Online Supplementary Material for

Nimmo, J.R., Hermann, P.M., Kirkham, M.B., and Landa, E.R., 2014, Pollen Dispersal by Catapult—Experiments of Lyman J. Briggs on the Flower of Mountain Laurel: Physics in Perspective, v. 16, no. 3.

[Figures are in the published paper.]

Biomechanics of pollen-flinging

Briggs's (1954-1958) analysis was the first attempt to apply rigorous physical theory to the pollen-flinging mechanism of the *Kalmia* flower. More recently, Niklas (1992) has given a physical description of the flinging biomechanics of a related species, *Kalmia angustifolia.* Here we present some of the physical reasoning and calculations apparent from the materials Briggs left behind, with updated interpretations made possible with recent knowledge of the filament geometry and the properties of related botanical materials

The bending of the filament of the *Kalmia* flower is an inherently two-dimensional problem involving curvature and transverse forces. Desirable simplifications result from transforming it into a largely one-dimensional problem of simple lengths and displacements. Briggs and Frankland did this by the standard method of extreme-fiber analysis. The filament is conceptualized as a tight bundle of infinitesimally thin hypothetical fibers. Here the word "fiber" refers to a hypothetical geometric element, and does not correspond to any physical botanical structure. Each fiber experiences a particular longitudinal stress and strain caused by the bending stress. Fibers at the edges that experience the greatest stress are called the extreme fibers; in the *Kalmia* filament these are at the extreme ad- and abaxial positions. Briggs' measured dimensions indicate extreme fiber strain of 4.7% for a filament bending through 270° as in figure 4.

Frankland calculated extreme fiber stress using the flexure equation, which defines bending stress as

(1)
$$\sigma_x(y) = \frac{My}{\int_A y^2 dA} ,$$

where M is the bending moment (the product of length and applied force of the filament, considered as a cantilever beam loaded at its distal end). Briggs's measurements give a bending moment of 2.0 μNm; A is the area of the beam's cross-section. The coordinate x is in the longitudinal direction of the beam, and the y-z plane is normal to it (figure 6). The coordinate y is in the direction of the bending force and has its origin on the neutral axis, defined as the set of points in the y-z plane at which the bending stress $\sigma_x(y)$ is zero. Conceptually the neutral axis is the line that stays fixed when the beam is bent, around which the off-axis portions of the beam tend to rotate. The integral in the denominator is frequently called the moment of inertia, though because it includes no inertial mass, it is less confusingly called the second moment of the cross-sectional area.

With limited knowledge of its actual physical characteristics, Frankland conceptualized the filament as tube of circular cross section filled with fluid (in some instances referred to a gas). He assumed the material was homogeneous, so the neutral axis was simply a diameter. Given an outside radius *R*, the extreme fiber stress is $\sigma_x(R)$. He calculated stress for various tube wall thicknesses. An actual filament internally comprises cells and intercellular spaces without a singular chamber resembling the interior of a tube, and it does not contain significant gas. Thus, the most relevant of Frankland's calculations is the one having tube wall thickness equal to the tube radius, i.e. a rod rather than a tube. The area of integration *A* being a circle, with Briggs' data and Frankland's assumed geometry, the calculated extreme fiber stress is 0.12 MPa.

Frankland, though he appropriately used the mid-filament thickness 250 µm when he was calculating extreme fiber strain, took the diameter of the circular cross section he used for calculating extreme fiber stress to be the basal lateral thickness of the filament, 560 µm. This unrealistically large size is apparent in figure 6. The distribution of stress from a given bending moment over a larger area makes any given fiber stress less; this large area in the integral in (1) leads to Frankland's value of extreme fiber stress. The small value he obtained was unrealistic for a beam whose own unaugmented stress could accomplish the *Kalmia's* flinging of pollen and thus contributed unwarranted support for the argued necessity of negative pressure contributing a major component of the stress.

Unlike the circular geometry, whose symmetry locates the neutral axis exactly on a diameter, the more realistic geometry requires a calculation of its position. For this, we assume homogeneity of the filament material, which is not strictly true (from figure 5 it is clear that the cross section contains different materials, cell sizes, and structures) but may be adequate for evaluating the reasonableness of computed values. Assuming also that the bending is entirely in the elastic range (Hooke's law applies throughout), stress and strain in the bent filament increase linearly with *y*, whose zero is on the neutral axis. For the static case, appropriate to the pinned filament, compressive stress over the area above the neutral axis must balance the tensile stress over the area below. This condition determines the location of the neutral axis (n.a.):

$$\int_{Area-above-n.a.} y\,dA = \int_{Area-below-n.a.} -y\,dA \qquad (2)$$

In words, the first moment of area must balance across the neutral axis.

Integration over the indicated polygonal shapes with the measured dimensions gives the neutral axis position as 74 µm from the abaxial edge. Integrating with the second moment of area in the flexure formula (1) gives the bending stress $\sigma_x(y)$. Using Briggs' measured bending moment M, the abaxial ($y = c$) extreme fiber stress is 1.45 MPa. Recalculating the extreme fiber strain (again for the filament going through the 270° bend shown in figure 4), using our estimates of the filament dimensions we obtain a value of 0.036, smaller than Frankland's 0.047 because of the smaller filament thickness. The ratio of stress to strain then indicates a Young's modulus of 40 MPa, larger by a factor 16 than what Briggs and Frankland's analysis would have given (Table I). This larger value indicates greater ability of the filament to apply force from unbending, and so diminishes the need for Briggs' hypothesized augmentation of the force with negative pressure.

The second area where new knowledge can enhance Briggs's interpretation is in the properties of relevant materials. Elastic limits of botanical materials are rarely measured outside of construction applications; most such measurements are for wood used as a construction material. In Table I we have compiled measured and computed values of such properties for the *Kalmia* filament and other materials selected for comparison. Young's modulus is the one property known for all items here.

TABLE I. Elastic properties of selected materials of botanical origin.

Material	**Extreme Fiber Strain**	**Extreme Fiber Stress (MPa)**	**Young's Modulus (MPa)**	**Strain at Elastic Limit**	**Stress at Elastic Limit (MPa)**
K. latifolia filament--Briggs/Frankland values (Briggs, 1954-1958)	0.047	0.12	2.5		
K. latifolia filament--our values	0.036	1.45	40		
Pine wood (Marks, 1930)			8030	0.00314	25
Riparian stems and branches (Sutili and others, 2012)			4540	0.015	45
Parenchyma (Niklas, 1992)			50		
Lignin (Cousins and others, 1975)			3300	0.067	220
Cellulose (Niklas, 1992)			400000		
Parenchyma of *Pachycereus pringlei* (Niklas and others, 1999)			4.6 to 9.6		
Stem rib tissue of *Pachycereus pringlei* (Niklas and others, 1999)			1900 to 2800		

The measurements of Sutili and others (2012) for stems and branches of four species of riparian plants are more appropriate for comparison than the wood (lumber) data available to Briggs. The motivation for these measurements was not to assess suitability for construction but rather to understand the performance of streambank vegetation in altering flow patterns within the river and reducing erosion. The stems and branches measured are relatively young and thin, so perhaps more similar to a *Kalmia* filament. Compared to wood used for construction, these have a smaller Young's modulus, greater capacity for stress in the elastic range, and much greater strain at elastic limit (1.1% to 1.5%). On the whole these properties suggest much closer resemblance to a *Kalmia* filament.

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