

REORIENTATION OF DAFFODIL (*NARCISSUS*: AMARYLLIDACEAE) FLOWERS IN WIND: DRAG REDUCTION AND TORSIONAL FLEXIBILITY¹

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Daffodil flowers extend laterally from the long axes of their stems; as a result, wind on a flower exerts torsional as well as flexural stress on the stem. Stems respond by twisting, and thus flowers reorient to face downwind in moderate winds, in the process reducing their drag by ~30%. This repositioning is facilitated by the stems' relatively low torsional stiffness. Daffodil stems have a ratio of flexural to torsional stiffness of 13.27 ± 0.96 (SD), compared with 8.33 ± 3.20 (SD) for tulip stems, which bear flowers as symmetrical extensions of their long axes, and compared with 1.5 for isotropic, incompressible, circular cylinders.

Key words: Amaryllidaceae; biomechanics; daffodil; drag; flowers; *Narcissus*; torsional stiffness; wind.

*All the blossoms turn their backs to the wind,
whenever the gale blows hard enough to endanger
their delicate parts.*

William Paley (1805)

While bearing flowers on long stems may improve the effectiveness of wind pollination or attractiveness to pollen-transferring animals, it will concomitantly make the flowers more vulnerable to potentially destructive winds. Many flowers, such as those of both wild and cultivated daffodils (genus *Narcissus*) are borne asymmetrically atop their stems, that is, the flower faces radially outward in a particular direction. Wind from almost any direction will cause the stem of such a flower to twist as well as bend. Thus wind might reorient the flower so it incurs less drag and is less prone to bending over irreversibly. Other flowers, such as those of tulips (genus *Tulipa*), are coaxial with their stems and should experience only minimal wind-induced torsional stress and reorientation.

The particular liveliness of daffodils in gusty winds has been noted, not just by William Paley, but by less scientifically oriented writers such as William Shakespeare (1564–1616; *The Winter's Tale*), Amy Lowell (1874–1925; *Patterns*), John Masefield (1878–1967; *The West Wind*) and, with the best known and most extensive allusion, William Wordsworth (1770–1850; *I Wandered Lonely as a Cloud*).

Here we ask about the biomechanical correlates of the behavior of daffodil flowers and their stems in wind. In particular, we investigate (1) the range of wind speed over which reorientation occurs, (2) the change in the drag of

flowers that accompanies reorientation, and (3) the relationship between the torsional flexibility of stems, which facilitates reorientation, and their flexural stiffness, which opposes simultaneous bending.

Item 1 tests whether reorientation occurs at environmentally relevant speeds. The context of item 2 is earlier work on how organisms use their lack of rigidity to permit flow-induced, drag-reducing reorientation (see, for instance, Koehl, 1977; Vogel, 1994). The context of item 3 is an on-going exploration of the usefulness of a dimensionless ratio of flexural to torsional stiffness in characterizing elongate, load-bearing biological structures (Vogel, 1992, 1995; Ennos, 1993; Etnier, 1997).

For (1), flowers with their stems were mounted in a wind tunnel and subjected, unrestrained in orientation, to wind speeds varying from near zero to speeds associated with storms. For (2), drag was measured on stemless flowers, restrained to face either upwind or downwind. Drag was expressed in terms of the drag coefficient,

$$C_d = 2D/\rho SU^2 \quad (1)$$

where C_d is the drag coefficient, D is the drag force, ρ is the density of air, S is frontal area, and U is wind velocity. This corrects drag for area and dynamic pressure and thus provides a dimensionless indication of the "dragginess" of a particular shape.

For (3), stems were first bent and then twisted, applying a known force or torque and measuring the resulting deflection. For bending, flexural stiffness (or flexural rigidity) expresses the relationship between force and deflection. Flexural stiffness is a composite variable, EI , where E is Young's modulus of elasticity, a material property, and I is ordinarily the second moment of area taken normal to the neutral (unstressed) plane of bending. For twisting, torsional stiffness (or rigidity) expresses the analogous relationship between torque and deflection. Torsional stiffness is given as GJ , where G is the shear modulus, a material property, and J (for many but not all shapes) is the polar second moment of area of a cross section about the axis of rotation. (For additional information on these variables, see Niklas, 1992).

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The ratio of flexural to torsional stiffness, EI/GJ , provides an index of the relative resistance of a beam to bending vs. twisting or, put conversely and more intuitively, its ease of twisting relative to its ease of bending (“twistiness to bendiness”). Since EI and GJ combine analogous material and geometric factors, their ratio is a dimensionless reflection of that combination. As the ratio has no dimension of length, it has no intrinsic variation with size. For a given material, a beam with a noncircular cross section gives a higher value than a circular beam of the same cross-sectional area—it twists relatively more easily (see, for instance, Gere and Timoshenko, 1984). Daffodil stems are lenticular in cross section, suggestive of a relatively high EI/GJ .

MATERIALS AND METHODS

Daffodils (*Narcissus pseudonarcissus* L.) were collected from the authors' gardens or from the vicinity of the Biological Science Building at Duke University, Durham County, North Carolina. Data reported here came from specimens of the King Alfred cultivar unless otherwise noted; data from less systematic investigation of specimens of other cultivars differed in no important way. All flowers and stems were fresh, fully opened, and undamaged upon collection, the bases of stems (cut at ground level) were placed in cool water within a few minutes of cutting, and all specimens were used within 2 h of collection. In addition, comparative mechanical testing was done on tulips (*Tulipa* sp.) collected and treated similarly.

Cross sections of daffodil stems for calculation of second moments of area, I and J , were cut with a double-edged razor blade and then traced onto paper using a stereomicroscope and camera lucida. Maximal and minimal diameters were measured at both ends with electronic calipers for stems used in mechanical tests. Frontal surface areas of stems were estimated from these morphological measures.

For measurement of drag, specimens were mounted in the working section of an open circuit wind tunnel (Tucker and Parrott, 1970) at winds up to 16 m/s. Speeds were calibrated by reference to the drag of a circular disk positioned perpendicular to the wind with an assumed drag coefficient of 1.17 (Eq. 1). The disk was mounted on a streamlined sting (whose drag was subsequently subtracted); the sting, in turn, extended from an aluminum beam equipped with a pair of foil strain gauges. The gauges were calibrated gravitationally by positioning the beam horizontally and applying weights to the tip of the sting.

The drag of isolated flowers was measured with each extending laterally from the top of a vertical, cylindrical metal sting (0.40 m in length and 2.4 mm in diameter) connected to the same aluminum beam equipped with strain gauges. Drag on each flower ($N = 6$) was determined for two orientations: facing upwind and downwind, in random order. The drag of the sting was subtracted from each datum. Wind speed was increased incrementally, and data at each speed were taken as the average of four readings.

Drag on minimally constrained flowers with their stems was measured for three specimens by attaching the basal end of each stem directly to the aluminum beam; stems were not free to rotate about the beam, so any rotation depended on stem torsion. At the beginning of each test, flowers pointed directly upwind. Drag was measured as the wind velocity was increased incrementally to 15.9 m/s. Additionally, speeds for repositioning and any reconfiguration of flowers were noted for these three flowers as well as for six others.

The frontal areas of flowers were determined by tracing their outlines as each faced (as if directed upwind) a collimated light source, cutting out and weighing each tracing, and comparing it to the weight of a known area of the same paper. Combination with frontal areas of stems gave overall measures of areas. Using those areas, data for drag were converted into dimensionless drag coefficients by Eq. 1. Thus all drag

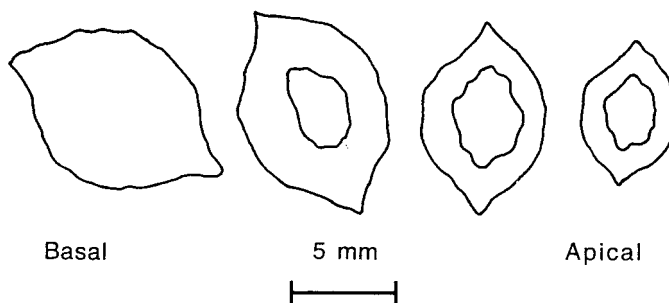


Fig. 1. Transverse outlines of a typical daffodil stem, from proximal (base) to distal (tip). Overall stem length is 270 mm, with sections taken at 85-mm intervals. Orientations are consistent, with the flower facing right.

coefficients are based on the original frontal areas of specimens as yet uninfluenced by wind.

Winds were reproducible to 1%, although systematic errors due to turbulence and spatial nonuniformity within the wind tunnel of up to 5% cannot be precluded. Determinations of drag have an estimated accuracy (with respect to both systematic error and imprecision) of 2%.

Flexural stiffness (EI) was measured on six daffodil and six tulip stems by extending each horizontally between a pair of supports 200–250 mm apart, loading the stem midway between the supports with standard weights, and noting deflections (to the nearest 0.5 mm) visually. In terms of applied weight (F), distance between supports (l), and deflection (y),

$$EI = Fl^3/48y \quad (2)$$

(Gere and Timoshenko, 1984). For each daffodil stem eight deflections were averaged, including four when bent in the plane of maximum diameter and four in the plane of minimum diameter. Individuals within each set of four varied very little in practice. For tulip stems, circular in cross section, four deflections were averaged. No deflection was more than 5% of length, ensuring that measurements reflected bending rather than shearing.

Torsional stiffness (GJ) was measured on the same stems as follows. The basal (lower) end of each was embedded with rapid-setting epoxy glue (DuroMaster Mend Epoxy, Quick Set, Loctite Corporation, Rocky Hill, Connecticut, USA) in a cut-off plastic test tube, 11 mm in diameter, and 30 mm long. The test tube was then inserted coaxially into a cylindrical capstan, 19.2 mm in diameter, from which weights could be hung tangentially. On the opposite end of the capstan, a shaft extended through a pair of ball bearings to a wheel, 110 mm in diameter, marked in radial increments of 1°. The apical (upper) end of each stem extended horizontally to an adjustable, padded laboratory clamp. The arrangement was similar to one used earlier (Vogel, 1995). In terms of the applied weight (F), the moment arm of half the capstan diameter (r), the twistable length of the stem (l), and the resulting angle (radians) of twist of the beam (θ),

$$GJ = Fr/l\theta \quad (3)$$

(Gere and Timoshenko, 1984). Four measurements were averaged for each stem. No twist exceeded 40° or, with lengths of 20–24 cm, 170°/m.

Determinations of both EI and GJ are estimated having both systematic errors and imprecision of <5%. As a check on the accuracy of our measures, a steel music wire of 0.67 mm diameter, treated as described for stems, gave a value of EI/GJ of 1.37. The expected value, from engineering handbooks, is 1.30.

RESULTS

Morphology—Cross-sectional shapes along a typical daffodil stem are shown in Fig. 1. The stem, lenticular

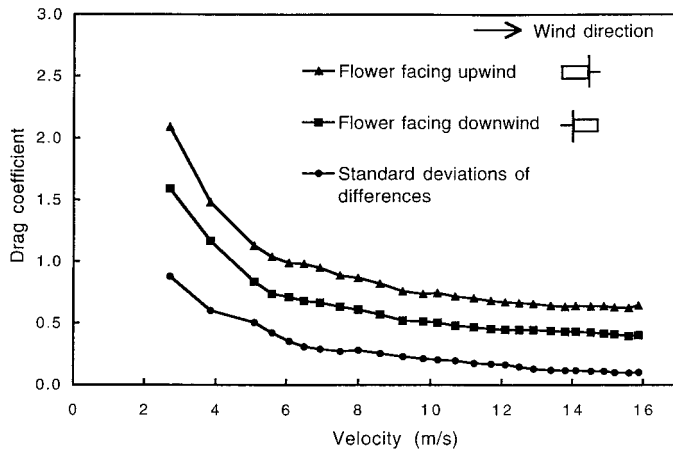


Fig. 2. Drag coefficient vs. speed for daffodil flowers facing into a wind and facing downstream. Data are averages of four determinations at each speed and orientation on each of six flowers. The bottom line shows the standard deviation of differences between upwind and downwind drag coefficients for each speed.

in shape (elliptical, with pointed ends on the long axis), has an average ratio of greatest to least diameter of 1.4 (± 0.1 SD). Unlike a traditional beam, the long and short axes of the ellipse do not remain in the same orientation throughout the length of the stem. Rather, they most often rotate around the central axis, as shown in the figure. The amount of rotation varies from zero to 180° and is highly variable, as is the position of the flower relative to the maximum diameter of the stem. The stem tapers along its length, and its apical portion is hollow. As is typical for monocots, individual bundles of fibers run lengthwise through the stem with no obvious interconnections or interweaving.

For a typical daffodil stem, the second moments of area for bending (I) in the plane normal to the greatest diameter are $161 \times 10^{-12} \text{ m}^4$ and $31.6 \times 10^{-12} \text{ m}^4$ at the base and tip of the stem, respectively; the second moments of area for bending normal to the least diameter are $303 \times 10^{-12} \text{ m}^4$ and $60.3 \times 10^{-12} \text{ m}^4$. The polar second moments of area (J , for twisting) are $464 \times 10^{-12} \text{ m}^4$ at the base and $91.9 \times 10^{-12} \text{ m}^4$ at the tip.

Reorientation and drag—As velocity increases, a flower undergoes several positional changes. At low velocities, the flower begins to rotate slightly, with very little bending of the stem. At higher velocities, the flower rotates to 90° from the wind direction and the stem begins to bend. As velocity increases further, it reaches $\sim 180^\circ$ from the wind direction and, facing downwind, continues to bend even farther. The flower now starts to reconfigure, with the distal tips of the sepals pointing downward to form a cone. As velocity continues to increase, this cone becomes increasingly tight and the distal portion of the stem bends until it is almost parallel to the wind. We observed no damage to stems and only rarely any damage, a slight tearing of sepals, to flowers.

Figure 2 gives the drag coefficients for artificially restrained flowers facing upwind and downwind. Reorientation to face downwind instead of upwind, with no other

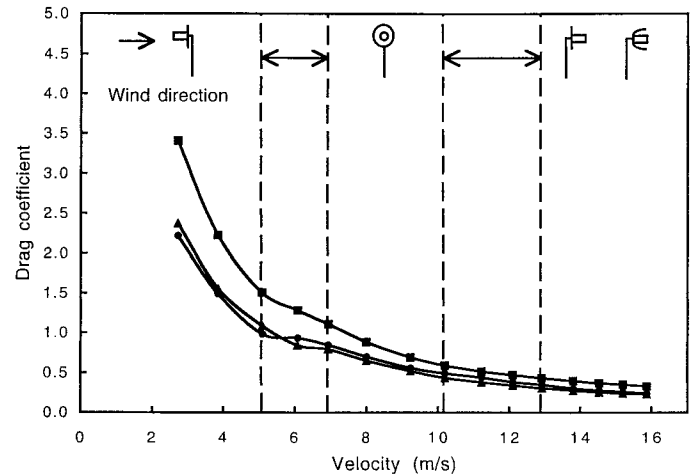


Fig. 3. Drag coefficient vs. speed for three entire flowers (stem and flower head) whose stems were free to move in nearly normal fashion, with speed ranges for the various orientations and configurations.

alteration of posture, reduces drag by an average of 30% at any windspeed.

Figure 3 gives the drag coefficients for unrestrained flowers on stems that initially faced upwind, along with the speeds at which changes in orientation and configuration occurred. As a result of these changes, the coefficient decreases more dramatically with increasing speed than for restrained flowers; a flower shifts, in effect, from the upper to the lower curve of Fig. 2.

Mechanical properties—Table 1 gives the principal results of the mechanical tests—flexural and torsional stiffnesses and the ratio of the two for the sets of six specimens. Daffodils have a significantly higher value of this latter size-adjusted mechanical descriptor than do tulips: a Mann-Whitney U test gives $P < 0.02$ for a comparison of the EI/GJ ratios. Equally relevant may be daffodils' much less scattered values for that ratio.

In addition, mechanical tests were performed on four specimens of a small cultivar of daffodils thought to be similar to older and less artificially manipulated varieties. Their values for EI/GJ , $12.2 (\pm 3.5 \text{ SD})$, although more variable, were not statistically distinguishable from those for the highly cultivated King Alfred daffodils.

DISCUSSION

Daffodil flowers change both shape and orientation in response to winds above 5 m/s, and both changes lead to reductions in drag coefficient. Between 3 and 5 m/s, drag coefficient also drops as speed increases, but neither shape nor orientation changes are yet evident. This latter is not merely the ordinary drop of drag coefficient with speed that occurs at low Reynolds number since the

TABLE 1. Flexural stiffness, EI , torsional stiffness, GJ , and their ratio for flower stems of daffodils and tulips, with standard deviations.

Species	EI ($\text{N}\cdot\text{m}^2$)	GJ ($\text{N}\cdot\text{m}^2$)	EI/GJ
Daffodil	$11.9 \pm 4.3 \times 10^{-3}$	$0.89 \pm 0.32 \times 10^{-3}$	13.27 ± 0.96
Tulip	$20.2 \pm 9.1 \times 10^{-3}$	$2.4 \pm 0.56 \times 10^{-3}$	8.33 ± 3.20

Reynolds number range, 12 000–20 000, is several orders of magnitude too high. It should be noted that at no point does an increase in speed lead to a decrease in drag itself, but merely to a decrease in the coefficient.

As a daffodil bends over in more extreme winds, it takes advantage of yet another mechanism for reducing drag. Bending of the stem will put the flower head closer to the ground and thus expose it to lower wind velocities. The relatively invariant speeds across the wind tunnel minimize the contribution of this last component in the present measurements. In nature the effect of the velocity gradient near the surface will almost certainly be both greater and more variable.

A beam of lenticular or elliptical cross section is most easily interpreted as a device to increase bending stiffness relative to material invested for loading in a particular direction. Such a cross section might reflect adaptation to an environment where the direction of external forces is consistent and predictable. Daffodil stems play a different game. Their noncircularity shows no obvious relationship to either load direction or flower orientation; indeed, many stems are slightly helical, with the orientation of the asymmetry varying along their length. Thus the noncircularity functions more likely as a device for decreasing the torsional stiffness of the stem. We expect that the stems of other large, nonaxially positioned flowers will have a relatively high EI/GJ ratio and that they will also respond to wind by twisting.

Noncircularity is both a contributor to and a sign of a high EI/GJ , but its contribution is relatively small. Were the stems made of an isotropic and incompressible material, EI/GJ would be ~ 2.0 , only slightly above the value of 1.5 for an isotropic, incompressible circular cylinder. Thus the high value of 13.27 found here reflects material (E/G) more than geometric (I/J) peculiarity. This relatively greater dependence on special material behavior characterizes all biological cases of high EI/GJ of which

we know. Presumably, high values of E/G require no drastic structural adjustment for composite structures with stiff elements running lengthwise, as in typical stems.

In practice, the second moments of area, I and J , have limited usefulness as structural descriptors for typically anisotropic and nonhomogeneous biological materials. While they can be determined easily and permit the Young's and shear moduli, E and G , to be calculated from measurements of flexural (EI) and torsional (GJ) stiffnesses, the results are not reliable for all shapes (Niklas, 1992). Conversely, the effective values of the latter composite variables are easy to measure, and their ratio is of immediate relevance to mechanical performance.

Daffodil stems, then, respond to wind by twisting so as to face downwind. By doing so they reduce their drag substantially. The motion is facilitated by their unusually low torsional stiffness relative to their flexural stiffness.

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