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Potential and Limitations of Plant Virus Epidemiology: Lessons from the *Potato virus Y* Pathosystem

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Abstract Plant virus epidemiology provides powerful tools to investigate key factors that contribute to virus epidemics in agricultural crops. When successful, epidemiological approaches help to guide decisions regarding plant protection strategies. A recent example is epidemiological research on *Potato virus Y* (PVY) in Finnish seed potato production; this study led to the identification of the main PVY vector species and helped to determine the timing of virus transmission. However, pathosystems rarely allow research to produce such clear-cut results. In fact, the notorious complexity of plant virus pathosystems, with multiple interactions between virus, vector, plant and environment, makes them often impenetrable even for advanced epidemiological models. This dynamic complexity questions the universal validity of employing epidemiological models that attempt to single out key factors in plant virus epidemics. Therefore, a complementary approach is needed that acknowledges the partly indeterministic nature of complex and evolving pathosystems. Such an approach is the use of diversity, employing functionally complementary elements that can jointly buffer against environmental changes. I argue that for a wider range of plant production problems, the strategy of combining mechanistic and diversity-based approaches will provide potent and sustainable solutions. In addition, to translate insights from plant virus epidemiology into practice, improvements need to be made in knowledge transfer, both within the scientific community and between researchers and practitioners. Finally, moving towards more appropriate virus control strategies is only possible if economic interests of stakeholders are in line with changing current practices.

Keywords Complexity · Determinism · Ecology · Knowledge transfer

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Introduction

In many crops, plant viruses are a major threat to productivity and farm economic viability (Waterworth and Hadidi 1998; Bos 1999; Martin and Shepherd 2009). Potato (*Solanum tuberosum* L.) as a main global staple is affected by several plant viruses (Stevenson 2001). Some of these, such as *Potato virus Y* (PVY), are of global economic importance, and their control is a high priority for potato research (Fuglie 2007). However, understanding underlying causes of virus disease epidemics is difficult. For potatoes, as for other plant species, pathosystems involving plant viruses are highly complex: In addition to the interactions between pathogen, plant and environment, further complexity is brought in by the vectors (such as aphids or nematodes) that transmit the virus from plant to plant (Bos 1999).

Plant virus epidemiology intends to disentangle the multiple interactions in plant virus pathosystems for a more thorough understanding of the driving forces behind outbreaks of virus diseases (Jeger et al. 2004; Jones et al. 2010). In principle, epidemiological approaches are therefore able to guide decisions on which strategies are the most promising one for the control of plant viruses (Kranz 1996; Jones et al. 2010). In this article, I demonstrate this potential by discussing recent advances made by virus epidemiology in a High Grade seed potato area in Northern Europe, where the incidence of *Potato virus Y* has become a serious problem over the last few years (Kirchner et al. 2011a).

At the same time, however, several factors prevent the potential of plant virus epidemiology from being fully realised. On the one hand, there are limitations that are inherent in plant virus pathosystems, in particular their complex, changeable and evolving nature (Jones 2009; Jones et al. 2010). In addition to this given limit of epidemiological approaches, there are further impediments to translating the insights of epidemiological research into practice. These include shortcomings in knowledge transfer activities, both within the agricultural research community and between researchers, breeders, seed merchants and farmers. Finally, economic interests of these stakeholders may interfere with the efforts to find the most efficient virus control strategies. Here, I discuss the ‘given’ as well as the ‘self-made’ limitations of plant virus epidemiology and suggest steps that can be taken to increase the impact of epidemiological findings in agricultural practice.

The Potential of Plant Virus Epidemiology

Epidemiological Approaches

Epidemiology looks at plant virus pathosystems by studying the factors that determine how the virus spreads from an infection source in a plant population through space and time (Kranz 1996; Jeger et al. 2004). Typical questions that can be answered with epidemiological methods are:

- What is the relative importance of various epidemiological factors, such as inoculum, plant resistance, vector abundance or environment, for virus incidence?

- Which environmental factors affect virus spread in the field?
- Which are the main vector species contributing to the dispersal of the virus?
- When does the main virus transmission take place in the growing season?
- How far are virus particles carried by vectors in the field?
- How quickly does a virus spread over a given distance?
- What are the effects of various virus control strategies on virus incidence in the field?

A powerful tool in epidemiological reasoning is mathematical modelling. Recently, the typology of models in plant virus epidemiology has been reviewed by Jones et al. (2010). Here, I use a much simplified classification to show two differing ways of epidemiological modelling—these can be termed theory-driven (synthetic) vs. data-driven (analytical). Proceeding synthetically one starts with theoretical assumptions. Based on logical relationships between defined variables, a set of equations is built that represents a simplified version of the pathosystem and makes explicit statements regarding the *mechanisms* of disease spread.

For example, in a model developed for *African Cassava Mosaic Disease* (ACMD) by Holt et al. (1997) and reviewed by Jeger et al. (2004), it is assumed that if t is time, X is the density of healthy (uninfected) plants, Y is the density of diseased plants, K is the maximal plant density, r is the rate of replanting uninfected seed, k is the rate of inoculation of healthy plants per infective vector, g is the rate of removing plants, either by harvesting or by roguing, V is the density of viruliferous vectors and a is the loss rate of plants (plant death) due to the virus disease; then, the rate of change in the density of uninfected plants (dX/dt) and of infected plants (dY/dt) can be expressed using the following linked differential equations:

$$\mathrm{d}X/\mathrm{d}t = rX[1-(X+Y)/K] + kXV - gX \tag{1}$$

$$\mathrm{d}Y/\mathrm{d}t = kXV - aY - gY \tag{2}$$

Both equations express that the rate at which plants become diseased (or are removed from the pool of healthy plants via infection) depends on the density of vectors. An important assumption in this model is that this relationship is linear, i.e. the rate dY/dt is proportional to XV (with a constant parameter k determining the strength of that relationship). A second set of equations is added by Holt et al. (1997) that describes the vector dynamics, by defining the factors that influence the rate of change of the density of infective vs. non-infective vectors. Refinements subsequently added to the model, e.g. by incorporating a stage of latent infection, are discussed by Jeger et al. (2004). In addition to these refinements, one can consider (a) that the susceptibility of the plant for the virus changes during the season (Sigvald 1985), (b) that virus transmission does not only depend on vector abundance but also on the movement activity of vector individuals among plants (Nemecek 1993) and (c) that vector efficiency may be dependent on the vector species if multiple vector species are involved in transmission; i.e. when moving from plant to plant, vector species may differ in the efficiency with which they are able to acquire the pathogen from a diseased plant and transmit it to an uninfected one (Sigvald 1984).

Such an epidemiological model can then be used to simulate the behaviour of the pathosystem by changing input parameter values. For instance, it can be simulated in which way the proportion of infected plants changes if the overall plant density, i.e. in the case of the ACMD model, the intensity of cassava cropping is increased (Jeger et al. 2004).

In principle, a very large number of parameters can be incorporated in such epidemiological models (e.g. Nemecek 1993). As a consequence, this approach to epidemiological modelling is highly flexible and limited only by computing power and the modeller's imagination. While each equation reflects relatively simple assumptions, the large set of linked equations in the model allows nontrivial insights (which do not merely reflect the assumptions) to be made. Because of the large number of assumptions in such models, however, it can be difficult to identify which assumptions may not reflect realistic conditions in the field. In any case, predictions of model simulations should be checked against data collected in the field to ensure that models produce reasonable outputs. Further, manipulative experiments can be performed to quantify parameters entering the model. Ideally, field-validated models are able to produce genuine insights into virus control options in the field (Jones et al. 2010).

In contrast to this synthetic approach that stacks explicit mechanisms together to construct a model, the analytical (empiric) way of epidemiological modelling starts with the data, mostly gathered in the field. Here, a large part of the mechanisms that link the various components of the pathosystem may be treated as a black box. Instead, statistical modelling is used to establish (correlative) relationships among the relatively limited number of variables that enter the model. Here, the aim is to *reduce* the number of variables entering the final model to the necessary minimum.

An application of this approach is forecasting of vector occurrence and virus incidence (Sigvald 1992; Thackray et al. 2004); following the analysis of datasets concurrently collected on weather and vector populations or virus incidence in the crop, forecasting models can be built that predict vector abundance or the risk of virus infection when a (limited) number of weather parameters are known. This may then allow the timing of vector or virus control options to be optimized (Thackray et al. 2004). A more detailed example of data-driven epidemiological modelling is presented in the next section.

Case Study: *Potato virus Y* in the High Grade Seed Potato Area in Finland

In many countries, one of the most serious virus diseases of potato is caused by *Potato virus Y* (PVY) (Weidemann 1988; Crosslin et al. 2006; Valkonen 2007; Boukhris-Bouhachem et al. 2010). As seed tubers infected with PVY yield substantially less than uninfected ones (Winiger and Bérces 1974; Whitworth et al. 2006), it is essential for potato production that seed lots have a low proportion of PVY-infected tubers. Transmission of PVY is experimentally possible by mechanical inoculation (sap transmission), and for some isolates, contact transmission has been reported. However, in the field, the only relevant mode of PVY transmission is transmission by aphids (Beemster and De Bokx 1987). PVY is transmitted in a nonpersistent manner (Bradley 1954), which means that a very short time span is sufficient for the aphid to acquire and transmit PVY from plant to plant because the virus is not acquired from the phloem but from epidermal cells.

Aphids do not need to be colonizers of potato to be able to transmit PVY. In fact, many non-colonizing aphid species are able to transmit PVY as they make brief probings on potato plants when they are searching for host plants (Harrington and Gibson 1989; Heimbach et al. 1998). These transient PVY vectors are extremely difficult to control with insecticides (Zellner 1998; Perring et al. 1999; Radcliffe and Ragsdale 2002; Kirchner et al. 2011b) because the active ingredients are often not able to have an effect on the vector before the acquisition or transmission of the virus has occurred.

Fortunately though, there are numerous alternative strategies for controlling potato viruses in seed potatoes (Zitter and Simons 1980; Radcliffe and Ragsdale 2002; Döring et al. 2006; Boiteau et al. 2009). One of these strategies is to grow the crop in regions where vector abundance is low (Wetzel and Franken 1975), for example in the high latitudes where low temperatures during winter keep vector populations low, especially by delaying the onset of population buildup in spring. In Europe, one of the five specialised seed potato growing areas that uses this strategy is the High Grade (HG) seed potato production zone in Northern Finland, with a total seed potato area of around 1,000 ha and an annual production of currently about 14,000 tonnes of seed potatoes.

Around 2005, however, PVY infections in this HG zone led to a surge of seed lot decertification—something that had been unusual before. It was clear that measures would need to be taken to prevent the situation from getting out of hand. However, nothing was known about potential virus vectors in the area. Therefore, a research project was initiated in 2007 to conduct an aphid survey in the HG region and to monitor PVY levels in the field to establish potential routes for virus control (Hiltunen et al. 2008; Kirchner et al. 2011a).

To monitor vector populations in the region, yellow pan traps were set up on several potato fields over 3 years. Winged aphids caught in the traps were identified using a combination of morphological identification and molecular fingerprinting (Kirchner et al. 2010). In addition, yellow pan trap data were supplemented by regional suction trap data. From the identification of the over 30,000 individuals caught in the pan traps, it emerged that about a third of the aphid individuals belonged to nine species known as PVY vectors (Kirchner et al. 2011a). Interestingly, no potato colonizing aphids were found on the potato plants in any of the years.

A modelling approach was then used to determine the relative importance of the various aphid species caught in the region for the transmission of PVY (Kirchner et al. 2011a). Models were constructed that used weekly cumulated vector counts as explanatory variables and the incidence of PVY in harvested tubers as the response variable. The difference between final and initial PVY incidence was taken as an alternative response variable. The importance of individual aphid species as PVY vector in the region was determined by removing one species at a time from the data set and comparing models based on this reduced data set with models based on the full data set. A large drop in model fit following the removal of a species was interpreted as a strong contribution of that species to the spread of PVY in the potato crop.

The modelling was further used to identify the most important epidemiological factors for PVY, based on published data for resistance of cultivars, collected vector data and the initial infection rate of the seed tubers. Results of this approach showed that the incidence of seed-borne PVY infection and the vector flight were the most important factors contributing to the incidence of PVY in the harvested tubers, while the resistance of cultivars played a less important role. Modelling further allowed the timing of the main virus transmission activity to be determined as the early part of the growing season, relatively shortly after the emergence of the potato crop. Finally, the black bean aphid (*Aphis fabae* Scop.) unambiguously emerged as the only relevant vector of PVY in the study area.

The outcomes most relevant for virus control are: (a) the earliness of virus transmission activities in the growing season, (b) the identity of the main vector, *A. fabae*, and (c) the fact that no aphids were colonizing the potato plants. These findings can be translated into a set of clear recommendations for virus control strategies in the HG area.

When vector flight occurs early, measures that interfere with the host locating and host contacting behaviour of the vectors have a great potential for virus control. In previous studies, straw mulch had been suggested to be an efficient tool for reducing virus diseases (Heimbach et al. 2000; Saucke and Döring 2004; Saucke et al. 2009). While the exact mechanisms of this effect are still not entirely understood, it is believed that straw mulch interferes with the host finding behaviour of the aphids, in particular with their ability to visually locate a plant (Döring et al. 2004; Döring and Chittka 2007). Therefore, it is expected that it is especially efficient under conditions of early vector flight (Saucke and Döring 2004). This was indirectly confirmed for the HG area in Finland where further trials showed straw mulch had an outstanding efficacy for controlling PVY (Kirchner et al. 2011b).

When initial data analysis showed the possible importance of *A. fabae* as a PVY vector in the region, the aphid's winter host, the snowball shrub (*Viburnum opulus*) was inspected in spring to determine at what time migration of winged adults from the winter host to secondary hosts takes place in the HG area. This revealed that monitoring populations of winged aphids on the winter host can give an early indication of the timing of main migration of this aphid species to its summer hosts, i.e. the main period of virus transmission. This part of the investigations also opened up possible control options of the PVY vector *A. fabae* on its winter host.

Finally, the absence of apterous aphids on the potato plants suggests that the practice of farmers in the study area to spray insecticides frequently fails to act against PVY and its vectors. This finding reiterates the point of low efficacy of insecticidal treatments for controlling nonpersistently transmitted viruses (Perring et al. 1999). It is further confirmed by replicated field experiments in the study area, showing poor control of PVY with several insecticides (Kirchner et al. 2011b).

From a theoretical point of view, the presented study on PVY in Northern Finland is still incomplete because the essential steps of model validation and sensitivity analysis are missing (Jones et al. 2010). Insofar, the study cannot really make any *predictions* about the future behaviour of the PVY pathosystem, but can only help to *explain* its behaviour in the past. Thus, more data are needed to validate the model. However, as mentioned above, one of its most important insights—the relative earliness of the transmission in the growing season—has already been indirectly confirmed through successful application in virus control experiments.

Limitations of Epidemiological Approaches

In the case presented above, the investigation of the PVY pathosystem yielded relatively clear-cut results and recommendations for the HG seed production area. However, despite a number of positive examples (Jones et al. 2010), this situation might not be entirely typical for plant virus pathosystems. Indeed, an epidemiological approach, although successful in this instance, faces several challenges that need be overcome before it may lead to an improved control of plant virus diseases in practice. These challenges can be broadly grouped into three main themes: (1) in the natural domain: ecological complexity and changeability; (2) in the social domain: knowledge transfer and knowledge exchange within scientific and farming communities; and (3) in the economic domain: interests of stakeholders involved in the control of the pathogen.

Complexity and Changeability

There are three types of complexity-related difficulties impeding the advances that epidemiological models can make: First, the multiple interactions between virus, vector, plant and environment make them often impenetrable even for highly sophisticated epidemiological models. Because there are so many factors and (potential) interactions involved that determine virus levels in the crop, it is necessary to collect large amounts of data before meaningful patterns can be detected, and this entails high costs for this type of research. Typically, not all potentially important epidemiological factors can be included in any single study focussing on a particular virus disease in a geographic region, so that some key factors may remain undetected. Even if patterns are established, however, the question remains how far insights can be generalised, e.g. by transferring them from one location to another. In most cases, it is unknown to which degree each location represents a unique combination of factor levels, so that models would need to be parameterized anew at each location.

Second, pathosystems are not static. Several factors influencing virus levels in the crop are extremely dynamic, and these fluctuations further reduce the predictability of the behaviour of plant virus pathosystems. Dynamic factors include the emergence of regionally new virus strains (Jones 2009), the constant turnover of crop varieties (Michelmore 2003), the large fluctuations in vector populations with complex underlying causes (Way 1967; Leslie et al. 2009), population dynamics of alternative hosts of virus and vectors (Boydston et al. 2008; Tugume et al. 2008) and changes in agricultural management, as for example the proportion and spatial distribution of non-cropped areas (Jones 2009).

Once a model is established, a substantial change in the level of just one of these factors could mean that the results obtained in the modelling are partly or entirely obsolete. An important point in this context is the prediction that global climate change will not only lead to changes in *average* temperature and rainfall but also to an increased *variability* of these factors around their means (Schär et al. 2004). Thus, important factors that affect plant virus pathosystems, such as temperature and rainfall, are going to become more difficult to predict as their frequency distributions broaden towards more extreme events.

Third, pathosystems evolve and respond to the selection pressures exerted by management strategies. Rather than just reducing predictability by adding another source of variability, such factors also respond to the very strategies that are designed and deployed to control plant virus diseases. The most important case is the evolution of new plant virus strains that can overcome plant resistance (Garcia-Arenal et al. 2003). Evolvability in viruses is aided by high genetic diversity in the pathogen. In the case of PVY, genetic diversity of the virus is facilitated by its ability to develop recombinant strains (Hu et al. 2009; Sztuba-Solinska et al. 2011).

Further examples of evolving components of plant virus pathosystems are the evolution of vectors in response to insecticide treatments (Rongai et al. 1998) and the evolution of virus strains that do not induce visible symptoms in the host and are therefore difficult to rogue. While the direction of such evolutionary changes and some general patterns may be relatively easy to predict (e.g. regarding which type of resistance management will result in faster resistance breakdown), it seems not possible to predict where a particular resistance breakdown event is going to happen, and when.

As a consequence of these three sources of uncertainty, there are genuine limits to the predictability of plant virus pathosystems. When faced with complex systems, researchers often make the point that more research (i.e. more data) is needed to better understand the system in question. However, although research will often help to suggest causes for *past* behaviour of a particular pathosystem, the attempt to make accurate *predictions* of future behaviour often fail in such dynamic situations (Taleb 2007; Goodwin and Wright 2009; Makridakis and Taleb 2009).

However, in the debate between the deterministic position (‘we just need more data to understand complex dynamic systems’) and an indeterministic position (‘we will never be able to predict the behaviour of complex dynamic systems’), the root problem is that the degree of uncertainty itself is unknown. If predictions based on epidemiological research were always entirely successful, indeterministic arguments would be pointless. Conversely, if predictions were always failing because of overwhelming uncertainties, it would be futile carrying on with expensive epidemiological research and modelling. Therefore, we need to acknowledge that plant virus epidemiology is firmly set in the middle ground: While it can demonstrate some successes, there are also limits set by the inherent dynamics of pathosystems, and these limits are unlikely to be overcome through gathering more data.

Knowledge Transfer

A key requirement for the adoption of appropriate virus control strategies in practice is efficient knowledge transfer (Fig. 1). Several stakeholders, including farmers, breeders, advisors, researchers, retailers, consumers and policy makers, are all involved in bi- or multi-directional knowledge transfer activities. Crucially, this includes knowledge transfer within the scientific community. In addition,

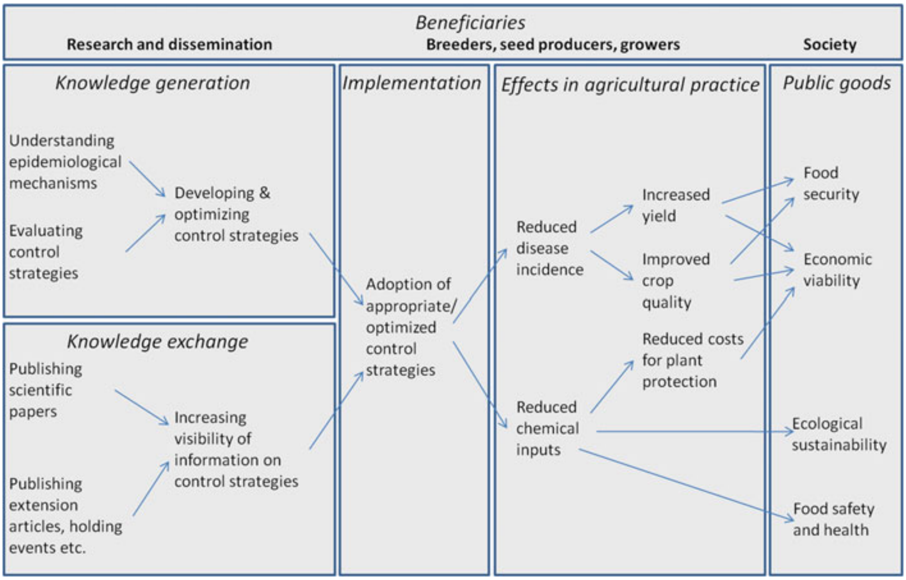

Fig. 1 A simplified and idealised effects model for control of insect vectored plant virus diseases such as *Potato virus Y*

knowledge transfer involves more than just communicating recent research findings to potential users; in fact, an important aspect of knowledge transfer is the visibility of knowledge for the various stakeholders over longer time periods, up to several decades.

What are knowledge transfer-related limits to making best use of research insights in plant virus epidemiology? An important point is that relevant knowledge can be poorly visible to relevant people. For instance, while the information on a particular way of controlling plant viruses may still be principally available, it may just not reach many practitioners because it is hidden in old literature or written in a foreign language. An example of limited information visibility with relevance to virus control was shown by a study on the options recommended for potato virus control in German extension literature. The average number of different options recommended in agricultural textbooks decreased continuously over the last five decades (Döring et al. 2006). Although most virus control options are still present somewhere in the current record, encountering a wide range of available control strategies in a single textbook has consistently become more unlikely over time.

At the same time, the study showed that the prevalence of one particular control option, spraying plants with insecticides for vector control, had substantially increased in the extension literature over time, despite the repeated criticism against this measure in the scientific literature (Döring et al. 2006). This finding highlights that insights from applied and epidemiological research on plant virus diseases are not automatically translated into appropriate recommendations for practice. Instead, these insights are competing with an increasing amount of product-centred information. Maintaining or establishing independent advisory bodies for agricultural knowledge transfer is therefore suggested to be of high priority for making best use of plant virus epidemiology research.

Economic Interests

Economic interests, often diverging between different stakeholders, are an integral part of any agricultural production system. One could assume that reducing the severity and incidence of plant virus diseases is a common aim of all groups involved in the production chain. However, economic interests do not always align themselves easily with the aim of virus control.

An example comes from the competition between different options of virus control. If plant varieties that exhibit good and durable resistance against a viral pathogen are available, both farmers and the breeders of these resistant varieties benefit. However, at the same time the perceived need to apply measures for direct vector control may decrease, which may have negative economic consequences for those stakeholders involved in direct vector control. Similarly, there may be competition between different geographical regions: Seed potato producers established in one region may not be interested in low virus levels in a competing region.

A further example is found in circumstances when, as in potato, the plant propagation material is a main source of virus infection. Because virus-infected seed tubers yield less than non-infected ones, potato growers are protected from buying low-performance seed by certification schemes that ensure virus levels in seed tubers do not go above defined thresholds. To meet the requirements of seed certification, potato growers who intend to sell their crop as seed need to put dedicated management practices in place in order to control virus and other diseases in the potato crops. However, the measures taken preventively to control PVY do not always succeed, so that there is the risk of decertification. Therefore, the efforts by seed potato growers entail a price premium on seed. As a consequence, there is an economic incentive for ware potato growers to cut seed costs by using their own farm-saved seed. Farmers saving seed, however, need to weigh these economic benefits against the risk of losing yield from planting infected seed. If this risk is very low (i.e. when virus pressure is generally low or virus resistance is high), the proportion of seed saving will increase, which in turn might not be in the long-term economic interest of seed producers, even though having resistant varieties on offer can also mean an advantage over competing seed merchants.

Even researchers may not be without conflicts of interest with regard to plant virus diseases. For obtaining research grants, researchers need to justify that the problem under investigation is indeed a substantial one. The current reward system of giving grants for *studying* potential solutions to a problem, rather than for actually *solving* the problem, means that researchers may benefit from the problem not being entirely solved as the continuation of the problem ensures an income stream for researchers.

Breaking the Limits

Dealing with Complexity and Changeability

With the uncertainties and vagaries pertinent to virus pathosystems, deterministic approaches aiming to predict their behaviour come to their limits. Therefore, a complementary approach is needed that acknowledges the partly indeterministic nature of complex and evolving pathosystems and that is able to reduce the disease even if the behaviour of the pathosystem in question is highly unpredictable. Such an approach is the use of diversity, employing functionally complementary elements that can jointly buffer against unforeseen and unforeseeable environmental changes.

The inspiration for this comes from the use of crop genetic diversity which has been shown to provide insurance against plant disease outbreaks (Finckh and Wolfe 1997) and provides resilience against environmental stress (Döring et al. 2010). Similarly, combining complementary virus control options can offer insurance in uncertain situations: For example, in a recent study on control of PVY in potatoes, mineral oil treatments and crop borders were trialled singly and in combination (Boiteau et al. 2009). The study concluded that "combining border and oil provided the best reduction in PVY incidence 3 years out of 3, providing producers with a tool to *reduce year-to-year variation in the effectiveness* of crop borders or oil sprays used separately" (italics added).

In a similar vein, the combination of straw mulch application and pre-sprouting seed tubers has been suggested as an insurance strategy for PVY control in seed potatoes (Saucke and Döring 2004). Because straw mulch is thought to be most effective when vector activity is relatively early, whereas pre-sprouting helps best when vector activity is relatively late, both treatments work in a complementary way. In combination, they therefore decrease the risk of failure and reduce the need to know when vector flight is likely to occur.

The use of functional diversity, i.e. combining measures or materials that are complementary in their way of action, is a logical and perhaps the most fundamental way of stabilising plant performance under fluctuating and uncertain environmental conditions (Döring et al. 2010; Döring et al. 2011). At the same time, however, this diversification strategy needs to be based on, and supported by the established, more deterministic approaches that aim to identify and understand the factors that drive plant pathosystems. In particular, plant virus epidemiological research can help in selecting the virus control measures which are to be combined and fine-tuning their combination. In general, it is therefore likely that not only for plant virus control, but for a much wider range of plant production problems, the strategy of combining deterministic and diversity-based approaches will provide effective and sustainable solutions.

Improving Knowledge Transfer

As demonstrated above, appropriate and efficient knowledge transfer does not automatically follow from good research. Maintaining the visibility of virus control options at the level of their actual relevance is a constant challenge. The system of evaluating scientists, which currently focuses almost entirely on peer-reviewed publications, needs to be restructured (Parnas 2007), especially in the agricultural sciences. In particular, researchers need to be better rewarded for publishing research that has a high impact in *practice* (rather than in terms of citations). Such impact, however, can only be achieved via disseminating in the extension literature, by writing textbooks, or by contributing to dissemination events addressing potential users.

At the same time, researchers will not be able to shoulder the full weight of transferring knowledge into agricultural practice. Therefore, more funds need to be made available for professional advisory services that can draw information from recent and old research alike and that can give balanced and detailed recommendations for best practice. Most importantly, as the examples of virus control in potatoes have shown, knowledge transfer needs to be more independent from direct commercial interests than is currently the case.

Sharing Risks and Benefits

For a fair approach to sharing the risks, costs and benefits of plant virus control, a necessary first step is to bring all stakeholders (farmers and farmer organizations, breeders, official plant health bodies and regulators, seed producers, processors, retailers and consumer organizations) together for an open and thorough dialogue. In this dialogue and beyond, maximum transparency of information on virus control options is needed, in particular regarding their economic performance.

In the case of potato virus control, due to the lack of economic data (Döring et al. 2006) research that can provide thorough economic evaluations of a variety of virus control options, both on the level of individual farms and on a macroeconomic level, is urgently needed. Finally, mechanisms for economic compensation should be developed that minimize costs of plant virus diseases to farmers and society while ensuring continued investment in new solutions.

Conclusions and Outlook

While plant virus epidemiology helps to identify successful virus control strategies, the complexities in plant virus pathosystems limit the transferability of insights across time and space. However, it is possible to buffer against such uncertainties by diversifying virus control strategies. In order to decide where deterministic vs. diversity-based approaches will be most appropriate, epidemiology tools could help to rank epidemiology factors according to the degree of their unpredictability. At the same time, knowledge transfer needs to improve and to become more systematic, more evidence-based and more economically specific to translate epidemiological insights into successful practice.

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