European Journal of Plant Pathology (2006) 115:53–59
DOI 10.1007/s10658-005-2025-y

The practical considerations of scale in plant pathology

W.W. Turechek
USDA-ARS Fruit Laboratory, Building 010A – BARC-W, Baltimore Avenue, 10300 Beltsville, MD 20705-2350, USA (E-mail: turechekw@ba.ars.usda.gov)

Accepted 28 June 2005

Key words: quantitative epidemiology, strawberry

Abstract

The concept of scale has only recently gained recognition as a central theme in ecology. The rise in significance of scale in ecology can be attributed to the increase in hypothesis-driven experimental ecology over the last quarter century, and the realization that experimental results do not sufficiently explain past, or predict future observations in nature. Plant pathologists, who rely heavily on hypothesis-driven research, have confronted these same issues for nearly a century. In this paper, I will provide a concise presentation and discussion of the important concepts of scale and how they apply to the discipline of plant pathology.

Introduction

The concept of scale has only recently gained recognition as a central or unifying theme in ecology. In an extensive review of the ecological literature, Schneider (2001a) showed a dramatic increase in publications of scale-related research during the 1990s. The rise in importance of scale can be attributed to the increase in hypothesis-driven, experimental ecology over the last quarter century and the realization that experimental results do not sufficiently explain past or predict subsequent observations in nature.

Plant pathologists have confronted these same issues for nearly a century. With few exceptions, this important component of systems, observation, and analysis has been conveniently – unknowingly is perhaps a better choice of words – disregarded, sometimes to the detriment of the hypothesis. Unfortunately, the common leap from laboratory/glasshouse to the field without sufficient consideration of how outcomes may differ vastly when rescaled is a theme repeated to this day. Scaling is generally of little concern to the organismal biologist where processes under study are often clearly defined by the organism's size.

In what follows, I will provide a concise presentation and discussion of the important concepts of scale. Most of what I will present is drawn from the ecological literature, as ecologists are generally at the forefront of advancing concepts and our knowledge of scale. Three books that have helped shape my understanding of scale are 'Quantitative Ecology: Spatial and Temporal Scaling' by Schneider (1994), 'Ecological Scale: Theory and Applications' edited by Peterson and Parker (1998), and 'Scaling Relations in Experimental Ecology' edited by Gardner et al. (2001). I recommend these books to anyone wishing to gain an ecological perspective on scale.

Definitions

"Scale has a good start on contesting niche as one of the vaguest yet most often used words in ecology" (Wiens, 2001). Scale can be defined *correctly* in a number of ways. The definition that likely comes to mind when used in everyday conversation is that of cartographic scale. Cartographic scale is the ratio of the distance on a map to the distance on the ground (Schneider, 2001a). Another common usage defines scale as the

"...physical dimensions of observed entities and phenomena" (O'Neill and King, 1998). Merriam and Webster offer this definition of scale "to arrange in a graduated series" (Merriam-Webster online dictionary). In practice, most ecologists would argue against this latter definition because, unlike the previous two, the notion of quantifiable measurement (i.e., distance, dimension) is not stated explicitly. A number of ecologists have argued recently, and I agree, that any definition of scale must consider scale as a quantity and involve, or at least imply, measurements or measurement units (O'Neill and King, 1998).

Hierarchical scale equates the organizational level in a hierarchy to independent or individual scales. Hierarchical scale forms the essence of hierarchy theory (Allen and Starr, 1982) where it is argued that ecosystem processes operate in a way such that upper level processes, structure, etc. regulate and/or constrain processes at lower scales in a quantifiable manner. Some ecologists have argued that hierarchical levels should not be thought of as scales because 'level' is often an arbitrary, ambiguous or unquantifiable term (O'Neill and King, 1998; Wiens, 2001). Again, the notion of quantity is not defined explicitly in the definition, e.g., in what units does one quantify the 'leaf' level? (Turechek and Madden, 2001).

An idealistic goal in experimental design is to conduct an experiment where measurements or observations are taken at the organisms or phenomenons 'characteristic scale'. This is defined as the system scale at which all relevant ecological and biological processes of a population or community occur. This ideal, however, is likely not achievable as biological processes occur and interact over a range of scales. A better way to approach this concept is to envisage ecological phenomena occurring within upper and lower limits (Schneider, 1994). Even still, this may be easily definable for certain phenomena, such as spore dispersal, but not others, e.g., patterns of plant disease.

Scaling concepts

Given an acceptable definition, a logical next question is how to apply the term scale in practice. In other words, what exactly needs to be scaled? Dungan et al. (2002) distinguished three categories to which scale-related terms are applicable. The first category is the phenomenon (process or structure) under study. For example, the spatial pattern of plant disease and the processes that generate it. The second is the experimental or sampling units used to acquire information or data about the phenomenon under study. The third is the analyzes used to summarize the data to describe the phenomenon. From herein, I will refer to these as the system scale, observational scale, and analysis scale, respectively.

In all cases, scale is bounded by *grain* at the lowest extreme and *extent* at the other. When applied to the systems scale grain refers to the smallest ecological unit to which a phenomenon affects a structure or process; extent is the total area affected by the phenomenon, process, or structure. Applied to the observational scale grain refers to the *resolution* of measurements (Dungan et al., 2002). The frequency of sampling in space and/or time determines the resolution of the data. Extent refers to the range over which experimental measurements are taken (Wiens, 2001). For example, consider measurements of precipitation. This is an important variable in many disease forecasters and one where estimates often need to be sufficiently accurate. The recording frequency of the rain gauge (i.e., hourly, daily, weekly, etc.) sets the temporal resolution or grain. The duration of time over which precipitation is measured determines the extent. Applied to the analysis scale, calculating means and grouping sampling units coarsens grain; subsampling reduces the extent. These are a few examples of how analytical tools alter scale (O'Neill and King, 1998).

The *scope* is defined at the observational scale for experimental design, surveys, model building, etc. as the ratio of extent to grain, and is an important and useful measurement for comparing scales across studies. "Scope can be thought of as the number of steps, once we know the step size" (Schneider, 1994). For example, the temporal scope of an experiment is the ratio of the time from the beginning to the end of the experiment, to the time-step of a single measurement. The spatial scope of a survey is the ratio of the maximum length or distance between measurements relative to the minimum length or distance of a single measurement.

Disease surveys are used commonly in plant pathology to estimate some unknown value or quantity of a population, typically disease severity

or incidence (Turechek and Mahaffee, 2004). In the terminology of survey sampling, the scope of a survey is the ratio of the sampling frame to the sampling unit, where the sampling unit is the smallest item sampled and the sampling frame is the total number of possible sampling units in the survey area. It is always the case that the precision of the estimate increases, and the uncertainly decreases, as the number of samples or observations is increased. Thus, the challenge is to collect an ample number of samples to sufficiently minimize uncertainty under the logistical and natural constraints that often limit the scope of most designed surveys.

For example, a typical raised-bed field of strawberry will contain about 43,750 plants ha^{-1}. An individual strawberry plant could be considered the sampling unit in a sampling frame of 43,750 plants. In a survey for Colletotrichum crown rot (caused by *C. acutatum*) a sample of 500 plants gives a sampling fraction (i.e., the ratio of the number of samples taken to the sampling frame) of 500/43750 or 1.14%. The inverse of the sampling fraction represents the magnification factor (MF). The magnification factor magnifies the result of the sample into an estimate for the entire population. For example, say 20% of the sample (100 plants) was diagnosed with crown rot. Multiplying the number of diseased plants by the MF (i.e., 87.7) informs us that we should expect to find 8770 plants with crown rot in the population, assuming a random distribution of infected plants. The magnification factor can be reduced by sampling more plants, but at a cost. Cluster sampling allows the sampler to observe a greater number of plants with the same number of sampling units (Hughes et al., 1996). This, in effect, will reduce the MF at the cost of decreasing resolution and, consequently, will give a reduced scope. The benefit of the trade-off needs to be determined for each study and can be represented in a scope diagram.

A scope diagram is one way of displaying or comparing the scope among different phenomena, events, or studies. Schneider (1994) demonstrates how a simple line diagram can be used to represent the scope of a survey. The line can be partitioned into two components, one representing the scope of the sample and the remainder the inference component of the sample represented by MF. This simple diagram can be used to compare survey strategies and help decide the best approach. Continuing with the strawberry example, assume that in a hectare of strawberries a single plant occupies a space of 0.1 m^2. Figure 1 depicts the scope diagrams for three 100 unit samples where: (1) single plants are observed or collected in a random sample, (2) groups of 10 plants are collected in a cluster sample, and (3) 10 m^2 grids are observed via aerial sampling. In this example, the number of samples collected or observed remains the same, but the size of the sampling unit changes resulting in a smaller magnification factor and a

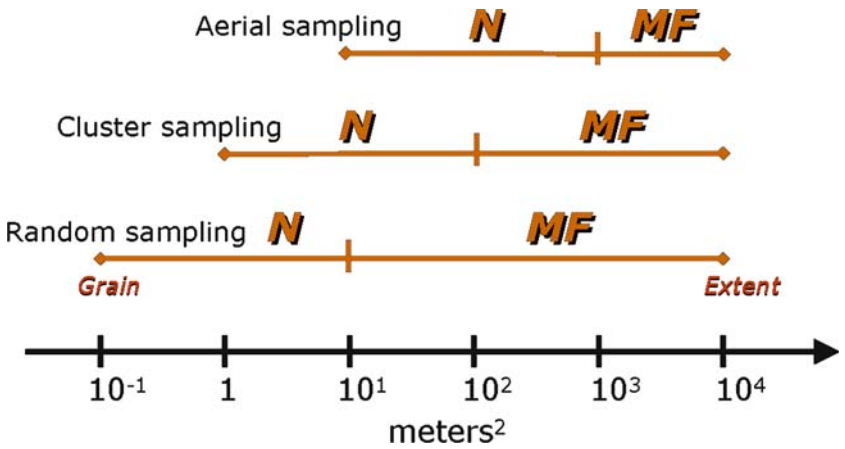

Figure 1. Scope diagrams for three 100 unit samples where: (1) single plants are observed or collected in a random sample, (2) groups of 10 plants are collected in a cluster sample, and (3) 10 m^2 grids are observed via aerial sampling. The starting point of each diagram represents the grain or resolution of the data at the observational scale, and the ending point represents the extent of the study (the sampling frame). The sample size is denoted by *N* and the magnification factor by MF.

reduced scope. Scope diagrams can be much more complex. Seem (2004) gives a good example of scope diagram and its applicability in disease forecasting.

Scaling in practice

The practice of *scaling* involves relating measurements made at one scale to measurements or predictions made at another. A scale-dependent process is one in which the process (e.g., rate) or property (e.g., density) changes with a change of grain or extent. An example of scale dependency encountered often in plant pathology is scale-dependent patterns of plant disease, i.e., patterns differing with sampling unit size and/or extent of the survey. Although these scaling dependencies can be represented through various modelling procedures (Allen, 2001), episodic dynamics, non-Euclidean structures, and/or biotic discontinuities that are typically associated with ecological processes or phenomena make modelling (scaling) a challenge.

Episodic dynamics generally make it difficult to scale temporal events. For example, 30 mm of rainfall over the course of an hour implies a rainfall rate of 0.5 mm min^{-1}; an increase in disease severity from 3 lesions/leaf to 52 lesions/leaf over the period of 7 days implies a rate of disease progress of 7 lesions day^{-1}. The process of calculating rates masks the fact that precipitation and lesion development occur as concentrated events (episodes) over some defined time period. Non-Euclidean structures (such as landscape surfaces) and patchy or heterogeneous environments generally make it difficult to scale spatial properties because they lead to fractal dimensions (i.e., greater than a plane, but less than a volume). For example, wind patterns contributing to larger scale patterns of spore dispersal and microclimatic variability are directly affected by variations in topography in a largely unpredictable manner, much more so than if these events were to occur over a strictly two-dimensional surface.

Biotic boundaries or discontinuities further contribute to modelling headaches. For example, a change of 3 °C from 27 to 30 °C straddles the critical temperature for conidial germination of *Podosphaera macularis*, the causal agent of hop powdery mildew (Mahaffee et al., 2003). Other biotic boundaries are often much more difficult to define and are not necessarily constrained by quantifiable units (Naeem, 2001). For example, the taxonomic groupings of race, subspecies, species, genus, and sometimes higher groupings can often be ambiguous. At the population level, the boundaries between patches, communities, metapopulations, etc. is often blurred due to fluctuations in growth, decline, and interactions among populations.

Considerations in experimental design

"The near absence of prescriptions for incorporating scale in experimental design may partially explain why explicit consideration of scale is not more prevalent in the design of terrestrial field experiments" (King et al., 2001). Readers interested in a statistical treatment of this topic are referred to two chapters by Dutilleul (1998a, b). I will touch on a broader aspect of design: the desire to have experimental results relate directly to natural observation. Every experiment is subject to a compromise between what Manly (1992) defines as internal vs. external validity (Naeem, 2001). "Internal validity concerns whether the apparent effects or lack of effects shown by the experimental results are due to the factor being studied, rather than some alternative factor. External validity concerns the extent to which the results of an experiment can be generalized to some wider population of interest." Naeem (2001) groups experiments into three general classes: (1) field, (2) model-ecosystem (micro-, meso-, and macrocosm), and (3) simulation. Field experiments have the highest level of external validity and, consequently, the lowest level of internal validity. Conversely, simulation experiments have the highest level of internal validity and lowest level of external validity.

More often than not, the type of experiment and the choice of scale (determined by plot size, duration, sampling extent, etc.) are a function of pragmatism. Available funding, personnel, experimental costs, measurement technology, etc. play a more central role in the design of experiments than does the theoretical consideration of scale and validity. In any event, it is likely (and is often the case) that to gain a full understanding of a process, sets of experiments that span the range of what Naeem (2001) refers to as the "scale-validity matrix" must be conducted. That is, a reasonable set

of field, microcosm, or simulation experiments conducted at different spatial, temporal, and possibly biotic scales are often necessary to fully interpret a process or to explain what was observed naturally.

Multiscale analysis

In the (failed) quest for a 'characteristic scale', multiscale analysis has evolved to play a central role in scaling. Multiscale analysis is defined as an analysis with respect to multiples of a unit of measurement (Schneider, 1994). In general, this type of analysis is done by first defining subsystems within a system. In a survey, this might be accomplished by superimposing a grid over the region of study or spatially referencing sampling units in the survey area. As one example, summing the components of the subsystem, grid, or sampling units (with correction factors introduced as needed) can be used to scale to larger areas (Schneider, 2001b). Quantities can be summed by either juxtaposing or superposing values. Summation by juxtaposing values extends the range of scale; summation by superposing leaves the scale unchanged. Summing the number of diseased plants in a series of contiguous plots is an example of juxtaposing; summing the number of newly diseased plants to the number of previously diseased plants in a single plot is an example of superposing.

The variance plays a central role in multiscale analysis. ''One of the major research challenges in ecology is understanding the creation and erosion of spatial variability as a function of spatial scale. Included in this challenge is the question of the degree to which variance generated at one scale is transformed into variance at another scale'' (Schneider, 1994). Across many disciplines, including plant pathology, methods have been developed for relating and/or predicting variance across scales (Hughes et al., 1997; Turechek and Madden, 2003). However, the mere ability to model these relations should not be mistaken as an understanding of how these relations came to be. For the most part, the mechanisms or biological processes generating these differences are only partially understood.

The sample variance is only one measure of spatial variability and has limited interpretation in multiscale analysis. Variances can also be calculated from grouped or lagged measurements or observations. (The term *lag* refers to the interval or spacing between neighbouring units.) Imagining a grid; grouping occurs when contiguous squares of the grid (sampling units) are combined to form larger units and the quantities are combined via juxtaposition (added); under these conditions the resolution of the data changes. Variances are obtained by re-calculating the variance of the combined quantities, and comparing it to the original or ungrouped variance and to variances calculated from successively larger groupings. The blocked quadrat-variance methods, such as the two-term local quadrat variance (TTLQV) method and the paired-quadrat variance (PQV) method, are examples of analyses that use grouped variances (Ludwig and Reynolds, 1988). Lagging, on the other hand, results from calculating deviances between grid components (sampling units) at increasingly greater separations (lags) across the grid. Again, these variances are compared to the original sample variance as well as to variances calculated at different lag distances. Autocorrelation and semivariogram analyses are examples of analyses that use lagged variances (Cressie, 1991). Variances calculated according to the lag manoeuvre can be used to calculate variances that would be obtained via grouping using a Fourier transformation (Schneider, 1994).

Scaled quantities cannot be treated as unitless numbers. The process of summing, multiplying, and taking derivatives of scaled quantities should not be done independently of the unit. For example, the sum of 52 lesions/leaf and 6 diseased trees/orchard is non-sensical. Biologically interpretable sums of scaled quantities are referred to as ensemble quantities (Schneider, 1994). Spatial and temporal averages, variances, and covariances are typical ensemble quantities. This definition differs from the traditional in which an ensemble refers to a collection of 'realizations' of an event or process; the ensemble average, for example, is the mean of the realizations. Although this concept is evident in plant pathology research, the terminology is infrequently used (one exception is Ferrandino, 2004).

Statistical tools

Over the past 20 years, the variety of statistical tools available for multiscale analyses has

increased tremendously; many have been applied to characterize spatial patterns of plant disease. The tests, however, can be categorized based on the general type of analysis, point-pattern vs. correlation (Upton and Fingleton, 1985), or on whether the data consist of mapped or unmapped observations (Diggle, 1983). The point-pattern approach is based on the location of individuals over an area of interest and analyses are conducted either using the distances between individuals (Perry, 1995; Ferrandino, 1998), or using the counts of individuals within sampling units such as quadrats (Pielou, 1977; Madden and Hughes, 1995). The latter methods include the distributional approach that involves fitting observed frequencies of counts per sampling unit to well-defined statistical distributions (e.g., Poisson, negative binomial, binomial, and beta-binomial). The methods based on counts per sampling unit provide direct measurements of heterogeneity of the data at the scale of the sampling units and below, but they do not explicitly define the spatial arrangement of the sampling-unit counts unless several sampling units are grouped in a series of steps (Ludwig and Reynolds, 1988).

Spatial autocorrelation and semivariograms (Cressie, 1991) use lagged variances to produce explicit information on the degree of association of disease intensity among sampling units. Unlike the distributional methods, these methods yield different results for different arrangements of counts within a field, although they are not specifically developed for counts within sampling units. Spatial Analysis by Distance IndicEs (SADIE) is a class of tests developed recently to quantify spatial pattern in the spirit of spatial autocorrelation, but uses data in the form of counts (Perry, 1995; Xu and Madden, 2004). The correlation-based methods characterize pattern at the scale of the sampling unit and above. The results from point-pattern and correlation-type analyses can jointly be used to better interpret patterns and possibly describe the biological phenomenon responsible for generating the observed pattern (Turechek and Madden, 1999).

Simulation and randomizations have also been used to study scale-related processes. For example, Turechek and Madden (2001) used Monte–Carlo methods and randomizations to determine how the variability of strawberry leaf blight at a lower scale impacted the variability at higher scales. Willocquet and Savary (2004) designed a simulation model to determine how varying auto-, allo-leaf, and allo-plant-deposition rates of infective propagules affected epidemic development observed at the plant and leaf level (in both examples, measurement units are implied). As discussed above, simulation studies have a high degree of internal validity and allow researchers to explore a range of conditions that may otherwise take years to observe.

Conclusion

The intent of this paper was to provide an overview of scale-related concepts and how they might apply to plant pathology. Although I did not provide prescriptive advice on how to include scale in designed studies, I hope I made it obvious where scaling is naturally applied in our discipline. I also hope that I impressed the importance of being vigilant in reporting the scale (grain, extent, and scope) of experiments and surveys to allow for drawing valid comparisons across studies.

To summarize briefly, before designing any experiment or survey, it would be prudent to acquire preliminary data on the structure of the population under study so that sampling units (i.e., grain) and the extent of the study can be appropriately chosen (Legendre and Legendre, 1998). Realize that this information may indicate that a single study may not be sufficient to gain a full understanding of the process or characteristic under study. It is also important to consider the units of measurement and how easily information can be rescaled. Pathologists should avoid describing the scale of study as, for example, the 'leaf scale' unless a unit of measurement is clearly implied. In many cases, it is likely that the scale can be defined within some narrow range of values, and these should be used to identify the scale (grain) of study. Lastly, be aware that many field studies or surveys of disease are the result of the interaction between two populations: the population of the host and the population of the pathogen. The scale at which the host population exists should be an important consideration of the pathogen population, because the host represents the possible extent of the pathogen. For example, knowing the scale of spore dispersal distance is not very informative unless the distance significantly overlaps the range of the host. Considering these aspects of scale in the design of an

experiment will help to minimize the possibly large discrepancies in scale between what is observed and what is being tested.

References

Allen TFH (2001) The nature of the scaling issue in experimentation. In: Gardner RH, Kemp WM, Kennedy VS and Peterson JE (eds) Scaling Relations in Experimental Ecology. Columbia University Press, New York

Allen TFH and Starr TB (1982) Hierarchy, University of Chicago Press, Chicago

Cressie N (1991) Statistics for Spatial Data, Wiley, New York

Diggle PJ (1983) Statistical Analysis of Spatial Point Patterns, Academic Press, London

Dungan JI, Perry JN, Dale MRT, Legendre P, Citron-Pousty S, Fortin M-J, Jakomulska A, Miriti M and Rosenberg MS (2002) A balanced view of scale in spatial statistical analysis. Ecography 25: 626–640

Dutilleul P (1998a) Incorporating scale in ecological experiments: Study design. In: Peterson DL and Parker VT (eds) Ecological Scale: Theory and Applications. Columbia University Press, New York

Dutilleul P (1998b) Incorporating scale in ecological experiments: Data analysis. In: Peterson DL and Parker VT (eds) Ecological Scale: Theory and Applications. Columbia University Press, New York

Ferrandino FJ (1998) Past non-randomness and aggregation to spatial correlation: 2DCORR, a new approach for discrete data. Phytopathology 88: 84–91

Ferrandino FJ (2004) Measuring spatial aggregation in binary epidemics: Correlative analysis and the advantage of fractal-based sampling. Phytopathology 94: 1215–1227

Gardner RH, Kemp WM, Kennedy VS and Peterson JE (eds) (2001) *Scaling Relations in Experimental Ecology*. Columbia University Press, New York

Hughes G, Madden LV and Munkvold GP (1996) Cluster sampling for disease incidence data. Phytopathology 86: 132–137

Hughes G, McRoberts N, Madden LV and Gottwald TR (1997) Relationship between disease incidence at two levels in a spatial hierarchy. Phytopathology 87: 542–550

King AW, Gardner RH, Hatfield CA, Naeem S, Peterson JE and Wiens JA (2001) Terrestrial perspectives on issues of scale in experimental ecology. In: Gardner RH, Kemp WM, Kennedy VS and Peterson JE (eds) Scaling Relations in Experimental Ecology. Columbia University Press, New York

Legendre P and Legendre L (1998) Numerical Ecology, Elsevier Science, Amesterdam

Ludwig JA and Reynolds JF (1988) Statistical Ecology: A Primer on Methods and Momputing, Wiley-Interscience, New York

Madden LV and Hughes G (1995) Plant disease incidence: Distributions, heterogeneity, and temporal analysis. Annual Review of Phytopathology 33: 529–564

Mahaffee WF, Turechek WW and Ocamb CM (2003) Effect of variable temperature on infection severity of *Podosphaera macularis* on hops. Phytopathology 93: 1587–1592

Manly BFJ (1992) The Design and Analysis of Research Studies, Cambridge University Press, Cambridge

Naeem S (2001) Experimental validity and ecological scale as criteria for evaluating research programs. In: Gardner RH, Kemp WM, Kennedy VS and Peterson JE (eds) Scaling Relations in Experimental Ecology. Columbia University Press, New York

O'Neill RV and King AW (1998) Homage to St. Michael; or, why are there so many books on scale? . In: Peterson DL and Parker VT (eds) Ecological Scale: Theory and Applications. Columbia University Press, New York

Peterson DL and Parker VT (eds) (1998) Ecological Scale: Theory and Applications. Columbia University Press, New York

Perry JN (1995) Spatial analysis by distance indices. Journal of Animal Ecology 64: 303–314

Pielou EC (1977) Mathematical Ecology, Wiley, New York

Schneider DC (1994) Quantitative Ecology: Spatial and Temporal Scaling, Academic Press, San Diego

Schneider DC (2001a) The rise of the concept of scale in ecology. Bioscience 7: 545–553

Schneider DC (2001b) Spatial allometry: Theory and application to experimental and natural aquatic ecosystems. In: Gardner RH, Kemp WM, Kennedy VS and Peterson JE (eds) Scaling Relations in Experimental Ecology. Columbia University Press, New York

Seem RC (2004) Forecasting plant disease in a changing climate: A question of scale. Canadian Journal of Plant Pathology 26: 274–283

Turechek WW and Madden LV (1999) Spatial pattern analysis of strawberry leaf blight in perennial production systems. Phytopathology 89: 421–433

Turechek WW and Madden LV (2001) Effect of scale on plant disease incidence and heterogeneity in a spatial hierarchy. Ecological Modeling 144: 77–95

Turechek WW and Madden LV (2003) A generalized linear modeling approach for characterizing disease incidence in a spatial hierarchy. Phytopathology 93: 458–466

Turechek WW and Mahaffee WF (2004) Spatial pattern analysis of hop powdery mildew in the Pacific Northwest: Implications for sampling. Phytopathology 94: 1116–1128

Upton G and Fingleton B (1985) Spatial Data Analysis by Example, Vol 1. Point Pattern and Quantitative Data, John Wiley & Sons, West Sussex

Wiens JA (2001) Understanding the problem of scale in experimental ecology. In: Gardner RH, Kemp WM, Kennedy VS and Peterson JE (eds) Scaling Relations in Experimental Ecology. Columbia University Press, New York

Willocquet L and Savary S (2004) An epidemiological simulation model with three scales of a spatial hierarchy. Phytopathology 94: 883–891

Xu XM and Madden LV (2004) Use of SADIE statistics to study spatial dynamics of plant disease epidemics. Plant Pathology 53: 38–49