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Information networks for disease: commonalities in human management networks and within-host signalling networks

K. A. Garrett

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Abstract Network models of human epidemics can often be improved by including the effects of behaviour modification in response to information about the approach of epidemics. Similarly, there are opportunities to incorporate the flow of information and its effects in plant disease epidemics in network models at multiple scales. (1) In the case of human management networks for plant disease, each node of a network has four main components: plant communities, microbial communities, human information (among researchers, extension agents, farmers, and other stakeholders), and environmental conditions, along with their interactions. The links between nodes, representing the rate of movement between them, have three parts: the rates for plant materials, the rates for microbes, and the rates for information. Network resilience for information flow is an important goal for such systems. Game theory can provide insights into how human agents decide how to invest their efforts in strengthening information networks, and how policies can support more resilient networks. (2) For the case of within-plant signalling networks, each node has a comparable set of four main components: plant signals (often in the form of phytohormones) and development status, microbial communities and plant disease status, microbial signals (often in the form of quorum sensing molecules), and micro-environmental conditions, along with their interactions. In effect, human information is replaced by plant signals and microbial signals in this second model. The links between nodes have three parts: the rates for microbes, the rates for microbial signals (which may move separately from the microbes, themselves), and the rates for plant signals. Understanding how to enhance adaptive plant signalling networks and microbial signalling networks that support plant productivity, and disrupt microbial signalling networks that contribute to pathogenicity, will be an important step for improved disease management.

Keywords Decision making · Dynamic networks · Host as habitat · Mesoscale networks · Multi-scale modelling · Quorum sensing · Systems biology · Biofilms

K. A. Garrett (✉)
Department of Plant Pathology, Kansas State University, Manhattan, KS 66506, USA
e-mail: kgarrett@ksu.edu

Introduction

Network models are used to describe processes where there are discrete nodes, such as individual people, plants, or political units, and each pair of individuals is joined (or not) by a link. Wider use of network models for plant disease epidemics is motivated by, for example, changes in the structure of horticultural trade that must be understood to protect against pathogen invasions (Dehnen-Schmutz et al. 2010). One of the simplest types of network models would be one representing a group of people (nodes),

where each pair of people is either acquainted or not (a link exists between the pair, or does not). Network models become more elaborate as more types of information are included. For example, the link between a pair of people might have a weight indicating how often the two see each other. Or the link might have a weight indicating how likely one of the pair is to infect the other with a disease. The inclusion of more and more interesting and useful features of interactions has led to complex weighted network models (Newman 2003; Barrat et al. 2004). Networks may describe features such as the relationship between species (nodes) in food webs, but this paper focuses on networks that explicitly describe processes in space (Dale and Fortin 2010; Barthelemy 2011). One particularly useful aspect of network models is that understanding the topology of interactions among the nodes leads to understanding of emergent properties of the system. For example, often threshold levels of pathogen movement and establishment that allow an epidemic to progress or not can be identified as a function of the network structure.

Network models offer a fresh perspective on plant disease epidemics (Jeger et al. 2007; Moslonka-Lefebvre et al. 2011). For example, it is useful to understand whether a plant pathogen is likely to move from a neighbouring field into a new field, by understanding principles of pathogen dispersal. Network models can provide insight into whether a disease is likely to move through a network of fields to reach a new field, as a function of how 'well-connected' those fields are to each other. Use of network models can help to partition the effects of spatial and temporal organization on the risk of pathogen spread (Brooks et al. 2008). The terminology of networks is helpful for developing a common vocabulary to understand similar processes acting across temporal and spatial scales in plant pathology, from individuals to landscapes (Jordán et al. 2010), where individual plants may constitute landscapes for microbes. As an example, consider the wheat plant in Fig. 1a and a corresponding network summarizing the wheat structure at the organ level in Fig. 1b, from the perspective of a plant-associated microbe.

This paper addresses network models to describe epidemic processes both within host plants and at larger scales. It emphasizes how information influences

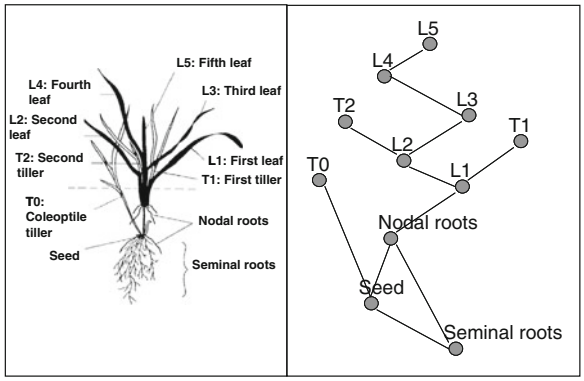

Fig. 1 **a** Vegetative wheat plant structure (image from Klepper et al. (1983)). **b** A corresponding network graph, where lines indicate direct physical links. (Note that the best formulation of this network can be debated, in terms of how leaves in a grass are linked.) Nodes are *adjacent* if connected by a link; for example, the nodes representing leaf 1 (L1) and leaf 2 (L2) are adjacent. In this model, only the most direct physical connections are treated as producing adjacency, but other processes such dispersal through air or water could produce additional links for microbes. If links are directional (*arcs*), such as processes related to xylem or, depending on growth stage, phloem, then the graph may be a *digraph* (= *directional graph*). The *degree* of a node is the number of links *incident*, or linked, to the node; L2 and the seed both have the highest degree in this model, three. In digraphs, the in-degree and out-degree can also be evaluated. A *walk* on a graph is an alternating sequence of nodes and links, and the *length* of the walk is the number of links the path includes; for example the length of the walk between L1 and L5 is four. A *path* is a walk without repeated links or nodes. A node is *reachable* from another node if a walk exists between them. A graph is *connected* if any node can be reached from any other node, as in this model; graphs for some processes within plants or between plants would not be connected

epidemics, as information moves through the same networks as do pathogens, or ideally can be made to move through more efficient networks. The objective of this paper is to contribute to the development of a conceptual framework for (1) linked epidemic networks and information networks for plant disease, and (2) mesoscale plant-microbe networks, scaled between epidemic networks of multiple host individuals and genetic networks of gene interactions.

Human networks for disease management

The spread of information and its effects on epidemics

The idea that the spread of ideas (or memes) is analogous to the spread of a disease (or genes in

a population) has been stimulating scientists for some time (Gerard et al. 1956; Goffman and Newill 1964; Dawkins 1976), with inroads in popular culture (e.g., Language is a Virus, Laurie Anderson). Intriguing models of networks of human relationships have also been developing rapidly across decades (Goffman and Newill 1964; Agliari et al. 2006), with a journal devoted to the topic: Social Networks. Evaluations of human communication, particularly, have taken this perspective, with increasing mathematical rigour, such as in 'theories of rumour' (Nekovee et al. 2007). Now there are many models of communication processes such as movement of information through the internet and networks of scientific citations. Epidemic and communication networks have been frequent topics for network modelling, but it is only recently that they have been considered simultaneously in systems in which information and epidemics interact as individuals use information about epidemics to guide decisions such as whether to vaccinate (Del Valle et al. 2005; Salathé and Bonhoeffer 2008; Perisic and Bauch 2009).

Social structures in human populations may affect movement of epidemics (Andersson 1997). A primary behaviour change in response to information about human epidemics may be change in how frequently people choose to encounter others and other attempts to avoid exposure, which may or may not slow epidemics (Del Valle et al. 2005; Meloni et al. 2011). Increasingly information is available about patterns of interaction among study groups of people (Edmunds et al. 1997; Eubank et al. 2004; Mossong et al. 2008; Scoglio et al. 2010). Individuals as nodes may choose to modify their network links, such that they have less exposure to potential infection sources (Gross et al. 2006).

Funk et al. (2010) have developed a classification for voluntary behaviour initiated by individuals (as opposed to behaviour imposed through outside rules) to manage their disease risk. They categorize models first in terms of the source of information: 'global' information that is publically available vs. 'local' information that comes from their social neighbourhood. Clustered beliefs about how best to manage disease may lead to clusters of lower or higher infection, depending on how well beliefs correspond to actual effective management strategies. Local spread of useful information has the potential to stop an epidemic (Funk et al. 2009). Second, there are different types of information. Information about incidence ('prevalence') and severity of disease is one important form, perhaps the type of information most commonly addressed in models of human disease. Funk et al. (2010) distinguish between 'prevalence-based' and 'belief-based' information. Belief-based information may relate to decisions in advance of the approach of disease, such as decisions about vaccination (Cornforth et al. 2011) (or, in the case of plant disease, decisions about what types of management are needed in terms of form of cultivar resistance, use of pesticides and cultural practices, etc., as discussed by Savary et al. (2006)). Not only beliefs about factors such as the costs and benefits of vaccination may move through networks, but also emotions (Hill et al. 2010), which may influence the likelihood that managers make optimal decisions for themselves and others in their network. Models of information flow through networks may also incorporate the degeneration of information as it moves from one agent to another (Agliari et al. 2006) or within an agent over time.

Plant disease networks

There are similarities whether information networks provide information about the risk of human disease or the risk of disease in plants managed by humans. For IPM, different types of information play a role. Irwin (1999) discussed three 'tiers' of information: a fundamental knowledge base (scientific fields such as plant pathology, aerobiology, etc.), tactical or methodological (biological control, chemical control, host resistance deployment, habitat manipulation), and operational (integration of tactics into a scalable strategy). For 'global' (in the sense of Funk et al. (2010)) plant disease, national and international diagnostic networks provide information about the types of disease found at different geographic nodes of epidemic/information networks, as well as information about how to identify pathogens and vectors (Stack et al. 2006; Miller et al. 2009). For some diseases, such as endemic soilborne diseases that have long-lived structures for survival when a host is not available, farmers primarily make use of information about management. New invasive pathogens may arrive at new locations, or familiar pathogens may make annual migrations to arrive at different times and so require different types of information for management. For pathogens such as soybean rust, each growing season represents a new invasion for the regions that do not support

overwintering (Li et al. 2010). Long-distance spore transport is also important for other rusts such as wheat stripe rust (Wang et al. 2010). The timing of arrival is critically important for decision-making in areas distant from overwintering sites for diseases such as soybean rust or wheat rusts, because appropriate management timing is necessary for efficiency (Isard et al. 2004; Isard et al. 2005; Isard et al. 2007). Application of network models supports analysis of the importance of information about disease at the nodes in such epidemic networks (Chadès et al. 2011), so that an efficient set of nodes can be selected for sampling (for example, for soybean rust in the US, shown by Sutrave, S., Scoglio C., Isard, S. A., Hutchinson, J. M. S., and Garrett K. A., in preparation).

The networks formed by landscapes of plant communities have been considered most commonly for variety mixtures or intercropping (Finckh et al. 2000), and sometimes at larger scales such as epidemic processes among fields or at larger scales (Margosian et al. 2009). Understanding of the current and potential structure of epidemic networks can potentially be used to design networks with lower disease risk (Liu et al. 2011; Schneider et al. 2011). Disruption of epidemic networks because of higher plant diversity can be a form of ecosystem service, while the presence of additional host species that strengthen networks by functioning as green bridges or other means can be a form of ecosystem disservice (Cheatham et al. 2009). In general, higher host diversity tends to decrease disease risk (Garrett and Mundt 1999; Keesing et al. 2006), so the diversity of hosts within networks will have important effects on epidemics, where immune or highly resistant hosts may essentially be removed from the network. For example, in a network analysis of important crop species in the US, each county was represented in the network by a node (Margosian et al. 2009). The resistance to movement between nodes was modelled as a function of the availability of the host crop species being evaluated. In order to evaluate the impact of host availability for a range of different types of invasive pathogens or vectors, the network was evaluated for a range of different threshold tolerances. For example, some species can only move short distances without contact with their hosts (without human help), and for these species only low levels of resistance to transmission would allow links to be retained in the network. This analysis provides perspective on the potential for host crop species distributions to influence epidemic spread. Agricultural and natural or unmanaged systems may be linked through their shared pathogens, such as links among tallgrass prairie, maize, sorghum, and soybean fields through the generalist pathogen *Macrophomina phaseolina* (Saleh et al. 2010). Networks formed by plants are also dynamic at different time scales as annual crops are sown and harvested. The conduciveness of the environment for disease also influences the effect of network structure on epidemics (Garrett et al. 2009).

Human information networks for plant disease management

A model of human information networks related to plant disease management might include the elements illustrated in Fig. 2. In this diagram, links join geographical nodes, where nodes might be individual plants, fields, farms, counties, regions, or countries. At each node, four main factors interact to determine the role that that node will play in the larger network. (1) The plant communities present at the node will determine what plant diseases may be present and what microbial communities may be supported. (2) The information available at this node will influence how plants are managed. Farmers may or may not act efficiently and effectively to manage disease, depending on factors such as the information they have access to, and their perceptions of risk and how those perceptions

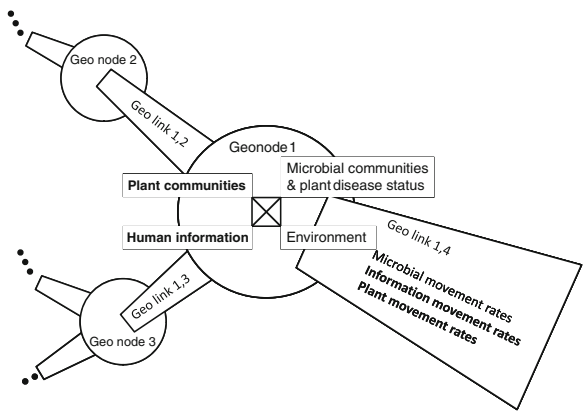

Fig. 2 Nodes and links within a geographic network, where a node might be a farm, county, region, or country

influence their decision-making (McRoberts et al. 2011). In scenarios where resource-poor farmers have limited access to information, programs such as farmer field schools may support better decision-making (Ortiz et al. 2004). (3) Environmental conditions will influence both plant-microbe interactions and human decision-making. For example, the increasing environmental variability predicted in climate change scenarios will change the utility of different weightings of past and present experience in farmers' decision-making (Garrett, K. A., Dobson, A., Kroschel, J., Natarajan, B., Orlandini, S., Randolph, S., Tonnang, H. E. Z., and Valdivia, C., in review). (4) The current microbial communities and disease status will directly affect the probability of disease movement from this node. The local structure at the beginning of an epidemic may be particularly important (Keeling 1999). These four factors will interact as generally described for the plant disease triangle, or plant disease tetrahedron. Between each pair of nodes, there may be a nonzero rate of influence for three of these factors (where movement of environments is less germane to the concepts discussed here). Rates are not necessarily related at all to the Euclidean distance between nodes. (1) Microbes may move between nodes, 'directly' as windborne spores or vectored by arthropods, for example. (2) Information moves between nodes, where cell phones and newer technologies for dispersing information can facilitate if valuable information is not lost in noise. Key people such as extension agents may act as information 'hubs' or 'superspreaders'. (3) Plant movement by humans may be a particularly important means for movement of microbes. Transport of plants through networks such as those of cargo ships is becoming more feasible to incorporate in models (Blasius et al. 2010). The capacity for inspection of plant materials is limited, so strategies for optimizing inspection are needed (Surkov et al. 2008). Moslonka-Lefebvre et al. (2011) review network models of plant pathogens including *Phytophthora ramorum*, the causal agent of sudden oak death and other diseases of trees and shrubs. In this system, it is important to consider both 'natural' spread and spread through trade networks. The effects of different changes to this epidemic network, such as inspection and eradication programs, have been evaluated in simulations to identify the best strategies for management (Harwood et al. 2009). The relationship between epidemic networks and information networks will also be an important consideration for climate change scenario analysis and adaptation (Garrett et al. 2011).

An important consideration is the resilience of human networks that process information related to the management of plant disease, where resilience is defined here as the ability of a system to continue with essentially the same desirable features despite perturbations to the system. There are many potential perturbations to the general system in Fig. 2. New pathogens may be introduced, for which there may be a lag in the availability of information at some nodes. Budget cuts for formal information networks, such as reduced funding for the US National Plant Diagnostic Network, disrupt established networks. Folke et al. (2005) review how the structure of human organizations determines the success of adaptive ecosystem-based management when there are abrupt changes. Social networks within governance systems can help in the process of transformation to a more desirable state during periods of crisis. The high level of uncertainty associated with complex ecosystem and management systems motivates regular adjustment of approaches through adaptive management. Especially when change is rapid, informal social networks can complement hierarchical bureaucracies. The social capital of a human group provides advantages through the 'citizenship behaviors' of group members (Bolino et al. 2002). The nature of human networks has the potential to contribute to effective problem solving, such as cooperation to stop an epidemic. 'Agency within networks requires specific skills from entrepreneurs, including ones that enable pattern generation, relationship building and brokering, knowledge and resource brokering, and network recharging' (Moore and Westley 2011). Biological networks have the potential to serve as examples for the construction of robust human information networks; for example, Tero et al. (2010) have compared networks formed by a slime mold to the Tokyo rail system.

Theoretical perspectives on epidemic and information networks

Theoretical analyses of the effects of network structure offer perspective on potential outcomes for plant disease epidemic and information networks. Moslonka-Lefebvre et al. (2011) also review some of the key traits of epidemic networks, where knowledge about the form of the network can provide insights for anticipating the likelihood of different types of outcomes for an epidemic. For example, the epidemic

threshold, the threshold above which an epidemic spreads and below which an epidemic dies out, is a function of the probability of transmission, the probability of persistence, and the network structure. Analysis of networks can give insights into how management actions to limit transmission and/or persistence, or to modify network structure, can most efficiently be used to move a system below the epidemic threshold. Other measures capture aspects of how well-connected a network is, such as connectance, the fraction of possible links that exist in the network. Many networks exhibit nodes with a scale-free power-law distribution (Barabasi and Albert 1999). 'Many existing natural, social, and technological networks have been shown to have small-world (local connectivity with short-cuts) and scale-free (presence of superconnected nodes) properties' (Moslonka-Lefebvre et al. 2011). Scale-free networks generally have a lower threshold than other network forms, which also holds true for small networks with a positive correlation between links in and out of nodes (Pautasso and Jeger 2008). Scale-free networks also support the spread of 'rumors'(Nekovee et al. 2007) or general information. In 'small world' scenarios, individuals that are particularly well-connected may be the most important for epidemic processes (e.g., Mossong et al. 2008). The goal for management is to break the short-cuts in epidemic movement, while introducing and strengthening the short-cuts in the movement of information contributing to management.

Game theory offers useful perspectives on human decision-making, as well as the co-evolution of plants and microbes. One game commonly considered, in many variations, is the Prisoner's Dilemma. In a simple form of the game, two prisoners must decide whether to confess to a crime or not, without being able to discuss the situation with each other. If neither confesses, they both go free. If both confess, they each have a shorter sentence. If one confesses and the other does not, the one who does not confess has a longer sentence. The trick for a prisoner is to weigh the different outcomes without knowing what the other prisoner will do, though perhaps with an estimate of the probability that the other prisoner will decide to confess. This game can be generalized to other situations where a person makes decisions without knowing other people's future actions. In the context of information networks, people must decide what information to collect and what to share, in part as a function of whether other people are likely to collect and share information, too. In general, plant pathologists in academia are motivated to share information (unless they are waiting until after it has been published), but time constraints and funding opportunities will determine how much effort they invest in collecting and distributing particular information resources. The Prisoner's Dilemma has also been evaluated for the case of decision makers in networks. If the prisoner's dilemma is considered on a small-world network, an intermediate optimum level of topological heterogeneity is observed for cooperation (Fu et al. 2007). In the Continuous Prisoner's Dilemma, agents may have different degrees of cooperation rather than an all-or-nothing scenario. In simulations of this game in networks, levels of cooperation evolve to higher levels when agents are clustered in networks (Ifti et al. 2004) and clusters of cooperators have higher success (Luthi et al. 2008). Network structure for mutualistic networks may be favoured by high levels of connection and nested architecture (Thebault and Fontaine 2010).

In addition to decisions about information sharing, game theory can provide insights into people's decisions about disease management. Decisions about vaccination have been studied in a game theoretic framework. Smaller network neighbourhoods may support greater protection through 'herd immunity' when not all people are vaccinated (Perisic and Bauch 2009). Herd immunity is the phenomenon by which a group of potential hosts is effectively protected even if not all members have protection through vaccination or other means, although opinion processes can lead to clusters of unprotected individuals (Salathé and Bonhoeffer 2008). In game theory models, the vaccination rates observed when individual agents act only in their perceived self-interest is generally below what would be optimal for the group (Funk et al. 2010). Individuals who do not vaccinate may still benefit from lower disease exposure because others have vaccinated, while the unvaccinated individuals have avoided the perceived costs of vaccination.

Analogously, farmers might decide to manage plant disease less strenuously if they believe that the management efforts of farmers around them will protect them from disease. A multi-state analysis of benefits from 'herd immunity' in maize suggests that non-Bt-maize has experienced lower European

corn borer damage as a result of being mixed with Bt maize (Hutchison et al. 2010). Conversely, non-Bt maize refugia are designed to reduce selection pressure for European corn borers to develop tolerance to Bt maize. In this case, farmers forego the potential immediate benefits of growing Bt maize on the refugia lands, to gain the future benefit of Bt maize that is still effective against local populations of European corn borer.

Within-host signalling networks

Networks within individual plants

There is an obvious analogy between these models of human communication, and communication within and among microbial communities and individual host plants. The mesoscale for plant-microbe network models might be defined as scales ranging from between-cells to between-individuals, in contrast to larger geographic networks or smaller genetic networks. Models of individual plant 'networks' have been available for many years, with 'the algorithmic beauty' of plants (Prusinkiewicz and Lindenmayer 1991) addressed particularly in the context of simulating plant structure and architecture. 'Trees' are one type of network graph, where branches come off from a central node. Cells are one natural choice for representation as network nodes. At the between-organs scale, the modular structure of many plant species results in a network of plant organs that may vary from one individual within a species to another. Organs in network models might include leaves and stems, roots, flowers, and seeds/fruits, with architecture changing over time. Network models for disease have also been developed to incorporate changes in the network structure, itself (Gross et al. 2006). Such an adaptation will be important for network models of plants, where plants may grow to quickly change their form and thus the network structure they provide for microbes and signalling (Fig. 3). Environmental cues change plant architecture through effects on hormones and responses to hormones (Wolters and Jurgens 2009). The genetic structure of networks of multiple plants has often been studied (Skelsey et al. 2005; Biek and Real 2010), and new tools for transcriptome analysis make it possible to similarly study the phenotypic structure of networks both between plants and within individual plants (Garrett et al. 2006). An interesting question in the context of within host networks is to what extent summary statistics at smaller scales can be used to approximate larger scale processes. For example, average status of cells within a leaf may be used to summarize the leaf processes, but process outcomes may not scale directly (e.g., Hughes 1996).

Microbial communities may be associated with plants on leaf or root surfaces, in intercellular spaces, or within cells. The structure of the microbial community may influence the likelihood of infection by any given potentially pathogenic species through processes such as competition for resources, antibiotic production, or through production of disease in the microbe. Some transitions from one within-individual 'zone' to another have been studied in detail, such as movement from epiphytic surfaces to within leaves through entry points such as wounds and stomates. Movement from one organ to another, or from one plant

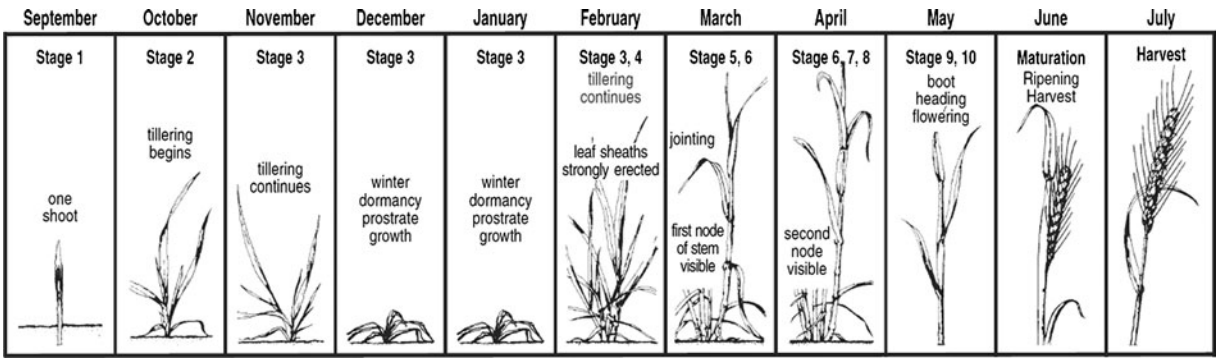

Fig. 3 Growth stages of wheat, illustrating the change in the network composed of a winter wheat plant in Kansas, USA (image from Kansas State University Agricultural Experiment Station and Cooperative Extension Service (1997))

to another, can be facilitated by wind, splashing, or arthropod vectors. For some pathogens such as *Tilletia indica*, an Allee effect, where reproduction decreases disproportionately as other members of the same species become rarer, will be important due to limits on the availability of mates (Garrett and Bowden 2002). Leaf surface features and the presence of other microbes may influence the survival of newly arrived microbes (Monier and Lindow 2005). Arthropod vector nodes are also important, both for movement of microbes and for influencing plant resistance. Sack and Holbrook (2006) represent the plant as a simplified electronic circuit based on water transport capacity, a network structure relevant for microbes that use the plant vascular system. Skirting the within-plant scale, network models have also been applied to microbial movement between individual plant hosts (Jeger et al. 2007; Lamour et al. 2007; Moslonka-Lefebvre et al. 2011), to evaluate the coexistence of plants and epiphytes (Blick and Burns 2009), and to model mycorrhizal networks (Southworth et al. 2005).

Plant signalling networks

In within-plant networks, information moves in the form of hormones and other molecules that signal biotic and abiotic stressors. The plant immune system can recognize pathogen molecules and activate a defence signalling network including a number of small-molecule hormones (Pieterse et al. 2009). This set of different hormones offers the potential for plants to present a range of different responses to microbes. Systemic acquired resistance utilizes the signal molecule salicylic acid (Durrant and Dong 2004). Signal molecules such as salicylic acid, jasmonic acid, and ethylene may function as part of complex networks, where there may be inhibition between signalling dependent on the different molecules (Glazebrook et al. 2003). As a generality, necrotrophic pathogens may be limited by defence responses from jasmonic acid and ethylene signalling, while biotrophic pathogens may be limited by responses from salicylic acid signalling (Glazebrook 2005). Growth and development are influenced by hormones such as auxin, cytokinin, gibberellin, and brassinosteroid, and these may also respond to stresses. More types of plant signalling interactions and forms continue to be recognized (Tsuda et al. 2009). Due to the modular structure of many plant species, these hormones influence the form of the within-plant network in terms of the number of nodes present and distances between nodes (Wolters and Jurgens 2009). Crosstalk between hormones can make the impact of hormonal concentrations more complex (Bostock 2005). Crosstalk can also occur between tissues, and could be incorporated into network models at the appropriate scale to study the effects of spatial structure. Between individual plants, volatile chemicals may alert plants to herbivore attacks on their neighbours so that they can activate their own defence systems (Baldwin et al. 2006).

Microbes may influence plant hormones and other forms of signalling for heightened susceptibility or resistance in a number of ways. Microbial processes include pathogenicity, disease suppression by biological control agents, and growth promotion. Associations with mycorrhizal fungi and endophytes may influence plant susceptibility to disease through mechanisms that are not always well-understood. Through their effects on plant processes such as induced and acquired resistance, microbes may influence resistance to their own or other species. RNA silencing as a response to viruses is another process by which plant resistance is altered in an effect that moves across plant organs. In some cases, microbes can manipulate plant signalling networks to disrupt phytohormone balance and so the plant immune response (Pieterse et al. 2009). Pathogens such as *Pseudomonas syringae* can manipulate plant defence systems through systemic induced susceptibility (Cui et al. 2005). Plants may select for microbes that provide benefits such as growth promotion and disease suppression (Smith and Goodman 1999).

Microbial signalling networks and environmental effects

The influence of microbes moves through within-plant networks through the presence of microbial cells, through influence on plant signalling and plant health or disease, and also through microbial signalling molecules that affect the development of microbial communities. Microbes can modify their group behavior through intercellular communication networks using small signal molecules (Atkinson and Williams 2009). When the concentration of signal molecules passes a threshold, gene expression is altered. Many bacteria modify their phenotypes in

response to these signals, which may result in greater fitness for the current conditions. Communication across species in different kingdoms can induce these changes, which may or may not be adaptive for all the linked species. "Different bacterial species may 'speak' the same QS [quorum sensing] 'language', some may possess sensors for specific QS signals that facilitate eavesdropping while others may manipulate the QS activities of neighbouring bacteria by degrading the QS signal molecules within their locality' (Atkinson and Williams 2009). The production of biofilms is an important outcome of phenotypic changes from QS, which can enhance the survival and pathogenicity of bacteria. Biofilms associated on leaves or root surfaces, or in intercellular plant spaces, provide a protected environment for bacteria (Morris and Monier 2003). Selection for biofilm polymer secretion may change over time, so that downregulation of polymer secretion is beneficial at higher levels when it can favour dispersal (Nadell et al. 2008). Thus, quorum sensing would tend to evolve through competition in and among biofilms. In simulations, cooperative and non-cooperative bacterial cells tend to segregate in space, which can support the evolution of cellular cooperation (Nadell et al. 2010). On leaf surfaces, other epiphytes may interfere with quorum sensing by pathogens, by limiting the availability of essential elements such as iron (Dulla et al. 2010). Quorum size for microbes associated with leaves can vary with environmental conditions, such as the availability of water (Dulla and Lindow 2008). Rather than being mixed together on leaf surfaces, different species of microbial epiphytes may tend to aggregate, and aggregation can lead to enhanced survival (Monier and Lindow 2003; Monier and Lindow 2005). The potential for human pathogens associated with plants to be 'conditioned' by signal networking with other plant-associated microbes is an interesting possibility that may be an important consideration for management (Tyler and Triplett 2008).

The microenvironment has important effects, particularly on microbes on plant surfaces. In addition to temperature, leaf surface wetness is a key factor for epiphytic communities (Huber and Gillespie 1992). Microbes inside plants are relatively more buffered from water stress, but are still exposed to ambient temperatures (in contrast to pathogens of warm-blooded animals). In many cropping systems, microenvironments, with all their impacts on network processes, will change over time as canopies close. Climate change may have profound effects on plant disease risk that scale from gene networks through mesoscale networks to epidemic networks (Garrett et al. 2006; Pautasso et al. 2010).

Within-plant information networks and plant disease

A model of within-host information networks related to plant disease might include the elements illustrated in Fig. 4. In this diagram, links join plant nodes, where nodes might be cells or organs, or potentially arthropod vectors. At each node, four main factors interact to determine the role that that node will play in the larger network. (1) Plant signals and development stage at the node will determine what microbial communities are supported, and will also determine the form of the network linked to the node in the future through their influence on plant growth. Plant signalling is an analog to human information for decision-making in comparison with Fig. 2. (2) Microbial information through signalling at this node will help to determine what microbes are present, whether they are pathogenic, and how their populations will change. (3) Environmental conditions will influence all processes. (4) The current microbial communities, themselves, and disease status, will directly affect the probability of disease movement from this node. Different pathogens may have different niches within a host, such as niches based on how close leaves are to senescence (Al-Naimi et al. 2005). The form of interaction between microbes and host can change as a function of the host life-cycle stage and environmental condition, where microbes may change from

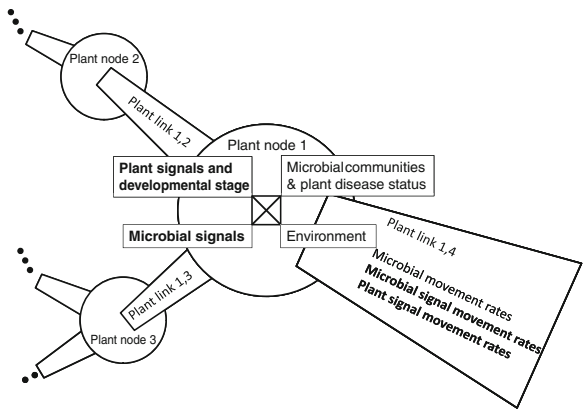

Fig. 4 Nodes and links within a plant, where nodes might be cells or organs (leaves, roots, flowers)

beneficial to detrimental to plants depending on these conditions (Newton et al. 2010), and plants will vary in the quality of environment they provide to microbes. Between each pair of nodes, there may be a nonzero rate of influence for three of these factors. As for larger networks, rates are not necessarily related to the Euclidean distance between nodes. (1) Microbes may move across plant surfaces or among plant cells, or be vectored by arthropods. (2) Microbial signals move between nodes, impacting processes beyond the immediate location of the microbes that produced them. (3) Plant signals similarly move beyond the immediate location of biotic stressors to influence plant-microbe interactions. Network models could include both directed and undirected components, in that movement between some nodes will be approximately equally likely in both directions, while movement between other nodes will be directional. For example, movement through phloem and xylem will often tend to be more directional, while the direction of movement of epiphytic microbes by rain splashing may be closer to random. A synthetic model of information networks within plants might include analysis of plant responses to stressors in the form of receiver operation characteristic (ROC) curves, evaluating whether a plant's response to a stressor is adaptive or non-adaptive. A synthetic model could address the structure of plants first in the context of their inherent structure, and its changes over time, and then in terms of the other ways that their components may be linked by air, water, and arthropod vectors.

Considering the full range of types of information flows in within-host networks will be a challenge, but would provide a number of benefits for plant disease management. Understanding of phenomena such as changes in the efficacy of resistance genes with temperature (Webb et al. 2010) will benefit from a more complete characterization of these within-plant networks. Clarification of these processes will also inform analysis of the evolution of plant network structure. There are trade-offs for plants, in that well-connected plant components may contribute to plant fitness in many ways, but also offer advantages to pathogens. This is analogous to 'single large' or 'several small' debates regarding nature reserves: large reserves are beneficial for most processes that benefit from connectivity, but multiple less connected reserves help to slow pathogen movement. Connectivity is a larger scale measure of network cohesion. In plant networks where some nodes may be quite distant compared to the size of a microbe, dispersal by air, water, or arthropod vectors can add links between the distant nodes to result in a small world scenario. Similarly, movement within plants may be more cohesive when it involves the plant vascular system.

New questions to be addressed

Formulating and estimating parameters for within-host network models will help to address questions such as the following.

1. Which types of interactions are most important, such that multi-factor experiments are necessary for understanding those system components?
2. As the model incorporates more and more biological features, at what point are there so many interactions that outcomes are unpredictable? Conversely, if fewer and fewer features are included, at what point do outcomes become predictable?
3. How do the results change with the scale of model considered? How can smaller scale processes best be used to predict larger scale processes, and vice versa?
4. If signalling is disrupted through a management intervention, when must the disruption occur and what degree of disruption is necessary for the approach to be effective and efficient? What minimal and optimal spatial patterns for disruption are needed?
5. What are the relative magnitudes of effects? Under what circumstances can the abiotic environment override the effects of microbial or plant communication?
6. What forms of engineering of plant resistance related to signalling may be most effective? How may crosstalk and buffering of signals through gene redundancy influence attempts to achieve results based on engineering small numbers of genes?
7. What are optimal sampling schemes to characterize these networks?
8. Are there emergent properties such that initially small changes in the system propagate to produce large changes?

Commonalities and impact

Evaluating the impact of research networks in the context of human information and within-plant

networks can produce an interesting hall of mirrors. Agricultural economists have often used supply and demand models of commodity markets in the analysis of agricultural research impacts, where decreases in the price of commodities and increases in consumption are one measure of success (Alston et al. 2009). Evaluation of benefits for producers is another element. Attributing the source of improvements is a problem because of the frequently long time-lag between research effort and benefit, as is dealing with 'spillover' benefits for systems that were not the original targets of the research (Alston et al. 2009). Ekboir (2003) argued that research impacts should be analyzed by treating the link between research and adoption of new products of research as a complex adaptive system. From this perspective, research impacts come about because of the whole network and it is the network that can be evaluated. Returning to ideas from game theory, the research network may be more or less successful as a function of the costs and benefits of participation in the network. Ekboir (2003) discusses the idea of a national innovation system (NIS) 'composed by all agents involved in the innovation process, their actions, interactions and the formal and informal rules that regulate the system' as formulated by the Organisation for Economic Co-operation and Development, where networks of agents develop technologies. Lack of sufficient connections between research networks and extension networks in NISs can reduce research impacts (Green et al. 2009; Shanley and Lopez 2009). Ekboir's (2003) conclusion is that increased research impacts result not from management of the research process but from providing conditions for effectively linking research institutions in innovation networks.

Systems biology in its broader sense can address the type of multi-scale modelling issues suggested by comparison of human information networks and within-host networks. Scaling is a challenge for models of epidemics, where new types of structures may be encountered at higher scales (Kleczkowski et al. 1997). Linking mesoscale models of within-plant epidemics and their associated experiments into the context of field-scale and larger epidemics will be an important step. New genomic tools will facilitate this, making it possible to characterize genotypic resistance (Rouse et al. 2011) and phenotypic resistance (Travers et al. 2010) even in natural plant communities such as tallgrass prairie. Network structures from one scale may inform another. For example, humans weight past and present information differently, and the system of weighting may differ from one social group to another (Johnson and Covello 1987; Slovic et al. 2002). Are there analogs for plant conditioning to biotic stresses, where some plants have the strategy of weighting the past heavier and others the present, perhaps as a function of their life span and reproductive strategies? Models of disease risk developed for smaller-scale decision-making may be adapted to different scales through approaches such as metamodelling (Sparks et al. 2011). The level of autoinfection, or infection from inoculum produced on the same host individual, can have important epidemiological consequences (Mundt 2009). Induced resistance may have important effects that scale to influence epidemic outcomes (Calonnec et al. 1996; Garrett et al. 2006). The study of information networks across scales in plant pathology will support the development of strategies to enhance information flows that support plant productivity, and to disrupt information flows that contribute to disease.

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