

Wind structure in relation to odour plumes in tsetse fly habitats

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Abstract. Key characteristics of airflow were measured in the African bush in a study of host odour plume structure. Wind speed, speed variance, direction, and directional variance were measured by conventional cup anemometers plus wind-vanes and by a solid state ultrasonic anemometer, on time scales from seconds to minutes. The two technologies gave opposite relationships between wind speed and turbulence measured as rate of angular direction change in the wind ($^{\circ} s^{-1}$). A positive correlation between turbulence and wind speed was observed with mechanical anemometers and wind-vanes, evidently caused by their inherent hysteresis (stalling in weak wind, overswinging after gusts). The same correlation was *negative* with the solid-state anemometer which, being hysteresis free, should have measured the true directional turbulence more accurately. Such fine-scale turbulence at a fixed point in space (on a scale of about ~ 15 cm diam.) decreased with wind speed up to ~ 1.5 m s^{-1} , as does large-scale (~ 1 m diam.) turbulence of air moving *through* space (Brady *et al.*, 1989). This decrease occurred both within vegetation and out in the open, but the slope and intercepts of the relationship depended on vegetation and topography. Variables for describing wind speed and turbulence are considered in the context of odour plume structure.

Key words. Wind structure, wind speed, turbulence, odour plumes, anemometer, tsetse fly, *Glossina*.

Introduction

The straightness of airflow, as measured by the displacement of puffs of smoke, increases as the wind speed increases up to about 1 m s^{-1} (Brady *et al.*, 1989, 1990). This is true, moreover, whether the wind is measured in thick vegetation or out in the open with no obstructions for hundreds of metres. Although it might seem that such weak winds would not be biologically significant for most large insects, there are two situations where they are typical.

The first occurs in thick vegetation, where resistance within the canopy slows down the airflow relative to that above it, so that the wind near ground level is at least an order of magnitude slower than that in the boundary layer (Brady *et al.*, 1990, Fig. 2; Businger, 1975). This uncouples the pressure differentials that drive the air movement within the vegetation from those above, so that large packets of air move through vegetation in effect independently of the mainly straight-line flow above.

The second occurs at night in tropical and subtropical climates, where local temperature inversions are set up as the air at ground level cools under a blanket of warm air left over from the daytime insolation. The wind is then no longer driven by large

topographical convection forces, so that stability ensues and the local airflow becomes weak to virtually zero.

The first situation is typical of the natural habitat of tsetse and other diurnal biting flies; it must also be true in most crops. The second is typical of the habitat of nocturnal insects such as moths and mosquitoes, and may well be relevant to crepuscular tsetse flies also. These insects all depend in large measure on finding their hosts (plant or animal) and mates by olfactory orientation up odour plumes emanating from some source of 'attractant'. For them all, airflow in the range below ~ 1 m s^{-1} will be the norm, and may present acute limitations for any optomotor-guided upwind steering they employ (see Kennedy, 1986; David, 1986). For anthropophilic mosquitoes, the situation is likely to be particularly difficult due to the darkness and stillness inside houses at night – other than as relieved by convection currents above sleeping hosts.

It is already apparent that the inevitably low wind speeds in vegetation cause insects substantial problems for odour source location, whether to a point source of pheromone by male moths in open woodland (Elkinton *et al.*, 1987) or to a large, CO₂-panting vertebrate by tsetse flies in thick bush (Brady *et al.*, 1989, 1990). For the former, the wind's meander may so reduce the correlation between local wind direction and 'true' source direction that male moths fail to find 'calling' females from more than about

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80 m away. For tsetse flies, the meander may be so great that the odour plume a few metres away from a host may 'point' away from it as much as 50% of the time.

As part of a long-term study of the relationship between the wind, odour plumes and host-finding in tsetse flies, we measured the airflow in a range of situations. This paper summarizes our findings on the 'structure' of the wind; two parallel papers (Griffiths *et al.*, 1995; Brady *et al.*, 1995) report on the performance of tsetse flies in locating odour sources in relation to the wind.

Materials and Methods

Observations were carried out between 1990 and 1992 at Rekomitjie Research Station in the Zambezi valley, northern Zimbabwe (alt. 500 m). This is an area of high tsetse density in the rather variable 'mopani-type' woodland described by Vale (1974; Vale *et al.*, 1988), and includes the bushy woodland studied by Brady *et al.* (1989, 1990).

Wind data were recorded in a variety of situations. In 1990 and 1991 the equipment was set up next to odour-baited electric nets that recorded the arrival of flies (Brady *et al.*, 1995). The 1990 observations were in low, partly treeless, wet season mopani scrub (= expt 1, *loc. cit.*), with a three-cup anemometer plus a light mechanical wind-vane (see below); the data had to be read off analogue print-outs. The 1991 observations were in dry season mopani scrub with leafless trees overhead (= expt 4, *loc. cit.*) and used a solid-state ultrasonic anemometer (below) to record wind speed.

In 1992 three measuring systems were run concurrently to test their relative performances in different situations, first in dense dry scrub bush ~2–2.5 m high, then in more open riverine bush with scattered trees, and finally on a large airstrip. The systems were set up in as nearly identical conditions of airflow as possible, 2 m apart across the mean wind line, and sampling the wind 0.8 m above the ground (slightly above the height at which tsetse flies fly in odour plumes over cleared ground; Gibson & Brady, 1988). This layout was a compromise between the theoretical need to have the instruments on exactly the same spot, and the practical need to avoid airflow interference between them.

The systems used were: (i) a Vector Instruments six-cup potentiometer-anemometer (threshold speed = 0.23 m s⁻¹; sample frequency = 1 Hz) and mechanical wind-vane (0.3 m s⁻¹; 1 Hz) linked to a Squirrel Data-logger; (ii) a Vector Instruments three-cup frequency anemometer (0.18 m s⁻¹; 0.2 Hz) and mechanical wind-vane (0.3 m s⁻¹; 1 Hz) linked to a Delta-T logger; (iii) a Gill Instruments, 'Solent Standard' 1012-S solid-state ultrasonic anemometer (offset speed = 0.02 m s⁻¹; sampling at 80 Hz to give 1 Hz mean readings) that measured and logged wind speed and direction simultaneously, downloading to a Philips PC. All three instruments were virtually new.

Results and Discussion

Measures of turbulence

'Turbulence', loosely, is an expression of the way the air tumbles in a series of vortices and eddies of decreasing scale, with

ever-diminishing energy being transferred down the scale until it is lost by viscous dissipation among the smallest eddies of around 1 cm diameter. Aerodynamicists use several definitions of this unstable air movement (see Elkinton & Cardé, 1984; Murlis *et al.*, 1992). From the point of view of the insect, however, the main aspect of turbulence that will affect its attempts to locate an odour source by responding to wind direction is how much the wind changes direction, and what the spatial scale and timing of these changes are.

In this paper, therefore, we consider turbulence mainly as the rate of change of direction of the air flow (expressed as ° s⁻¹) at a point in space where an anemometer plus its coupled wind-vane is situated. In effect this measures the direction of wind eddies about 10–20 cm in diameter on a time scale of about 1 s. We also consider, more briefly, the engineers' conventional measure of *turbulence intensity*, which is rate of fluctuation of the wind speed expressed as the standard deviation of the mean wind speed, sometimes converted to a dimensionless quantity by dividing it by the mean speed (the statistical equivalent of its coefficient of variation).

Note that these two measures of 'turbulence' correlate in opposite directions with wind speed (see e.g. Fig. 4A vs Fig. 4C or Fig. 4D), but we repeat that it is rate of change of direction that should matter most to insects, whereas the turbulence intensity would seem largely irrelevant.

Effect of sample length

The effect of sample duration was examined using the data from the 1991 ultrasonic anemometer records. Sample duration markedly affects the apparent statistical variance of the wind speed because of the semi-random distribution of wind speed over time, with calm episodes alternating unpredictably with gusts. Thus, even though the mean wind speed was scarcely affected by changing the sampling length (Fig. 1A), the variance of the mean increased markedly (Fig. 1B), and levelled off only when samples were at least 2 min long.

This might seem counter-intuitive, but arises because the shorter the samples, the more likely they are to fall in either a calm episode or a gust, but not both. The average variance of short samples of, say, ten readings at 1-s intervals thus under-represents the wind's more general variance (and may also misrepresent the 'true' mean wind speed). Conversely, the average variance of longer samples of, say 100 readings at 1-s intervals, tends to cover the full range of instantaneous speeds and therefore shows the, much greater, full wind speed variance.

The same relationship occurred with turbulence: the rate of change of wind direction was not much affected by sample duration (Fig. 1C), but the full level of the wind's directional variance at any one time was not revealed until samples were at least 2 min long (Fig. 1D). Still longer time samples showed no further 'improvement' because the whole gamut of speed and turbulence was normally covered within about 120 s.

Notwithstanding the lack of effect of sampling duration on the mean wind speed and turbulence (Figs 1A and 1C), there was a steep increase in the strength of the correlation between these two functions and the duration over which they were measured

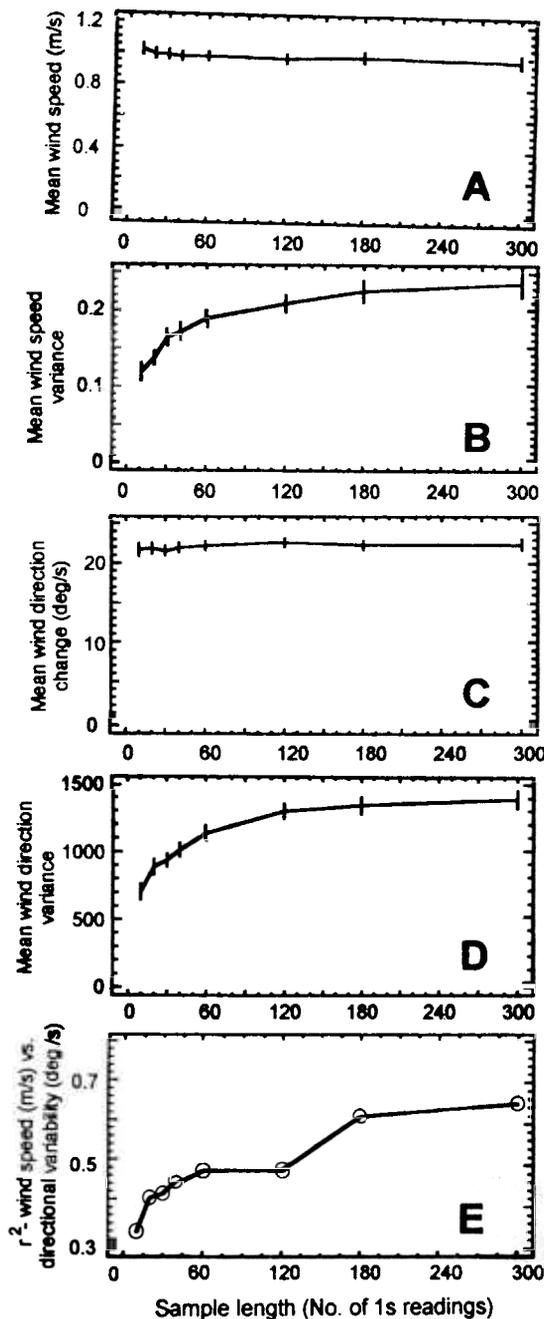


Fig. 1. The effect of sample length on wind parameter means (ultrasonic anemometer). Plotted against sample duration is: A, mean wind speed (m s^{-1}); B, variance of wind speeds about their mean; C, mean rate of change of wind direction ($^{\circ} \text{s}^{-1}$); D, variance of the mean rate of change in direction; E, correlation coefficients (r^2) for the relationship between wind speed and its rate of change of direction.

(Fig. 1E). Longer samples apparently reflected better the mean turbulence that resulted from the wind's speed over the same interval.

Sampling effects may thus markedly colour one's interpretation of the wind's structure. For example, in a mark-release-recapture experiment (Griffiths *et al.*, 1995), spurious correlations were found between the time a fly took to find an upwind odour source and both the wind's speed variance and its directional variance during the flight – precisely because longer sampling intervals (i.e. longer flight times) led to higher variance.

Comparison of three wind recording systems

The three anemometers, being set just 2 m apart and 0.8 m above flat ground, measured air flow and turbulence at virtually the same point in space and over the same spatial scale, ~ 15 cm in diameter for each instrument. They should therefore have 'read' almost identical segments of the wind. The data, recorded in 1992, were therefore analysed (in 5-min blocks) to compare the 'answers' provided by the three systems to questions about wind structure.

Speed. Wind speed recorded by the mechanical anemometers agreed closely with each other at any given time or situation, and with that recorded by the solid-state ultrasonic anemometer (Fig. 2A). Similarly, the standard deviations of the wind speeds (the turbulence intensity) measured by the two types of system also agreed closely (Fig. 2B). The fact that the six-cup anemometer consistently indicated slightly higher mean wind speeds than the three-cup is presumably due to this particular three-cup instrument's slightly worse performance in the low wind episodes that always occurred within any 5-min samples (its specification stalling speed was supposed to be lower than the six-cup's (see Methods), but we had no means to calibrate the instruments' performance independently in a wind-tunnel).

As the curves of the different comparisons are all very close to a slope of one, it seems that over the whole range of mean wind speeds observed (0.5 – 5 m s^{-1}) the moving mechanical anemometers and the solid state ultrasonic anemometer measured the same function of wind speed. However, the y-axis scatter about the standard deviations regression in Fig. 2B is at least twice that about the means regression in Fig. 2A, suggesting a greater variability in the mechanical anemometer measurements. This is made more apparent by plotting the instantaneous wind speed indicated by a mechanical anemometer over a short wind sequence against that indicated simultaneously by the solid-state anemometer. That exposes a very wide scatter in the 'answers' given by the two machines (Fig. 2C); scatter which is almost completely smoothed out in the much longer samples shown in Fig. 2A.

The output errors in ultrasonic anemometers (i.e. the difference between the measured and actual wind speed (or direction)) are linear, and for the 'Solent Standard' we used are quoted as $\pm 3\%$ from 30 m s^{-1} right down to the offset speed of 0.02 m s^{-1} . This contrasts markedly with the accuracy of mechanical anemometers, whose output is subject to a notional absolute error ($\pm 0.1 \text{ m s}^{-1}$ below 10 m s^{-1} for our instruments) and which, as a percentage of wind speed, therefore increases exponentially as

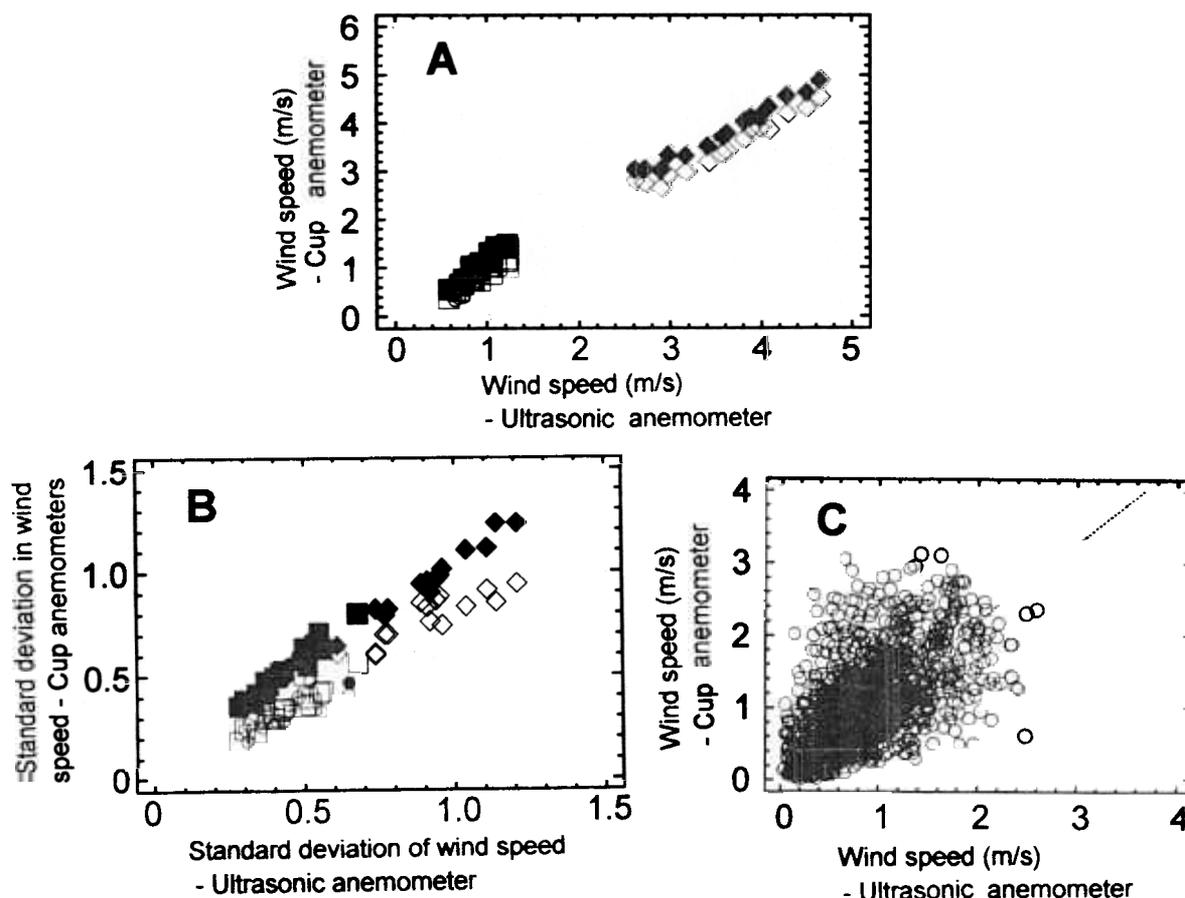


Fig. 2. Direct comparisons of the readings from mechanical rotating cup anemometers with simultaneous readings from an ultrasonic anemometer (300-s samples): A, mean wind speed; B, standard deviation of wind speed (closed symbols = six-cup; open symbols = three-cup anemometer); records from thick dry bush (circles), medium density riverine bush with trees (squares), large gravel airstrip (diamonds). In C the instantaneous (1-s) wind speed readings from the six-cup anemometer are plotted against the synchronous readings from the solid-state anemometer, data from one 20-min sequence in the thick dry bush (regression = $0 + 1.1x$, $r^2 = 18\%$).

the wind falls, approaching 100% near the instruments' threshold speed of $\sim 0.2 \text{ m s}^{-1}$.

Errors thus arise from the hysteresis inherent in the moving parts of mechanical anemometers: they stall in very low winds, have a take-up lag before they accelerate with the arrival of a gust of wind, and then overrun as the gust ends. These errors will be particularly serious within vegetation, because the low winds there typically consist of relatively long periods ($>10 \text{ s}$) with almost no air movement interspersed with brief gusts ($<10 \text{ s}$) of light wind. In that situation the stall and overrun characteristics of mechanical instruments are at their worst. Ultrasonic anemometers, on the other hand, are free of any such problems, and thus represent much more accurately the real wind speed (and turbulence) at the low wind speeds we are concerned with.

Fig. 2C illustrates the wide range of errors that can arise even in high precision, sensitive mechanical anemometers in their representation of the wind on the fine time-scales that matter to flying insects – errors that will be much worse in old, dirty, or less sensitive equipment. Furthermore, the fidelity between the two systems implied in Fig. 2A is in fact misleading, because

the plotted points are of 5-min wind samples, in which stalls and overruns tend to cancel each other out; the fidelity is in any case only good in winds above $\sim 2.5 \text{ m s}^{-1}$.

Turbulence. For the high wind speeds over the airstrip there were no significant correlations between the directional variability of the wind and the wind speed (Fig. 3, right-hand regressions). But for the low wind speeds in the two bush sites the correlations were significant in all three systems, most strongly so with the mechanical anemometers (Fig. 3, legend). The *direction* of this correlation, however, was crucially dependent on the equipment used. Measured with the rotating cup anemometers and mechanical wind-vanes, the correlation was positive (Figs 3A and 3B); measured with the solid-state anemometer it was negative (Fig. 3C). The mechanical vanes started with a low apparent turbulence of $\sim 1^\circ \text{ s}^{-1}$ which grew towards 12° s^{-1} as the wind speed rose to 1 m s^{-1} , whereas the ultrasonic system started high, at around 15° s^{-1} , and fell towards 8° s^{-1} over the same wind speed range.

The different directions of these slopes are not due to mechanical hysteresis in the cup anemometers, because the slopes for the

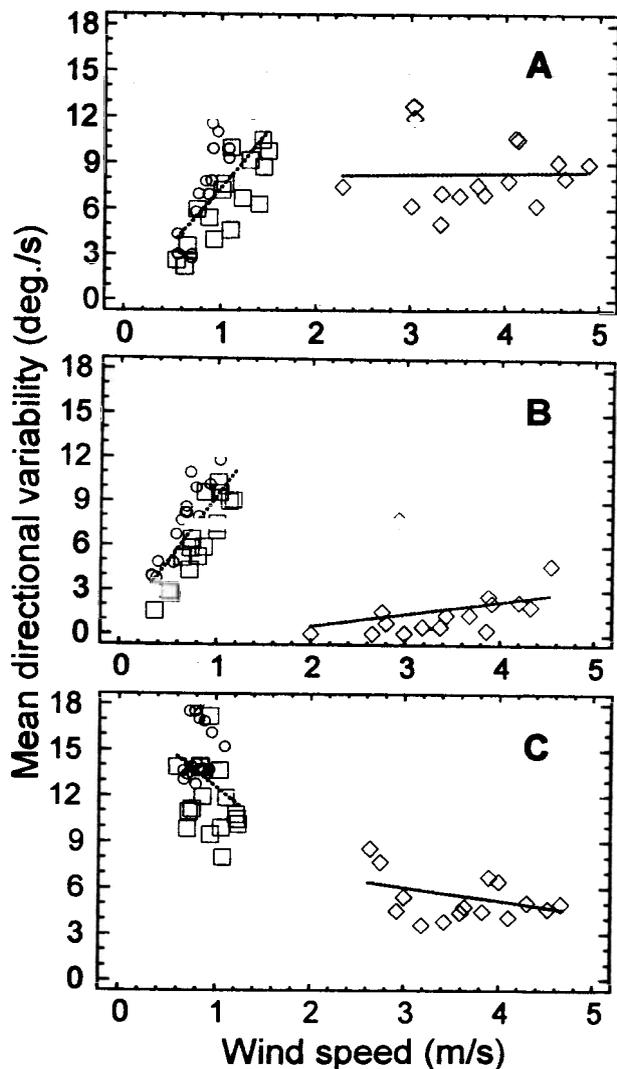


Fig. 3. Rate of change of direction of the wind plotted against wind speed in three habitats (details as in Fig. 2). A, a six-cup anemometer with mechanical wind-vane (combined bush regression = $-0.1 + 7.5x$, $r^2 = 45\%^{**}$; airstrip regression = $8.0 + 0.1x$, $r^2 = 0\%^{NS}$); B, a three-cup anemometer with mechanical wind-vane (combined bush regression = $0.37 + 9.0x$, $r^2 = 56\%^{**}$; airstrip regression = $-1.2 + 0.84x$, $r^2 = 9\%^{NS}$); C, ultrasonic anemometer (combined bush regression = $17.7 - 5.0x$, $r^2 = 12\%^*$; airstrip regression = $8.4 - 0.86x$, $r^2 = 14\%^{NS}$). $*P = 0.05$; $**P < 0.01$; $NS > 0.05$.

swinging arm wind-vanes remain almost unchanged when plotted against the wind speed recorded simultaneously by the solid-state anemometer. The positive relationship is therefore evidently an additional artefact arising from the hysteresis in the wind-vanes themselves, as they stall in low winds and over-swing in high. [Why the airstrip turbulence should have been recorded as being so much lower with the three-cup set-up (Fig. 3B) than with the six-cup (Fig. 3A) is unclear; it seems not to be due to a malfunctioning wind-vane, since that readily recorded 12° s^{-1} in the bush.]

A negative correlation between the rate of change of direction of air flow and wind speed is what is also observed with the

movement of puffs of smoke (Brady *et al.*, 1989, 1990). *A priori*, the same relationship might not have been expected, because the solid-state anemometer measures turbulence over time at a $\sim 15\text{-cm}$ point fixed in space, whereas the displacement of smoke puffs does so over both time and space on a scale of metres. However, it is what would be predicted from the negative relationship between the standard deviation of the wind direction and wind speed mentioned by Elkinton & Cardé (1984, p. 85), which we measured and show in Fig. 4D. Evidently, as turbulence transfers the energy from larger eddies to smaller, the declining rate of direction change with falling wind speed occurs simultaneously over a range of spatial scales.

[The slope in Fig. 4D might appear to be due to increasing instrument error at very low wind speeds, but is in fact a genuine function of wind speed. Instrument error in the wind direction parameter of ultrasonic anemometers becomes significant only at close to the offset speed of 0.02 m s^{-1} , because they measure wind direction by integrating their measures of its speed in the three planes (x , y and z). The error in the reported direction is therefore the same as that in the speed, namely $\pm 3\%$ for our instrument (see *Speed* above).]

Effect of vegetation

The ranges of wind speeds covered by the two regressions in Fig. 3C do not overlap. It is thus not clear whether they represent two separate relationships, one for wind movement in vegetation the other for wind out in the open, or whether they represent different parts of a single negative exponential relationship. They certainly differ markedly in slope, being much steeper within the bush than in the open.

However, the slope without vegetation cover (-0.86 , albeit non-significant) is about a sixth of that in the bush (-5.0), which is almost precisely what Brady *et al.* (1989, Fig. 4) observed with smoke puffs measured over a fully overlapping range of low wind speeds ($< 1 \text{ m s}^{-1}$): the slope for winds out in the open was a fifth of that in thick bush. It seems most likely, therefore, that the curves in Fig. 3C indicate two different linear relationships in the two different topographical situations.

These relationships cannot, of course, be linear over the whole range of wind speeds. As revealed by the much larger data set in Figs 4C and 4D, when the air is almost stationary its movement becomes nearly random, so that it then changes direction at a high rate. Conversely, once it has achieved a certain speed it flows virtually straight, just as shown with smoke puffs by Brady *et al.* (1989), and as observed by David *et al.* (1982, 1983) over short grass. It is only in the range of wind speeds from ~ 0.2 to 1.0 m s^{-1} that the relationship is approximately linear.

The point where the wind straightened out in the present 15 cm -scaled observations in 'mopani' woodland was at $\sim 1.5 \text{ m s}^{-1}$ (Fig. 4C). That is very close to the 1 m s^{-1} asymptote for the metre-scaled movement of smoke puffs (triangles in Fig. 4C). Whether it is the 15-cm or the 1-m turbulence that is the more important from the insect's point of view is unclear. The one will presumably indicate the apparent direction of the instantaneous wind to the stationary, perched fly; the other will indicate the more general direction of odour movement more relevant for the flying fly.

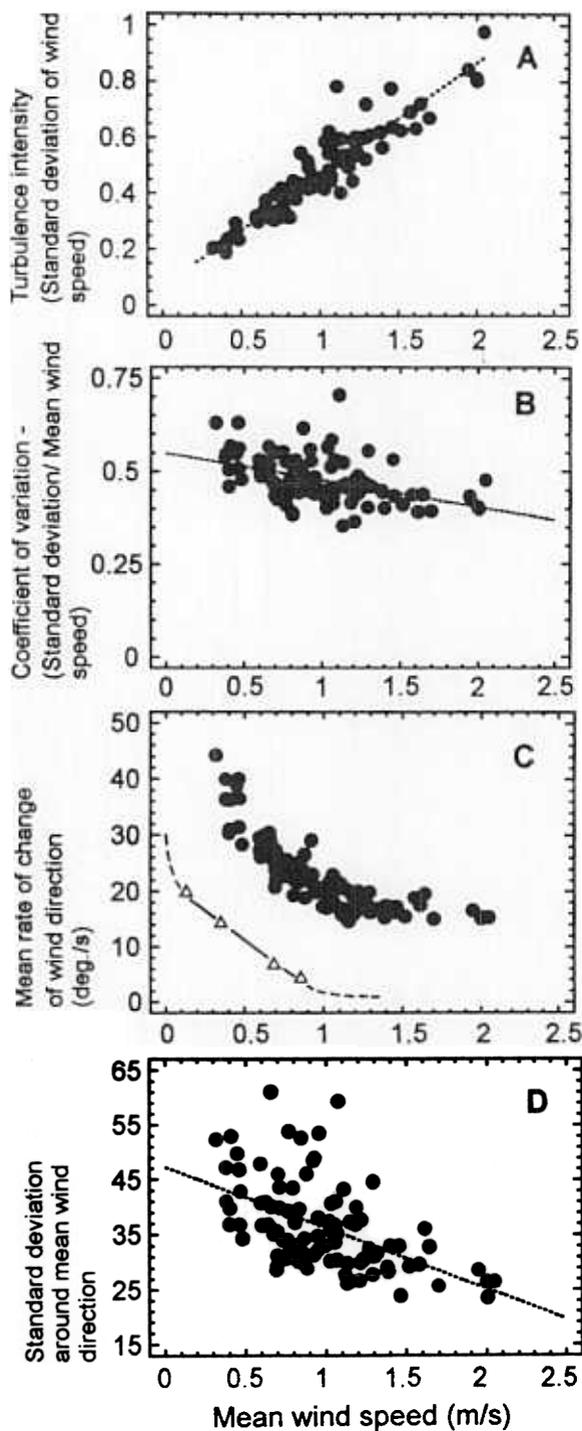


Fig. 4. Relationships between the wind's mean speed and various aspects of its 'turbulence': A, the standard deviation of its speed (the turbulence intensity) (regression = $0.067 + 0.4x$, $r^2 = 88\%$); B, the coefficient of variation of its speed (standard deviation/mean) (regression = $0.54 - 0.07x$, $r^2 = 19\%$); C, its mean rate of change of direction (triangles show curve for smoke puff tracks in thick bush, from Brady *et al.*, 1989); D, the standard deviation of its mean rate of change of direction (regression = $47 - 11x$, $r^2 = 28\%$). Data taken from 300-s samples measured by ultrasonic anemometer during eleven afternoons at one site in medium density dry mopani bush with scattered trees (during the observations reported in Griffiths *et al.*, 1995).

Wind speed measures

The above correlations relate to the mean of the wind's speed over the length of some given time-sample. However, such means may in fact be a poor measure of the wind's speed from the insect's point of view, since the speed distribution is usually strongly skewed to episodes below 0.5 m s^{-1} , especially in thick vegetation (Brady *et al.*, 1989, Fig. 4). We therefore examined alternative measures, including the variance, standard deviation and coefficient of variation of the speed, and the percentage of time the wind ran at <0.25 , >0.25 , >0.5 and $>1.0 \text{ m s}^{-1}$. These measures always correlated with the mean speed, usually very closely (Figs 4A and 5). They sometimes also correlated better with the flies' success at finding odour sources than did the mean speed (Brady *et al.*, 1995).

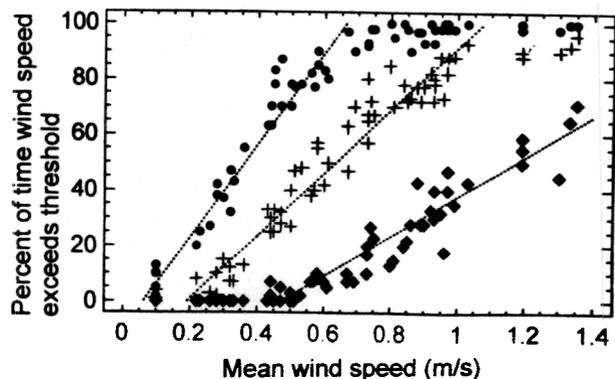


Fig. 5. Alternative measures of wind speed compared with the mean wind speed, measured as 10-min samples with a six-cup anemometer. Circles, percent of wind flowing at more than 0.25 m s^{-1} (regression up to $0.7 \text{ m s}^{-1} = -10 + 166x$, $r^2 = 95\%$). Crosses, percent of wind at $>0.5 \text{ m s}^{-1}$ (regression from 0.2 to $1.1 \text{ m s}^{-1} = -21 + 112x$, $r^2 = 94\%$). Diamonds, percent of wind at $>1.0 \text{ m s}^{-1}$ (regression from $0.4 \text{ m s}^{-1} = -34 + 72x$, $r^2 = 89\%$).

Variance in speed (turbulence intensity)

There were considerable differences in the speed distribution of the wind between different sites. For example, although the mean speeds measured in one 1990 situation at Rekomitjie and another measured in similar bush in Kenya (Brady *et al.*, 1995) were nearly identical (0.64 vs 0.65 m s^{-1}), the standard deviation of these means (the turbulence intensity) varied by a factor of 2 (± 0.65 vs $\pm 0.34 \text{ m s}^{-1}$). Thus, although there was always a positive correlation between the wind speed means and standard deviations in any one experiment (as in Fig. 4A), r^2 ranged from 30% to over 90% in different sets of observation.

The turbulence intensity was therefore markedly different in different habitats. This may be due in part to the differences in vegetation causing differential effects on wind flow, but other causes may also be indicated, such as differences in local topography and climate. Despite the similarity of mean wind speeds, therefore, the overall 'gustiness' of each habitat (which will be the more critical factor affecting odour dispersion), may be quite distinct.

Because of the positive correlation between wind speed and turbulence intensity (Fig. 4A), it might be expected that the coefficient of variation of the wind speed ($\text{CV} = \text{SD}/\text{mean}$) would

be moderately constant with wind speed, but in fact it tended to correlate negatively, albeit weakly (Fig. 4B). Thus, the turbulence intensity as a proportion of the mean speed decreased slightly in higher winds. This implies that for these relatively low winds there is an increasing consistency of the wind's speed as it increases, presumably because faster winds include longer periods of sustained air movement.

Conclusions

We conclude that turbulence measured by mechanical wind-vanes is likely to provide misleading artefacts. Although solid-state anemometers are much more expensive (currently around US\$6000), they are the only wind-monitoring systems that provide reliable and consistent speed and direction measurements in weak winds, especially the kind of very weak winds typical of thick vegetation and temperature inversions. Moreover, even in strong winds, mechanical vanes may be prone to overswing effects that exaggerate the true turbulence. For measuring the variance of the wind's speed or direction – with any system – it is also advisable to monitor the wind in samples of at least 2 min, since shorter samples may lead to misrepresentative sampling errors.

The significance of wind speed on the likely navigability of odour plumes by insects is complex. Wind speed profoundly affects turbulence and hence the structure of odour plumes. It therefore affects both the odour distribution and the optomotor input used by flying insects orienting upwind in odour. In general, the faster the wind the straighter its flow, both in terms of fine-scale (<20 cm) direction change and in terms of large-scale (>1 m) displacement. This will, in turn, increase the probability that any odour encountered is travelling directly from the true source direction (Brady *et al.*, 1989, 1990; David *et al.*, 1982, 1983).

However, as pointed out by Elkinton & Cardé (1984; and also Murlis *et al.*, 1992), the greater turbulence intensity of faster wind speeds will lead to a greater 'volume' of the plume and hence to greater average dilution at all distances downwind. This will result in a reduction of the above threshold 'active space' of the plume from the insect's point of view, even though the flux of the odour molecules passing the insect's antennae may not change in proportion to the dilution. In any case, faster, straighter wind will lead to narrower plumes with lower lateral meander, so that less bush is 'covered' by the plume. These plume dynamics will also be influenced by temperature, which will affect vertical flux (convection) and air turbulence on all spatial scales, and may also affect odour release rates from hosts.

The relative importance of each of these effects for the navigational success of tsetse flies will depend on the behavioural mechanisms and cues which the flies employ. For example, although slow winds may increase the probability of flies encountering odour, by spreading the plume's active space wider, the reliability of the wind's directional cues for upwind anemotaxis will be diminished. Conversely, although increasing wind speeds should improve directional fidelity, the area of potential recruitment of the plume will be reduced. We explore the problems these phenomena pose for tsetse flies more fully in an associated paper (Brady *et al.*, 1995).

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