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# A survey of highly influential studies on plant pathogen effectors during the last two decades (2000-2020)

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## Abstract

Plant effector biology is a research area that describes how plant-associated organisms modulate host structures and functions to promote colonization by using small molecules (effectors). In this article, we analyzed the 249 most highly-cited publications focused on plant pathogen effectors (aka Highly Influential studies on plant Pathogen Effectors; thereafter HIPEs) published between 2000 and 2020. This analysis identified outstanding countries, organizations, and journals that contributed HIPEs, as well as the evolution of research trends, model molecules, and model organisms over the last two decades. We notably show an increasing proportion of studies focused on effectors of biotrophic and hemibiotrophic fungi upon time. Our snapshot of the top tier plant effector biology papers will help readers gain a comprehensive and analytical understanding of this research area.

## Keywords

Bibliometric pipeline, Web of Science, plant immunity, avirulence, virulence, pathogenicity, receptor

## Introduction

Plant pathogens threaten agricultural production by triggering dramatic yield losses worldwide (Savary *et al.*, 2019). The effector biology research field explains how pathogens manipulate their host(s) to promote infection through the modulation of host structures and processes, and aims at leveraging that knowledge to ultimately improve plant health (Win *et al.*, 2012). Since the 2000s, this field of research grew spectacularly, with an exponential increase in the number of publications (<https://www.webofscience.com;Supplementary Figure S1>). During these two decades, our understanding of effector diversity and functions has improved, notably thanks to functional genomic studies. However, there are only a few studies that comprehensively inventory the major findings and concepts of plant effector biology, which makes it difficult for junior researchers to gain a broad expert and conceptual understanding of the research field.

To build a snapshot of top tier research in plant effector biology, we implemented the 'HIP in' ('Highly-Influential Publication in' ...) method that we recently described (Petre *et al.*, 2021). We report here a bibliometric analysis of 249

Highly Influential (*i.e.* highly cited) papers on plant Pathogen Effectors (thereafter HIPEs) published between 2000 and 2020. We describe the concepts, model objects, and findings shared by HIPEs, as well as the research community that shared them. We notably show the increasing importance of fungi as model pathogens over time, and highlight key fungal species.

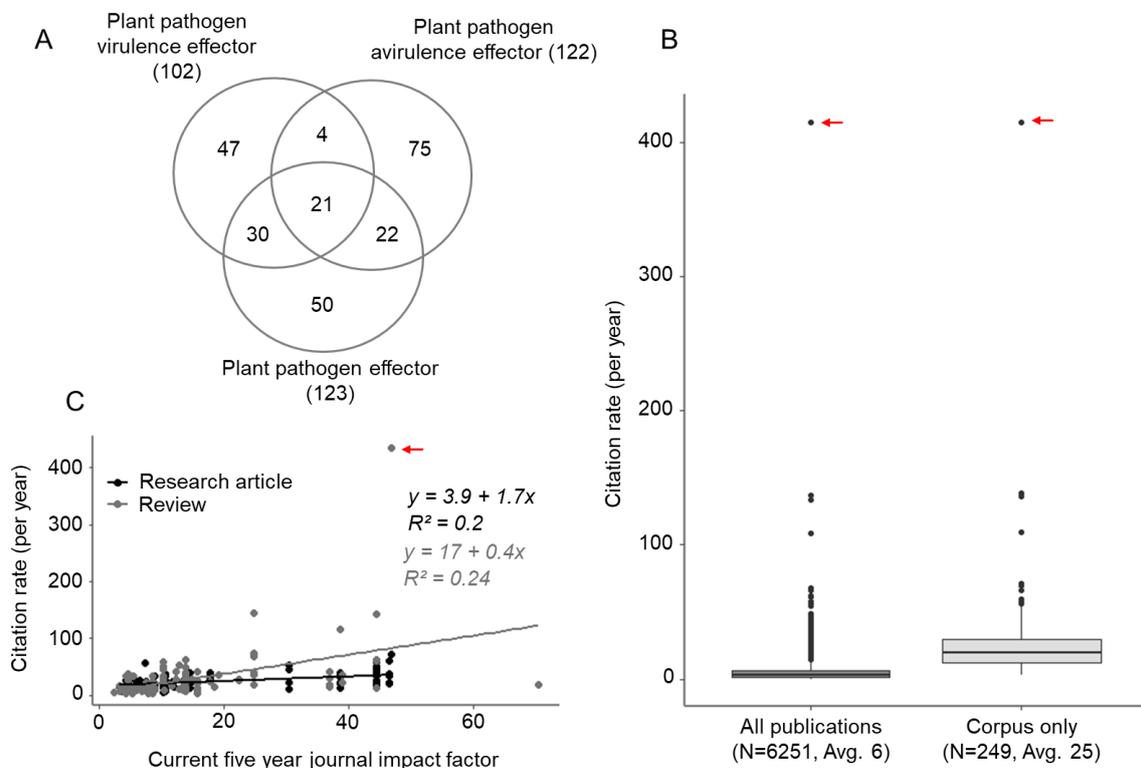
## A bibliometric pipeline identifies 249 highly influential publications addressing plant pathogen effectors

To identify the most influential publications that addressed plant pathogen effectors over the last two decades, we implemented a previously-described bibliometric pipeline (Petre *et al.*, 2021), which mostly uses the Web of Science database (<https://www.webofscience.com>) and a reference management software (here Mendeley). We selected the top three most cited research articles or reviews for each year between 2000 and 2020, which we identified via three successive searches using the key words 'plant pathogen effectors', 'plant pathogen avirulent effectors', and 'plant pathogen virulent

effectors' ([Figure 1A](#); [Dataset 1](#); see [Supplementary Methods](#) and [Supplementary Figure S2](#) for details). In total, we collected and archived 249 HIPEs (127 research articles and 122 reviews; hereafter the 'HIPE collection') on the following public web address: [https://www.zotero.org/groups/4410902/hipe\\_collection/library](https://www.zotero.org/groups/4410902/hipe_collection/library).

The HIPEs represents 4% of all the publications identified *via* the three searches above mentioned, but their annual citation rate is approximately four times higher (25 *vs.* 6 on average; [Figure 1B](#)). The HIPE with the highest number of citations (6503) and annual citation rate (414) is the review that presented the

seminal zig-zag model (Jones and Dangl, 2006). Interestingly, the current five years impact factors of the journals in which HIPEs were published do not correlate with HIPEs annual citation rate, indicating that the journal impact factor is a poor indicator of HIPEs influence ([Figure 1C](#)). As a note, only 19 out of 249 HIPEs overlap with the collection of highly-cited papers in plant immunity (HIPPYs) described in our previous paper (Petre *et al.*, 2021; [Dataset 1, column B](#)). To summarize, HIPEs represent an original collection of influential studies that pertains to plant pathogen effectors, and that is suitable for further analyses.



**Figure 1. HIPEs are highly cited studies addressing plant pathogen effectors**

(A) Venn diagram indicating the number of overlapping publications between the three group of key words ('plant pathogen effectors', 'plant pathogen avirulence effectors' and 'plant pathogen virulence effectors') used to build the HIPE collection. The number of publications is shown between parentheses. (B) Boxplots displaying the annual citation rate of all publications identified with the keyword searches (left-hand side; 'All publications') and the HIPEs only (right-hand side; 'Corpus only'). The boxplot outliers are indicated as dots. The number and the average of publications considered is indicated below each boxplot (N and Avg value, respectively). (C) Scatterplot displaying the annual citation rate of individual HIPEs according to the value of the current five-year journal impact factor of the journal in which the HIPEs were published. Black and grey dots indicate research articles and reviews, respectively. Linear trendlines are indicated for each article type along with trendline equations and r-squared values, with the same color-code as previously. In (B) and (C), the red arrow indicates the HIPE with the highest annual citation rate, which corresponds to the 2006 review by Jones and Dangl that presented the zig-zag model of the plant immune system. The raw data used to build this figure are available in the [Dataset 1](#).

### A small influential community publishes the majority of the HIPEs

To identify the research community that publishes the HIPEs, we extracted from HIPEs metadata the main countries and institutions to which HIPEs corresponding authors are affiliated, as well as the journals that published them. Overall, 19 countries, 87 institutions (comprising 154 affiliated corresponding authors), and 67 journals published the HIPEs ([Dataset 1](#)). Interestingly, only a handful of scientific actors contributed most of the collection ([Table 1](#)). Indeed, three countries (USA, UK, and Germany) published 62% of the

HIPEs, whereas four institutions published a quarter of the HIPEs: the Max Planck Institute (MPI, Germany), The Sainsbury Laboratory (TSL, UK), the National Research Institute for Agriculture, Food, and Environment (INRAE, France) and the Wageningen University & Research (WUR, Netherlands). Also, four journals (Science, Annual Review of Phytopathology, PNAS, and The Plant Cell) contributed over a quarter of the HIPEs. Altogether, this analysis indicates that HIPEs are shared by a restricted number of academic actors mostly based in Western Europe and in the USA.

**Table 1. Top countries, institutions, and journals that publish the most HIPEs.**

Country, institution, or journal <sup>a</sup>	Number of HIPEs	Number of citations	Number of corresponding authors	Current 5-year journal impact factor
USA	88	25,167	52	-
UK	35	13,939	25	-
Germany	31	7,581	19	-
INRAE (France)	18	3,099	13	-
TSL (UK)	15	10,082	7	-
MPI (Germany)	15	4,034	10	-
WUR (Netherlands)	14	3,190	6	-
Science	20	7,013	-	44.37
Annual Review of Phytopathology	19	4,925	-	13.87
PNAS	17	4,702	-	10.62
The Plant Cell	17	3,686	-	10.14

<sup>a</sup> USA: United States of America; UK: United Kingdom; INRAE: Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement; TSL: The Sainsbury Laboratory; MPI: Max Planck Institute; WUR: Wageningen University & Research; PNAS: Proceedings of the National Academy of Science of the USA.

### HIPEs collectively address seven main research questions, whose relative importance within the HIPE collection evolved over time

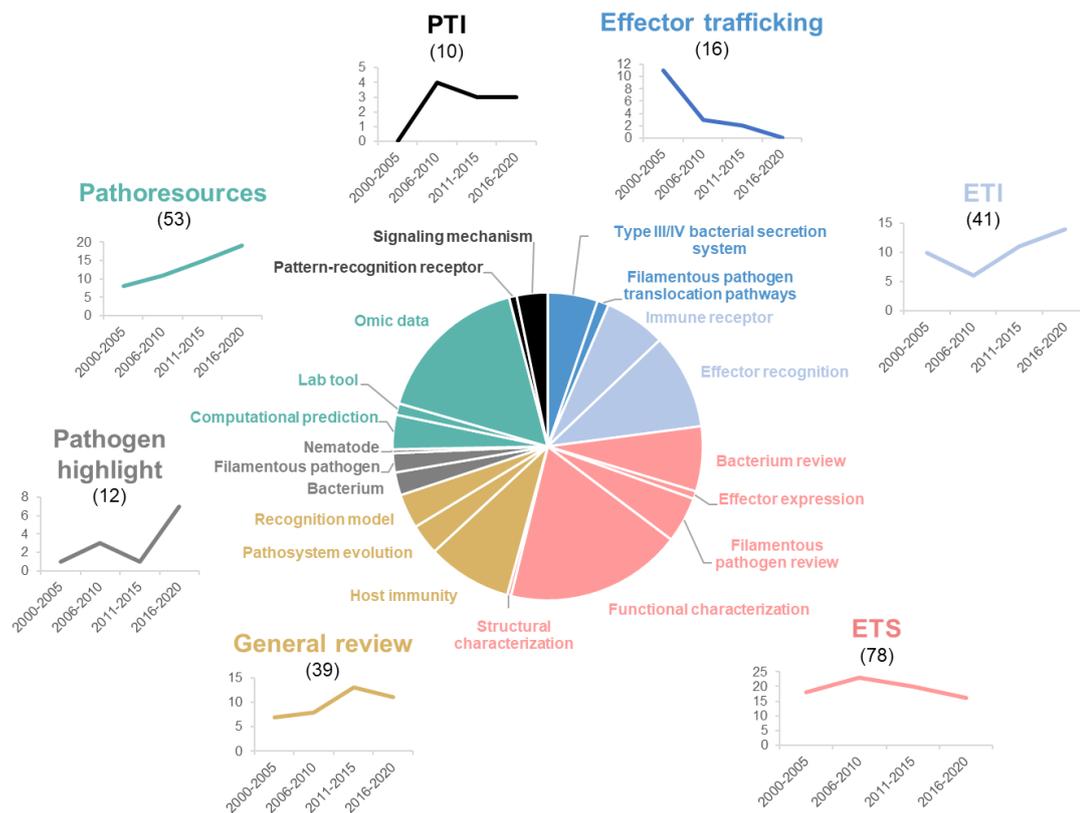
To identify the main research questions addressed by the HIPEs, we performed an iterative analytical reading combined with key word tagging of all the collection aimed at identifying HIPEs main research topics and sub-topics. This analysis identified seven main research topics as follow: 1) the 'PTI (PAMP-triggered immunity; *what is the interplay between PTI and effectors?*; 10 HIPEs), 2) the 'ETI (Effector-triggered immunity; *what is the interplay between ETI and effectors?*; 41 HIPEs), 3) the 'ETS' (Effector-triggered susceptibility; *how do effectors modulate host functions?*; 78 HIPEs), 4) the 'Effector

trafficking' topic (*how do pathogens deliver effectors to the host?*; 16 HIPEs), 5) the 'Pathogen highlight' topic (*what is the current knowledge in the field for specific pathogen species?*; 12 HIPEs), 6) the 'Pathoresources' topic (*how to build and leverage technological innovation and resources to better understand plant-pathogen interactions?*; 53 HIPEs), and 7) the 'General review' topic (*how do we conceptually understand the role of effectors in plant-pathogen interactions?*; 39 HIPEs) (see [Supplementary Text](#) for details). Interestingly, the annual citation rate is comparable between these main research topics ([Supplementary Figure S3](#)).

To gain a more accurate understanding of HIPEs research questions, we further grouped HIPEs into 20 sub-topics ([Figure 2](#)). Thus, each of the

seven main research topics comprises two to five sub-topics that pertain to a more specific research question. For example, the ETI topic comprises two sub-topics: 'Immune receptors' (*what are the receptors that recognize effectors?*) and 'Effector recognition' (*how do immune receptors recognize effectors and signal*

*that recognition?*). Overall, these sub-topics highlight several specific research questions and the main addressed are: '*what is the function of pathogenic effectors in the host?*' (18% of HYPEs, ETS topic) and '*how do we develop and use omics data to identify pathogenic effectors?*' (16% of HYPEs, Pathoresources topic).



**Figure 2. HYPEs pertain to seven main research topics**

Pie chart displaying the seven main research topics and 20 sub-topics addressed by the HYPEs and their publication trends over time. The main research topics, sub-topics and trendlines associated are color-coded as indicated in Figure S3. Research sub-topics are indicated as separated pie segments within a main topic. The categorization of each HYPEs was based on iterative expert reading and key word association of the entire HYPE collection. Numbers above the main research topics indicate the total number of HYPEs for each topic. Trendlines indicate the number of HYPEs for each topic according to four five-year time frames: 2000-2005; 2006-2010; 2011-2015 and 2016-2020. PTI: PAMP-triggered immunity; ETI: Effector-triggered immunity; ETS: Effector-triggered susceptibility. The raw data used to build this figure are available in the [Dataset 1](#).

To identify potential research trends within the HYPEs, we analyzed the evolution of the number of publications in each of the seven main topic between 2000 and 2020, by five-year time frames (*i.e.* 2000-2005, 2006-2010, 2011-2015, and 2016-2020). That analysis showed that most topics remain stable over time. In contrast, the two topics Effector trafficking and Pathoresources showed marked trends of

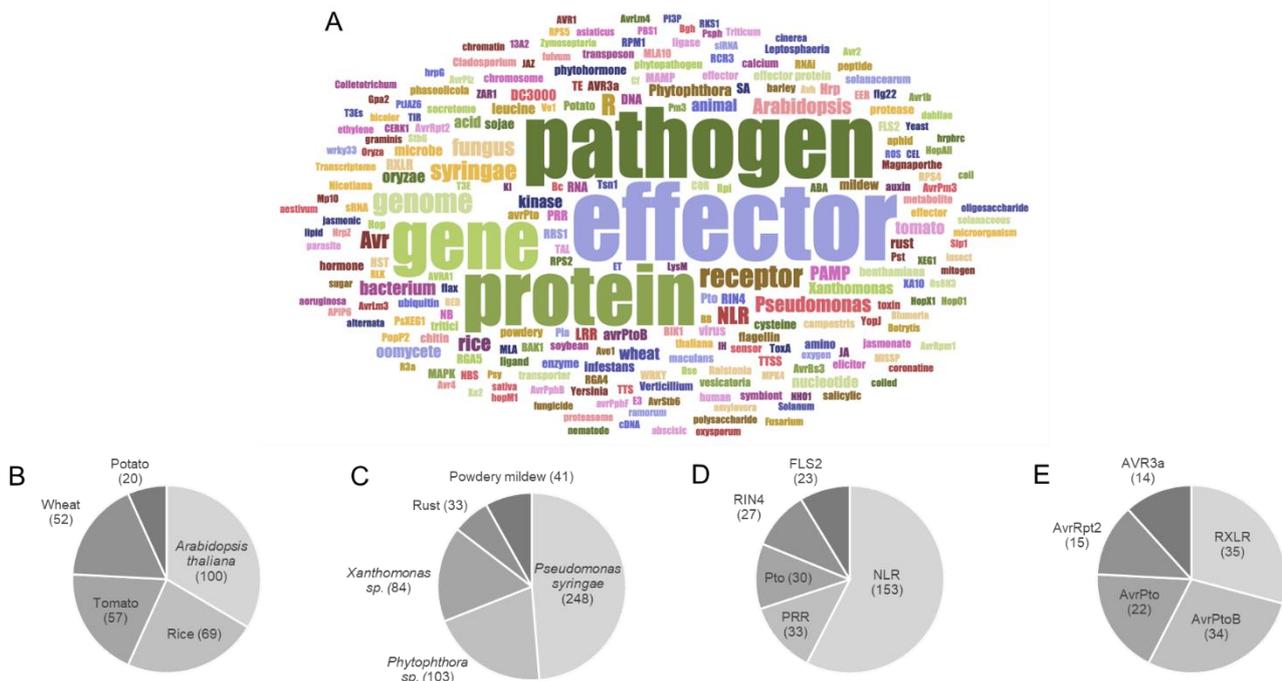
decrease and increase over time, respectively. The Effector trafficking topic declined markedly over the years, mainly due to the reduction of HYPEs addressing the bacterial Type III or Type IV secretion system. The strong controversy on the mechanisms of delivery of filamentous pathogen effectors may also explain the decline of this topic (Anderson *et al.*, 2015; Tyler *et al.*, 2013; Wawra *et al.*, 2013; Wawra *et al.*, 2017).

At the opposite, the Pathoressources topic steadily increased, probably benefiting from the progresses in genomics that helped the identification of candidate effectors (Figure 2). In conclusion, this set of analyses show that HYPEs pertain to key research questions that address well-defined aspects of the molecular interaction between plants and pathogens; the relative importance of some of those increased (*i.e.* Pathoressources) or declined (*i.e.* Effector trafficking) over the last two decades.

### HYPEs address a handful of key organisms and proteins

To identify the main objects (*i.e.* organisms or molecules) investigated by the HYPEs, we performed a word occurrence analysis of the title and abstracts combined with word cloud generation and iterative text enrichment for words referring to organisms or molecules

(Dataset 2; see Supplementary Methods for details). That pipeline helped to generate a world cloud of the 200 most frequently used words referring to organisms or molecules (Figure 3A). As expected, the most used words refer to key groups of organisms (pathogen, *Arabidopsis*, bacterium, fungus, *Pseudomonas*) or groups of molecules (effector, receptor, NLR, gene, protein, genome). We further quantitatively analyzed Dataset 2 to identify the top five most frequently referred to plant species, pathogen species, immune receptors, and effectors (Figure 3B-E). Firstly, the top five model plants comprise a Brassicaceae (*Arabidopsis thaliana*), two Poaceae (*i.e.* cereals; rice and wheat), and two Solanaceae (potato and tomato). The fact that three out of these five model plants are key crops providing staple food worldwide (*i.e.* rice, wheat, and potato; Savary *et al.*, 2019) shows the alignment of research efforts with agricultural efforts to meet global food security (Figure 3B).



**Figure 3. HYPEs rely on a handful of model organisms and proteins**

(A) Word cloud displaying the most frequent words referring to organisms or molecules in the title and abstract of the HYPEs. The word cloud was built using a filtered text file including HYPEs metadata (publication title and abstract) deprived from words that did not explicitly refer to organisms or molecules. Word colors were randomly generated to assist visual word discrimination. The word cloud displays 200 words. The size of the words positively correlates with their frequency in the text file. A top five of plant organisms (B), plant-associated pathogens (C), immune receptors (D) and pathogen effectors (E) was identified based on the Dataset 2. Specific additional key words were considered for the following topics: *Arabidopsis thaliana* ('*Arabidopsis*' and '*thaliana*'), *Pseudomonas syringae* ('*Pseudomonas*', '*syringae*', 'DC3000' and 'pst'), *Phytophthora sp.* ('*Phytophthora*', '*infestans*', '*ramorum*' and '*sojiae*'), *Xanthomonas sp.* ('*Xanthomonas*', '*campestris*' and '*oryzae*' if used in a

meaningful context), Powdery mildews ('Powdery' and 'mildews'), NLR ('NLR', 'LRR', 'NB-LRR', 'TNL', 'CNL', 'sNLR' and 'hNLR'). NLR: nucleotide-binding/leucine-rich-repeat receptor; PRR: pattern recognition receptors. The raw data used to build this figure are available in the [Dataset 2](#).

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Secondly, the top five model pathogens comprise two bacteria (*Pseudomonas syringae* and *Xanthomonas* species), two groups of fungi (Pucciniales and Erysiphales, causing rust and powdery mildew diseases), and one genus of oomycetes (*Phytophthora* species) ([Figure 3C](#)). These pathogens collectively cause a wide range of diseases that significantly impact agricultural production worldwide (Fones *et al.*, 2020; Savary *et al.*, 2019). Thirdly, the top five model receptors comprise two general groups of immune receptors (NLRs and PRRs), as well as three specific proteins: FLS2 (the PRR responsible for flagellin recognition), Pto (a cytosolic kinase), and RIN4 (a regulator of immunity). The prominence of NLRs mirrors their importance in ETI, and the importance of ETI as a research topic within HIPEs ([Figure 3D](#)). Finally, the top five model groups of effectors comprise three *P. syringae* effectors (AvrPto, AvrPtoB, and AvrRpt2) and two oomycete effector families (the RXLR superfamily, and the AVR3a family) ([Figure 3E](#)). Altogether, these analyses reveal the prominence of *A. thaliana*, *P. syringae*, as well as receptor and effector gene families as model objects in effector biology. We refer readers to [Supplementary Text](#) for a more detailed and contextualized analysis of the organisms and molecules listed above.

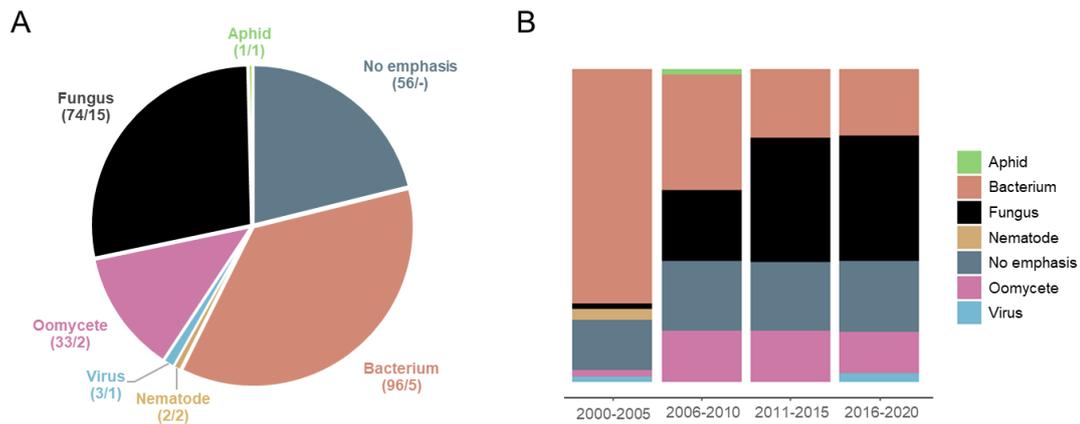
### **Temporal analysis of model pathogens reveals the increasing importance of plant pathogenic fungi**

To get a more detailed understanding of the model pathogens addressed in HIPEs, we performed an iterative analytical reading of all HIPEs and categorized them according to the taxonomic group of the pathogens they emphasized (if any). This analysis revealed that 80% of the HIPEs emphasize a specific pathogen; we grouped those HIPEs into six

categories: bacteria (96 HIPEs), fungi (74), oomycetes (33), viruses (3), nematodes (2), and aphids (1) ([Dataset 1](#)) ([Figure 4A](#)). Only a handful of HIPEs emphasize aphids, viruses and nematodes, suggesting that the effector biology community revolves mostly around bacterial, fungal and oomycete model systems. Notably, the categories bacteria of oomycetes (33% and 13% of the collection, respectively) show low diversity, as they mostly address *Pseudomonas* and *Phytophthora* species, respectively ([Dataset 1](#)). In contrast, the fungal group (28% of the HIPEs) shows a high diversity, as it addresses 15 different fungal genera ([Dataset 1](#)). This indicates that bacteria and oomycete groups are dominated by a limited number of key model species, while the fungal group addresses a broader diversity of species. Interestingly, the size of the categories evolved drastically between 2000 and 2020 ([Figure 4B](#)). Indeed, between the 2000-2005 and the 2016-2020 time periods, studies focusing on bacteria declined from 75% to 21% of the HIPE collection, while studies focusing on oomycetes and fungi increased from 2% to 13% and from 2% to 40%, respectively. These results indicate that in the early 2000s model bacterial systems vastly dominated effector biology, but that over time filamentous pathogens (*i.e.* fungi and oomycetes) gained importance. This likely reflects the impact of pathogenomics and the possibility for systematic effectors prediction in sequenced genomes of a larger number of microbes, particularly fungi.

### **The influence of publications addressing fungal effectors increased over time: analysis of the 'HIPE-fun' collection**

To perform an objective analysis of the most prominent fungal species in influential publications addressing fungal plant pathogen effectors, we repeated the bibliometric analysis



**Figure 4. Studies emphasizing fungi gain importance over time.**

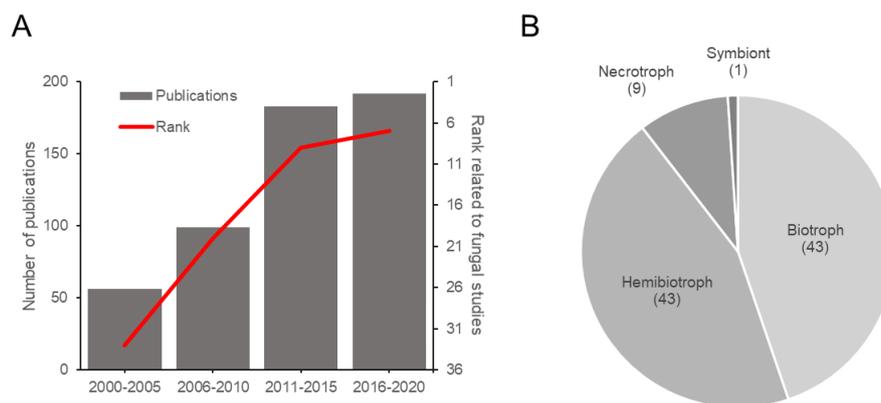
(A) Pie chart displaying the seven taxonomic groups of pathogens emphasized (if any) addressed by the HIPEs. The assignment of each HIPE was based on iterative expert reading of the publications. For each taxonomic group, the number of HIPEs and the total number of species are indicated (e.g. '74/15'). (B) Percent stacked bar chart displaying the evolution of the relative size of taxonomic groups over four five-year time periods: 2000-2005; 2006-2010; 2011-2015 and 2016-2020. Color code is the same as in (A). The raw data used to build this figure are available in the [Dataset 1](#).

that identified the HIPE collection, by considering only the research articles on fungi. This helped to build a collection of 100 HIPEs focusing on fungi (thereafter referred to as 'HIPE-funs'; [Dataset 3](#); see [Supplementary Methods](#) and [Supplementary Figure S2](#) for details), archived on the following public web address: [https://www.zotero.org/groups/441090/5/hipe-fun\\_collection/library](https://www.zotero.org/groups/441090/5/hipe-fun_collection/library).

To understand the expansion of publications focus on fungi in HIPEs, we extracted the number of publications addressing plant pathogen effectors and the citation rank over years of the HIPE-funs (i.e. rank of the publication on the Web of Science database based on the number of citations). This analysis highlighted an obvious increase in the citation rank over years of the HIPE-funs associated with the expansion in the number of publications addressing plant pathogen effectors. Between 2000-2005 and 2016-2020, studies on fungi were ranked on average from 33<sup>rd</sup> place out of 56 publications to 7<sup>th</sup> place out of 192 publications ([Figure 5A](#)). This result displays the significant increase in the influence of publications related to fungi over time, and more precisely by two predominant trophic lifestyles: biotrophy and hemibiotrophy (45% for both; [Figure 5B](#)).

### The HIPE-funs are related to influential fungal species in the field of molecular plant pathology

In 2012, Dean and colleagues surveyed hundreds of mycologists who voted for the most important fungal species in molecular plant pathology based on their scientific and economic importance (495 votes in total). We performed a comparative analysis to evaluate the correspondence between the fungal species addressed in HIPE-funs and the top 10 list from Dean et al. (2012). We first identified a total of 21 fungal genera covered in the HIPE-funs. We ranked fungal genera according to HIPE-funs numbers and annual citation rates, and then we compared this ranking with the list by Dean and colleagues ([Table 2](#)). First, this analysis showed that all top 10 species occur in at least one HIPE-fun, highlighting an excellent correspondence between the two lists ([Dataset 3](#)). Notably, the genera *Magnaporthe* and *Puccinia* appear in the top of both lists ([Table 2](#); Dean et al., 2012). These genera comprise species that trigger dramatic epidemics on rice and/or wheat, threatening global food security (Figuroa et al., 2018; Talbot, 2003; Wilson and Talbot, 2009). That may explain why they represent important fungal models in the field of fungal effector



**Figure 5. Publications addressing effectors of (hemi)biotrophic fungi gain prominence over time.**

(A) Evolution of the number of publications related to plant pathogen effectors and the citation rank for HIPE-funs. Each citation rank was calculated based on the mean of rank of publications by time frames (*i.e.* position of the publication on the Web of Science website based on the number of citations). (B) Pie chart displaying the proportion of each lifestyle of plant pathogenic fungi studied in the HIPE-funs. The categorization of each lifestyle was based on iterative expert reading and association with the pathogenic species studied for the entire HIPE-fun collection. Numbers above lifestyle topics indicate the total number of HIPE-funs for each topic. The raw data used to build this figure are available in the [Dataset 3](#).

biology. In contrast, the ranking of some species differs between the two lists. For instance, the genus *Botrytis sp.* dominates the top 10 list of Dean et al. (2012), but it is barely represented in the HIPE-funs (2<sup>nd</sup> place in the previous report vs. 13<sup>th</sup> place in this study; [Table 2](#)). This genus, and notably the species *Botrytis cinerea*, is a strong model for molecular plant pathology but not in effector biology. This is probably because

of its necrotrophic lifestyle (poorly represented by the HIPE-funs; [Figure 5B](#)); a lifestyle that is though not to rely much on effectors during host infection, but rather on toxins. To conclude, our analysis of HIPE-funs confirms the importance of well-established fungal pathogens as agronomical models in both effector biology and molecular plant pathology.

**Table 2. Main fungal plant pathogens with the highest number of publications and annual citations based on HIPE-funs.**

Fungal pathogen	Rank	Number of publications	Citation rate (per year)	Rank based on Dean <i>et al.</i> , 2012 top 10 list
<i>Blumeria sp.</i>	1	12	240	6
<i>Magnaporthe sp.</i>	2	10	206	1
<i>Leptosphaeria sp.</i>	3	10	136	-
<i>Cladosporium sp.</i>	4	9	171	-
<i>Puccinia sp.</i>	5	9	73	3
<i>Verticillium sp.</i>	6	6	163	-
<i>Melampsora sp.</i>	7	6	121	10
<i>Zymoseptoria sp.</i>	8	6	117	7
<i>Fusarium sp.</i>	9	6	84	4 & 5
<i>Colletotrichum sp.</i>	10	4	124	8
<i>Ustilago sp.</i>	11	4	87	9
<i>Sclerotinia sp.</i>	12	4	67	-
<i>Botrytis sp.</i>	13	2	117	2

## Conclusion and outlook

To conclude, the present study shows that top tiers plant effector biology has developed as a well-structured research area, with key academic actors and objects (*i.e.* molecules or organisms). The study also reveals that the focus of the most cited publications in the field has partially shifted over time, from bacterial pathogens to filamentous pathogens (notably fungi). As an outlook for the next twenty years, we anticipate that the research area will continue to diversify the organisms it addresses (*i.e.* aphids, herbivores, viruses), which may help understand better the diversity of virulence strategies that arose throughout evolution.

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## Authors contribution

CL acquired data and wrote the manuscript. CL performed data analysis and interpretation, with inputs from BP and SD. All authors conceived and designed the study, as well as critically revised and edited the manuscript.

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## Conflict of Interest

The authors declare that there is no conflict of interest.

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## References

- Anderson, R.G., Deb, D., Fedkenheuer, K. and McDowell, J.M.** (2015) Recent progress in RXLR effector research. *Molecular Plant-Microbe Interactions*. **28**, 1063–1072.
- Dean, R., Kan, J.A.L. Van, Pretorius, Z.A., et al.** (2012) The Top 10 fungal pathogens in molecular plant pathology. *Molecular Plant Pathology*. **13**, 414–430.
- Figueroa, M., Hammond-Kosack, K.E. and Solomon, P.S.** (2018) A review of wheat diseases—a field perspective. *Molecular Plant Pathology*. **19**, 1523–1536.
- Fones, H.N., Bebbler, D.P., Chaloner, T.M., Kay, W.T., Steinberg, G. and Gurr, S.J.** (2020) Threats to global food security from emerging fungal and oomycete crop pathogens. *Nature Food*. **1**, 332–342.
- Jones, J.D.G. and Dangl, J.L.** (2006) The plant immune system. *Nature*. **444**, 323–329.
- Petre, B., Louet, C., Lintz, J. and Duplessis, S.** (2021) 2000-2019: twenty years of highly influential publications in plant immunity.
- Savary, S., Willocquet, L., Pethybridge, S.J., Esker, P., McRoberts, N. and Nelson, A.** (2019) The global burden of pathogens and pests on major food crops. *Nature Ecology and Evolution*. **3**, 430–439.
- Talbot, N.J.** (2003) On the trail of a cereal killer: exploring the biology of *Magnaporthe grisea*. *Annual Review of Microbiology*. **57**, 177–202.

**Tyler, B.M., Kale, S.D., Wang, Q., et al.** (2013) Microbe-independent entry of oomycete RxLR effectors and fungal RxLR-like effectors into plant and animal cells is specific and reproducible. *Molecular Plant-Microbe Interactions*. **26**, 611–616.

**Wawra, S., Djamei, A., Albert, I., Nürnberger, T., Kahmann, R. and West, P. Van** (2013) In vitro translocation experiments with RxLR-reporter fusion proteins of Avr1b from *Phytophthora sojae* and AVR3a from *Phytophthora infestans* fail to demonstrate specific autonomous uptake in plant and animal cells. *Molecular Plant-Microbe Interactions*. **26**, 528–536.

**Wawra, S., Trusch, F., Matena, A., et al.** (2017) The RxLR motif of the host targeting effector AVR3a of *Phytophthora infestans* is cleaved before secretion. *The Plant Cell*. **29**, 1184–1195.

**Wilson, R.A. and Talbot, N.J.** (2009) Under pressure: investigating the biology of plant infection by *Magnaporthe oryzae*. *Nature Reviews Microbiology*. **7**, 185–195.

**Win, J., Chaparro-Garcia, A., Belhaj, K. and Yoshida, K.** (2012) Effector biology of plant-associated organisms: Concepts and perspectives. *Cold Spring Harbor Symposia on Quantitative Biology*. **77**, 235–247.

## SUPPLEMENTARY METHODS

### Building of the HIPE and HIPE-fun collections

To identify and extract publications in plant pathogen effectors that have been published between 2000 and 2020 and that have been highly cited, we used a step-by-step pipeline that used the Web of Science website as described previously by Petre et al. (2021), with the following modifications. We used the Mendeley software instead of Zotero. We selected publications following searches with three groups of keywords: 'plant pathogen effector', 'plant pathogen avirulence effector' and 'plant pathogen virulence effector'. We defined 12-time periods (2000-2001; 2002-2003; 2004-2005; 2006-2007; 2008-2009; 2010-2011; 2012-2013; 2014-2015; 2016-2017; 2018; 2019; 2020). The last three years have been considered separately due to low citation numbers (grouping them in pairs would have excluded publications from the most recent year). Three publications per year were considered (*e.g.* we selected six publications for the time period 2000-2002 and only three publications for the year 2020). In order to import all the metadata of the publications (*e.g.* PDF, title, abstract, author list, journal, ...), we used the 'Mendeley Web Importer' tool. Finally, we removed all redundant publications between the three different extraction to obtain a collection of 249 non-redundant publications (HIPE collection). In addition, we reperformed this step-by-step pipeline included all variations cited above in order to extract a corpus of 100 research articles focused only on fungal pathogens (HIPE-fun collection). We archived both HIPE and HIPE-fun collections in a public Mendeley web folder as follow: 'HIPE collection' ([https://www.zotero.org/groups/4410902/hipe\\_collection/library](https://www.zotero.org/groups/4410902/hipe_collection/library)) and 'HIPE-fun collection' ([https://www.zotero.org/groups/4410905/hipe-fun\\_collection/library](https://www.zotero.org/groups/4410905/hipe-fun_collection/library)).

### Categorization of publications into research topics and organisms studied

To group HIPEs according to their research topics, we performed an iterative analytical reading of the publications and keywords aimed

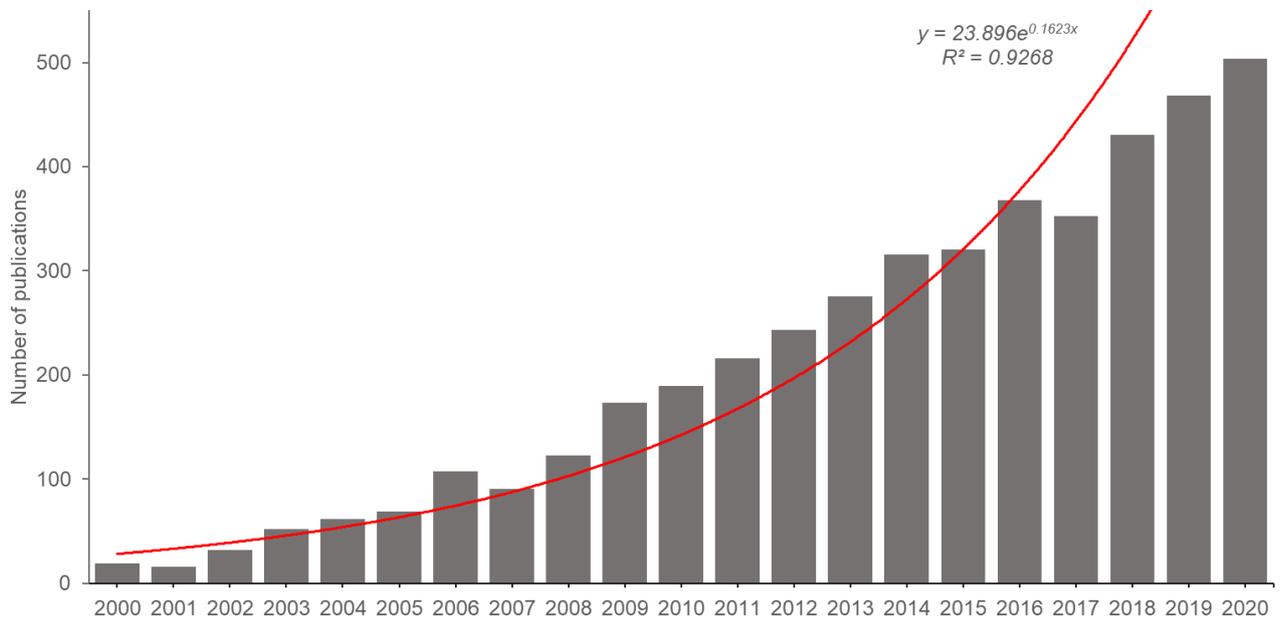
at identifying their main research questions and the organism studied, as described previously (Petre *et al.*, 2021). Throughout this process, we grouped the HIPEs into (i) topics and subtopics according to the main research and specific questions they address or (ii) the pathogenic organisms or group of pathogenic organisms addressed by HIPEs (Dataset 1). In addition, to evaluate the temporal distribution of the HIPEs within each group cited above, we quantified their number per five-year time frames: 2000-2005, 2006-2010, 2011-2015 and 2016-2020.

### Generation of word clouds and analysis of key organisms and molecules

To analyze text content, we built the text files using Microsoft Excel and Text Wrangler softwares, as described previously (Petre *et al.*, 2021). We first manually copied and pasted the relevant text from Mendeley metadata (publication title and abstract) into a Microsoft Excel spreadsheet (Dataset 1) and we then generated the word clouds containing only words referring to organisms and molecules with filtered text files (Dataset 2). An accurate quantification of the most frequent words was performed using the online WordClouds generator (<https://www.wordclouds.com/>). To generate Excel spreadsheets with the word occurrences, we imported our filtered text files and we used the 'Word list' function to export them.

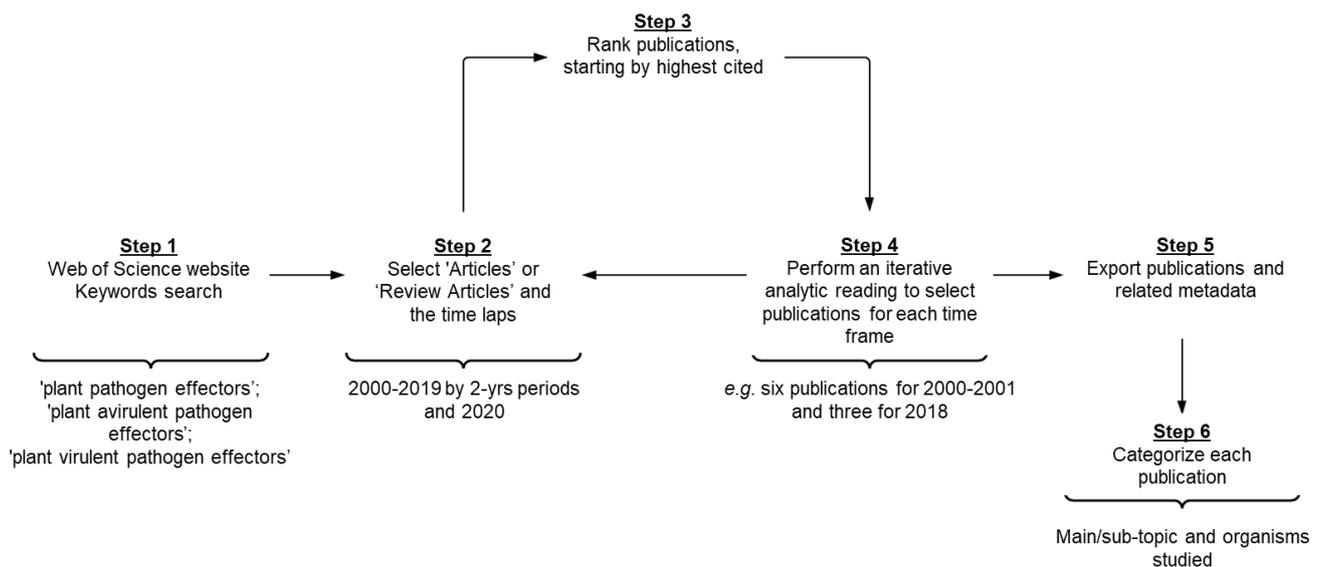
## SUPPLEMENTARY MATERIAL

**Figure S1**



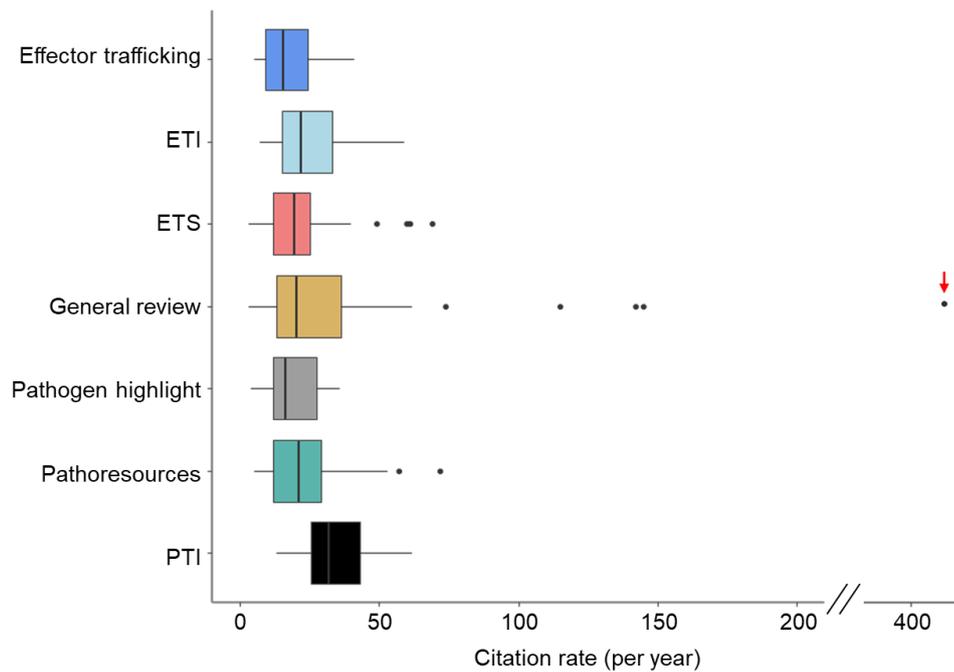
**Figure S1. The number of publications pertaining to plant pathogen effectors increases exponentially over time.**

**Figure S2**



**Figure S2. Operational diagram displaying the step-by-step pipeline used to build the HIPE and HIPE-fun collections.**

**Figure S3**



**Figure S3. The seven main research topics show comparable citation rates.**

Boxplots indicating the annual citation rate of the seven main research topics addressed by the HIPes. The red arrow indicates the HIPE with the highest annual citation rate, which corresponds to the 2006 review by Jones and Dangl that presented the seminal zig-zag model of the plant immune system. The raw data used to build this figure are available in the [Dataset 1](#).

**Dataset 1. Raw dataset including the 249 HIPes and main meta data.**

**Dataset 2. Filtered text file of the 249 HIPE titles and abstracts.**

**Dataset 3. Raw dataset including the 100 HIPE-funs and main meta data.**

## SUPPLEMENTARY TEXT

### **Effector trafficking topic studies how pathogens secrete effectors in the host**

The 'Effector trafficking' topic comprises 16 publications (six research articles and ten reviews) that collectively gathered around 4.4k citations. Among them, bacterial studies predominate, as only three publications focused on filamentous pathogens. The topic comprises two subtopics. The 'Type III/IV bacterial system' subtopic comprises 13 publications. The majority address the current knowledge on the Type III secretion system (TTSS) and associated effectors (Alfano and Collmer, 2004; Büttner and Bonas, 2002a; Büttner and Bonas, 2002b; Cornelis and Van Gijsegem, 2000; Galán *et al.*, 2014; He *et al.*, 2004; Jin *et al.*, 2003; Lindeberg *et al.*, 2012) and the Type IV secretion system (Christie, 2001; Christie and Vogel, 2000). On another hand, three publications describe and analyze how *hrp/hrc* genes encode the Hrp (type III secretion) system and other putative effectors as well as its associated secretion mechanisms (Alfano *et al.*, 2000; Collmer *et al.*, 2000; Lee *et al.*, 2001). The 'Filamentous pathogen translocation pathways' subtopic comprises three publications. One publication addresses the functioning of the biotrophic interfacial complex (BIC) of *Magnaporthe oryzae* (Khang *et al.*, 2010), and two publications focus on how effectors traffic to the host cell cytosol (Whisson *et al.*, 2007) (Kale *et al.*, 2010).

### **ETI (Effector-triggered immunity) topic highlights the immune resistance with the specific recognition of effectors**

The 'ETI (Effector-triggered immunity) topic comprises 41 publications (30 research articles and 11 reviews) that collectively gathered around 9.7k citations. Near 76% of those publications emphasize a specific organism (or group of organisms), including notably fungi and bacteria (41 and 27%, respectively). This topic comprises two subtopics. The 'Immune receptor' subtopic comprises 17 publications that summarize and discuss recent findings on the diversity, the structure, and the function of NLRs (nucleotide-binding leucine-rich repeat receptors) (Bai *et al.*, 2012; Belkhadir *et al.*, 2004; Cesari *et al.*, 2014; DeYoung and Innes, 2006; Jubic *et al.*, 2019; Lu *et al.*, 2016; Marchal *et al.*, 2018; Martin *et al.*, 2003; McHale *et al.*, 2006; Pedley and Martin, 2003; Saintenac *et al.*,

2018; Shen *et al.*, 2007; van Der Vossen *et al.*, 2000; Wang *et al.*, 2019a; Wang *et al.*, 2019b; Williams *et al.*, 2014) or compare plant and animal immune systems (Maekawa *et al.*, 2011). The 'Effector recognition' subtopic comprises 24 publications. The first set of publications addresses direct and indirect recognition of pathogens by the plant immune system (Ellis *et al.*, 2007; Kourelis and Van Der Hoorn, 2018; Petit-Houdenot and Fudal, 2017). A second set is focused on the direct recognition model following the gene-for-gene model (Allen *et al.*, 2004; Bourras *et al.*, 2015; Bourras *et al.*, 2019; Dodds *et al.*, 2006; Gu *et al.*, 2005; de Jonge *et al.*, 2012; Navathe *et al.*, 2020; Paulus *et al.*, 2020; Saur *et al.*, 2019; Vleeshouwers *et al.*, 2011; Yang *et al.*, 2006). The last set of publications studies the indirect recognition of pathogen effectors (Tian *et al.*, 2014) following the guard model (Axtell and Staskawicz, 2003; Deslandes *et al.*, 2003; Mackey *et al.*, 2002; Shao *et al.*, 2003) and finally the recognition mediated by NLR-ID following the decoy model (Cesari *et al.*, 2013; Kroj *et al.*, 2016; Le Roux *et al.*, 2015; Sarris *et al.*, 2015; Sarris *et al.*, 2016).

### **ETS (Effector-triggered susceptibility) topic explains how pathogens deploy effectors to promote infection disease**

The 'ETS' (Effector-triggered susceptibility) topic comprises 78 publications (45 research articles and 33 reviews) that collectively gathered around 17k citations. Nearly 94% of those publications emphasize a specific or a group of organisms with a preponderance of bacterial studies in contrast to studies focused on filamentous pathogens (60 and 40%, respectively). This topic comprises five subtopics. The 'Bacteria review' subtopic comprises 17 publications. A first well-defined set of publications summarizes our knowledge on Type III bacterial effectors (Boch and Bonas, 2010; Büttner, 2016; Greenberg and Vinatzer, 2003; Gürlebeck *et al.*, 2006; Macho, 2016; Macho and Zipfel, 2015; Oh and Beer, 2005; Winstanley and Hart, 2001). Another set of publications reviews the recent investigations on intricate molecular interactions with bacterial elicitation and evasion of plant innate immunity (Abramovitch *et al.*, 2006; Deslandes and Rivas, 2012) and comprises comparative analyses with the fungal pathogens (Hogenhout *et al.*, 2009;

Khan *et al.*, 2018) or animal-specific bacteria (Büttner and Bonas, 2003; Orth, 2002). One publication studies the impact of auxin on pathogenesis and during the interactions with bacterial pathogens (Kunkel and Harper, 2018). Finally, a last set of publications summarize researches on the infection pathways of the genus *Xanthomonas sp.* (Büttner and Bonas, 2010) and more precisely the contribution of transcription activator-like effectors (TALEs) (Perez-Quintero and Szurek, 2019). The 'Effector expression' subtopic comprises two publications and highlights the epigenetic regulation of effector gene expression in the fungus *Leptosphaeria maculans* (Soyer *et al.*, 2014) and the regulation of the *hrp* gene cluster encoding the type III protein secretion system (TTSS) (Noël *et al.*, 2001). The 'Filamentous pathogen review' subtopic comprises 12 publications reviewing the recent findings on fungal effectors (Anderson *et al.*, 2015; Franceschetti *et al.*, 2017; Giraldo and Valent, 2013; Han and Kahmann, 2019; Lo Presti *et al.*, 2015; de Sain and Rep, 2015; Selin *et al.*, 2016; Stergiopoulos *et al.*, 2013; Stergiopoulos and de Wit, 2009; Tsuge *et al.*, 2013), on oomycete effectors (Schornack *et al.*, 2009), and on the use of effectors as cellular probes (Toruño *et al.*, 2016). The 'Functional characterization' subtopic comprises 46 publications. Nearly 71% of those publications study the modulation of immune responses by effectors (Bos *et al.*, 2006; Feng *et al.*, 2012; Gao *et al.*, 2019; Gimenez-Ibanez *et al.*, 2009; Göhre *et al.*, 2008; Hou *et al.*, 2019; Houterman *et al.*, 2008; Kim *et al.*, 2005; Li *et al.*, 2005; Mackey *et al.*, 2003; Nomura, 2006; Park *et al.*, 2012; Rooney, 2005; Wang *et al.*, 2016; Weiberg *et al.*, 2013; Xia, 2004; Xiang *et al.*, 2008; Zhang *et al.*, 2007; Zhang *et al.*, 2010), compare bacterial and fungal modulation of plant immunity (Göhre and Robatzek, 2008), address phytohormone modulation (Gimenez-Ibanez *et al.*, 2014; Kazan and Lyons, 2014; Liu *et al.*, 2014; Plett *et al.*, 2014), or focus on plant trafficking modulation (Aung *et al.*, 2020; Brooks *et al.*, 2005; Chen *et al.*, 2010; DebRoy *et al.*, 2004; de Jonge *et al.*, 2010; Kay *et al.*, 2007; Mentlak *et al.*, 2012; Orth, 2000; Shan *et al.*, 2008; de Torres-Zabala *et al.*, 2007). A second set of publications identifies avirulence genes and validates their Avr activity (Tsiamis *et al.*, 2000; Zhong *et al.*, 2017) and highlights the masking model as a counter-defense of pathogen to evade the immune system (Ma *et al.*, 2017; Plissonneau *et al.*, 2016). Five publications

characterize the activity of type III bacterial effectors (Abramovitch *et al.*, 2003; Abramovitch and Martin, 2005; He *et al.*, 2006; Jamir *et al.*, 2004; Nimchuk *et al.*, 2000) and the associated environmental influences (Xin *et al.*, 2016). Finally, two publications study the virulence activity and virulent motifs of effectors secreted by the soybean pathogen *Phytophthora sojae* (Dou *et al.*, 2008; Ma *et al.*, 2015). The 'Structural characterization' subtopic comprises one publication that reports the crystal structure of the TALE PthXo1 of *Xanthomonas oryzae* (Mak *et al.*, 2012).

### **General review topic conceptualizes our knowledge on plant-pathogen interactions**

The 'General review' topic comprises 39 publications (all reviews) that collectively gathered around 18k citations. Nearly 77% of those publications do not emphasize on a specific or a group of organisms. It comprises three subtopics. The 'Host immunity' subtopic comprises 22 publications. A first series of nine publications summarizes recent findings on ETI (Cui *et al.*, 2015; Thordal-Christensen, 2020; Wu *et al.*, 2014), PTI (PAMP-triggered immunity) (Boller and Felix, 2009; Hématy *et al.*, 2009), compares them (Chisholm *et al.*, 2006; Dodds and Rathjen, 2010; Liu *et al.*, 2013; Qiu *et al.*, 2008; Thomma *et al.*, 2011; Tsuda and Katagiri, 2010), or emphasize some taxonomic groups (Liu *et al.*, 2014; Zvereva and Pooggin, 2012). The other set of publications describes the contribution of phytohormones to plant immunity (Zhang and Li, 2019), the regulation and the signaling pathways of host immunity (Feys and Parker, 2000; Hacquard *et al.*, 2017; Wang *et al.*, 2020), the antiviral immunity (Calil and Fontes, 2017; Gouveia *et al.*, 2017), the defense priming (Conrath, 2011), or the non-host resistance in plant (Nürnberger and Lipka, 2005). Finally, two publications compare immunity between plants and animals (Staskawicz *et al.*, 2001) and between bacteria and fungi (van't Slot and Knogge, 2002). The 'Pathosystem evolution' subtopic comprises eight publications that summarize our knowledge on evolutionary models and mechanisms of plant-pathogen interactions (Brown and Tellier, 2011; Dong *et al.*, 2015; Frantzeskakis *et al.*, 2019; Raffaele and Kamoun, 2012; Schulze-Lefert and Panstruga, 2011) with a focus on climate change (Velásquez

*et al.*, 2018) and R-Avr (Resistance gene – Avirulence gene) interactions (Białas *et al.*, 2018). Finally, one publication compares the evolution in bacterial and fungal pathosystems (Dou and Zhou, 2012). The 'Recognition model' subtopic comprises nine publications and proposed different conceptual models focused on the plant immune system (Bent and Mackey, 2007; Bonas and Lahaye, 2002; van Der Hoorn and Kamoun, 2008; Jones and Takemoto, 2004; Jones and Dangl, 2006; Nimchuk *et al.*, 2001; Stotz *et al.*, 2014) and comparative analyses with the animal immune system (Jones *et al.*, 2016). Finally, one publication summarizes specifically bacterial recognitions models (Khan *et al.*, 2016).

### **Pathogen highlight topic emphasizes on specific organisms**

The 'Pathogen highlight' topic comprises 12 publications (all reviews) that collectively gathered around 1.6k citations. These reviews emphasize bacteria (6), fungi (4), oomycetes (1) and nematodes (1). It comprises three subtopics. The 'Bacterium' subtopic comprises six publications and summarize recent findings on the genera *Xanthomonas* (An *et al.*, 2020; Kumar *et al.*, 2020; Niño-Liu *et al.*, 2006; Timilsina *et al.*, 2020) and *Pseudomonas* (Xin *et al.*, 2018; Xin and He, 2013). The 'Filamentous pathogen' subtopic comprises five publications and summarize recent findings on the oomycete *Phytophthora infestans* (Fry, 2008), the fungus *Cladosporium fulvum* (de Wit, 2016), the rust fungi (Lorrain *et al.*, 2019), the mycorrhizal fungi (Genre *et al.*, 2020) and an overview of selected fungal species with a focus on PAMPs and associated effectors (de Wit *et al.*, 2009). The 'nematode' subtopic comprises one publication on the model species *Caenorhabditis elegans* (Alegado *et al.*, 2003).

### **Pathoresources uses omics approaches and technological innovations to study plant-pathogen interactions**

The 'Pathoresources' topic comprises 53 publications (42 research articles and 11 reviews) that collectively gathered around 11k citations. It comprises three subtopics. The 'Omic data' subtopic comprises 41 publications. Almost half of those publications provides genomic data (Baltrus *et al.*, 2011; Buell *et al.*, 2003; Cooke *et al.*, 2012; Dale *et al.*, 2019; Duan *et al.*, 2009; Faino *et al.*, 2016; Genin and

Boucher, 2004; Genin and Denny, 2012; Grandaubert *et al.*, 2014; Haas *et al.*, 2009; Joardar *et al.*, 2005; Kema *et al.*, 2018; Laflamme *et al.*, 2020; Levy *et al.*, 2018; Li *et al.*, 2020; O'Connell *et al.*, 2012; Rouxel *et al.*, 2011; Salanoubat *et al.*, 2002; Spanu *et al.*, 2010; Thieme *et al.*, 2005; Tyler *et al.*, 2006; Wyatt *et al.*, 2020; Yoshida *et al.*, 2009) and four publications perform comparative analyses of genomic data (Fouché *et al.*, 2018; Fouché *et al.*, 2020; Spanu, 2012; de Wit *et al.*, 2012). A second set of publications reports effectoromic analyses (Jiang *et al.*, 2008; Vleeshouwers *et al.*, 2008), secretomic analyses (Bos *et al.*, 2010; Kamoun, 2006; Kamoun, 2007; Poueymiro and Genin, 2009; Vincent *et al.*, 2020), transcriptomic analyses (Rudd *et al.*, 2015; Wang *et al.*, 2011) and studies of the effector-target interactome network (Mukhtar *et al.*, 2011; Weßling *et al.*, 2014). Finally, three publications describe the pathogen–host interactions database (PHI-base) providing curated molecular and biological information on gene catalogues associated with pathogen–host interactions (Urban *et al.*, 2015; Urban *et al.*, 2017; Urban *et al.*, 2020). The 'Lab tool' subtopic comprises three publications and describe molecular genetic tools to enhance lab investigations for a better comprehension of plant-pathogen interactions (Fang and Tyler, 2016; Ghislain *et al.*, 2019; Nowara *et al.*, 2010). Finally, the 'Computational prediction' subtopic comprises nine publications which describe pipelines to identify and characterize effectors of filamentous pathogens (Saunders *et al.*, 2012; Sperschneider *et al.*, 2016; Sperschneider *et al.*, 2017; Sperschneider *et al.*, 2018a; Sperschneider *et al.*, 2018b), of bacteria (Chang *et al.*, 2005; Collmer *et al.*, 2002; Lindeberg *et al.*, 2005), or to annotate NLRs (Steuernagel *et al.*, 2020).

### **PTI topic describes the basal disease resistance of plant**

The 'PTI' topic comprises ten publications (four research articles and six reviews) that collectively gathered around 2.7k citations. Among them, five publications do not focus on a specific organism or a group of organisms, four study specifically focus on a bacterium and only one on a fungus. It comprises two subtopics. The 'Pattern-recognition receptor' (PRR) subtopic comprises two publications. These two reviews summarize and discuss recent findings on plant PRRs, their diversity to recognize different

ligands, and the ability of pathogen effectors to interfere with early PRR signaling (Tang *et al.*, 2017; Zipfel, 2009). The 'Signaling mechanisms' subtopic comprises eight publications. Four publications describe downstream molecular events with: two summarize the complex network of signaling pathways occurring during PTI with an emphasis on mitogen-activated protein kinases (MAPK) and effectors employed to suppress it (Bigeard *et al.*, 2015; Meng and Zhang, 2013); and two highlight the activity of MAPK4 (Qiu *et al.*, 2008) and BIK1 (Lu *et al.*, 2010) in the early signaling pathways and effectors associated with that process. On another hand, two publications study the contribution of phytohormones to the effector recognition (Tsuda and Katagiri, 2010; Yang *et al.*, 2019), one addresses the role of reactive oxygen species (ROS) in signaling and defense reactions against filamentous fungi and fungal effectors that suppress the host oxidative burst (Heller and Tudzynski, 2011), and one provides evidence of calcium-dependent PAMP-triggered immunity in plants (Tian *et al.*, 2019).

## References

- Abramovitch, R.B., Anderson, J.C. and Martin, G.B.** (2006) Bacterial elicitation and evasion of plant innate immunity. *Nature Reviews Molecular Cell Biology* **7**, 601–611.
- Abramovitch, R.B., Kim, Y.J., Chen, S., Dickman, M.B. and Martin, G.B.** (2003) *Pseudomonas* type III effector AvrPtoB induces plant disease susceptibility by inhibition of host programmed cell death. *The EMBO Journal* **22**, 60–69.
- Abramovitch, R.B. and Martin, G.B.** (2005) AvrPtoB: a bacterial type III effector that both elicits and suppresses programmed cell death associated with plant immunity. *FEMS Microbiology Letters* **245**, 1–8.
- Alegado, R.A., Campbell, M.C., Chen, W.C., Slutz, S.S. and Tan, M.W.** (2003) Characterization of mediators of microbial virulence and innate immunity using the *Caenorhabditis elegans* host-pathogen model. *Cellular Microbiology* **5**, 435–444.
- Alfano, J.R., Charkowski, A.O., Deng, W.L., Badel, J.L., Petnicki-Ocwieja, T., Van Dijk, K. and Collmer, A.** (2000) The *Pseudomonas syringae* Hrp pathogenicity island has a tripartite mosaic structure composed of a cluster of type III secretion genes bounded by exchangeable effector and conserved effector loci that contribute to parasitic fitness and pathogenicity. *PNAS* **97**, 4856–4861.
- Alfano, J.R. and Collmer, A.** (2004) Type III secretion system effector proteins: double agents in bacterial disease and plant defense. *Annual Review of Phytopathology* **42**, 385–414.
- Allen, R.L., Bittner-Eddy, P.D., Grenville-Briggs, L.J., Meitz, J.C., Rehmany, A.P., Rose, L.E. and Beynon, J.L.** (2004) Host-parasite coevolutionary conflict between *Arabidopsis* and downy mildew. *Science* **306**, 1957–1960.
- An, S.Q., Potnis, N., Dow, M., et al.** (2020) Mechanistic insights into host adaptation, virulence and epidemiology of the phytopathogen *Xanthomonas*. *FEMS Microbiology Reviews* **44**, 1–32.
- Anderson, R.G., Deb, D., Fedkenheuer, K. and McDowell, J.M.** (2015) Recent progress in RXLR effector research. *Molecular Plant-Microbe Interactions* **28**, 1063–1072.
- Aung, K., Kim, P., Li, Z., Joe, A., Kvitko, B., Alfano, J.R. and Hea, S.Y.** (2020) Pathogenic bacteria target plant plasmodesmata to colonize and invade surrounding tissues. *The Plant Cell* **32**, 595–611.
- Axtell, M.J. and Staskawicz, B.J.** (2003) Initiation of RPS2-specified disease resistance in *Arabidopsis* is coupled to the AvrRpt2-directed elimination of RIN4. *Cell* **112**, 369–377.
- Bai, S., Liu, J., Chang, C., et al.** (2012) Structure-function analysis of barley NLR immune receptor MLA10 reveals its cell compartment specific activity in cell death and disease resistance. *PLoS Pathogens* **8**, e1002752.
- Baltrus, D.A., Nishimura, M.T., Romanchuk, A., et al.** (2011) Dynamic evolution of pathogenicity revealed by sequencing and comparative genomics of 19 *Pseudomonas syringae* isolates. *PLoS Pathogens* **7**, e1002132.
- Belkhadir, Y., Subramaniam, R. and Dangl, J.L.** (2004) Plant disease resistance protein signaling: NBS-LRR proteins and their partners. *Current Opinion in Plant Biology* **7**, 391–399.
- Bent, A.F. and Mackey, D.** (2007) Elicitors, effectors, and R genes: the new paradigm and a

lifetime supply of questions. *Annual Review of Phytopathology* **45**, 399–436.

**Bialas, A., Zess, E.K., De La Concepcion, J.C., et al.** (2018) Lessons in effector and NLR biology of plant-microbe systems. *Molecular Plant-Microbe Interactions* **31**, 34–45.

**Bigeard, J., Colcombet, J. and Hirt, H.** (2015) Signaling mechanisms in pattern-triggered immunity (PTI). *Molecular Plant* **8**, 521–539.

**Boch, J. and Bonas, U.** (2010) *Xanthomonas* AvrBs3 family-type III effectors: discovery and function. *Annual Review of Phytopathology* **48**, 419–436.

**Boller, T. and Felix, G.** (2009) A renaissance of elicitors: perception of microbe-associated molecular patterns and danger signals by pattern-recognition receptors. *Annual Review of Plant Biology* **60**, 379–407.

**Bonas, U. and Lahaye, T.** (2002) Plant disease resistance triggered by pathogen-derived molecules: Refined models of specific recognition. *Current Opinion in Microbiology* **5**, 44–50.

**Bos, J.I.B., Kanneganti, T.D., Young, C., Cakir, C., Huitema, E., Win, J., Armstrong, M.R., Birch, P.R.J. and Kamoun, S.** (2006) The C-terminal half of *Phytophthora infestans* RXLR effector AVR3a is sufficient to trigger R3a-mediated hypersensitivity and suppress INF1-induced cell death in *Nicotiana benthamiana*. *Plant Journal* **48**, 165–176.

**Bos, J.I.B., Prince, D., Pitino, M., Maffei, M.E., Win, J. and Hogenhout, S.A.** (2010) A functional genomics approach identifies candidate effectors from the aphid species *Myzus persicae* (green peach aphid). *PLoS Genetics* **6**, e1001216.

**Bourras, S., Kunz, L., Xue, M., et al.** (2019) The *AvrPm3-Pm3* effector-NLR interactions control both race-specific resistance and host-specificity of cereal mildews on wheat. *Nature Communications* **10**, 2292.

**Bourras, S., McNally, K.E., Ben-David, R., et al.** (2015) Multiple avirulence loci and allele-specific effector recognition control the *Pm3* race-specific resistance of wheat to powdery mildew. *The Plant Cell* **27**, 2991–3012.

**Brooks, D.M., Bender, C.L. and Kunkel, B.N.** (2005) The *Pseudomonas syringae* phytotoxin

coronatine promotes virulence by overcoming salicylic acid-dependent defences in *Arabidopsis thaliana*. *Molecular Plant Pathology* **6**, 629–639.

**Brown, J.K.M. and Tellier, A.** (2011) Plant-parasite coevolution: bridging the gap between genetics and ecology. *Annual Review of Phytopathology* **49**, 345–367.

**Buell, C.R., Joardar, V., Lindeberg, M., et al.** (2003) The complete genome sequence of the *Arabidopsis* and tomato pathogen *Pseudomonas syringae* pv. *tomato* DC3000. *PNAS* **100**, 10181–10186.

**Büttner, D.** (2016) Behind the lines-actions of bacterial type III effector proteins in plant cells. *FEMS Microbiology Reviews* **40**, 894–937.

**Büttner, D. and Bonas, U.** (2003) Common infection strategies of plant and animal pathogenic bacteria. *Current Opinion in Plant Biology* **6**, 312–319.

**Büttner, D. and Bonas, U.** (2002a) Getting across - bacterial type III effector proteins on their way to the plant cell. *The EMBO Journal* **21**, 5313–5322.

**Büttner, D. and Bonas, U.** (2002b) Port of entry - the type III secretion translocon. *Trends in Microbiology* **10**, 186–192.

**Büttner, D. and Bonas, U.** (2010) Regulation and secretion of *Xanthomonas* virulence factors. *FEMS Microbiology Reviews* **34**, 107–133.

**Calil, I.P. and Fontes, E.P.B.** (2017) Plant immunity against viruses: antiviral immune receptors in focus. *Annals of Botany* **119**, 711–723.

**Cesari, S., Kanzaki, H., Fujiwara, T., et al.** (2014) The NB-LRR proteins RGA4 and RGA5 interact functionally and physically to confer disease resistance. *The EMBO Journal* **33**, 1941–1959.

**Cesari, S., Thilliez, G., Ribot, C., et al.** (2013) The rice resistance protein pair RGA4/RGA5 recognizes the *Magnaporthe oryzae* effectors AVR-Pia and AVR1-CO39 by direct binding. *The Plant Cell* **25**, 1463–1481.

**Chang, J.H., Urbach, J.M., Law, T.F., Arnold, L.W., Hu, A., Gombar, S., Grant, S.R., Ausubel, F.M. and Dangl, J.L.** (2005) A high-throughput, near-saturating screen for type

III effector genes from *Pseudomonas syringae*. *PNAS* **102**, 2549–2554.

**Chen, L.Q., Hou, B.H., Lalonde, S., et al.** (2010) Sugar transporters for intercellular exchange and nutrition of pathogens. *Nature* **468**, 527–532.

**Chisholm, S.T., Coaker, G., Day, B. and Staskawicz, B.J.** (2006) Host-microbe interactions: shaping the evolution of the plant immune response. *Cell* **124**, 803–814.

**Christie, P.J.** (2001) Type IV secretion: intercellular transfer of macromolecules by systems ancestrally related to conjugation machines. *Molecular Microbiology* **40**, 294–305.

**Christie, P.J. and Vogel, J.P.** (2000) Bacterial type IV secretion: conjugation systems adapted to deliver effector molecules to host cells. *Trends in Microbiology* **8**, 354–360.

**Collmer, A., Badel, J.L., Charkowski, A.O., et al.** (2000) *Pseudomonas syringae* Hrp type III secretion system and effector proteins. *PNAS* **97**, 8770–8777.

**Collmer, A., Lindeberg, M., Petnicki-Ocwieja, T., Schneider, D.J. and Alfano, J.R.** (2002) Genomic mining type III secretion system effectors in *Pseudomonas syringae* yields new picks for all TTSS prospectors. *Trends in Microbiology* **10**, 462–469.

**Conrath, U.** (2011) Molecular aspects of defence priming. *Trends in Plant Science* **16**, 524–531.

**Cooke, D.E.L., Cano, L.M., Raffaele, S., et al.** (2012) Genome analyses of an aggressive and invasive lineage of the irish potato famine pathogen. *PLoS Pathogens* **8**, e1002940.

**Cornelis, G.R. and Gijsegem, F. Van** (2000) Assembly and function of type III secretory systems. *Annual Review of Microbiology* **54**, 735–774.

**Cui, H., Tsuda, K. and Parker, J.E.** (2015) Effector-triggered immunity: from pathogen perception to robust defense. *Annual Review of Plant Biology* **66**, 487–511.

**Dale, A.L., Feau, N., Everhart, S.E., et al.** (2019) Mitotic recombination and rapid genome evolution in the invasive forest pathogen *phytophthora ramorum*. *mBio* **10**, e02452-18.

**DeRoy, S., Thilmony, R., Kwack, Y.-B., Nomura, K. and He, S.Y.** (2004) A family of conserved bacterial effectors inhibits salicylic acid-mediated basal immunity and promotes disease necrosis in plants. *PNAS* **101**, 9927–9932.

**de Jonge, R., Van Esse, H.P., Kombrink, A., et al.** (2010) Conserved fungal LysM effector Ecp6 prevents chitin-triggered immunity in plants. *Science* **329**, 953–955.

**de Jonge, R., Van Esse, H.P., Maruthachalam, K., et al.** (2012) Tomato immune receptor Ve1 recognizes effector of multiple fungal pathogens uncovered by genome and RNA sequencing. *PNAS* **109**, 5110–5115.

**Deslandes, L., Olivier, J., Peeters, N., Feng, D.X., Khounloham, M., Boucher, C., Somssich, I., Genin, S. and Marco, Y.** (2003) Physical interaction between RRS1-R, a protein conferring resistance to bacterial wilt, and PopP2, a type III effector targeted to the plant nucleus. *PNAS* **100**, 8024–8029.

**Deslandes, L. and Rivas, S.** (2012) Catch me if you can: bacterial effectors and plant targets. *Trends in Plant Science* **17**, 644–655.

**de Torres-Zabala, M., Truman, W., Bennett, M.H., Lafforgue, G., Mansfield, J.W., Rodriguez Egea, P., Bögre, L. and Grant, M.** (2007) *Pseudomonas syringae* pv. *tomato* hijacks the *Arabidopsis* abscisic acid signalling pathway to cause disease. *The EMBO Journal* **26**, 1434–1443.

**de Wit, P.J.G.M.** (2016) *Cladosporium fulvum* effectors: weapons in the arms race with tomato. *Annual Review of Phytopathology* **54**, 1–23.

**de Wit, P.J.G.M., Van Der Burgt, A., Ökmen, B., et al.** (2012) The genomes of the fungal plant pathogens *Cladosporium fulvum* and *Dothistroma septosporum* reveal adaptation to different hosts and lifestyles but also signatures of common ancestry. *PLoS Genetics* **8**, e1003088.

**de Wit, P.J.G.M., Mehrabi, R., Van Den Burg, H.A. and Stergiopoulos, I.** (2009) Fungal effector proteins: past, present and future. *Molecular Plant Pathology* **10**, 735–747.

**DeYoung, B.J. and Innes, R.W.** (2006) Plant NBS-LRR proteins in pathogen sensing and host defense. *Nature Immunology* **7**, 1243–1249.

- Dodds, P.N., Lawrence, G.J., Catanzariti, A.-M., Teh, T., Wang, C.-I.A., Ayliffe, M.A., Kobe, B. and Ellis, J.G.** (2006) Direct protein interaction underlies gene-for-gene specificity and coevolution of the flax resistance genes and flax rust avirulence genes. *PNAS* **103**, 8888–8893.
- Dodds, P.N. and Rathjen, J.P.** (2010) Plant immunity: towards an integrated view of plant-pathogen interactions. *Nature Reviews Genetics* **11**, 539–548.
- Dong, S., Raffaele, S. and Kamoun, S.** (2015) The two-speed genomes of filamentous pathogens: Waltz with plants. *Current Opinion in Genetics and Development* **35**, 57–65.
- Dou, D., Kale, S.D., Wang, Xinle, et al.** (2008) Conserved C-terminal motifs required for avirulence and suppression of cell death by *Phytophthora sojae* effector Avr1b. *The Plant Cell* **20**, 1118–1133.
- Dou, D. and Zhou, J.M.** (2012) Phytopathogen effectors subverting host immunity: different foes, similar battleground. *Cell Host and Microbe* **12**, 484–495.
- Duan, Y., Zhou, L., Hall, D.G., et al.** (2009) Complete genome sequence of citrus huanglongbing bacterium, “*Candidatus liberibacter asiaticus*” obtained through metagenomics. *Molecular Plant-Microbe Interactions* **22**, 1011–1020.
- Ellis, J.G., Dodds, P.N. and Lawrence, G.J.** (2007) Flax rust resistance gene specificity is based on direct resistance-avirulence protein interactions. *Annual Review of Phytopathology* **45**, 289–306.
- Faino, L., Seidl, M.F., Shi-Kunne, X., Pauper, M., Van Den Berg, G.C.M., Wittenberg, A.H.J. and Thomma, B.P.H.J.** (2016) Transposons passively and actively contribute to evolution of the two-speed genome of a fungal pathogen. *Genome Research* **26**, 1091–1100.
- Fang, Y. and Tyler, B.M.** (2016) Efficient disruption and replacement of an effector gene in the oomycete *Phytophthora sojae* using CRISPR/Cas9. *Molecular Plant Pathology* **17**, 127–139.
- Feng, F., Yang, F., Rong, W., Wu, X., Zhang, J., Chen, S., He, C. and Zhou, J.M.** (2012) A *Xanthomonas* uridine 5'-monophosphate transferase inhibits plant immune kinases. *Nature* **485**, 114–118.
- Feys, B.J. and Parker, J.E.** (2000) Interplay of signaling pathways in plant disease resistance. *Trends in Genetics* **16**, 449–455.
- Fouché, S., Badet, T., Oggenfuss, U., Plissonneau, C., Francisco, C.S. and Croll, D.** (2020) Stress-Driven Transposable Element De-repression Dynamics and Virulence Evolution in a Fungal Pathogen. *Molecular Biology and Evolution* **37**, 221–239.
- Fouché, S., Plissonneau, C. and Croll, D.** (2018) The birth and death of effectors in rapidly evolving filamentous pathogen genomes. *Current Opinion in Microbiology* **46**, 34–42.
- Franceschetti, M., Maqbool, A., Jiménez-Dalmaroni, M.J., Pennington, H.G., Kamoun, S. and Banfield, M.J.** (2017) Effectors of filamentous plant pathogens: commonalities amid diversity. *Microbiology and Molecular Biology Reviews* **81**, e00066-16.
- Frantzeskakis, L., Di Pietro, A., Rep, M., Schirawski, J., Wu, C.H. and Panstruga, R.** (2019) Rapid evolution in plant-microbe interactions – a molecular genomics perspective. *New Phytologist* **225**, 1134–1142.
- Fry, W.** (2008) *Phytophthora infestans*: the plant (and *R* gene) destroyer. *Molecular Plant Pathology* **9**, 385–402.
- Galán, J.E., Lara-Tejero, M., Marlovits, T.C. and Wagner, S.** (2014) Bacterial type III secretion systems: Specialized nanomachines for protein delivery into target cells. *Annual Review of Microbiology* **68**, 415–438.
- Gao, F., Zhang, B. Sen, Zhao, J.H., Huang, J.F., Jia, P.S., Wang, S., Zhang, J., Zhou, J.M. and Guo, H.S.** (2019) Deacetylation of chitin oligomers increases virulence in soil-borne fungal pathogens. *Nature Plants* **5**, 1167–1176.
- Genin, S. and Boucher, C.** (2004) Lessons learned from the genome analysis of *Ralstonia solanacearum*. *Annual Review of Phytopathology* **42**, 107–134.
- Genin, S. and Denny, T.P.** (2012) Pathogenomics of the *Ralstonia solanacearum* species complex. *Annual Review of Phytopathology* **50**, 67–89.
- Genre, A., Lanfranco, L., Perotto, S. and**

- Bonfante, P.** (2020) Unique and common traits in mycorrhizal symbioses. *Nature Reviews Microbiology* **18**, 649–660.
- Ghislain, M., Byarugaba, A.A., Magembe, E., et al.** (2019) Stacking three late blight resistance genes from wild species directly into African highland potato varieties confers complete field resistance to local blight races. *Plant Biotechnology Journal* **17**, 1119–1129.
- Gimenez-Ibanez, S., Boter, M., Fernández-Barbero, G., Chini, A., Rathjen, J.P. and Solano, R.** (2014) The bacterial effector HopX1 targets JAZ transcriptional repressors to activate jasmonate signaling and promote infection in *Arabidopsis*. *PLoS Biology* **12**, e1001792.
- Gimenez-Ibanez, S., Hann, D.R., Ntoukakis, V., Petutschnig, E., Lipka, V. and Rathjen, J.P.** (2009) AvrPtoB targets the LysM receptor kinase CERK1 to promote bacterial virulence on plants. *Current Biology* **19**, 423–429.
- Giraldo, M.C. and Valent, B.** (2013) Filamentous plant pathogen effectors in action. *Nature Reviews Microbiology* **11**, 800–814.
- Göhre, V. and Robatzek, S.** (2008) Breaking the barriers: microbial effector molecules subvert plant immunity. *Annual Review of Phytopathology* **46**, 189–215.
- Göhre, V., Spallek, T., Häweker, H., Mersmann, S., Mentzel, T., Boller, T., de Torres, M., Mansfield, J.W. and Robatzek, S.** (2008) Plant pattern-recognition receptor FLS2 is directed for degradation by the bacterial ubiquitin ligase AvrPtoB. *Current Biology* **18**, 1824–1832.
- Gouveia, B.C., Calil, I.P., Machado, J.P.B., Santos, A.A. and Fontes, E.P.B.** (2017) Immune receptors and co-receptors in antiviral innate immunity in plants. *Frontiers in Microbiology* **7**, 2139.
- Grandaubert, J., Lowe, R.G.T., Soyer, J.L., et al.** (2014) Transposable element-assisted evolution and adaptation to host plant within the *Leptosphaeria maculans*-*Leptosphaeria biglobosa* species complex of fungal pathogens. *BMC Genomics* **15**, 891.
- Greenberg, J.T. and Vinatzer, B.A.** (2003) Identifying type III effectors of plant pathogens and analyzing their interaction with plant cells. *Current Opinion in Microbiology* **6**, 20–28.
- Gu, K., Yang, B., Tian, D., et al.** (2005) *R* gene expression induced by a type-III effector triggers disease resistance in rice. *Nature* **435**, 1122–1125.
- Gürlebeck, D., Thieme, F. and Bonas, U.** (2006) Type III effector proteins from the plant pathogen *Xanthomonas* and their role in the interaction with the host plant. *Journal of Plant Physiology* **163**, 233–255.
- Haas, B.J., Kamoun, S., Zody, M.C., et al.** (2009) Genome sequence and analysis of the Irish potato famine pathogen *Phytophthora infestans*. *Nature* **461**, 393–398.
- Hacquard, S., Spaepen, S., Garrido-Oter, R. and Schulze-Lefert, P.** (2017) Interplay between innate immunity and the plant microbiota. *Annual Review of Phytopathology* **55**, 565–589.
- Han, X. and Kahmann, R.** (2019) Manipulation of phytohormone pathways by effectors of filamentous plant pathogens. *Frontiers in Plant Science* **10**, 822.
- He, P., Shan, L., Lin, N.C., Martin, G.B., Kemmerling, B., Nürnberger, T. and Sheen, J.** (2006) Specific bacterial suppressors of MAMP signaling upstream of MAPKKK in *Arabidopsis* innate immunity. *Cell* **125**, 563–575.
- He, S.Y., Nomura, K. and Whittam, T.S.** (2004) Type III protein secretion mechanism in mammalian and plant pathogens. *BBA* **1694**, 181–206.
- Heller, J. and Tudzynski, P.** (2011) Reactive oxygen species in phytopathogenic fungi: signaling, development, and disease. *Annual Review of Phytopathology* **49**, 369–390.
- Hématy, K., Cherk, C. and Somerville, S.** (2009) Host-pathogen warfare at the plant cell wall. *Current Opinion in Plant Biology* **12**, 406–413.
- Hogenhout, S.A., Van Der Hoorn, R.A.L., Terauchi, R. and Kamoun, S.** (2009) Emerging concepts in effector biology of plant-associated organisms. *Molecular Plant-Microbe Interactions* **22**, 115–122.
- Hou, Y., Zhai, Y., Feng, L., et al.** (2019) A *Phytophthora* effector suppresses trans-kingdom RNAi to promote disease susceptibility. *Cell Host and Microbe* **25**, 153-165.e5.

- Houterman, P.M., Cornelissen, B.J.C. and Rep, M.** (2008) Suppression of plant resistance gene-based immunity by a fungal effector. *PLoS Pathogens* **4**.
- Jamir, Y., Guo, M., Oh, H.S., Petnicki-Ocwieja, T., Chen, S., Tang, X., Dickman, M.B., Collmer, A. and Alfano, J.R.** (2004) Identification of *Pseudomonas syringae* type III effectors that can suppress programmed cell death in plants and yeast. *The Plant Journal* **37**, 554–565.
- Jiang, R.H.Y., Tripathy, S., Govers, F. and Tyler, B.M.** (2008) RXLR effector reservoir in two *Phytophthora* species is dominated by a single rapidly evolving superfamily with more than 700 members. *PNAS* **105**, 4874–4879.
- Jin, Q., Thilmony, R., Zwiesler-Vollick, J. and He, S.Y.** (2003) Type III protein secretion in *Pseudomonas syringae*. *Microbes and Infection* **5**, 301–310.
- Joardar, V., Lindeberg, M., Jackson, R.W., et al.** (2005) Whole-genome sequence analysis of *Pseudomonas syringae* pv. *phaseolicola* 1448A reveals divergence among pathovars in genes involved in virulence and transposition. *Journal of Bacteriology* **187**, 6488–6498.
- Jones, D.A. and Takemoto, D.** (2004) Plant innate immunity - direct and indirect recognition of general and specific pathogen-associated molecules. *Current Opinion in Immunology* **16**, 48–62.
- Jones, J.D.G. and Dangl, J.L.** (2006) The plant immune system. *Nature* **444**, 323–329.
- Jones, J.D.G., Vance, R.E. and Dangl, J.L.** (2016) Intracellular innate immune surveillance devices in plants and animals. *Science* **354**, aaf6395.
- Jubic, L.M., Saile, S., Furzer, O.J., Kasmi, F. El and Dangl, J.L.** (2019) Help wanted: helper NLRs and plant immune responses. *Current Opinion in Plant Biology* **50**, 82–94.
- Kale, S.D., Gu, B., Capelluto, D.G.S., et al.** (2010) External lipid PI3P mediates entry of eukaryotic pathogen effectors into plant and animal host cells. *Cell* **142**, 284–295.
- Kamoun, S.** (2006) A catalogue of the effector secretome of plant pathogenic oomycetes. *Annual Review of Phytopathology* **44**, 41–60.
- Kamoun, S.** (2007) Groovy times: filamentous pathogen effectors revealed. *Current Opinion in Plant Biology* **10**, 358–365.
- Kay, S., Hahn, S., Marois, E., Hause, G. and Bonas, U.** (2007) A bacterial effector acts as a plant transcription factor and induces a cell size regulator. *Science* **318**, 648–651.
- Kazan, K. and Lyons, R.** (2014) Intervention of phytohormone pathways by pathogen effectors. *The Plant Cell* **26**, 2285–2309.
- Kema, G.H.J., Mirzadi Gohari, A., Aouini, L., et al.** (2018) Stress and sexual reproduction affect the dynamics of the wheat pathogen effector AvrStb6 and strobilurin resistance. *Nature Genetics* **50**, 375–380.
- Khan, M., Seto, D., Subramaniam, R. and Desveaux, D.** (2018) Oh, the places they'll go! A survey of phytopathogen effectors and their host targets. *The Plant Journal* **93**, 651–663.
- Khan, M., Subramaniam, R. and Desveaux, D.** (2016) Of guards, decoys, baits and traps: pathogen perception in plants by type III effector sensors. *Current Opinion in Microbiology* **29**, 49–55.
- Khang, C.H., Berruyer, R., Giraldo, M.C., Kankanala, P., Park, S.Y., Czymmek, K., Kang, S. and Valent, B.** (2010) Translocation of *Magnaporthe oryzae* effectors into rice cells and their subsequent cell-to-cell movement. *The Plant Cell* **22**, 1388–1403.
- Kim, M.G., Da Cunha, L., McFall, A.J., Belkhadir, Y., DebRoy, S., Dangl, J.L. and Mackey, D.** (2005) Two *Pseudomonas syringae* type III effectors inhibit RIN4-regulated basal defense in *Arabidopsis*. *Cell* **121**, 749–759.
- Kourelis, J. and Van Der Hoorn, R.A.L.** (2018) Defended to the nines: 25 years of resistance gene cloning identifies nine mechanisms for R protein function. *The Plant Cell* **30**, 285–299.
- Kroj, T., Chanclud, E., Michel-Romiti, C., Grand, X. and Morel, J.B.** (2016) Integration of decoy domains derived from protein targets of pathogen effectors into plant immune receptors is widespread. *New Phytologist* **210**, 618–626.
- Kumar, A., Kumar, R., Sengupta, D., et al.** (2020) Deployment of genetic and genomic tools toward gaining a better understanding of rice-Xanthomonas oryzae pv. oryzae interactions for

development of durable bacterial blight resistant rice. *Frontiers in Plant Science* **11**, 1152.

**Kunkel, B.N. and Harper, C.P.** (2018) The roles of auxin during interactions between bacterial plant pathogens and their hosts. *Journal of Experimental Botany* **69**, 245–254.

**Laflamme, B., Dillon, M.M., Martel, A., Almeida, R.N.D., Desveaux, D. and Guttman, D.S.** (2020) The pan-genome effector-triggered immunity landscape of a host-pathogen interaction. *Science* **367**, 763–768.

**Lee, J., Klüsener, B., Tsiamis, G., et al.** (2001) HrpZPsph from the plant pathogen *Pseudomonas syringae* pv. *phaseolicola* binds to lipid bilayers and forms an ion-conducting pore *in vitro*. *PNAS* **98**, 289–294.

**Le Roux, C., Huet, G., Jauneau, A., et al.** (2015) A receptor pair with an integrated decoy converts pathogen disabling of transcription factors to immunity. *Cell* **161**, 1074–1088.

**Levy, A., Salas Gonzalez, I., Mittelviehhaus, M., et al.** (2018) Genomic features of bacterial adaptation to plants. *Nature Genetics* **50**, 138–150.

**Li, X., Lin, H., Zhang, W., Zou, Y., Zhang, J., Tang, X. and Zhou, J.M.** (2005) Flagellin induces innate immunity in nonhost interactions that is suppressed by *Pseudomonas syringae* effectors. *PNAS* **102**, 12990–12995.

**Li, Y., Xia, C., Wang, M., Yin, C. and Chen, X.** (2020) Whole-genome sequencing of *Puccinia striiformis* f. sp. *tritici* mutant isolates identifies avirulence gene candidates. *BMC Genomics* **21**, 247.

**Lindeberg, M., Cunnac, S. and Collmer, A.** (2012) *Pseudomonas syringae* type III effector repertoires: last words in endless arguments. *Trends in Microbiology* **20**, 199–208.

**Lindeberg, M., Stavrinides, J., Chang, J.H., Alfano, J.R., Collmer, A., Dangl, J.L., Greenberg, J.T., Mansfield, J.W. and Guttman, D.S.** (2005) Proposed guidelines for a unified nomenclature and phylogenetic analysis of type III hop effector proteins in the plant pathogen *Pseudomonas syringae*. *Molecular Plant-Microbe Interactions* **18**, 275–282.

**Liu, T., Song, T., Zhang, X., et al.** (2014) Unconventionally secreted effectors of two filamentous pathogens target plant salicylate

biosynthesis. *Nature Communications* **5**, 4686.

**Liu, W., Liu, J., Ning, Y., Ding, B., Wang, X., Wang, Z. and Wang, G.L.** (2013) Recent progress in understanding PAMP-and effector-triggered immunity against the rice blast fungus *Magnaporthe oryzae*. *Molecular Plant* **6**, 605–620.

**Liu, W., Liu, J., Triplett, L., Leach, J.E. and Wang, G.L.** (2014) Novel insights into rice innate immunity against bacterial and fungal pathogens. *Annual Review of Phytopathology* **52**, 213–241.

**Lo Presti, L., Lanver, D., Schweizer, G., Tanaka, S., Liang, L., Tollot, M., Zuccaro, A., Reissmann, S. and Kahmann, R.** (2015) Fungal effectors and plant susceptibility. *Annual Review of Plant Biology* **66**, 513–545.

**Lorrain, C., Gonçalves dos Santos, K.C., Germain, H., Hecker, A. and Duplessis, S.** (2019) Advances in understanding obligate biotrophy in rust fungi. *New Phytologist* **222**, 1190–1206.

**Lu, D., Wu, S., Gao, X., Zhang, Y., Shan, L. and He, P.** (2010) A receptor-like cytoplasmic kinase, BIK1, associates with a flagellin receptor complex to initiate plant innate immunity. *PNAS* **107**, 496–501.

**Lu, X., Kracher, B., Saur, I.M.L., Bauer, S., Ellwood, S.R., Wise, R., Yaeno, T., Maekawa, T. and Schulze-Lefert, P.** (2016) Allelic barley MLA immune receptors recognize sequence-unrelated avirulence effectors of the powdery mildew pathogen. *PNAS* **113**, E6486–E6495.

**Ma, Z., Song, T., Zhu, L., et al.** (2015) A *Phytophthora sojae* glycoside hydrolase 12 protein is a major virulence factor during soybean infection and is recognized as a PAMP. *The Plant Cell* **27**, 2057–2072.

**Ma, Z., Zhu, L., Song, T., et al.** (2017) A paralogous decoy protects *Phytophthora sojae* apoplastic effector PsXEG1 from a host inhibitor. *Science* **355**, 710–714.

**Macho, A.P.** (2016) Subversion of plant cellular functions by bacterial type-III effectors: beyond suppression of immunity. *New Phytologist* **210**, 51–57.

**Macho, A.P. and Zipfel, C.** (2015) Targeting of plant pattern recognition receptor-triggered immunity by bacterial type-III secretion system

- effectors. *Current Opinion in Microbiology* **23**, 14–22.
- Mackey, D., Belkhadir, Y., Alonso, J.M., Ecker, J.R. and Dangl, J.L.** (2003) *Arabidopsis* RIN4 is a target of the type III virulence effector AvrRpt2 and modulates RPS2-mediated resistance. *Cell* **112**, 379–389.
- Mackey, D., Holt, B.F., Wiig, A. and Dangl, J.L.** (2002) RIN4 interacts with *Pseudomonas syringae* type III effector molecules and is required for RPM1-mediated resistance in *Arabidopsis*. *Cell* **108**, 743–754.
- Maekawa, T., Kufer, T.A. and Schulze-Lefert, P.** (2011) NLR functions in plant and animal immune systems: so far and yet so close. *Nature Immunology* **12**, 818–826.
- Mak, A.N.S., Bradley, P., Cernadas, R.A., Bogdanove, A.J. and Stoddard, B.L.** (2012) The crystal structure of TAL effector PthXo1 bound to its DNA target. *Science* **335**, 716–719.
- Marchal, C., Zhang, J., Zhang, P., et al.** (2018) BED-domain-containing immune receptors confer diverse resistance spectra to yellow rust. *Nature Plants* **4**, 662–668.
- Martin, G.B., Bogdanove, A.J. and Sessa, G.** (2003) Understanding the functions of plant disease resistance proteins. *Annual Review of Plant Biology* **54**, 23–61.
- McHale, L., Tan, X., Koehl, P. and Michelmore, R.W.** (2006) Plant NBS-LRR proteins: adaptable guards. *Genome Biology* **7**, 212.
- Meng, X. and Zhang, S.** (2013) MAPK cascades in plant disease resistance signaling. *Annual Review of Phytopathology* **51**, 245–266.
- Mentlak, T.A., Kombrink, A., Shinya, T., et al.** (2012) Effector-mediated suppression of chitin-triggered immunity by *Magnaporthe oryzae* is necessary for rice blast disease. *The Plant Cell* **24**, 322–335.
- Mukhtar, M.S., Carvunis, A.R., Dreze, M., et al.** (2011) Independently evolved virulence effectors converge onto hubs in a plant immune system network. *Science* **333**, 596–601.
- Navathe, S., Yadav, P.S., Chand, R., Mishra, V.K., Vasistha, N.K., Meher, P.K., Joshi, A.K. and Gupta, P.K.** (2020) ToxA-TSN1 interaction for spot blotch susceptibility in Indian wheat: an example of inverse gene-for-gene relationship. *Plant Disease* **104**, 71–81.
- Nimchuk, Z., Marois, E., Kjemtrup, S., Leister, R.T., Katagiri, F. and Dangl, J.L.** (2000) Eukaryotic fatty acylation drives plasma membrane targeting and enhances function of several type III effector proteins from *Pseudomonas syringae*. *Cell* **101**, 353–363.
- Nimchuk, Z., Rohmer, L., Chang, J.H. and Dangl, J.L.** (2001) Knowing the dancer from the dance: R-gene products and their interactions with other proteins from host and pathogen. *Current Opinion in Plant Biology* **4**, 288–294.
- Niño-Liu, D.O., Ronald, P.C. and Bogdanove, A.J.** (2006) *Xanthomonas oryzae* pathovars: model pathogens of a model crop. *Molecular Plant Pathology* **7**, 303–324.
- Noël, L., Thieme, F., Nennstiel, D. and Bonas, U.** (2001) cDNA-AFLP analysis unravels a genome-wide *hrpG*-regulon in the plant pathogen *Xanthomonas campestris* pv. *vesicatoria*. *Molecular Microbiology* **41**, 1271–1281.
- Nomura, K.** (2006) A bacterial virulence protein suppresses host innate immunity to cause plant disease. *Science* **313**, 220–223.
- Nowara, D., Schweizer, P., Gay, A., Lacomme, C., Shaw, J., Ridout, C., Douchkov, D., Hensel, G. and Kumlehn, J.** (2010) HIGS: Host-induced gene silencing in the obligate biotrophic fungal pathogen *Blumeria graminis*. *The Plant Cell* **22**, 3130–3141.
- Nürnberg, T. and Lipka, V.** (2005) Non-host resistance in plants: new insights into an old phenomenon. *Molecular Plant Pathology* **6**, 335–345.
- O’Connell, R.J., Thon, M.R., Hacquard, S., et al.** (2012) Lifestyle transitions in plant pathogenic *Colletotrichum* fungi deciphered by genome and transcriptome analyses. *Nature Genetics* **44**, 1060–1065.
- Oh, C.S. and Beer, S. V.** (2005) Molecular genetics of *Erwinia amylovora* involved in the development of fire blight. *FEMS Microbiology Letters* **253**, 185–192.
- Orth, K.** (2000) Disruption of Signaling by Yersinia Effector YopJ, a Ubiquitin-Like Protein Protease. *Science* **290**, 1594–1597.

- Orth, K.** (2002) Function of the *Yersinia* effector YopJ. *Current Opinion in Microbiology* **5**, 38–43.
- Park, C.H., Chen, S., Shirsekar, G., et al.** (2012) The *Magnaporthe oryzae* effector AvrPiz-t targets the RING E3 ubiquitin ligase APIP6 to suppress pathogen-associated molecular pattern-triggered immunity in rice. *The Plant Cell* **24**, 4748–4762.
- Paulus, J.K., Kourelis, J., Ramasubramanian, S., et al.** (2020) Extracellular proteolytic cascade in tomato activates immune protease Rcr3. *PNAS* **117**, 17409–17417.
- Pedley, K.F. and Martin, G.B.** (2003) Molecular basis of *Pto*-mediated resistance to bacterial speck disease in tomato. *Annual Review of Phytopathology* **41**, 215–243.
- Perez-Quintero, A.L. and Szurek, B.** (2019) A Decade Decoded: Spies and Hackers in the History of TAL Effectors Research. *Annual Review of Phytopathology* **57**, 459–481.
- Petit-Houdenot, Y. and Fudal, I.** (2017) Complex interactions between fungal avirulence genes and their corresponding plant resistance genes and consequences for disease resistance management. *Frontiers in Plant Science* **8**, 1072.
- Plett, J.M., Daguere, Y., Wittulsky, S., et al.** (2014) Effector MiSSP7 of the mutualistic fungus *Laccaria bicolor* stabilizes the *Populus* JAZ6 protein and represses jasmonic acid (JA) responsive genes. *PNAS* **111**, 8299–8304.
- Plissonneau, C., Daverdin, G., Ollivier, B., Blaise, F., Degrave, A., Fudal, I., Rouxel, T. and Balesdent, M.-H.** (2016) A game of hide and seek between avirulence genes *AvrLm4-7* and *AvrLm3* in *Leptosphaeria maculans*. *The New phytologist* **209**, 1613–24.
- Poueymiro, M. and Genin, S.** (2009) Secreted proteins from *Ralstonia solanacearum*: a hundred tricks to kill a plant. *Current Opinion in Microbiology* **12**, 44–52.
- Qiu, J.L., Fiil, B.K., Petersen, K., et al.** (2008) *Arabidopsis* MAP kinase 4 regulates gene expression through transcription factor release in the nucleus. *The EMBO Journal* **27**, 2214–2221.
- Raffaele, S. and Kamoun, S.** (2012) Genome evolution in filamentous plant pathogens: why bigger can be better. *Nature Reviews Microbiology* **10**, 417–430.
- Rooney, H.C.E.** (2005) *Cladosporium* Avr2 inhibits tomato Rcr3 protease required for Cf-2-dependent disease resistance. *Science* **308**, 1783–1786.
- Rouxel, T., Grandaubert, J., Hane, J.K., et al.** (2011) Effector diversification within compartments of the *Leptosphaeria maculans* genome affected by repeat-induced point mutations. *Nature Communications* **2**, 202.
- Rudd, J.J., Kanyuka, K., Hassani-Pak, K., et al.** (2015) Transcriptome and metabolite profiling of the infection cycle of *Zymoseptoria tritici* on wheat reveals a biphasic interaction with plant immunity involving differential pathogen chromosomal contributions and a variation on the hemibiotrophic lifestyle. *Plant Physiology* **167**, 1158–1185.
- Sain, M. de and Rep, M.** (2015) The role of pathogen-secreted proteins in fungal vascular wilt diseases. *International Journal of Molecular Sciences* **16**, 23970–23993.
- Saintenac, C., Lee, W.S., Cambon, F., et al.** (2018) Wheat receptor-kinase-like protein Stb6 controls gene-for-gene resistance to fungal pathogen *Zymoseptoria tritici*. *Nature Genetics* **50**, 368–374.
- Salanoubat, M., Genin, S., Artiguenave, F., et al.** (2002) Genome sequence of the plant pathogen *Ralstonia solanacearum*. *Nature* **415**, 497–502.
- Sarris, P.F., Cevik, V., Dagdas, G., Jones, J.D.G. and Krasileva, K. V** (2016) Comparative analysis of plant immune receptor architectures uncovers host proteins likely targeted by pathogens. *BMC Biology* **14**.
- Sarris, P.F., Duxbury, Z., Huh, S.U., et al.** (2015) A plant immune receptor detects pathogen effectors that target WRKY transcription factors. *Cell* **161**, 1089–1100.
- Saunders, D.G.O., Win, J., Cano, L.M., Szabo, L.J., Kamoun, S. and Raffaele, S.** (2012) Using hierarchical clustering of secreted protein families to classify and rank candidate effectors of rust fungi. *PLoS ONE* **7**.
- Saur, I.M.L., Bauer, S., Kracher, B., et al.** (2019) Multiple pairs of allelic MLA immune receptor-powdery mildew AVR effectors argue for a direct recognition mechanism. *eLife* **8**.
- Schornack, S., Huitema, E., Cano, L.M., et al.**

- (2009) Ten things to know about oomycete effectors. *Molecular Plant Pathology* **10**, 795–803.
- Schulze-Lefert, P. and Panstruga, R.** (2011) A molecular evolutionary concept connecting nonhost resistance, pathogen host range, and pathogen speciation. *Trends in Plant Science* **16**, 117–125.
- Selin, C., Kievit, T.R. de, Belmonte, M.F. and Fernando, W.G.D.** (2016) Elucidating the role of effectors in plant-fungal interactions: progress and challenges. *Frontiers in Microbiology* **7**, 600.
- Shan, L., He, P., Li, J., Heese, A., Peck, S.C., Nürnberger, T., Martin, G.B. and Sheen, J.** (2008) Bacterial effectors target the common signaling partner BAK1 to disrupt multiple MAMP receptor-signaling complexes and impede plant immunity. *Cell Host and Microbe* **4**, 17–27.
- Shao, F., Golstein, C., Ade, J., Stoutemyer, M., Dixon, J.E. and Innes, R.W.** (2003) Cleavage of Arabidopsis PBS1 by a bacterial type III effector. *Science* **301**, 1230–1233.
- Shen, Q.-H., Saijo, Y., Mauch, S., et al.** (2007) Nuclear activity of MLA immune receptors links isolate-specific and basal disease-resistance responses. *Science* **315**, 1098–1103.
- Soyer, J.L., Ghalid, M. El, Glaser, N., et al.** (2014) Epigenetic control of effector gene expression in the plant pathogenic fungus *Leptosphaeria maculans*. *PLoS Genetics* **10**, 1004227.
- Spanu, P.D.** (2012) The genomics of obligate (and nonobligate) biotrophs. *Annual Review of Phytopathology* **50**, 91–109.
- Spanu, P.D., Abbott, J.C., Amselem, J., et al.** (2010) Genome expansion and gene loss in powdery mildew fungi reveal tradeoffs in extreme parasitism. *Science* **330**, 1543–1546.
- Sperschneider, J., Catanzariti, A.M., Deboer, K., Petre, B., Gardiner, D.M., Singh, K.B., Dodds, P.N. and Taylor, J.M.** (2017) LOCALIZER: Subcellular localization prediction of both plant and effector proteins in the plant cell. *Scientific Reports* **7**.
- Sperschneider, J., Dodds, P.N., Gardiner, D.M., Singh, K.B. and Taylor, J.M.** (2018a) Improved prediction of fungal effector proteins from secretomes with EffectorP 2.0. *Molecular Plant Pathology* **19**, 2094–2110.
- Sperschneider, J., Dodds, P.N., Singh, K.B. and Taylor, J.M.** (2018b) ApoplastP: prediction of effectors and plant proteins in the apoplast using machine learning. *New Phytologist* **217**, 1764–1778.
- Sperschneider, J., Gardiner, D.M., Dodds, P.N., Tini, F., Covarelli, L., Singh, K.B., Manners, J.M. and Taylor, J.M.** (2016) EffectorP: predicting fungal effector proteins from secretomes using machine learning. *New Phytologist* **210**, 743–761.
- Staskawicz, B.J., Mudgett, M.B., Dangl, J.L. and Galan, J.E.** (2001) Common and contrasting themes of plant and animal diseases. *Science* **292**, 2285–2289.
- Stergiopoulos, I., Collemare, J., Mehrabi, R. and de Wit, P.J.G.M.** (2013) Phytotoxic secondary metabolites and peptides produced by plant pathogenic Dothideomycete fungi. *FEMS Microbiology Reviews* **37**, 67–93.
- Stergiopoulos, I. and de Wit, P.J.G.M.** (2009) Fungal effector proteins. *Annual Review of Phytopathology* **47**, 233–263.
- Steuernagel, B., Witek, K., Krattinger, S.G., et al.** (2020) The NLR-annotator tool enables annotation of the intracellular immune receptor repertoire. *Plant Physiology* **183**, 468–482.
- Stotz, H.U., Mitroussia, G.K., de Wit, P.J.G.M. and Fitt, B.D.L.** (2014) Effector-triggered defence against apoplastic fungal pathogens. *Trends in Plant Science* **19**, 491–500.
- Tang, D., Wang, G. and Zhou, J.M.** (2017) Receptor kinases in plant-pathogen interactions: more than pattern recognition. *The Plant Cell* **29**, 618–637.
- Thieme, F., Koebnik, R., Bekel, T., et al.** (2005) Insights into genome plasticity and pathogenicity of the plant pathogenic bacterium *Xanthomonas campestris* pv. *vesicatoria* revealed by the complete genome sequence. *Journal of Bacteriology* **187**, 7254–7266.
- Thomma, B.P., Nurnberger, T. and Joosten, M.H.** (2011) Of PAMPs and effectors: The blurred PTI-ETI dichotomy. *The Plant Cell* **23**, 4–15.
- Thordal-Christensen, H.** (2020) A holistic

view on plant effector-triggered immunity presented as an iceberg model. *Cellular and Molecular Life Sciences* **77**, 3963–3976.

**Tian, D., Wang, J., Zeng, X., et al.** (2014) The rice TAL effector-dependent resistance protein XA10 triggers cell death and calcium depletion in the endoplasmic reticulum. *The Plant Cell* **26**, 497–515.

**Tian, W., Hou, C., Ren, Z., et al.** (2019) A calmodulin-gated calcium channel links pathogen patterns to plant immunity. *Nature* **572**, 131–135.

**Timilsina, S., Potnis, N., Newberry, E.A., Liyanapathirana, P., Iruegas-Bocardo, F., White, F.F., Goss, E.M. and Jones, J.B.** (2020) *Xanthomonas* diversity, virulence and plant–pathogen interactions. *Nature Reviews Microbiology* **18**, 415–427.

**Toruño, T.Y., Stergiopoulos, I. and Coaker, G.** (2016) Plant–pathogen effectors: cellular probes interfering with plant defenses in spatial and temporal manners. *Annual Review of Phytopathology* **54**, 419–441.

**Tsiamis, G., Mansfield, J.W., Hockenhull, R., et al.** (2000) Cultivar-specific avirulence and virulence functions assigned to *avrPphF* in *Pseudomonas syringae* pv. *phaseolicola*, the cause of bean halo-blight disease. *The EMBO Journal* **19**, 3204–3214.

**Tsuda, K. and Katagiri, F.** (2010) Comparing signaling mechanisms engaged in pattern-triggered and effector-triggered immunity. *Current Opinion in Plant Biology* **13**, 459–465.

**Tsuge, T., Harimoto, Y., Akimitsu, K., Ohtani, K., Kodama, M., Akagi, Y., Egusa, M., Yamamoto, M. and Otani, H.** (2013) Host-selective toxins produced by the plant pathogenic fungus *Alternaria alternata*. *FEMS Microbiology Reviews* **37**, 44–66.

**Tyler, B.M., Tripathy, S., Zhang, X., et al.** (2006) *Phytophthora* genome sequences uncover evolutionary origins and mechanisms of pathogenesis. *Science* **313**, 1261–1266.

**Urban, M., Cuzick, A., Rutherford, K., et al.** (2017) PHI-base: a new interface and further additions for the multi-species pathogen–host interactions database. *Nucleic Acids Research* **45**, D604–D610.

**Urban, M., Cuzick, A., Seager, J., et al.** (2020)

PHI-base: The pathogen–host interactions database. *Nucleic Acids Research* **48**, D613–D620.

**Urban, M., Pant, R., Raghunath, A., Irvine, A.G., Pedro, H. and Hammond-Kosack, K.E.** (2015) The pathogen–host interactions database (PHI-base): additions and future developments. *Nucleic Acids Research* **43**, D645–D655.

**van Der Hoorn, R.A.L. and Kamoun, S.** (2008) From guard to decoy: a new model for perception of plant pathogen effectors. *The Plant Cell* **20**, 2009–2017.

**van't Slot, K.A.E. and Knogge, W.** (2002) A dual role for microbial pathogen–derived effector proteins in plant disease and resistance. *Critical Reviews in Plant Sciences* **21**, 229–271.

**Velásquez, A.C., Castroverde, C.D.M. and He, S.Y.** (2018) Plant–pathogen warfare under changing climate conditions. *Current Biology* **28**, R619–R634.

**Vincent, D., Rafiqi, M. and Job, D.** (2020) The Multiple Facets of Plant–Fungal Interactions Revealed Through Plant and Fungal Secretomics. *Frontiers in Plant Science* **10**.

**Vleeshouwers, V.G.A.A., Raffaele, S., Vossen, J.H., et al.** (2011) Understanding and exploiting late blight resistance in the age of effectors. *Annual Review of Phytopathology* **49**, 507–531.

**Vleeshouwers, V.G.A.A., Rietman, H., Krenek, P., et al.** (2008) Effector genomics accelerates discovery and functional profiling of potato disease resistance and *Phytophthora infestans* avirulence genes. *PLoS ONE* **3**, e2875.

**Vossen, E.A.G. van Der, Voort, J.N.A.M.R. van Der, Kanyuka, K., Bendahmane, A., Sandbrink, H., Baulcombe, D.C., Bakker, J., Stiekema, W.J. and Klein-Lankhorst, R.M.** (2000) Homologues of a single resistance-gene cluster in potato confer resistance to distinct pathogens: a virus and a nematode. *The Plant Journal* **23**, 567–576.

**Wang, Jizong, Hu, M., Wang, Jia, et al.** (2019a) Reconstitution and structure of a plant NLR resistosome conferring immunity. *Science* **364**, eaav5870.

**Wang, Jizong, Wang, Jia, Hu, M., et al.** (2019b) Ligand-triggered allosteric ADP release primes a plant NLR complex. *Science* **364**, eaav5868.

- Wang, M., Weiberg, A., Lin, F.M., Thomma, B.P.H.J., Huang, H. Da and Jin, H.** (2016) Bidirectional cross-kingdom RNAi and fungal uptake of external RNAs confer plant protection. *Nature Plants* **2**, 16151.
- Wang, Q., Han, C., Ferreira, A.O., et al.** (2011) Transcriptional programming and functional interactions within the *Phytophthora sojae* RXLR effector repertoire. *The Plant Cell* **23**, 2064–2086.
- Wang, W., Feng, B., Zhou, J.M. and Tang, D.** (2020) Plant immune signaling: advancing on two frontiers. *Journal of Integrative Plant Biology* **62**, 2–24.
- Weiberg, A., Wang, M., Lin, F.-M., Zhao, H., Zhang, Z., Kaloshian, I., Huang, H.-D. and Jin, H.** (2013) Fungal small RNAs suppress plant immunity by hijacking host RNA interference pathways. *Science* **342**, 118–123.
- Weßling, R., Epple, P., Altmann, S., et al.** (2014) Convergent targeting of a common host protein-network by pathogen effectors from three kingdoms of life. *Cell Host and Microbe* **16**, 364–375.
- Whisson, S.C., Boevink, P.C., Moleleki, L., et al.** (2007) A translocation signal for delivery of oomycete effector proteins into host plant cells. *Nature* **450**, 115–118.
- Williams, S.J., Sohn, K.H., Wan, L., et al.** (2014) Structural basis for assembly and function of a heterodimeric plant immune receptor. *Science* **344**, 299–303.
- Winstanley, C. and Hart, C.A.** (2001) Type III secretion systems and pathogenicity islands. *Journal of Medical Microbiology* **50**, 116–126.
- Wu, L., Chen, H., Curtis, C. and Fu, Z.Q.** (2014) Go in for the kill: how plants deploy effector-triggered immunity to combat pathogens. *Virulence* **5**, 710–721.
- Wyatt, N.A., Richards, J.K., Brueggeman, R.S. and Friesen, T.L.** (2020) A comparative genomic analysis of the barley pathogen *Pyrenophora teres* f. *teres* identifies subtelomeric regions as drivers of virulence. *Molecular Plant-Microbe Interactions* **33**, 173–188.
- Xia, Y.** (2004) Proteases in pathogenesis and plant defence. *Cellular Microbiology* **6**, 905–913.
- Xiang, T., Zong, N., Zou, Y., et al.** (2008) *Pseudomonas syringae* effector AvrPto blocks innate immunity by targeting receptor kinases. *Current Biology* **18**, 74–80.
- Xin, X.-F., Nomura, K., Aung, K., Velásquez, A.C., Yao, J., Boutrot, F., Chang, J.H., Zipfel, C. and He, S.Y.** (2016) Bacteria establish an aqueous living space in plants crucial for virulence. *Nature* **539**, 524–529.
- Xin, X.F. and He, S.Y.** (2013) *Pseudomonas syringae* pv. *tomato* DC3000: a model pathogen for probing disease susceptibility and hormone signaling in plants. *Annual Review of Phytopathology* **51**, 473–498.
- Xin, X.F., Kvitko, B. and He, S.Y.** (2018) *Pseudomonas syringae*: what it takes to be a pathogen. *Nature Reviews Microbiology* **16**, 316–328.
- Yang, B., Sugio, A. and White, F.F.** (2006) *Os8N3* is a host disease-susceptibility gene for bacterial blight of rice. *PNAS* **103**, 10503–10508.
- Yang, J., Duan, G., Li, C., Liu, L., Han, G., Zhang, Y. and Wang, C.** (2019) The crosstalks between jasmonic acid and other plant hormone signaling highlight the involvement of jasmonic acid as a core component in plant response to biotic and abiotic stresses. *Frontiers in Plant Science* **10**, 1349.
- Yoshida, Kentaro, Saitoh, H., Fujisawa, S., et al.** (2009) Association genetics reveals three novel avirulence genes from the rice blast fungal pathogen *Magnaporthe oryzae*. *The Plant Cell* **21**, 1573–1591.
- Zhang, J., Li, W., Xiang, T., et al.** (2010) Receptor-like cytoplasmic kinases integrate signaling from multiple plant immune receptors and are targeted by a *Pseudomonas syringae* effector. *Cell Host and Microbe* **7**, 290–301.
- Zhang, J., Shao, F., Li, Y., et al.** (2007) A *Pseudomonas syringae* effector inactivates MAPKs to suppress PAMP-induced immunity in plants. *Cell Host and Microbe* **1**, 175–185.
- Zhang, Y. and Li, X.** (2019) Salicylic acid: biosynthesis, perception, and contributions to plant immunity. *Current Opinion in Plant Biology* **50**, 29–36.
- Zhong, Z., Marcel, T.C., Hartmann, F.E., et al.** (2017) A small secreted protein in

*Zymoseptoria tritici* is responsible for avirulence on wheat cultivars carrying the *Stb6* resistance gene. *New Phytologist* **214**, 619–631.

**Zipfel, C.** (2009) Early molecular events in PAMP-triggered immunity. *Current Opinion in Plant Biology* **12**, 414–420.

**Zvereva, A.S. and Poogin, M.M.** (2012) Silencing and innate immunity in plant defense against viral and non-viral pathogens. *Viruses* **4**, 2578–2597.