

## PHYSIOLOGY

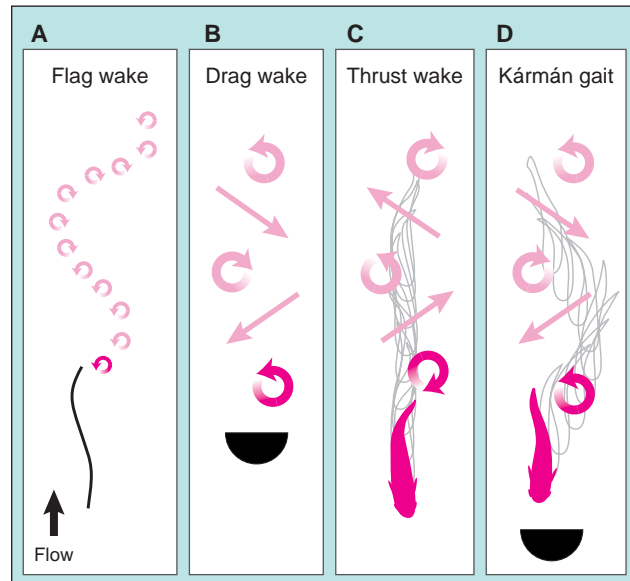
### Fish 'n Flag

Ulrike K. Müller

Flags flutter, even in a completely steady breeze. In an analogous way, fish undulate their bodies in order to swim against a steady current. A flag is a passive aerofoil, whereas a fish is an active swimmer. Yet, evidence is accumulating that it is not large oscillating forces that undulate flags and fish, but rather it is their natural oscillations that get amplified to generate visible motion. On page 1566 of this issue, Liao *et al.* (1) show that trout behave almost like a passive hydrofoil when they swim behind stationary objects. These fish exploit the vortices generated by water flow around stationary objects, modifying their own swimming behavior most likely to reduce the energy cost of locomotion.

Similarities and differences between flags and fish become apparent in the flow patterns that they leave behind. Four simple cases illustrate the relationship between thrust, drag and wake structure (see the figure). A fluttering flag extracts energy from the flow of air, and sheds an undulating vortex ribbon (2) (panel A). A solid obstruction also sheds a characteristic drag wake called a von Kármán vortex street (3) (panel B). Fish, on the other hand, swim actively. Their muscle activity adds energy to the water, and the flow pattern shed behind the fish is called a thrust wake or reverse von Kármán vortex street (4) (panel C). Both von Kármán wakes consist of two rows of counter-rotating vortices with a jet meandering between them. The jet behind an obstruction points forward, against the background flow, whereas the jet behind an actively swimming fish points backward. Yet from the standpoint of the jet, thrust and drag wakes look very similar. Fish and insects exploit this apparent similarity of thrust and drag wakes when they let their body, fins, or wings interact with their own wake or other wakes to enhance performance (4, 5).

The advent of time-resolved flow visualization has enabled the detailed interaction between wakes and active or passive hydrofoils to be explored experimentally. Several years ago, Zhang and colleagues (2) showed that the similarity between fish swimming and flag flapping is not superficial. Flags flutter not because the wind itself flutters,



**Going with the flow.** Vortices (pink circles) and jets (pink arrows) behind a flag (A), a dowel (B), and a swimming fish in flowing water (C and D). The most recent event is indicated in bright pink, and previously shed vortices are in pale pink. (A) The wake behind a fluttering flag. (B) The drag wake behind a dowel (black semicircle). (C) The thrust wake behind a swimming fish (fish shown in outline). The undulating fish sheds vortices that travel downstream with the flow, generating a cross-sectional vortex pattern akin to the drag wake behind a dowel, but with an opposite sense of rotation (pink silhouette and pink vortex; previous outlines in gray plus their corresponding vortices in pale pink). (D) Trout performing the Kármán gait behind a dowel. The fish weaves through the dowel's drag wake to keep clockwise vortices to the right and anticlockwise vortices to the left of its tail as if it were generating a thrust wake.

but because the flag's inertia and elasticity exert forces on the air while the air's dynamic pressure and drag act on the flag (2). In addition to inertial and elastic forces, a swimming fish exerts muscle forces on the water. Both flag (2) and fish (6) exhibit natural oscillations when they "wave." Yet, when one places a flag in the wake of a flagpole or a fish in the wake of a stationary object, something new happens.

Liao *et al.* (1) demonstrate that trout behave like a passive hydrofoil when swimming in the wake of other objects. The authors placed a trout in the flow downstream of a vertical dowel, then recorded the swimming motions and vortex structure simultaneously (1, 7) (see the figure, panel D). Rather than simply swimming in the lee of the dowel—like one cyclist "drafting" in another's wake—the trout locks its swimming

movements into phase with the oncoming drag vortices. The trout weaves through the wake to let each oncoming vortex pass it on the same side as a thrust wake vortex would. The fish moves considerably from side to side, undulating its body with large amplitudes, a behavior termed the "von Kármán gait" by the investigators (1, 7). Liao *et al.* also show that trout adapt this gait to suit the particular vortex spacing of wakes behind large and small dowels in slow- and fast-flowing water (1). The fish's body behaves much like a passive hydrofoil or a fluttering flag. In the wake of a flagpole, flags flutter in response to the pole's drag wake (2). Similarly, the trout's considerable body undulations might not be the result of extra-strong muscle contractions. This fact is confirmed by Liao and co-workers with their comparison of electromyogram recordings of trout swimming in an unperturbed (uniform) free stream with those of trout swimming in the wake generated by stationary dowels. In contrast to free-swimming fish, fish adopting the von Kármán gait only activate the most anterior group of

their swimming muscles. This suggests that their body wave is generated passively by interaction with the oncoming flow of water. This reduced muscle activity is the first direct evidence for the energy-saving benefits of swimming in a wake. It hints at the benefit that could be gained by fish swimming in schools and gives valuable pointers for the design of fish ladders (structures that allow fish to migrate past obstacles).

Fish might not be the only animals that recycle vortices that they encounter in their path. Like all flying animals, birds generate vortices as they flap their wings (8). At cruising speed, the wings beat with low amplitude and shed vortices mainly from their tips. Because energy conservation and efficiency are paramount during migration, birds might exploit the wake of neighboring birds in

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the same flock. Even individual fish with their multiple fins recycle the wake of their own upstream propellers for increased power and control. An improved understanding of these natural mechanisms should help engineers to design better foil propulsors. The next step will be to seek more examples of phase-

locked swimming and flight movements in nature to ascertain how widely vortex recycling is exploited during swimming and flight.

## References

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## ATMOSPHERIC SCIENCE

# Nitrogen and Climate Change

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Human activities, particularly burning fossil fuel, have increased atmospheric carbon dioxide (CO<sub>2</sub>) concentrations. Because CO<sub>2</sub> traps heat, continued emissions are expected to change global climate. The extent of this change will depend not only on the rate of emissions, but also on carbon uptake by the oceans and the land.

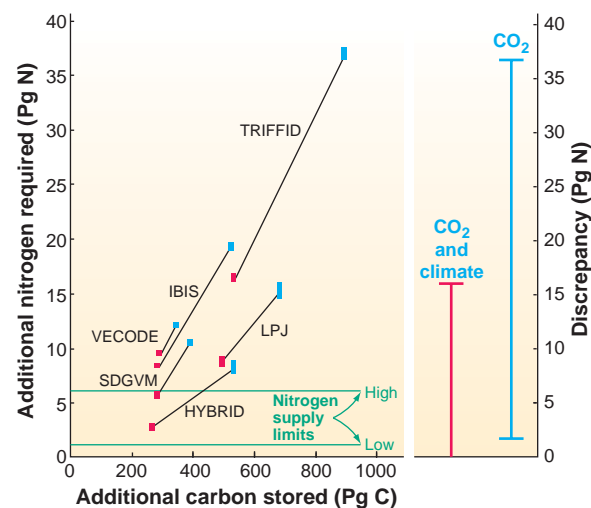
According to some models, land ecosystems can sequester carbon fast enough to help to counteract CO<sub>2</sub> emissions. Models featured in the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) suggest that increasing atmospheric CO<sub>2</sub> alone could cause 350 to 890 Pg of carbon (1 Pg = 10<sup>15</sup> g) to accumulate in the terrestrial biosphere by 2100. These amounts are equivalent to 22 to 57% of expected anthropogenic CO<sub>2</sub> emissions in an intermediate emissions scenario (1, 2). The models suggest that atmospheric CO<sub>2</sub> and climate change together could cause 260 to 530 Pg of carbon to accumulate, or 16 to 34% of emissions (1, 2).

These models probably exaggerate the terrestrial biosphere's potential to slow atmospheric CO<sub>2</sub> rise. Ecosystem carbon accumulation may be constrained by nutrients, particularly nitrogen (3, 4), through mechanisms that are not well developed in or absent from the models.

How much nitrogen do the model projections require? The models distribute the future terrestrial carbon sink roughly equally between trees and soils. With no change in the carbon:nitrogen (C:N) ratios of trees (200) and soils (15), the CO<sub>2</sub>-only projections require 7.7 to 37.5 Pg of nitrogen; the CO<sub>2</sub>-climate projections require 2.3 to 16.9 Pg of nitrogen (see the figure) (5).

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Can increasing ecosystem C:N ratios reduce the nitrogen required? Tree C:N increases with atmospheric CO<sub>2</sub> concentration (6, 7). But even allowing all the simulated increase in tree carbon to occur as wood (C:N = 500) only slightly reduces the amount of additional nitrogen required (see the figure). Soil C:N could also increase with rising atmospheric CO<sub>2</sub> concentration, allowing soil carbon accumulation without additional nitrogen. This mechanism could allow some nitrogen transfer from soil to trees (6, 7), lowering the nitrogen demand associated with increased tree carbon. However, experimental studies show that when CO<sub>2</sub> enrichment increases soil C:N, decomposing microorganisms require more nitrogen. This effect can reduce nitrogen mineralization, the main source of nitrogen for plants (8, 9). It is thus



**Supply and demand.** (Left) Nitrogen required to support terrestrial carbon uptake (1), compared to likely limits of nitrogen supply (green). For each model (2), values are shown for CO<sub>2</sub>-only (blue) and CO<sub>2</sub>-climate (red) projections. The upper nitrogen requirement assumes a fixed tree C:N of 200; the lower value assumes that all new tree carbon is allocated to wood. (Right) Discrepancy between nitrogen required for projected carbon uptake and likely nitrogen availability for CO<sub>2</sub>-only (blue) and CO<sub>2</sub>-and-climate-change (red) scenarios. Upper value: maximum calculated nitrogen required minus low nitrogen supply limit. Lower value: minimum nitrogen required minus high nitrogen supply limit.

unlikely that increases in soil C:N could yield large increases in ecosystem carbon stocks.

With little contribution from increasing C:N, the carbon-uptake projections (1, 2) almost certainly require nitrogen accumulation. Nitrogen enters the terrestrial biosphere through atmospheric deposition and biological fixation, and is mainly lost through leaching and gaseous fluxes. We have estimated high and low nitrogen fluxes for each of these mechanisms (10).

To estimate future anthropogenic nitrogen deposition based on population-growth projections (11), we assume that per capita nitrogen deposition remains constant (low) or increases linearly to that of North America today (high) (12). We assume that 5% (low) to 10% (high) of that deposited nitrogen supports increased carbon storage (9). We estimate biological nitrogen fixation (12) to increase linearly by 10% (low) or 45% (high) with CO<sub>2</sub> doubling (9). We further assume that nitrogen leaching losses are currently 36 Tg of nitrogen per year (13), and that nitrogen leaching would decline linearly with CO<sub>2</sub> doubling by 0 (low) to 20% (high) (9).

Combining our high estimates, 6.1 Pg of nitrogen could accumulate by 2100 (see the figure). This amount is less than is required by all CO<sub>2</sub>-only simulations and by four of the six CO<sub>2</sub>-climate simulations (1, 2) (see the figure). Our low estimates of nitrogen accumulation yield only 1.2 Pg of nitrogen, insufficient for all simulations.

We have focused on nitrogen, but the situation may be worse for other nutrients, such as potassium and phosphorus, which are less subject to human or biological control than is nitrogen fixation. Models that incorporate nutrient cycling predict much less CO<sub>2</sub> carbon uptake than models lacking these feedbacks (14). The next IPCC assessment must include models taking into account these feedbacks.