Series

Living in a physical world
VII.
Gravity and life on the ground

STEVEN VOGEL

Department of Biology, Duke University, Durham, NC 27708-0338, USA

(Fax, 919-660-7293; Email, svogel@duke.edu)

1. Introduction

Unless some energy-demanding process counteracts its effect, gravity inevitably makes aerial life descend. For terrestrial life, gravity acts less obviously, less immediately, and less consistently. Sometimes it matters; sometimes other agencies eclipse its effects. Sometimes it acts as impediment or nuisance; sometimes it plays a crucial positive role. In short, gravity has more diverse consequences and has elicited a wider range of biological devices for organisms that live on the ground.

For one thing, much more depends on the distinction between gravity, thus weight, and inertia, thus mass. Steadily lift an object, and you work against gravity; pull downward, and you enlist gravity's assistance. Sliding an object steadily sideways may entail no irreduceable resistance, but the frictional force you do feel still comes from gravity, from the press of the object against the substratum. But accelerate an object, and you work against its mass. Big Neanderthal thrusting spears put gravity to use, working best with heavy bodies that leaned forward over well-planted feet to get sufficient purchase on the ground. Lighter, thrown spears depended more on inertial mass – a running body, in effect no purchase at all, could aid a launch. Similarly, a lighter person has to lean further outward when opening a substantial door. The lesser weight needs to be more effectively applied to produce the sideways force that will accelerate the mass of the door. Muscularity is a secondary matter.

For another, organisms consist of both solids and liquids. In practice the two phases of matter face gravity in slightly different guises that reflect the difference between compressive stress and hydrostatic pressure. Both variables have dimensions of force per unit area, but in a specific direction for stress while omnidirectional for pressure. Stack solid bricks ever higher (with pads between to ensure uniform force transfer), and eventually the lowest will crush. That crushing point is reached when the compressive strength of brick, or force-resistance relative to cross section, of about

20 MPa (or MN m^{-2}), equals the weight of the column relative to cross section. If made of bricks whose density is 2000 kg m^{-3}, the column will be about 1000 m high. Taper changes the picture – a column tapering upward can extend farther; one expanding upward will not reach as far. With similar reasoning, Weisskopf (1975) estimated the maximum height of a mountain as 10 km, about 10% higher than our present highest; in his analysis, plastic flow rather than crushing set the limit, so taper mattered little.

Extend a pipe of liquid water upward in the air, and the pipe eventually bursts at ground level. The column of water extending upward stresses (in the sense above) the material of the pipe, but it does so in proportion only to the height of the column – cross section and contained volume have no direct relevance. The pressure difference, Δp, across the walls of the pipe will be the product of the liquid's density, ρ, gravitational acceleration, g, and the column's height, h, in the familiar equation for both manometry and conversions of pressure units:

$$\Delta p = \rho g h. \tag{1}$$

Transforming that pressure to tensile stress (σ_t) in the wall of the pipe depends, obviously, on the thickness of the wall of the pipe (Δr, assumed well below the radius r) and, less obviously, on its size, here the radius:

$$\sigma_t = \frac{\Delta p \, r}{\Delta r} = \frac{\rho g h r}{\Delta r}. \tag{2}$$

This last equation is prescient with biological implications. For a given pressure and a wall material of a given tensile strength, a narrower pipe (lower r) will manage with a thinner wall (Δr). For example, your capillaries withstand pressures about 1/3 of that in your aorta despite having walls 2000X thinner. They manage that apparently paradoxical feat (convenient for material exchange) because their diameters are about 4000X less than that of the aorta. As one can see from eq. (2), they feel about 6X less tensile stress in their walls rather than the many times more that one might guess (Zweifach 1974; Caro *et al* 1978). Or,

anticipating just a bit, since neither cardiac blood pressure (Δp) nor maximum muscle stress (σ_t) changes with body size, the thickness of the ventricular wall (Δr) will remain a constant fraction of heart radius itself (r) (Seymour and Blaylock 2000).

Here I will examine three situations in which gravity plays a role, asking what sets blood pressures for animals of different sizes and with what consequences; what determines the gait transition speeds for legged animals; and what sets the heights of trees and forests.

2. Circulation and hydrostatics

The scaling of the circulatory components of vertebrates, especially mammals, has come in for renewed attention in recent years. Heart mass and total blood volume increase in direct proportionality to body mass ($\propto m_b^{+1}$). Capillary length goes up slightly with mass ($\propto m_b^{+1/5}$), while capillary density ($\propto m_b^{-1/6}$) and maximum heart rate ($\propto m_b^{-1/5}$) go down. Maximum oxygen consumption and cardiac output go up but not as fast as body mass itself (both $\propto m_b^{+7/8}$). But not all variables vary with mass; in particular, blood viscosity, capillary and red blood cell diameters, aortic flow speed, and average arterial blood pressure remain nearly the same. (Exponents from Baudinette 1978, Calder 1984 and Dawson 2005.)

In looking for gravity's consequences, we ought to take a closer look at that size-independence of blood pressure. That constancy, first noted over half a century ago, has become ever better supported. For mammals, the average of systolic peaks and diastolic minima (often taken as a third of systolic plus two-thirds of diastolic to get closer to a true time-averaged mean), is about 12,900 Pa (97 mm Hg). So we humans are typical, with our systolic pressure of about 16,000 Pa (120 mm Hg) and diastolic pressure of 10,500 Pa (80 mm Hg). For birds average pressure runs somewhat higher, 17,700 Pa (133 mm Hg) (Grubb 1983).

From our present viewpoint, constancy of blood pressure seems paradoxical. Terrestrial animals amount to ambulatory manometers, obeying eq. (1), with a blood density of about 1,050 kg m^{-3} for ρ, and thus with a pressure gradient of 10,300 Pa m^{-1} from head to toe. Without auxiliary pumps, blood pressure at head height has to drop as body height increases. Thus a normal human has a diastolic blood pressure of about 5,300 Pa (40 mm Hg) in the head and 20,000 Pa (150 mm Hg) in the feet (Schmidt-Nielsen 1997). While gravity cannot be turned off, the relatively high pressure gradient needed to keep blood flowing through the resistive vessels ordinarily exceeds that gravitational gradient. Health care people learn to cuff the arm at heart height when taking blood pressures, although (by my informal survey) almost none of them know just why or what error an improper height introduces. With that 5,300 Pa (a little

lower if hypotensive) we manage to keep blood flowing steadily and our brains decently supplied with oxygen – I have seen no claim that mental agility decreases with body height. Roughly 4,000 to 6,000 Pa (diastolic) appears sufficient to keep a mammalian brain in business.

An animal with its head a meter above its heart should be in serious trouble at standard mammalian cardiac output pressure – during diastole, blood will cease flowing at all. Half a meter should be about the limit, with gravity dropping diastolic pressure by 5,100 Pa (almost 40 mm Hg).

In fact, animals that hold their heads high do not have normal mammalian blood pressure. Most sources of scaling exponents include some parenthetical remark such as "excluding the giraffe" (Calder 1984) after noting the standard and its nearly size-independent scaling. That exclusion represents not some special case but a necessary threshold for gravitational compensation. We might view the situation with the aid of a dimensionless ratio, a "gravitational hazard index" (*GHI*). Such an index puts the height of animal in pressure units, that is, as if it were a blood-filled manometer obeying eq. (1); it divides this "manometric height" (ρgh) by average arterial (heart-high) blood pressure:

$$GHI = \frac{\rho gh}{\Delta \bar{p}}. \tag{3}$$

Figure 1 considers average blood pressures relative to this *GHI*. (One should recall just how labile a variable is one's own pressure and recognize the limitations of data from animals of even less certain disposition.) Two limits on blood pressure can be discerned. A lower horizontal line must represent the minimum average arterial pressure needed to overcome the resistance of the systemic system of conduits; it has a value of about 10,000 Pa (75 mm Hg). A vertical line to the right of the data points represents the limit set by the need to supply a brain at some minimum pressure after gravity exacts its tax on cardiac output. It appears to have a value (dimensionless) of about *GHI* = 1.7. Bear in mind the use of overall height instead of heart-to-head height and zero rather than some necessary minimum cranial pressure.

Small mammals can ignore gravity, while large (at least tall) ones most definitely must care. In effect, mammals tolerate the gradual diminution of cranial blood pressure with increasing height – up to a point. That point corresponds to animals only slightly taller than ourselves. (And thus slightly hypotensive or unusually tall humans manage quite well.) While we have too few reliable data for mammals taller than ourselves, we have no reason to suppose that their blood pressure does anything other than tracking the sum of two components, that set by the resistance of the system and that set by the need to raise blood against gravity.

The perceptive reader may think of a simple evasion of this problem of getting blood up to the head – in a word,
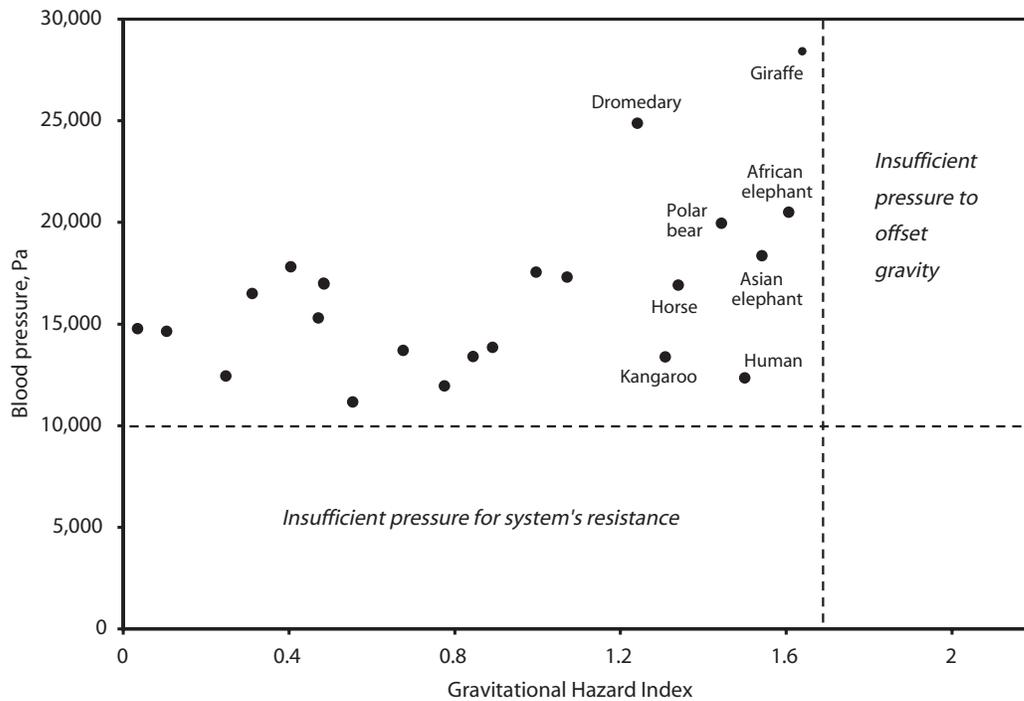
Figure 1.   Blood pressures of mammals, with names of the larger ones, plotted against gravitational hazard index (*GHI*). Most of the pressure data come from Seymour and Blaylock (2000), with a few additions and confirmations from *www.ivis.org;* heights have been estimated from the photographs and shoulder heights in Nowak (1991).

siphoning. Since vessels are full, descending blood could draw blood upward, reinvesting the energy of decent to raise blood. The issue of siphoning has provoked no small amount of controversy; at present the weight of evidence opposes it (Pedley *et al* 1996). Tall mammals do generate the high pressures needed to raise blood without siphoning – one of the incentives for work on giraffes. Blood vessels in the head appear reinforced against conventional outward aneurysms rather than inward collapse. And the descending veins are all too collapsible, so blood commonly descends in boluses rather than a continuous stream. Of course one should not rule out the possibility that at least some siphoning still occurs under some circumstances, perhaps during vigorous aerobic activity.

At the same time, blood vessels in the legs must be strong enough to take both the higher cardiac pressure and the extra gravitational component. Which, not surprisingly, they are. In addition, the entire legs must be wrapped with an especially inextensible integument lest the extracellular space become oedematous. Which they are as well. In giraffes in particular, the vessels of head and neck need similar reinforcement, almost certainly important in preventing aneurysms when an animal lowers its head to drink.

Between their higher average blood pressures and lack of very tall extant members, birds should never hit an equivalent limit. One does wonder about giant moas, extinct for the

past 800 years – the wall thickness of some miraculously preserved artery would probably allow reasonable estimation of their blood pressure. By contrast, reptiles (or "other reptiles" to some) present a much more interesting issue. Blood pressures run about a third of those of mammals, so the vertical limit line of figure 1 should occur at a third of the equivalent mammalian body height – about 0.57 rather than 1.7. Most extant reptiles are either small or lie low to the ground and should have no problem with gravitational pressure loss even so. Not all, though; in particular, some fairly long snakes climb trees and go over obstacles, making "fairly long" into "fairly tall." In fact, the average heart-level blood pressures of long snakes vary widely, from about 3,300 Pa (25 mm Hg) in aquatic species to around 10,500 Pa (80 mm Hg) in terrestrial climbers. More remarkably, terrestrial climbers position their hearts substantially closer to their anterior ends— in a comparison of a python and a file snake of about equal length, about 25% of snout-vent distance versus 37%. In addition to these differences, climbers have reinforced body walls in their posterior regions and especially well-developed baroregulatory reflexes (Seymour and Arndt 2004).

No basic inferiority of reptilian heart muscle should rule out the giraffe's trick. More likely, their basic lung-shunting scheme, dividing cardiac output between interconnected systemic and pulmonary circulations, presents a barrier. We

mammals (and birds) have no such connection and an unalterably serial circulation. Volume flow (Q) through the lungs must exactly equal volume flow through the systemic circulation, depriving us of the ability to reduce pulmonary flow during, for instance, diving. But we gain the ability to run the pulmonary circuit at a different pressure (Δp) (typically a fifth or sixth) than that elsewhere. In effect, we keep the cost ($\Delta p Q$) of pulmonary pumping low with a reduced Δp; reptiles keep the cost low with a reduced Q. (Crocodilian reptiles, with optional shunting, may have the best of both worlds; but they live in a severely horizontal world so the problem is moot.)

Extant reptiles may mainly keep their heads down, but one must wonder about dinosaurs, those famously tall reptiles. To take an extreme case, *Brachiosaurus* may have carried its head as much as 8 m above the heart, with an overall height of 12 m (Gunga *et al* 1995). A *GHI* limit of 1.7 suggests an average heart-level blood pressure of 73,000 Pa (550 mm Hg). Recognizing the atypically low heart and using ($10,000 + \rho g h$) instead gives a pressure of 92,000 Pa (690 mm Hg). Either far exceeds that of a giraffe. One must assume that *Brachiosaurus* kept its head up – as Carrier *et al* (2001) pointed out, carrying a head so far in front of the center of gravity would have severely impeded turning, and the vertebrae certainly permit such posture. Still, we can imagine a variety of solutions or evasions. Brief cranial anoxia may have been tolerated. Or perhaps these creatures had subambient cranial blood pressures, driving flow by the pull of siphons rather than the push of pumps. A partial solution may not be especially obscure. Birds evolved from (or are) dinosaurs, and birds have fully serial circulatory systems. That dinosaurs did likewise thus involves no great stretch of any evolutionary scenario, according to one of their intimates, Kevin Padian (personal communication).

3. To walk or to run

Almost all our terrestrial vehicles move on rotating wheels. Occasionally we even use temporary, axle-less wheels, moving heavy objects on rollers by shifting them from rear to front as they emerge, one by one. Physics imposes no irreducible minimum cost – only imperfect stiffness of wheels and path, friction of wheel bearings, accelerations, slopes, and air resistance impede motion. Railroads, with metal wheels and level, metallic tracks, could provide economic transport with the inefficient steam engines of two centuries ago, long before road vehicles could shift from draft animals. Wheels, especially with axles, are splendid devices.

No terrestrial animal goes from place to place on wheels and axles. One can argue (as did Gould 1981) that evolutionary constraints preclude their appearance. Or one can argue (as did LaBarbera 1983) that we easily overrate the utility of wheels, that they lack versatility and, in particular, work badly on either soft or bumpy surfaces. That latter argument receives at least tacit endorsement by recent attention (mainly military) to legged robots for off-road use, emulating the general arrangements of animals such as ourselves.

The use of legs may be widespread but it cannot be described as energetically efficient. However many legs an animal uses, it faces a basic difficulty that rolling wheels circumvent. Legs work by reciprocating rather than rotating, which means that any leg of finite mass must waste work accelerating at the start of a cycle and then decelerating again at the end. Of course an evasion comes immediately to mind – bank the decelerative work for reuse in the subsequent acceleration. What kind of short-term battery, then, might store that work? Electrochemical storage could be used, like the regenerative brakes of some hybrid automobiles, but no natural examples have yet come to light. Or inertial storage might serve, as in a flywheel. Again we can point to no obvious natural case, although bicycles, passive locomotory prostheses, make some use of the scheme.

Two kinds of brief batteries do find widespread use – lifting and then lowering masses against and with gravity, and straining and then releasing springs. Interestingly, animals cannot be dichotomized by their use of one or the other of these fundamentally different ways to store energy. Instead, most legged terrestrial animals depend on both, shifting from one to the other at a specific speed. At low speeds, gravitational energy storage does the job in what we call walking gaits; at higher speeds elastic energy storage serves in the various running gaits. It would be a rare culture that lacks specific words for at least these two gaits, so obvious is the distinction.

Quite recent – surprisingly recent – is the recognition that this shift from gravitational to elastic energy storage underlies the abrupt transition. Traditionally, walking gaits have no fully aerial phase while running gaits include at least a brief aerial phase. True enough, except for elephants (at least), which trot without an entirely aerial phase, but that classic distinction holds far less prescience. The realizations both that the basic game consisted of offsetting the inefficiency of legged locomotion and of the role of gait shifting we owe to R McNeill Alexander and his associates (Alexander 1976; Alexander and Jayes 1983 and other papers and books). In addition they have done as much perhaps as everyone else put together in working out its implications. The crux of the matter takes few words. In walking gaits, whether bipedal or polypedal, gravitational storage does the job, and almost the entire body mass contributes to the functional weight. In running and hopping gaits (trotting, galloping, cantering, skipping, bounding, etc.) stretched tendon does most of the work of elastic storage, with substantially lesser contributions from muscle and bone.

How gravitational energy storage can ease a task can be easily demonstrated. Swing a lower leg back and forth while sitting on the edge of a desk and measure the period. Plug that time, *t*, into the standard equation for a pendulum,

$$t = 2\pi \sqrt{\frac{l}{g}},   \tag{4}$$

and you get an effective length, *l*. My 1.1 s swing predicts a length of 30 cm, a reasonable measure of the distance from knee to the leg's center of gravity. The exercise is not entirely trivial – it illustrates the ease with which one's neuromuscular system phases its output to maintain that frequency. Put on a heavy shoe, and you swing with a longer period, again with no initial awkwardness. Try to change swinging frequency and you find yourself working a lot harder. Similarly, when you walk, you immediately adopt a 'natural' pace, increasing or decreasing speed as much by changing stride length as by changing frequency. A pendulum length for a normal adult pace of 1.4 s per stride is about 50 cm, not unreasonable for hip to center of gravity of a leg – ignoring some bias and complications from the constrained motion of a leg in contact with the ground. About the location of the pendulum, though, the extrapolation from leg swing to walking misdirects us.

Just how gravitational storage operates in walking gaits turns out to be less easily specified; indeed it operates in a distinctly odd manner – perhaps the reason it escaped analysis for so long. Were our walking to resemble the swinging of an ordinary pendulum, we would reach greatest speed and our centers of gravity would be lowest in mid-step. In fact, we are highest, not lowest, and slowest, not fastest, in mid-step, as we vault over relatively extended legs. In addition, as we walk, we sway slightly side to side at half the frequency at which we move up and down.

Walking, again whether bipedal or polypedal, is commonly described in terms of the motion of an inverted pendulum.

The head and torso provide almost all the relevant mass whose center of gravity matters, rather than the mass of the legs, despite their more rapid motion. As shown in figure 2, head and torso travel in a series of arcs, convex upward rather than downward, as in a conventional pendulum. One gets some idea of the way kinetic and gravitational energies interchange by thinking of an egg rolling end-over-end down a slope – speed and height of center of gravity peak at opposite phases of its motion. While an inverted pendulum does not correspond to an intuitively obvious physical model, the analogy has proven analytically powerful.

One might think of walking as a process of lifting one's center of mass and then allowing it to fall forward, the combination forming an arc. Gravity then imposes a distinct limitation by setting the downward acceleration of that forward fall. That allowed Alexander and Jayes (1978) to estimate the maximum speed of walking, using only a few empirically-supported assumptions. First, in walking, at least one leg must always be on the ground – that is, the "duty factor" or temporal ground contact fraction cannot be less than 0.5. And second, relative stride length – stride length over hip-to-ground length – should peak at the same value for walkers of any size. Finally, the walkers should be similarly proportioned and walk with similar maximum arc angles for their strides. They predicted that the limit on downward acceleration would limit walking speeds to a value no more than about 0.4 or 0.5 times a particular dimensionless ratio, v^2/gh. The latter is the quotient of forward speed, *v*, squared to gravity times a height, *h*, taken as that of the hip joint from the ground.

The ratio happens to have the same arrangement of variables as that between kinetic energy and gravitational potential energy,

$$\frac{mv^2}{mgh} = \frac{v^2}{gh},   \tag{5a}$$
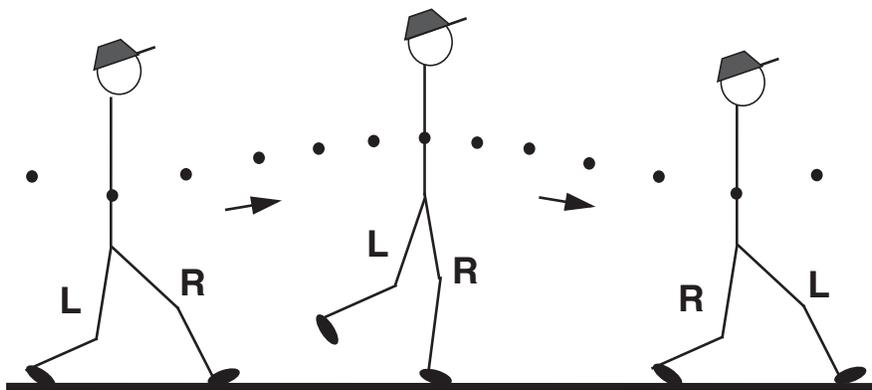

Figure 2.   The motions of the body in a half-step of walking. At mid-stride the body is highest and the speed (indicated by distances between spots at standard intervals) is lowest. Changes in both have been exaggerated. (Adapted from Vogel 2003; see also Biewener 2003.)

where m is body mass and the factor of 2 in kinetic energy has been ignored. It also appears if inertial force is divided by gravitational force,

$$\frac{ma}{mg} = \frac{v^2}{gh} = Fr \,, \tag{5b}$$

noted as the Froude number, Fr, in the last essay (Vogel 2006) – the ratio introduced by William Froude in the 19th century as a scaling rule for models of the hulls of ships. In this last guise, it will reappear in the next essay. It can also be derived by ignoring the constant factor and squaring what is left of both sides of eq. (4), which itself can be obtained by simple dimensional analysis.

The ratio provides a specific rule for the relationship between animal size and maximum walking speeds, a rule with both explanatory and predictive value. And the rule works well for a very wide range of walkers, which hit maximum speeds at Froude numbers between 0.3 and 0.5 (Biewener 2003). Above that range of size-adjusted dimensionless speeds, animals switch to other gaits – we begin to jog, a dog begins to trot, a crow begins to hop. The greatest distance covered per unit energy expenditure occurs at about $Fr = 0.25$, the size-independent optimum walking speed. Had Alexander not pointed out Froude's precedence (albeit in relating at the wave lengths and speeds of surface waves), we would now be talking about the Alexander number. The diversity of organisms that follow the rule makes it a remarkable generalization. It stands as the classic illustration of how dimensionless ratios can serve biomechanics just as they serve mechanical (mostly fluids) engineering.

Animals of whatever size stress their bones to similar maxima when moving – about twice standing during walking and about five times standing in running – but do not exceed 50–100 MPa (Biewener 1990). With this range of maximal bone stress and the transition range of Froude numbers we can ask about the speeds of dinosaurs. The combination implies that the largest theropods such as *Tyrannosaurus* ran gingerly if at all (Alexander 1976; Hutchinson and Garcia 2002); conversely, they could walk exceedingly fast. And from the skeletal dimensions and trackways the walking speed of the 3-million year old Laetoli (Tanzania) hominids can be estimated. They were about a third shorter than modern humans and should have been slower by a similar factor (Alexander 1984).

We can also ask what might happen were the value of gravitational acceleration altered. Greater g should give a higher transition speed; lower g should give a lower transition speed. Humans on the moon, with a sixth of terrestrial g, found that hopping was a better way to get around than walking, which would have been (ignoring the effect of space suits) less than half as fast as on earth. Skipping, as done by children here on earth, was a useful gait as well

(Minetti 2001). When walking on a (terrestrial) treadmill, partly supported by a traveling overhead harness, humans maintained the characteristic exchange of kinetic and potential energy of walking (Griffin *et al* 1999). And in brief exposures to truly altered gravity in maneuvering aircraft, maximum walking speed increased with the value of g, as expected from eq. (5) (Cavagna *et al* 2000).

One of the benefits of a rule is how it directs attention to apparent exceptions. Emperor penguins walk long distances at an especially high cost for their size. Their short legs mean that they are not geometrically similar to other birds – for their size, they make especially quick strides. That may preclude the usual arrangement for energy interchange, but they have another, side-to-side waddling. The high cost, then, does not come from abandonment of the interchange, but from the high rates at which the muscles running their short legs must generate force (Griffin and Kram 2000). Penguin walking appears to be close to a model developed by Coleman and Ruina (1998), a bipedal toy or robot (a "passive-dynamic walker") that goes down a slope with a side-to-side pendulum motion – a description of an easily-built model can be found at *http://ruina.tam.cornell.edu/research/topics/locomotion_and_robotics/*.

Bear in mind that on a level path, the entire cost of locomotion (ignoring drag) represents inefficiency. Although walking costs energy, the relative (mass specific) cost of body transport decreases as the size of animal increases. Most likely, its cost traces to a basic disability of muscle, the need to expend energy to produce force, even when moving nothing. The more rapidly we ask a muscle to develop force, the greater the cost, as just mentioned for penguins; the smaller the animal, the greater its stride frequency, and the greater the cost of level walking relative to its mass.

If the path slopes upward, walking incurs an additional cost, that of working against gravity, which scales with body mass. Combining the cost of level walking with the additional price of going upward explains a curious but familiar phenomenon. The relative difficulty of ascent depends on an animal's size. A horse walks more efficiently on the level than does a dog, but even a slight slope extracts a great fractional increase in demand for energy – quite familiar where animal-drawn vehicles provide transport. A small rodent handles slopes more easily than any dog, and those ants that construct roadways do so with magnificent indifference to slope, caring only about overall path length. Minetti (1995) applied treadmill data to predict the optimum slope of mountain paths, assuming a goal of gaining altitude cheaply. The slopes of paths in the Italian Alps corresponded nicely to the predictions, with switchbacks wherever the critical steepness would be exceeded. In theory, at least, one could predict the size of an unknown animal (perhaps a yeti) from the slopes of its paths.

4.   To trot or to gallop

We bipeds have only a few variants on walking, such as flexed-leg rather than stiff-legged walking, race-walking and goose-stepping. To these we add several gaits that depend on elastic energy storage, such as running, hopping and skipping. Quadrupeds have a considerably wider range of possibilities for gaits that use elastic storage; of these the two most common are trotting and galloping. In trotting each of four legs strike the ground in a left-right symmetrical sequence – front-left plus hind-right, front-right plus hind-left. In galloping almost paired front and almost paired hind legs alternate, 'almost' because a leading side and thus some minor asymmetry is typical. Like trotting, galloping mainly stores energy from stride to stride as stretched tendon.

Several questions immediately occur. First, why gallop? Simply because by doing so an animal can go faster. Among other things, galloping permits recruitment of an additional mass of elastic in the back and elsewhere for energy storage (Alexander 1988). Moreover, after rising as trotting speed increases, cost relative to distance drops again following the shift to a gallop. The speeds of this second gait transition raise a second and more peculiar question. Among quadrupeds that gallop, the trot-to-gallop transition occurs within a fairly specific Froude number range, between 2 and 3 (Biewener 2003). Froude number, again, represents a ratio of inertial to gravitational force. In this second transition, oddly, both gaits use elastic energy storage and neither uses gravitational storage. So why should Froude number matter?

Perhaps we need to reverse the argument that explained the first transition. What determined that one was the upper practical speed for walking. Here, by contrast, what matters may not be an upper limit of trotting but a lower limit of galloping, a limit set by the maximum practical aerial period. Trotting has (elephants, again, excepted) only short periods when no foot makes contact with the ground, while galloping involves considerably longer aerial periods. And while airborne, an animal must fall earthward – with gravitational acceleration. Too long a fall, and an animal will not be easily able to position one or more feet on the ground beneath its torso. What can we make of that intuitively argument?

Assume an animal can fall a fixed fraction of leg length,

$$d \propto h \propto gt^2,$$ (6)

where d is distance fallen, h is leg length, and t is the time in free fall. What we need to know is how the speed at transition, v, varies with leg length. Heglund and Taylor (1988) report that it varies as one might expect, with leg length divided by stride time – basically all gallopers gallop in about the same way at the transition point. So

$$v \propto h/t.$$ (7)

Combining the two proportionalities to eliminate t and taking the reciprocal (if you are constant, so is your reciprocal) yields, in fact, the Froude number:

$$Fr = \frac{v^2}{gh}.$$ (8)

Can we go a step further and rationalize the particular value (or range) of Froude number at which transition occurs? We might assume that value and estimate the fraction of leg length that a galloper drops while airborne. Breaking speed into length per stride (l) and time per stride (t), we get

$$Fr = \frac{l^2}{hgt^2}.$$ (9)

Heglund *et al* (1974) reported a minimum galloping speed for a particular horse of 5.6 m s^{-1} at a frequency of 2.0 Hz. Alexander *et al* (1980) found that the stride length of a galloping horse is about 5 times its hip height. Adjusting that down from average to minimum speed (using the speeds of Heglund *et al* 1974 and Heglund and Taylor 1988) gives 3.4 times hip height, the later about 1 m (from a skeleton). The final item needed is the fractional duration of the airborne periods at minimum galloping speed. Here specific data seems lacking – people care far more about how rapidly than how slowly horses can gallop! I will assume two periods, each of 25% of stride duration, noting that relative time airborne will be at its lowest at minimum galloping speed.

These data give a stride duration of 0.69 s and thus airborne periods of 0.172 s each. During each period, gravity will make the horse fall 0.145 m, about 15% of the hip to ground distance. That does seem a practical maximum for getting feet positioned for the next stride, again noting the very rough character of the estimate.

5.   The height of trees

Surely trees provide the paradigmatic examples of gravitationally responsive organisms. Each is a tall column that keeps a crown of photosynthetic structures elevated in the face of a gravitational force that would prefer otherwise. It does so to win access to sunlight in competition with other trees – greater height cannot bring it significantly nearer the sun. Each of the lineages in which tree-like organisms have evolved from shrubbier or herbaceous ancestors has used the same basic material, wood. In each tree or tree-like system, water must be extracted from the substratum and lifted to leaf level, typically through evaporation at the top and consequent suction below. Despite considerable structural

and developmental diversity among the lineages, their tallest members have achieved about the same maximum heights, roughly 25 to 100 m (Niklas 1997). Explaining such consistency tests our understanding of the biological consequences of gravity.

Perhaps the column of stacked bricks invoked at the start of this essay might provide an instructive analogy. Wood has a compressive strength of about 50 MPa and a density of about 500 kg m^{-3} – better specifications than brick, incidentally. A column (as in figure 3a) could extend 10 km upward even with no taper, a hundred times the height of the tallest contemporary tree. Clearly resistance to compressive crushing imposes no limit.

But crushing mainly afflicts short, wide columns. A more likely failure mode is so-called Euler buckling, the sudden collapse that occurs when the middle of a column bows ever further outward (as in figure 3b). Elastic modulus, rather than compressive strength, now becomes the operative material property. For fresh wood we can assume a value of 5 GPa (Cannell and Morgan 1987), noting that the compressive moduli run slightly lower than the tensile (Young's) moduli but that trees compensate for the difference with some tensile prestressing. Trunk thickness becomes relevant because buckling stretches one side and compresses the other. The standard equation for Euler buckling (see Vogel 2003 or standard handbooks for mechanical engineers) gives a height of well over 100 m for a trunk diameter of 1 m. This assumes that the tree does not taper and that its entire weight is concentrated at the top – an unrealistically harsh scenario. Offsetting (at least in part) those biases, trunks are assumed straight and their bases firmly fixed. Even admitting the simplifications, though, it appears that gravitational loading through buckling imposes no practical limit.

We might look at the tree in yet another way, a simplified version of Greenhill's (1881) classic analysis. Consider a brief lateral perturbation near the top of a tree from wind or some other cause. That will move the center of gravity laterally, tending to make the tree topple. At the same time, it will generate an opposing elastic restoring force in the wood. In effect, this treats the tree as a self-loaded cantilever beam (as in figure 3c), albeit one extending upward rather than outward. If lever arm and restoring force scale linearly with deflection distance, then that distance drops out. Young's modulus also drops out since in practice it varies directly with the density of the wood. Again adopting standard equations and the standard relationship between Young's modulus and density, our 1 m tree can extend upward about 120 m before the wood of the tree reaches maximum tolerable stress. Again, trees rarely approach that value. And, again, more realistic assumptions would raise the limiting height – I have once more assumed that the tree does not taper, which raises the center of gravity, and I have assumed that it pivots at the bottom rather than bending, which moves its mass too far outward.

Still, while both views – a column subject to Euler buckling and a cantilever beam – give unrealistically great heights, both say that height will scale with diameter$^{2/3}$. The girth of the taller tree will be disproportionately great, something easily observed. Quite a few sources note that particular scaling rule, going back at least to Greenhill's (1881) prediction and including McMahon's (1973) compilation from data on 576 trees in the United States, each of either record height or record girth for its species. The arguments for the rule have become much more sophisticated, in particular accounting for taper and crown weight (Niklas 1992 has a good discussion).
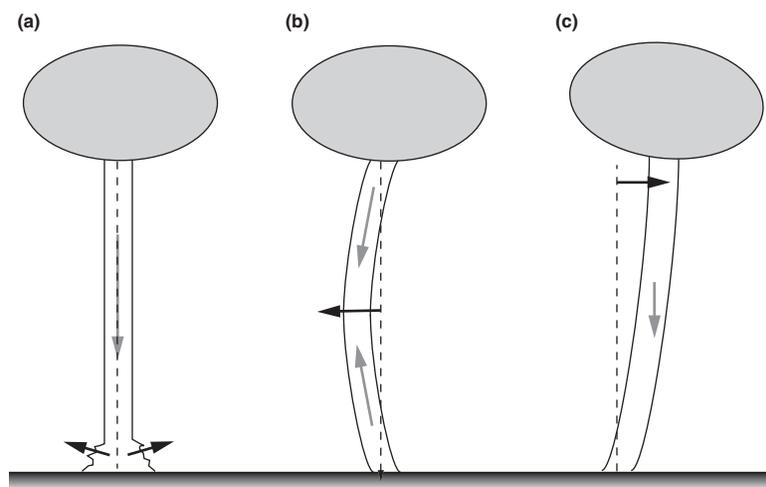

Figure 3. (a) A column failing by simple compressive failure – crushing. (b) A column, also end-loaded, failing by "Euler buckling," a mode in which, paradoxically, one side experiences tensile loading. (c) A column loaded sideways as if a cantilever beam, in which, once bent, its own weight generates a turning moment about the base.

That each of several starting assumptions yields the same scaling rule gives little help in choosing among them. Worse, we should not place great confidence in that exponent of 2/3, however often it gets cited. For few biological systems can we find so much data to test such a rule – for obvious reasons, books on practical silviculture, forest mensuration, and so forth pay great attention to the height and girth of trees. I tried a few regressions on published data and was rewarded with exponents ranging from about 1/3 to 4/3. Unsurprisingly, practical people concerned with timber production rely on other, more complex formulations – see, for instance, Johnson and Shifley (2002).

Moreover, many sources question the whole notion that the strength, density, and elastic moduli of wood determine the maximum heights and proportions of trees. The most common alternative views the limit as hydraulic, the problem of lifting water from the roots to such biologically prodigious heights. Our hearts develop systolic pressures during exercise of perhaps 25,000 Pa, and tall mammals when running probably approach twice that. Just working against gravity, a 100 m tree has to move water against a pressure difference of 1,000,000 Pa, 40 times better than our personal best. Worse, the main pump depends on suction from above rather than pushing from below, that is, on negative rather than positive pressure.

The main mechanism for raising water needs a few words, especially because at first encounter nearly every physical scientist expresses skepticism or outright incredulity. Evaporation across tiny interfaces in the feltwork of fibers of the cell walls of cells within leaves draws water out of the soil and up through a large number of small conduits (xylem) just beneath the bark. Surface tension at these interfaces (around 0.1 μm across) should have no trouble keeping air from being drawn in at the top – the surface tension of pure water can sustain a pressure difference of nearly 3,000,000 Pa, almost 30 atmospheres, across such a tiny interface (Nobel 1999).

But then things get decidedly unconventional. Atmospheric pressure can push water up to a maximal height, defined by eq. (1), that corresponds to a pressure difference of 101,000 Pa at sea level – the difference between that of the atmosphere and a full vacuum. For water (or xylem sap), with a density of 1,000 kg m^{-3}, that height is 10.3 m. Evacuate a vertical tube and place the open end in water, and the water will rise to that height, with a vacuum above. Of course if a clean pipe a bit longer than 10.3 m is initially fully filled with water containing little dissolved gas, one may have to bully the system a bit for the water level to drop and the vacuum to appear. In the interim, the water column will have developed a pressure below 0 Pa, a slight and brief negative pressure.

Even if water is freely available at ground level and can be raised without frictional loses, trees should be able to grow no higher than 10.3 m – unless they can capitalize to a

fabulous degree on such negative pressure. Before taking offence at the notion of negative pressure, pause to observe that the water in question is liquid, not gaseous. The internal intermolecular cohesion that makes a liquid a liquid rather than a gas should render it perfectly capable of withstanding tension, the more sanitary term for negative pressure. The difficulty comes from containing a liquid while subjecting it to tensile stress. Not only must its intermolecular cohesion withstand the stress, but the adhesion of the liquid to the walls of the container must do the same – neither grip can fail or a vacuum will appear. In addition, very little gas or other impurities can be dissolved in the water, so ordinary soil water must be pre-processed before entering the main conduits.

Trees apparently meet these demanding conditions and raise sap despite severely negative pressures. A field-usable device (a so-called Scholander bomb – see Scholander *et al* 1965) makes possible routine measurements of negative pressures in plants by indicating the positive pressures required to counterbalance them. –1 or –2 MPa (–10 or –20 atm) pressures are common, and values as extreme (one hesitates to say 'high') as –12 MPa. (–120 atm) have been reported (Schlesinger *et al* 1982). In laboratory tests, macroscopic quantities of water have resisted tensile stresses of hundreds of atmospheres, so the picture does not rely solely on calculated intermolecular forces.

Other things being equal, the taller the tree, the more extreme the negative pressures. And the more extreme the pressures, the greater the danger that liquid within some conduit will cavitate, interrupting the process and putting that conduit out of action as if it were an unprimed pump. Cavitation does occur with some regularity – this is no hypothetical hazard – with a large fraction of the conduits in a normal tree sometimes embolized. In practice, the greater the diameter of the conduits running up the tree, the greater the likelihood of cavitation (Ellmore and Ewers 1986; Maherali *et al* 2006). But recent work (see, for instance Holbrook and Zwieniecki 1999 and other papers by each of these authors) has revealed specific devices to minimize the propagation of embolisms and to repair embolized conduits.

Trees face a curious balancing act. Their demands for water vary over a wide range, low in conifers, for instance, and high in many broad-leaved trees. Beyond the gravitational loss of 9,800 Pa m^{-1} (from eq. 1), making the water move raises another kind of loss, that due to the fluid-mechanical resistance of the conduits. The general rule for pressure drop per unit length ($\Delta p/l$) due to laminar flow in circular conduits is the Hagen-Poiseuille equation (here given in terms both of total flow, Q, and maximum, axial, flow speed, v_{max}):

$$\frac{\Delta p}{l} = \frac{8\mu Q}{\pi r^4} = \frac{4\mu v_{max}}{r^2} \, . \tag{10}$$

μ is the fluid's viscosity and r the radius of the conduit. Whether one considers total flow or flow speed, the smaller the conduit the worse the pressure drop. In addition, passage of sap between adjoining conduits entails additional losses – see, for instance, Lancashire and Ennos (2002). One might argue that a tree should move water in pipes large enough to keep the cost of flow low but not so large that embolizing becomes an excessive risk. And in enlarging pipes to reduce losses from flow, trees must meet diminishing returns – after all, that gravitational loss of 9,800 Pa m^{-1} remains.

Thus we expect conduit sizes will strike a balance, large enough to keep flow losses down to the same order as gravitational losses but not much larger. What do we find? Maximum flow speeds *in vivo* can be measured by heating a trunk locally and then timing the interval before a thermocouple located somewhat higher detects a temperature change. I calculated pressure drops per unit length for a variety of trees (and a liana) from a variety of sources, using measured averages of maximum speeds and conduit diameters from Milburn (1979), Zimmermann (1983), Gartner (1995) and Nobel (1999). The data cover a 10-fold range of diameters and a 100-fold range of speeds; the resulting pressure drops range from 1,300 to 20,000 Pa m^{-1}, that is, from 13% to 200% of the gravitational drop, with little evident regularity. But the data is highly heterogeneous, reflecting spread in conduit diameters within individual trees, uncertainty about which ones happen to be active and not embolized at a particular time, variation in flow speeds with time of day and wetness of season, and so forth.

Nonetheless, the values do not disagree with the notion that trees balance the diminishing returns and increasing risk of enlarging conduits, keeping a fairly fixed relationship between flow and gravitational losses. Put another way, why should a tree risk making conduits large enough to reduce flow loss much below the unavoidable gravitational pressure loss? At the same time, the values provide at least indirect support for the idea that the difficulty of lifting water imposes a general limitation on forest height.

That, though, is hard to reconcile with lots of data showing that gravitational pressure drops and the flow losses predicted from the Hagen-Poiseuille equation commonly do not represent the largest part of the overall negative pressures measured at tree-top heights. A further pressure drop come from extracting water from less-than-saturated soil ("matrix potential" sometimes), osmotic processes in roots, and (as noted) flow through the pits and plates that divide the ascending tubes of xylem. Trees 20 or 30 meters high often develop pressures of –2 MPa or more, far above a twice gravitational drop of –0.4 to –0.6 MPa. For that matter, the record of –12 MPa mentioned earlier comes from measurements on a desert shrub, not a tree, and mainly results from the scarcity of soil water. By contrast, Koch *et al* (2004) measured an extreme pressure of –1.8 MPa 4 M

below the top (112 M) of the tallest known tree, a redwood (*Sequoia sempervirens*). They found in the laboratory that a pressure of –1.9 MPa imposes serious loss of hydraulic conductivity on such material and therefore argued that hydraulics limits height. The skeptic wonders if the closeness of those figures, –1.8 and –1.9 MPa, merely tells us that such trees conduct and utilize water no better than they have to.

We also face the awkward fact that especially wide conduits occur in woody vines (lianas), with diameters sometimes exceeding 300 μm. But vines, unlike trees, need not support themselves; their dry densities are concomitantly low. Xylem, we remind ourselves, is wood, both a conductive and a supportive tissue. One suspects that relaxation of their supportive function at least in part underlies the size of these conduits. And that suspicion points back to mechanical support as the main limitation on height.

Before dismissing hydraulics, though, we should note another way it might bear relevance. Recently Niklas and Spatz (2004) have related both maximum tree height and the basic 2/3-power scaling to the problem of supplying an ever-increasing overall leaf area with water – an argument based on supply rather than pumping cost. I like their rationale but remain bit skeptical. The quantities of water that trees raise and transpire are almost as impressive as the pressures against which they do so. But these quantities far exceed the amounts used in photosynthesis and vary widely. Nobel (1999) notes a 40-fold range in water use efficiency – rate of carbon fixation divided by rate of water use. Furthermore, just as with pressure, the most extreme values (here high ones) come from plants living in dry habitats rather than from especially tall trees.

In short, the original question remains without a satisfactory resolution. We may even be looking at the wrong variables. In trying to choose between two different routes through which gravity might affect tree height, we presumed a gravitational limit. Even that presumption may be suspect. First, healthy trees rarely fail by gravitationally driven mechanical collapse. (Occasional windless ice storms where I live do cause trees to fail gravitationally.) Second, the correspondence between conduit size and flow speed and acceptance of a considerable rate of cavitation suggests that still wider conduits could be tolerated – conduits such as those of lianas. Finally, the fact that negative pressures at tree top level exceed, sometimes by large factors, the sum of both gravitational and flow-induced pressure drops suggests that still greater losses from these latter quarters could be tolerated.

Perhaps the limit on height, paradoxically, might sometimes come from something other than gravity. Trees blow over in storms, most often by uprooting, less often by snapping of their stems near their bases, still less by shear-induced snapping higher up. Whichever way, failure most

likely results from drag, acting on the crown; the taller the tree, the longer the lever arm and the greater the turning moment. In such a scenario, the lateral drag of the crown, mainly due to its leaves, imposes the critical disadvantage of height. Several structural features of leaves and trees (and bamboo culms, etc.) make functional sense as devices to reduce vulnerability to drag, often termed "wind throw", and their ubiquity argues that drag surpasses gravity as a hazard.

The commonness of uprooting, in particular, implies that much of the problem of a tree must come from a peculiarity of tree substratum, the limited resistance of soil to tensile forces. Shear and compression soil can resist, and its weight above buried roots may assist, but many trees may not be able to pull on the ground with particular effectiveness. At one time, perhaps somewhere still, large stumps were pulled directly upward by teams of horses solely with the aid of simple windlasses that could be moved from stump to stump.

Trees may stay upright in winds in several ways (Vogel 1996):

(i) With a long, stiff taproot that extends the trunk downward a tree can take advantage of the shear and compression resistance of soil. If lateral roots near ground level fix the location of the base of the tree, blowing the trunk one way asks that the taproot be forced the other way, compressing and shearing soil. The array of smaller, vertical 'sinker' roots from larger horizontal ones may work the same way, as well as providing significant resistance to uprooting tension through shear numbers and area covered. That combination of tap root, laterals, and sinkers seems to be central to the support system of many trees (pines, paradigmatically) of temperate and boreal forests, trees whose trunks obviously bend in winds.

(ii) Some tension resistance in the most superficial soil layer can come from the tangle of roots of surrounding vegetation, something many tropical trees take advantage of with large, thin, upwind buttresses. These act like diagonal cables from trunk to roots rather than the compression-resisting buttresses of Gothic architecture – the misleading linguistic analogy confused things until recently (Smith 1972; Ennos 1993). Again, sinker roots assist. Trees with such tensile buttresses tend to be thin relative to their heights.

(iii) Ground level lateral extensions of the trunks of many big temperate-zone broad-leaved trees are lower and thicker; they most likely work as conventional downwind buttresses that take advantage of soil's reliable compression resistance – as well as providing attachment points for sinker roots. Trees with these wide, heavy bases ('plates' sometimes) typically have thick trunks of dense wood that do not bend noticeably in winds. The arrangement comes into use as a tree matures and shifts from system (i).

The wide bases and stiff trunks of system (iii) may convey another message. I have argued that the vulnerability of trees to wind-throw shows that gravity need not always be the physical agency that limits height. Compressive buttressing and thick, stiff trunks suggest that gravity may at times operate on the other side of the equation, assisting a tree in staying erect. When trees such as large oaks blow over, the bases of the trunks often lie 1 or 2 m above the ground; by contrast, pine trunks lie directly on the ground. Thus in uprooting, compressively buttressed trees pivot around a horizontal axis well to the side of the axis of the trunk, as in figure 4. To make a tree uproot, the turning moment must exceed the stabilizing moment – the product of drag times the height of the center of the crown must
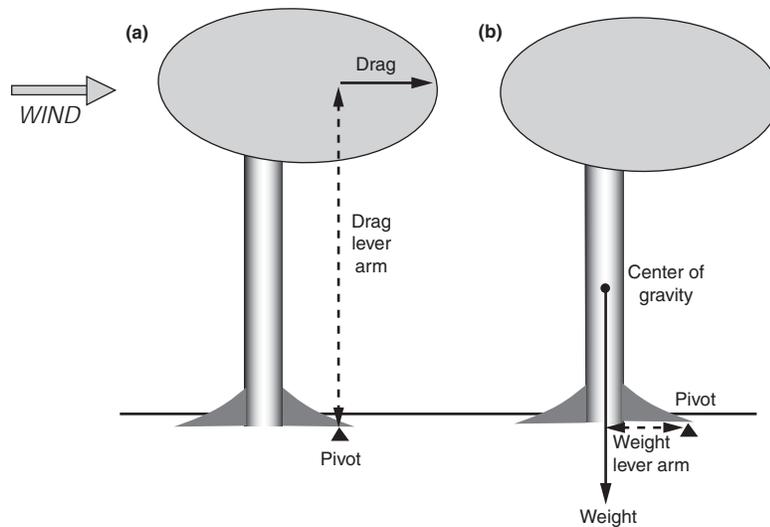

Figure 4. The drag of a wind loads a tree not as a column but as an end-loaded cantilever beam. A tree with stiff trunks and basal, compression-resisting buttresses, will suffer "wind-throw" when the turning moment from drag and the height of the crown (**a**) exceeds the opposing moment from its weight and the width of the buttressing (**b**).

exceed the product of the weight of the tree times the distance from trunk axis to turning axis. That simple view ignores any contribution from soil around the roots, of sinker roots, and so forth. But it exposes the possibility that such a tree might use its weight to stay upright with its sinker roots to keep from sliding sideways.

Does such a model survive quantification? Consider a tree with 30 m of cylindrical trunk, 0.7 m in diameter, of a density of 1000 kg m^{-3}, a pivot point 1.5 m to one side of the trunk's vertical axis, an otherwise weightless basal plate, and a weightless, spherical crown of branches and leaves. Using symbols for the variables described in figure 4, the stabilizing moment will be

$$\rho_{tree}\ \pi\ r_{tree}^{\ 2}hgr_{base}. \tag{11}$$

The tipping moment will be the drag of the crown times the height of the tree,

$$0.5C_d\,\rho_{air}\ \pi r_{crown}^{\ 2}v^2h. \tag{12}$$

Assuming a drag coefficient, C_d, of 0.1, appropriate for a large sphere in fast flow, an air density of 1.2 kg m^{-3}, and a speed of 35 m s^{-1}, we equate (11) and (12) and solve for the radius of the crown. It comes to almost 5 m, and thus a diameter of nearly 10 m. While perhaps a little smaller than one observes in nature, it comes close enough to suggest taking this model of an oddly detached tree seriously.

Still, I must emphasize its crudeness. We have distressingly little information on the real drag of this kind of broad-leaved tree in high winds. I did some work on the drag of individual leaves and small clusters (Vogel 1989), enough to undermine confidence in any extrapolation or estimate for whole crowns, something Ennos (1999) has reemphasized. Besides the obvious logistical problems, people who run sufficiently large wind tunnels do not take kindly to tests of items expected to fail by detaching pieces just upwind from valuable and vulnerable fans and motors.

Note, though, what the model says about the relevant variables. First, wind speed has a severe effect on the result. Second, height does not directly matter, since it equally affects the weight of the tree and the moment arm of its drag. Greater height does, though, require that the trunk be wider to have the additional flexural stiffness needed to minimize lateral movement of its center of gravity. Of course wider means heavier and thus gives further improvement of a tree's stability. Finally, gravity itself aids stability, as in eq. (11), so if gravity were greater, such a tree might be able to grow taller – unless, as suggested in the last essay (Vogel 2006) air density (and thus drag) were thereby also increased. But whatever the specific value of *g*, in this model the tree depends on gravity to stay erect.

Whatever the limitation on height, it must most often operate through the competitive interactions of individual trees. If height does scale with diameter to the 2/3 power

and thus cross section to the 1/3 power, then successive increments in height demand making ever increasing amounts of wood. Better access to sunlight than one's peers extracts an ever increasing constructional penalty. Furthermore, growing significantly above canopy level should disproportionately increase peak wind speeds and thus drag. So any cost-benefit analysis ought to include competitive interactions and growth. And growth depends on a host of other factors; thus the dipterocarp forests of Southeast Asia, growing on rich, volcanic soils, achieve greater canopy height than tropical forests elsewhere on earth. Givnish (1995) expands on this kind of argument, noting the ever-decreasing ability of a tree in a forest to compensate for cost with increased leaf area.

I must admit some attachment to a picture that emphasizes the lateral force of wind, a bias stemming from my own interest in air flow and drag. So I hasten to remind the reader (and myself) of the old adage that when one's tool is a hammer, all problems resemble nails. It well may be a case, as said of raccoon- and opossum-hunting dogs in this part of the world, of barking up the wrong tree.

6. The diverse roles of gravity

In aerial systems, gravity impels dense bodies downward, with only the relationship between size and descent speed at all negotiable. In terrestrial systems gravity may be less insistently intrusive, but it plays a wider range of roles. Here we moved from cases where the role of gravity was straightforward to ones in which it played increasingly subtle roles – clearly important, but in ways that challenged our analyses. But I conclude with a mild caution, noting that many other cases might have been considered as well as the present ones, that this essay just scratches the surface. The present essay might have compared impact loading with gravitational loading in various forms of locomotion. It might have noted the shift in mammalian posture from flexed-legged to straight-legged, a likely consequence of the way body weight scaled with volume, while postural muscle force scaled with cross-section. Or it might have suggested that an alteration gravity's strength (or wood's strength-density relationship) would affect the length and taper of branches more than it would the overall height of trees.

In these essays I have made much of scaling rules and their particular exponents; the way blood pressure depends on body size illustrates one hazard of the approach – a real threshold effect that would be missed by the normal regression-based scaling analysis. For gait transitions we do have a scaling rule, based on Froude number, but here the rule itself applies to thresholds. For tree height, we examined the near constancy of forest heights over space and time, suggestive of mechanical (solid or hydraulic) limitation. Not

only could we not pinpoint the limitation, but we could not either confirm or discredit a scaling rule – or even convince ourselves fully that gravity contributed to the limit.

Acknowledgements

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