Aerodynamics of Wind Pollination

Many plants are almost perfectly engineered to capture pollen from the wind. Cones, flower clusters and other structures channel the airflow—and sperm-producing pollen—toward reproductive surfaces

by Karl J. Niklas

The gusts of pollen that seasonally vex the sinuses of hay-fever sufferers are a by-product of the reproductive strategy of many plant species. Such plants loft showers of pollen grains (sperm-producing spores) into the air. If all goes well, wind currents then convey the grains to other plants of the same species. Pollen that lands on ovules (specialized egg-producing bodies), or on structures that encase them, fertilizes the eggs and enables the ovules to develop into seeds.

Biologists have traditionally considered wind dispersal, the oldest surviving method of pollination, to be more wasteful than the strategies of many other plants, which depend on insects, birds or other animals to transfer pollen. Perhaps one in 1,000 grains of pollen entrusted to the wind reaches the female organ of a target plant. Most of the rest collide with a variety of unreceptive objects, such as leaves, branches, telephone poles or human nasal passages.

Wind pollination might be more wasteful than other methods, but I believe it is less extravagant than it might seem. After all, if the method were truly inefficient, thousands of plant species would not have retained it over the course of evolutionary history or—what is more striking—have recently adopted it. Many gymnosperms (nonflowering seed plants), including the conifers and certain of the palmlike plants known as cycads, are pollinated by wind. So are certain members of the other main group of seed plants: the angiosperms (flowering plants), which evolved some 200 million years after the gymnosperms. Grasses, one of the largest and most successful families of flowering plants, are almost all wind-pollinated. In addition solid evidence now shows that pollen capture is often far from random. My colleagues and I at Cornell University, in collaboration with workers at the University of Arizona and the Fairchild Tropical Garden in Coral Gables, have found that many plants are aerodynamically designed to filter large amounts of pollen from the air.

An understanding of our findings requires some knowledge of the reproductive machinery of seed plants. In gymnosperms the ovule lies unenclosed on modified branches or leaves. ("Gymnosperm" literally means naked seed.) Pollen needs only to land on or near the opening of the ovule—the micropyle—for the pollen grain to mature and ultimately release sperm that can fertilize an egg. In angiosperms, in contrast, the ovule is enclosed within the bulbous part of a flask-shaped body known as a carpel. Pollination is complete when the grain lands on the stigma, the carpel's upper tip. The pollen then extends a long tube in order to reach the egg for fertilization.

In some species of seed plants the sexes are divided: pollen-bearing and ovulate organs grow on different individuals. Most species, however, are bisexual; even so, many do not pollinate their own eggs. (There is a reasonable explanation for this apparent inefficiency: cross-pollination preserves genetic diversity.)

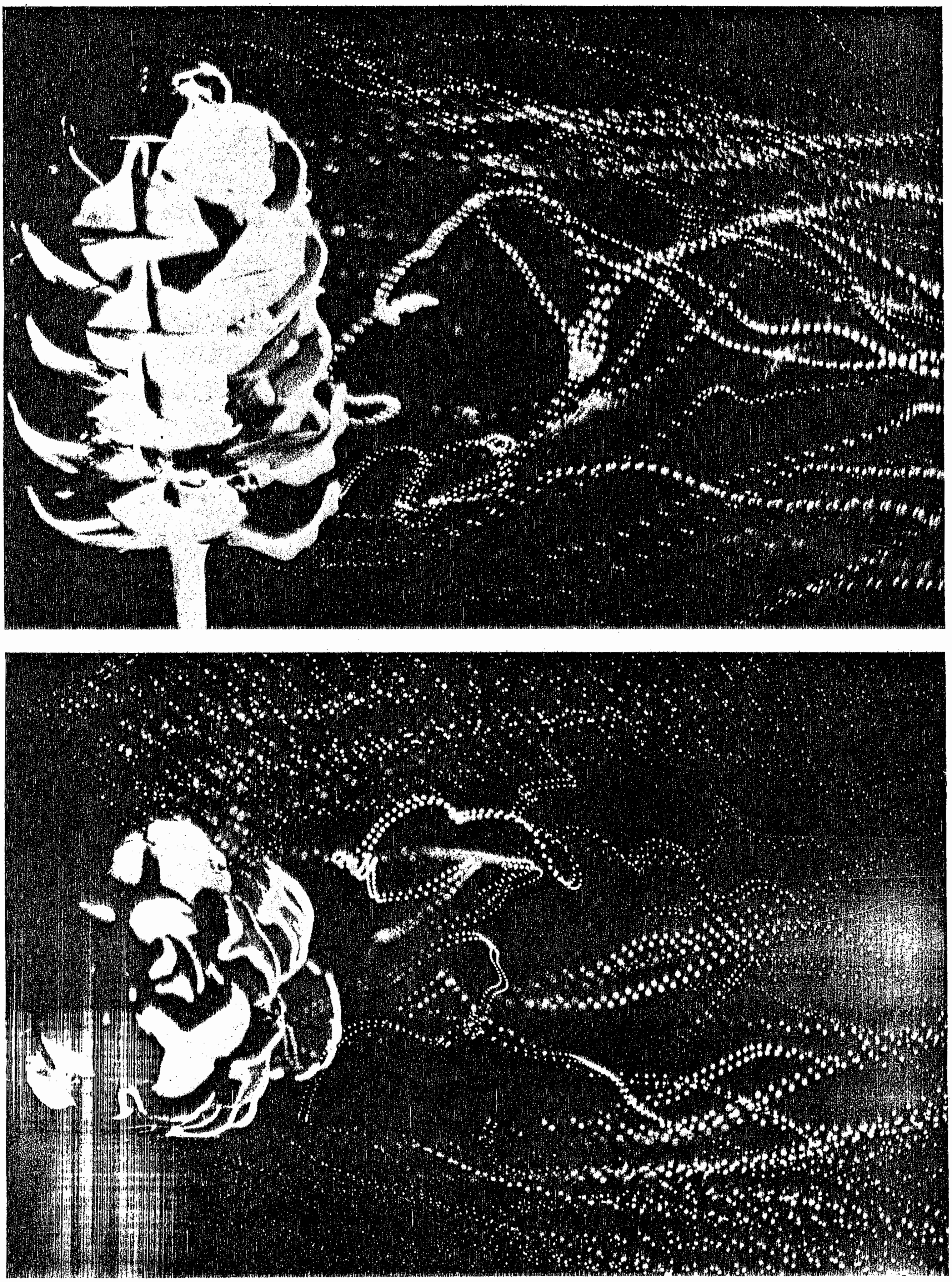
Pine trees, which are bisexual as adults yet rely on cross-pollination to fertilize 95 percent of their eggs, provide an excellent illustration of the influence of a plant's aerodynamic design on its ability to snare pollen from the wind. The male reproductive organs of these conifers are small cones that usually grow in clusters. When a cone is completely grown, its pollen-producing chambers rupture, releasing their contents into the air. The female cones, on the other hand, are larger and can grow singly. Their scales, which have small leaves known as bracts at the base, bear two ovules on their upper surface. When the cone is ready to be pollinated, the scale-bract complexes separate slightly from one another, giving airborne pollen access to the micropyle.

When my colleagues and I began to study female pinecones, we were particularly intrigued by a puzzling structural feature: the ovules are buried close to the axis (the cone's stemlike core), and their micropyles open toward the axis and not the external environment. This seemed a poor design for fostering contact between pollen and micropyle. Could it be, we wondered, that the scales and bracts somehow obstruct the flow of air in such a way as to deflect pollen toward the oddly placed ovules?

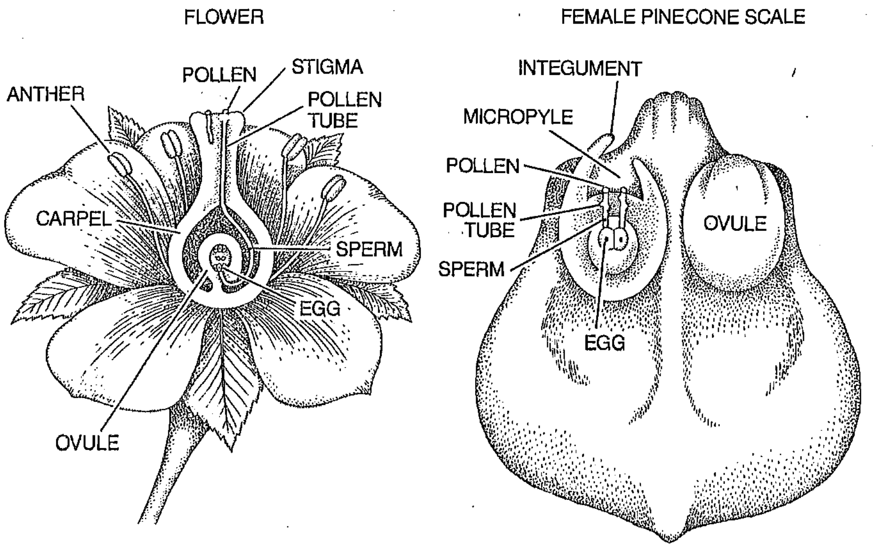
We sought the answer by placing a larger-than-life model of a pinecone in a wind tunnel. We visualized the airflow disturbances around the model by releasing helium-filled bubbles into the wind; such bubbles trace airflow with excellent precision and can pass through tight spaces at a high speed without bursting. We then recorded the trajectories of these bubbles with stroboscopic photography: a camera "shot" the bubbles as a strobe light flashed at preset intervals. A computer analyzed the images to yield data on the speed and direction of the wind in various "cells," or tiny regions, in the microenvironment around the cone.

The computer indicated that the model disturbed the linear movement of the wind in three basic ways [*see bottom illustration on page 74*]. First, it deflected the wind into the core of the cone. There the air circled the axis, washing over the upper (ovule-bearing) surface of the scale-bract complexes. Second, wind passing over each scale dropped toward the base and swirled chaotically near the micropyles. Third, the cone as a whole, with its many protrusions, resulted in significant turbulence along the leeward (downwind) side. There the wind was sucked downward and back (upwind), striking the leeward scales.

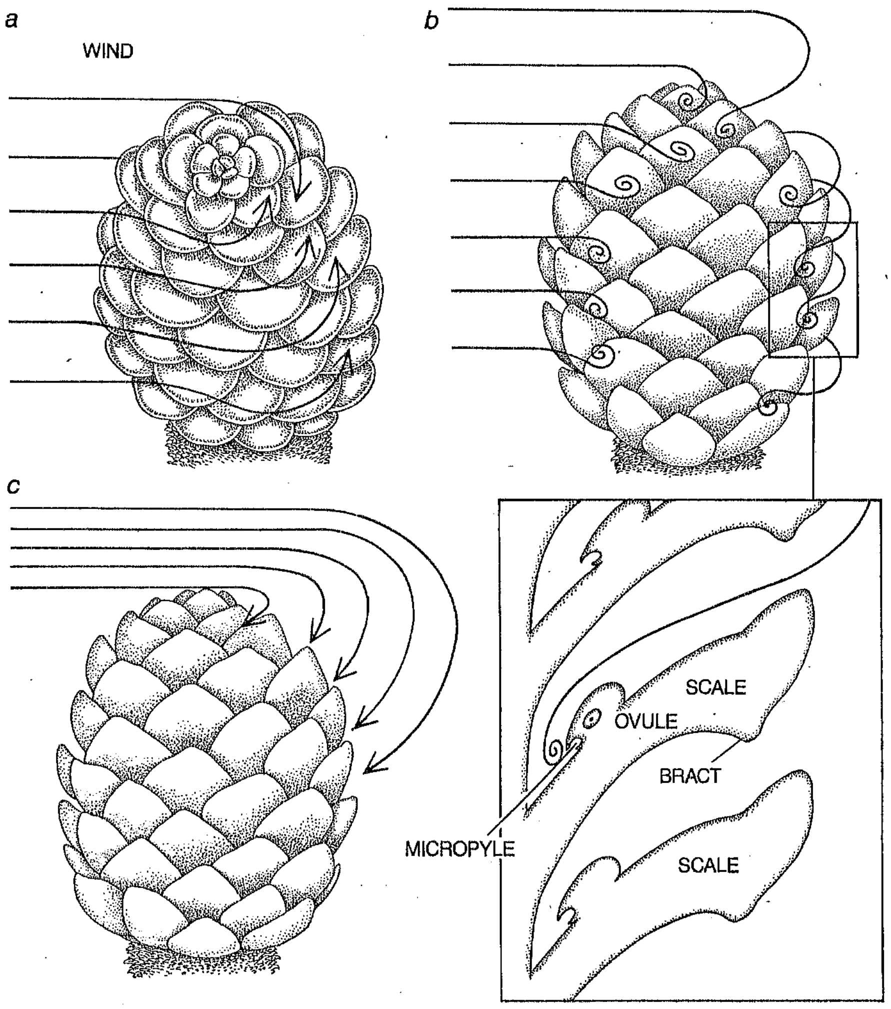
All three of the patterns suggested



HELIUM-FILLED BUBBLES in a wind tunnel reveal the turbulence created by a model of a female pinecone, which is seen from the side (*top*) and from above (*bottom*). The wind is blowing from left to right. Such turbulence fosters collisions between airborne pollen grains (sperm-producing spores) and a cone's ovules: the egg-bearing structures on the upper surface of each scale. The airflow around the model was photographed by a stroboscopic technique in which the bubbles were illuminated at preset intervals.



FERTILIZATION of an egg follows pollination: the delivery of pollen to the stigma of a flower (*left*) or, in a nonflowering plant, to the micropyle (opening) of an ovule (*right*). The pollen then matures, if necessary extending a tube to reach the egg. Eventually the pollen releases sperm, fertilizing the egg and causing the ovule to develop into a seed. A pine scale bears two ovules, each of which holds two or three eggs; only one egg becomes an embryo, however. (The left ovule is rotated 90 degrees to show the inner structure.)



THREE PATTERNS of airflow are typically generated around a female pinecone that is ready to be pollinated. Wind is deflected into the core of the cone (*a*), where it circles the axis, or central stem, brushing over the upper (ovule-bearing) surface of the scales. The air also swirls chaotically above each scale (*b*), near the micropyle (*inset*). On the leeward (downwind) side of the cone air is drawn down and is pulled toward the scales (*c*).

that pollen grains suspended in the wind brushing over an actual cone have a good chance of colliding with the micropyles. Other experiments involving real cones and pollen confirm the suggestion. The same basic turbulence patterns were evident, and pollen moving around ovulate cones roughly followed the course of the wind. We also determined that a large fraction of the spores settled on the inward-facing micropyles.

Knowing that female organs of conifers can deflect airborne pollen toward their ovules, we confronted another question: What prevents the pollen grains of one plant species from being "wasted" on the ovules of another? In plants, as in animals, sperm can generally fertilize eggs from the same species only.

Our studies reveal that the unique shape of the cone produced by each plant species results in idiosyncratic modifications of the airflow patterns described above. The specific patterns are influenced by such factors as the diameter and length of the cone, the number of scales attached to the central axis, their shapes, the angle at which each scale meets the axis and the speed of the wind. Similarly, each type of pollen has a distinctive size, shape and density, causing the pollen to interact with the turbulence in a unique way. Pollen grains from one species, for example, may be too dense to follow precisely the currents generated by a cone from another species; instead particles on the leeward side may settle out of the air currents, falling to the ground before they can be pulled back toward the scales.

Apparently many varieties of cones generate wind-flow patterns that best suit the pollen of their species; most of the cones we studied filtered their "own" pollen from the air but not that of other species. This filtering ability has obvious benefits. In addition to capturing the appropriate pollen, female pinecones also deflect undesirable particles, such as fungal spores, that can damage the ovules.

The cone itself is not the only part of the conifer to exert an aerodynamic influence on pollination; the leaf clusters that typically surround a female cone also have an effect. These leaves act much like a snow fence: a slatted fence that screens a roadway from blowing snow. The spaces between the slats create eddies that slow the wind and therefore the flakes it carries. As a result the flakes drift to the ground on the downwind side of the fence instead of streaming onto the roadway. Similarly, the leaves around a pinecone can decrease the speed of the air, thereby showering the cone with pollen grains, which are then sucked into eddies above and around the scales. Because the leaves are arranged symmetrically around the cone, they can trap windborne particles coming at them from any direction.

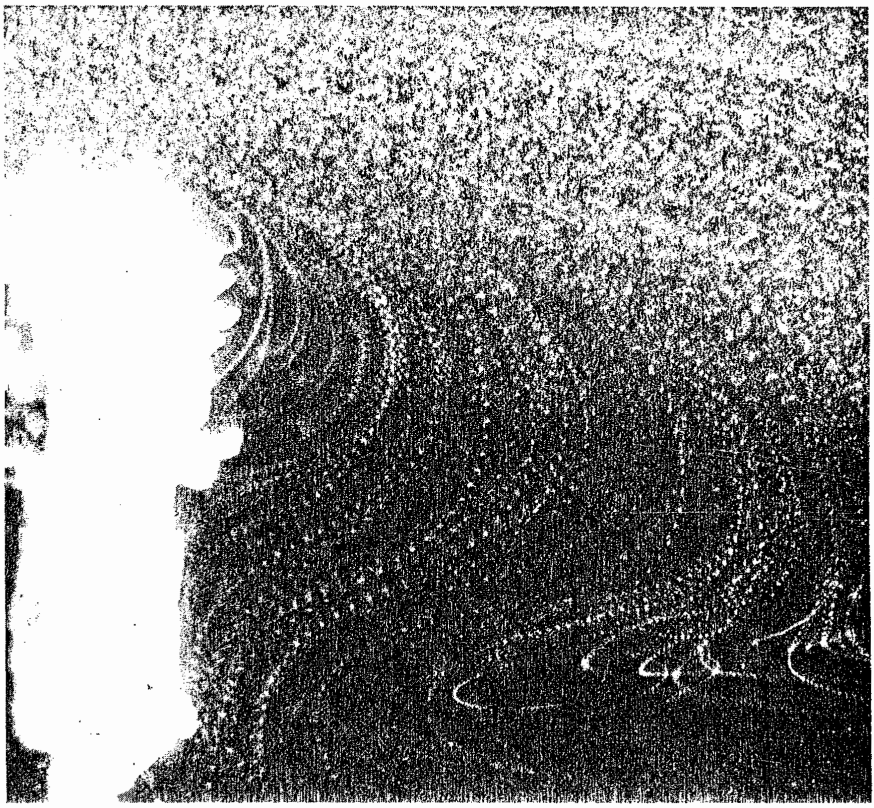
One additional characteristic of pine trees also facilitates pollen capture. Ovulate organs generally grow at branch tips. As the wind blows it can cause branches to undulate in a nearly circular path, enabling the cones to harvest spores from various levels of the air.

Like pinecones, the reproductive organs of grasses also generate unique turbulence patterns. Some grass inflorescences, or clusters of flowers, are borne at the tips of flexible stems and consist of numerous flowers arranged around a central stalk, much as scales are arranged around a pinecone. Not surprisingly, the flow of air around these "tight" inflorescences resembles the flow around a female pinecone. Floral surfaces deflect pollen into the spaces between flowers, and the inflorescence as a whole creates an aerodynamic sink for other grains on its leeward side. When the stem sways in the breeze, it plunges the flowers into this sink, increasing their uptake of pollen.

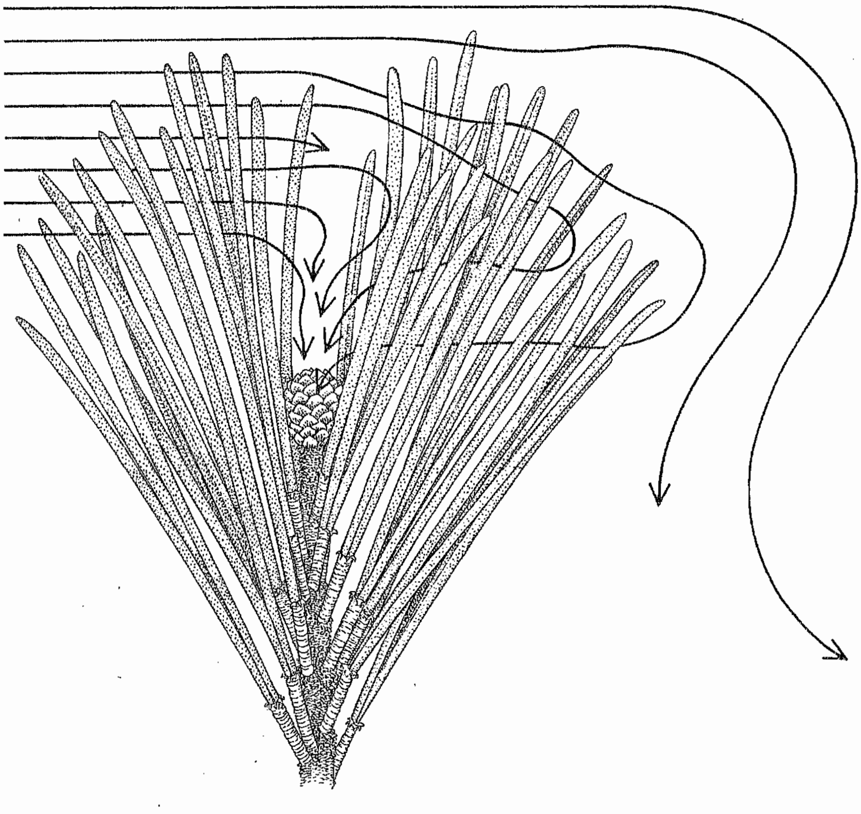
The inflorescences of certain grass species consist not of dense aggregates but of a main stem bearing several small stems, each of which supports one or more flowers at the tip. These "loose" inflorescences create little local turbulence, but they compensate in part by traversing a broad area when the wind stirs them. As the main stem is set into harmonic motion, the smaller stems follow the same trajectory and also oscillate independently, creating a highly complex motion that allows the flowers to intercept much of the pollen in their vicinity.

The studies discussed thus far have been primarily descriptive, but research into the physics of pollination has also extended to prediction. Computer models make it possible to estimate the likelihood that a particular ovulate organ will entrap pollen grains having a hypothetical structure. One goal of such modeling is to determine whether the spore produced by a given plant is aerodynamically ideal. Even if an ovulate organ is known to take up its own species of pollen in preference to other types, the possibility remains that the plant could improve its rate of pollination if the grain had slightly different features.

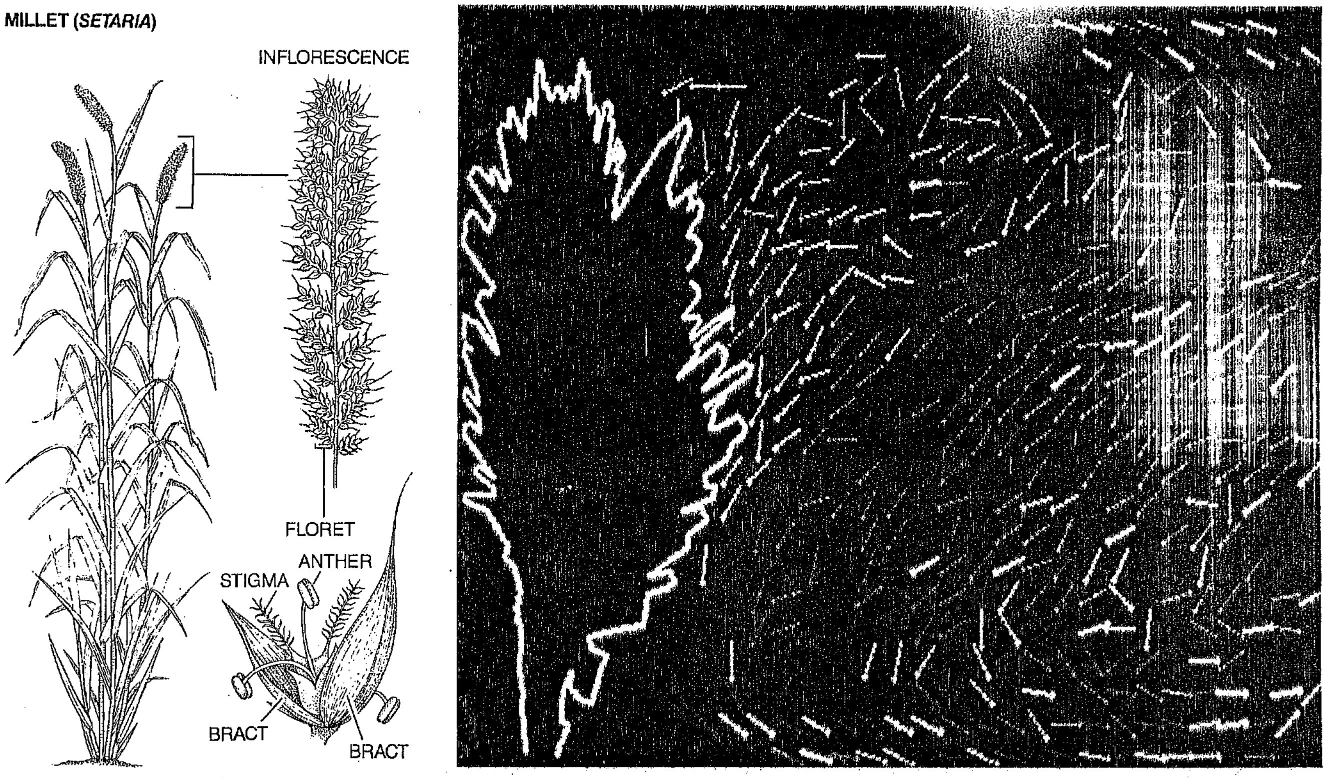
As in our descriptive studies, we set up a cone or an inflorescence in the wind tunnel and determined its characteristic patterns of airflow. We then



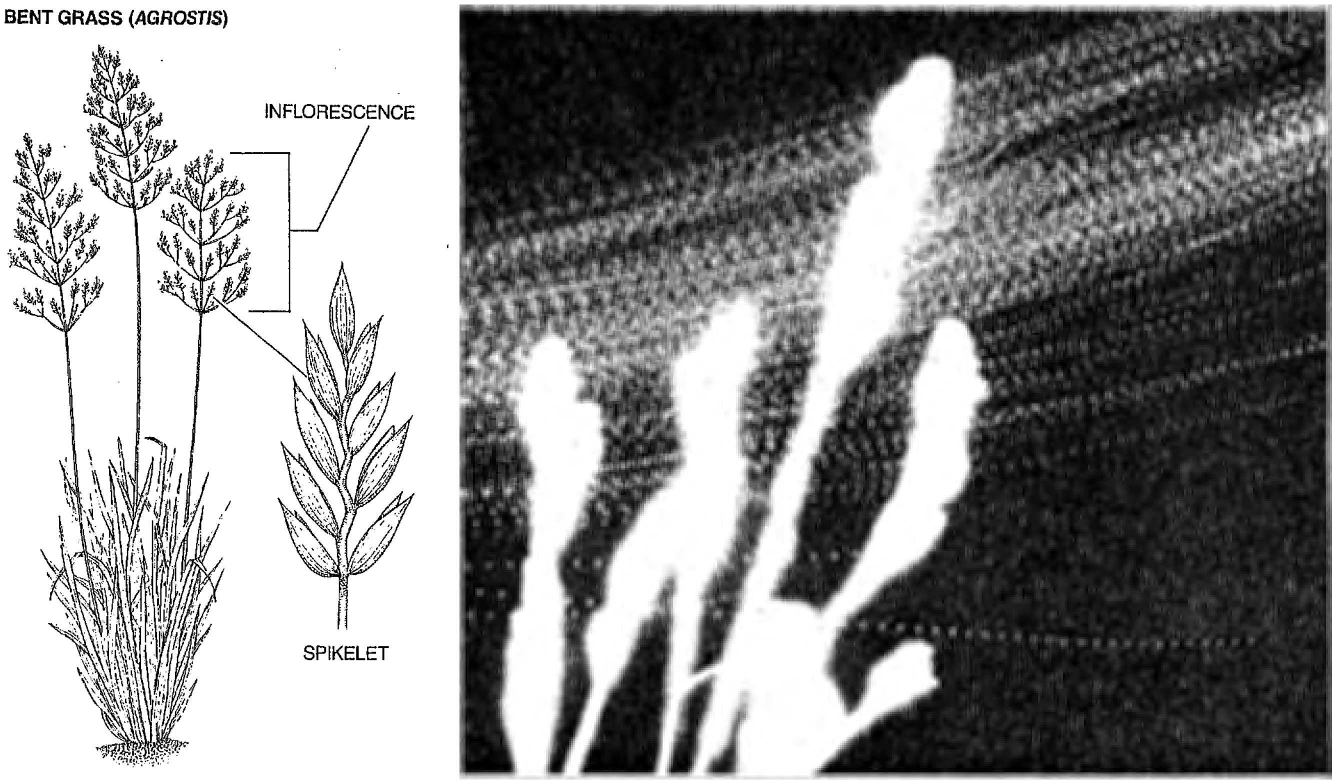
AIRBORNE POLLEN blowing past a female cone of the species *Pinus taeda* is shown by stroboscopic photography; the flow is from left to right. Many grains hit windward surfaces or continue beyond the cone, but others fall back and collide with leeward scales.



LEAVES around a female pinecone act much like a snow fence: a slatted barrier set parallel to and at a distance from a roadway to keep the road free of snow. The spaces between the slats of such a fence hamper the airflow, causing snowflakes to settle to the ground immediately downwind of the fence. Similarly, the leaves upwind of a pinecone cause airborne pollen to settle on their downwind side, showering the cone with spores.



INFLORESCENCE, or flower cluster, of *Setaria geniculata*, a species of millet (*left*), produces leeward turbulence similar to that of a pinecone. A computer analysis (*right*) reveals that pollen grains carried by the wind follow a Z-shaped trajectory and slow as they drift back toward the inflorescence. The computer determined the pattern by calculating the average direction (*round-headed arrows*) and speed (*colors*) of all the pollen in every cell of an imaginary grid superposed on the air around the inflorescence. Green represents the highest speed and is followed in decreasing order by dark blue, white, purple, yellow, red and light blue. The turbulent, slow-moving pollen constitutes a virtual reservoir into which the inflorescence may plunge when it sways in the breeze.



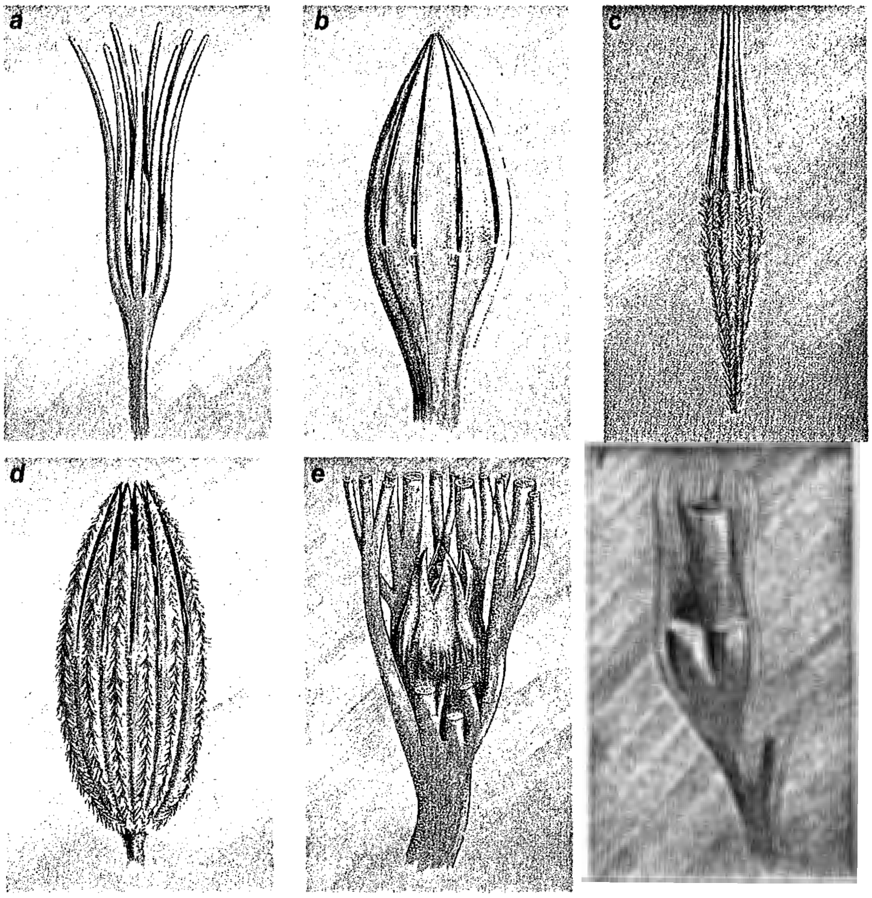
GRASS *Agrostis hiemalis* (*left*) produces "loose" inflorescences: each has a main stem that branches into several smaller stems bearing flowers at the tip. Pollen brushing across such an inflorescence (*right*) does not become trapped in turbulence as it would when passing over a more compact cluster of flowers. Loose inflorescences do have one aerodynamic advantage, however. When the wind blows, their parts move in complex patterns that enable them to capture pollen scattered throughout a large volume of air.

specified the size, shape and density of a hypothetical pollen grain. On the basis of the known air patterns and basic aerodynamic principles, the computer estimated the number of spores that would be likely to reach an ovule (or a stigma).

We have now evaluated approximately 20 plant species that are pollinated by the wind. Most of these have evolved a type of pollen that well suits the aerodynamic environment of their female cones or inflorescences. Certain of the remaining species, however, produce grains whose physical properties appear to be far from optimal. In some of those instances it turns out that the plants do not rely solely on the wind to deliver pollen. A few species are pollinated by insects as well; others reproduce by sprouting cloned offshoots. These plants apparently survive with a "sloppy" match between aerodynamic design and pollen structure because they have reproductive alternatives.

The fact that plants with no alternative methods tend to have the most effective systems of wind pollination suggests aerodynamic design may be an evolutionary adaptation to the need for capturing pollen. It is possible, however, that the architecture of the plants is only a fortunate by-product of adaptations to other demands in the environment. For instance, the tight clustering of ovules in a pinecone or in a grass inflorescence could result solely from the selective pressure to package numerous reproductive units into a small volume. In a similar vein, the arrangement of scales and flowers could be the result of several different pressures, all of which happen to have the same design solution.

This issue is extremely difficult to resolve, but studies of plant fossils carried out by my colleagues and me do support the notion that the need to filter pollen from the air may well have played a role in shaping wind-pollinated species. In particular we evaluated the pollen-capturing abilities of the fossil ovule, often the only part of ancient plants that has been preserved.



FOSSIL OVULES became aerodynamically more efficient as they evolved. Some of the oldest varieties (*a–d*), dating from more than 300 million years ago, consisted of an inner, barely visible egg chamber surrounded by a truss, or ring, of branches. The turbulence created by these protrusions was not focused at the open tip of the chamber and so was inefficient at delivering pollen to the egg. In later ovules (*e, f*), shown within a different set of branches (a cupule), the truss appears to have melded and become shorter. At the rim of the new design an eddy formed a sink for airborne pollen. Modern ovules resemble the inner part of figure *f;* the egg chamber is encased by tissue known as the integument.

Ovule-bearing plants first appeared some 350 million years ago. Although no one is certain of their pollination method, there is a good chance that they depended on the wind. Working under this assumption, my group made life-size models of fossil ovules, put them in our wind tunnel and released various types of pollen around them. A simple conclusion emerged: Among the many ovule shapes in the history of seed plants, the ones that resulted in the most efficient trapping of pollen from the wind were those most similar to the shapes of modern ovules. Nature seems to have culled the least efficient structures.

One such inefficient ovule (or, more properly, ovule precursor) consisted of a short, central egg chamber surrounded by a truss, or ring, of branchlike protrusions; pollen grains reached the egg by falling into a hole at the tip of the chamber. In our studies the protrusions acted like a snow fence, slowing the airflow, but they generated little turbulence over the hole. As a result much of the pollen fell onto the outside of the central body, missing the entryway. In contrast, the egg chambers of modern ovules are encased not by branches but by a continuous layer of tissue known as the integument, which is open only at the rim (the micropyle). In many plants with naked ovules, air that strikes the integument is channeled toward the micropyle and into an eddy above it. This turbulence forms a reservoir for pollen grains, many of which drop into the ovule.

The fossil record suggests that the integument is a reduced and melded form of the ancient protrusions, and our findings indicate that the need to improve pollen capture influenced the alteration. It may well be that plants with the most streamlined ovules were favored by natural selection because they had a higher probability of being pollinated successfully and hence of producing a high yield of seeds that could grow into new plants.

Regardless of the selective forces responsible, it is clear that many wind-pollinated plants leave as little as possible to chance. Botanists have long known that some species exude sticky droplets or extend tentaclelike outgrowths to trap pollen. Most wind-pollinated plants also grow in stands, or clusters, thereby limiting the distance that pollen must travel. Now my colleagues and I have discovered that certain plant species also employ an additional stratagem: by channeling the local airflow, they harness the wind for reproduction.