

# Landscape-Scale Disease Risk Quantification and Prediction

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## Abstract

The study of plant disease epidemics at a landscape scale can be extended to allow for predictions about disease occurrence at this scale. Examined within the context of the disease triangle, systems developed to incorporate information primarily about the pathogen and conditions conducive to the infection process. Parametric methods can be used to relate environmental conditions to disease, and specifically relate environment to the inoculum production, the resulting infection process, or both. Aspects relating to the presence or absence of the host plant within the landscape, or patterns of the host within the landscape, are much rarer in disease prediction, although analyses incorporating these factors have been conducted. Predictive systems at the landscape scale may concentrate only on the conditions for infection or possible migratory paths of pathogen propagules. Incorporation of all components of the disease triangle may be one way to improve these systems.

## INTRODUCTION

Plant disease epidemiology, which in this review refers to the study of plant diseases in populations, has traditionally been focused on fields as the units of interest. More recently, in part driven by studies of plant disease in natural systems but also by a realization that it is often insufficient to define the systems of study as individual fields, plant diseases are examined in a landscape context. In this review, we have considered a field to be cultivated and planted with a limited number of crop species, often only one. A landscape would not only include fields (often with different crops) but also the surrounding areas that are not cultivated but rather populated with diverse vegetation or used for human activities. Fields are thus a component in the landscape (**Table 1**). The relevant scales are different, in that the landscape encompasses more than a field (63). A logical extension of the studies of plant disease epidemics in a landscape context would be to try to make inferences about these diseases in a predictive manner. In this review, we first briefly review plant disease epidemiology in a landscape context and then cover the possibilities for making disease risk quantifications and predictions on a landscape scale. In both cases, we use the disease triangle (the necessity of having a susceptible host, a pathogen, and a suitable environment for the disease to develop) as a theme to assist in structuring the information needed to quantify the risk or predict a plant disease at the landscape scale.

One way of describing landscape ecology is to refer to it as the art and science of analyzing patterns of and processes in ecosystems. We can qualify this description and use it to define landscape epidemiology as the art and science of analyzing patterns and processes of disease development in ecosystems. These patterns and processes describe disease development per se but also include other processes that are indirectly related to development of disease. Static snapshots show the patterns, and dynamic modeling is probably the best way to describe the processes. Observation-based empirical models are the most common (39), and most of these are static

**Table 1** Differences between predictions on landscape and field scales

Component <sup>a</sup>	Landscape scale	Field scale
Present (or incorporated) components of disease triangle	Often not all	Can have all three
Data available to quantify relationships among components	Limited	Extensive
Investigation and description of underlying processes involved	Not easy	Possible
Parameter estimation of factors used to describe components of disease triangle	Complicated, interactive	Can be described with simple functions, although in reality complicated and interactive
Degree of knowledge of interactions among components of disease triangle	Limited	Extensive
Quantitative nature of interactions among components of disease triangle	Nonlinear	Frequently nonlinear but can be sufficiently described with linearity
Spatial dimensions associated with distribution of host, pathogen, and environmental factors that are the components of the disease triangle	Latitude, longitude, and elevation	Latitude and longitude

<sup>a</sup>We use the disease triangle and its three components—the susceptible host, the pathogen, and the suitable environmental conditions for the disease to develop—as a core theme to discuss epidemiology in the landscape and field scales.

in nature. Geographic information systems (GISs) persist as one of the most extensively used methods of describing and displaying these static snapshots. Most GIS software allows the creation of data surfaces through interpolation of point data, using statistical methods such as variograms and kriging (7, 48, 50, 68). Spatially linked data surfaces then can be analyzed using statistical approaches, such as multiple regression, that account for spatial dependency and autocorrelation (31, 48, 68).

Parametric methods, particularly logistic regression (9, 42, 69), have been extensively used because they are well known for balancing model parsimony and prediction robustness while providing interpretation of straightforward ecological relationships. Implementation methods and input variables differ based on whether the purpose is inference or prediction. Most published studies are inferential rather than predictive (39). One key difference is that an inferential analysis seeks to explain the given data, whereas a predictive model attempts to make predictions about what might happen in a different time or different setting (39). Another important aspect to keep in mind when evaluating or conducting analyses of this type is the selection criteria for the units of interest. Ideally, the units that are sampled should be selected in a random nature, but this may not always be possible (35). If analyses are performed on material selected on the basis of the presence or absence of disease, in a manner similar to a case/control study, rigorous criteria are needed to maintain valid results (24). The definition of the studied population in turn affects the scope of possible inferences. A brief summary follows as to how each of the components of the disease triangle has been addressed in landscape-scale analyses of plant disease epidemics.

## Pathogen

Largely, time and resources dictate the amount of available data. Thus, the sources, distance, and routes of dispersal of infective propagules are poorly known for most crop diseases, as it takes a lot of resources to track inoculum in a large geographic area. For most analyses, the pathogen of interest is assumed to be present or just ignored. In some other cases, researchers prefer to conduct investigations at the smaller scale, which enables them to capture more details of the pathosystem being studied, and then extrapolate the findings to a larger scale. This has been successfully implemented for long-distance airborne pathogens such as those that cause downy mildews (33). In this case, report of the disease (or the pathogen) by a network of collaborators is indispensable and is the basis of any long-distance dispersal and thus of landscape epidemiology of downy mildews. The report is evaluated to weigh the source of potential inoculum. A model that calculates trajectories from temporal data about wind directions and speeds, called HYSPLIT (10), can then calculate and estimate ground deposition of inoculum in a new location and potential risk for a new outbreak (33). The basis of estimating this risk comes from experiments on the biology of the pathogen conducted under controlled environments. Developing new tools to track the movement of pathogens at the landscape scale would be beneficial and especially informative for air- or waterborne pathogens. Even the use of existing tools, such as those used (or developed) at the molecular level, would allow a great improvement of our knowledge in this aspect of the disease triangle at the landscape scale.

## Environment

Most landscape epidemiological studies utilize GISs and other geospatial technologies (e.g., remote sensing) to assimilate the large, spatial data sets that enable analysis of relationships between the distribution of disease and landscape heterogeneity. For example, Smith et al. (57) examined patterns of white pine blister rust infection in the Rocky Mountains by correlating geographically

referenced field observations of disease prevalence with GIS-derived environmental variables in a Poisson regression model. In almost all cases, these environmental variables are indirect or surrogate variables. In other words, they presumably have an effect because they are close relatives of well-studied environmental variables that affect disease development in the modeled system at the field level. The relationship between these variables and disease development could also result from studies of the pathogen under controlled conditions. For instance, Mila et al. (42) quantified the prevalence of *Sclerotinia* stem rot of soybeans in four states of the north-central United States using monthly average summer temperatures and precipitation. Although those were highly generic variables to describe multiple aspects of the disease cycle of this pathogen, the variables were very efficient in their ability to describe the prevalence of the disease across a large area. A similar approach was used in the initial work that led to the *Fusarium* head blight (FHB) forecasting system (9). In this research, combinations of temperature, relative humidity, and rainfall or durations of specified weather conditions for seven days prior to anthesis and ten days beginning at crop anthesis were identified as potential predictor variables. One potential pitfall with these approaches is that indirect variables may influence multiple processes in a nondescriptive way. This methodology provides only static snapshots and cannot describe dynamic processes. Within the context of the disease triangle, it is difficult to disentangle whether these variables influence the infection process, the production of inoculum, or both.

## Host

The host portion in the disease triangle is not frequently considered in the analysis of epidemics at the landscape scale. There may be different explanations for this, such as the difficulty to collect data on large scales, the complexity of the system, or simply that plant pathologists are inherently trained to study diseases at the field level. An additional complication is that the patterns of agricultural crops vary as a result of the ephemeral nature of many plantings (crop rotation). There are, however, some stellar examples in the literature that demonstrate how the landscape (host) may play a unique role at this level. Haas et al. (18) demonstrated links between forest species diversity and disease risk. In this study, sites with greater biodiversity had lower infection risk from the emerging plant pathogen *Phytophthora ramorum* after accounting for landscape heterogeneity and spatial dependence in infection. Another aspect that has not generally been addressed is topology, e.g., the existence or absence of lakes, rivers, and other sources that could spread pathogens that are primarily disseminated in water. Another important aspect may be the distribution of the host. In contrast to the field level, where host may be a binomial variable (i.e., presence implies potential disease and absence no disease), this component may have a more sophisticated function in landscape epidemiology. Host patches, corridors, or density (what is called landscape connectivity) in general might facilitate or impede high disease severity or spread (22, 62). There are few examples of landscape epidemiology of plant diseases in which the host distribution is included even in the simplistic form of a GIS map that depicts the host structure (see, for example, 2, 11). Examples that incorporate the functionality of the host (62), such as the effect of host density on disease severity (16, 56) or the effect of rivers and roads (29, 30) on the occurrence of a plant disease at the landscape scale, are even scarcer.

## CAN THE RISK OF PLANT DISEASE BE ESTIMATED AT THE LANDSCAPE SCALE?

The prediction of plant disease has become an important part of modern disease management. In most cases, the objective is to optimize different management strategies, notably the use of

## MEASURING UNCERTAINTY

Uncertainty in knowledge or understanding exists in every biological process and structure. More uncertainty is inherent in disease development and spread in the landscape compared with those in controlled laboratory experiments because in the latter a few aspects can be isolated and investigated in extensive detail. The development and implementation of Bayesian methods have assisted significantly in quantifying uncertainty. Uncertainty in parameter estimates in empirical models such as the examples given above can be quantified with Bayesian approaches (40, 42). Bayesian methods offer further advantages to landscape epidemiology because (a) they allow for explicit modeling of complex systems using a hierarchical structure in which hypotheses can be investigated in each level of hierarchy separately and (b) potential structured and unstructured spatial effects can be incorporated (41, 47).

Behind spatial effects there are usually a number of factors, some of which may have a spatial structure and others may be present only locally (unstructured) in a given spatial unit. If standard statistical methods are used to analyze spatially correlated data, the standard error of the covariate parameters is underestimated and thus the statistical significance is overestimated (12). This pitfall may have a profound effect on the significance of differently sized geographic areas, particularly small areas. Bayesian methods easily allow us to distinguish between the two kinds of effects by splitting them up and investigating the significance of each one separately (12, 41, 47).

fungicides. Initial systems aimed at predicting when fungicides should be applied generally and when in specific fields were composed of rules that were derived from critical parts of the disease cycle (8). Examples of early rule-based decision aids include those for potato late blight, caused by *Phytophthora infestans* (3), and apple scab, caused by *Venturia inaequalis* (43). Although these early predictive systems were generally based on knowledge about the biology of the pathogen, the relative importance of each of the factors was generally derived through a trial-and-error basis. More recently, statistical techniques were proposed not only to calibrate the rules (69) but also to place the results of the rules into a Bayesian framework, incorporating information about uncertainty in the predictions (72) (see sidebar, Measuring Uncertainty). The quality of the decisions arising from the rules could then be compared with respect to both sensitivity and specificity (34, 52, 64, 69, 72).

These predictive systems were developed to be used at the field scale. Given that most of these systems utilized information culled from knowledge of the pathogen life cycle, current crop information, and relevant past field history, they also needed field-specific information. One question that arises is whether predictions can be made at a higher spatial integration level. Here, we examine whether the predictive systems can be applied at a landscape scale, preserving our theme of the disease triangle concept.

One major difference in scaling up to the landscape scale is that landscapes are not individual units that can become diseased. If we are to employ the disease triangle framework on a landscape scale, the susceptible plant portion could be modified to state that susceptible plants are present in the landscape. The presence of the pathogen and the mapping of suitable conditions for disease development are most often the factors considered when trying to predict disease at a landscape scale. Given that the techniques that are used have varying levels of uncertainty and are possibly used to look into the future, one ends up predicting the risk of disease development.

Systems that attempt to predict the risk of disease development generally focus on two components of the disease triangle: (a) the presence of the pathogen and (b) the occurrence of suitable conditions for disease development. In general, these predictive systems are designed as tools for assisting in decision making in pest management, so there is little concern with whether a disease will develop if the corresponding host crop is not present. In practice, predictive systems are rarely

developed for diseases if the corresponding crop is not present, and either experience or simple models show whether plants can be grown in specific areas. This important aspect is not currently a major component of landscape-scale plant disease predictions.

### **Predicting Suitable Conditions for Disease Development**

Current climate models provide varying levels of resolution (both spatial and temporal) and can be used to predict the occurrence of suitable conditions for disease development (22). Obviously, enhanced resolution in the form of a finer grid leads to more accurate and precise predictions, although a robust understanding of the relationship between the climate data and disease development is needed. The estimation of the relationship between disease risk and various climatic or meteorological factors is a critical part of predicting disease risk at a landscape scale.

### **Predicting Pathogen Presence**

The other component of the disease triangle that has received considerable attention in predicting disease risk at a landscape scale is the presence of the pathogen. The spatial spread of pathogens can be monitored with spore traps, for example, or pathogen collections, possibly followed by phenotypic or genotypic characterization, and can contribute to the disease triangle component relevant to the presence of the pathogen. The predicted movement of pathogens can also be calculated using suitable models, such as the HYSPLIT model (10), if suitable climatic data are available. This approach, however, needs information regarding the possible sources of the pathogen.

### **Predicting Host Presence**

There are mechanistic models, such as the EcoCrop portion of DIVA-GIS (23), that can predict where crops can be grown based on temperature and rainfall data. In practice, there are other factors that determine whether or not a specific crop is grown on a particular field. The Spatial Analysis Research Section (SARS) of the National Agricultural Statistics Service (NASS) of the United States Department of Agriculture (USDA) provides crop and land-use data for the continental United States on a suitable spatial scale (30 or 56 m resolution) (20), but the database, called CropScape, has not been used in predicting plant disease on a landscape scale.

Ideally, predicting disease risk would have all three components of the disease triangle (or at least two if it is assumed that the end user would supply information as to the presence of a suitable crop). In practice, one of these two components is emphasized. This often depends on the nature of the disease in question. If the assumption is made that the conditions will always be favorable for disease development, the predictive system focuses on whether the pathogen is present. Likewise, if the pathogen is generally thought to be present, then the prediction of conditions suitable for disease development is more important. Certain types of information presented on a landscape scale, such as mapping of disease occurrence, contain elements of both pathogen presence and suitable conditions.

## **EXAMPLES OF LANDSCAPE-SCALE PREDICTIONS OF DISEASE AND DISEASE RISK**

The origin and development of landscape-scale predictors are variable. This is illustrated below using the examples of potato late blight, FHB, and more. None of these explicitly incorporate information about the presence and the distribution of host plants (i.e., the plant side of the

disease triangle). They each include varying amounts of information representing other parts of the disease triangle (whether conditions are suitable and whether the pathogen inoculum is present or produced) in their predictions.

## Potato Late Blight

A range of models and algorithms to predict the occurrence of potato late blight, caused by *P. infestans*, have been utilized. The early tables, such as those produced by Hyre (25) and Wallin (66), generally referred to the risks within a particular field (and relied on specific data from that field). Adjustments have been made, and the new models and algorithms can be used at the landscape scale. Given that the original calculations made by Wallin (66) relied on information regarding periods of high humidity in the crop canopy (the temperature during the period and the period length), the adjustments entail using relative humidity estimated without surrounding foliage and at a standard height, along with changes as surrogate variables (1). One common aspect in these systems is the general assumption of inoculum presence, which is not an unreasonable assumption for potato late blight. Most of these systems date to a period when infected tubers were the primary inoculum because they pre-date the discovery of the A2 mating type outside of the Toluca Valley in Mexico (15). Thus, unless high-quality certified seed was used in a large area, the logical assumption is that inoculum was present. If, however, oospores are a major source of inoculum, such as in Scandinavia (71), then these assumptions and models are not representative of the disease cycle, because of earlier primary infections (70). After the prediction of the first infections to initiate fungicide applications, these predictive systems use different rules that typically indicate when fungicide applications should continue and then how often these sprays should take place. Comparisons of different predictive systems have been made (61).

The derivation of these early predictive systems was based in part on the temperature and humidity requirements of the pathogen but also on field observations of potato late blight (3). Exactly how these data were then translated into the rules that predicted late blight is not always clear, although the general impression is that this took place through empirical, often trial-and-error, methodology and was also dependent on the available weather data. The rules proposed by Hyre (25) and Wallin (66) were then merged into a computer-based system called Blitecast (32). One predictive system, SimCast (14, 17), was based on the original Blitecast model (32), but was calibrated and tested using output from a process-based dynamic simulation model of potato late blight development (4, 5, 6, 14). Thus, the logical bases for many of these predictive systems are related.

If the purpose of these landscape-scale predictions is to provide near-real-time information for potato producers, the systems generally have an Internet-based interface. For example, a system used in Michigan employs a prediction algorithm derived from that proposed by Wallin (66), with periods of relative humidity over 80% as a surrogate for the high humidity threshold in the crop canopy (<http://www.lateblight.org>). This also permits late blight risk forecasting to be made on the basis of weather predictions. In a similar manner, a system active in New York State can provide predictions based on standard Blitecast, with predicted values, and SimCast (<http://newa.cornell.edu/index.php?page=potato-late-blight-dss>). A system active in Norway (<http://www.vips-landbruk.no>) provides predictions based on Försund's rules (13), Negativprognose (65), and a new late blight model still under development and testing (Nærstadmodellen) (21). Other systems, with varying degrees of involvement from commercial firms, are also available (19).

These models provide information as to the suitability of the environment for production of inoculum as well as the suitability of the environment for infection. One system that is active in

Scandinavia utilizes geo-referenced early reports of the pathogen (<http://euroblight.net/late-blight-survey-mapper>). The occurrence of early infections indicates that all three components of the disease triangle were present and allowed for the development of disease. A decision maker would then learn that inoculum is present if he used this system and could focus attention on the conditions relevant for the infection process. One advantage here is that the differences between initial infections from tubers, or from oospores, are not significant to the prediction of fungicide application because this system documents the presence of inoculum in a particular region, and thus protective measures would be required in any case. Conversely, it may be too late to initiate fungicide applications, since inoculum is already present. In most cases, though, the role of weather and its effect on the production of sporangia, and the subsequent infection process, are the overriding factors in prediction of potato late blight on a landscape scale. The influence of spatial heterogeneity of the potato fields has been studied via simulation models (56). However, the inclusion of this information is not generally available in landscape-scale disease forecasts. For instance, in the potato late blight case this simulation analysis could describe the effects of reducing potato production in a region, clustering potato production, or mixing resistant and susceptible potatoes (56), but the detailed data required by this process-based simulation is not generally available.

A divergent approach was used to estimate how climate change will affect the future risks of late blight on a global scale (59). Given that future climatic data consist of monthly averages and that the processes that are modeled in late blight require data at a much finer temporal scale (such as daily or even hourly measurements), the first step was to develop a metamodel that could be used with these monthly data (58). The metamodel was generated via generalized additive models and an existing model driven by hourly data. This metamodel, based on a portion of SimCast and referred to as SimCastMeta, was then used with monthly data from different future climate scenarios to calculate the cumulative blight units for each grid cell. The optimal time for potato cultivation for each cell, as well as the suitability of the cell for potato production, was estimated with the EcoCrop model (23). This information was then used to calculate the number of blight units within each cell on the globe that had potato production. SimCastMeta evaluates how favorable the climate is for late blight development, and the EcoCrop model supplied information about the presence of a host. Here, it is still assumed that the pathogen is present, as is the case with other late blight prediction systems. The purpose of this global prediction of late blight was different from the systems designed to provide near-real-time advice regarding the initiation and intensity of fungicide applications. In this case, the authors were able to draw conclusions regarding the predicted severity of the disease and identify areas where late blight may become more severe in the future (59).

### **Fusarium Head Blight**

FHB, caused by *Fusarium graminearum* (teleomorph: *Gibberella zeae*), has become problematic in wheat production, causing reduced yields but also quality problems due to reductions in seed quality and the presence of the mycotoxin deoxynivalenol (37, 38). This disease is exacerbated by the presence of extended periods of wet weather and/or high humidity during flowering and the early grain-filling period (38). Whereas the review presented in 1997 (38) described the disease as re-emerging due to wet weather as well as changes in cultural practices, the review in 2012 presents data suggesting that the problem has persisted (37). Although a number of predictive models have been proposed in Asia, South America, and North America, a systematic analysis of the risk of FHB was initiated by a consortium of researchers in the United States, and the first phase of this analysis (9) used data from a collection of 50 fields. In this study, outcomes from logistic regression models were used to relate the probability of a major epidemic of FHB to a



number of predictor variables. The binary outcome, a major FHB epidemic, corresponded to a threshold of more than 10% disease incidence in the field, and the independent variables were different weather factors, generally temperature, relative humidity, and precipitation, and different interaction terms. This initial model was then adjusted for factors related to crop residues and host reaction, using additional data from 2004 and 2005 (44). Several iterations of the predictive model have been implemented, first at the state level, and subsequently on a regional basis (L. Madden, personal communication; <http://www.wheatscab.psu.edu/>).

Whereas the initial model had a resolution of 20 km<sup>2</sup>, the resolution has been improved to 2 km<sup>2</sup> based on improved geospatial interpolation surface information. Additional analyses exploring different alternatives to logistic regression have been completed (51, 52) but are not yet part of the predictive system. In this system, the presence or absence of the crop is not an explicit part of the prediction system, and the different independent variables used in the regression models are related to the conditions that favor infection as well as the production of inoculum.

## Rust on Small Grains

For rusts of cereals, most landscape-scale mapping has been confined to the occurrence of the pathogen and pathotype (race) information. The success of resistant cultivars with race-specific resistance in controlling disease depends on the pathogen population lacking virulence to the cultivar grown (36). Hence, the geographical distribution of the different pathotypes is critical information and has played a major role in controlling rust diseases. Another factor is that the environment is usually not a limiting factor in the development of rust. Geographic movement of rust spores has been described by the *Puccinia* pathway in North America (60) and within continents or regions, including Europe (73), India (46), and the Rift Valley (45). Currently, spore rust mapping is coordinated by the FAO (49) at the Rust Spore web portal (<http://www.fao.org/agriculture/crops/rust/stem/en/>). At this site, a large emphasis has been placed on stem rust and the Ug99 variant (54, 55). The NOAA HYSPLIT model (10) is used to calculate future trajectories of rust spores from known sources within 24, 48, or 72 hours (55). In this case, there are no explicit predictions made about whether conditions are suitable for infection. The presence or absence of the host plant (and its resistance or susceptibility) is also not part of this predictive system.

Current information and maps of stripe rust can be found at the Global Rust Reference Center Web site (<http://www.wheatrust.org>) (28). The geo-referenced data on the occurrence of *Puccinia striiformis* pathotypes in different countries have been registered over time, and one way of examining these data is to visualize them as a map in a manner similar to the presentation of the different genotypes of *P. infestans* at the Late Blight Survey Mapper (<http://euroblight.net/late-blight-survey-mapper>). These maps only inform the user as to what is already present, perhaps subdivided by genotype, and although they provide a basis for making decisions in the future, e.g., to change the host cultivar, such a map does not provide any additional information with regard to risk. The migration of pathotypes of *P. striiformis* in China has also been studied with the HYSPLIT model to make inferences on potential inoculum sources (67).

## Other Systems

Following the incursion of soybean rust (caused by *Phakopsora pachyrhizi*) into the continental United States, a pest information system was launched that combined elements of information technology together with information from the USDA Soybean Rust Information System (53). Building on this concept, a system that combined weather data and a variety of predictive and

reporting systems called IPM PIPE (Integrated Pest Management Pest Information Platform for Extension and Education; <http://www.ipmpipe.org>) was started in the United States (27). The website has several components, some of which map only the occurrence of the disease, whereas others also present information regarding risks for infection. A series of processes were modeled in a soybean rust aerobiology predictive system (SRAPS) that covered spore production, canopy escape, turbulent transport and dilution in the atmosphere, survival, deposition, and colonization (26). The resulting model was used to calculate areas in which there could be potential depositions of urediniospores of *P. pachyrhizi* in the continental United States and guided the search that led to the discovery of the pathogen in Louisiana (26).

The field-oriented decision support systems for applying fungicides against potato late blight represent one type of system that uses the same weather-based algorithms to make predictions on a landscape scale. This is done by substituting other measurements for the leaf-wetness information. The weather information is related to factors affecting inoculum production and infection, although the landscape scale system has, in principle, all the characteristics of the field-based system. For the FHB systems, the algorithms were developed to be used on a landscape basis, and the statistical connection between the different predictor variables and the outcome of interest is well documented (9, 44). In this case, both inoculum production and conditions suitable for the infection process are considered by the predictive system. The rust prediction systems include only the inoculum presence component of the disease triangle.

## ESTIMATING THE RELATIONSHIP BETWEEN THE COMPONENTS OF THE DISEASE TRIANGLE AND DISEASE RISK

To utilize the disease triangle conceptual model to evaluate estimates of disease risk at a landscape scale different kinds of data would be required. Detailed weather information at finer spatial scales is becoming more widely available, but data regarding the distribution of the pathogen and the host at a similar scale are much harder to obtain, if they are available at all. Although dynamically updated weather data are a built-in component of modern weather forecasting, no such motivation exists in collecting temporally and spatially detailed information about crop plants and their pathogens. Thus, the prediction systems that have evolved use these data to make inferences about the conditions for inoculum production and subsequent infection of the plants (e.g., late blight and FHB) or to make inferences about pathogen movement (e.g., rust and IPM PIPE systems). No systems have evolved to date that rely on all three components of the disease triangle. Incorporation of information from all three components on a landscape scale would provide a substantial improvement in predictions of disease risk and provide transformational change in disease management approaches.

## CONCLUSION

Landscape epidemiology is a new field of research within plant pathology and human and veterinary epidemiology. Thus, it is a field that is still trying to find its underlying principles and methods. Its development has been slow because most researchers, even those trained in quantitative epidemiology, are more familiar with the field than with spatially large-scale modeling. Some progress has been made in the prediction of plant diseases at the landscape scale with diseases such as FHB and potato late blight. This could, in part, be due to economic interests, but the availability of suitable data, the need for disease predictions, and a well-connected IT system (computers, mobile devices, and the supporting infrastructure) make the implementation and use of such systems easier.

The availability of detailed, regularly updated weather data with a finely gridded spatial framework provides a wealth of possible input data for a predictive system. Other, nonmeteorological factors may also be available that will assist in the prediction. Just how this input data can be transformed into a prediction of disease on a landscape scale becomes a statistical problem. Clearly, we need more information on how spatial discontinuities of both pathogen and host plants affect disease development to connect the remaining parts of the disease triangle.

Determining the relationship between this input data and the resulting disease also requires verification of known biological relationships, as well as a determination of the relevant quantitative relationships. For some systems, the weather affects the production of inoculum, but for many diseases it also has large effects on infection and subsequent disease development. The distinctions between inoculum production and subsequent disease development are not always clear in the estimation process. The availability of relevant outcomes, such as disease or inoculum, along with the corresponding input data are necessary to perform this statistical analysis. If regression techniques are to be used to estimate parameters on a landscape scale, the statistical units in question are often fields. Given that these fields define the population of interest, it is important to know just how these fields are selected and whether there is any bias in the selection. A selection bias would reduce the scope in which a predictive system could be used, and if this bias is undocumented, then the application domain for the resulting system is not defined. In practice, though, possible bias in the selection of fields is seldom mentioned or discussed.

Currently, there are limited data available that can be used to answer several practical but also fundamental questions related to landscape epidemiology and the prediction of plant diseases at the landscape scale. Yet, even when data are available or could be collected, one must still confront the challenge of balancing epidemiological and landscape parameters needed to capture disease dynamics without (*a*) exceeding computational and data collection costs or (*b*) overfitting models that contain large numbers of free parameters that are difficult to interpret. Developments in data science may create significant opportunities in the near future. New methods are being developed that combine different sources of numerical and even text types of data, and new algorithms allow sophisticated models to be implemented. All this means new opportunities (but also challenges) in how we look at epidemics, analyze data, and make inferences. If the prediction of plant diseases at the landscape scale is to be improved, a combination of analytical techniques, together with different forms of data, should lead to better predictions. The disease triangle framework may be useful in categorizing the different types of data.

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# Contents

The Wayward Hawaiian Boy Returns Home <i>Dennis Gonsalves</i> .....	1
Playing on a Pathogen's Weakness: Using Evolution to Guide Sustainable Plant Disease Control Strategies <i>Jiasui Zhan, Peter H. Thrall, Julien Papaix, Lianhui Xie, and Jeremy J. Burdon</i> .....	19
Dissecting the Molecular Network of Virus-Plant Interactions: The Complex Roles of Host Factors <i>Aiming Wang</i> .....	45
Molecular Mechanisms of Nematode-Nematophagous Microbe Interactions: Basis for Biological Control of Plant-Parasitic Nematodes <i>Juan Li, Chenggang Zou, Jianping Xu, Xinglai Ji, Xuemei Niu, Jinkui Yang, Xiaowei Huang, and Ke-Qin Zhang</i> .....	67
Priming for Enhanced Defense <i>Uwe Conrath, Gerold J.M. Beckers, Caspar J.G. Langenbach, and Michal R. Jaskiewicz</i> .....	97
Genome-Enabled Analysis of Plant-Pathogen Migration <i>Erica M. Goss</i> .....	121
<i>Citrus Tristeza Virus</i> : Making an Ally from an Enemy <i>William O. Dawson, Moshe Bar-Joseph, Stephen M. Garnsey, and Pedro Moreno</i> .....	137
Practical Benefits of Knowing the Enemy: Modern Molecular Tools for Diagnosing the Etiology of Bacterial Diseases and Understanding the Taxonomy and Diversity of Plant-Pathogenic Bacteria <i>Carolee T. Bull and Steven T. Koike</i> .....	157
Genomics Spurs Rapid Advances in our Understanding of the Biology of Vascular Wilt Pathogens in the Genus <i>Verticillium</i> <i>Anna Klimes, Katherine F. Dobinson, Bart P.H.J. Thomma, and Steven J. Klosterman</i> .....	181
Soil Health Paradigms and Implications for Disease Management <i>Robert P. Larkin</i> .....	199

Epidemiology and Population Biology of <i>Pseudoperonospora cubensis</i> : A Model System for Management of Downy Mildews <i>Peter S. Ojiambo, David H. Gent, Lina M. Quesada-Ocampo, Mary K. Hausbeck, and Gerald J. Holmes</i> .....	223
Identifying and Naming Plant-Pathogenic Fungi: Past, Present, and Future <i>Pedro W. Crous, David L. Hawksworth, and Michael J. Wingfield</i> .....	247
Impact of Diseases on Export and Smallholder Production of Banana <i>Randy C. Ploetz, Gert H.J. Kema, and Li-Jun Ma</i> .....	269
Evolution of Plant Parasitism in the Phylum Nematoda <i>Casper W. Quist, Geert Smant, and Johannes Helder</i> .....	289
Lipo-chitoooligosaccharides Modulate Plant Host Immunity to Enable Endosymbioses <i>Erik Limpens, Arjan van Zeijl, and Rene Geurts</i> .....	311
Range-Expanding Pests and Pathogens in a Warming World <i>Daniel Patrick Bebber</i> .....	335
Sharka Epidemiology and Worldwide Management Strategies: Learning Lessons to Optimize Disease Control in Perennial Plants <i>Loup Rimbaud, Sylvie Dallot, Tim Gottwald, Véronique Decroocq, Emmanuel Jacquot, Samuel Soubeyrand, and Gaël Thébaud</i> .....	357
A Moving View: Subcellular Trafficking Processes in Pattern Recognition Receptor-Triggered Plant Immunity <i>Sara Ben Khaled, Jelle Postma, and Silke Robatzek</i> .....	379
Roots Shaping Their Microbiome: Global Hotspots for Microbial Activity <i>Barbara Reinhold-Hurek, Wiebke Bünger, Claudia Sofia Burbano, Mugdha Sabale, and Thomas Hurek</i> .....	403
Identification of Viruses and Viroids by Next-Generation Sequencing and Homology-Dependent and Homology-Independent Algorithms <i>Qingfa Wu, Shou-Wei Ding, Yongjiang Zhang, and Shuifang Zhu</i> .....	425
Quantitative Resistance to Biotrophic Filamentous Plant Pathogens: Concepts, Misconceptions, and Mechanisms <i>Rients E. Niks, Xiaoquan Qi, and Thierry C. Marcel</i> .....	445
Landscape-Scale Disease Risk Quantification and Prediction <i>Jonathan Yuen and Asimina Mila</i> .....	471



Torradoviruses <i>René A.A. van der Vlugt, Martin Verbeek, Annette M. Dullemans, William M. Wintermantel, Wilmer J. Cuellar, Adrian Fox, and Jeremy R. Thompson</i> .....	485
Durable Resistance of Crops to Disease: A Darwinian Perspective <i>James K.M. Brown</i> .....	513
Understanding Plant Immunity as a Surveillance System to Detect Invasion <i>David E. Cook, Carl H. Mesarich, and Bart P.H.J. Thomma</i> .....	541
Leaf Rust of Cultivated Barley: Pathology and Control <i>Robert F. Park, Prashant G. Golegaonkar, Lida Derevnina, Karanjeet S. Sandhu, Haydar Karaoglu, Huda M. Elmansour, Peter M. Dracatos, and Davinder Singh</i> .....	565
Highways in the Sky: Scales of Atmospheric Transport of Plant Pathogens <i>David G. Schmale III and Shane D. Ross</i> .....	591
Grapevine Leafroll Disease and Associated Viruses: A Unique Pathosystem <i>Rayapati A. Naidu, Hans J. Maree, and Johan T. Burger</i> .....	613

## Errata

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