

Impact of novel methods and research approaches in plant pathology: Are individual advances sufficient to meet the wider challenges of disease management?

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ABSTRACT

Advances continue to be made by plant pathologists on topics in plant health, environmental protection, and food security, whether in terms of novel methods or research approaches. Many advances have been made for individual crops, pathogens, and diseases that in many cases have led to their successful management. A wider impact of research depends on recognition of the multifaceted challenges posed by plant diseases and the need to integrate studies in a systems level approach. The adoption of high throughput sequencing for diagnosis and detection is widespread but impact depends upon the agricultural and ecological context combined with improved surveillance. Deployment of host resistance in the field needs to be aligned with a greater appreciation of plant genetic diversity and the complementary contribution made by tolerance of disease. Epidemiological understanding of the spatiotemporal spread of plant diseases has improved through population dynamic and genetic analyses. Research emphasis on the plant microbiome has invigorated soil microbial studies especially for disease complexes and declines, but the challenge is to move to interventions that benefit plant health. Analysis of the impacts of climate change has been made for single-crop disease studies, but seldom have these been placed in the context of pathogen adaptation, new crops, wild plants, vectors, and soil microbes. Advances in informatic analysis illustrate the global impacts of plant disease introductions, but also the challenges inherent in marshalling and integrating information. Advances have been made in applying artificial intelligence technologies across many areas of plant pathology but have yet to be integrated within any co-ordinated research agenda.

INTRODUCTION

Scientific advances continue to be made by plant pathologists on specific topics relevant in plant health, environmental protection, and food security (IPPC Secretariat, 2023, Ristaino et al., 2021). Key areas of plant pathology research and discovery that have impacted on practical disease management over the last five decades have recently been summarised (Wang & Scherm, 2023) based on an online survey of members of the American Phytopathological Society. Successes in the commercial use of greater host diversity in crops have been difficult to demonstrate but as with many previous studies the use of intraspecific crop diversity can increase yield and quality, stability of production, soil fertility and microbial diversity while reducing aggressiveness of the pathogen,

e.g., as shown recently for *Phytophthora infestans* (He et al., 2016, 2021). These advances have led to successes in improved management of important crop diseases, but equally there have been failures due to a lack of durability in host resistance, development of resistance to pesticides in pathogen and vector populations, emergence or re-emergence of novel pathogens or strains associated with increasing trade and travel, and through unintended consequences of changes in cropping systems often linked to socio-economic factors. It is important for the scientific community to evaluate the impact of these advances when faced with the challenges of the mid 21st century, especially in relation to food security (Smil, 2000; Flood, 2010). The first International Day of Plant Health was celebrated at an International Conference of Plant Health on 21-23 September 2022 in London (IPPC Secretariat, 2023) to provide a forum for discussing and evaluating global scientific, technical, and regulatory plant health issues, paying particular attention to the attainment of the United Nations Sustainable Development Goals (SDGs), especially SDGs 1, 2, 13, and 15. With the UN 2030 Agenda for Sustainable Development at midpoint, the United Nations convened a Summit on 18-19 September 2023 to carry out a comprehensive review of the state of the 17 SDGs. Progress for many of the goals has been disappointing, requiring remedial action to get back on track (United Nations, 2023).

Responding to the impact of multiple interconnected challenges facing the world must include accelerated actions in agriculture (Streimikis & Baležentis, 2020) and plant health (Chakraborty, 2021; Streich et al., 2020). Achieving impact in relation to plant diseases will depend on recognition of the multidimensional nature of the challenges, their interconnectedness, and the ability to transcend discipline-based research and taxonomic boundaries by integrating studies from the molecular to the ecological in a systems level approach (FIGURE 1). In a review on the global challenges facing plant pathology (Jeger et al., 2021a), a set of concluding observations were made relevant to this approach (TABLE 1). Significant scientific advances in relation to these challenges have led to successful disease management outcomes, or at least have demonstrated a clear pathway for implementation, for individual crop diseases over the last five years as noted in TABLE 1, but not in all instances. New developments in disease management, as noted in the closing plenary session of the International Congress of Plant Pathology (ICPP 2023) in Lyon, France, are also aligned against the concluding observations of Jeger et al., (2021a) in TABLE 1. A 'word-cloud' analysis of written feedback from 276-311 participants at ICPP 2023 was analysed to identify major achievements, changes, and challenges in plant pathology. A word-cloud analysis of the responses (Höfte, 2023) gave "High Throughput Sequencing" as the major achievement over the last 20 years, "Artificial Intelligence" as the major change over the next 20 years, and "Climate Change" as the top challenge in plant health. These topics are considered further in this review.

Advances in plant pathology research which have led to individual successes in disease management are not the main emphasis of this review but rather the extent to which advances have been integrated to provide broader impact and success. Whether the wider impact of plant pathology research is conditional on such integration, is assessed. Herein we review impact in different areas, concerned with either novel methods or research approaches: diagnosis and detection of plant pathogens, surveillance of plant disease, sustainable disease management, approaches to analysing spatiotemporal spread of disease, applications of microbiome research, global change in terms of both climate and plant trade, the uses of informatic research, and the increasing use of artificial intelligence. We point out some unintended consequences of successful implementation in practice in these areas. It should also be noted that not all improvements in disease management practices can be attributed directly to advances in plant pathology research (Jeger, 2004).

DIAGNOSIS AND DETECTION

90 There have been remarkable developments in diagnosis and detection over the last decade. High
 91 Throughput Sequencing (HTS) technologies were first used in plant pathology applications in 2009
 92 (Adams et al., 2009; Al Rwahnih et al., 2009; Kreuze et al., 2009). Since then, the applications of the
 93 technology in its various forms have been refined and further developed. New scientific and
 94 technological advances have been made in HTS for molecular diagnostics and disease surveillance
 95 for monitoring of pathogen emergence and spread, including for fungi and other eucaryotes
 96 (Abarenkov et al., 2023). An exemplar for the use of HTS in plant pathology has been its adoption by
 97 virologists over the last decade (Bester et al., 2021; Valenzuela et al., 2022), now adopted widely for
 98 other pathogen and pest taxa (Maasart et al., 2022), including fungi, oomycetes, bacteria, and
 99 nematodes (Campos et al., 2021; Espindola et al., 2022). HTS has been used to investigate diseases
 100 of unknown aetiology (Adams et al., 2014; Malapi-Wight et al., 2016), to support post entry
 101 quarantine and biosecurity applications (Bag et al., 2015; Fox et al., 2019; Whattam et al., 2021), and
 102 to investigate the virome from the individual plant to the landscape scale (Maclot et al., 2020;
 103 Rumbou et al., 2020). Using the technology in each of these applications has led to the discovery of
 104 an unrecognised diversity of plant-infecting viruses, at a previously unmatched rate. This increased
 105 rate of discovery was highlighted as early as 2012, and was considered likely to continue (Roossinck,
 106 2012). Whilst this increased rate in virus discovery has been greatest in fields such as
 107 marine/aquatic viruses and bacterial viruses (known as bacteriophage or phage), the plant viruses
 108 present a greater technical challenge to deal with due to the potential risks posed to food security
 109 and environmental impacts. To help both researchers and regulatory bodies manage the application
 110 of HTS in plant health a series of guidelines have been produced to support the implementation of
 111 the technology (Lebas et al., 2022; Massart et al. 2022).

112 To prevent movement of damaging plant pests and pathogens there is a global biosecurity system
 113 administered by national and regional plant protection organisations (NPPOs and RPPOs) and
 114 coordinated by the International Plant Protection Convention. Using the IPPC international
 115 standards on phytosanitary measures (ISPMs), NPPOs have set standard approaches, not just for
 116 performing diagnostics, but for performing surveillance and most importantly assessing the risk of
 117 emerging plant pests and pathogens. Before a pathogen becomes the focus of regulatory actions,
 118 such as being declared a quarantine pest, the risk posed by that pest should be assessed through a
 119 formal Pest Risk Analysis (PRA) process (IPPC, 1996, 2004, 2006,). An essential element of that PRA
 120 is to have a characterisation of the pathogen which includes determining its taxonomic placement,
 121 lifecycle, host range, transmission characteristics, distribution, and likely impact, as this information
 122 will then support decisions to regulate the pest/pathogen. There may be a reaction to a novel
 123 discovery in one territory which provokes a reaction from another NPPO, implementing trade
 124 restrictions without having the necessary data to support a PRA. In some cases this may be a
 125 pragmatic precautionary measure, such as the discovery of novel tuber infecting viruses in *Ullucus*
 126 *tuberosus* (Fox et al., 2019) which led to the species being listed in Commission Implementing
 127 Regulation (EU) 2018/2019 as ‘High risk plants, plant products and other objects’, with prohibited
 128 entry to the EU, until a commodity risk assessment could be completed (EFSA, 2021). To assist with
 129 supporting the decision making on these new virus findings, guidelines have recently been updated
 130 to provide an optimized scientific and regulatory framework for their characterization and risk
 131 analysis (Fontdevila Pareta et al., 2023).

132 An unintended consequence of the use of HTS, particularly for plant viruses, is that the rate of
 133 pathogen discovery is increasing more rapidly than the ability to biologically characterise all the
 134 pathogens being discovered, a trend that is likely to become apparent for other taxonomic groups. A
 135 recent study by Hou et al. (2020) highlighted this issue and coined the term the “emerging biological
 136 desert” to highlight the increasing disparity between the publication of molecular characterisation

137 data as compared to the limited biological characterisation data of the type needed to support risk
138 assessment. For example, in the Hou et al. (2020) study on fruit tree viruses, over 90% of the
139 published works presented a diagnostic assay for the detection of the putative pathogen and/or a
140 near complete genome, however, fewer than 50% presented distribution data based on survey, and
141 fewer than 40% presented infectivity or transmission data. Some of these discrepancies may be due
142 to the relative speed at which practical work can be completed, creating a lag between discovery
143 and biological characterisation, however, in many cases these reports without biological evidence
144 may stand alone due to the associated costs and timescales of generating biological data.

145 The need for an increased focus on generating fundamental biological data such as host range,
146 distribution and transmission, as well as the need for territories to implement baseline surveillance
147 studies prior to plant health action being implemented, was highlighted by MacDiarmid et al. (2013).
148 A framework for dealing with these novel pathogen discoveries was proposed (Massart et al., 2017),
149 however, many of the approaches required traditional skills and, when faced with a large number of
150 novel viruses, prioritisation would be required (Fox, 2019). Even basic requirements such as
151 determining if the discovered virus was a pathogenic agent linked to disease could be technically
152 challenging due to dealing with unknown transmission mechanisms or disease being the result of
153 complex infections. Therefore, traditional approaches, such as demonstrating causation via Koch's
154 postulates, have proven unsuitable for plant virology and alternative approaches need to be found
155 (Fox, 2020). In animal virology there have been attempts to predict host reservoirs and vectors
156 based on RNA sequence (Babayan et al., 2018), an approach which could be tried in plant virology,
157 however, the much greater range of hosts and potential vectors may again prove challenging for this
158 type of predictive work. The other untapped source of data on host range and distribution may be
159 the public sequence database short read archive (SRA). These databases can be used to exploit the
160 sequence accessions for previously undiscovered viruses by searching for a characteristic virus gene
161 sequence such as the RNA-dependent RNA polymerase. Edgar et al. (2022) used this approach to
162 analyse 5.7 million ecologically diverse samples from across the globe (10.2 petabases of data) and
163 reported finding 10^5 putative novel viruses. Whilst this may initially appear to exacerbate the gap
164 between discovery and characterisation, as these data are from a range of environmental sources
165 the discoveries could help to provide supporting data for host range and global distribution of novel
166 viral pathogens if used in conjunction with targeted searching; such as the recent example from
167 Rivarez et al. (2023) in which a newly discovered ilarvirus was found across a wider range of plant
168 families, atypically for ilarviruses. Taking account of these alternative approaches, the updated
169 framework proposing how to deal with this deluge of new virus findings (Fontdevila Pareta et al.,
170 2023) should prove a useful tool in dealing with the increasing levels of uncertainty in the gulf
171 between molecular sequence and biological data.

172 This problem with the use of HTS technology is not unique to plant viruses. HTS of itself will make
173 little impact on disease management or the emergence of new or novel pathogens (Ristaino et al.,
174 2021) unless the agricultural and ecological context of studies is provided to make interpretation
175 meaningful, and the diagnostics are combined with improved surveillance in the field, whether
176 through remote sensing or other novel surveillance techniques. The availability of genome-
177 sequences of pathogens on wild species or non- pathogenic relatives is vital to be able to use HTS for
178 fungal pathogens, especially where airborne microbial populations captured at different scales form
179 the basis for sequencing (Karlsson et al., 2020; Redondo et al., 2020). An innovative approach
180 combining detection and surveillance technologies has been taken in the development of MARPLE
181 (Mobile And Real-time PLant disEase) diagnostics (Radhakrishnan et al., 2019), based on portable,
182 genomics-based equipment for in-field use. The approach is specifically tailored to identify individual
183 strains of complex fungal plant pathogens such as the rusts, which have large genome sizes and

cannot be cultured in vivo. The possibility of using sequencing to detect and monitor fungal strains presenting fungicide resistance has also been shown (Samils et al., 2021).

SURVEILLANCE

Surveillance covers a wide range of activities ranging from traditional methods based on symptoms, molecular tests and odor detection by dogs or electronic noses, to remote sensing. Remote sensing, in particular *in situ* and imaging spectroscopy, has proven highly effective for detecting and monitoring plant diseases (Gold, 2021; Oerke 2020; Terentev et al. 2022). Also known as “hyperspectral imaging,” imaging spectroscopy in the visible to shortwave infrared light range (VSWIR, 400-2400nm) can quantify chemistry in soil, rock, and vegetation based on the interaction of light with chemical bonds (Curran, 1989). This underlying capacity is what enables the ability to use imaging spectroscopy for early and non-destructive biotic stress detection in both natural ecosystems and agroecosystems (Gold, 2021). Plant pathogens damage, impair, and/or alter plant function, thus changing foliar composition, including elements such as production of systemic effectors or secondary metabolites, or by physical presence of pathogen structures such as hyphae and spores (Agrios, 2009). The changes imparted by plant disease alter how solar radiation interacts with leaves, canopy, and general plant constitution, which results in spectral responses readily capturable in VSWIR imagery both before and after visible symptoms appear (Couture et al., 2018; Herrmann et al., 2018; Fallon et al., 2020; Gold et al. 2020). Recent work has established that multiple economically important diseases caused by bacterial (Zarco-Tejada et al., 2018), fungal (Sapes et al., 2022), oomycete (Hornero et al., 2021), and viral (Romero Galvan et al., 2023) pathogens can be asymptotically detected with VSWIR hyperspectral imagery collected via aircraft, and can be differentiated from abiotic stresses.

In the context of remote sensing, disease detection differs from disease surveillance in that “detection” refers to disease identification at a particular location and point in time, while “surveillance” means consistent, ongoing monitoring for plant disease status. Disease detection is a critical first step in building operational disease surveillance systems with remote sensing. Disease detection technologies aim to accurately identify a specific cause of crop stress, while surveillance systems seek to provide this via repeated measures of the same location(s) over time to direct resources to areas that deviate from a healthy baseline. In 2018, the first report of successful asymptomatic disease detection with airborne spectroscopy was published (Zarco-Tejada et al., 2018). Their discovery is now being used by the European Union to detect existing *Xylella fastidiosa* infestation zones and establish new quarantine zones. The detection capacity underlying the EU’s *Xylella* program has begun to advance towards disease surveillance, buoyed by the team’s long speculated, but only recently confirmed, finding that that abiotic and biotic stresses with similar visual appearance (e.g. wilt) but different biological origins (e.g. drought and root disease) have divergent spectral pathways, explaining why airborne VSWIR and thermal spectroscopy can be used to differentiate between them (Zarco-Tejada et al., 2021). This success in suborbital, airborne detection has turned plant pathologists’ attention towards looking to orbitally based platforms, like satellites, as the logical next step.

When the goal is surveillance, and not simply detection, spaceborne sensing has a clear advantage over suborbital sensing due to an unparalleled landscape coverage. Suborbital platforms like aircraft provide extraordinary spatial and spectral resolution, but with highly variable temporal coverage due to the logistics and realities of funding expensive flights. Broadband and multispectral methods relying on visible (VIS, 400-700nm) and near-infrared (NIR, 700-1000nm) reflectance indices, such as normalized difference vegetation index (NDVI), from spaceborne platforms have been used to sense

late-stage plant disease since the 1980s (Jackson, 1986; Nagarajan et al., 1984). Widely available indices such as the NDVI from both commercial and from space agency sources have proven useful for general targeting and risk assessment, but have proven insufficient for disease diagnosis, especially in multi-stress environments (Cotrozzi & Couture 2019) where there may be a critical dependency on external environmental conditions. Recent engineering innovations and advances in satellite constellation design have improved the temporal and radiometric consistency and scalability of both space agency and commercial spaceborne sensing platforms. Examples of commercial platforms include DigitalGlobe's World View fleet (0.5-1.2 m spatial resolution, 8-38 spectral bands) and Planet Lab's SuperDove (3 m, 8 bands) and SkySat-C (0.5 m, 4 bands) fleets (Yang, 2018; Frazier & Hemingway, 2021; Saunier et al., 2022). As teams around the world have begun to explore novel satellite technology for detection and surveillance, we see an emerging dependency on canopy size for whether spaceborne multispectral observations can be used for disease mapping at actionable intervention stages, with capacity diminishing as plant size shrinks. For example, commercial Earth observations from Worldview 2 and 3 could detect intermediate and advanced disease, but early detection of the symptoms required airborne hyperspectral data (Poblete et al., 2023). Other teams studying different pathosystems have found both similar, and dissimilar results, owing to differences in underlying pathosystem characteristics. Scientists studying oak wilt (*Bretziella fagacearum*) found that space agency observations are indeed sufficient to detect and map the disease from space when phenology is taken into account (Guzmán et al., 2023). However, others studying grapevine downy mildew (*Plasmopara viticola*) found that multispectral satellite imagery alone is insufficient for early stage disease detection and that canopy density was a critical dependency in whether moderate-to-late stage disease could be mapped (Kanaley et al., 2023). Use of shortwave infrared (SWIR) reflectance from satellites greatly improves disease detection in the absence of, and/or prior to, a greenness response (Bhattacharya & Chattopadhyay, 2013; Dutta et al., 2014; Mirik et al., 2010). Historically, narrowband SWIR data have not been widely available from spaceborne systems, but this is soon to change. For example, NASA's EMIT mission began collecting "postage stamps" of VSWIR imagery across the Earth in early 2023. Forthcoming satellite systems with launches planned for the late 2020s such as ESA's Copernicus Hyperspectral Imaging Mission for the Environment (CHIME; (Nieke & Rast, 2018) and NASA's Surface Biology and Geology (SBG; Schneider et al., 2019) will make global imaging spectroscopy data widely available for agricultural decision making.

Identifying plant diseases prior to them becoming symptomatic is especially valuable but challenging. For example, the fastidious plant pathogenic bacterium *X. fastidiosa* can infect more than 350 plant species worldwide, and early detection is critical for its eradication in areas where it has been introduced. Quick olive decline syndrome is the result of a recent introduction of the pathogen to southern Italy. Before symptoms are visible, changes in plant traits detected by imaging spectroscopy and thermography revealed *X. fastidiosa* infection in olive trees with 94.03% accuracy, visualised using receiver operating characteristic (ROC) analysis from the pool of plant functional traits (Zarco-Tarjeda et al., 2018). In a similar study on almond on the island of Majorca, research applying machine learning showed early detection of *X. fastidiosa* infection based on spectral changes related to pigments, canopy structural traits, fluorescence emission and transpiration, resulted in an accuracy of detection of >90% (Camino et al., 2022). Global trade exposes natural and agricultural systems to non-native pathogens (Pautasso & Jeger, 2014). As a consequence, physiology-focused remote sensing methods at large spatial scales relying on plant traits will prove important to prevent and manage plant disease epidemics worldwide, as well as being a contributing component of precision agriculture in managing established diseases (Gold, 2021). The idea of plant functional traits has emerged as a unifying framework in remote sensing to understand natural and

276 stress-induced variation in vegetation (Wright et al., 2004; Ustin et al., 2004; Verrelst et al., 2019).
277 Recent research has begun to disentangle divergent spectral pathways associated with shared
278 physiological symptoms (Couture et al., 2018; Fallon et al., 2020; Gold et al., 2019a, 2019b, 2020;
279 Sapes et al., 2022; Guzman et al., 2023; Zarco-Tejada et al., 2018, 2021). For example, Zarco-Tejada
280 et al. (2021) found spectral plant traits contribute differently to airborne scale detection across host
281 species (olive vs. almond) and vascular plant pathogens (*X. fastidiosa* vs. *Verticillium dahliae*).
282 Further, accounting for distinct spectral plant traits associated with water-induced stress greatly
283 improved early and pre-symptomatic disease detection algorithm performance. Overall, quantifying
284 spectral plant traits linked to stress-induced biological mechanisms has been shown to greatly
285 improve model accuracy and generalizability in contrast to empirical approaches based on single-
286 band and vegetation indices alone (Camino et al., 2021; Hornero et al., 2021; Poblete et al., 2021;
287 Zarco-Tejada et al., 2018). Quantifying plant traits, either through statistical (e.g., partial least
288 squares regression [PLSR]; Serbin & Townsend, 2020) or Radiative Transfer Modeling (RTM;
289 Kattenborn & Schmidtlein, 2019), from imaging spectroscopy data allows us to measure, map, and
290 model the pathosystem processes that underly the diseased plant phenotype, and will become more
291 important as we seek to further scale research to application.

292 As plant pathologists seek to move proof-of-concept detection discoveries in plant disease sensing
293 towards surveillance application with these forthcoming systems, it will be critical that systems we
294 build employ multi-modal and multi-scale observations and integrate epidemiological modeling to
295 inform risk (Gold et al. in review). Imaging spectroscopy alone is not sufficient to fully inform plant
296 disease risk, as its greatest strength, the ability to precisely capture wide ranging traits related to
297 environmental chemistry and constitution, is also its greatest weakness. Hyperspectral imagery is
298 highly sensitive to numerous factors, ranging from atmospheric variability and sensor position to
299 topology and geography (Schweiger, 2020). The impact of this sensitivity can be reduced through
300 contextualization with other data streams and methodologies. For example, scientists studying *X.*
301 *fastidiosa* recently discovered that remote sensing can quantify the explanatory power of
302 epidemiological modeling by capturing the effect of host spatial structure and landscape
303 connectivity, substantially improving prediction accuracy (Camino et al., 2021). Poblete et al. (2023)
304 found that supplementing spaceborne multispectral imagery with thermal airborne imagery was
305 able to improve prediction accuracy of *X. fastidiosa* and *V. dahlia* infection by 10-15%, highlighting
306 the need for multi-modal observations for early detection to inform actionable intervention. As
307 forthcoming hyperspectral satellite systems come online, the need for operational research to
308 address how to integrate them with data streams that can further contextualize risk, such as
309 environmental sensors and epidemiological modeling, and to make information in a timely and
310 accessible manner will become more important.

311 Currently, research is lacking in plant pathology on how to operationalize discovery into publicly
312 accessible applications via easily interpretable information for decision support systems at spatial
313 scales relevant to the end user (Rose et al., 2016). Imagery from space agency (e.g., NASA, ESA)
314 sources is an ideal foundation for risk assessment systems, the data is free, and any changes to
315 accessibility are announced and documented well in advance. Data may be freely available but
316 often has been obtained for other purposes. . For example, NASA's Airborne Visible and Infrared
317 Imaging Spectrometer Next Generation system captured, opportunistically, high resolution
318 hyperspectral imagery of almost 1 million acres of vineyards in California over the past 5 years
319 during missions focused on non-agricultural objectives (Trolley et al., 2021). Better tools and user-
320 interfaces for accessing, searching through, and processing remote sensing imagery for non-expert
321 users will be essential for utilizing spaceborne data to the fullest potential. Key to achieving this goal

will be interdisciplinary training and collaboration between plant pathologists, engineers, and computer scientists to build usable decision support and risk assessment systems for both researchers and stakeholders (Heim et al., 2019).

STRATEGIES FOR SUSTAINABLE DISEASE MANAGEMENT

The areas of plant pathology research that have had successful outcomes in disease management (Wang & Scherm 2023) were deployment of host resistance genes (Norman et al., 2023), use of disease models in forecasting systems (González-Domínguez et al., 2023), introduction of modern systemic fungicides (Beckerman et al. 2023) and resistance inducers (Reglinsky et al., 2023), improved management of fungicide resistance (Yin et al., 2023), and a better utilisation of biological control (Sarrocó, 2023) and suppressive soils (Sagova-Mareckova et al., 2023). Collinge et al. (2022) reviewed achievements in biological control of plant diseases. The prospects for biological control were considered promising rather than demonstrated but at the very least biocontrol can supplement other sustainable disease management practices such as disease resistance. The contribution that recent microbiota research can make to biological control in the broader context of plant health is considered in a later section of this review. The significant progress made in understanding plant disease resistance mechanisms have been summarised (Khan et al., 2023). In most cases successful outcomes refer to individual plant pathogen combinations rather than taking a broader view of impact on disease management, such as how best to deploy resistance genes in a crop population.

The principles behind sustainable plant disease management are easy to state but it is more difficult to demonstrate their implementation in practice. Emphases should be placed on rational adaptation of resistance, avoidance, elimination, and remediation strategies, individually and collectively, guided by traits of specific host-pathogen associations and evolutionary ecology principles. The overall objective would be to sustain biotic and abiotic environmental conditions favorable for host growth and development while being averse to pathogen reproduction and evolution, consistent with economic and sociological considerations (He et al., 2016, 2021). A gamut of solutions has been proposed to meet this challenge, ranging from regenerative agriculture to precision agriculture. Much of the argument is made in terms of host defence, and the relationship with diversity in host and pathogen populations at different system levels.

Plants have developed complex defence systems against plant pathogens based on pathogen recognition, signal transduction, and the defence response, but tempered by the pathogen's ability to subvert these defences (Andersen et al., 2018). Questions over the durability of resistance have led to renewed interest in quantitative or partial resistance providing a background to major gene resistance which otherwise would give a bimodal segregation into resistant or susceptible phenotypes (Pilet-Nayel et al., 2017). There have been major advances in genetic techniques that have the potential to transform the development of disease-resistant crops by genetic modification (van Esse et al., 2020), genome-editing (Yin & Qiu, 2019), gene drive and synthetic biology (Pixley et al., 2019). If such advances are to have impact in plant breeding and the development of disease resistant crops then they must be matched by similar advances in the use of high throughput phenotyping in the field (Mahlein et al., 2019; Shakoor et al., 2017). These advances are also limited by insufficient attention being given to how novel resistances can be deployed in the field under the range of agronomic, climatic and pathogen challenges to be faced. Advances in cropping system research and the role of genetic diversity in relation to plant diseases have been made in two areas, corresponding to a whole agroecosystem perspective and responses to biotic and abiotic stressors at the individual host plant level.

At the system level, deployment of novel resistances to specific pathogens needs to be aligned with a wider appreciation of biodiversity-ecosystem function relationships (Brooker et al., 2021), ecosystem services (Paseka et al., 2020), within- and between-crop diversification (Wang et al., 2021; Newton & Skelsey, 2023, Newton & Karley, 2023), soil biodiversity (Bakker, 2019) and microbiota-mediated resistance (Vannier et al., 2019). Successes in the commercial use of greater host diversity in crops have also been difficult to demonstrate but as with many previous studies the use of cultivar mixtures can increase yield and quality, stability of production, soil fertility and microbial diversity while reducing aggressiveness of the pathogen, e.g., with *Phytophthora infestans* (He et al., 2016, 2021). Many examples of successful outcomes in field experimental work can be cited and the ecological principles that underly these can be defined (Kopp et al., 2023; Brooker et al., 2023) but evidence of success on a wider scale is limited due to many unsuccessfully controlled disease issues. The main issues are a lack of uptake of greater host diversity due to market resistance, practical application issues and the requirement for greater management input (Newton & Karley, 2023; Hus et al., 2022). However, use of more diverse crops is becoming mainstream in the approach of 'regenerative agriculture' practitioners (Newton et al., 2024) and therefore the system benefits may facilitate adapted market development, new precision agriculture technology, and an expanding set of supporting resources, such as the DIVERSify Guide to Farmers and Agronomists, Decision Support Tool, and Toolbox for Policy Makers <https://plant-teams.org/#guidestoolboxes>. The question remains as to the extent trends towards sustainability and regenerative agriculture can be aligned with the opportunities presented by precision agriculture.

Tolerance of plant disease, as with abiotic stressors, can be expressed at all stages of plant growth, can be induced by environmental conditions, and can ameliorate reproductive fitness (Ganie & Foyer, 2023). The question of how best tolerance of disease can be combined with host resistance to pathogens has only recently been posed. The complementary contribution that tolerance of plant disease can make in protecting crops (Jeger, 2023; Mikaberidze & McDonald, 2020; Schneider, 2021; Pagán & García-Arenal, 2018, 2020), whether as an alternative or combined with host resistance, needs critical examination with some suggestion there may be counterindications; i.e. those farmers who grow tolerant crops may suffer less yield loss per unit of disease and also benefit from neighbouring farmers who grow resistant crops, but in so doing they may disadvantage the latter farmers, termed "selfish grower behaviour" (Murray-Watson & Cunliffe, 2022). There may be a fine balance in determining what constitutes successful deployment of tolerance or failure. Specific tolerance traits have rarely been identified in individual plants, but equally relevant is identifying traits in plants grown as crops and especially the role of diversity including in intercropping (Newton, 2016). Disease escape related to breeding for plant ideotypes/architecture has been little exploited; examples for wheat pathogens include *Zymoseptoria tritici* (Robert et al., 2018; Vidal et al. 2018), *Rhizoctonia cerealis* (Guo et al., 2017), and *Gaeumannomyces tritici* (Palma-Guerrero et al., 2021).

Multiple pathogen species or strains on a single diseased tissue present problems in assessing pathogen diversity, for example with *Fusarium* head blight (Wang et al., 2022). A single diseased head could contain more than 10 *Fusarium* operational taxonomic units (OTU), where OTUs based on sequence similarity are the basic analytical unit in microbial ecology (He et al. 2015). Deoxynivalenol, 15-acetyldeoxynivalenol and zearalenone concentrations showed a significant negative correlation with *Fusarium* diversity on diseased heads while a significant positive correlation between nivalenol concentration and *Fusarium* diversity was observed.

Both discussions above at the system and whole plant levels describe deployment of 'diversity' but as with other popular terms such as 'sustainability' (Spadaro & Gullino, 2019; Berlin et al., 2018; Frac et al. 2022) and 'regenerative' (Sherwood & Uphoff, 2000; Giller et al., 2021; Khangura et al., 2023)

these represent different things to different people in different contexts. To optimise effective deployment, diversity with respect to both disease management and the crop and environmental context needs to be defined and parameterised (Newton & Karley, 2023).

More benign disease control options such as chemical induced resistance agents or resistance elicitors have been proposed and tested. Addressing whether these have been a great success, Yassin et al. (2021) concluded that generally, they have had small, variable, and inconsistent effects, occasionally with some deleterious side-effects and therefore compare unfavourably against 'conventional' pesticides. Nevertheless, in the context of IPM and lower-input agriculture such as 'regenerative' cropping, they may have important roles (Yassin et al., 2021). In this context Yassin et al. (2021) argue that developing complementary and synergistic combinations of resistance elicitors, or elicitors with reduced dose conventional pesticides, are likely to offer both effective and resilient or durable crop protection as part of IPM protocols. However, independent evaluation of such products and the funding to develop effective combinations and IPM protocols, is lacking. Their impact has, therefore, been far lower than their potential, and the challenge to change this is daunting. A way forward could be to harness and enhance farmer-led on-farm trialling and the knowledge exchange found commonly amongst 'regenerative' agriculture communities (Newton et al., 2024). In a similar vein the broader use of signalling molecules such as semio-chemicals to provide a wider range of protection against insect pests and pathogens across crops, with additional benefits for biological control and pollinators, has been reviewed (Thomas et al., 2023). Successful outcomes with insect pests have been realised using the "push-pull" strategy, also applied for management of virus vectors, such as *Bemisa tabaci* (Pouët et al. 2022), or the ambrosia beetle/symbiotic fungal association involved in laurel wilt disease (Kendra et al. 2017).

TEMPORAL AND SPATIAL SPREAD OF DISEASE

Spatiotemporal spread is the main driver of plant disease outbreaks, their predictability, and subsequent consequences in terms of crop damage and loss. The associated environmental factors contributing to disease spread have been studied in many cases even for complex aetiologies involving multiple pathogens, e.g., for *Phytophthora* and other oomycete pathogens causing oak defoliation and mortality (Sánchez-Cuesta et al., 2021). Epidemiological understanding of the temporal and spatial spread of plant diseases has been enhanced by advances in population genetic approaches, especially in relation to pathogen diversification and evolutionary potential, e.g., *Melampsora lini* (Susi et al. 2020) and *Zymoseptoria tritici* (McDonald et al., 2022) as thoroughly discussed for rust fungi in reviews on the evolution of virulence (Figueroa et al., 2020) and their global dispersal and diversity (Hovmøller et al., 2023). It is still the case that combining population genetic and dynamic models in an overall epidemiological approach has proved elusive except for cases where dispersal pathways or over-wintering (or over-summering) locations have been demonstrated (Corredor-Moreno & Saunders, 2020; Ristaino et al., 2021).

Modelling the potential spatial range of invasive plant pathogens in new geographic areas relies on environmental data to predict habitat suitability to infer risk of establishment (Andersen et al. 2004). This informs the need for quarantine measures at potential points of pathogen entry and surveillance requirements if a pathogen has already entered. Species distribution models adapted from ecology, such as BIOCLIM (Booth et al., 2013), CLIMEX (Sutherst et al., 2007) and MAXENT (Phillips et al., 2008) have been widely used for plant disease and pest risk analyses. Climatic inputs come from publicly available gridded global climate databases, such as WorldClim, which provides monthly averages of weather variables from 1970-2000 at a spatial resolution from 1–340 km² (Fick & Hijmans, 2017). More recently, the ERA ERA5-Land global dataset has been made available with a

total of 50 environmental variables from 1950 to the present hourly and at a spatial resolution of 0.1 X 0.1° (Muñoz-Sabater et al., 2021). The NAPPFAST modelling platform was specifically developed for plant disease risk assessment (Magarey et al., 2007) and derives disease-specific climatic variables from monthly averaged data from 1978 onwards at 55 km spatial resolution (Climatic Research Unit, Norwich, UK; Jones & Harris, 2008).

All these models use either correlative approaches such as climate matching to derive climatic predictor variables from areas where a pathogen already occurs, or process-based approaches using physiological information about a pathogen's environmental requirements derived from controlled experiments. The risk maps resulting from the above are static spatial representations of long-term average disease risk and although they include seasonal trends by virtue of the monthly time step in the climate databases, they cannot represent episodic climatic variation and extreme events associated with, for example, the El Niño Southern Oscillation, or other oceanic climate drivers. However, fine time-resolution spatial climatic data is becoming more readily available for disease modelling because of advances in numerical weather modelling and computing power. This allows weather models to produce simultaneous fine scale spatial and temporal disease risk prediction in near-real time or even ahead of time using forecast weather. Recently, machine learning combined with geo-regionalisation methods have been applied to make predictions of the temporal and spatial spread of wheat powdery mildew for the German federal state of Schleswig-Holstein (Hamer et al., 2020). The new challenge for high resolution spatiotemporal disease modelling concerns visualisation and interpretation by the human brain of the dynamic disease risk information generated. Static representations can be made using a sequence of risk maps over time, or a set of time-series graphs for different locations but both are difficult to assimilate. Computer animation of mapped disease spread over time helps visualisation and interpretation but requires an interactive computer interface, which challenges current methods of scientific publication, but may also challenge the intended users of risk maps such as growers or policymakers.

An additional and often overlooked problem in the analysis of spatial data is that models usually assume stationarity (i.e., the spatial effect is invariant to the map translation) and isotropy (i.e., the spatial effect is invariant to the map rotation), that is, the autocorrelation between two locations only depends on the Euclidean distance. However, relying on these two assumptions can produce misleading results, with unrealistic associations and/or bias in the prediction of the species distribution, when elements such as barriers that are an obstacle to the movement of the species are present in the study area. Different types of barriers (i.e., geographic, agronomic, etc.) are often present when diseases spread by natural means and they are also intrinsic to the principles of plant disease control, i.e., exclusion, eradication, protection, and resistance. Bakka et al. (2019) introduced an approach that makes it possible to deal with nonstationary spatial processes. This approach has been initially applied in marine species distribution studies (Bakka et al., 2019; Martínez-Minaya et al., 2019) and more recently by Cendoya et al. (2022) to analyze the occurrence of *X. fastidiosa* in Alicante, Spain, using hierarchical Bayesian spatial models with the incorporation of barriers. The predicted probability of *X. fastidiosa* presence in the area outside the barrier was substantially reduced when the nonstationary spatial effect was considered in the models. However, the approach by Bakka et al. (2019) assumes that barriers are completely impermeable, meaning that the pathogen cannot be present or cross these barriers, which is a very strong assumption rarely met in practice. New modeling methods are, therefore, needed to be developed to accommodate the incorporation of barriers with different levels of permeability, to address more realistic scenarios in plant health. More generally, we note that stochastic representation of spatiotemporal spread based within a Bayesian framework is increasingly applied to obtain a realistic appreciation of the key

parameters and uncertainties and the implications for improved disease management (Kwame Adrakey et al., 2023).

In the context of outbreaks of quarantine pathogens for which eradication or containment is foreseen by regulations, individual-based models allow the incorporation of the interactions between individual plant hosts and the pathogen within a spatially explicit landscape. This approach captures the effects of host heterogeneity as well as the spatial structure of disease dynamics, which are essential to design and evaluate outbreak management plans (Cunniffe et al., 2015). Nevertheless, one of the problems faced when fitting this type of model is that the temporal and geographical characteristics of the initial foci of the outbreak are unknown. Moreover, in most cases a no-intervention scenario is not available as disease control measures are implemented as soon as the disease is detected. The scale of ambition of this approach can extend over large geographical areas. For example, a predictive spatiotemporal model was proposed for the spread of cassava brown streak disease, for which surveillance data was sparse Godding et al. (2023). The model included disease control interventions and could in principle be extended to all sub-Saharan cassava producing countries and contribute to regulatory decisions at national and regional levels.

Examples of applications

Applications of advanced techniques in epidemiological analysis based on spatial data, dynamic models, and climatic variables has proved successful, as shown for established populations of *Puccinia striiformis* f. sp. *tritici* in China, invasive populations of *Austropuccinia psidii* in New Zealand, and emerging populations of *Xylella fastidiosa* in Spain.

Puccinia striiformis f. sp. *tritici*

Population genetic analysis was made of yellow rust of wheat (*P. striiformis* f. sp. *tritici*, *Pst*) collected from spatially separated sampling locations in Gangu County in Gangsu Province in China (Huang et al., 2021) (FIGURE 2(a)). Samples were collected in relation to elevation from two mountain regions separated by a valley. Samples collected from different altitudes in the spring showed close genetic similarity with several shared multilocus genotypes (FIGURE 2(b), Panel A). In the fall the level of genetic relatedness decreased with increasing altitude with many distinct multilocus genotypes (Panel B). In terms of geographical separation there was close genetic similarity between the north and south mountain regions in spring (Panel C), whereas the over summering populations had separated into two groups (Panel D). Results showed the extent of genetic diversity in the population, supporting the interpretations of different migrating populations with altitude, a level of isolation with altitude, and that sexual recombination occurred in the mountain regions. *Pst* spread and epidemic development across the entirety of China using a wider range of molecular markers and other approaches has recently been published (Li et al., 2023). Forward and backward trajectory analyses were used to develop a spread simulation model for *Pst* in China. By means of trajectory tracking, historical migration studies, genetic introgression analyses, and field surveys, *Pst* sources and their contributions to wheat stripe rust epidemics were investigated (FIGURE 2(c)). The regions with the highest population diversities (Longnan, the Himalayan region, and the Guizhou Plateau) were identified as the *Pst* sources in China.

Austropuccinia psidii

Myrtle rust (*A. psidii*) is an invasive species affecting plants in the Myrtaceae that has recently spread throughout the Southern Hemisphere (Chock, 2020) and is also a threat to the Northern Hemisphere (Paap et al. 2023). Myrtle rust affects many plants in the Myrtaceae and was first reported in New Zealand in 2017. The Myrtle Rust Process Model (MRPM) is a spatiotemporal model that predicts epidemiological parameters of infection risk, latent period, and spore production risk from gridded

hourly data at 1.5 km spatial resolution generated by the New Zealand Convective Scale Model (NZCSM) numerical weather model (Beresford et al., 2018; Moore et al. 2016). The high-resolution output is processed into weekly risk maps which are used for planning disease surveillance and management. The MRPM and NZCSM have also been adapted as a decision support tool for timing fungicides against myrtle rust in plant nurseries (Beresford and Wright 2022), to predict climate change effects on myrtle rust (Campbell et al., 2020) and to identify ecological refugia in natural areas, where the climate is suitable for susceptible Myrtaceae host species but less so for the pathogen (McCarthy et al., 2021). To identify ecologically important refugia outside the predicted geographical range of the pathogen, McCarthy et al. (2021) constructed Myrtaceae species distribution maps and rust infection risk maps used to define areas of climatic tolerance for four species based on gradients of annual temperature and precipitation. Refugia were identified as natural habitat areas where susceptible hosts could exist with little or no pathogen impact, whereas restorable refugia, which were climatically similar, had anthropological disturbance which could potentially be restored to function as refugia. Two disease severity assumptions were examined: Scenario 1 represented the core infection risk where climate is most suitable for infection and Scenario 2 represented the entire pathogen range. Species distributions for a total 15 New Zealand endemic species were examined, with four illustrated to represent a range of niche combinations (FIGURE 3). These two scenarios provided insights into how different assumptions about level of infection risk could influence the spatial distribution of refugia.

Xylella fastidiosa

Almond leaf scorch caused by *X. fastidiosa* was first reported in Alicante, Spain, in 2017 (Cendoya et al. 2022) (FIGURE 4). A study area within the demarcated infected zone consisted of more than 366K trees distributed over 1300 km². The test area had almost 30000 trees. An individual tree-based compartmental (healthy, asymptotically infected, infectious) model was defined with spatial dependencies and configurations included. Simulations were done over a period of 120 months. The outcome of the simulations depended on the initial introduction and a range parameter describing the distance at which locations can be considered spatially uncorrelated. With an aggregated initial distribution there was a great variability in the maximum and minimum number of infected individuals depending on the location of the initial infected individuals. With a random initial distribution, the maximum and minimum numbers were very close to the median. Such analyses show the importance of accounting for the initial distribution of disease, whether aggregated or with multiple sources of primary inoculum (Ojwang' et al., 2021). Recently, it was discovered that remote sensing can quantify the explanatory power of epidemiological modeling by capturing the effect of host spatial structure and landscape connectivity that substantially improved *X. fastidiosa* prediction accuracy (Camino et al., 2021).

Recently, Cendoya et al. (in review) used molecular epidemiology studies to date the possible origin of the introduction of *X. fastidiosa* in Alicante, Spain, in the mid-1990s by sequencing and comparing different *X. fastidiosa* strains (Landa et al., 2020), as well as epidemiological and dendrochronological data on *X. fastidiosa* infected almond trees (Moralejo et al., 2020). Control measures for *X. fastidiosa* have been implemented only recently in this area and thus official survey data provided an approximation of the extent of the infested zone that the disease would have reached without any interventions. Through this approach, it was possible to simulate with an individual-based model the progression of the disease over time in the absence of diagnosis-based evidence on the date of introduction. Different survey strategies and disease control measures were then simulated to determine their effectiveness and efficiency for outbreak management in relation to the baseline scenario without interventions.

596 MICROBIOT AND HOLOBIONT RESEARCH

597 Recent research emphasis on the microbiome has invigorated plant-soil microbial studies in relation
598 to sustainable agriculture and food security (Chouhan et al., 2021), plant breeding (Nerva et al.,
599 2022; Karlström et al., 2023; Zhang et al., 2023), malfunctional microbiota and disease (Arnault et
600 al., 2023), stress resistance (Liu et al., 2020), and crop resilience and biodiversity (Vassilev et al.,
601 2021). The ecological and evolutionary dynamics of the plant microbiome communities have been
602 reviewed (Company et al., 2019; Fields & Friman, 2022; Morales Moreira et al., 2023).

603 Beneficial effects of soil microbes in sustaining plant health and their role in complex declines and
604 disease syndromes have long been described (Gómez-Aparicio et al., 2022). Microbiont research has
605 started to shed light on the etiology and ontogeny of a variety of disease complexes and declines as
606 opposed to diseases caused by single pathogens (Mannaa & Sao, 2021). Examples include oak
607 declines (Scarlett et al., 2021), grapevine declines (Bettenfeld et al., 2020), and root pathogen
608 complexes in grain legumes (Wille et al., 2019). The abundance and diversity of soil microbial
609 communities associated with asymptomatic and symptomatic oak trees with declines was
610 investigated in relation to soil nitrogen status (Scarlett et al., 2021) (FIGURE 5). Piecewise structural
611 equation modelling was used to evaluate direct and indirect relationships among soil abiotic
612 variables and N-cycle microbial gene abundance, and tree health status. The resulting path diagram
613 showed that asymptomatic trees were positively associated with ammonia oxidizing bacteria (AOB)
614 genes with increased abundance in high pH soils.

615 The outstanding and unique role of soil as a microbiome reservoir opens new perspectives for
616 applications of soil microbial inoculants to improve plant responses to abiotic and biotic stressors.
617 Plant root recruitment of beneficial microbiomes through root exudates (Santoyo et al., 2022;
618 Dastogeer et al. 2020; Chialva et al. 2022) can be partially genetically controlled by hosts. This was
619 shown by the significant variability in the rhizosphere microbiome between host genotypes,
620 e.g., in cotton (Wei et al., 2019) and apple (Cook et al., 2023). Such a recruitment process may reach a
621 steady state rapidly even for perennial tree fruit crops such as apple (Cook et al., 2023). Specific
622 beneficial microbial organisms in the phytobiome may be associated with cultivar resistance or
623 diseased status (Wei et al., 2019; Tilston et al., 2018; Cook et al., 2023). However, pathogens might
624 utilize secreting proteins/effectors to overcome the defence barriers associated with the
625 microbiome, leading to disease development (Hassani et al., 2018; Li et al., 2021; Chen et al., 2018;
626 Snelders et al., 2020).

627 Santos & Olivares (2021) proposed two approaches for converting microbiome knowledge into a
628 potential biotechnological product applied to agriculture systems. Firstly, agronomic intervention
629 may be used to influence the microbiota community composition towards benefiting crop
630 development and production. Among other things, these practices may include use of cover crops,
631 organic materials, soil management, and nutritional and irrigation management. Secondly, key
632 beneficial micro-organisms in the resident microbiome are identified, isolated, evaluated, and finally
633 formulated into commercial biological products. Adopting the first approach is severely constrained
634 by our current limited understanding of the complex dynamics of the microbiome in relation to
635 external perturbations. Thus, developing commercial products based on a few specific strains has
636 been commonly adopted, including biofertilizers and biopesticides (Malusà et al., 2021). Managing
637 plant diseases can also be achieved by specific beneficial microbes that prime or induce host defence
638 mechanisms (Ali et al., 2023). This was recently demonstrated by the fact that dipping rice roots in
639 microbial products at transplanting increased crop productivity in addition to suppressing rice blast
640 development (Murunde et al., 2022; 2023). However, biocontrol efficacy may be considerably

affected by other factors, such as environmental conditions (Tut et al., 2023) and nutrient application (Berg & Koskella, 2018).

Detailed studies have been carried out with specific plant-microbiome systems worldwide, and here we highlight two: one on wilt management in cotton, and the other on apple canker management at leaf scars. *Verticillium* wilt caused by *Verticillium dahliae* is a serious soil-borne disease in cotton worldwide. Banning broad-spectrum chemical soil fumigants necessitated the search for alternative management methods, including exploitation of beneficial microbes associated with roots. Wilt resistant and susceptible cotton genotypes differ in their overall rhizosphere and endosphere microbial communities, including several well-known taxonomic groups containing beneficial microbes with higher relative abundance in resistant cultivars (Wei et al., 2019a). In wilted plants, the variability in the fungal/bacterial biomass ratio is much smaller than in either fungal or bacterial total biomass (Wei et al., 2021). Many rhizosphere microbial groups differ in their abundance between healthy and wilted plants; in particular, there is a decrease in arbuscular mycorrhizal fungi and an increase in several plant pathogen and saprophyte guilds in diseased plants. Soil origin predominantly shapes rhizosphere microbiome assembly, while cotton genotype fine-tunes this recruitment process by changing the abundance of specific microbial members (Yang et al., 2022). Coating seeds with fungicides leads to significant changes in bulk soil microbiome, with the exact effects depending on soil types (Ma et al., 2023). Results also showed that there are strong links between soil microbial communities, metabolites, and enzymatic activities. Finally, a specific cotton endophytic fungal strain, *F. solani* CEF559, can confer protection against *V. dahliae* (Wei et al., 2019b).

European apple canker, caused by *Neonectria ditissima*, is one of the most devastating diseases of apple that urgently requires new control measures. Infection by *N. ditissima* is through wounds, including leaf scars. Recent research has been focussed on searching for microbial-based solutions as there is a lack of effective fungicidal solutions. Initial amplicon sequencing study showed clear differences in fungal communities in the leaf scar tissue between susceptible and resistant cultivars (Saville & Olivieri, 2019), leading to an identification of *Epicoccum nigrum* as a putative biocontrol organism against *N. ditissima*. Both in vitro and in planta experiments indicated that this strain could reduce canker development (Papp-Rupar et al., 2023a). Furthermore, the abundance of this specific strain in plants within a growing season can be increased by augmented foliar spray or root drenching. This demonstrated that a targeted approach to search for biocontrol organisms based on amplicon-sequencing can be fruitful. The overall endophyte communities at leaf scars are largely affected by locations, sampling time and, to a much lesser extent, rootstock, and scion genotypes (Papp-Rupar et al., 2023b, Olivieri, 2021). Bacterial endophytes may persist over growing seasons better than fungal endophytes in the leaf scar tissues (Papp-Rupar et al., 2023b). Several microbial groups differed in their relative abundance between canker susceptible and resistance cultivars, including several *Sphingomonas* taxa, associated with tree health and canker resistance. In a canker resistance mapping population, relative abundance of several endophyte taxonomic groups in the apple leaf scar tissues is correlated with canker development (Papp-Rupar et al., 2022). Furthermore, there is evidence for partial genetic control of many endophytes by apple hosts. Quantitative trait loci (QTL) mapping has identified a number of QTL associated with relative abundance of specific endophytes and a couple of the QTLs are located in close proximity to QTLs for host canker resistance (Karlstrom et al., 2023), suggesting breeding for a specific endophyte could be a viable option.

Although the microbiome concept has invigorated plant and soil microbiological research, the potential for impact has not fully been realised. Publication of results was often largely a

687 categorisation exercise but are now more difficult to publish unless combined with functional
688 studies. Data show many associations of potential functions or plant traits with specific microbiome
689 components but testing specific hypothesis on such association is difficult within the context of a
690 specific microbiome. Furthermore, microbiome knowledge has only recently led to specific
691 microbial manipulations or interventions to improve biological control or plant health more
692 generally. Consequently, it remains a challenge to predict outcomes on soil microbiome and/or
693 phytobiome, hence crop performance, after specific management interventions.

694 GLOBAL CHANGE

695 Global change includes considering the impacts of climate warming and variability and of plant
696 disease introductions from the worldwide trade in plants and plant products. The impacts of climate
697 change on individual crops and plant pathogens have long been studied and reviewed, e.g., Hunjan
698 & Lure (2020). The impacts of climate warming on different groups of plant pests have been
699 comprehensively described in terms of a general poleward latitudinal movement of different
700 taxonomic groups (Bebber et al., 2013, 2015). Speculations on the impact of global change on
701 individual plant diseases have been made, but it is only relatively recently that a framework for
702 methodological approaches to study the impact has been proposed (Raza & Bebbber, 2022), involving
703 observational studies, process-driven disease models, and experimental comparisons of plant
704 pathogen systems under current and presumed future climates. The relationship between projected
705 yields for 12 crops under climate change scenarios to 2080 was examined using three crop models
706 and cardinal temperatures defining infection risk for 80 fungal and oomycete pathogens (Chaloner et
707 al., 2021). It was projected that at high latitudes crop yield would generally increase under climate
708 change; there would be an additional burden placed by infection risk that would need to be met by
709 host resistance and crop protection methods. Although climate change impacts have been assessed
710 mainly in terms of temperature-driven effects, there is likely to be direct and indirect effects of soil
711 moisture as predicted for *Phytophthora cinnamomi* (Homet et al., 2019). In the Mediterranean basin
712 this invasive oomycete is devastating native evergreen oaks. Although on average climate change is
713 projected to lead to a drier climate, an increased frequency of extreme rainfall events, waterlogging
714 and flooding is likely to exacerbate infection risk and spread that makes the average soil moisture
715 conditions irrelevant to disease epidemiology. Episodic and extreme climatic events present many
716 challenges in predicting the impact of climate change on plant pathogens, as shown for outbreaks of
717 bark beetle in Sweden (Kärvemo et al., 2023) and *P.striiformis* in the USA (Gardner et al., 2023).

718 Still lacking in climate change projections are the cascading ecological interactions and impacts at
719 various spatial scales occurring with climate warming. It has been claimed that the challenge of
720 climate change cannot be met with single pathogen-single crop studies but requires these to be
721 placed in the context of shifting populations of new as well as existing crops, wild plants, and soil
722 microbes (Jeger et al., 2022a). Equally it has been argued that the current conceptual framework for
723 climate change impacts on plant diseases is deficient and that a combination of ecological and
724 evolutionary concepts should be introduced into research to improve mechanistic understanding
725 and prediction of pathogen spread and disease outbreaks in future climates (Singh et al., 2023), and
726 thus improve modelling strategies (Yang et al., 2023). As an example, *Candidatus Phytoplasma solani*
727 affects grapevine ('bois noir') and solanaceous crops ('stolbur') as incidental hosts, with bindweed
728 (*Convolvulus arvensis*), stinging nettle (*Urtica dioica*) as wild hosts for the pathogen and reproductive
729 hosts for the planthopper vector *Hyalesthes obsoletus*. The question is then how will climate
730 warming affect the individual components and epidemiology of disease?

731 As well as climate warming, human actions, and the introduction of exotic plant pathogens through
732 global plant trade needs continuing evaluation (Pautasso & Jeger, 2014). Non-native plants

introduced through trade may become invasive and, if carrying pathogens, may threaten native plants in the natural environment. This situation is analogous to that described for parasites of invasive alien animal species, e.g., helminth parasites of fish, where effectively the parasite is a co-invader. It was found that virulence on native species where a host switch of the parasite had occurred was greater than on the alien invasive species (Lymbery et al., 2014). Plant disease introductions have consequences that are multidimensional (Jeger et al., 2021b) and although plant health risk assessments have been developed rapidly in recent years, whether this leads to improved regulation at national and regional levels remains an open question. The challenge in assessment and in regulation is how best to marshal and interrogate large data sets from across the world, often inconsistent in format and content, and to prioritise risks according to the threats posed. Advances in informatics research, as described in the next section, have the potential to help meet this challenge.

INFORMATICS

Advances in informatics research make the marshalling and interrogation of large data bases more amenable but is still challenging, particularly the extent to which automated searches can serve the purpose without ‘ground truthing’ through human interpretation. Extensive data bases on plant pathogens, compiled by different public and private agencies, are now available, ranging from the conventional scientific literature to governmental or industry-based publications, media reports, and internet-based social platforms. The challenge is to extract relevant information from these myriad forms of communication that can be used and acted upon in response to real-time plant disease problems. Informatic studies of the peer-reviewed scientific literature has advanced beyond conventional bibliographic analyses (e.g., Arya, 2015) and can provide authenticated information but reflect inevitable delays in publication (Jeger et al., 2023). Another problem is the publication bias towards positive results, whereas in practice negative results can also provide equally important information in disease management. They can be applied to individual species and crops (dos Santos et al., 2021; Singh et al., 2019) and broader categories such as in forest health and suites of diseases affecting crops and trees (Pautasso, 2016; Muniz et al., 2020), or specific topics in plant pathology such as methodologies used in disease assessment (Del Ponte et al., 2017).

Systematic reviews

Citation bias is common and can have unintended consequences, particular for practice-relevant questions (Pandey & Burch-Smith, 2023). To avoid this, one way of examining the available scientific evidence is to use evidence synthesis, which is based on a robust, transparent, and repeatable method for searching the literature and collecting evidence, often called a systematic review. This type of systematic overviews has revolutionised medicine, is widely used in the humanities, and is increasingly applied in many other fields, including environmental and agricultural sciences (Haddawy et al., 2016). A systematic review is a synthesis and analysis of all available information on a specific research question (Moher et al., 2016), whereas a systematic mapping is a description of the available knowledge and the amount of research within a defined area (James et al., 2016). The processes for both types of systematic overviews follow reporting standards that include systematic and defined methods for searching for, selecting, and critically appraising relevant research and should be designed to avoid biases (Page et al., 2021). Systematic reviews and maps can be used to identify and summarise evidence on different methods of disease management (Vilvert et al. 2022), and some are already available (Wyckhuys et al., 2023). These types of reviews have the potential to identify knowledge gaps and biases that are difficult to identify in other types of studies, and they facilitate the possibility of developing new and better research questions to support evidence-based decision-making (Cooke et al., 2023; Lázaro et al., 2021).

779 Systematic reviews can be used to identify available knowledge and knowledge gaps relevant to
780 plant protection for different crops (Berlin et al., 2018). The reviews have great potential to support
781 plant health and can be used as an encyclopaedia for the selection of agronomic and control
782 methods. The outcome and quality of the systematic review or map depends largely on the selection
783 of eligibility criteria. When assessing the available literature, the economically most important
784 diseases of the most valuable crops are far more studied than diseases of minor crops, and the
785 production of a crop within a region often correlates with the number of studies published from that
786 area (Vilvert et al., 2021; Wallenhammar et al., 2022). The most frequently studied control methods
787 were resistant crops, indicating the importance of breeding resistant varieties in crop production.
788 The second most studied control method was fungicides or pesticides. As several active ingredients
789 in pesticides are banned, new or re-emerging plant diseases are emerging. Various types of
790 agronomic practices were also identified as control methods. There was also a trend towards
791 increasing publications on different types of biological control agents and tools. One example is the
792 increase in insect-transmitted viruses in warmer climates and when insecticides are banned. In the
793 oilseed rape map, only three articles were identified on aphid-transmitted turnip yellows virus
794 (TuYV), a disease that is expected to increase in the warmer Swedish climate (Puthanveed et al.,
795 2023).

796 Horizon scanning

797 Informatic studies when combined with expert knowledge can be used in horizon scanning (EFSA,
798 Mannino et al. 2021) and prioritization of pathogen problems (EFSA, Tayeh et al. 2022), although in
799 the case of novel and/or emerging pathogens there is often a lack of both data and expert
800 knowledge, necessitating new forms of analysis such as provided by methods described in the next
801 section. There is also the question of whether 'hard' scientific literature (validated but mostly with a
802 time-lag in publication) can be combined with 'soft' media information (often not validated but
803 available in real-time) to provide the best means of prioritising plant health risks. There can be a real
804 contrast between the relative proportions of pathogen groups reported in these two sources of
805 information. Arthropods and bacteria dominate reports in the media compared with fungi,
806 oomycetes, viruses and viroids, and nematodes; whereas although arthropods still dominate in the
807 scientific literature, there is a more even representation across the pathogen groupings (See Figures
808 5 and 14 in Mannino et al. 2021). Social media is a further source of information on plant pest
809 invasions (Tateosian et al. 2023) and can contribute to horizon scanning, but comparison with other
810 forms of media information is premature, and is explicitly excluded in systematic review
811 methodology.

812 ARTIFICIAL INTELLIGENCE, MACHINE LEARNING, AND DEEP LEARNING

813 Artificial intelligence (AI) (Winston, 1984) guiding is rapidly opening new opportunities that affects
814 individuals, businesses, and society more generally (Winston, 1984; Zhang & Lu, 2021) and could
815 affect the achievement of the UN Sustainable Development Goals (Goralski & Tan, 2019; Galaz et al.,
816 2021), including those mentioned in the introduction as relevant for agriculture and plant pathology.
817 New developments in computer technology, referred to variously as AI, machine learning (ML), and
818 deep learning (DL), are cutting across all areas of plant pathology (Prabha, 2021; Liu & Wang, 2021;
819 Li et al., 2021; Hassan et al., 2020; Streich et al., 2020; Garrett et al., 2022). Applications can be
820 found in all areas of plant pathology covered in this review (TABLE 2): plant disease detection and
821 diagnosis, surveillance, sensing, resistance gene discovery, analysis of spatial data, genomic
822 sequencing, microbiota data, climate change, and informatics. Although these techniques overlap,
823 there are differences which are not always reflected in how they are referred to by authors. Clear

824 definitions of AI and machine learning can be found in Joshi (2019), the distinction between ML and
825 DL by Sujatha et al. (2021) and Jackulin & Murugavalli (2022), and the distinctions across all three
826 approaches by Ongsulee (2018), with the additional epithet for the techniques being “explainable”
827 (Emmert-Streib 2020).

828 Obtaining large, accurate, and annotated datasets is the key limiting factor to further use of AI in
829 plant pathology. Standardizing methods and aggregating data in a comprehensible manner will be
830 instrumental in overcoming challenges related to liability, scalability, and generalizability in data-
831 driven plant pathology (Del Ponte et al., 2022). Universally accepted protocols for plant disease risk
832 measurement and reproducibility across scales remain undeveloped (Sparks et al., 2023). Assessing
833 disease severity, even by trained plant pathologists, is complex (Bock et al., 2022). Leveraging non-
834 supervised learning methods such as self-supervised learning can help address this challenge by
835 enhancing model parameterization using large, unannotated datasets, so that subsequent
836 supervised model training is more efficient and generalizable. Even still, initiatives targeting risk
837 prediction at broader scales will require meticulous, universal protocols or computer-vision-based
838 machine learning classifications archived in searchable databases to standardize disease severity
839 assessments to ensure uncertainty isn’t propagated through surveillance predictions. While
840 extensive repositories such as the United States National Fungus Collections Fungus-Host Dataset
841 (Castlebury et al., 2023.) certainly exist, there are few existing searchable databases that aggregate
842 specific disease incidence, severity, and damage data at scales sufficient for regional-global scale
843 inferences.

844 As the demand for AI in plant pathology advances it is vital that we adopt “explainable” to ensure
845 that all systems guiding stakeholder decision-making are accurate, efficient, transparent, and
846 interpretable. Recent breakthroughs in DL have revolutionized tasks like natural language processing
847 and computer vision, but many models remain enigmatic, yielding results without clear underlying
848 mechanisms (Grün et al., 2016). Unintended consequences can result, a particularly unacceptable
849 outcome for plant disease, which can influence management decisions with substantial public and
850 financial impacts. Explainable AI (XAI) is a groundbreaking approach that overcomes the causal
851 obscurity of black-box AI models (Arrieta et al., 2020; Ryo, 2022; Vilone & Longo, 2020). XAI seeks to
852 enhance transparency and interpretability of ML and DL models, granting researchers and
853 stakeholders improved clarity into the underlying decision-making processes (Arrieta et al., 2020).
854 XAI can (1) create models with interpretable components and controlled behaviors and (2) interpret
855 existing black-box models using activation maps to reveal decision-making processes. XAI can
856 therefore improve our ability to understand models’ driving predictors, fostering informed,
857 transparent decision-making and trust, while addressing AI-associated issues of bias, ethics, and
858 regulatory compliance; aspects that are crucial for disease detection since epidemics and the actions
859 taken to mitigate them carry significant financial, environmental, and societal consequences (Garrett
860 et al. 2022).

861 Training and deploying ML, DL, and XAI models demand considerable computation and storage
862 resources (Marr, 2015; Mell et al. 2011; Minh et al. 2022). Most recent advances in XAI have been
863 enabled by cloud computing, which has fundamentally transformed data storage and processing by
864 offering on-demand and virtually unlimited access to storage and computing devices. Edge
865 computing complements cloud computing by placing storage and computing nearer to data sources,
866 enabling timely and accurate modeling development and deployment (Rubambiza et al., 2023). The
867 distributed (edge and cloud) computing model enables models to be trained and housed in the cloud
868 but deployed at the edge, including on users’ devices, which optimizes system performance for

Commented [KMG1]: Del Ponte, E. M., Cazón, L. I., Alves, K. S., Pethybridge, S. J., & Bock, C. H. (2022). How much do standard area diagrams improve accuracy of visual estimates of the percentage area diseased? A systematic review and meta-analysis. *Tropical Plant Pathology*, 47(1), 43–57. <https://doi.org/10.1007/s40858-021-00479-5>

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869 agricultural decision-making. This is especially important, as agricultural areas tend to have pervasive
870 challenges with reliable internet connectivity. Distributed computing has been increasingly applied in
871 agricultural use cases, including disease detection (Rubambiza et al. 2023). The demanding
872 computation and storage resources for AI development and deployment also present challenges in
873 terms of sustainable deployment, critical for long term usage of any such systems to inform plant
874 disease management decision-making (Wu et al. 2022). The private sector (e.g., large technology-
875 based companies) are investing in capital infrastructure to host large common datasets, train general
876 AI models (e.g., GPT 4 for natural language processing), and deploy them for commercial
877 applications (e.g., GPT 4 for ChatGPT), but there is no clear pathway or plan on how to make these
878 resources available in the long run to sustainably support derived applications for the public sector,
879 such as plant disease analysis. It is urgent that plant pathologists support initiatives to 1) connect the
880 public and private sectors so resources can be effectively and efficiently shared for societal good,
881 and 2) push for resource-efficient AI solutions.

882 CONCLUSIONS

883 The main conclusion we draw is that a systems-based research agenda that builds upon successes in
884 the management of individual plant diseases, as well as learning from the failures and 'negative'
885 data which are often overlooked, is needed to meet the wider challenges in plant pathology.
886 Multidimensional solutions across different disciplines, which are themselves interconnected, are
887 needed (FIGURE 6).

888 More specifically, we need to:

- 889 1. Determine how best to mitigate the combined impacts of physical and biotic stress in moving
890 towards a sustainable agroecology. Determine how best tolerance to disease and abiotic
891 stressors in crop plants can be combined with host resistance to pathogens.
- 892 2. Ensure the agronomic and ecological context is provided for interpretation of huge data sets
893 collected in high throughput sequencing studies and genome-based detection methods,
894 including the sequencing of related but not crop infecting pathogens. With big data as referred
895 to in many of the studies addressing the issues in the review, there is the need for standards and
896 providing data/methods/metadata for reproducibility.
- 897 3. Ensure that advances in molecular diagnostics and disease surveillance technologies are
898 compatible and well-integrated. In the research community, there is much knowledge about
899 specific detection/diagnosis tools, but to what extent are the technologies implemented in
900 practice.
- 901 4. Move towards physiology-based characterization for disease detection and surveillance with
902 multi-modal and multi-scale observations.
- 903 5. Protect and restore ecological habitats that could function as refugia for vulnerable native plants
904 threatened by invasive pathogens. Characterise the initial distributions of emerging pathogens
905 through epidemiologically based surveillance.
- 906 6. Characterise and manipulate the beneficial components of the soil microbiome and/or
907 phytobiome for improving plant health. Be able to predict likely outcomes on soil microbiome
908 and/or phytobiome when specific intervention measures are applied. Determine whether there
909 are commonalities in the causative microbial factors seen across plant declines.
- 910 7. The effects of climate warming on the individual components affecting epidemiology of disease
911 (wild hosts, vectors, microbes) and their interactions have been poorly studied.
- 912 8. Marshal and interrogate large data sets from across the world and prioritise plant health risks
913 arising from plant introductions. Determine the time-lags in assessing the epidemiological
914 significance of new pathogen reports and identifying emerging diseases.

- 915 9. Reconcile sources of information from the scientific literature and media reports to prioritise
916 plant health risks, including a systematic review on how knowledge from science is
917 communicated with stakeholders.
- 918 10. Combine the use of artificial intelligence with more traditional approaches in addressing
919 research questions and implementing disease management actions.
- 920 11. Challenge research funders and regulatory authorities to develop and respond to a
921 multidimensional research agenda. Policy needs to be formulated or conducive in a way to
922 provide an environment to nurture such an agenda.
- 923 12. Operationalize proof-of-concept discoveries to proof-of-practice with stakeholder involvement.

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928 assessment.

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1830 **FIGURE LEGENDS**

1831 **FIGURE 1: Multidisciplinary approaches to meet food security and environmental challenges (Jeger**
1832 **et al. 2021)**

1833 **FIGURE 3: Migration routes of *Puccinia striiformis* f. sp *tritici* (Pst) in China: (a) and (b), regional**
1834 **migration (Huang et al. 2021); (c) long-distance dispersal across China (Li et al. 2023).**

- 1835 (a) Location of Gangu county within Gansu province in China. Sampling sites/elevations where
- 1836 Pst isolates were collected are shown as dots (Huang et al. 2021).
- 1837 (b) Minimum spanning networks with colors indicating the population, and size of circles
- 1838 reflecting the number of samples for each multilocus genotype. The population from
- 1839 different altitudes in spring are shown in A, and in fall in B. The populations from the south
- 1840 and north mountain regions in spring are shown in C, with over-summering survival on
- 1841 volunteer wheat shown in D.
- 1842 (c) Major migration routes of Pst from sources in China inferred from population genetics
- 1843 analysis, air trajectories, and disease occurrence (Li et al. 2023). Red arrows represent
- 1844 migration routes supported by all analyses. Dark blue arrows show migration routes
- 1845 supported by population genetics and air trajectories. Green arrows indicate migration
- 1846 routes supported by disease surveys and air trajectories. The solid lines indicate direct
- 1847 migration from the Pst sources, whereas the dashed lines indicate indirect migration. The
- 1848 width of each arrow shows the probability of the migration route.

1849 FIGURE 4: Environmental niches of four Myrtaceae species and our two myrtle rust scenarios. The
 1850 environment is characterised across two primary climate gradients (precipitation and temperature;
 1851 grey hexagons with dashed lines showing extremities). Myrtle rust scenario polygons encompass
 1852 95% of the climate values. Species points show the mean (\pm SD) for all occurrence records (McCarthy
 1853 et al. 2021).

1854 FIGURE 5: Simulations with which the maximum (a) and minimum (b) of individuals infected by
 1855 *Xylella fastidiosa* after 120 months, in the test area of Alicante, Spain, with initial introduction of 10
 1856 asymptomatic infected individuals at a focus (Cendoya et al. 2022).

1857 FIGURE 6: Path diagram showing significant direct and indirect effects of soil abiotic variables and N-
 1858 cycle microbial communities on tree health status. Numbers on arrows are standardised path
 1859 coefficients with width of arrows proportional to the strength of path coefficients. Solid and dashed
 1860 arrows indicate positive and negative relationships, respectively. Double-headed arrows indicate
 1861 covariance between variables, single-headed arrows indicate a one-way relationship. Blue arrows
 1862 indicate the relationship between soil variables, red arrows between soil variables and gene
 1863 abundances, grey arrows between gene abundances, and green arrows between gene abundances
 1864 and tree health status (Scarlett et al. 2021).

1865 FIGURE 8: A multidisciplinary research agenda is needed to meet future challenges in plant
 1866 pathology.