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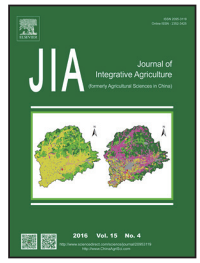

REVIEW

Problems, challenges and future of plant disease management: from an ecological point of view

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Abstract
Plant disease management faces ever-growing challenges due to: (i) increasing demands for total, safe and diverse foods to support the booming global population and its improving living standards; (ii) reducing production potential in agriculture due to competition for land in fertile areas and exhaustion of marginal arable lands; (iii) deteriorating ecology of agro-ecosystems and depletion of natural resources; and (iv) increased risk of disease epidemics resulting from agricultural intensification and monocultures. Future plant disease management should aim to strengthen food security for a stable society while simultaneously safeguarding the health of associated ecosystems and reducing dependency on natural resources. To achieve these multiple functionalities, sustainable plant disease management should place emphases on rational adaptation of resistance, avoidance, elimination and remediation strategies individually and collectively, guided by traits of specific host-pathogen associations using evolutionary ecology principles to create environmental (biotic and abiotic) conditions favorable for host growth and development while adverse to pathogen reproduction and evolution.

Keywords: disease resistance, avoidance, elimination and remediation, ecological plant disease management, evolutionary principle, food security, plant disease economy

1. Introduction

Plant disease has been a major factor influencing food production and human societal development over thousands of years (Palmgren *et al.* 2015). Throughout the early agricultural era, the occurrence of plant disease epidemics was seen as a punishment from the gods and overt plant disease management approaches were extremely limited. Given generally low yields and the general lack of significant food reserves, once disease epidemics occurred food shortages could easily develop resulting in disastrous effects on human society — such as the Irish Famine caused by potato late blight in the 1840s and the 1943 Bengal famine caused by rice brown spot (Bourke 1964; Padmanabhan 1973; Strange and Scott 2005). Despite the contribution of scientific and technological advances to significant reductions in the frequency and intensity of epidemics in recent times, 20–30% of actual production is still lost due to plant diseases per year (Oerke and Dehne 2004; Oerke 2005). These losses reflect incomplete knowledge relating to the causes and mechanisms behind epidemic development, a situation that unsurprisingly reflects a lack of adequate approaches

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to even efficiently manage them, let alone eliminate them. Furthermore, many plant disease management strategies together with many agronomic practices used in modern agriculture have also generated unintended problems including loss of biodiversity and other natural resources (Lucas 2011; Gonthier *et al.* 2014), environmental deterioration (Enserink *et al.* 2013), and accelerated evolution in pathogens (Zhan *et al.* 2002; Sommerhalder *et al.* 2010; Zhan and McDonald 2013).

Over agricultural history, plant disease management has experienced four major phases: (i) limited intervention in ancient farming systems; (ii) mechanical and temporal disease suppression approaches (rogueing, ploughing, rotations); (iii) widespread use of major gene resistances and pesticides before and following the first Green Revolution; and (iv) integrated pest management and ecological management emphasizing synergic effects on the economy, society and both the agricultural and natural environments. Ecological management of plant diseases is not a simple return to farming systems of ancient times. Rather, it aims to use evolutionary principles and thinking to maximize the regulatory functions of nature to create suitable environments for healthy hosts ensuring high and stable yield through the efficient use of natural and societal resources including high disease resistance to create environments adverse for the infection, reproduction, transmission and evolution of pathogens (Zhan and McDonald 2013; Zhan *et al.* 2014, 2015). In addition, short- and long-term economic and societal impacts should be evaluated for each plant disease management scheme. To achieve the goal of sustainable plant disease management, multidisciplinary collaboration involving natural and biological sciences such as plant pathology, breeding, agronomy, soil science, environmental science, economics and social science is needed.

2. The nature of plant disease epidemics and current situation of management

In natural systems, host plant and pathogen are constantly changing with pathogens evolving new pathogenicity to overcome host defense systems and plants evolving to reduce pathogen attack. These coevolutionary interactions occur within ecological settings in which pathogen evolution and impact are tempered by environmental patchiness while host evolution is constrained by small population sizes and long generation times (Burdon and Thrall 2009; Iranzo *et al.* 2015). In contrast, in modern agriculture systems, increasing requirements for high productivity and good quality of some specific crops and/or varieties forces the shift of agricultural practices to large-scale, intensive and specialized cultivation. In turn, this disrupts the co-evolutionary dynamics between host plants and pathogens as observed in natural systems, increasing the frequency and severity of disease epidemics and the spread of new diseases. However, largely due to a failure to place relationships among agricultural practices, disease epidemics and economic returns in an ecological and evolutionary context, plant disease management strategies adopted over the past 50–100 years rarely reflected these changes in risk and patterns of disease occurrence. Consequently, plant disease management can easily fall in the conumdrum where increasing efforts to control plant diseases actually promotes further disease problems.

Plant disease results from complex interactions among biotic and abiotic factors including hosts, pathogen and environments, to which should be added vectors for some diseases and human activities that modify the interaction intentionally or unintentionally through agricultural practices such as cropping systems, resistance gene deployment (Burdon *et al.* 2014) and application of pesticides (Fig. 1). In past decades, plant disease management and other agricultural practices have created ecological environments favorable for pathogen infection, reproduction, transmission and evolution as described in the following sections. This increases the negative impacts of plant disease on food security and human society.

2.1. Ecological environments adverse to host plants but favorable for pathogens

Healthy soils are the key to sustainable agriculture including plant disease management through their impact on pathogen density particularly of soil-borne diseases (Magdoff 2001; Janvier *et al.* 2007), the structure of beneficial microbe communities and the availability of organic and inorganic nutrition for plant growth and development (Larkin 2015;

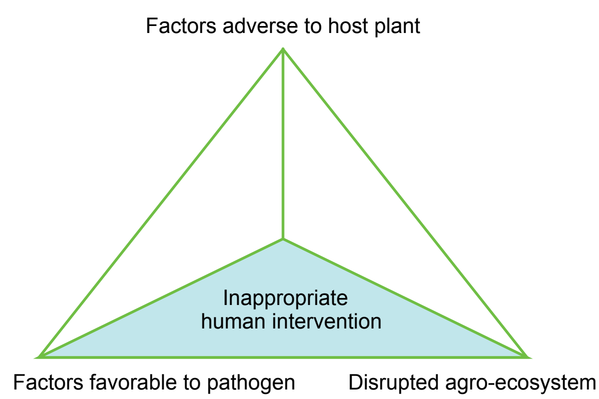

Fig. 1 The mechanism of plant disease epidemics in agricultural system. Plant disease epidemiology in modern agriculture is driven by disrupted eco-systems that create conditions favorable for pathogens but adverse to hosts due to inappropriate human intervention.

van Bruggen *et al.* 2016). Over past decades, water and air pollution resulting from industrial emission and agricultural wastes, and over-use of chemicals to nurse plants and manage pests and weeds has generated many near-irreversible changes reducing farmland quality through soil compaction, reduced organic material, mineral imbalances, and heavy metal and pesticide residue contamination (Kosalec *et al.* 2009; Lu *et al.* 2015; Tripathy *et al.* 2015). Furthermore, this deterioration in farmland quality may further reduce host plant immunity against pathogen infection.

Agricultural management strategies can have a major impact on soil quality (Bancal *et al.* 2008) with consequent effects on disease incidence. Thus most practices designed to improve soil quality by increasing beneficial microorganisms and the microbial biodiversity of farmland through activities such as organic matter supplementation also help to suppress the development of most diseases (Welbaum *et al.* 2004; Bonilla *et al.* 2012; Page *et al.* 2013). Crop rotation typically improves the physical and chemical properties of soil such as nutrition balance as well as the diversity of microbial communities (Ball *et al.* 2005). On the other hand, field management and production techniques such as continuous cropping and monocultures of single crops or varieties increase the risk of disease occurrence and epidemics by allowing pathogens to accumulate high inoculum loads. This is especially the case for soil-borne diseases but is also true of many foliar diseases. Such strategies also facilitate the breakdown of disease management strategies based on the use of limited numbers of resistance genes or pesticides due to the enhancement of selection pressures on pathogens due to reduced host diversity and the widespread use of pesticides with the same modes of action (Zhan *et al.* 2002; Sommerhalder *et al.* 2010).

2.2. Single and static management strategies increasing the intensity of plant disease outbreaks

Plant pathogens are difficult to control partly due to their rapid spatio-temporal dynamics and rapid evolution (Strange and Scott 2005) associated with high genetic diversity and short generation times that together promote their ability to overcome the currently most effective disease control approaches based on major R gene resistance and industrial pesticides. Integrated pest management (IPM) approaches advocated in the last century were intended to manage plant diseases by assembling diverse approaches according to particular diseases, time and locations. However, the application of chemical pesticides has almost become the main and even only one approach of IPM strategy, particularly for crops lacking major resistance (Guedes *et al.* 2015). It has been reported that the rate of increased pesticide application has been far more than that of gained food production in recent decades (Popp *et al.* 2013), indicating the reduced efficiency and economic return of using pesticides to manage plant diseases. Usually, pesticides are used in a prescribed manner that standardizes type, time, frequency and dosage of application regardless of the particular crop's plant resistance status, environmental conditions and pathogen chemical sensitivity. Such a fixed and static strategy of pesticide application not only reduces management efficiency and increases costs, but also brings many unnecessary negative effects to environments and society such as toxicity to humans and livestock, and ecological degradation as discussed earlier.

2.3. The grey box of plant disease epidemic mechanisms

To achieve efficient and sustainable plant disease management, it is important to use an integrated systems thinking approach to understand the entire interaction between host and pathogen and its interplay with the broader environment (Burdon and Thrall 2008). Thus while an understanding of the pathogenesis and epidemic principles of plant pathogens, and of the genetic, biological and physiological mechanisms of host plant defenses is important, so too is the knowledge of interactions with other microbial populations, and the ecological niche of the pathogen. More importantly, efforts should be made to comprehensively understand the effects of human activities such as agricultural practices (e.g., monoculture, rotation, etc.), international trading, and application of pesticides on the generation and evolution of new virulence, health of plant development and interactions among plants, pathogens, vectors and the environment (Xie *et al.* 2009). This is essential because it is commonly believed that many major disease outbreaks in history were mainly induced by human.

Correct and quick disease diagnosis, identification and forecasting are always fundamental (Miller *et al.* 2009). Technologies for diagnosis and identification have been well established and have been greatly assisted by the rise of molecular diagnostic kits. Despite this, their application in commercial production is still highly variable with some agri-companies and farmers still relying on experience, which can cause misdiagnoses and improper use of management approaches. In comparison with diagnosis and identification, disease forecasting requires a much deep understanding of pathogenesis and epidemic principles and the ecological and environmental interactions of plant pathogens with other biotic and abiotic factors. Because of this complexity, with a very few notable exceptions (for example, potato late blight in the north-eastern USA), accurate disease forecasting is still very limited.

2.4. Lack of models including externalities in the economic analysis of plant disease management

Externalities emerges when the effect of plant disease management on other parties is not reflected in the calculation of cost and profit. Externalities associated with plant disease management may be positive or negative and can be divided into short- and long-term ecological, social and economic components (biotic and abiotic, see Table 1). Negative externalities of plant disease management include environmental pollution, toxin production affecting humans or livestock, ecological damage, resource depletion, reduced disease management efficiency and costs associated with meeting minimum chemical residues on produce. Positive externalities include benefits to disease management in neighboring farms, reduced evolutionary potential of pathogens, and ensuring social stability and safety. Currently, these externalities are not included in economic analyses of plant disease management. Farmers are only responsible for the direct costs associated with pesticide application but not the costs associated with residue removal and ecology restoration, while those who apply ecologically-friendly approaches to disease management receive no additional benefit. Because farmers only pay the direct costs associated with plant disease management, they strongly select strategies that generate the best immediate economic returns while largely discounting potential negative impacts on the environment. To date, some highly effective disease management strategies have been used without sufficient regard to their long-term ecological impacts.

Regulatory policy associated with industrial sewerage management provides a model for how externalities could be captured in assessing plant disease management strategies. The system levies the discharge of industrial wastes into surroundings to alleviate environmental pollution. Due to the transformation of externality to products, net profits of management strategies depend not only on the quality of the commodity but also the level of potential damage to environments. Taking pesticide and ecological management of plant diseases as examples, actual profits are substantially reduced for the former but increased for the latter when externalities are included in economic analysis (Fig. 2).

Table 1 Short- and long-term goals of plant disease management

Short-term benefit	Long-term benefit
High and stable yields	High efficiency and security (without residue, pollution and catastrophic effects)
Quality improvement	Sustainable production capacity
Low input	Reduced speed of pathogen evolution
High output	Social stability

3. Challenges of plant disease management — rational management

Plant pathology faces ever-growing challenges. On one hand, societal demand for total, high quality and diverse food increases due to booming global population which is expected to reach 9 billion in 2050 (Godfray *et al.* 2010), and improving life standards. On the other hand, diminishing arable lands, and depleting natural resources reduce the potential for increasing agricultural productivity (Ray *et al.* 2013). Furthermore, monocultures, intensification and other high resource (fertilizer, water and pesticides) input agriculture practices aimed at maximum yield as the sole target, thereby facilitating the evolution and epidemics of

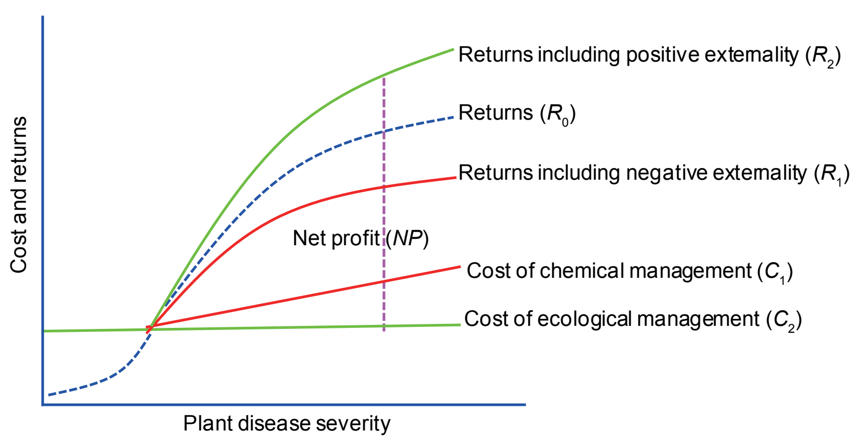

Fig. 2 Externality of plant disease management. If plant diseases are controlled by chemical application, management cost is positively associated with disease severity. On the other hand, if plant diseases are managed with ecological approaches aiming to improve plant health, cost is relatively stable with less negative impact to environments. According to Diminishing Marginal Returns principle, the profit (R_1–C_1) of chemical management is progressively reduced after peak disease, while the profit (R_2–C_2) of ecological management remains stable.

plant diseases globally (Zhan *et al.* 2014, 2015). Into the future, much greater emphasis must be given to sustainable plant disease management strategies that ensure food security and societal development but also have less adverse impacts on environments and natural resources.

To meet the challenge, plant disease management strategies, current agricultural practices and plant disease management strategies must change. Three components (society, economics and ecology) should be considered in future plant disease management strategies. Providing safe and adequate food for society is always the most important task of plant disease management. Plant disease management should strike to ensure food security and social stability by increasing crop productivity, reducing food contamination by microbial toxins, and guaranteeing the supply of diverse and reasonable priced foods. In regard to economic considerations, the ratio of input and return of plant disease management approaches should be better measured and evaluated including direct and indirect economic benefits and costs in a short- and long-term framework including externalities, opportunity costs, technical benefits, etc. In an ecological context, plant disease management should not only consider how to use ecological principles to reduce disease epidemics through changing agricultural practices but also how the strategies may impact on agricultural and ecological sustainability.

4. The ecological way to rational management of plant disease

4.1. Changes in the philosophy of plant disease management

To achieve rational and sustainable outcomes, the philosophy of plant disease control should shift the focus from managing pathogens (or insect vectors) to managing host plants and from the sole goal of high productivity to multiple goals of high yield, efficiency, good quality and safety.

4.2. Ecological management of plant disease

The key to sustainable plant disease management is to establish an agro-ecological system that is favorable to plant growth and development at the population level and adverse to pathogen evolution and epidemic development based on interactions among plants, pathogens, vectors and environments (Xie 2003; Acosta-Leal *et al.* 2011). This management system includes two main components: multiple goals (high yield, efficiency, good quality, and safety) and dynamic and integrated approaches guided by a comprehensive understanding the evolutionary ecology of particular host-pathogen interactions. This integrated approach shows great promise in overcoming the problems and challenges associated with current strategies of plant disease management to optimize its economic, ecological and social benefits.

4.3. The core of ecological plant disease management

The core of ecological plant disease management is to manipulate the environments of host-pathogen interactions in the favor of hosts through the balanced application of RAER (resistance, avoidance, elimination and remedy) strategy (Fig. 3). Agricultural pathogens vary substantially in disease ecology, epidemic patterns, evolutionary potential and economic impact (Table 1) and RAER strategy should be applied according to specific conditions of the host-pathogen interactions involved (Xie and Lin 1984; Xie *et al.* 1984, 1994). Some plant disease management approaches such as crop rotation may achieve the equivalent of resistance, avoidance, elimination and remedy effects simultaneously

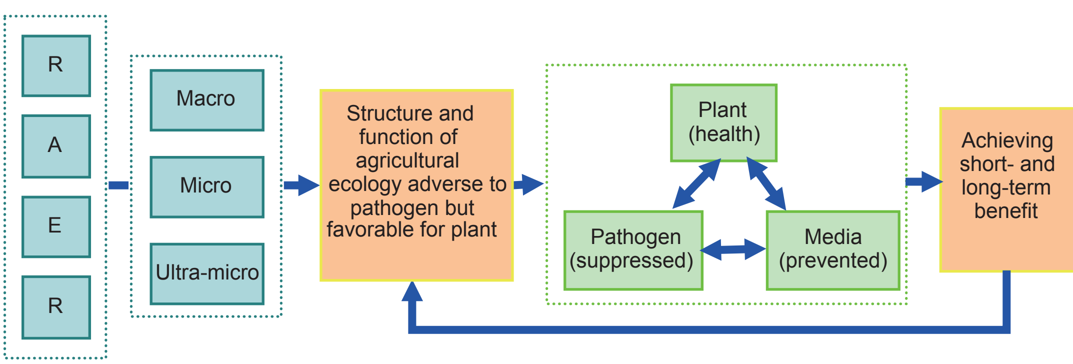

Fig. 3 Ecological management of plant disease. The ecological management of plant disease is to regulate host-pathogen interaction through the rational application of RAER (resistance, avoidance, elimination, and remediation) principle to create the environment favorable for host plant population but adverse to the spread and evolution of pathogen and/or vector for sustainability.

and could be applied widely to future agriculture despite some practical constraints (Pywell *et al.* 2015).

Resistance Host resistance is the most effective and convenient approach for plant disease management (Xie *et al.* 1983, 1994). Host resistance can be induced or constitutive, systematic or local and qualitatively or quantitative. Most resistances in crops are introduced from land-races or wild relatives through plant breeding (Manosalva *et al.* 2015; Palmgren *et al.* 2015). Qualitative (or major gene) resistance is highly effective but due to elevated evolution of plant pathogens under modern agricultural practices (Hall *et al.* 2010; Fraile *et al.* 2011; Thrall *et al.* 2012), many qualitative resistances lose their effectiveness only a few years after commercial release (Kiyosawa 1982; Fry 2008), particularly when they are used in large-scale monocultures. Compared with this qualitative resistance, quantitative resistance is less effective, reducing disease epidemics rather than preventing infection, but more durable due to the lower selection pressure it places on pathogens. On the other hand, induced resistance is thought to have an advantage over constitutive resistance primarily due to lower resource allocation when it is not needed (Anderson and O'Toole 2008; Wei *et al.* 2015).

In addition to the genetics of host resistance, other elements termed the 'ten principles of agricultural practices' (soil, nutrition, water, seed, population density, plant protection, field management, farming machine technology, light and air, Fig. 4) can also affect the resistance level of host plants (Savary *et al.* 2011; Szechyńska-Hebda *et al.* 2015). Changing any of these elements may modify the environment in a way that is either favorable or adverse to plant or pathogen (Table 2). Though managing plant diseases through a whole farming system approach (Plantegenest *et al.* 2007; Yuen and Mila 2015) may still allow some disease development, may need more labor and other inputs particularly on establishment, and may need supplementary support from other strategies such as the application of pesticides, it has been used successfully to control rice blast (*Magnaporthe oryzae*) and tungro (*Rice tungro virus*) disease on a large scale (Xie *et al.* 1983; Xie and Lin 1988; Xie 2003).

Increasing host heterogeneity through intercropping or mixing crop varieties with different genetic and physiological properties such as type of resistance (quantitative versus quantitative) has been proved to be one of the most effective ecological approaches to manage plant diseases. This approach not only reduces disease epidemics, increases nutrition efficiency, productivity and yield stability in short term but also improves soil fertility and slows down pathogen evolution (Burdon and Thrall 2008; Parnell *et al.* 2010; Pérez-Reche *et al.* 2010; Brooker *et al.* 2015; Papaïx *et al.* 2015; Tack *et al.* 2015), thereby extend the lifespan of resistant varieties (Table 2). For example, increasing host population heterogeneity by intercropping different rice varieties greatly reduced dependence on fungicide application to manage rice blast, while simultaneously increasing the quality and quantity of production significantly (Zhu *et al.* 2000, 2003). Varietal mixture has also been used successfully to control potato late and early blights (data not shown). In addition to mixture or intercropping technologies,

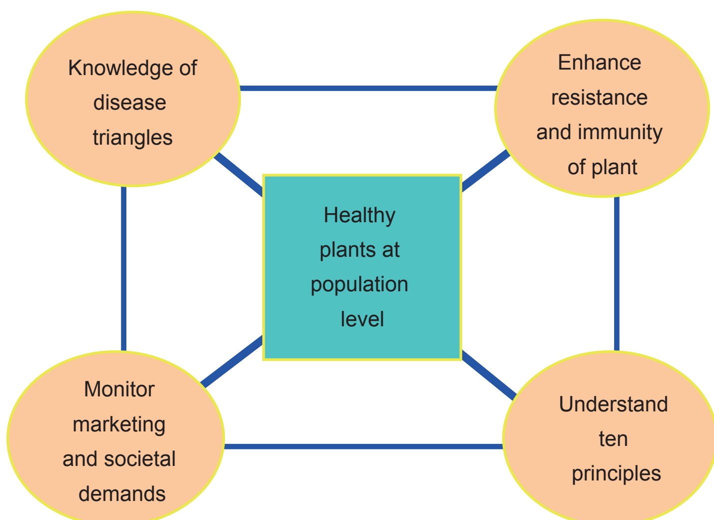

Fig. 4 Solution to improve healthy condition of plant population in agro-ecological system. Sustainable plant disease management that aims at improving plant health at population level can be achieved through a comprehensive understanding the mechanisms of plant disease epidemics, and multi-functions of agro-ecosystems, and interactions among biotic and abiotic conditions, marketing and societal demands. "Knowledge of disease triangles" means plant-pathogen-environment interaction and plant population-biotic factors-abiotic factors interaction. "Ten principles" mean soil, nutrition, water, seed, population density, plant protection, field management, farming machine technique, light and air.

Table 2 The RAER function of each plant disease management approach

Approach	Resistance (R)[1)]	Avoidance (A)[2)]	Elimination (E)[3)]	Remediation (R)[4)]
Single R gene	√			
R gene mixture	√	√		
R gene rotation	√	√		
R gene pyramid	√	√		
R gene regional deployment	√	√		
R induced	√			√
Tolerance	√	√		
Quarantine			√	
Isolation		√	√	
Hygiene	√	√	√	
Seed cleaning			√	
Cropping system adjustment	√	√	√	
Rotation	√	√	√	
Interplant	√	√	√	
Planting time adjustment		√	√	
Species diversity	√	√	√	
Field landscape	√	√	√	
Forecasting		√	√	
Pesticide		√		√
Bio-control agent				√
Physical treatment		√	√	√

[1)] Resistant to the infection of pathogen for host plant.
[2)] Avoid peak and key stage of pathogen reproduction.
[3)] Eliminate infectious sources.
[4)] Kill pathogen and/or vector.

other approaches in resistance gene deployment, such as R gene rotation and pyramiding, can also be used to assist in the ecological management of plant diseases (Coutts *et al.* 2011).

Disease avoidance This approach aims to ensure a mismatch between critical periods of crop and pathogen development by changing the cultivation pattern of host plants spatially and temporally such as through variation in planting time, planting location or cultivation system (Table 2). It is a complex approach that requires a comprehensive understanding of host susceptibility through different phenological development stages, likely meteorological conditions, disease ecology, and pathogen and pathotype distributions. The efficiency of spatial avoidance including regional R gene deployment and varietal mixture is mainly determined by pathogen distribution and transmission modes. Spatial avoidance may be effective to manage plant disease caused by soil- or water-borne pathogens such as many diseases caused by nematodes and bacteria but this approach is unlikely to be useful for the management of air-borne diseases which can be spread over a significant distance over a single course of epidemics.

Temporary avoidance approaches include changing crop planting times and crop rotation. The effectiveness of changing planting times to control plant diseases is heavily dependent on within-season climatic conditions particularly for polycyclic pathogens in which primary inoculum does not play a determinant role in disease epidemics. However, in rice virus disease, this approach shortens the exposure of plants to the pathogen during their most sensitive period by avoiding the peak stage of vectors transmission (Xie *et al.* 1983, 1984, 2001; Xie and Lin 1988; Tiongco *et al.* 1990). A second class of temporary avoidance, i.e., crop rotation, is expected to be particularly effective in controlling plant diseases caused by soil-borne pathogens. Indeed, rotation has been shown to be very effective to control bacterial wilt of potato, banana, tobacco (Ong *et al.* 2007; Peeters *et al.* 2013) and black and root rot of sweet potato (Huang *et al.* 2014). For pathogens transmitted by insect vector such as many viruses, the key for disease avoidance is to understand the ecology — overwintering site, migration patterns, wind direction — as well as the reproductive biology of the insects (Acosta-Leal *et al.* 2011).

Elimination Some methods (Table 2) that eliminate overwintering sites (places and hosts) of pathogens and their transmission vectors generate remarkable plant disease management outcomes with no or minimum adverse ecological impacts by eradicating or reducing inoculum sources. The key obstacle to using an elimination strategy to managing plant diseases is to identify the correct sources of primary inoculum. Misidentification of primary inoculum sources not only reduce management efficiency but also result in resource waste. If a disease exhibits epidemics continuously over many years despite heavy human intervention, it is necessary to re-check whether the crucial points of the disease cycle have been misidentified, to determine whether eradication at those points is actually feasible and to general rethink the strategies for management.

A large number of agricultural practices have proved to be very effective in eliminating or reducing sources of pathogen inoculum by adapting farming systems to remove diseased plant tissues, volunteer host plants and secondary crops, etc. Foremost among these practices, crop rotation is a convenient method of disease elimination that can not only eliminate the pathogen (especially some of those that are soil-borne) and potential reservoir hosts, but may also improve soil quality (nutrition balance and physical structure) supporting healthier crop populations. The practice of ploughing soils after harvesting dramatically reduces the population density of the insect vector, *Nephotettix virescens*, and therefore, the viral source of rice tungro disease (Hirao and Ho 1987) by reducing the vector's overwintering sites. Similar to disease resistance and avoidance, a disease-elimination strategy should also be built on a proper understanding of the various interactions occurring among hosts, pathogens, vectors in an ecological and epidemiological context as well as with due consideration of the economic threshold of management (Figs. 2–4).

A successful case of applying an elimination strategy to control plant disease comes from wheat stem rust in China. Several major epidemics of the disease occurred in spring wheat in Northeast China and winter wheat in Fujian Province, southern China between 1948 and 1965 despite the wide use of major resistant varieties and chemical pesticides. Investigation found that *Puccinia graminis* var. *tritici*, the causal agent of wheat stem rust, overwintered on cultivated winter wheat sown in August in Putian County, Fujian Province. Elimination of these *P. graminis tritici* overwintering sites by persuading Putian farmers to change their cropping systems from growing winter wheat to potatoes and broad beans has been marked by the occurrence of no major epidemics of wheat stem rust since then. Indeed, the disease almost disappeared in the China after the 1990s (Xie 2003). Another successful example of application of an elimination strategy to control plant disease comes from rice stripe disease. The disease has been rampant in Jiangsu Province, the main rice production area of China for nearly 10 years (2001–2010). Due to a lack of resistant varieties, the disease was mainly controlled by insecticide application to kill the insect vector, *Laodelphax striatellus*. However, after 2008, the strategy of managing *Rice stripe virus* was switched from sole insecticide application to the combined use of insecticides with primary inoculum source elimination achieved by abandoning a local common practice of wheat-rice rotations (this removed the overwintering sites of the vector). The disease was eventually brought under full control in the past few years.

Remedy Spraying pesticides to kill pathogens and/or their insect vectors is an inseparable part of plant disease management when other approaches cannot achieve the required level of pathogen population density reduction and epidemic amelioration. However, the use of pesticides in an integrated disease management system is not to eradicate the disease completely but to control it to the most appropriate extent as guided by ecological and economical thresholds. During pesticide application, factors such as action modes and pathogen resistance should be considered (Siegwart *et al.* 2015). To increase their efficiency of application and reduce negative impacts on the environment, pesticides should be used in combination with disease forecasts and knowledge of the pathogen population genetic structure (Zhan *et al.* 2015) to determine the best time and frequency of application and to choose the type and utilization dosage of the pesticides (van den Berg *et al.* 2013).

Remedy successes could also be achieved by other approaches (Table 2) than synthetic fungicides (Xie 2003), such as naturally occurring plant compounds with biological control activity — for example protein y^3 that is extracted from edible fungi and other microbes (*Bacillus* spp.) (Wu *et al.* 2003; Luna *et al.* 2011; Chen *et al.* 2013; Kumar *et al.* 2014). To ensure effective use of such bio-pesticides a better understanding of their properties and application procedure is important as is information about relevant biological features and the transmission mode of pathogens. For example, adding viral therapeutic agents or biological control agents in 1–2 sprays at the rice seedling and turning green stage can not only reduce viruliferous insect population density, but also protect the plant from further infection (Xie *et al.* 1979). Combining pesticides with other biotic and abiotic approaches such as biological agents, soil pH adjustment and UV irradiation has proved to be very effective in long-term control of tomato and lettuce root rot (Tu 2002; Lee 2015).

5. The future of plant disease management

Sustainable plant disease management (Figs. 3 and 4) requires a multi-dimensional consideration of the impacts of management approaches on economics, sociology and ecology by fully understanding the mechanisms of plant disease epidemics, the functioning of healthy agro-ecosystems and individual and collective roles of RAER approaches on disease management. This model of plant disease management seeks not only to increase agricultural productivity and improve food quality but also to protect the ecological environment and natural resources. To achieve this goal, future research in ecological plant disease management should focus on: (i) epidemic and evolutionary patterns of plant disease under changing environments and agricultural production philosophies; (ii) the role of ecological considerations in agricultural productivity and crop health; (iii) social-economic analysis of plant disease epidemics and management; and (iv) technology development for integrating management of major crop diseases with ecological principles.

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