Jerry M. Davis and Charles E. Main
North Carolina State University, Raleigh

Applying Atmospheric Trajector to Problems in Epidemiology

Plant pathologists are using the principles of atmospheric physics to explain many of the complex biological processes associated with long-range inoculum transport in disease outbreaks and subsequent epidemics. This article focuses on the use of computer-generated atmospheric trajectory analyses to help identify potential inoculum source regions and to trace in time and space the probable movement of inoculum-laden air parcels.

Several recent papers (3,5,6) have examined the long-range atmospheric transport of *Peronospora tabacina* Adam sporangiospores in an attempt to explain the spatial and temporal aspects of tobacco blue mold epidemics. Our experience over the past 5 years with analyses of the 1980–1982 blue mold epidemics has convinced us that the U.S. Air Resources Laboratories Atmospheric Transport and Dispersion (ATAD) model (7) and an improved version known as the Branching Atmospheric Trajectory (BAT) model (8) have the potential to identify inoculum source areas and to predict the future course of epidemics of this disease. Both models are adaptable to interactive computer use and can be used in a real-time forecasting mode.

Tobacco Blue Mold

Tobacco blue mold (Fig. 1) is an ideal pathosystem to use in a case study of long-distance transport. The disease is a polycyclic downy mildew restricted to cultivated tobacco (*Nicotiana tabacum* L.) and certain other *Nicotiana* spp. (9). The pathogen overwinters in the winter-grown tobacco areas of the Caribbean and Latin America as well as on wild *N. repanda* Willd. populations in south central Texas (12). Each growing season, air parcels laden with asexual sporangiospores of *P. tabacina* are carried northward along a "blue mold pathway" to Canada. Although commercial tobacco is widely planted across the pathway, plantings are highly concentrated in certain agricultural regions within the eastern United States. Since 1930, when *P. tabacina* was first introduced into the United States, the disease was largely restricted to localized epidemics in tobacco plant beds during wet, cool spring months. The pathogen was very sensitive to temperatures ≥30 C and only occasionally and sporadically spread to field-grown tobacco (9,10).

The blue mold situation changed dramatically in the summer of 1979 when the disease occurred as a general field epidemic throughout the entire tobacco-growing area from the Caribbean to Canada (9). The disease persisted in the field throughout the hot summer growing season, resulting in an estimated $250 million loss (10,11). Renewed and urgent research on blue mold, from both economic and scientific viewpoints, led us to examine long-distance inoculum transport as an important component of the epidemiology and control of this now recurring, apparently temperature-tolerant pathogen.

We have used North Carolina (1980) and Kentucky (1981 and 1982) blue mold documentation and interpretations (11) to show how atmospheric trajectory analysis provides a much needed and valuable tool for understanding spore transport, which occurs primarily, though not exclusively, in the atmospheric boundary layer.

Atmospheric Boundary Layer

The atmospheric boundary layer (ABL) is the lowest part of the atmosphere in contact with the biosphere. The ABL forms as a result of the interactions between the underlying land surface and the atmosphere over time scales of a day or less (1). This layer, which can be thought of as a transition zone between conditions existing at the earth's surface and those existing outside the ABL, undergoes major diurnal structural changes. Within the ABL, energy is transferred from the surface to

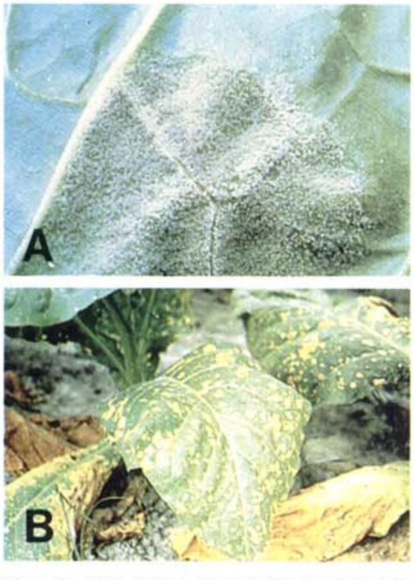

Fig. 1. (A) Blue mold (*Peronospora tabacina*) lesion on a tobacco leaf and (B) tobacco plant severely infected with blue mold.

Paper No. 10194 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh 27695-7601. The use of trade names in this publication does not imply endorsement by the North Carolina Agricultural Research Service of the products named or criticism of similar ones not mentioned.

nalysis

the atmosphere and vice versa in the form of momentum, heat, and water vapor. It is within this layer that virtually all human and biological activities take place.

In the atmosphere, the boundary layer is almost always turbulent. Turbulence is generated by both mechanical and buoyancy forces. Buoyancy-generated turbulence results from the surface absorption of a portion of the incident solar radiation that warms the surface relative to the overlying air, yielding an unstably stratified ABL. The convective circulation patterns (plumes, thermals, dust devils, convection cells, etc.) that result from the surface-air temperature difference are responsible for the transfer of heat and other quantities from the surface to the atmosphere (1). When the atmosphere is neutrally stratified, only mechanical turbulence is produced, because of wind shear in the ABL. The turbulent convection that occurs is referred to as forced convection. Free convection occurs in an unstable atmosphere when the mechanical production is relatively small and buoyancy production is the main source of turbulence. In the daytime unstable atmosphere, both sources of production are usually important, with forced convection dominating near the surface, provided airflow is sufficient. The importance of free convection increases as one moves away from the surface. At night under inversion or stable conditions, mechanically generated turbulence is considerably weakened and is sometimes suppressed altogether by negative buoyancy forces in a stably stratified atmosphere. Decreased turbulence results in the uncoupling of atmospheric processes at the surface from those aloft. The net effect can be large directional and speed shears in the horizontal wind with increasing height.

Unstable stratification refers to the situation in which the temperature within a vertically displaced parcel of air is greater than that in the surrounding air, resulting in upward acceleration of the parcel because of its lower density. The eventual mixing of the parcel with the surrounding air results in vertical transfer of heat. In a neutral atmosphere, a vertically displaced parcel remains at the same temperature and, therefore, the same density as the surroundings. In a stable atmosphere, a parcel displaced upward tends to return to its original position, since it is cooler and, therefore, denser than the surrounding air.

There is a large diurnal variation in the thickness of the ABL. During daytime unstable and convective conditions, the boundary layer usually extends up to the base of the lowest temperature inversion, which is about 1–2 km above ground level. Nighttime is characterized by a surface-based inversion caused by the rapid cooling of the ground through the efficient emission of infrared radiation. If nocturnal winds are strong, mechanical turbulence is generated and heat is lost to the ground by turbulent mixing throughout the boundary layer. On clear nights when the winds are weak, only the bottom portion of the inversion layer may be turbulent. The top of the ground-based inversion is typically about 300–400 m above ground level late at night and early in the morning. This inversion plays an important role in spore transport. Spores emitted into the daytime ABL are soon mixed throughout the lower atmosphere. As night approaches, the stable ABL becomes established and a ground-based inversion begins to develop. The inversion insulates the main body of spores, which remains above the inversion, from the effect of ground absorption through dry deposition. Turbulence in the layer above the inversion gradually decays, since the energy sources needed to maintain it are no longer available (4,13).

The dispersion of material such as spores released into the lower atmosphere depends on atmospheric mixing processes that occur at various temporal and spatial scales. Mixing depends mainly on the turbulence generated in the ABL. Distribution of material released into the atmosphere is usually quite patchy and changes constantly because of the complex and highly variable nature of atmospheric turbulence.

Pasquill and Smith (14) provide guidelines on the progression of dispersion based on different time scales for a near-surface release of material. In the first minutes after release, a spore cloud has traveled hundreds of meters and has grown both vertically and horizontally within the boundary layer under the action of small-scale dispersive eddies.

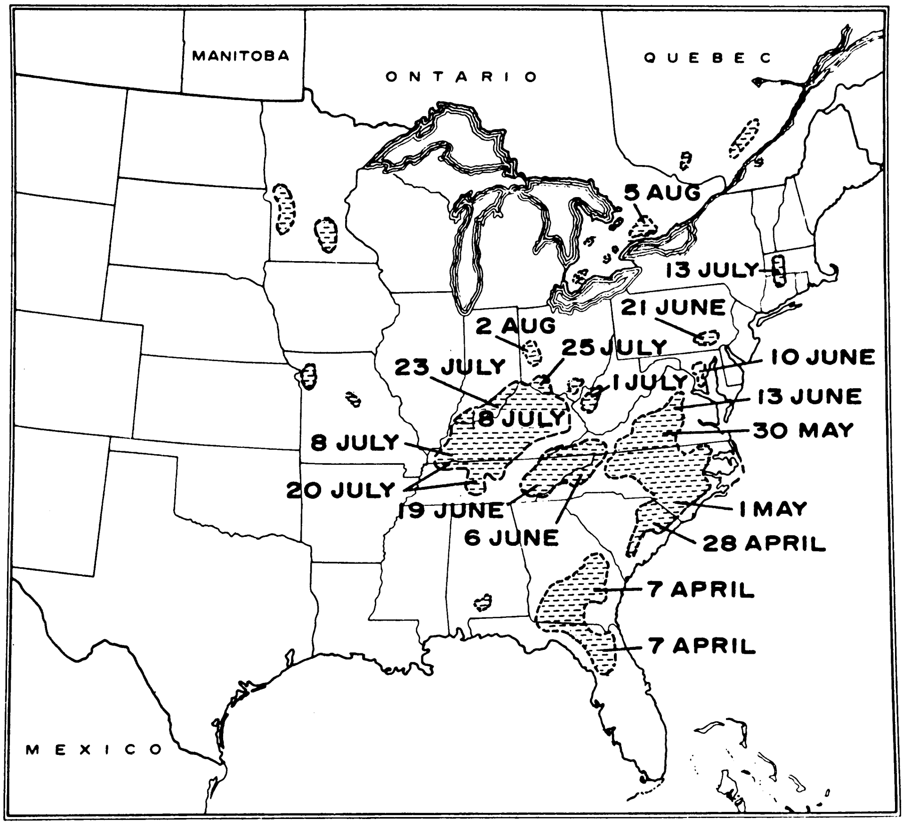

Fig. 2. Tobacco production areas and dates of the first report of blue mold in the eastern United States and Canada for 1980. (Reprinted with permission from: Davis, J. M., and Main, C. E. 1984. A regional analysis of the meteorologic aspects of the spread and development of blue mold on tobacco. Boundary-Layer Meteorology Vol. 28, p. 287. Copyright © 1984 by D. Reidel Publishing Company, Dordrecht, Holland.)

Modeling Long-range Transport: The Trajectory Analysis Models

The Atmospheric Transport and Dispersion (ATAD) model calculates trajectories using a data base containing upper-air winds, temperature, and heights obtained from atmospheric sounding stations in North America. Four trajectories are calculated per 24 hours, at 0000, 0600, 1200, and 1800 hours Greenwich mean time. A trajectory is made up of a series of 40 3-hour segments, yielding a total duration time of 5 days. The calculated trajectories can move either forward or backward in time. Each trajectory segment calculation is based on an average wind in a transport layer, the depth of which is determined by the model. Dispersion calculations are made only on the forward trajectories. In addition to the meteorologic input data, the model requires the user to select a set of parameter values (e.g., start time and location) that describe a particular run.

To find the transport layer depth (which is essentially the mixing depth), the model employs procedures that depend on whether the trajectory begins during the day or at night. The day procedure centers around the search for the lowest critical inversion, which is one means of delineating the top of the atmospheric boundary layer (ABL). The critical inversion must meet certain criteria with regard to strength. If no critical inversion is present, the transport layer depth is assumed to be 3,000 m. For trajectories that begin at night, the transport layer depth is taken to be twice the standard deviation of the vertical Gaussian pollutant distribution. The model applies this technique throughout the night, then the daytime method for the remainder of the trajectory.

The Branching Atmospheric Trajectory (BAT) model, a revised version of the ATAD model, addresses the problems related to modeling the diurnal structural changes in the ABL encountered in the ATAD model. The BAT model trajectory branches at the day/night transition and branches and mixes at the night/day transition. The model approaches trajectory branching by dividing the lower troposphere into three layers, based on whether it is night or day and on the vertical temperature profile at each atmospheric sounding station. The first layer, the surface layer, exists only at night and is assumed to have a constant height of 300 m above the surface. The second layer, the boundary layer, extends from the top of the surface layer at night or from the surface during the day to a height determined by the same critical inversion criteria used in the ATAD model. The third layer, the upper layer, extends upward from the critical inversion to a fixed height of 3,000 m. When no critical inversion exists, the boundary layer height is assumed to be 3,000 m, and no upper layer is defined.

The ATAD model makes dispersion and deposition calculations that lead to time-averaged surface-air concentrations of the pollutant and deposition amounts. The BAT model makes only dispersion calculations. Application to the release of *P. tabacina* sporangiospores requires that we consider the transport of a puff of material released instantaneously into the atmosphere. This approach is appropriate when anticipated puff travel time is long compared with release time.

After several hours, the cloud has traveled tens of kilometers and has reached the top of the boundary layer and continues to be spread laterally by mesoscale eddies. Over several days, during which the spore cloud has traveled hundreds or even thousands of kilometers, escape of spores from the boundary layer is possible and synoptic-scale (i.e., weather-map-scale) dispersive eddies become important.

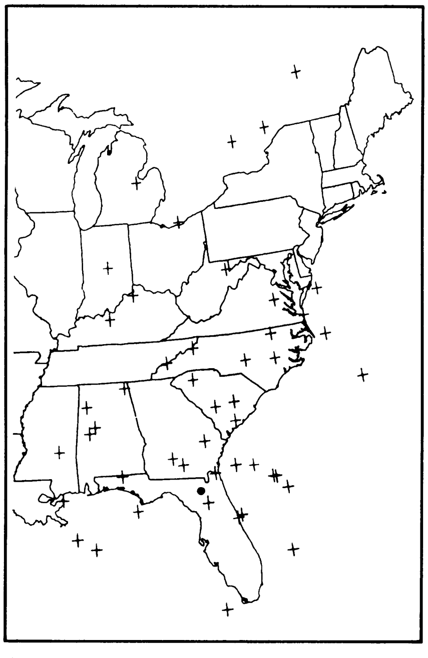

Fig. 3. ATAD model calculation of air parcel positions (+) 48 hours after leaving north Florida at 1300 EST on each day during April, May, and June 1980.

In arriving at this description of dispersion, no allowance has been made for strong stabilization of the lower atmospheric layers during nighttime. The described dispersive processes will cause dilution, whereas dry deposition (sedimentation and impaction on the underlying surface) and precipitation scavenging (rain-out [uptake in cloud droplets] or wash-out [uptake into precipitation as it falls through the mixed layer below the cloud]) will result in spore depletion. After the spore-containing air parcel has traveled some distance, impaction processes may have depleted the bottom part of the parcel, leaving greater spore concentrations at higher altitudes. If the spore-laden air parcel passes over fields where the disease is active and spores are being produced, uptake of spores into the passing air parcel is possible. If no such replenishment occurs, spores at higher altitudes can be brought to the surface by precipitation scavenging.

Trajectory Analysis

A trajectory is a curve in space tracing the positions successively occupied by a moving air parcel—in the present case, a spore cloud. An example of how a trajectory is constructed can be found in the standard text on meteorologic analysis by Saucier (15). When trajectories are constructed for the movement of spores, two sources of error are common: the analysis of the windfield data and the timing of the movement of the spores. Uncertainties in windfield analysis arise because of the sparseness of data in both the horizontal and the vertical direction, unrepresentativeness of some individual observations, and the sampling time.

In timing of spore movement, a typical scenario for an initial outbreak of blue mold might be as follows: The sporangiospores arrive at the leaf surface, after which spore germination, germ tube development, and penetration occur within 2–48 hours under favorable weather conditions. The incubation period under ideal conditions can be as short as 4 days but typically is closer to 5–7 days. The appearance of yellow lesions serves as the point in time when the disease is first detectable.

Ideally, a surveillance team could detect the first blue mold outbreak in a state or region by observing primary lesions on plants in well-defined initial foci. Backward trajectories could then be calculated using a reasonable estimate of the date and location of the outbreak. In practice, however, several problems arise. As stated, the incubation period can vary owing to microenvironment. Depending on the type of spore cloud and deposition pattern (16), i.e., small and localized vs. broad-scale, uniform, and dense, the probability of early detection of blue mold might be quite different. In the case of localized deposition of a few spores, blue mold in an initial small focus might need to go through two or three secondary disease cycles before damage is readily observable; hence, primary, secondary, and perhaps tertiary lesions would all be present at the time the surveillance team arrives. Fixing a time of inoculum arrival under these circumstances would be tentative at best. In practice, spore arrival dates are usually estimated as a "window in time" during which the movement of synoptic-scale weather systems can lead to large variations in the path an air parcel will take. Consequently, we routinely calculate a family of backward trajectories that should encompass in time the estimated arrival date.

This backward trajectory analysis thus becomes a valuable tool for identifying inoculum source regions. Once a region has been identified, forward trajectories can be calculated. Forward trajectories serve three purposes. First, they confirm the evidence provided by the backward trajectories by showing that, for a specific spore release time, the spore-laden air parcel will have passed over the outbreak site. Second, model dispersion calculations are made only on forward trajectories. And third, forward trajectories indicate the path of the air parcel after it has moved beyond the outbreak site, thus identifying other potential outbreak locations.

Given that fields with actively sporulating lesions have been identified, the calculation of forward trajectories requires certain biological information on spore release times and duration. *P. tabacina* sporangiospores are typically released between 0800 and 1500 EST, with the peak between 1000 and 1300 EST. Aylor and Taylor (2) estimate that $0.14\text{–}1.4 \times 10^{11}$ spores can be released into

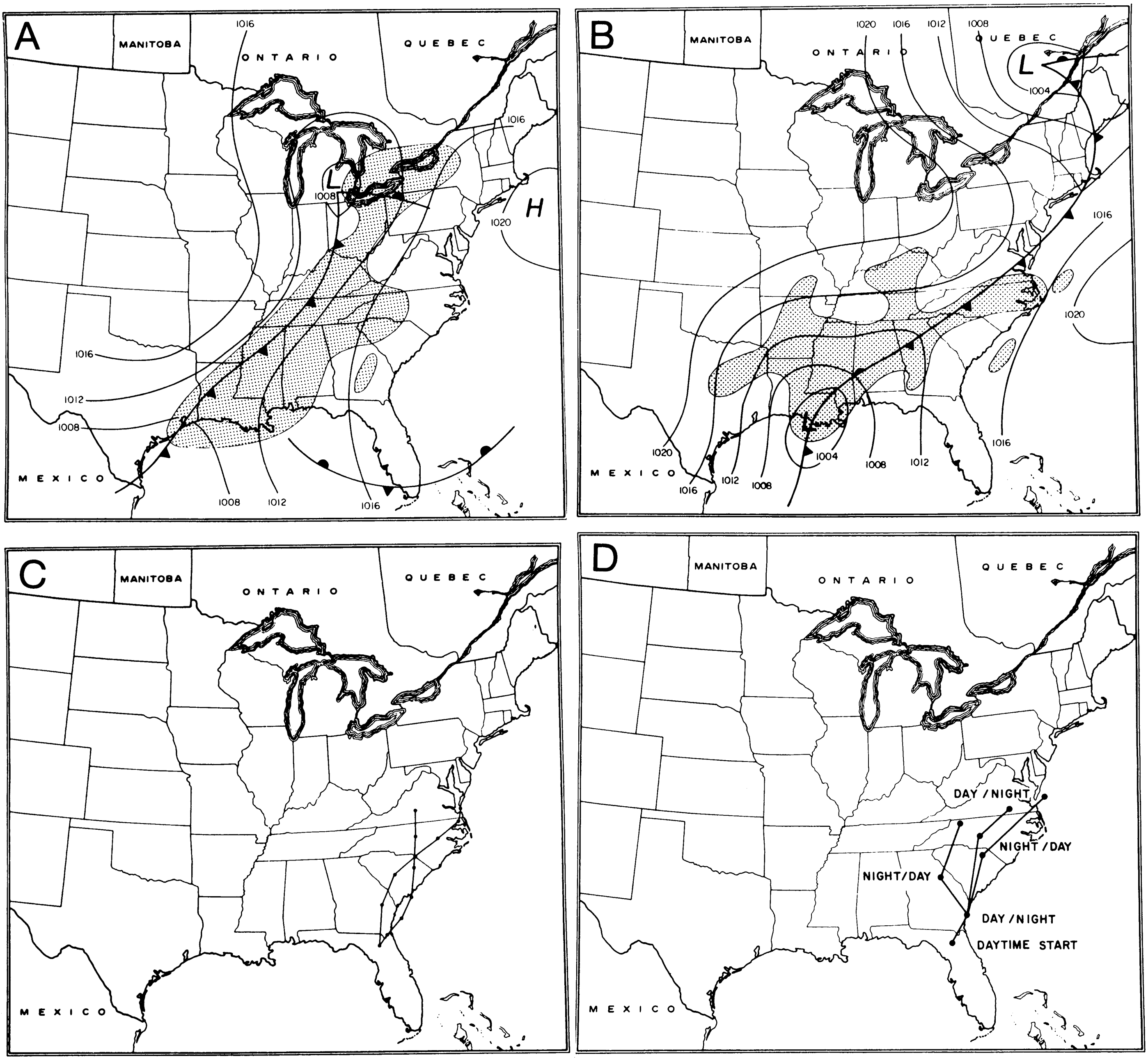

Fig. 4. North Carolina trajectory event, 1980. (A) Surface weather map, 0700 EST, 12 April. (B) Surface weather map, 0700 EST, 13 April. (C) The ATAD model trajectory over Georgia leaves the source at 0700 EST and the trajectory passing over water leaves the source at 1300 EST, 12 April. (D) BAT model trajectory leaves the source at 1000 EST, 12 April. (A, B, and C reprinted with permission from: Davis, J. M., and Main, C. E. 1984. A regional analysis of the meteorologic aspects of the spread and development of blue mold on tobacco. Boundary-Layer Meteorology Vol. 28, pp. 288-289. Copyright © 1984 by D. Reidel Publishing Company, Dordrecht, Holland.)

the air from 100 ha of severely infected tobacco during a 2-hour period. Spore liberation requires a rise in temperature, a decrease in relative humidity (which for a constant vapor pressure must, by definition, occur with a rise in temperature), and an increase in insolation.

The successful movement of inoculum and spread of an epidemic have both meteorologic and biological components. Of the many hundreds of trajectories possible, only those of sufficient duration and appropriate orientation need be considered. To aid in selecting the most likely spore-transporting air parcels, a set of guidelines has been developed so that only those forward trajectories are considered where:

1. Sporulation at the point of origin of the forward trajectory is either very highly probable or confirmed;
2. Weather conditions along the transport route are conducive to maintaining spore viability and the chances of precipitation scavenging are not limiting;
3. The spores arrive at a location with substantial numbers of host fields and susceptible plants;
4. Weather conditions in the target area are favorable for spore deposition, germination, and infection; and
5. The spores arrive at the proper time, i.e., one or two latent periods before the first occurrence of the disease.

Evidence for Long-range Transport of *P. tabacina*

Our examination of blue mold covers the 1980 epidemic in North Carolina and the 1981 and 1982 epidemics in west central Kentucky. We selected these cases because of the contrasts they present. North Carolina tobacco fields are part of the contiguous tobacco region extending from Florida to Virginia. Thus, during the 1980 epidemic, tobacco fields to the south were capable of providing abundant inoculum of *P. tabacina* for North Carolina fields. Windborne spores could have arrived in North Carolina from South Carolina, Georgia, or Florida or from all three, implying both short- and long-range transport. Given the first occurrence date (1 May) for blue mold in southeastern North Carolina, only infected fields to the south could have served as inoculum sources. The synoptic weather patterns that facilitate south-to-north transport occur frequently in the eastern United States during the time of the year when blue mold is most active. In addition, because fungicides for blue mold control were not yet in widespread use in 1980, growers and extension agents closely monitored tobacco fields for the disease. For this reason, the reported first occurrence dates and the actual first occurrence dates are thought to be nearly coincidental. The trajectories presented for this case provide a highly probable scenario for south-to-north spore transport along the East Coast in 1980.

The Kentucky situation is not as clear-cut. The first reports of blue mold in Kentucky in early July 1981 and in mid-June 1982 came from the unlikely west central region of the state. Pathologists usually expect blue mold to occur first in southeastern Kentucky because of its proximity to the major tobacco production areas in western North Carolina and eastern Tennessee. First occurrence in west central Kentucky implies a different inoculum source region. Short-range transport to west central Kentucky from infected tobacco fields in central Tennessee was ruled out in both years because blue mold appeared in Kentucky either first or at the same time as in Tennessee. Pathologists speculated that the inoculum originated to the southwest. Tobacco distribution maps show no significant production areas in those regions, but perique tobacco is grown in Louisiana and populations of wild tobacco (*N. repanda*) flourish just south of the Edwards plateau in south central Texas. Whether the hectarage of tobacco infected with blue mold is sufficient, on the average, in these areas to serve as inoculum sources for blue mold in Kentucky is largely speculative.

An examination of the weather records in the Texas source region (6) showed that sporulation in 1981 and 1982 occurred even though temperatures were much higher than the upper end of the temperature range proposed for sporulation by Lucas (9).

Evidence to support the Texas inoculum source comes from Nesmith and Jones (12), who reported a pathogen causing downy mildew on *N. repanda* in Texas and who successfully transmitted the disease to cultivated tobacco. The lesions and asexual fructification that occurred on the inoculated plants were indistinguishable from common blue mold caused by *P. tabacina*.

The North Carolina trajectories. Figure 2 shows the first occurrence dates of blue mold by counties in the eastern United States in 1980. We will focus our attention on the 1 May first occurrence in southeastern North Carolina. Backward trajectories were calculated for a segment of time containing, to the best of our knowledge, the actual spore arrival date. These calculations indicated that the inoculum source was located to the south.

Given that the first occurrence of blue mold was reported in early April in north Florida/south Georgia and that the backward trajectories from North Carolina had identified this area as a potential inoculum source region, we wanted to know in what direction a parcel of air originating in this region would travel. To answer this question, we examined a large number of trajectories leaving this source region.

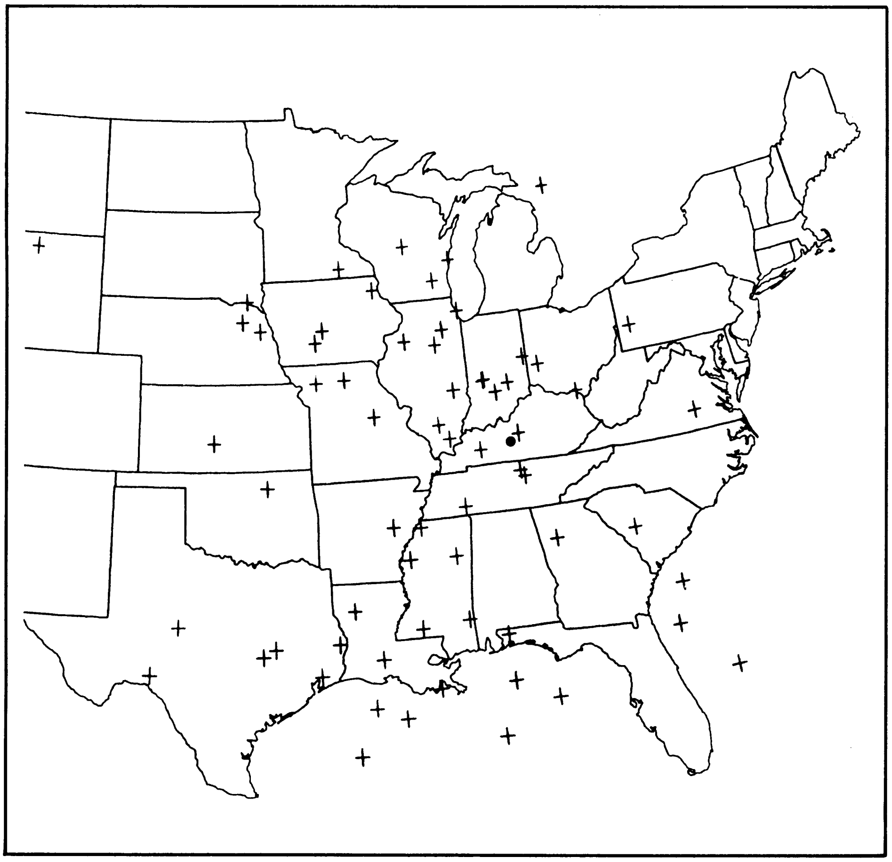

Fig. 5. ATAD model calculation of air parcel positions (+) 48 hours *before* arriving in west central Kentucky at 1800 CST on each day during 1 April–19 June 1982.

Figure 3 shows the 48-hour positions of air parcels originating in north Florida at 1300 EST for each day in April, May, and June 1980. Trajectory locations could not be plotted for days with missing data or when the locations were beyond the map boundaries. During these 3 months, air parcels leaving north Florida traveled in many directions. Many of the parcels were positioned over North Carolina at the end of the 48 hours, and many of those to the north had passed over North Carolina on the way to their 48-hour positions.

We believe that the 1 May first occurrence of blue mold in southeastern North Carolina was caused by spores that arrived from the south in mid-April. Figure 4 shows trajectories calculated for this period of time using BAT and ATAD models. Synoptic conditions favorable for spore transport occurred again from 24 to 27 April. When allowance is made for the disease incubation period and the difference in time between reported and actual first occurrence dates, however, these spores probably arrived too late to initiate the 1 May occurrence. Both the synoptic situation and the trajectories for this late April case were similar to the mid-April transport events. For the ATAD trajectories, air parcel departure times of 0700 and 1300 EST were selected, since parcels leaving at these times have a high probability of containing a large number of spores (2). Each trajectory segment represents a 6-hour travel time. A BAT model trajectory leaving north Florida at 1000 EST on 12 April (Fig. 4D) is shown for a time midway between the ATAD trajectories. The rather dramatic branching that occurs at the first day/night interface indicates the presence of vertical directional and speed shears in the horizontal winds. It is this branching property that makes the BAT model assessment of transport so useful. Spores in the lowest atmospheric layer moved into central Georgia during the night, while those in the two layers above moved

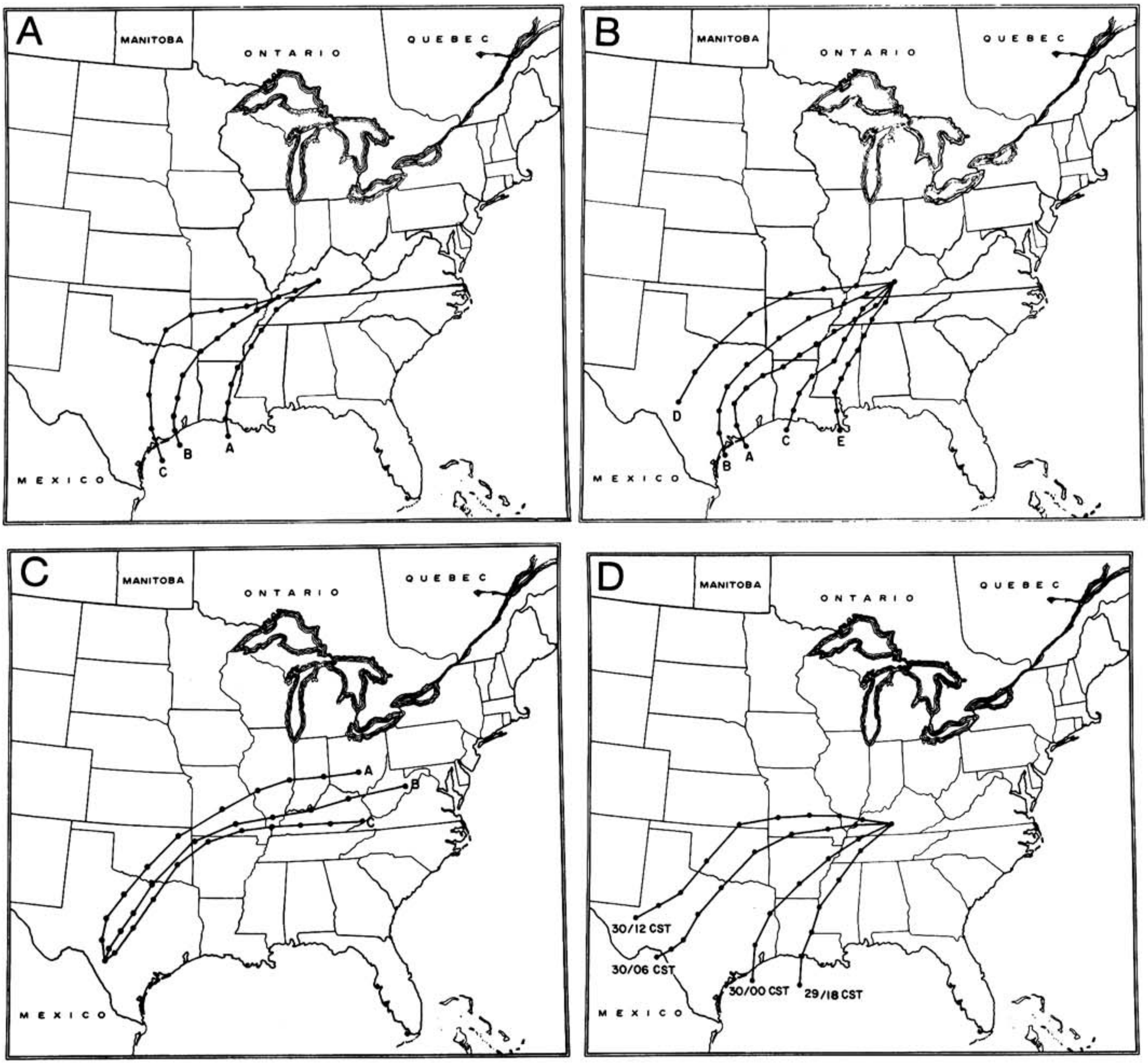

Fig. 6. Kentucky ATAD model trajectories for May 1982. (A) Backward trajectories for 20–22 May; A = 20 May, B = 21 May, C = 22 May. (B) Backward trajectories for 27–31 May; A = 27 May, B = 28 May, C = 29 May, D = 30 May, E = 31 May. (C) Forward trajectories for 27–28 May; A = 1800 CST 27 May, B = 0000 CST 28 May, and C = 0600 CST 28 May. (D) Diurnal variation in trajectory position for 29–30 May. (A and B reprinted with permission from: Davis, J. M., Main, C. E., and Nesmith, W. C. 1985. The biometeorology of blue mold of tobacco. Part II: The evidence for long-range sporangiospore transport. Pages 471-496 in: Movement and Dispersal of Agriculturally Important Biotic Agents. D. R. MacKenzie, C. Barfield, T. G. Kennedy, and R. D. Berger, eds. Claitor's Publishing Company, Baton Rouge, LA.)

north toward North Carolina. Figures 4A and 4B show the basic synoptic weather features at the time of transport. The winds in advance of the frontal system were from the south. The stipled areas on the synoptic charts are composite radar summaries for the time closest to the map time. The presence of showers in the transport area would have meant that precipitation scavenging of some of the spores during transport was a strong possibility. Spores lost from the air parcel on its northward trip because of dry deposition and precipitation scavenging could have been replenished as the parcel passed over other sporulating fields.

When blue mold inoculum arrived in mid-April in southeastern North Carolina, 5–15% of the acreage had been transplanted. By 5 May, planted acreage had risen to 59%. Occurrence of the disease was not widespread at this time—a fact we attributed to the lack of moisture and the absence of host plants (5). The resurgence of the disease later in May resulted from increased supplies of both moisture and host plants. At no time did we find temperatures to be a limiting factor in the spread of blue mold.

The Kentucky trajectories for 1982. Reported first occurrences of blue mold in west central Kentucky in 1982 were in mid-June (15 June). Figure 5 shows parcel positions 48 hours *before* arrival in west central Kentucky at 1800 CST on each day during 1 April–19 June. Air parcels arrived from virtually every direction, including many from areas where tobacco is grown.

What this case presents is a detective problem: Given what we know about the occurrence of blue mold in 1982, where did the spores come from? To complicate matters, our knowledge of the time difference between actual first occurrence and reported first occurrence is not as firm as it was in the North Carolina case. On the basis of the presence of three generations of lesions when the disease was detected in 1982, Kentucky pathologists estimated that the spores arrived about 3 weeks before the reported first occurrence date. Figures 6A and 6B show backward trajectories for two time periods (20–22 May and 27–31 May) that would come close to meeting our criteria for spore arrival dates. Spores following these trajectories would have arrived in west central Kentucky at 0600 CST on the date indicated. The source regions designated seem to support the hypothesis that inoculum came from the southwest. Travel times back to the indicated source regions would require about 2 days. Figure 6C shows forward trajectories from south central Texas for the period from 1800 CST on 27 May to 0600 CST on 28 May. Given the release time of the spores, the air parcel departing at 0600 CST would appear to have the highest probability of being spore-laden. The spore content of the parcels departing at 1800 and 0000 CST would depend on the fate of spores released after sunrise on 27 May. The travel time from Texas was about 2 days. As in the North Carolina case, precipitation scavenging and dry deposition along the route could have depleted the air parcel of some spores with little or no possiblility of replenishment, since the parcel was not likely to have passed over other infected fields.

Jerry M. Davis **Charles E. Main**

Dr. Davis is professor of meteorology and plant pathology at North Carolina State University. He received his B.S. degree in applied mathematics from North Carolina State University, his M.S. degree in meteorology from the University of Michigan, and his Ph.D. degree in climatology/meteorology from The Ohio State University. Since 1973 he has been an active researcher in agricultural meteorology, concentrating on the relationship between the environment and plant diseases. For the past 5 years his research has focused on the effects of temperature, moisture, and long-range spore transport on the occurrence of blue mold on tobacco.

Dr. Main is a professor in the Department of Plant Pathology at North Carolina State University in Raleigh. He received his B.Sc. and M.Sc. degrees at West Virginia University and his Ph.D. degree in plant pathology and plant physiology from the University of Wisconsin. For the past 15 years he has focused his research on tobacco diseases and his teaching toward epidemiology and crop loss assessment. Since 1981 he has served as coordinator of the North Carolina research program on tobacco blue mold, involving studies in epidemiology, biology of the pathogen, development and testing of resistant germ plasm, disease control, and impact assessment.

Figure 6D shows the diurnal variation in the backward trajectories for 29–30 May. The labels at the end of each trajectory show the date and time the air parcel arrived in west central Kentucky. Thus, the air parcel that arrived at 0600 CST on 30 May followed a different route than the parcel that arrived at 1200 the same day. The backward trajectory labeled 30/06 CST in Figure 6D coincides with the backward trajectory labeled D in Figure 6B. By 0600 CST on 31 May, the air parcel route had returned to the more southerly orientation shown by the trajectory labeled E. These dramatic shifts in trajectories caused by the movement of synoptic-scale weather systems are quite common and make the identification of potential inoculum source regions more challenging.

The trajectories in Figure 6C illustrate another interesting aspect of the Kentucky case. Although the trajectories traversed the entire state, the disease occurred initially only in west central Kentucky. If one assumes that spores were deposited over a wide area, the observed disease pattern could have been caused by the lack of spatial homogeneity in favorable weather conditions, fungicide application, presence and susceptibility of host plants, or a combination of several of these factors. If plants were uniformly susceptible over a wide area, the observed patterns could have been the result of localized spore deposition caused by precipitation scavenging.

Conclusion

Our work demonstrates the usefulness of trajectory analysis in identifying potential inoculum source regions for large-scale plant disease epidemics. Such analysis must proceed with caution because of problems inherent in the basic calculation procedures and because of problems associated with ascertaining spore arrival dates. The latter become clear in the Kentucky case, where serious errors in the assumptions we used to estimate spore arrival times could mean the trajectories we calculated would not apply. The trajectory evidence for Kentucky indicates that the spores came from the southwest. A whole new set of questions now needs to be answered. How large is the population of *N. repanda* in south central Texas? What is the sporulation rate of the pathogen? On the basis of the answers to these questions, how realistic is it to consider Texas as an important source region? How often in the past has this area served as a source region, and what should we expect in the future? Can the sporangiospores of *P. tabacina* survive in a possibly hostile radiation environment during what is potentially a long trip? In the North Carolina case, there is little doubt that the state was showered with spores in the spring of 1980. When this fact was coupled with an abundant supply of susceptible hosts plants and favorable environmental conditions, all the ingredients were on hand for an explosive epidemic.

Acknowledgments

We thank W. C. Nesmith, extension plant pathologist at the University of Kentucky, for the data and interpretation pertaining to the blue mold occurrences in Kentucky during 1981 and 1982. We also thank John Clark, meteorologist with the Environmental Protection Agency at Research Triangle Park, North Carolina, for initial assistance and suggestions in using the ATAD model, and Kim McDonough and David Epperson for running the trajectory analyses and producing the computer graphics. Support for these studies was provided by R. J. Reynolds, Inc., the North Carolina Tobacco Foundation, and the National Crop Loss Design Committee, USDA-CSRS.

Literature Cited

1. Arya, S. P. 1982. Atmospheric boundary layers over homogeneous terrain. Pages 233-267 in: Engineering Meteorology. E. Plate, ed. Elsevier Scientific Publishing Company, Amsterdam. 740 pp.
2. Aylor, D. E., and Taylor, G. S. 1983. Escape of *Peronospora tabacina* spores from a field of diseased tobacco plants. Phytopathology 73:525-529.
3. Aylor, D. E., Taylor, G. S., and Raynor, G. S. 1982. Long-range transport of tobacco blue mold spores. Agric. Meteorol. 27:217-232.
4. Businger, J. A. 1984. Equations and concepts. Pages 1-36 in: Atmospheric Turbulence and Air Pollution Modeling. F. T. M. Nieuwstadt and H. van Dop, eds. D. Reidel Publishing Company, Dordrecht, Holland. 358 pp.
5. Davis, J. M., and Main, C. E. 1984. A regional analysis of the meteorological aspects of the spread and development of blue mold on tobacco. Boundary-Layer Meteorol. 28:271-304.
6. Davis, J. M., Main, C. E., and Nesmith, W. C. 1985. The biometeorology of blue mold of tobacco. Part II: The evidence for long-range sporangiospore transport. Pages 471-496 in: Movement and Dispersal of Agriculturally Important Biotic Agents. D. R. MacKenzie, C. Barfield, T. G. Kennedy, and R. D. Berger, eds. Claitor's Publishing Company, Baton Rouge, LA.
7. Heffter, J. L. 1980. Air Resources Laboratories Atmospheric Transport and Dispersion model (ARL-ATAD). NOAA Tech. Memo. ERL-ARL-81. National Oceanic & Atmospheric Administration, Silver Spring, MD. 17 pp.
8. Heffter, J. L. 1983. Branching Atmospheric Trajectory (BAT) model. NOAA Tech. Memo. ERL-ARL-121. National Oceanic & Atmospheric Administration, Silver Spring, MD. 16 pp.
9. Lucas, G. B. 1980. The war against blue mold. Science 210:147-153.
10. Main, C. E., Davis, J. M., and Moss, M. A. 1985. The biometeorology of blue mold of tobacco. Part I: A case study in the epidemiology of the disease. Pages 451-469 in: Movement and Dispersal of Agriculturally Important Biotic Agents. D. R. MacKenzie, C. Barfield, T. G. Kennedy, and R. D. Berger, eds. Claitor's Publishing Company, Baton Rouge, LA.
11. Nesmith, W. C. 1984. The North American blue mold warning system. Plant Dis. 68:933-936.
12. Nesmith, W. C., and Jones, R. 1984. The downy mildew of *Nicotiana repanda*, a pathogen of burley tobacco. (Abstr.) Phytopathology 74:631.
13. Panofsky, H. A., and Dulton, J. A. 1984. Atmospheric Turbulence. John Wiley & Sons, New York. 397 pp.
14. Pasquill, F., and Smith, F. B. 1983. Atmospheric Diffusion. Ellis Horwood Limited, Chichester, England. 437 pp.
15. Saucier, W. J. 1955. Principles of Meteorological Analysis. University of Chicago Press, Chicago. 438 pp.
16. Zadoks, J. C., and Schein, R. D. 1979. Epidemiology and Plant Disease Management. Oxford University Press, New York. 427 pp.