THE AERODYNAMICS AND HYDRODYNAMICS OF PLANTS

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Summary

Because they grow away from their substratum to compete for light, plants have to withstand hydrodynamic or aerodynamic drag. Both water and land plants reconfigure in response to this drag, and this is presumed to reduce the risk of mechanical failure. However, there is little unequivocal evidence of drag reduction in large trees as a result of reconfiguration. Land plants must also transport water internally to their tissues, and many have developed xylem tracheids and vessels that help speed up this process. Recent evidence that tree height is limited by water supply suggests that water transport efficiency must be a crucial element in tree design. However, the resistance of many parts of the xylem is still unknown. More focused work is urgently required to shed light on the evolution and ecology of plants in relation to the flow of fluids.

Key words; aerodynamics, hydrodynamics, tree, drag.

Introduction

The importance of aerodynamics and hydrodynamics in plants results from competition for light which drives the evolution of taller and taller plants (Alexander, 1970). Taller plants can shade out their competitors and, being further out of the boundary layer, will receive a better carbon dioxide supply. The inevitable drawback is that water plants will be exposed to greater hydrodynamic drag and land plants to greater aerodynamic drag. In addition, taller land plants will have more difficulty supplying their leaves with water because it has further to travel up their stems. The hydrodynamic drag as well as the gravitational resistance will therefore be greater.

In many biomechanical studies, there are three main areas in which study needs to be concentrated: quantification, adaptation and ecology. In this particular research area, it is essential to be able to measure the drag on plants, to investigate the mechanisms they use to minimise it, and to relate these to the life of the plants in their particular habitats. Unfortunately, as I will show, little work has been carried out in these areas, particularly compared with the mass of research that has been devoted to the solid mechanics of plants (Niklas and Spatz, 1999; Spatz et al., 1999). Consequently, far too many of our ideas about the adaptation and acclimation of plants to their hydrodynamic and aerodynamic environments are still based on conjecture and remain unsubstantiated 'Just So stories' (Ennos, 1997).

Hydrodynamics of water plants

Surprisingly little work has been carried out on the mechanics of aquatic plants, especially compared with the large literature on seaweeds (Denny, 1999). Indeed, so popular have seaweeds been to zoologists that they seem to have reached the status of honorary animals.

Even the most cursory examination of the plants of fast-flowing streams suggests that they have given up the unequal task of standing up to the large forces that would beset a rigid structure in the water. They trail away downstream from their roots, seeming to present a streamlined shape to the flow. However, only two studies of the hydrodynamics of these plants have been carried out recently (Usherwood et al., 1997; Biehle et al., 1998). They both quantified drag by placing live plants in water tunnels; they investigated adaptation by examining the shape, anatomy and mechanics of the shoot systems and related their findings to the mode of life of the plants.

In the first study, Usherwood et al. (1997) tested *Ranunculus fluitans* plants, ranging in length from 0.5 to 1.5 m, in a flow tank whose speed ranged from 0.5 to $1.3 \, \mathrm{m \, s^{-1}}$, giving Reynolds numbers in the range of 10^6. Plants trailed downstream in the flow and displayed drag that was approximately proportional to the first power both of the velocity and the length, rising to a maximum of 0.3 N. The linear relationships between drag and velocity, and drag and length, are both somewhat surprising, but can be related to aspects of the morphology and mechanics of the plant.

The fact that drag varies nearly linearly with velocity rather than with its square, as would be expected in a rigid plant, can be related to reconfiguration of the shoot. The stems bend downstream more in faster flow, so that the frontal area is reduced, lowering profile drag, while the long strap-like leaves can fold against the stem, reducing friction drag. Stem

reconfiguration in turn can be related to the anatomy and mechanics of the stem. The central portion of the stem encloses an air-filled central lumen, so at low velocities the shoots float to the surface. However, the rigidity of the stem is only around one-hundredth of that of the land plant *Ranunculus acris* because of the lower stiffness and central positioning of the vascular bundles.

The fact that drag varies with the first power of velocity rather than with its square suggests that the flow separation that occurs around flags (Hoerner, 1965) and in the blades of some seaweeds (Koehl and Alberte, 1988) does not occur. Neither do the stems show the rapid fluttering movements that result from flow separation. The reasons for this are not known. It may be because of residual bending rigidity in the stems or because fluttering is prevented by the extreme narrowness of the stems and leaves. These suggestions could be tested using model leaves of varying widths and rigidities. The rarity of plants with flattened leaves in fast-moving streams suggests that the latter explanation might be correct.

Even the longest plants at the highest speed had high factors of safety, around 7, against failure, so the drag reduction seems to work well enough to prevent breakage in all but the fastest floods and longest plants.

In contrast to *Ranunculus fluitans*, the water moss *Fontinalis antipyretica* showed little sign of reconfiguration (Biehle et al., 1998). Operating at lower Reynolds numbers of 10^4–10^5, its drag was again roughly proportional to length but increased approximately with the square of flow velocity. This was not surprising because the single unbranched stems that were tested were so flexible they hung almost perfectly downstream even at low velocities. The majority of resistance was therefore due to friction drag. As in *Ranunculus fluitans*, there was no suggestion of flag-like behaviour.

Fontinalis antipyretica also showed morphological plasticity similar to that seen in some seaweeds (Koehl and Alberte, 1988). Plants from fast-moving streams had leaves with low branching angles, which produced a smooth surface. In contrast, in plants from slow-moving water, the branching angles of the leaves were higher and the leaves stuck out more into the flow, presenting a rough surface. This change increased the drag coefficient by 35 %, but resulted in the production of small vortices behind the leaves that would increase the supply of CO_2 and nutrients. This would increase the maximum rate of photosynthesis and, hence, growth. Differences in form could therefore be related, *via* hydrodynamic observations, to the ecology of the plants.

Aerodynamics of trees

Compared with water plants, trees have a much greater problem with reconfiguration because, living in air, they must support their own weight. This precludes the evolution of the sort of flexibility seen in water plants; trees can therefore be regarded as at best semi-flexible structures. This is especially true of large trees because, to provide adequate support, the diameter of the trunk must scale at least with length to the power 3/2 (McMahon, 1973); large trees must have relatively thicker trunks than small ones. The consequences are far-reaching. Young trees can bend right over in gales, reducing both their drag and the height of the centre of pressure of the force. Therefore, they are unlikely to be broken or uprooted by wind forces. Tall trees, in contrast, can be regarded as rigid columns with small trees or shrubs attached near the top (Bertram, 1989). Thus, although they can reduce drag by reconfiguration of their canopy, they cannot reduce the height of the centre of pressure. They are therefore vulnerable to windsnap and windthrow.

The main problem with finding out whether trees do reduce drag by reconfiguring in the wind is one of scale; no wind tunnels are large enough to take full-sized trees! Some tests have been carried out on young trees which suggest that reconfiguration does work. Fraser (1962) placed young conifers into wind tunnels operating at speeds of 9–38 m s^{-1}. Analysing his results, Mayhead (1973) showed that drag increased more nearly with the first than the second power of velocity, with drag coefficients based on full frontal area falling from almost 0.5 to 0.15. These changes were accompanied by a progressive decrease in the exposed area as branches and twigs bent back in the wind. In an unpublished study on young larch trees carried out at Manchester, R. H. C. Bonser obtained similar results.

Similar work has also been carried out on very small holly seedlings and branches (Vogel, 1984), and Vogel (1989) performed more extensive work on the behaviour of isolated leaves and small branches of a range of angiosperm trees. Vogel showed that very small trees, single leaves and branches show effective drag reduction by means of reconfiguration. Lobed leaves roll up into a streamlined tube, while compound leaves and leaves on whole branches fold up together, producing a streamlined surface with a lower surface area. These changes result in large reductions in the drag coefficient, especially in the branches.

The picture seems conclusive, but there are problems with extrapolating the results of this investigation to whole trees. Vogel's (1984, 1989) leaves and branches were held pointing downwind, and when on the tree would be the ones on the sheltered lee side of the tree. The behaviour of leaves and branches held out towards the wind has not been explicitly studied. Because their petioles will bend, the leaves might even be held out more nearly at right angles to the wind and have increased drag due to reconfiguration. Certainly this seems to have been exactly what occurred in the wind-pruned trees examined by E. C. Brown (cited in Vogel, 1984). When these trees, which had most branches pointing away from the prevailing wind, were placed in the opposite direction in the wind tunnel, the drag coefficient rose dramatically up to speeds of 10 m s^{-1}. Even if all leaves do show efficient reconfiguration, it is uncertain whether this would reduce the drag of the whole tree. It would depend on the permeability of the canopy; highly permeable canopies would let more air through and enable reconfiguration of leaves and branches to reduce drag, whereas in impermeable canopies, reconfiguration would just allow wind to penetrate further in the canopy.

Attempts to measure the drag coefficients of broadleaved trees in the field have been beset by problems. Single trees standing

in a flat landscape are extremely rare, though some good work might be carried out in the English landscape gardens of Capability Brown. Second, it is hard to measure the actual force on a tree without digging it up. Investigators have to examine lateral movements of the crown, or strains on the trunk, and calculate the drag by estimating the position of the centre of pressure of the tree. Third, wind is notoriously variable, both spatially and temporally. Trees are in the earth's boundary layer, so winds will be strongest at the top of their crown. Large numbers of anemometers may be needed to estimate the mean wind speed around the tree at any instant. Finally, the drag on a tree might well depend on the point in a gust, since it will take time for reconfiguration to take place, and trees move about quite a lot in the wind, oscillating at their natural frequency.

The results so far from whole mature trees (Roodbaraky et al., 1994; R. H. C. Bonser and A. R. Ennos, unpublished observations) have been inconclusive, partly because of huge scatter in the data and the difficulty in sampling a wide enough range of windspeeds. The slope of the regression lines of logged data of force against velocity are not significantly different from either 1 or 2. The only results from constant monitoring of trees over a period of years are those of Blackburn (1997), who showed that drag increased even faster than with the square of wind velocity. However, this was in Sitka spruce trees grown in a forest. Only during strong gusts does wind penetrate the canopy in these cases. Consideration of what goes on in these situations would bring us into the esoteric world of forest aerodynamics (Finnigan and Brunet, 1995; Gardiner, 1995).

In summary, then, the role of reconfiguration in reducing the drag of large trees is far from proven. It could be important, but more practical work is needed before we can say one way or the other. This is unfortunate because many of our ideas about the ecology and functional morphology of trees are based on the idea that reconfiguration is important. The relative drag of conifers and angiosperm trees is uncertain, although it has been suggested that conifers should have lower drag (Vogel, 1981, 1984). It has also been suggested that a major advantage of dense woods, as used in branches and in long-lived climax trees, is that they can reconfigure more in strong winds than can less-dense woods (King and Loucks, 1978). Similar arguments have been invoked to explain certain growth responses of trees to wind such as flagging and the production of spiral grain (Kubler, 1991; Telewski, 1995) and the production of smaller leaves with more flexible petioles (Niklas, 1996). Clearly, we will need to develop better methods to investigate the relationship between wind speed and drag and carry out far more work before we can answer many important questions about tree design.

The internal hydrodynamics of trees

There are many aspects of the internal hydrodynamics of vascular plants that have yet to be quantified and which therefore block our understanding of the functional morphology of wood. Using a computer modelling approach, Roth et al. (1994a,b) have clearly demonstrated the vital importance of a stele of open vascular conduits to maintain an adequate water supply to land plants. They have also shown how the evolution of the more complex stele arrangements seen in higher plants might have been driven by water supply considerations; siphonosteles and eusteles are favoured because the nearer the stele is to the surface, the better the water supply to the outside of the stem.

In modern plants, however, most physiologists have concentrated on the behaviour of the stomata, which are usually seen to be the most important resistance element to transpiration. Only recently has the theory that tree height is limited by the hydraulic resistance of its wood been taken seriously (Ryan and Yoder, 1997), and it is now receiving strong experimental support (Menduccini and Grace, 1996). This makes it vital to understand the factors that affect hydrodynamic resistance to flow. The hydrodynamics itself should be fairly straightforward; since water travels up the thin cells very slowly, the Reynolds numbers are well below 1, so viscous flow predominates. In these conditions, it is clearly better to have fewer, wider conduits, because the hydrodynamic resistance of pipes falls with the fourth power of their radius. However, large columns of water under the large negative pressures seen during transpiration are vulnerable to embolisms, not only during winters and dry spells but each day (Canny, 1997; Sperry and Ikeda, 1997; Zwieniecki and Holbrook, 1998). Much interest has been shown by physiologists on how embolisms may be prevented and vessels refilled. This has focused interest on the morphology of the water-conducting elements.

The water-conducting elements are not, in fact, open-ended tubes because they are made up of cells. In conifers, the water-conducting elements are thin, tapered tracheids, joined only by complex toroid-bordered pits. The much wider vessels of angiosperm trees are made up of columns of cells joined by perforation plates that vary between multi-barred scalariform plates and simple plates with a large central hole. The ends of the vessels are then joined by large numbers of pits without toruses. Many studies have attempted to quantify the importance of the pits and perforation plates.

The most common method has been to measure the resistance of a piece of wood and compare it with the expected resistance of the same number of open-ended tubes of the same diameter (Petty, 1978). There are many problems with this approach: some conduits might be blocked; wood conductivity measurements can fluctuate greatly; and, because of the dependence of resistance on the fourth power of radius, small inaccuracies in morphological measurements can result in large inaccuracies in the expected resistance. Other studies have overcome these problems by using finite element modelling to investigate the effects of helical wall thickenings (Roth, 1996) and scalariform plates (Schulte and Castle, 1993a,b). The disadvantage of this method is its cost and the difficulty in modelling complex shapes. A cheap alternative is to use large-scale models filled with glycerol to maintain low-Reynolds-number flow (Ellerby and Ennos, 1998).

The results of these studies show that the overall resistance of perforation plates is very low: less than 20 % of the resistance of the tubes themselves. However, no study has been able to investigate the effect of the much more complex pores. Future

work should try to make up for this deficiency. One method might be to make models of the pores, but this would be very tricky. It might be necessary to investigate the resistance of single pores by carrying out a sort of hydrodynamic 'patch-clamping' on small areas of cell wall containing single pores. It is also important that researchers not only examine the fine details of the flow regimes within cells, but ask much broader questions about the relative resistances of angiosperm and conifer wood.

Conclusion

Although some progress has been made in recent years, far less work has been put into examining the aerodynamics and hydrodynamics of plants than that of animals. More work in this area is urgently required. It also needs to be focused more on answering the type of question that appeals more widely to biologists and indeed to a general audience. Why do water plants have so little drag? How effectively can trees reconfigure? How can trees pipe water up their trunks so efficiently? The answers might help us answer important evolutionary questions such as why there are so few conifers in tropical rainforests or why there are no coniferous lianas.

The hope is that, in the future, biomechanical books about plants may be written which cover fluid dynamics as comprehensively as solid mechanics.

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