The functional morphology of the petioles of the banana, *Musa textilis*

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Abstract

Bananas are among the largest herbs in the world and their lightweight petioles hold up huge leaves. This study examined how the petioles manage to achieve adequate rigidity to do this, while allowing extensive and reversible reconfiguration in high winds. Morphological and anatomical examination of the petioles and leaves of *Musa textilis* suggested how these two apparently incompatible abilities are achieved. The hollow U-shaped section of the petiole and the longitudinal strengthening elements in its outer skin give it adequate rigidity, while its ventral curvature help support the leaf without the need for thick lateral veins. These features, however, also allow the petiole to reconfigure by twisting away from the wind, while the leaf can fold away. In addition, two sets of internal structures, longitudinal partitions and transverse stellate parenchyma plates, help prevent dorsoventral flattening, allowing the petiole to flex further away from the wind without buckling. These ideas were tested and verified by a range of mechanical tests. Simple four-point-bending and torsion tests showed that the petioles are indeed far more compliant in torsion than in bending. Axial bending tests and crushing tests showed that petioles could be flexed twice as far and were four times as resistant to dorsoventral flattening when intact than when the internal tissue is removed. The banana petiole, therefore, seems to be an excellent example of natural integrated mechanical design.

Key words: Banana, petiole, mechanics, buckling, torsion.

Introduction

Bananas are among the largest herbs in the world. They are perennials with tall aerial shoots that arise from swollen, fleshy corms (Tomlinson, 1969). The petioles are arranged spirally in the aerial shoots, and their long overlapping bases form a stout pseudostem, through the centre of which the terminal inflorescence grows. Higher up, the petioles bend away from the pseudostem to hold the huge oval leaves at an oblique angle (Fig. 1A). The design of the petioles is clearly extremely efficient from a structural viewpoint because, even though they are extremely lightweight and lack any woody tissue, they can support the huge leaves. In addition, they can also withstand hurricanes. They, and the leaves they support appear to flex and fold away from the wind to produce a streamlined crown in such winds before returning to their rest position apparently unharmed.

The ability for a lightweight beam to be both extremely rigid and to survive such great deflections is highly unusual; most lightweight beams, such as hollow tubes are rigid, but are vulnerable to buckling at even small deflections (Gordon, 1978), while solid rods can deflect further but, weight for weight, lack rigidity. This paper examines the petiole of the banana (*Musa textilis*) to determine how it possesses two so apparently irreconcilable properties and allows the banana to reconfigure so well. To do this anatomical and morphological examinations of the petiole and leaf were combined with hand manipulations in order to develop ideas that could then be tested using quantitative mechanical investigations.

Morphology and anatomy of the petiole

The petiole of the banana (Figs 1, 2) has several characteristic morphological features. First, the petiole is not
Fig. 1. (A) Overall view of the shoot system of a banana, showing the petioles, which form the lower regions of the pseudostem bending away from it higher up to support the leaves. (B) Transverse section of the stem, showing the U-shaped cross-section and unusual semi-hollow structure, with longitudinal partitions splitting up the internal air space.

straight, but has a gentle ventral curvature of around 0.3 m\(^{-1}\). Second, the petiole is not circular but U-shaped in cross-section with the channel on the upper surface and the lamina emerging from the upper arms of the U. Third, the lamina is not held out flat from the petiole by thick strut-like veins as it is in most dicots. Instead, it is joined to it by numerous parallel fibrous veins that run along the petiole before diverging through the lamina at an angle of approximately 60°, and it appears free to hinge up and down at its join with the petiole.

The anatomy of the petiole is even more characteristic. The outer layers of tissue (Fig. 1B; Fig. 2) are similar to the stems and petioles of other monocotyledonous plants, being composed of parenchyma that is reinforced longitudinally by vascular bundles which include xylem tissue and lignified sclerenchyma fibres. Internally, however, the structure is unusual in being pierced by large air canals that are separated by narrow longitudinal parenchyma partitions that contain very few vascular bundles. In turn, these partitions are joined at intervals of 0.8–1 mm (Fig. 2B) by single transverse layers of porous stellate parenchyma (Fig. 2C). The structure is therefore unlike that of most monocots. It is not solid like the petioles of palms or the stems of sedges (Ennos, 1993); nor is it hollow, like the stems of grasses (Spatz et al., 1997). It is best described as semi-hollow, like the leaves of rushes, but with a much more ordered structure, since rush leaves are merely packed with a foam of stellate parenchyma (Esau, 1977). In fact, with its combination of longitudinal ‘stringers’ and transverse ‘bulkheads’ the petiole is more reminiscent of quite different structures: the spines of hedgehogs and porcupines (Vincent and Owers, 1986), and even more of the hulls of ships (Gordon, 1978).

**Suggested mechanical function**

So how do these design features confer rigidity on the petiole and leaf, while allowing extensive controlled reconfiguration? Two features that should increase the flexural rigidity of the petiole are its hollowness and the extensive longitudinal reinforcement of the outer layer of tissue. The resistance of the fibres to changes in length should strongly resist any bending, particularly as they are held well away from the neutral axis of the structure. Together these should help prevent the petiole from bending downwards appreciably under the weight of the leaf.

Support for the leaf itself appears to result from the ventral curvature of the petiole that means that the leaf is cambered downwards along its length. This curvature will greatly stiffen the leaf and prevent it drooping under its own weight, just as the camber in the wings of butterflies and other insects stiffens them against aerodynamic forces (Wootton, 1981; Ennos, 1997).

Manipulation of the petiole and leaf shows how strong lateral winds cause them to reconfigure. When a lateral force is applied to the petiole and leaf, the petiole does not
bend away from the force initially, but twists away (Fig. 3B). Since the petiole is bent downwards, twisitng it means that it curves away from the force with its ventral surface orientated away from it. Once in this orientation, application of further force causes no further torsion. Instead, anatomically ventral bending of the petiole allows it to curve even further away from the force (Fig. 3C). The leaf, meanwhile is folded back along the join with the petiole and, though corrugated, hangs like a flag ‘downwind’. These movements would all reduce drag dramatically, and would help reduce the force acting on the stem of the banana. When the force is removed the petiole reverts to its original position and the leaf, if it has not been torn, springs back up.

The results of previous studies suggest ways in which the design of the petiole might be adapted to allow such
reconfiguration. The low torsional rigidity, that would be required to allow the petiole to twist easily, might be conferred by two anatomical features: by its non-circular cross-section (Vogel, 1992; Ennos, 1993; and by its isolated longitudinal strengthening elements (Ennos, 1993, 1997). Other structures that combine these elements can be much easier to twist than to bend. The flower stems of the sedge Carex acutiformis (Ennos, 1993), with similar isolated fibres, but concave triangular cross-section have twist-to-bend ratios, a ratio of torsional to flexural compliance (Vogel, 1992), of up to 100, compared with only around 1.2–1.5 for solid metal rods.

The ability to flex without undergoing harmful local buckling might be conferred by another anatomical feature: the presence of the longitudinal partitions and the transverse stellate parenchyma. Certainly, Vincent and Ower’s study of hedgehog and porcupine spines showed the efficiency of similar stringers and bulkheads at preventing local buckling in an otherwise hollow structure (Vincent and Ower, 1986). They limit the flattening of the cross-section when the structure is bent and hence increase the curvature it can withstand without being damaged. In the banana petiole, the longitudinal partitions joining on to the inside surface of the lower wall (i.e. the wall on the convex side of the petiole) certainly seem well placed to prevent inner movement of the lower wall, since they are all placed more-or-less at right angles to it (Fig. 1B), like the spokes of a wheel. The ‘bulkheads’ of stellate parenchyma in turn seem well placed to prevent buckling of these ‘stringers’.

To investigate their functional morphology further, a range of mechanical tests were carried out on the petioles. As well as examining their overall mechanical performance, the tests sought to test the ideas generated in the last section. The ability to twist away from the wind was investigated by measuring the twist-to-bend ratio of the petiole. And the ability of the internal tissue to prevent flattening of the petiole when it is subjected to extensive ventral flexion was tested by carrying out axial flexion tests and crushing tests on intact and manipulated sections.

Materials and methods

Banana petioles

Complete petioles and leaves of the banana (Musa textilis Nee) were removed, at the point at which they left the pseudostem, from specimens growing in the heated glasshouses of the Freiburg Botanical Garden. The base of the petioles were immediately placed in water, and used within a day of removal. In between tests individual parts of the petiole were kept in water and, if they were to be kept overnight, placed in a refrigerator at 4 °C. They were then subjected to a range of mechanical tests.

Morphology and overall mechanical performance

To investigate the mechanical performance and morphology of petioles all the way along their length, and to investigate the twist-to-bend ratio, two petioles were subjected to a range of measurements.

(i) Overall petiole morphology: Each intact petiole was weighed, and the length, maximum width and distance of attachment from the base of the petiole, where it joined the stem, to the leaf were measured. The two halves of the leaf were then cut from the petiole, removed and weighed, allowing the weight of the petiole to be calculated.

(ii) Four point bending tests: The petiole was then cut up into 45 cm long sections to carry out a series of four point bending tests to investigate the flexural rigidity of the petiole at several points along its length. Sections were laid horizontally, with the channel of their cross-section facing upwards, on two supporting rods placed 16 cm apart. A weighing boat with arms 26 cm apart was then suspended, one arm hanging on each of the protruding ends of the petiole, 5 cm away from each of the rods (Fig. 4). Weights were then progressively added to the weighing boat which caused the petiole to bend, curving upwards. This mimics the effect of the weight of the leaf lamina on the petiole in calm conditions, and the force of the wind on the twisted petiole in gales. The upward movement of the mid-point of the section was measured using a travelling microscope. Weights were added progressively at 10 s intervals until the petiole had bent upwards about 10 mm. The weights were then removed.

This process allows the flexural rigidity, EI, of the stalks to be determined since the flexural rigidity of a beam in four point bending is given by the equation (Roark and Young, 1975)

$$EI = Fy (Ic^2/8)$$

(1)

where $F$ is the load applied at each of the outer loading points, $y$ is the upward movement at the centre point, and hence $Fy$ is the initial slope of the force/displacement curve. $I$ is the distance between the central rods and the outer loading points (here 5 cm) and $c$ is the distance between the two central
(iii) Torsion tests: The petiole sections were removed from the bending apparatus and cut into 18 cm lengths whose centre points were at 13, 32, 58, 77, 103, and 122 cm from the stem end of the petiole. These lengths of petiole were then mounted at each end in a torsion balance. One end was held firm, while the other end was located into a mounting which was free to rotate within an outer mounting but which was connected to it via a spiral spring that had a stiffness of 0.0541 Nm rad\(^{-1}\). In this way, rotation of the outer mounting applied a torsional moment to the piece of petiole, tending to twist it. The stiffer the petiole the less it would twist at any given torque. For each stem segment the outer casing was moved by 20, 40, 60, 80, 100, and 120\(^\circ\) and the movement of the inner casing recorded. The torsional rigidity, \(GK\), of the petiole section was then calculated using the following equation.

\[
GK = 0.0541L(\theta_n - \theta_i)/\theta_i
\]  

where \(L\) is the free length of the petiole segment, \(\theta_n\) is the displacement of the outer mounting and \(\theta_i\) is the displacement of the inner mounting in radians.

The results from the bending and torsion tests were finally combined to calculate the ‘twist-to-bend’ ratio \(EI/GK\) (Vogel, 1992), a ratio describing the relative ease of twisting to bending, for each section.

(iv) Morphology, mass and density: Sections of petiole were removed from the torsion apparatus and 2 cm long sections centred at 13, 32, 58, 77, 103, and 122 cm were cut. The width and depth of the centre point of each section was measured using callipers and it was weighed. Its volume was then measured by submerging it in water and measuring the volume of water displaced. No water entered into the centre of the petiole through the stellate parenchyma. This allowed the density of each 2 cm section to be calculated. Finally, the internal tissue (the partitions and stellate parenchyma) was removed from each 2 cm section and the wet weight of the internal and external tissue separately measured. The tissue was oven dried at 80 °C and finally the dry weights were taken.

Axial bending tests

To investigate the resistance of petioles to local buckling when flexed caused by flattening of their cross-section, a second series of mechanical tests were carried out on 21 more petioles.

(i) Tests on intact petiole sections: Petioles were cut into 30 cm long sections and the mechanical properties of 22 sections of varying diameter were investigated by carrying out Euler buckling tests under displacement control, using an axial bending test machine (designed by Spatz et al., 1993, and improved by Spatz and Speck, 1995). In such tests the ends of the specimen are held in rotatable cups (Fig 5A) which are moved inwards at a constant speed, forcing the petiole section to bow upwards along its length (mimicking the curvature seen due to the weight of the lamina). The inward force, \(P\), required is recorded continuously, along with the distance, \(d\), between the two ends of the specimen. The upward movement, \(D\), of the centre of the stalk is recorded by a video camera which automatically follows the movement of the vertex in the vertical direction. These measurements allow the bending moment, \(M\), to be calculated using the equation

\[
M = PD
\]

while curvature at the vertex, \(C\), is given by the equation

\[
C = 12D/d^2
\]

(ii) Calculating properties of the structure: The results were plotted on a bending moment/curvature graph, which allows the flexural rigidity and strength of the section to be calculated, since the flexural rigidity, \(EI\), is the initial slope of the curve (\(dM/dC\)), and the strength is the maximum value of the bending moment, \(M_{\text{max}}\). The critical curvature, \(C_{\text{crit}}\), is defined as the curvature at the point of the graph at which there is the first significant drop in the bending moment minus the original curvature. The tests also allow the examination of the mechanism of bending failure, since failure occurs at the vertex of the curve, well away from any supports and this point was continuously examined.

(iii) Calculating properties of the material: Both \(EI\) and \(M_{\text{max}}\) will depend strongly on the dimensions of the section; thicker, wider sections will tend to be both stronger and more rigid. For this reason, more measurements and calculations were carried out to investigate the material properties of the section. After failure had occurred, the petiole section was removed from the apparatus and a transverse section was cut near to the point of failure. The section was photographed using a video camera, and the captured image was used to calculate the dorsoventral axial second moment of area \(I\), where \(I\) is given by the equation

\[
I = \Sigma x^2 \, dA
\]

where \(x\) is the perpendicular distance of each small area of the petiole section, \(dA\), away from the neutral axis, which is the line along which the material is neither stretched nor compressed when the structure is bent. The neutral axis and second moment of area were determined graphically. Only the outer tissues were considered, since it was felt that the partitions and the pith would have very little effect on the bending rigidity of the petiole. They are composed largely of relatively weak parenchyma, they have a comparatively small cross-sectional area, and they are located mostly towards the centre of the cross-section.
from a single petiole, six each from around points 15, 30, and 60 cm from the base of the petiole. Two of each six were kept intact, two had the stellate parenchyma removed, and two had all the inner tissue removed. One of each was then subjected to a dorsoventral or lateral compression test. In dorsoventral compression the segments were crushed between a flat platten and a cylindrical rod of radius 3 mm (Fig. 5B) which was attached to a universal mechanical testing machine (Instron Ltd). In lateral compression they were crushed between two flat plottens (Fig. 5C). The machine continuously recorded the force required as compression proceeded and calculated the initial slope of the force/displacement graph.

**Results**

**Morphology, mass and density**

The morphology and mechanical properties were similar for the two petioles that were studied. Results are given for petiole 1, which was somewhat larger. It was 170 cm long, weighed 54.4 g, and supported a lamina of length 122 cm and width 28.5 cm which weighed 45.5 g.

The petiole tapered gradually down its length, the height and width of the cross-section being given in Fig. 6A. Petiole shape and anatomy showed little change along its length, though since the thickness of the outer wall did not fall so fast as the dimensions of the section, the petiole became noticeably less hollow towards its tip. This pattern is reflected in the density of the stalk, which rose from below 0.6 g cm$^{-3}$ near the base (Fig. 6C) to near 0.8 g cm$^{-3}$ towards the tip. The mass of internal tissue was small compared with the outer tissue: it made up only 20.3 ± 4.4% of the wet weight and only 9.8 ± 1.9% of the dry weight of sections.

**Mechanics of whole petioles**

Both the flexural and torsional rigidity of the petiole fell along its length as it got thinner (Fig. 6D, E). Each section was rigid in bending but relatively easy to twist, so the twist-to-bend ratios (Fig. 6F) were very high, ranging between 45 and 100, though there was no obvious pattern with distance down the petiole.

**Axial buckling tests**

**Intact stalks**: On being bent, the intact petioles maintained their cross-sectional shape until the curvature was well over 2. Only late in the process of Euler buckling did small creases appear in the lower surface of the petioles, but the sections never completely flattened out. A typical graph of bending moment/curvature is shown in Fig. 7A. This shows that, unlike hollow tubes, the bending moment does not fall dramatically either, as it would do for a hollow tube such as the stem of *Arundo donax* (Spatz et al., 1997), but after reaching a peak slowly declined. The rigidity, EI, and strength, $M_{\text{max}}$, of the petioles rose with their cross-sectional area, being
more-or-less proportional to the axial second moment of area, $I$, and section modulus, $I/X_{\text{max}}$, respectively (Fig. 8). The slope of neither of these log/log graphs line was significantly different from 1, implying that the material properties of the outer tissue were similar all the way along its length. The calculated mean and standard deviation of values for these material properties are given in Table 1.

**Manipulated petioles:** The petioles that had been hollowed out showed similar behaviour to intact ones (Fig. 7B). Their calculated material properties were also very similar (Table 1). One way ANOVA showed that there was no significant difference between manipulated and intact petioles in either the structural modulus of elasticity, $E$, or the maximum compressive stress, $s_{\text{max}}$.

However, the petioles which had all their internal tissue removed had significantly reduced values of critical curvature, $C_{\text{crit}}$ and critical strain, $\varepsilon_{\text{crit}}$ (Table 1); values were only about half those of intact petioles. These reduced values were clearly related to dorsoventral flattening of the hollow petioles when they were much less bent than those that retained internal tissue.

**Crushing tests on petiole segments**

Qualitatively, at least, the stabilizing influence of the partitions and stellate parenchyma can be demonstrated by the results of the crushing tests. In all of the tests the force required to compress the sections increased linearly with displacement at first, before reaching a peak. After a brief decline the force then increased again as the sample was consolidated. Such results are typical for compression tests on hollow or porous samples.
Table 1. Mechanical properties of the petioles of Musa textilis and the material properties of the outer tissue derived from axial bending tests on intact or manipulated stem sections

Mean ± standard deviations are given, along with the number of specimens tested. For critical curvature and strain, averages were calculated only from the larger samples, in which $I > 100 \text{ mm}^4$. Properties of manipulated specimens which were significantly different from intact ones are marked by asterisks ($***$, $P < 0.001$).

<table>
<thead>
<tr>
<th></th>
<th>Intact petiole</th>
<th>Minus stellate parenchyma</th>
<th>Hollow petiole</th>
</tr>
</thead>
<tbody>
<tr>
<td>Structural modulus of elasticity, $E$ (Gpa)</td>
<td>0.63 ± 0.51</td>
<td>0.65 ± 0.44</td>
<td>0.55 ± 0.42</td>
</tr>
<tr>
<td></td>
<td>$n = 22$</td>
<td>$n = 10$</td>
<td>$n = 14$</td>
</tr>
<tr>
<td>Maximum compressive stress, $s_{\text{max}}$ (MPa)</td>
<td>5.52 ± 2.83</td>
<td>5.47 ± 2.20</td>
<td>4.40 ± 1.56</td>
</tr>
<tr>
<td></td>
<td>$n = 21$</td>
<td>$n = 9$</td>
<td>$n = 13$</td>
</tr>
<tr>
<td>Critical curvature $C_{\text{crit}}$ (m$^{-1}$)</td>
<td>6.15 ± 1.31</td>
<td>5.66 ± 1.84</td>
<td>3.07 ± 0.89</td>
</tr>
<tr>
<td></td>
<td>$n = 13$</td>
<td>$n = 6$</td>
<td>$n = 12^{***}$</td>
</tr>
<tr>
<td>Critical strain $e_{\text{crit}}$</td>
<td>3.36 ± 0.87</td>
<td>2.73 ± 0.99</td>
<td>1.78 ± 0.24</td>
</tr>
<tr>
<td></td>
<td>$n = 13$</td>
<td>$n = 6$</td>
<td>$n = 12^{***}$</td>
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![Log/Log graphs showing the relationship between (A) the flexural rigidity of petiole sections with their axial second moment of area, $I$, and (B) the maximal moment and section modulus, $M_{\text{max}}$, of the sections. The relationship between both is more-or-less linear with a slope not significantly different from 1, suggesting that the material properties of the petiole remain constant along its length. (■) Intact petioles; (●) stellate parenchyma removed; (▲), hollow petioles.](image)

The initial slope of the force/displacement curves (Table 2) which represents its initial resistance to compression were analysed using 3-way ANOVA to investigate separately the effects of the direction of compression, the position of the section along the petiole, and the degree of intactness of the segments. All three factors (but not the interactions) had a highly significant effect (Table 2). First, sections were on average 47% more resistant to dorsoventral than lateral flattening ($P < 0.001$). Second, sections 60 cm along the petiole were on average 83% more resistant to flattening than those 30 cm along, and 66% more resistant than those 15 cm along ($P < 0.01$). Third, removing the stellate parenchyma reduced flattening resistance by on average 25%, while removing all the internal tissue reduced it by on average 75% ($P < 0.001$).

**Discussion**

The results of the mechanical tests in most ways confirmed the ideas about petiole design and function that had been built up following morphological examination and manipulation. First, the hollow design, and the longitudinal strengthening elements do produce a structure with a low density but high flexural rigidity. Undoubtedly the hollowness of the petioles greatly increases their flexural rigidity and strength, because tissue is thereby located well away from the neutral axis. The U-shaped cross-section must also help it to resist downward bending because on loading, the arms of the U will tend to move
inwards, increasing its second moment of area (Wootton, 1981; Ennos, 1997).

In contrast to its flexural rigidity the petiole is extremely flexible in torsion, as predicted, with values of the twist-to-bend ratio of between 40 and 100, far higher than the values for tree petioles of 1.6 to 9 measured previously (Vogel, 1992), and on a par with the exceptional values measured on the triangular stems of the sedge Carex acutiformis (Ennos, 1993). These high values, which can be related to the U-shaped cross-section and isolated reinforcing strands of the petiole, mean that the ventrally curved petiole will initially twist rather than bend away from lateral forces such as the wind. This means that the petiole will almost never have to resist lateral flexion.

The results of the axial bending tests, meanwhile, support the idea that the internal tissue acts to prevent dorsoventral flattening of the petiole, and hence allows it to flex further away from the wind without buckling. Removing all the internal tissue did not reduce the strength or stiffness of the petiole, but it did reduce their critical curvature by about 50%, since they flattened out much more easily. Removing the stellate parenchyma on its own had no significant effect, but the role of this tissue in preventing dorsoventral flattening is shown by the results of the crushing tests, since its removal reduced the resistance of the sections to flattening by about 25%. They seem to help prevent the spoke-like longitudinal partitions from buckling. Together, therefore, the two inner tissues can be seen to have a major mechanical role, despite making up only around 9% of the dry mass. They enable intact petioles to flex reversibly to curved angles of over 6 m⁻¹. The petioles should therefore be able to flex in a hurricane until they and their attached leaves all point downwind without being damaged.

In conclusion, it is the combination of the many distinctive features of the banana petiole into a clever integrated design that seem to confer its ability to be both rigid and deform reversibly downwind in gales. Its U-shaped outer shell, with isolated longitudinal reinforcement, makes it light but rigid in bending, while the ventral curvature of the petiole cambers the leaf and so helps support it. However, both these features also allow the structure to reconfigure. The shape and anatomy of the outer shell makes the petiole very compliant in torsion, and combined with the ventral curvature this allows it to twist away from the wind. The leaf, since it does not require rigid veins for support, can also fold downwind readily once the petiole has twisted in this way. Meanwhile, the internal structures, the longitudinal partitions that are orientated like spokes, and the lateral plates of stellate parenchyma, both prevent dorsoventral flattening. This allows the petiole to bend even further away from the wind without getting damaged. Consequently, the plant can fold up far better in the wind and avoid damage both to itself and to the stem (rather like the kelp studied by Johnson and Koehl, 1994).

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References


