Principles of the Atmospheric Pathway for Invasive Species Applied to Soybean Rust

SCOTT A. ISARD, STUART H. GAGE, PAUL COMTOIS, AND JOSEPH M. RUSSO

*Aerial transport alone is seldom responsible for the introduction of nonindigenous species into distant regions; however, the capacity to use the atmospheric pathway for rapid spread in large part determines the invasive potential of organisms once they are introduced. Because physical and biological features of Earth's surface influence the routes and timing of organisms that use the atmospheric pathway, long-distance movement of aerobiota is largely regular and thus predictable. Soybean rust (*Phakopsora pachyrhizi*), potentially the most destructive foliar disease of soybean, recently invaded North America. The concepts presented in this article form the basis of the soybean rust aerobiology prediction system (SRAPS) that was developed to assess potential pathogen movement from South America to the United States. Output from SRAPS guided the scouting operations after the initial discovery of soybean rust in Louisiana. Subsequent observations of *P. pachyrhizi* *in the southeastern United States provide validation of the modeling effort.*

Keywords: invasive species, aerobiology, movement and dispersal, soybean rust, atmospheric transport

Some organisms can move among terrestrial habitats by floating, soaring, or flying in the air. Others float or swim in water. Floating, soaring, flying, or swimming takes much less energy per unit of body mass than crawling, walking, or running on land (Isard and Gage 2001). The atmospheric pathway is a concept whereby organisms utilize dynamic but definable routes created by airflows across landforms on the earth's surface to move among geographic positions. Because many organisms can significantly increase the efficiency of their movement by taking advantage of air currents, it is not surprising that a greater proportion of those organisms that spread rapidly across landscapes use air rather than land surface or water (Dingle 1996).

Pests are species that threaten the performance, survival, and reproduction of plants and animals considered important by humans. They include plants (primarily weeds), animals (especially insects and other arthropods), and microorganisms (e.g., plant and animal viruses, fungi, and bacteria), and may be native or nonindigenous. Invasive species are nonindigenous organisms that proliferate and spread rapidly (Mack et al. 2000). Many nonindigenous species are not invasive, however, and are beneficial to humans; for example, most of the important crops, horticultural plants, and livestock in North America are nonindigenous species that require cultivation or rearing to thrive (NRC 2002). Only a very few nonindigenous species become invasive (Mack and Lonsdale 2001). Nonetheless, the cost of these invasive organisms to the United States is approximately $137 billion per year (Pimentel et al. 2000).

The introduction of nonindigenous species to faraway places by completely natural means is rare; almost all introductions are assisted by human activities (NRC 2002, Ruiz and Carlton 2003). Higher plants and animals now considered invasive were generally imported for pleasure or for economic reasons. Arthropod and pathogen pests often arrive in association with trade commodities (Campbell 2001). Some vertebrates, invertebrates, and fungi have been intentionally released for biological control of pests, and a small number of these have themselves become invasive species (Howarth 1991).

Regardless of the pathway of introduction, invasive species from many taxa influence our daily lives, and the histories of some are legendary. The English sparrow (*Passer domesticus*) and European starling (*Sturnus vulgaris*), for example, were introduced into New York and then quickly spread throughout North America (Shigesada and Kawasaki 1997). Lady beetles have been imported, reared, and released as biological control agents (Obrycki and Kring 1998). For many years these aesthetically pleasing insects were touted as beneficial

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predators; however, now the multicolored Asian lady beetle (*Harmonia axyridis*) has become notorious as a proliferous and noxious household pest (Jones and Boggs 2005). More recently, the Asian longhorned beetle (*Anoplophora glabripennis*) and the emerald ash borer (*Agrilus planipennis*), imported in woody packing material, have resulted in the destruction of thousands of shade trees in the Chicago, Detroit, and New York City metropolitan areas (McCullough and Roberts 2005, USDA FS 2005).

The majority of North Americans would be surprised to learn that the common dandelion (*Taraxacum officinale*), chickweed (*Stellaria media*), and plantains (*Plantago* spp.) were transported to North America as pot herbs (Foy et al. 1983). Perhaps the most demoralizing of all unwitting introductions, however, was that of chestnut blight (*Cryphonectria parasitica*), which arrived on Asiatic chestnuts planted for nut production. This pathogen subsequently devastated the American chestnut (*Castanea dentata*), the most important hardwood tree species in the United States (Smith 2000). Having learned hard lessons from these and many other biotic invasions, the US Department of Agriculture invested many millions of dollars preparing for an invasion of soybean rust (Smith 2005). *Phakopsora pachyrhizi,* an exceptionally aggressive species of soybean rust, has spread rapidly over the past decade, moving from Asia to Africa and then to South America (Miles et al. 2003). During autumn 2004, soybean rust invaded North America.

Although aerial transport alone is seldom responsible for the introduction of nonindigenous species into distant regions, the capability to use the atmospheric pathway for rapid spread in large part determines the invasive potential of organisms once they are introduced. For each organism that moves in the atmosphere, only processes that occur within a specific range of space and time scales result in aerial dispersal. Some biota may only be able to float for a few seconds to neighboring plants, while others may fly for days between regions. The principles that govern atmospheric transport of organisms apply regardless of the duration and distance of movement, however, making knowledge of the atmospheric pathway critical for understanding how invasive species influence biological diversity and ecosystem function (Isard and Gage 2001). From a pest-management perspective, failure to consider the relative probabilities of spread by atmospheric transport compared with alternative pathways (human-mediated dispersal) is likely to lead to inappropriate and inefficient containment and regulatory strategies for invasive species (Aylor 2003).

Introductions of invasive species, an important component of the modern biological landscape, always lead to compensating losses in the diversity of native species (Lonsdale 1999). Clearly, without quantitative theories regarding the impact of nonindigenous organisms on ecosystem diversity and functioning, the capability to predict changes that follow environmental perturbations is limited (NRC 2000).

Understanding the regulation and functional consequences of biological diversity and developing approaches for sustaining ecosystem composition and processes is one of the "grand challenges" in the environmental sciences (NRC 2000). Human habitation of a geographic region generally results in severe degradation of the natural environment, threatening ecosystems and their functioning (NRC 1995). A thorough understanding of the factors that govern movements of organisms through the air, and of associated effects on biological diversity, is required to assess the impacts of human activities on diversity at genotype, species, and ecosystem scales.

Aerobiology is the study of the biological process involving the movement of organisms in the atmosphere from one geographic position to another (Moulton 1942, Gregory 1973). Organisms that utilize air to change locations (aerobiota) range from large birds (e.g., tundra swans) to small spores produced by plant pathogens (e.g., soybean rust). This biotic process is inexorably linked to atmospheric movement systems that facilitate aerobiota transport over space. Benninghoff and Edmonds (1972) recognized the components of the aerobiological process and their functional relationships (figure 1) while working with the International Biological Program. Their model is the starting point for developing a logical framework to understand, predict, and deliver relevant knowledge concerning invasive organisms that use the atmosphere to spread.

Aerobiota proceed in order through each of the five components in the model—preconditioning, takeoff and ascent, horizontal transport, descent and landing, and impact—and in each stage, they are strongly influenced by ecological and environmental processes. Of particular relevance are the multiple temporal scales associated with each of the components, ranging from seconds to years.

The concept of the aerobiological process has been developed into a predictive tool by integrating atmospheric transport models that function at nested spatial scales with phenological models that characterize the processes regulating the growth and development of plant and animal communities (Gage et al. 1999). Atmospheric pathways are tightly coupled to ecosystems that support mobile organisms before, during, and after the organisms' dispersal. Organisms are usually functionally adapted to the ecosystems in which they begin and end their airborne travel, as well as to the habitats where some aerobiota rest temporarily during their migration (Brower 1995). Environmental conditions in source, resting, and receptor areas are typically very different. Many organisms that move long distances in the air also move locally within source and destination ecosystems. This general model of the aerobiological processes was used as the foundation of the integrated aerobiology modeling system (IAMS), built to forecast invasions of important species that use the atmospheric pathway.

Figure 2 shows the essential components of IAMS. It depicts information flows from observation and knowledge systems (e.g., meteorological, biological, and physical) into relational databases. Some of this information, including ecological boundaries, climate, political regions, and species biology, is essentially static, whereas dynamic observations—

measurements of changes in weather, vegetation phenology, and organism abundance, for example—are required in near-real time. This information is used in turn to estimate organism emission from ecosystems, organism transport distances and directions, and receptivity to colonization in potential destination ecosystems.

Model results are deposited in relational databases for linkage with socioeconomic data to assess risk from movement. A decision support system assesses field observations, model results, and information on ecosystem susceptibility and socioeconomic impacts. IAMS provides access to the user community through geographic information systems and visualization tools on the Internet. Spatial time series of ecological change, organism flows, and potential ecological and social impacts, among other products, are delivered to enable practitioners and decisionmakers to evaluate the risk of invasion by organisms at multiple temporal and spatial scales. IAMS can aid in rapid decisionmaking concerning invasive species, inform policymakers about the impacts of changes in regulations, and facilitate public and private education.

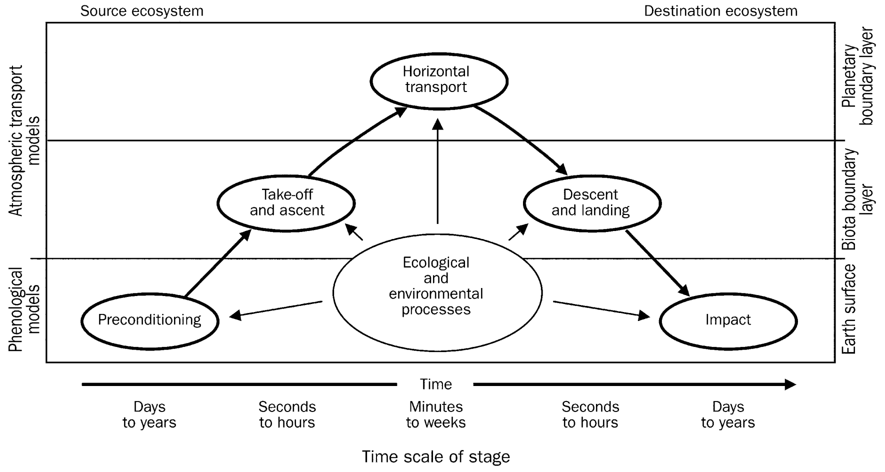

Figure 1. Aerobiology process model. Developed during the 1970s, this model provides a unifying approach to synthesize knowledge of processes associated with the aerial movement of biota. It was intended to focus research on ecological and environmental factors that affect aerobiota and to facilitate the study of organisms that use the atmospheric pathway as an integral part of dynamic ecological systems (Edmonds 1979). The time scales associated with these processes typically range from days to years for preconditioning and impact, minutes to weeks for horizontal transport, and seconds to hours for takeoff and ascent as well as descent and landing. Preconditioning and impact stages occur in ecosystems to which the aerobiota are functionally adapted. Takeoff and ascent as well as descent and landing occur within the biota boundary layer, which varies in depth with organism, weather conditions, time, and space. Winds encountered during the horizontal transport stage govern aerial pathways and consequently geographic destinations of aerobiota. Quantification of the atmospheric pathway requires the integration of phenological models that characterize aerobiota and their hosts in source and destination ecosystems with multiscale atmospheric transport models.

The case of soybean rust

During the past few years, the US Department of Agriculture has been working to prepare for the invasion of soybean rust by supporting breeding experiments for identifying host plant resistance, offshore fungicide evaluation trials, and research for assessing fungicide penetration into soybean canopies. There have also been education, training, and surveillance programs; purchases of new equipment for diagnostic facilities; risk assessments; and deployment of disease forecasting systems. A detailed response plan was developed and tested, to be used in the event the soybean rust pathogen was identified in continental North America (Smith 2005). The sense of urgency stemmed not only from the capacity for *P. pachyrhizi* to rapidly spread over large geographic areas but also from its potentially serious effects on crops: yield losses from infected fields can reach as high as 80%. Brazil may have lost between 5% and 10% of its annual soybean production in 2003 to this pathogen alone (Miles et al. 2003, Yorinori et al. 2005). This foresight and preparation proved extremely valuable when, on 6 November 2004, soybean rust was found infesting soybean fields in Louisiana (Schneider et al. 2005).

The development of the soybean rust aerobiology prediction system (SRAPS), an application of the more general IAMS (figure 2), was part of this preparatory effort. Figure 3 depicts the basic processes affecting the movement of fungal spores, as influenced by environmental and ecological controls. This conceptual model, based on figure 1, is the SRAPS template. Although much is known about the pathogen and its relationship with soybean, there are substantial gaps in knowledge that limit our capability to predict its aerial movement.

Spore production. Global circulation patterns dictate that likely sources of spores transported by aerial currents to the continental United States would be from either South America or Africa (Nagarajan and Singh 1990, Isard and Gage 2001). In collaboration, researchers from Africa, South America, and the United States constructed maps and calendars of spore production for these potential source regions (Ariatti 2005). The number of hectares (ha) planted with soybean is more than three orders of magnitude greater in South America than in Africa (UNFAO 2005), making South American soybean the most likely source of the spores blown to the United States, even though *P. pachyrhizi* is known to have at least 96 alternative hosts (Miles et al. 2003).

Researchers have investigated the relationships among weather, soybean plant growth, and the epidemiology of soybean rust as it relates to urediniospore development on soybean plants (e.g., Bromfield 1984, Tschanz 1984). Yang and colleagues (1990) expressed many of these relationships as functions of the physiological age of the plant and pathogen, which is especially useful for modeling.

Canopy escape. Very little is known about environmental factors that influence the flux of *P. pachyrhizi* spores from a vegetation canopy into the air above. Although clouds of spores escape from fields in many crop-pathogen systems, the vast majority of spores released into the air land on leaf surfaces and the ground within the crop canopy (Aylor 1986). The timing of *P. pachyrhizi* spore release as it relates to (a) environmental factors such as daylight, temperature, and humidity, (b) crop development factors such as stage and canopy density, and (c) the role of wind and turbulence in entraining spores and lifting them out of the canopy are critical, yet poorly understood, components of soybean rust dispersal.

Turbulent transport and dilution of spores in the atmosphere. The physical processes that affect the movement and concentration of particles such as spores in the air have been reviewed by Westbrook and Isard (1999). NOAA (National Oceanic and Atmospheric Administration) agencies routinely provide atmo-

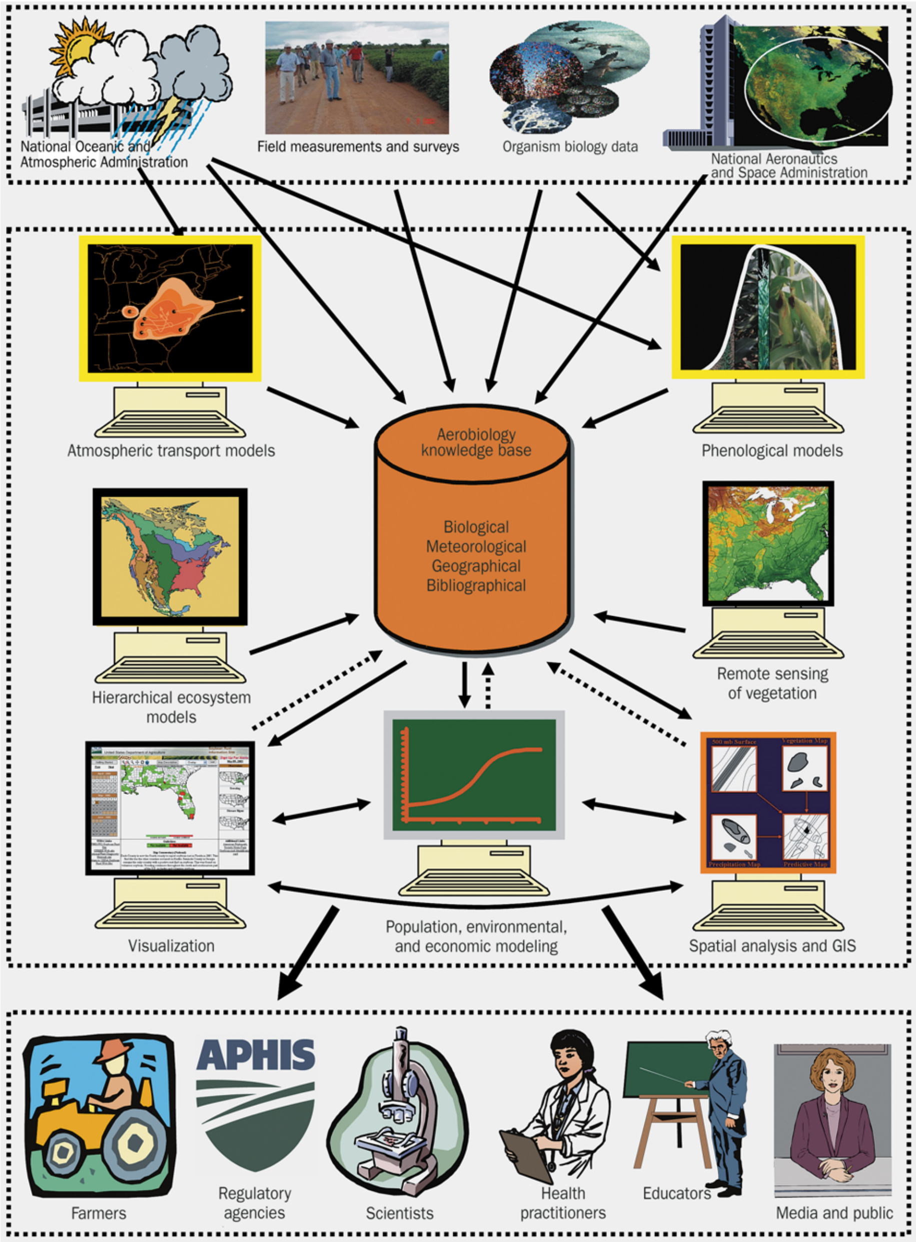

Figure 2. The integrated aerobiology modeling system (IAMS). To forecast the movement of important aerobiota, IAMS requires four categories of external information: (1) measurements and calculations of meteorological and climatological variables and fields, (2) near-real-time and historical satellite imagery, (3) an extensive knowledge base of aerobiota life histories and important ecological and environmental factors in North American ecosystems, and (4) near-real-time measurements and reports from scouts of aerobiota at critical times and locations. Appropriate atmospheric transport models, hierarchical systems of ecoregions, and satellite image access have been incorporated into IAMS; however, these components are frequently being updated as new, improved models become available. Many of the phenological models for aerobiota and their hosts have been published, but this is an area where continued work is critical. Creating life histories for aerobiota, quantifying temperature- and moisture-dependent development rates for their various stages, and then linking these models to those of their host vegetation in geographical units is a task for researchers who have studied specific organisms and their environments. The aerobiology knowledge base is organized and managed using a set of relational databases. Tools for analysis, internal to IAMS, include population environmental and economic modeling, spatial analysis/geographic information systems, and visualization. There are two basic types of output from the integrated aerobiology modeling system: (1) feedbacks of information from the analysis systems that enlarge the aerobiology knowledge base (dotted arrows) and (2) products designed to support decisionmaking by user groups in society (thick arrows), including ecosystem managers (especially farmers and their scouts), national regulatory and security agencies, scientists, health organizations and practitioners, educators, and the media and general public.

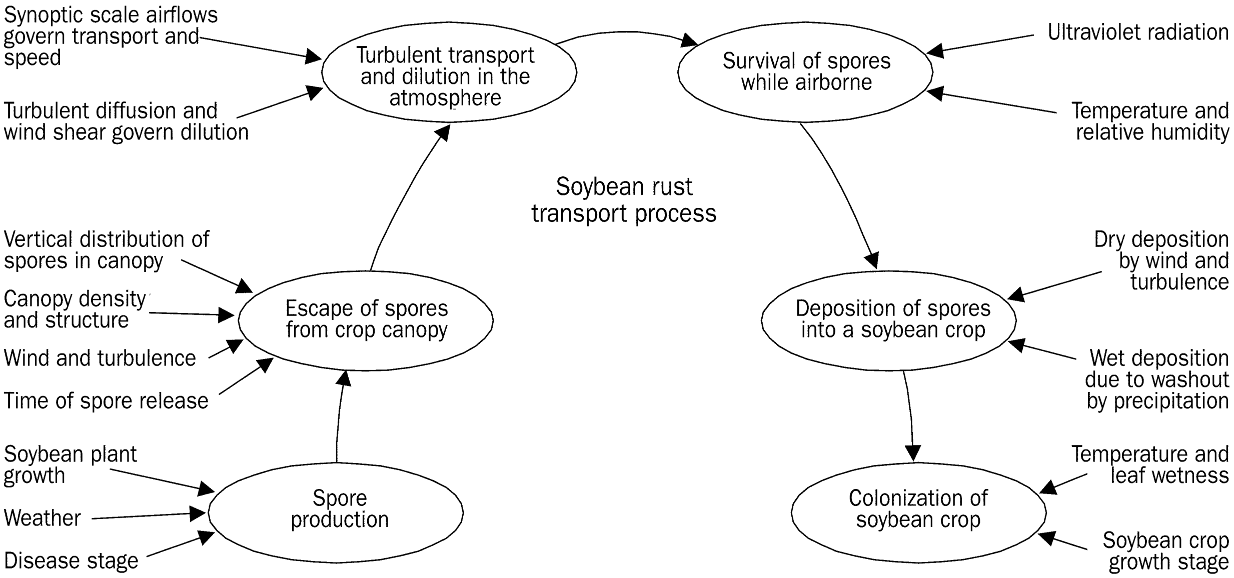

Figure 3. Conceptual model of the soybean rust transport process, depicting the processes that affect the movement of fungal spores as influenced by environmental and ecological controls.

spheric data, model output, and forecasting services. Of the various atmospheric transport models, the most widely used for aerobiological applications is HYSPLIT (hybrid single-particle Lagrangian integrated trajectory), which is maintained by the NOAA Air Resources Laboratory (ARL) (NAPDFC 2005, NOAA 2005).

Survival of spores while airborne. Solar radiation, temperature, and humidity can affect spore survival in the atmosphere (Gregory 1973). Most spores are extremely sensitive to even a few hours of intense sunlight (Maddison and Manners 1972, Bashi and Aylor 1983, Rotem et al. 1985). However, the relationship between duration of exposure to sunlight and *P. pachyrhizi* viability has not been investigated. The air temperatures and relative humidity levels to which spores are usually exposed while being transported in the atmosphere during summer are within the range that *P. pachyrhizi* can tolerate (see Melching et al. 1989, Aylor 1999).

Deposition of spores on a host. The deposition of spores is influenced by gravitational settling and turbulence (Gregory 1973). However, spores are also washed out of the air by rain. Wet deposition is especially important for initiating plant disease epidemics because "rainout" can result in the accumulation of many spores on a host in a relatively small area at a time when environmental conditions (e.g., leaf wetness and cloud cover) are conducive to plant infection (Aylor 1986).

Colonization. Deposition must occur on a host at a suitable stage of development for the spore to have an impact at its destination. When a *P. pachyrhizi* spore is deposited on a soybean leaf, it takes as few as 9 days to complete a cycle that includes germination, appressorial formation, penetration into the epidermis of the leaf, colonization, uredinial development, and sporulation (Bromfield 1984). Relationships between the establishment of soybean rust epidemics, moisture availability on plant surfaces, and environmental temperature have been investigated in field and greenhouse studies (Marchetti et al. 1976, Desborough 1984, Melching et al. 1989). The effect of the pathogen on soybean yield depends on the crop stage at infection (Yang et al. 1990). Once sporulation begins, the crop represents a new source from which urediniospores can initiate long-distance aerial dispersal.

SRAPS application. The model is configured in a modular format to include all of the stages in the aerobiology process. Host development and disease progression submodels driven by weather data are used to characterize source strength and distribution as well as colonization and disease progression in the impact stage at destinations. SRAPS also includes spore release and canopy escape in source areas, mortality due to exposure to solar radiation during atmospheric transport, and wet deposition in destination regions. The model assumes no dry deposition (spores are suspended until rained out). The spatial extent of the model includes the continents of North and South America, Africa, and Europe. Computations are conducted on a 0.125° × 0.125° (approximately 14 × 14 kilometers [km]) grid using a 6-hour time step. For applications confined to North America, the model can be run on a 10 × 10 km grid. SRAPS uses the National Center for Environmental Prediction–Department of Energy Reanalysis 2 data set (Kalnay et al. 1996, Kanamitsu et al. 2002). Global coverage includes 25 years (1979–2004) of historical surface and upper-air meteorological observations and model simulations. Details of the model and the results of an evaluation of the sensitivity of the SRAPS output to both input parameters and spatial resolution are reported by Isard and colleagues (2004).

For the applications presented below, spore release and escape from the crop canopy in a source area are computed using the following assumptions: (a) 25% of the soybean crop is heavily infected with soybean rust, (b) 6 million spores are released per day per heavily infected soybean plant (Melching et al. 1989, Yang et al. 1990), (c) planting density is 500,000 soybean plants per ha, (d) 33% of soybean rust spores are released during the late-morning-to-noon optimal transport period (applicable for *Peronospora tabacina* spores; Aylor 1986, Davis and Main 1989), and (e) 15% of the spores released escape from the soybean canopy (applicable for *Pe. tabacina* spores; Aylor and Taylor 1983).

The mathematical model computes the distribution of spores that escape the soybean canopy, first in the lateral or downwind direction, and then vertically. Lateral transport is computed for a 15° arc (dispersion angle) centered on the wind vector from each point source (grid cell center). A 15° dispersion angle approximates an increase in spore cloud radius with travel time (Heffter 1983, Aylor 1986, Davis and Main 1989). The distance of the arc from the point source is the average wind speed multiplied by the 6-hour time step. Each arc is subdivided into 40 equally spaced transport radii, and the spores associated with the grid cell during the previous time step are allocated uniformly among them. The wind-determined lateral transport distance is the same along each radius and is used to calculate destination grid cells. The computations are conducted separately for six standard pressure levels (1000, 925, 850, 700, 600, and 500 millibars). After the horizontal transport computations are complete, the spores are moved vertically (up or down) between pressure levels using vertical wind vectors. This procedure is followed for each point source (grid cell containing spores). After the trajectories from each grid cell containing spores are computed, the spores arriving at each grid cell and pressure level (potentially from multiple point sources) are summed in preparation for calculating soybean rust mortality due to solar radiation and deposition due to rainfall. The proportion of airborne spores that are eliminated at each time step because of mortality from radiation exposure and wet deposition are equal for each of the six pressure levels.

Spore mortality due to ultraviolet-B radiation exposure in the atmosphere is proportional to total cloud-adjusted, surface incoming solar radiation (Aylor 1999). Total incoming radiation ranges between a clear, sunny day (0% cloud cover, 75% of the total radiation at the top of the atmosphere) to an overcast day (100% cloud cover, 25% of the total radiation at the top of the atmosphere). Observed percent cloud cover between 0% and 100% was used to adjust the amount of radiation between the two radiation limits. In model iterations, spores are exposed to incoming solar radiation after transport to the destination point and before wet deposition. The expired fraction (E_f) is calculated as a function of incoming solar radiation (Rad) in megajoules (MJ) per square meter (m^2):

$$E_f = 1.0 - e^{-Rad/14.0}.$$

A solar radiation level of 14.0 MJ per m^2 results in a mortality of 63.2% of the exposed spore population. This value represents the mean of the critical doses of solar radiation for survival for *Pe. tabacina* and dry bean rust (*Uromyces appendiculatus*) (see table 1 in Aylor 1999). The number of expired spores (E, spores per ha per day) is the total number of spores arriving at a grid cell (A) multiplied by the expired fraction for that destination:

$$E = E_f A.$$

Wet deposition of viable spores after transport to a destination point is proportional to the observed surface precipitation total (Precip), in millimeters (mm), for the grid cell and time step. The wet deposition fraction (WD_f) is calculated as follows:

$$WD_f = 1.0 - e^{-Precip/25.4}.$$

A precipitation total of 25.4 mm results in a wet deposition of 63.2% of the spore population. The number of spores deposited on the ground by precipitation (WD, spores per ha per day) is the difference between the total number of spores arriving at a grid cell and the number of expired spores multiplied by the wet deposition fraction for that destination:

$$WD = WD_f (A - E).$$

Consequently, the number of spores that transition to the next iteration of model computations (S, spores/ha/day) is the number of arriving spores minus the expired spores minus spores deposited during the previous time step:

$$S = A - E - WD.$$

Total daily values of S, E, and WD are obtained by integrating spore concentrations over the pressure levels in the air column above each grid cell. Wet deposition is also accumulated through time for each grid cell and release date for mapping. These values are used to visualize the temporal and spatial extent of the SRAPS outputs.

Although not pertinent to the applications below, a "greening function" is used in SRAPS to evaluate the receptivity of deposition areas in North America to colonization by *P. pachyrhizi* (see figure 1). Computations of accumulated heat were correlated to NDVI (normalized difference vegetation index) values from the AVHRR (Advanced Very High Resolution Radiometer) for each of the 10 × 10 km grid cells in North America, using data collected over a 5-year period. Soybean planting and harvesting dates for spatial units in which the crop is prominent were also estimated as a function of accumulated heat. The resulting greening function can be used to determine whether hosts in a deposition region are available in appropriate growth stages to make colonization feasible. It also can be used to initiate a soybean development submodel for appropriate spatial units. A soybean rust disease progression submodel is coupled to the soybean growth model and started once spore deposition occurs in a grid cell. Together, these submodels predict the progression and intensity of an epidemic in the affected region and the time when the spatial unit is expected to become a source of *P. pachyrhizi* spores for further atmospheric spread.

Predictions of soybean rust transport to North America. During February and March 2004, historical data were used to evaluate likely aerial pathways for spread of the rust from the South American soybean production region north of the equator that includes portions of Venezuela, Roraima State in Brazil, Guyana, and Suriname. Soybean rust had been reported, although not confirmed, in this area. Since planting and harvesting in this region usually begin in May and September, respectively (USDA FAS 2004), it was assumed that if the disease was present, spore production would peak between mid-July and late August. SRAPS simulations were created for all days between July and September in the years 1999–2003. The vast majority of the simulations resulted in wet deposition of spores in Central America. Figure 4 shows a typical pattern of spore deposition for simulations initiated on days in mid-July. As the summer progresses and the Intertropical Convergence Zone shifts farther north, the deposition region extends to southern and eastern Mexico, including the Yucatán Peninsula. Model simulations showed that direct soybean rust transport from the South American soybean production area north of the equator to the United States could have been associated with only two tropical weather systems in the 5-year record (figure 5).

An advanced soybean rust infestation was observed along the Río Cauca in central Colombia in July 2004, most likely initiated by spores arriving in the fields during late May or early June (Glen L. Hartman, National Soybean Resarch Laboratory, Urbana, IL, personal communication, 22 June 2005). In response to this discovery, SRAPS simulation experiments were conducted daily for the period January through August 2004 to evaluate likely aerial pathways for spread of the pathogen from the heavily rust-infected soybean production area in equatorial Brazil. Figure 6 illustrates a typical pattern of spore deposition for simulations initiated for days in mid-May 2004. The pattern of wet deposition accumulated over the 2-week period subsequent to the 12 May release date shows potential spread to a large region that includes the soybean rust infestation areas in Colombia.

During the 2004 tropical cyclone season in the Caribbean basin, Zaitao Pan and X. B. Yang forecast a possible incursion of soybean rust spores into North America (Stokstad 2004). During the previous March, their model output had also indicated the possibility of soybean rust spread into northwestern South America. Pan and Yang used short-term climate model output from the Scripps Institute of

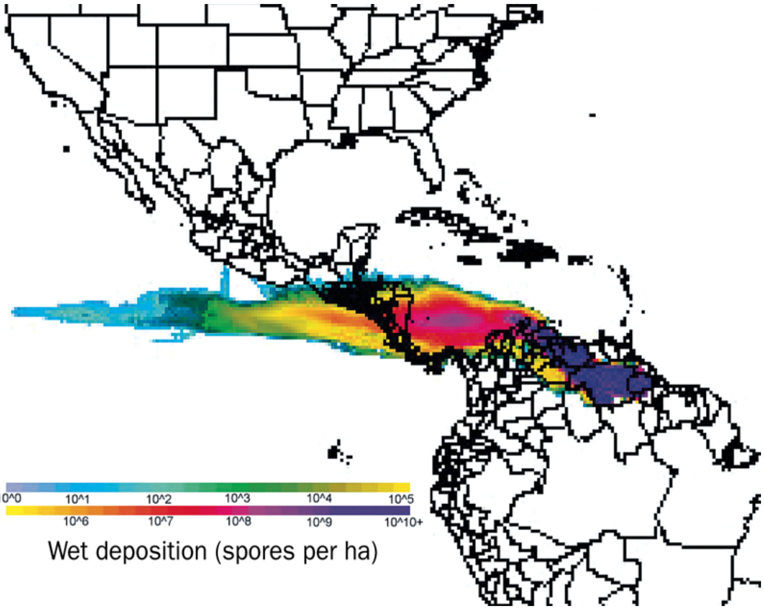

Figure 4. Typical pattern of spore deposition for SRAPS (soybean rust aerobiology prediction system) simulations using the South American soybean production area north of the equator in Venezuela, Brazil, Guyana, and Suriname as the source region and mid-July weather data for 1999–2003. Because the quantity of spores released in the source region is unknown, the map only provides a relative measure of spore deposition intensity.

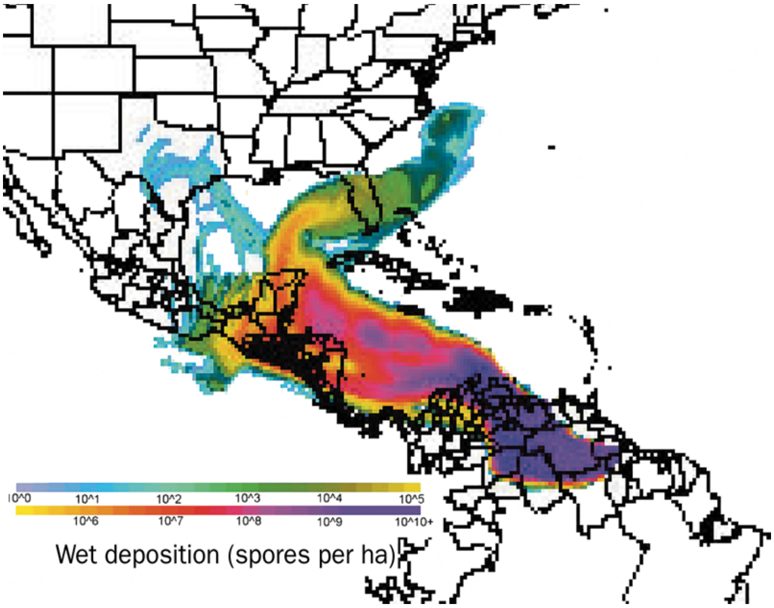

Figure 5. Pattern of spore deposition associated with a tropical cyclone that could have transported soybean rust spores directly to the United States from South American soybean fields had they been infected with soybean rust. SRAPS (soybean rust aerobiology prediction system) simulations were initiated from the soybean production area north of the equator in Venezuela, Brazil, Guyana, and Suriname for 22–29 August 2003. Because the quantity of spores released in the source region is unknown, the map only provides a relative measure of spore deposition intensity.

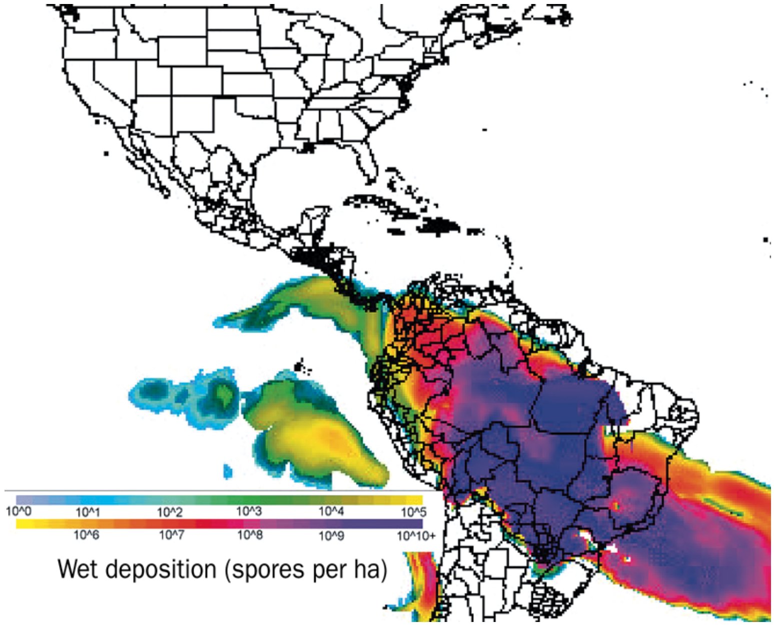

Figure 6. Typical pattern of spore deposition for SRAPS (soybean rust aerobiology prediction system) simulations using the confirmed soybean rust infestation area in Brazil as the source of inoculum and weather data for days between mid-May and late June 2004. Model output suggests that most spores released into the air were blown to the southeast over the Atlantic Ocean or to the northwestern region of South America that includes the Río Cauca region of Colombia, where a soybean rust infestation was identified in August 2004. Because the quantity of spores released in the Brazilian source region is unknown, the map only provides a relative measure of spore deposition intensity.

Oceanography global climate model as input to the Pennsylvania State University/National Center for Atmospheric Research mesoscale model (MM5) to create fields of meteorological variables, which in turn were used as inputs to the NOAA ARL HYSPLIT_4 trajectory model (NOAA 2005). The model accounts for the dispersion of spores at multiple altitudes in the lower atmosphere and incorporates both dry and wet spore deposition processes (X. B. Yang, Department of Plant Pathology, Iowa State University, Ames, personal communication, 24 April 2005). The 40-day forecasts produced in early August and again in early September 2004, using the newly confirmed Colombia source region, showed a spore deposition region encompassing most of central America and Mexico and extending to the northeast along the Gulf Coast as far as the Mississippi River delta (Stokstad 2004).

Historical analysis of soybean rust transport from Colombia to the United States by Hurricane Ivan. Inspection of digital images of infected soybean foliage sent via the Internet from Louisiana to the National Soybean Research Laboratory in Illinois on 8 November 2004 (two days after the pathogen was first found and two days before official confirmation) suggested that soybean rust had been present in Louisiana for 4 to 8 weeks (Glen L. Hartman, National Soybean Resarch Laboratory, Urbana, IL, personal communication, 22 June 2005). SRAPS simulations were immediately conducted for each day in August and September 2004. Results show that airflows converging into Hurricane Ivan as it made landfall in Alabama on 16 September had the potential to transport rust spores directly to the United States from the Colombia infestation area. Predictions from SRAPS (figure 7) indicated that many *P. pachyrhizi* spores from cohorts that initiated movement from the Río Cauca source area on 7, 8, and 9 September remained viable during transport and were deposited by the precipitation that occurred in the southeastern United States between 15 and 18 September. Output from the model, in map format, was provided to members of the APHIS Soybean Rust Rapid Response Team and was used to guide monitoring in soybean fields for the pathogen. Within three weeks of the initial discovery, *P. pachyrhizi* was confirmed (by polymerase chain reaction [PCR] assays; Frederick et al. 2002) in diseased plant tissue in late-planted soybean fields and wild kudzu (*Pueraria montana*) at multiple locations within nine states in the Mississippi River valley and southeastern United States (figure 7). Symptoms of soybean rust were identified at many additional locations in the same region but not confirmed with PCR analysis.

Close inspection of figure 7 reveals that although most of the positive observations correspond to the predicted area of spore deposition, the model failed to account for infections observed in counties along the Mississippi River in southwestern Tennessee, northeastern Arkansas, and southeastern Missouri. Potentially, these infections could have resulted from the subsequent spread of inoculum from sources along the coast of the Gulf of Mexico after the initial transport event. However, disease progression in these fields appeared to be similar to that observed in the predicted spore deposition area, and soybean rust was not reported to have spread to the many volunteer soybean plants that emerged in late autumn from spilt seed in the southeastern United States (Glen L. Hartman, National Soybean Resarch Laboratory, Urbana, IL, personal communication, 22 June 2005). The nonrandom pattern of observations (figure 7) precludes statistical comparison of model predictions with observations.

Through the Internet, the SRAPS system provides US soybean growers with decision support for managing soybean rust (USDA APHIS 2005). In this application, both preconditioning in source areas and impact in destination regions are included (see figure 1). A nationwide network of sentinel plots supplies inputs on the geographic distribution of the pathogen as well as inoculum levels on soybean and kudzu. Each day, SRAPS-generated maps showing deposition of spores, phenological development of soybean and kudzu, and disease progression on these hosts are provided to extension specialists who, in turn, may update their disease

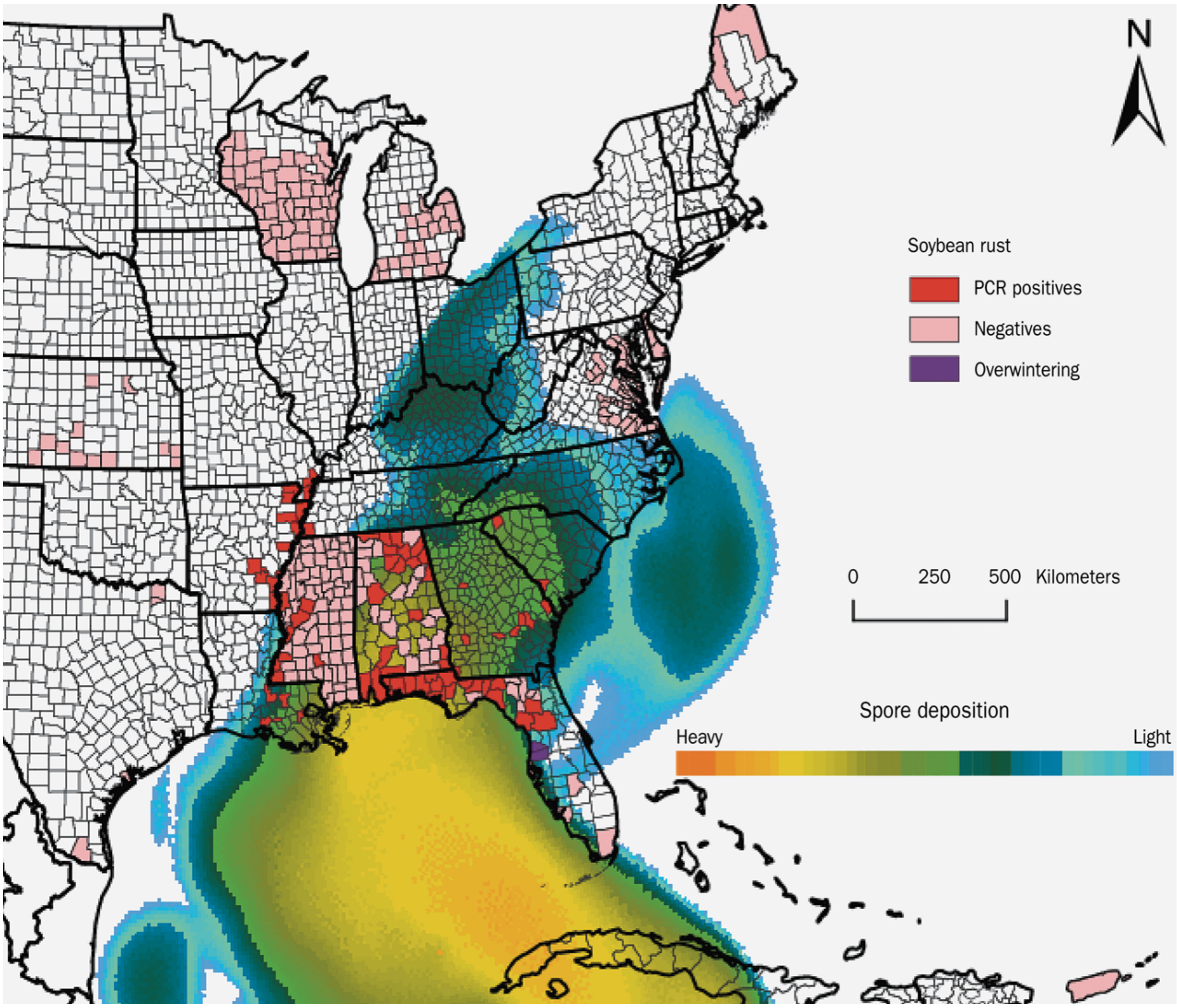

Figure 7. Predicted deposition pattern for SRAPS (soybean rust aerobiology prediction system) simulation using hypothetical cohorts of spores released from the Río Cauca source area on 7, 8, and 9 September 2004. Because the quantity of spores released in the Colombian source region is unknown, the map only provides a relative measure of spore deposition intensity (decreasing from yellow to light blue). Soybean tissues from many counties across the country were subject to polymerase chain reaction (PCR) analyses to confirm the presence or absence of soybean rust inoculum (CERIS 2005). Periods of cold temperatures during January through March 2005 eliminated soybean rust from most of the infected region, and Phakopsora pachyrhizi *was only observed overwintering on kudzu in Pasco and Hernando Counties in Florida (USDA APHIS 2005).*

management recommendations for their state. As the season progresses, scouting observations and measurements of spore deposition in rainwater from the sentinel plot network will be used to validate SRAPS model output.

Challenges for the future

Development of a comprehensive approach to understand and forecast aerial movements of invasive species is in its infancy. Further progress will require teams of professionals integrating biological knowledge and monitoring techniques with information technologies. The SRAPS example illustrates the potential to anticipate and assess movement of invasive organisms on a global scale before they become a problem in a locality, region, or country. The effort highlights the importance of an aerobiological framework to anticipate the threat of invasive species that utilize the atmospheric pathway. The framework also made possible the rapid construction of a nationwide decision support system for managing soybean rust. Because IAMS is a general framework, it can be applied to many other invasive species that may become important in the near future. Regardless of whether long-distance aerial movement is a major component of the life history of these future invaders, the use of the IAMS framework will enable rapid and comprehensive response to complex processes.

To enable a successful program to address the invasion of aerobiota that move at global scales, new sensor systems are needed to quantify the flows of organisms in the atmosphere. Assessment of aerial invasions by organisms is limited by a dearth of knowledge about the biological content of the atmosphere. Identification of the presence of exotic organisms in the air over a region, and of new patterns of movement in the atmosphere, requires a quantitative assessment of the spatial and temporal variations in airborne species and their abundance. Currently, aerobiology monitoring networks are few in number, have sparse spatial coverage, focus on a single or narrow range of taxa (e.g., aphids [Tatchell 1991], plant pollen [Emberlin et al. 2000], soybean rust [USDA APHIS 2005]), and occur mostly in western Europe and North America. The systematic operation of these limited systems has been very useful for investigating population fluctuations, providing pest management decision support, evaluating human risk from allergenic pollens, assessing impacts of climatic changes on spatial and temporal abundance of species, and, in a few instances, monitoring biological invasions (e.g., ragweed in Europe and soybean rust in North America). A vital challenge in aerobiology is to develop cost-effective technologies to build and maintain a global network for monitoring plant pollen, spores, insects, and other important aerobiota. Image recognition systems must be developed to allow automatic identification and quantification of specific aerobiota. Standardized measurement, efficient databasing procedures, and rapid Internet communications should allow near-real-time evaluation of rare or exotic aerobiota by scientists at diagnostic centers.

Humans have very significant inadvertent and advertent impacts on the dispersal of invasive species. Our roles range from transporting organisms into new environments with minimal natural regulatory mechanisms to developing global-scale systems for movement of goods and services to satisfy commercial enterprise. It is as yet unknown how the increase of human transport of organisms will interact with a changing climate regime, but the surprises associated with new introductions are not likely to diminish, and the potential hazard of invasive organisms to ecological systems (e.g., Asian longhorned beetle and emerald ash borer) and agricultural commerce (e.g., soybean rust) is immense. Incorporating a capacity to account for the effect of human actions in the IAMS framework is a significant challenge for the future. Because it is essential that new science and policies replace traditional strategies for managing invasive species, agencies must become willing to adopt strategic planning and invest in long-term research to address these regional-scale assaults on the biosphere.

Additional societal benefits will result from a more complete understanding of the flow of life in the atmosphere. Millions of waterfowl, songbirds, and butterflies move across continents to optimize reproductive requirements and thus provide a significant ecological service to humans. Their use of the atmospheric pathway is governed by the same principles that apply to invasive species. The survivorship of invasive species is also governed by the changing nature of air, land, and aquatic systems. As humans continue to exploit natural resources, the survival of beneficial organisms will suffer. For both applied and theoretical reasons, the study of the movement of organisms that use the atmospheric pathway is desperately needed. We believe that this arena of study is one of the least understood ecological processes on Earth.

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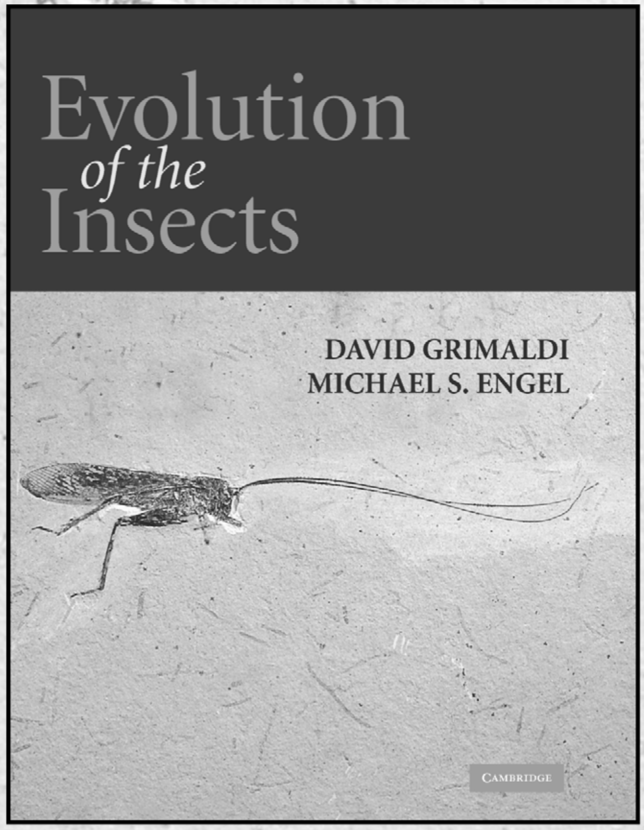

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