria japonica	japanese knotweed
Equisetum arvense	horsetail
Angelica archangelica	angelica
Foeniculum vulgare	fennel
Levisticum officinale	lovage
Lupinus perennis	lupinus

Table 3. Latin and English names of 84 flower species with a square stem [28]

latin name	english name
Pentaglottis sempervirens	green alkanet
Lamiastrum galeobdolon	yellow archangel
Melittis melissophyllum	bastard balm
Clinopodium vulgare	wild basil
Galium saxatile	heath bedstraw
Campanula trachelium	nettle-leaved bellflower
Betonica officinalis	betony
Bryonia dioica	white bryony
Ajuga reptans	bugle
Poterium sanguisorba ssp. balearicum	fodder burnet
Buddleja×weyeriana	Weyer's butterfly bush
Centaurium erythraea	common centaury
Stellaria neglecta	greater chickweed
Salvia nemorosa	balkan clary
Galium aparine	cleavers
Diphasiastrum alpinum	alpine clubmoss
Valerianella rimosa	broad-fruited cornsalad
Melampyrum pratense	common cow-wheat
Lysimachia nummularia	creeping jenny
Cruciata laevipes	crosswort
Clinopodium ascendens	common calamint
Leucanthemum vulgare	oxeye daisy

(*Continued.*)

Table 3. (*Continued.*)

latin name	english name
Lamium hybridum	cut-leaved dead-nettle
Rumex conglomeratus	clustered dock
Viola riviniana	common dog-violet
Phygelius capensis	cape figwort
Erigeron acris	blue fleabane
Gentianella amarella	autumn gentian
Lycopus europaeus	gipsywort
Parnassia palustris	grass of parnassus
Glechoma hederacea	ground ivy
Erica×darleyensis	darley dale heath
Galeopsis bifida	bifid hemp-nettle
Ballota nigra	black horehound
Persicaria campanulata	lesser knotweed
Stachys byzantina	lamb's ear
Lythrum salicaria	purple loosestrife
Pulmonaria officinalis	lungwort
Sherardia arvensis	field madder
Origanum vulgare	wild marjoram
Polygala vulgaris	common milkwort
Mentha suaveolens	round-leaved mint
Nonea lutea	zellow monkswort
Leonurus cardiaca	motherwort
Cerastium fontanum	mouse-ear
Brassica nigra	black mustard
Urtica dioica ssp. galeopsifolia	fen nettle
Solanum nigrum	black nightshade
Atriplex laciniata	frosted orache
Viola arvensis	field pansy
Aethusa cynapium	fool's parsley
Mentha pulegium	pennyroyal
Mentha×piperita	peppermint
Anagallis arvensis ssp. foemina	blue pimpernel
Ajuga chamaepitys	ground pine
Plantago lanceolata	ribwort plantain
Senecio inaequidens	narrow-leaved ragwort
Rhinanthus minor	yellow-rattle
Hypericum calycinum	rose-of-sharon

(*Continued.*)

Table 3. (*Continued.*)

latin name	english name
Salvia officinalis	sage
Prunella vulgaris	selfheal
Jasione montana	sheep's bit
Scutellaria galericulata	skullcap
Euonymus europaeus	spindle
Asperula cynanchica	squinancywort
Stellaria alsine	bog stitchwort
Hypericum maculatum	imperforate St John's-wort
Tanacetum vulgare	tansy
Vicia hirsuta	hairy tare
Thymus polytrichus	wild thyme
Thesium humifusum	bastard-toadflax
Legousia hybrida	Venus's-looking-glass
Verbena officinalis	vervain
Vicia sepium	bush vetch
Viola odorata	sweet violet
Galium odoratum	woodruff
Stachys germanica	downy woundwort
Achillea millefolium	yarrow
Inula helenium	elecampane
Phlomis russeliana	Jerusalem sage
Verbena bonariensis	Argentinian vervain
Nepeta×faassenii	catmint
Chimonobambusa quadrangularis	square bamboo
Lamium album var. barbatum	mint

Appendix B: bending and twisting plant stems

To bend a plant at a given position of its stem, the following bending moment is necessary [2,4]:

$$M_{\text{bend}} = \frac{E}{R} I, \quad I = \int_A z^2 \cdot \mathrm{d}A, \tag{B 1}$$

where E is the Young's modulus of the stem material, R is the local radius of curvature, and I is the second moment of inertia of the cross-section; I is a surfacial integral of $z^2{\cdot}\mathrm{d}A$ for the whole cross-section, where $\mathrm{d}A$ is an infinitesimal area at distance z from the axis crossing the geometrical centre of the cross-section.

To twist a plant stem of length L around its longitudinal axis by an angle φ, the following torsion moment is necessary [2,4]:

$$M_{\text{torsion}} = \frac{G\varphi}{L}(I_{\text{u}} + I_{\text{v}}), \quad I_{\text{u}} = \int_A v^2 \mathrm{d}A, \quad I_{\text{v}} = \int_A u^2 \mathrm{d}A, \tag{B 2}$$

where G is the shear modulus of the stem material, I_u and I_v are the moments of inertia calculated for two arbitrary orthogonal axes crossing each other at the geometrical centre of the stem cross-section, dA is an infinitesimal area at distances v and u from axes u and v, respectively. According to equations equations (B 1) and (B 2), bending or twisting a plant stem requires the larger bending or torsion moments M_{bend} or M_{torsion}, the larger are the moments of inertia I or I_v+I_u, respectively.

It follows that if a plant stem has to endure the mechanical strains induced by wind load and gravitation without fracture, then the stem I needs to be large enough. That is why we calculate and compare the moments of inertia of quadratic and cylindrical stems.

Appendix C: calculation of the moment of inertia in a rotated coordinate system

Consider an arbitrary cross-section of a plant stem in the Descartes system of coordinates x and y, shown in figure 9. The moments of inertia I_x and I_y calculated for the orthogonal axes x and y crossing each other at the origin O are

$$I_x = \int_A y^2 \mathrm{d}A, \quad I_y = \int_A x^2 \mathrm{d}A, \tag{C 1}$$

where dA is an infinitesimal area. The moments of inertia I_u and I_v calculated for the orthogonal axes v and u rotated by angle α from axes x and y are

$$I_u = \int_A v^2 \mathrm{d}A, \quad I_v = \int_A u^2 \mathrm{d}A. \tag{C 2}$$

According to Goldstein *et al*. [2]:

$$I_u = I_x\cos^2\alpha + I_y\sin^2\alpha - I_{xy}\sin 2\alpha,$$

$$I_v = I_x\sin^2\alpha + I_y\cos^2\alpha - I_{xy}\sin 2\alpha, \quad \text{where} \quad I_{xy} = \int_A xy\mathrm{d}A. \tag{C 3}$$

Appendix D

Using equation (2.13), the expression of the curve $z(k_{\text{circle}})$ separating the upper green and lower red regions in figure 7*a* is determined by the following equation:

$$J(k_{\text{circle}}, Q = z) = \frac{I_{\text{square}}}{I_{\text{circle}}} = \frac{16z^4}{3\pi(1-k_{\text{circle}}^4)}\left\{1-\left[1-\frac{\pi(1-k_{\text{circle}}^2)}{4z^2}\right]^2\right\} = 1$$

from which we get

$$z(k_{\text{circle}}) = \sqrt{\frac{\pi(1-k_{\text{circle}}^2)+3(1+k_{\text{circle}}^2)}{8}}, \quad 0 \le k_{\text{circle}} < 1,$$

$$z(k_{\text{circle}}=0) = \sqrt{\frac{\pi+3}{8}} \approx 0.8762, \quad z(k_{\text{circle}}=1) = \sqrt{\frac{3}{4}} \approx 0.8660. \tag{D 1}$$

In figure 7, the horizontal coordinate $k_{\text{circle}} = k^* = \sqrt{(\pi-3)/(\pi+3)} \approx 0.1518$ of the intersection point of curves $z(k_{\text{circle}})$ and $q(k_{\text{circle}})$ can be obtained from the following equation: $z(k^*) = \sqrt{\left[\pi(1-k^{*2})+3(1+k^{*2})\right]/8} = q(k^*) = \sqrt{\pi(1-k^{*2})/4}$.

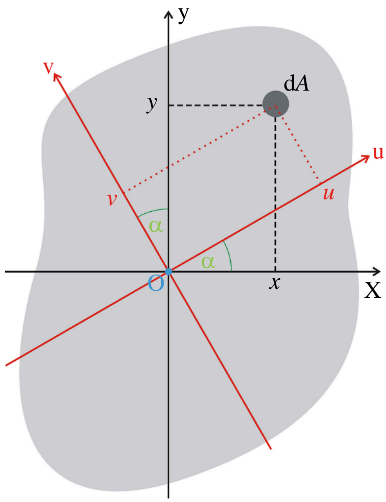

Figure 9. Calculation of the moment of inertia *I* of an arbitrary cross-section (grey) of a plant stem in the *x*–*y* (black) Descartes system of coordinates and in the system *u*–*v* (red) rotated by angle *α* around the origin O.

Using equation (2.17), the expression of curve $p(k_{\text{square}})$ separating the upper green and lower red regions in figure 8*a* is determined by the following equation:

$$J\left(k_{\text{square}}, Q = p\right) = \frac{I_{\text{square}}}{I_{\text{circle}}} = \frac{4\pi Q^2\left(1 + k_{\text{square}}^2\right)}{6\pi - 12Q^2\left(1 - k_{\text{square}}^2\right)} = 1,$$

from which we obtain

$$p\left(k_{\text{square}}\right) = \sqrt{\frac{3\pi}{2\pi\left(1+k_{\text{square}}^2\right) + 6\left(1 - k_{\text{square}}^2\right)}}, \quad 0 \le k_{\text{square}\ \S\text{lt;}1},$$

$$p\left(k_{\text{square}} = 0\right) = \sqrt{\frac{3\pi}{2\pi + 6}} \approx 0.8760, \quad p\left(k_{\text{square}} = 1\right) = \sqrt{\frac{3}{4}} \approx 0.8660. \tag{D 2}$$

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