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Monitoring the phenology of plant pathogenic fungi: why and how?

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ABSTRACT

Phenology is a key adaptive trait of organisms, shaping biotic interactions in response to the environment. It has emerged as a critical topic with implications for societal and economic concerns due to the effects of climate change on species' phenological patterns. Fungi play essential roles in ecosystems, and plant pathogenic fungi have significant impacts on global food security. However, the phenology of plant pathogenic fungi, which form a huge and diverse clade of organisms, has received limited attention in the literature. This diversity may have limited the use of a common language for comparisons and the integration of phenological data for these taxonomic groups. Here, we delve into the concept of 'phenology' as applied to plant pathogenic fungi and explore the potential drivers of their phenology, including environmental factors and the host plant. We present the *PhenoFun* scale, a phenological scoring system suitable for use with all fungi and fungus-like plant pathogens. It offers a standardised and common tool for scientists studying the presence, absence, or predominance of a particular phase, the speed of phenological phase succession, and the synchronism shift between pathogenic fungi and their host plants, across a wide range of environments and ecosystems. The application of the concept of 'phenology' to plant pathogenic fungi and the use of a phenological scoring system involves focusing on the interacting processes between the pathogenic fungi, their hosts, and their biological, physical, and chemical environment, occurring during the life cycle of the pathogen. The goal is to deconstruct the processes involved according to a pattern orchestrated by the fungus's phenology. Such an approach will improve our understanding of the ecology and evolution of such organisms, help to understand and anticipate plant disease epidemics and their future evolution, and make it possible to optimise management models, and to encourage the adoption of cropping practices designed from this phenological perspective.

Key words: environmental change, epidemics, fungal disease, phenology, phenological scale, plant pathogen.

CONTENTS

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I. INTRODUCTION

Phenology concerns the successive and irreversible stages of development of an organism during the completion of its life cycle and the ways in which the organism relates to seasonal environmental variations (Forrest & Miller-Rushing, 2010). Studying the timing of these events is central to understanding the fitness and dispersal patterns of organisms, species interactions and distribution, synchrony between organisms, and the assembly of communities in ecological niches (Chuine, 2010). Phenological events are influenced by environmental, organism-related, and populational mechanisms (Chmura *et al.*, 2019). The phenological response (e.g. when an organism begins to develop in the spring, when it reproduces, when it enters dormancy or migrates) to environmental factors has been studied in a large range of plant, animal, insect, and fungal species (e.g. Bebber, 2015; Forrest, 2016; Flynn & Wolkovich, 2018; Thackeray *et al.*, 2016). The phenology of most organisms is driven by temperature, photoperiod and water availability. As a result, phenological shifts provided the first biological evidence of climate change (Menzel *et al.*, 2020), and phenology is now considered an essential biodiversity variable requiring particular efforts in terms of monitoring and data sharing (Pereira *et al.*, 2013). Interest in phenology has recently increased, due to potential links and uncertainties relating to global changes in climate, land use, and cropping practices. Phenological studies can improve our understanding of the responses of natural and cultivated ecosystems to new abiotic and biotic combinations of conditions (Hamann *et al.*, 2021; Iler, Caradonna & Forrest, 2021).

Phenology drives species interactions in different trophic networks (Tylianakis *et al.*, 2008; Kharouba & Wolkovich, 2023). Phenological changes have been observed in plants (e.g. earlier dates of leaf unfolding, flowering or fruit ripening; Menzel *et al.*, 2020), insects (e.g. increased numbers of generations per year; Pöyry *et al.*, 2011) and pathogens (e.g. earlier spore release dates after overwintering; Garrett *et al.*, 2006). These changes can modify the synchrony between the host and biotic agents (Ouyang *et al.*, 2016; Morente-López *et al.*, 2018), and between the pathogen and its vector (Desprez-Loustau *et al.*, 2020) or its natural enemies (Forrest, 2016).

Decreases in generation time, associated with changes to phenological synchrony in food networks, can trigger species range expansion, emergence, or extinction (Régnière, St-Amant & Duval, 2012; Popova, 2014; Chaloner, Gurr & Bebber, 2021). Indeed, the spatial expansion and emergence of plant pathogens has greatly increased in recent years, with the emergence of new phenological niches due to global changes (Bebber, 2015; Corredor-Moreno & Saunders, 2020).

Phenology is particularly difficult to monitor in fungi, as most stages of the life cycle of these organisms are not visible to the naked eye. However, the timing of key events in the fungal life cycle has been studied at different spatial and temporal scales. Many studies have considered the timing of reproduction (fungal fruiting; Gange *et al.*, 2013). Andrew *et al.* (2018) and others have focused on the timing of dispersal (spore release; Peay *et al.*, 2012). Fungi and fungus-like organisms (such as oomycetes) are highly diverse. A number of fungal ecological guilds have been defined: saprotroph, endophyte, mycorrhizal, and pathogenic fungi. The traits of fungal pathogens have been less frequently recorded than those of other fungal guilds, with most of the traits recorded for pathogens relating to fungal genetics (Zanne *et al.*, 2020). The phenology of plant pathogenic fungi has rarely been formally explored *per se*, although the timing and duration of life-cycle traits have been described for fungal pathogens (e.g. dates of spore release or fructification, or latency period or cycle duration; Précigout *et al.*, 2020). In addition, epidemic events, such as the appearance of the first symptoms in the field, are also recorded, to anticipate disease outbreak severity (Clay, Duffy & Rudolf, 2020) or the effect of climate on infection dynamics (Daugherty, Zeilinger & Almeida, 2017). The term 'phenology' has only been applied to plant pathogenic fungi to our knowledge in two studies focusing on host–pathogen synchrony in oak populations (Desprez-Loustau *et al.*, 2010; Marçais, Kavkova & Desprez-Loustau, 2009). We argue here that studies of the phenology of plant pathogenic fungi and the creation of a common and global phenological coding system for these organisms will open up new research perspectives for quantifying and predicting the impact of global changes on plant health.

II. THE DRIVERS OF THE PHENOLOGY OF PLANT PATHOGENIC FUNGI

As a means of encompassing the various drivers of the phenology of plant pathogenic fungi, we assumed the perspective of plant pathologists, which targets disease occurring at the interface of three factors: a favourable environment, a susceptible host, and the presence of a pathogen. Using this

'disease triangle' (Francl, 2001), we considered the phenology of plant pathogenic fungi to be directly influenced by environmental conditions (biotic, abiotic, and anthropic) and by the host plant (Fig. 1). Pathogen phenology is expected to vary in response to these factors in interaction at different scales: (*i*) the timing of the entire pathogen life cycle or any of its steps may be shortened, extended, postponed, or delayed (e.g. in response to host phenology or in the face of competitors); and (*ii*) the presence or absence of particular stages in specific conditions (e.g. a survival stage under unfavourable conditions, asexual reproduction under optimal conditions, or interruption of the cycle if a primary or secondary host is missing).

(1) Environment

The abiotic (physical, chemical), anthropic, and biotic elements of the environment affect the phenology of pathogenic fungi at different scales. The climate and microclimate at plant canopy level are probably the main drivers of the phenology of pathogenic fungi. For example, spore germination, mycelial growth, sporulation, and fructification are all highly dependent on temperature (Chaloner *et al.*, 2021), in tight interaction with the duration of leaf wetness for many fungal species (Gullino *et al.*, 2022). Environmental conditions may also indirectly alter disease development likely through modifications of plant physiology or plant resistance level (Bortolami *et al.*, 2021; Desaint *et al.*, 2021). Plant–environment interactions

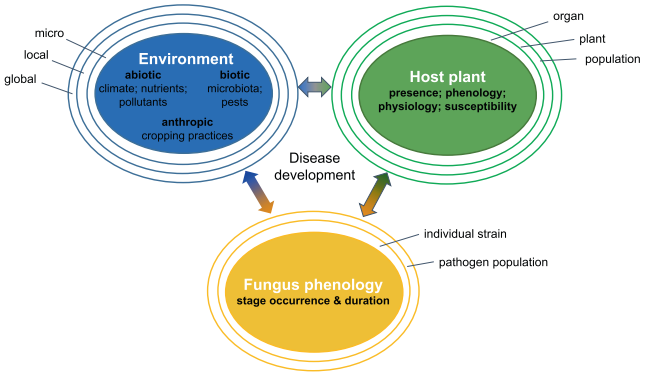

Fig. 1. Schematic representation of the biotic and abiotic drivers of the phenology of plant pathogenic fungi and associated disease development. Environmental conditions – biotic, abiotic, and anthropic – directly influence the phenology of plant pathogenic fungi. The host plant also modifies fungus phenology through its presence, phenology, physiology, and susceptibility. Environmental conditions may indirectly alter fungus phenology through modifications of host physiology and resistance level, *via* cropping practices or plant biodiversity management for example. The double-headed arrows symbolise the feedback interactions between elements of the environment, host plant traits and phenology, and fungal phenology. The various circles around the drivers represent the micro, local, and global scales (environment), the organ, plant, and population scales (host plant), and the individual and population scales (fungus).

shape the plant microbiome, thereby activating plant defence pathways and immunity (Pélissier, Violle & Morel, 2021) and enabling the plant microbiome to compete with the pathogen for resource requirements (Wei *et al.*, 2015), which can inhibit or enhance the achievement of key pathogen developmental stages (Liu *et al.*, 2020). These responses highlight the importance of trophic levels in the pathogen life cycle. Cropping practices can also modify pathogen phenology through effects on the environment and host in the long term or at a regional level (Fig. 1). Low-nitrogen farming accelerates leaf senescence (Agüera & De la Haba, 2018), limiting the host area available for biotrophic pathogens to invade (Robert, Bancal & Lannou, 2004). Sowing density modifies the early canopy microclimate, thereby altering the probability of infection. The synchrony between crops and pathogens varies considerably with sowing date (e.g. Van de Wouw *et al.*, 2021), varietal precocity (e.g. Tresson *et al.*, 2020) and the timing of the release of natural enemies to regulate pest populations (e.g. Nicot *et al.*, 2019; O'Sullivan, Belt & Thatcher, 2021). Moreover, plant biodiversity plays a key role in the evolution of pathogen phenology at the farm and landscape levels, the spatial organisation of cultivated and non-cultivated plants favouring the synchrony between natural enemies and pathogen phenology (Vialatte *et al.*, 2021). At the field level, a wider range of winter/summer crops or longer rotations including more non-host crops (Debaeke, Casadebaig & Langlade, 2021) can modify the fungal life cycle, such as switching to survival (Umaerus, Scholte & Turkensteen, 1989) or altering timing of key stages of fungal phenology (Newbery, Qi & Fitt, 2016). Finally, the introduction of new less-susceptible or non-host species may affect pathogen phenology through the host–pest coevolution process (Marburger *et al.*, 2015).

(2) Host plant

The host plant drives the phenology of plant pathogenic fungi directly through its presence, phenology, physiology, and susceptibility at different scales (organ, individual and population; Fig. 1). Host phenology affects the appearance of susceptible organs, such as leaves or flowers, and allows the spore germination stage to occur. The physiological traits of the host plant, including its nitrogen and water status, also alter pathogen phenology. For example, water stress can limit symptom development in vascular disease (Bortolami *et al.*, 2021) and leaf nitrogen content can affect the duration of the latency period (as assumed by Précigout *et al.*, 2020). Host plant resistance levels may depend on ontogeny, as resistance can be expressed at juvenile or adult stages (e.g. Jain *et al.*, 2020; Huang *et al.*, 2019), or even at a specific developmental stage (Calonnec *et al.*, 2021). In many cases, quantitative resistance in the host plant further modulates the duration of fungal phenological stages (as for latency period; Delmas *et al.*, 2016). The spatial distribution of host and alternative plants over the diverse plant community may also result in genetic dilution and discontinuity in pathogen resources (Schellhorn, Gagic & Bommarco, 2015), or empower the completion

of a particular stage (e.g. for the causal organism of wheat stem rust, sexual reproduction occurs on *Berberis vulgaris*; Barnes, Saunders & Williamson, 2020). Considering the evolution of the plant and fungal populations, there may be a selective advantage in individual plants that escape disease and in individuals of fungal species that adapt rapidly to phenological changes in the host. Global warming accelerates the life cycle, favouring pathogen survival (Aboukhaddour *et al.*, 2020; Olivera Firpo *et al.*, 2017). However, it may also lead to a disruption of the temporal and spatial phenological match between host and pathogen, resulting from dissimilar thermal performance curves (Caubel *et al.*, 2017; Marçais & Desprez-Loustau, 2014).

Detailed knowledge of the key phenological stages of living organisms is therefore crucial for pest management, especially in an agroecological context in which increased anticipation is required. Pathogen phenology responds to multiple interactions between environment, host and crop management. By observing and understanding pathogen phenology, we should be able to stay one step ahead. We therefore built a coding system for fungi and fungus-like organisms, taking their diversity into account, to assess objectively the effects of different drivers on pathogen phenology. This should help us to face epidemics in a more efficient and agroecological manner.

III. HOW TO SCORE THE PHENOLOGY OF PLANT PATHOGENIC FUNGI

(1) The diversity of plant pathogenic fungi

Fungi and fungus-like organisms (i.e. oomycetes, which belong to the Stramenopiles) are tremendously diverse, with at least 2.2–3.8 million species (Fig. 2; Hawksworth & Lücking, 2017; Hyde *et al.*, 2020; James *et al.*, 2020; Li *et al.*, 2021). Most are microscopic, and some are pathogenic for plants (Zeilinger *et al.*, 2016), with fungi and oomycetes together accounting for most eukaryotic plant pathogens. There are 8000 to 10,000 species of plant pathogenic fungi (Agrios, 2005; Petit & Lavigne, 2019; Fisher *et al.*, 2020) capable of causing disease in plants and major losses of global food production (Fisher *et al.*, 2012; Oerke, 2006; Strange & Scott, 2005). Most belong to the phyla Ascomycetes and Basidiomycetes (Zanne *et al.*, 2020). These two phyla are the most abundant fungal phyla, with 92,000 and 50,000 species, respectively, in the *Catalogue of Life 2022* (https://www.catalogueoflife.org/data/taxon/F).

(2) Revealing common main phenological stages of plant pathogenic fungi

Phytopathogenic fungi and fungus-like species differ in several ways (e.g. morphology, life-cycle stages). To identify potential shared phenological stages among them, we first selected several detrimental plant pathogens that are widespread globally and belong to different divisions (Oomycetes with *Phytophthora* spp. and *Plasmopara* spp.; Ascomycetes with common fungal pathogens causing rot such as *Sclerotinia* spp. and *Botrytis* spp.; and Basidiomycetes with a variety of fungal pathogens causing rust and leaf spot diseases). We compared their life cycles and identified common and specific stages for each (Figs 3 and 4). This comparison shows that, despite considerable diversity, five key features and developmental stages were common to these species: production of spores, spore germination, mycelial growth, reproduction, and survival (Fig. 3; Table 1). With rare exceptions (e.g. *Rhizoctonia*), fungal pathogens of the Ascomycetes and Basidiomycetes divisions as well as Oomycetes produce spores (the reproductive unit of fungi consisting of one or more cells, in function analogous to the seed of green plants; Agrios, 2005), which may play different roles in dispersal or reproduction (Fig. 4). In all three divisions, spore germination initiates a new cycle and is dependent on infection efficiency (Fig. 4). A mycelium (the hypha or mass of hyphae that make up the body of a fungus) is then produced, which colonises the host tissue (mycelial growth; Fig. 4). The next step is the production of reproductive organs from the mycelium. Reproduction may be asexual or sexual (involving mitosis or meiosis, respectively) and produces spores that can initiate a new cycle (Fig. 4). Depending on the fungal species, unfavourable periods during the life cycle may result in spores or mycelium becoming a survival organ (Fig. 4), avoiding spore germination or growth in environments that are not optimal, and enhancing fungal survival (also called dormancy).

We confirmed from the fungal literature that these five primary stages (Figs 3 and 4; Table 1) are suitable for use with life-cycle diagrams for other fungal and fungal-like plant pathogen species, as well as non-pathogenic fungi.

(3) The *PhenoFun* scale, a phenological coding system for fungi

The existing phenological coding systems (i.e. phenological scales) built for various plant and animal species describe successive phenological events (i.e. phenological traits). They are used at the level of the organism (the observer records the date at which a new organ appears) or at the level of the population (the observer records the date at which a trait reaches a given frequency in the population). Phenological scales have mostly been developed for crop species, as exemplified by the widely used Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie (BBCH) scale (Meier, 2018). This system is a useful tool that provides a code for similar development stages in each plant species (first digit) and a complementary code for the secondary development stages (second digit). Implementation of a similar system for fungi will make it possible to link observation dates with observed phenological stages.

We developed the *PhenoFun* scale, a phenological coding system for fungi and fungus-like taxa such as Oomycetes based on the BBCH scale. The *PhenoFun* scale can be freely downloaded *via* the permanent link: https://entrepot.

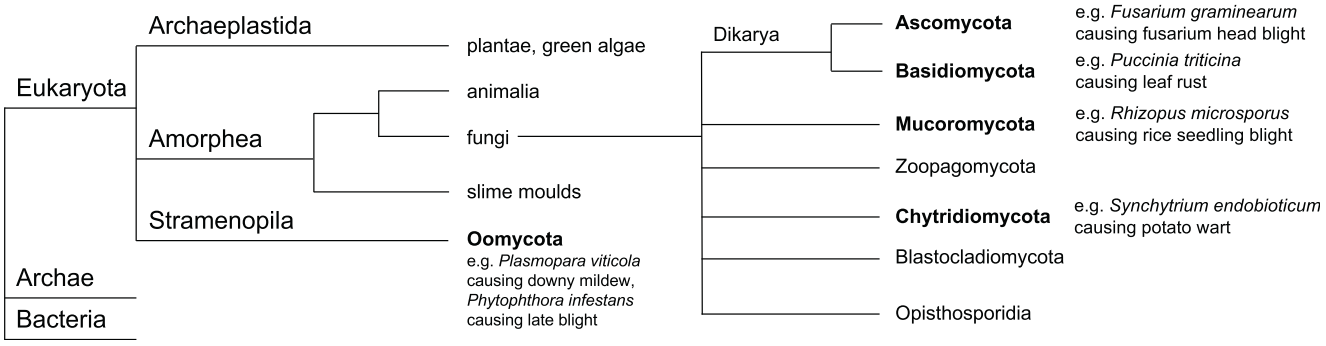

Fig. 2. Schematic phylogenetic tree of fungi and fungus-like organisms. Divisions including plant pathogenic fungal species are shown in bold and examples of well-known diseases are provided. Adapted from Burki *et al.* (2020), James *et al.* (2020) and Li *et al.* (2021).

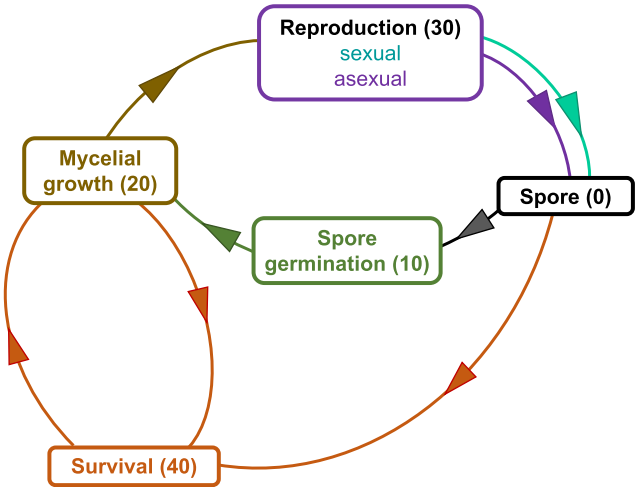

Fig. 3. Primary stages of the phenological scoring system developed for plant pathogenic fungi and the associated primary stage code from the *PhenoFun* scale. These different stages were identified by comparing species from the Oomycetes, Ascomycetes and Basidiomycetes divisions (see Fig. 4). These five primary stages are suitable for any fungal and fungal-like plant pathogen species, as well as non-pathogenic fungi. Changes in primary stages are indicated by arrowheads and each of the primary stages is identified by a specific colour code. The spore phase is represented in black, the germination phase in dark green, mycelial growth in brown, and the survival phase in orange. Sexual and asexual reproductive phases are represented in blue and purple, respectively. The phenological stage numbers are indicative of the primary phenological stages described in Table 1 and in the *PhenoFun* scale (version 1.0; Delmas *et al.*, 2024).

recherche.data.gouv.fr/dataset.xhtml?persistentId=doi:10.57745/CNM2XJ; (Delmas *et al.*, 2024). We associated each of the main five stages described above (production of spores, spore germination, mycelial growth, reproduction, and survival) with a 'primary stage code' (first digit) as detailed in Fig. 3 and Table 1. Fungi and fungus-like taxa have a number of patterns in common, but they also have specific features, particularly in terms of their secondary development stages, with differences in the types of reproduction observed and the types of spores produced, for example (Fig. 4). The *PhenoFun* scale thus includes specific secondary stages (second digit) within the same primary phenological stage as illustrated in Fig. 4 and Table 1. For example, in the primary Stage 30 'reproduction', stages 31–33 are related to asexual reproduction with the appearance of sporocarps or conidiophores followed by sporulation; stages 34–37 are related to sexual reproduction with formation of the gametangium and gamete fusion, production of fruiting bodies and then sporulation. We also include tertiary stage information (decimal digits, for example stages 32.2 to 32.11 for different sporocarp types within the 32 phenological secondary stage 'mature sporocarps/conidiophores'), which describes the types of spores and fruiting bodies of the major phyla of plant phytopathogenic fungi and fungus-like organisms (Ascomycetes, Basidiomycetes, Oomycetes, Chytridiomycetes) (see the *PhenoFun* scale; Delmas *et al.*, 2024 for details). In the examples shown in Fig. 4, the primary stages (0, spore; 10, spore germination; 20, mycelial growth; 30, reproduction; and 40, survival; each represented by a different colour code) are common to the three organisms considered, but their fruiting bodies, disseminated spores, and survival forms are markedly different. This results in different spore names and different secondary phenological stages, further highlighting different sequences of stages across species. For example, *Botrytis cinerea* (Fig. 4A), *Puccinia striiformis* f. sp. *tritici* (Fig. 4B) and *Plasmopara viticola* (Fig. 4C) have the primary stage 'survival' in common (code 40). However, their strategies for survival or overwintering involve different conservation organs. For example, *B. cinerea* (Fig. 4A) overwinters as a mycelium (secondary stage code 41.1, 'mycelium in debris'), whereas *P. striiformis* f. sp. *tritici* (Fig. 4B) and *P. viticola* (Fig. 4C) produce survival spores (secondary stage 41.3, teliospores and 41.7, oospores, respectively). Reproduction (primary Stage 30) is another good example to illustrate common patterns and specificities as illustrated by the different sequences of reproductive phases in Basidiomycota (Fig. 4B). The *PhenoFun* scale provides an exhaustive panel of phenological stages that can

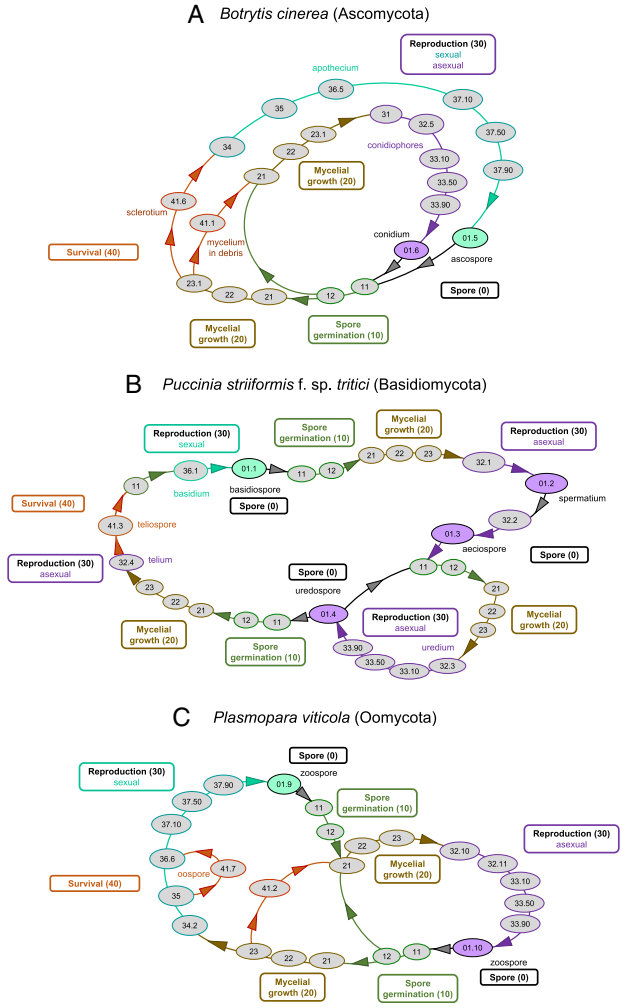

Fig. 4. Examples of life cycles of different fungal divisions: (A) Ascomycota (*Botrytis cinerea*); (B) Basidiomycota (*Puccinia striiformis* f. sp. *Tritici*); and (C) Oomycota (*Plasmopara viticola*). These three pathogens cause large yield losses in various crops, wheat, and grapevine, respectively. Changes in primary stages are indicated by arrowheads and a specific colour code. The spore phase is represented in black, the germination phase in dark green, mycelial growth in brown, and the survival phase in orange. Sexual and asexual reproductive phases are represented in blue and purple, respectively. The primary (first digit) and secondary (second digit) stages are described in Table 1 and the list of all tertiary stages (decimal digit) are available in the *PhenoFun* scale (version 1.0, Delmas *et al.*, 2024). Note that at particular developmental stages (e.g. stage 12 in *B. cinerea*), various alternative pathways may arise (symbolised by multiple arrows) depending on the pathogen's response to the environment. Polycyclic fungal pathogens complete multiple reproductive cycles in the same season, symbolised by repeating sequences of cycle arrows starting with a new spore germination stage 10.

be observed and dated with the naked eye (e.g. the fruiting bodies of Ascomycetes and Basidiomycetes) or by appropriate observation or detection methods for microscopic stages. However, not all fungal pathogens necessarily exhibit all of the secondary and tertiary stages during their life cycle. This is also the case for the BBCH plant scale, for example *Citrus* spp. have a score for only eight of the 10 primary stages. The absence of a stage thus does not call into question the use of this scale, and the code of the missing stage is simply not used.

IV. POTENTIAL APPLICATIONS OF THE *PhenoFun* SCORING SYSTEM

PhenoFun, calibrated and shared between observers and data scientists, can be used to characterise and recognise the different phenological stages of plant pathogenic fungi, and thus record their dates of occurrence.

It allows the identification and rigorous monitoring of changes in the phenology of fungi in relation to their environment, and makes it possible to analyse these changes, and even to anticipate them. The *PhenoFun* scale may therefore be key to understanding and analysing the major biophysical and global changes, because the phenology of fungi reflects their responses to biotic and abiotic environmental drivers. The presence, absence or predominance of a particular phenological stage, the rate of progression through the phenological phases, desynchronisation between the fungus and its host plant, and distribution patterns can reveal changes in climate, cropping practices, or land use. Phenology thus is a discipline that allows the measurement and dating of life-history traits associated with the development of fungi. The life-history strategy characterises how and when an organism acquires resources and uses them for growth and reproduction (Chagnon *et al.*, 2013). In the case of fungal pathogens, it may result in earlier spore release, shorter generation times or delayed reproductive stages, all of which can be observed through studies of phenology. The *PhenoFun* scale could therefore be used in comparative ecological and evolutionary research to understand the emergence and persistence of distinct life-history strategies across environments in relation to phenology (Pau *et al.*, 2011). The application of this scale to fungal pathogens of crops could prove useful for surveying, anticipating, and managing situations in which there is a risk of epidemics, and could facilitate the adoption of alternatives to pesticides, based on natural regulation within ecosystems, for example. Phenological scales can also serve as tools for structuring and combining different databases, and from plant health epidemiological surveillance platforms in particular, as they provide a generic and exhaustive representation of the biological cycles of plant pathogenic fungi. They can provide a common framework for the acquisition of observational data in various temporal and spatial situations. Finally, they are also a useful methodological tool for upstream modelling to build or improve models, and for downstream modelling as part

Table 1. Main stages of fungal life cycles (for an ascomycete, basidiomycete, or oomycete) and the corresponding phenological scoring system developed for plant pathogenic fungi (the *PhenoFun* scale, adapted from the BBCH phenological scale). The primary and secondary stage codes and names are presented here. Tertiary stage codes for each group of fungi (Ascomycetes, Basidiomycetes, Oomycetes) can be accessed at: https://entrepot.recherche.data.gouv.fr/dataset.xhtml?persistentId=doi:10.57745/CNM2XJ. During germination, the spore produces a germ tube, a specialised structure that grows for a very short distance before differentiating into an appressorium (Agrios, 2005). The mycelium (the hypha or mass of hyphae that make up the body of a fungus) then grows out by apical extension of slender hyphae, which then branch subapically to form a fractal, tree-like mycelium (Fricker *et al.*, 2007). The sporocarps (fruiting structure bearing spores) and conidiophores (a specialised hypha on which one or more conidia are produced) expel spores by a squirting or puffing action resulting in successive or simultaneous spore release (Agrios, 2005).

Primary stage code	Name of the primary stage	Secondary stage code	Name of the secondary stage
0	Spore	01	Spore without mycelium
10	Spore germination	11	Spore germination
		12	Development of the appressorium if present
20	Mycelial growth	21	Start of mycelium growth (without branching)
		22	Onset of branching
		23	Actively growing mycelium
30	Reproduction	31	Asexual reproduction (AR) – appearance of sporocarps/conidiophores (immature)
		32	AR – mature sporocarps/conidiophores
		33	AR – sporulation
		34	Sexual reproduction (SR) – formation of the gametangium and gamete fusion
		35	SR – immature fruiting bodies
		36	SR – fruiting bodies
		37	SR – sporulation
40	Survival	41	Dormancy of mycelium or spores

of a heuristic approach to model evaluation and questioning.

V. FUTURE DIRECTIONS FOR STUDIES OF THE PHENOLOGY OF PLANT PATHOGENIC FUNGI

(1) Perspectives

Plant fungal diseases result from an interplay between many different factors, integrating the respective effects of climate, land use, cropping practices, and their interactions (Fig. 1). However, the concept of 'plant disease', reflecting environmental variations in an integrative manner, provides no possibility of prioritising and weighting the different factors governing disease development or of separating the sensitivity of the pathogen to environmental cues from variations in the environmental cues themselves (Chmura *et al.*, 2019). Understanding and anticipating plant disease epidemics, and their past and future changes in terms of nature, intensity and frequency, will require a downscaling approach. This involves focusing on the interacting processes occurring between the pathogenic fungi, their hosts and their biological, physical, and chemical environment during the life cycle of the pathogen. Our aim here is to break down the processes involved into a pattern orchestrated by the phenology of the fungus. Identifying the drivers of the phenology of pathogenic fungi thus emerges as a relevant conceptual framework for structuring studies and combining epidemiological observations according to pathogen phenology. This approach may also counter the lack of availability of long-term data about disease dynamics (Garrett *et al.*, 2021). The *PhenoFun* phenological scoring scale proposed here provides a common lexicon and ontology for combining independent data sets. A common phenological scoring system can provide a conceptual framework for building mechanistic models simulating the development of fungi, or of an epidemic (e.g. Caubel *et al.*, 2012). Such frameworks may be useful for the epidemiological modelling of rarely studied fungi or of fungi responsible for emerging diseases ('knowing the enemy' is the lifeblood of disease control; Fones *et al.*, 2020) based on similarity to well-known fungal biological cycles or their drivers. Finally, studies of the phenology of pathogenic fungi may improve our ability to anticipate disease evolution according to changes in climatic and/or socio-economic scenarios, as new bioclimatic niches appear and accompany the spread or progression of diseases (Behzad, Mineta & Gojobori, 2018). In a crop pathogen-management modelling approach (Aubertot & Robin, 2013), the *PhenoFun* scoring system will facilitate and improve integration of the interplay between cropping practices and pathogen phenology, and can be used to optimise the efficacy of agronomic levers. This approach is especially relevant when an agronomic lever targets a specific life stage of a pathogen, such as destruction of an overwintering form (e.g. eyespot; Robin *et al.*, 2013).

(2) Outstanding questions

The application of the concept of phenology to plant pathogenic fungi and the use of a phenological scoring system will open new perspectives on the understanding of the ecology and evolution of these organisms, making it possible to address important questions.

(1) To what extent does climate change, as the main driver of the phenology of living organisms, lead to changes in plant health and epidemics and the reconfiguration of agroecosystems? Understanding and quantifying the impact of phenological mismatches between a plant pathogen and its host can shed considerable light on the impact of climate change on disease outbreaks. This knowledge can make a significant contribution to simulation and anticipation of the emergence, invasion or disappearance of certain pathogens, and, thus, expansions or contractions in the areas under certain crops.
(2) Are phenological strategies of plant pathogens evolving with global changes? The *PhenoFun* scale could be used in comparative studies of ecology and evolution to understand the rise and maintenance of distinct phenological strategies. Research on fungal phenology from an evolutionary perspective requires a multi-species approach that will enable predictions regarding the adaptive potential of fungal species in response to potential global change scenarios.
(3) How can we control the phenology of microbial control agents to ensure that they are effective against phytopathogens? Microbial biocontrol agents (including fungi) are increasingly employed to reduce the use of chemical pesticides. As living organisms, their efficacy depends on their viability, climatic conditions at the time of application, and, potentially, their phenology and its match with that of the targeted pathogen.
(4) How do innovative or alternative cropping practices and landscape management affect the phenology of plant pathogens? Diversification of the plant component of agricultural areas over different spatial and temporal scales (field, landscape, crop cycle or even rotation) is currently explored as an agroecological lever for pest regulation. Indeed, this diversification drives many processes involved in pathogen phenology that are still little studied, such as synchrony between natural enemies and pathogens, the presence of survival forms, host–pest coevolution or genetic dilution and the discontinuity of resources.
(5) How do breeding and cultivar resistance management alter the evolution of pathogen phenology? Breeding new cultivars capable of dealing with increasing abiotic stresses, such as drought and heat, or with resistance to various pests, and the diffusion of these cultivars at regional scales can modify pathogen life cycles through the co-evolution of pathogen populations.
(6) How can we collect large data sets on microscopic organisms, such as fungal pathogens? There are many data sets relating to plant disease symptoms or epidemic development, but very few on fungal phenology. The immediate challenges will be both to collect original data sets relating to the phenology of plant pathogenic fungi and to re-analyse existing data sets through the lens of phenology. The use of a common phenological scoring system framework should make it possible to homogenise these data, and to increase the size of data sets, thereby facilitating large-scale temporal and/or spatial analyses.

VI. CONCLUSIONS

(1) Plant pathogenic fungi are a diverse clade of organisms that interact with a broad diversity of plant species, limiting the use of a common language to describe them. Phenology is a key adaptive trait shaping biotic interactions in response to the environment, but this concept is not currently used in plant pathology. Herein we extended the concept of phenology to plant pathogenic fungi and presented a common scoring system for the phenology of fungal pathogens (*PhenoFun*).
(2) Plant pathogens are facing new selective pressures induced by global change, the reduction of pesticide use in favour of biocontrol and the switch from energy-intensive synthetic inputs towards more diversified and resilient systems. As has been largely studied in plants, the response of plant pathogen phenology to such selective pressures would be an excellent marker of climate, land-use and cropping practice changes.
(3) The use of a global phenological scoring system suitable for all fungal plant pathogens allows the collection and homogenisation of data from various pathosystems. Studying the phenology of plant pathogenic fungi will shed light on the ecology and evolution of such organisms. Accounting for pathogen phenology in the design of new cropping systems is essential not only to optimise pathogen management models, but also to promote the adoption of more beneficial cultivation practices.

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VIII. DATA AVAILABILITY STATEMENT

The *PhenoFun* scale is available in the INRAE dataverse: Delmas, Chloé; Bancal, Marie-Odile; Leyronas, Christel; Robin, Marie-Hélène; Vidal, Tiphaine; Launay, Marie, 2024, 'PhenoFun: a phenological scale for fungi and fungus-like organisms', https://doi.org/10.57745/CNM2XJ, Recherche Data Gouv, V1, UNF:6:AkTLFmkuPTEEasPel0eD0w== [fileUNF].

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