Drag and Flexibility in Sessile Organisms[1]

Steven Vogel

*Department of Zoology, Duke University,
Durham, North Carolina 27706*

Synopsis. Most large, sessile organisms when exposed to rapid flows of air or water are markedly deformed as a consequence of their structural flexibility. Responses to air and water movement are similar, although both extreme and typical forces generated by water flows are greater, and erect organisms are commonly shorter in water than in air. A useful way of viewing data on the scaling of drag with flow speed is with a graph of speed-specific drag (drag divided by the square of speed) against speed. Since an ordinary solid body usually gives a horizontal line on such a plot, deviations from the ordinary are immediately evident. The slopes of the double logarithmic version of these graphs provide useful numerical comparisons. All of the cases considered here—trees, macroalgae, sea pens, etc.—give negative slopes at high flow rates, indicating that speed-specific drag drops with increasing flow. Such results may be taken as evidence that the flexible response commonly constitutes an adaptively useful reconfiguration as opposed to a mere incidental consequence of the material economy afforded by flexibility.

Introduction

Perhaps the sharpest contrast in mechanical design between the larger products of natural selection and those of human contrivance is in stiffness. We find relatively rigid structures comfortable to manufacture and use while nature seems to make better and more extensive use of more flexible materials and structures. The solid biomechanician might hasten to point out that, in general, it takes less material to achieve a given strength or toughness if rigidity can be ignored then if substantial rigidity is a functional necessity. In short, faced with a given force, it is cheaper (and probably safer) to accept a fair amount of deformation—better bent than broken.

Consider, though, the use of the words "faced with a given force." One common origin of force or stress on an organism is motion of the fluid around it; the force will most often be in the direction of flow and hence properly called "drag." The fluid biomechanician might add an emphatic corollary to the argument that flexibility is a route to strength at low cost. As Koehl (1977) put it, "The shape, size, flexibility, texture, and behavior of an organism affects the flow forces it encounters . . . ." With

appropriate flexibility, the stress-causing force may itself be reduced—an organism may deform in rapid flows so its drag is no simple extrapolation from that in slow flows. Shape becomes a function of speed, and the scaling of drag with speed assumes unusual interest. Indeed the word "reconfiguration" may be more appropriate than "deformation"—we suspect specific adaptation and the latter carries some pathological odor of disfunction.

Flow-dependent shape, then, may be viewed as a way in which an organism can arrange that the flows which it encounters not generate excessive forces, analogous to streamlining, keeping deep within the velocity gradient on a surface, or otherwise, as it were, seeking shelter from the storm. For sessile organisms, flexibility may be a particularly efficient way to limit forces—a flow-tolerant shape need occur only during periods of high flow, so any consequent hypofunctionality can be of short duration, down to the period of a single wave or gust of wind.

The Highest Flows and Forces

In viewing adaptations which minimize drag, we might usefully focus on cases where drag is expected to be extreme; we ought thereby to reduce complications stemming from the non-mechanical functions of organisms. Thus we need to know values for extremes of flow within different

habitats in order to determine our partic-
ular experimental arrangements. These
extreme values are both more important
for present purposes and less commonly
measured than are temporal averages.

It is of some interest to ask just how fast
the flows of water and air to which organ-
isms are exposed ever get. For water cur-
rents, the maximal values seem to occur on
exposed rocky coasts, where the energy of
large waves is suddenly converted to,
among other things, very rapid local flows.
Only rarely has recording equipment been
mounted near enough to the rocks to be
exposed to maximum flows; one hopes that
the apparatus devised by Denny (1982) has
a major impact on our uncertainties. From
the forces recorded by Jones and Deme-
tropoulos (1968), I have estimated top
speeds as about 15 m/sec (34 mph) (Vogel,
1981). Some separate indication that this
figure is realistic can be obtained by assum-
ing that the local flow is occasionally
directed upward, a clump of water is thrown
free, and it decelerates without drag from
the air. An initial speed of 15 m/sec should
yield a height of 11.5 m (38 feet)—a value
which seems reasonable from anecdotal
observations and photographs of coastal
storms.

As a loose rule of thumb, flows of air in
nature are about fifteen times faster than
flows of water, but the rule seems inappli-
cable to extreme values. Winds of over 100
m/sec (220 mph) have been recorded on
mountain top instruments, but it is unlikely
that any organism extends into the full flow.
Some interesting data are supplied by
Oliver and Mayhead (1974) from a destruc-
tive gale of an intensity which occurred on
the average only one year in ten and which
eventually destroyed much of their appa-
ratus. Just above the forest canopy the
maximum speeds were about 17.5 m/sec
(40 mph), surprisingly low velocities; within
the canopy values were much lower still.
Well-spaced vegetation on hills and moun-
tains is probably at least occasionally
exposed to winds of above 25 m/sec (56
mph).

A flow of water of 15 m/sec can generate
very much higher forces than can an air-
flow of 25 m/sec. Consider a flat plate of
about 0.012 m² held normal to the flow—
approximately an outstretched hand with
fingers together. In air it experiences a
force of 5 N, roughly one pound; in water
it will be subjected to about 1,500 N, about
the weight of a 330 lb object. Another
comparison is that the maximum force
experienced by an object 1 × 1 cm in pro-
jecting area in water will be about the same
as the force on an 18 × 18 cm object in
air. Erect organisms of any great height
are unlikely to successfully colonize an
exposed rocky littoral! In passing, we might
note that the maximum speeds of airflow
are not unreasonable to produce in the lab-
oratory; flows of water of 15 m/sec are
rather more heroic. Fortunately, most
aquatic organisms should never encounter
any speeds near this latter value, so flow
tanks which achieve one or a few meters
per second are quite useful.

COMPARING DATA ON DRAG AND SPEED

One commonly hears that drag (D) is
proportional to the square of the speed of
flow (U). In fact, the statement applies rea-
sonably well to little other than non-
streamlined objects (bluff bodies) and to
these only in a limited range of speeds and
sizes. In water, the product of the length
of the object (in meters) and speed (in m/
sec) must be between about 10^{-4} and 10^0;
in air the figures are fifteen times greater.
Still, this is a biologically interesting range,
containing everything from a tree trunk,
1.5 m across in an airflow of 10 m/sec to
organisms in streams or tidal currents as
small as a millimeter in a flow of 0.1 m/
sec. And a non-streamlined object is an
essentially ordinary thing. So the relation-
ship

$$D \propto U^2 \qquad (1)$$

is a useful baseline. If the exponent of
velocity is less than two we may presume
some specialization toward reducing rela-
tive drag at high speeds. For streamlined
objects and for flat plates oriented parallel
to flow, the exponent is 1.5 for the same
size and speed range.

The usual practice in fluid mechanics is
to express both drag and speed in dimen-

sionless terms. For drag, the so-called "drag coefficient" is used, defined as

$$C_D = \frac{2D}{\rho S U^2} \qquad (2)$$

where ρ is the density of the fluid and S the area (defined in one of several possible ways) of the object. The drag coefficient can be viewed as the drag corrected for size, speed, and the particular fluid—a measure of the drag-suffering character-istics of a specific shape and a good param-eter for comparing different shapes. For speed, the "Reynolds number" is used, defined as

$$Re = \frac{\rho l U}{\mu} \qquad (3)$$

where l is a linear dimension of the object and μ is the viscosity of the fluid. The Reyn-olds number can be seen as the speed of flow corrected for the size of the object and the particular fluid—a measure of the effective speed with respect to such phe-nomena as the appearance of turbulence. I have elsewhere given a more complete account of the origin and use of C_D and Re. Note that if drag is proportional to the square of speed, then C_D no longer varies with speed, and

$$C_D \propto Re^0 \qquad (4)$$

This exponent of zero provides a better baseline: in a plot of C_D (ordinate) against Re (abscissa) any regular deviation from a horizontal line should signal something of interest.

I should like to suggest an alternative transformation of data for drag and speed, one less general in the comparisons it per-mits but which, although simpler in prac-tice, still focuses attention on the way drag scales with speed as a contrast with a bluff body. Let us assume we care only about the exponent of the proportionality between speed and drag; let us forgo direct com-parisons among objects of different sizes or from different fluid media; let us rec-ognize that plots of one dimensionless index against another may be intuitively unsatis-fying to the biologist; and let us recognize that "l" and "S" are awkward to define for biologically interesting shapes. We're left with

$$\frac{D}{U^2} \propto U^0 \qquad (5)$$

as our baseline, plotting D/U^2 (ordinate) versus U (abscissa) and looking for devia-tions from horizontality. D/U^2 might be termed the "speed specific drag." For regions on a graph without inflection points, the exponent can be derived by a linear regression as the slope of the plot of the logarithms of D/U^2 and U. This slope, then, can be taken as a "figure of merit"— the lower (more negative) the value, the more noteworthy the *relative* reduction of drag as speed is increased; we will denote the slope or exponent as "E." If flexibility permits a reduction in drag at high speeds, the fact should be signalled by a value of E below that which would hold for a similar but rigid object. All values of E cited or alluded to here have been collected in Table 1.

COMPARISONS AMONG ORGANISMS

At the start, it is useful to distinguish among several situations in which flexible organisms meet flows. (1) An organism may be either erect or non-erect; if erect it must withstand forces which tend to bend it as well as merely stretch it—it will experience compressive and perhaps torsional stresses as well as tensile stresses. In general, the erect organism will be more vulnerable to the effects of drag and will require more material to withstand a given drag, as pointed out by Koehl (1982). Trees, hard corals, and most sponges are erect; many large algae and much other aquatic vege-tation and a variety of sea whips, sea fans, sea lilies, and sea anemones might be best regarded as semi-erect. (2) Organisms (on a short time scale) may or may not maintain constant volume. Creatures such as sea anemones (Koehl, 1977) which can shrink or deflate perhaps make the most extreme use of flexibility. (3) An organism may or may not have a constant surface area. For flat structures parallel to flow, drag increases with exposed surface. While the surface of, say, a single flag is essentially fixed, elongate flags on the same mast might

TABLE 1. *Values of E for various cases, where $D/U^2 \propto U^E$.*

System	Condition		E	Source
Bluff body	Re:	1,000–500,000	0	Vogel, 1981
Streamlined body, laminar flow		1,000–500,000	−0.50	Vogel, 1981
Flat plate, parallel to flow		1,000–500,000	−0.50	Vogel, 1981
Flat plate, parallel to flow		10–1,000	−0.60	Janour, 1951
Cylinder, axis normal to flow		20–120	−0.29	White, 1974
Miscellaneous solid objects		<1.0	−1.00	Vogel, 1981
Hedophyllum sessile	U:	1–3 m/sec	−1.14	Armstrong (p.c.)
Sargassum filipendula		0.2–1.5 m/sec	−1.06	Pentcheff (p.c.)
Sargassum filipendula		0.5–1.5 m/sec	−1.47	Pentcheff (p.c.)
Pinus sylvestris		9–38 m/sec	−0.72	Mayhead, 1973
Pinus taeda, 1 m high		8–19 m/sec	−1.13	Present study
Ilex opaca, 1 m high		8–19 m/sec	−1.30	Present study
Pinus taeda, branch		8–19 m/sec	−1.16	Present study
Ilex opaca, branch		8–19 m/sec	−0.10	Present study
Pinus taeda, control		8–20.5 m/sec	−1.11	Present study
Pinus taeda, shaken		8–20.5 m/sec	−1.12	Present study
Ptilosarcus gurneyi		0.02–0.26 m/sec	−0.86	Best (p.c.)
Ptilosarcus gurneyi		0.11–0.26 m/sec	−1.14	Best (p.c.)
Locusta migratoria, antenna	Re:	20–120	−0.56	Gewicke and Heinzel, 1980

be arranged to layer in rapid flows and thus to reduce exposed area. Leaves on branches or highly dissected laminate algae may, in effect, have surfaces of variable area. (4) One might distinguish between cases in which strong flows are a constant environmental factor and those in which they are uncommon or episodic. In the former cases less compromise of other functions in order to withstand such flows is likely to be tolerable: an organism on a rock in a torrential stream or atop a mountain must be fully functional in the flow. A tree need not bother much with photosynthesis in a gale or a coral with suspension feeding in a typhoon. Thus some of the structural differences between, for example, trees high on mountains and those in valleys may reflect more the issue of whether the organism is fully functional in fast flows than any difference in actual breaking strength.

Thus even before examination of any data for drag as a function of speed, it is amply evident that flexibility raises the possibility of a range of kinds of adaptations which might reduce drag. While we have available a figure of merit for the scaling of drag with speed we ought, *a priori*, to recognize its limitations in comparisons of systems of markedly diverse arrangements.

Non-erect systems

One might expect that an elongate, laminate alga would behave much like either a streamlined body or a flat plate oriented parallel to the direction of flow, with a value of E of −0.50 at moderate Reynolds numbers—the alga should continuously reorient so, whatever the local flow, the blade should be parallel to it, lying essentially on a streamline. In fact, the drag of a freely fluttering flag is greater than that of a rigid weathervane of the same area (Hoerner, 1965) due to the flutter and the resulting "separation" of flow from the surface, at least at quite high Reynolds numbers. If separation of flow is the culprit, then the effect ought to be more pronounced at high speeds: the value of E should be above −0.50. One set of measurements on a sheet of polyethylene trailing behind a batten in a flow tank gave a value of +0.76—worse even than a bluff body (D. J. Law, personal communication). But further measurements indicate that E varies with experimental conditions in ways we do not yet understand.

Many aquatic plants, both algae in marine systems and vascular plants in fresh water, have ruffled edges. The ruffles may alter flow in a way which helps exchange of dissolved material between plant and water (Koehl and Alberte, work in progress) and/or they may reduce stress concentrations at the edges and therefore any tendency to tear. Koehl (personal communication) reports that ruffles on macroalgae seem to increase drag. Work on polyethylene stretched to produce ruffles has so far given ambiguous results suggestive of increased drag.

A few specific data exist for marine macroalgae, from which I have calculated values of E. From the data of S. L. Armstrong (personal communication) for *Hedophyllum sessile* towed alongside a boat at 1 to 3 m/sec, I obtain a value of -1.14: certainly low enough to make one suspect some degree of adaptive design and "deliberate" reconfiguration. The particular form of *Hedophyllum* tested (from Cattle Point, San Juan Island, Washington) is well-ruffled but undissected. A similar value, -1.06, comes from the data of N. D. Pentcheff (personal communication) for *Sargassum filipendula* from a wharf piling at Beaufort, North Carolina, tested in a flow tank at speeds up to 1.4 m/sec. *Sargassum*, though, is a highly branched alga of a lacey appearance. Looking only at speeds above 0.5 m/sec, E decreases to -1.47 (with a higher correlation coefficient). This figure begins to crowd the value of -2.00 at which drag becomes independent of speed. In fact, for certain specimens at the highest speeds, drag did not increase with increases in speed. Apparently at high speeds *Sargassum* reconfigures quite drastically, with the branches coalescing into a rather rope-like structure from their original fan form. These algae, though, live in a harbor area, where exposure to really rapid flows must be intermittent.

Erect systems

The paradigmatic erect sessile organism exposed to fluid motion is, of course, a tree. Photosynthetic efficacy dictates a high surface area even more inescapably than does,

say, suspension feeding. The basic resource, light, comes from above, so the competitive advantage of standing tall is clearly manifest. And, as argued earlier, the forces imposed by flows of air are rarely high enough to preclude an erect posture. Only in an occasional habitat is wind direction consistent, and shapes optimized for interception of sunlight are unlikely to yield low values of drag. Yet trees grow to great height and achieve impressive longevity— the chance of a healthy adult breaking or uprooting is really quite low.

Mayhead (1973) cites data for a Scotch pine tree (*Pinus sylvestris*) exposed to wind in a large wind tunnel at speeds from 9 m/sec to a value, 38 m/sec, at which irreversible structural changes occurred. From these data I calculate a value of E of -0.72: the tree performs better than an ordinary bluff body, better even than a streamlined object. As the wind increases, it gradually reconfigures itself. The process is indeed gradual and regular—the curve of D/U^2 versus U shows no inflections, and the correlation coefficient for the logarithmic regression is 0.986. The drag at the highest speed tested is only about a third of the drag which would be extrapolated from the lowest speed with an E of zero. And the lowest speed, 9 m/sec (20 mph), is high enough for us to doubt that it elicits a still air posture.

The availability of a smaller wind tunnel, originally designed for work on bird flight (Tucker and Parrott, 1970) permitted me to test smaller and presumably more flexible trees and speeds below 9 m/sec. The limitation of a meter in height is, admittedly, cramping and incites Procrustean pruning of trunks. And the extensive bending in winds shifts a tree's center of gravity, adding weight to drag as a component of torque on the base; the latter problem, though, is nearly eliminated by averaging figures for a tree in erect and inverted posture.

Two kinds of trees were tested, and representative results are plotted in Figure 1. The differences between loblolly pine (*Pinus taeda*) and holly (*Ilex opaca*) are worth some emphasis—their similarities scarcely
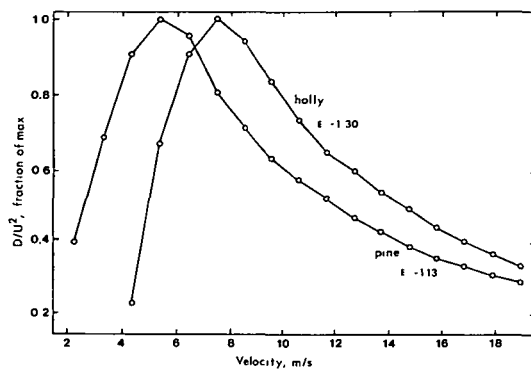
FIG. 1.   Speed-specific drag as a function of airspeed for loblolly pine (*Pinus taeda*) and holly (*Ilex opaca*). *E* is the exponent of the proportionality between D/U^2 and *U*, with values given for the descending portion of each curve. For each tree, the maximum value of D/U^2 has been set at 1.0.

extend beyond retention of leaves at the end of November, the basis for their selection. Small pines in the Carolina piedmont colonize open fields and are likely to meet substantial winds in their youth. Their flexible needles are clustered in fascicles, the latter flexibly attached to branches, themselves quite flexible. Hollies seem stiffer—brittle leaves attached by short petioles to branches—and grow beneath a preexisting forest canopy, presumably somewhat more sheltered. Thus the similarity of the results proved somewhat of a surprise. The stiffer response of the holly is evident in the shift of its peak value of D/U^2 to the right; otherwise the lack of sharp differences is suggestive of a common response of small trees and perhaps branches on large trees to winds.

The initial rise in speed specific drag appears to be associated with configurational changes which bring more needles, leaves, and branches broadside to the wind—the shapes of the trees are getting "worse"; but, of course, the actual levels of drag are not especially high at these speeds. As speed is further increased there is a surprisingly sudden change in the results of further reconfiguration, and the speed-specific drag curves drop even more drastically (lower *E*'s) than in Mayhead's full-size pine. The drastic configurational

changes at the highest speed appear to be entirely reversible. This is a far from obvious result for the holly in particular—individual leaves have had their petioles bent and twisted and are in most cases layered, one leaf on another, against the branch, with their spiked tips and surface contours preventing much movement. The pine needles gradually point more distally on the branches, a cluster forming a cone with its apex proximal and which becomes more acute as the wind increases. Thus individual needles become more nearly parallel to the wind and the mutual sheltering of the needles increases. Both graphs and appearances are persuasive indications of the pervasive hand of natural selection, tuning the form and flexibility of the system for an efficient response to wind.

The orderly wind-induced reconfigurations of these trees raises a host of questions with respect to both solid and fluid aspects of the response. Some are not easy to address—the drag cannot be simply partitioned into leaf and branch components since, as a result of flexibility, a leafless tree will not reconfigure its branches in the ordinary manner and since reciprocal sheltering of parts must be extensive. Conversely, the decrease in overall drag in winter as a result of the deciduous habit is not hard to determine. A few deciduous trees retain dead leaves through the winter, perhaps as a shield for buds which might reradiate excessively to a cold sky. Is the occasional leafed tree at especial hazard when surrounded by bare-branched neighbors; or can it shed its leaves in a rare, severe wind, in effect avoiding whichever factor is the forest's prime evil? At this point all I know is that a steady wind of 20 m/sec is insufficient to blow the leaves from a post oak (*Quercus stellata*) in winter.

Some indication of the components of the drop in speed specific drag at high speeds may be obtained by testing parts of trees. I tested small branches of pine and holly in the same tunnel as used previously; the results from the two species contrast sharply. For a branch of pine, the resulting *E* of − 1.16 (8–19 m/sec) is not appreciably different from that of the entire tree, suggesting that the main drag reducing adjust-

ment in pine consists of changes in orientation of needles and fascicles. For a branch of holly, E is -0.10: the speed-specific drag is nearly constant despite the conspicuous reorientation of leaves against the branch. Evidently, reorientation of branches so all tips point downstream is of greater consequence. The final result may be the same, but these preliminary data imply that holly and pine employ somewhat different tactics.

The adaptation of a tree to the prevailing pattern of winds in its habitat may be quite a subtle and elaborate complex of genetic and somatic factors. Some evidence exists indicating that a tree can make a "judgment" early in its life about the likelihood of encountering winds later on. F. Telewski (personal communication) has raised loblolly pines, each of which as seedling he shook gently for 30 sec on alternate days. The resulting meter-high saplings show a suite of morphological changes compared with unshaken controls. Among other differences, the shaken trees are shorter, on average, and have thicker trunks of greater flexural stiffness. Of particular interest, their drag at 20 m/sec averages 30% greater than the controls, although E is the same as for the controls and for the wild pines cited earlier. What might be the significance of these differences? Perhaps a tree in a windy place finds it advantageous to remain more nearly fully functional in moderate wind and so builds a stiffer and stronger trunk in compensation or overcompensation for its greater drag. This notion of the importance of maintaining non-mechanical functions in persistent wind is consistent with the results of Tranquillini (1969) and Caldwell (1970) on the changes in photosynthetic rates with changes in wind speed in woody plants from different habitats.

More drastic alterations are, of course, well known for trees living on ocean fronts and mountains where not only are winds strong but the direction of airflow is fairly certain. Indeed, the orientation of these "flag form" trees permits good mapping of the direction of prevailing winds. E. C. Brown (personal communication) measured the drag of eastern redcedars (*Junip-*
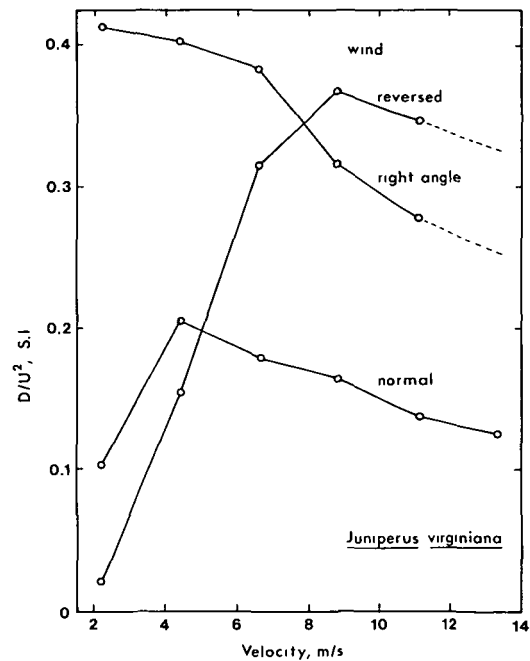

FIG. 2. Speed-specific drag as a function of airspeed for a flag-form eastern redcedar from a coastal dune front. "Normal" corresponds to the orientation in nature to a landward wind. The units for D/U^2 are N sec² m⁻².

erus virginiana) from the dunes of Bogue Bank (North Carolina). Trees from locations surrounded by dunes appeared symmetrical and gave curves for speed-specific drag similar to the pines and hollies. Trees from the first line of dunes above the beach were conspicuously flag-formed, and their drag curves (Fig. 2) depended strongly on orientation. At all but the lowest speeds, drag was minimized in the normal orientation with respect to landward wind. Perhaps the assumption that such changes in shape are a kind of passive damage is overly facile and tacitly maligns the evolutionary process.

The situation of a tree is not very different from that of some animals, in particular of that of erect, flexible suspension feeders. B. A. Best (personal communication) has measured the drag of sea pens (*Ptilosarcus gurneyi*) in a flow tank. These cnidarians can rotate (slowly) about a kind of joint near the base and can deflect in currents without retraction of individual

polyps. Over the range of speeds tested (0 to 0.26 m/sec), E is -0.86 ($r^2 = 0.969$), but the reconfiguration, like that of *Sargassum*, is more pronounced at the higher speeds, with an E of -1.14 for 0.11 to 0.26 m/sec ($r^2 = 0.997$). The latter figure is satisfyingly convergent with the results for loblolly pines.

A final erect system is the antenna of a locust (*Locusta migratoria*). The data of Gewicke and Heinzel (1980) gives a value for E of -0.56 for this small, tapering, flexible cylinder of some surface roughness. Due to the small size of the antenna and the consequently low Reynolds number, a base line of $E = 0$ is no longer appropriate. But it is a simple matter to calculate E for a circular cylinder from the formula given by White (1974) for the appropriate range as -0.29. Even with this more realistic comparison, flexibility seems to be a good thing.

CONCLUSIONS

The various bits of data cited here may be taken as strong (if circumstantial) evidence of the adaptive reconfiguration of flexible organisms to minimize drag in rapid flows, certainly not a novel notion. I could find no case in which flexibility failed to confer a decrease in speed-specific drag at high speeds when rigid bluff bodies or flat plates formed the basis for comparison. But flexibility is not automatically or intrinsically drag reducing—recall the increase in speed-specific drag for small trees at low airspeeds and the likelihood that speed-specific drag sometimes rises with speed for flexible laminae. So it is not unreasonable to invoke the idea of specific adaptation. And the latter is very much our stock-in-trade as functional biologists or biomechanicians.

For flexibility to work in drag reduction it thus must be a finely tuned feature of the design of an organism. And to investigate the phenomenon, one must do more than either assume a constant force and consider the mechanical response or assume a constant shape and consider how it might be designed to minimize force or stress. The message here is then a call for investigations which shrewdly combine solid and fluid mechanics, taking the pres-

ent information as evidence that such a combination cannot fail to produce enlightening results. Indeed, biomechanics might even uncover situations of relevance in the design of practical devices.

REFERENCES

Caldwell, M. M. 1970. Plant gas exchange at high wind speeds. Plant Physiol. 46:535–537.

Denny, M. W. 1982. Forces on intertidal organisms due to breaking ocean waves: Design and application of a telemetry system. Limnol. Oceanogr. 27:178–183.

Gewicke, M. and H. G. Heinzel. 1980. Aerodynamic and mechanical properties of the antennae as air-current sense organs in *Locusta migratoria*. I. Static characteristics. J. Comp. Physiol. A. 139:357–366.

Hoerner, S. F. 1965. *Fluid-dynamic drag.* S. F. Hoerner, Brick Town, N.J.

Janour, Z. 1951. Resistance of a plate in parallel flow at low Reynolds numbers. Nat. Adv. Comm. Aero. Tech. Mem. #1316.

Jones, W. E. and A. Demetropoulos. 1968. Exposure to wave action: Measurements of an important ecological parameter on rocky shores in Anglesey. J. Exp. Mar. Biol. Ecol. 2:46–63.

Koehl, M. A. R. 1977. Effects of sea anemones on the flow forces they encounter. J. Exp. Biol. 69: 87–105.

Koehl, M. A. R. 1982. The interaction of moving water and sessile organisms. Sci. Amer. 247(6): 124–134.

Mayhead, G. J. 1973. Some drag coefficients for British forest trees derived from wind tunnel studies. Agric. Meteorol. 12:123–130.

Oliver, H. R. and G. J. Mayhead. 1973. Wind measurements in a pine forest during a destructive gale. Forestry 47:185–194.

Tranquillini, W. 1969. Photosynthese und Transpiration einiger Holzarten bei verschieden starkem Wind. Zentralbl. Gesamte Forstwes. 86:35–48.

Tucker, V. A. and G. C. Parrott. 1970. Aerodynamics of gliding flight in a falcon and other birds. J. Exp. Biol. 52:345–367.

Vogel, S. 1981. *Life in moving fluids: The physical biology of flow.* Willard Grant Press, Boston, MA.

White, F. M. 1974. *Viscous fluid flow.* McGraw Hill Publishing Co., New York.