Effector Proteins in Plant–Microbe Interaction

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Oomycete and fungal interactions with plants can be neutral, symbiotic or pathogenic with different impact on plant health and fitness. Both fungi and oomycetes can generate so-called effector proteins in order to successfully colonize the host plant. These proteins modify stress pathways, developmental processes and the innate immune system to the microbes’ benefit, with a very different outcome for the plant. Investigating the biological and functional roles of effectors during plant–microbe interactions are accessible through bioinformatics and experimental approaches which can broaden our knowledge about structural biology, sequence motif and domain knowledge of effector proteins from filamentous microbes.

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1. All Lifestyles of Filamentous Microbes Use Effector Proteins to Establish Colonization

Oomycetes and fungi are filamentous eukaryotic organisms. In contrast to fungi that contain species of symbiotic and pathogenic lifestyle, oomycete species are mostly limited to a pathogenic lifestyle. Nevertheless, some oomycetes of the *Pythium* class are considered beneficial to plants and are in use as bio-control organisms. Examples are *Pythium olingandrum* and *Pythium periplocum*, which are known to be mycoparasites that antagonizes fungal plant pathogens [1][2].

Until recently, effector proteins have been studied mainly in context with pathogenic fungi and oomycete species. Nevertheless, recent advances have shown that symbiotic organisms such as endophytes and mutualistic microorganisms also secrete effector proteins [3][4] (**Table 1**). According to Rovenich *et al*., 2014 effector proteins contribute to niche colonization and most likely to microbial competition [5]. In mutualistic connections, identical to pathogenic invasions, the microorganism is identified by the plant’s recognition system and needs solutions to evade the plant’s immune strategies to maintain a mutual beneficial connection [6]. Apoplastic secreted effectors, such as secreted proteins (SP’s), β-glucan, [7] or RiSLM that binds to chitin [8], are known to play a role in early establishment of mycorrhiza–plant interaction. Recently, effectors translocated into the host’s cytosol originating from symbiotic fungi become more and more the focal point of ongoing research (**Table 1**) and we start to understand that oomycetes and fungi of all lifestyles use effector proteins to establish an interaction with the host plant [9][10]. This includes translocated effector proteins containing RxLR motifs and crinklers (CRN’s), which will be reviewed in more detail in the next chapter. Effectors are likely to be used by plant growth promoting fungi to limit the activation of the plant's immune system by decreasing the amount of specific MAMPs recognized by the plant's PRRs. However, many questions remain unresolved about the molecular mechanisms governing mycorrhiza–plant interaction—with one being how they can establish interaction with such a broad host spectrum. Future research in this field will need to establish collaborative approaches, combining ecology (bigger picture), molecular interaction studies of microbe and host on the cellular level (organismal and cell level) and protein biochemistry approaches (molecular level) to resolve these important questions.

Table 1. List of effector proteins identified for beneficial fungi, their host species and biological function.

Effector Protein	Fungal Species	Host Species	Characterized Biological Function	References
SP7	*Glomus intraradices*	*Medicago truncatula*	Interacts with JA/ethylene inducible ERF19 transcription factor and down regulates PTI	[8]
Lysm effector Tal6	*Trichoderma atroviride*	*Arabidopsis thaliana*	Binds to chitin of plant's cell wall and protects the fungi hyphae from plant's chitinase favoring *Trichoderma* interaction and increasing mycoparasitic effect	[11]
Lysm effector RiSLM	*Rhizophagus irregularis*	*Medicago truncatula*	Binds to chitin and chitooligosaccharides of plant's cell wall and interferes with chitin-triggered immune response protecting hyphae from plant's chitinase and enabling symbiotic reactions	[12]
MiSSP7	*Laccaria bicolor*	*Populus trichocarpa*	Suppresses JA-mediated immune response by preventing JA-dependent degradation of PtJAZ6, a negative regulator of JA-induced genes	[13]
RiCRN1	*Rhizophagus irregularis*	*Medicago truncatula* *Nicotiana benthamiana*	Establishes a functional AM symbiosis and Arbuscules phosphate transporter gene-MtP4-expression	[14]
Strigolactone induced secreted protein 1 (SIS1)	*Rhizophagus irregularis*	*Medicago truncatula*	Essential for AM symbiosis, gene silencing causes suppression of colonization and production of stunted arbuscules	[15]
RP8598 and RP23081	*Rhizophagus proliferus*	*Medicago truncatula* *Nicotiana benthamiana*	Interacts with JA/ethylene inducible ERF19 transcription factor and down regulates PTI	[16]

Effector Protein	Fungal Species	Host Species	Characterized Biological Function	References
		Allium schoenoprasum		
Nuclear localizing effector (RiNLE1)	*Rhizophagus irregularis*	*Medicago truncatula*	Interferes with mono-ubiquitination of 2B histone and decreases the expression of defense-related genes while enhancing AM colonization process	[17]
Hydrophobin-like OmSSP1	*Ericoid mycorrhiza*	*Vaccinium myrtillu*	Mutants are unable to colonize *V. myrtillu* roots and OmSSP1 may strengthen the attachment of the fungi to the root protecting the hyphae from plant's immune system	[18]
PIIN_08944	*Piriformospora indica*	*Arabidopsis thaliana*	Mutants show delayed colonization and PIIN_08944 expression reveals impairment of SA-defense pathway and reduced expression of flg-22	[19]
Did1 (PIIN_05872)	*Piriformospora indica*	-	Interferes with iron-mediated defense response which plays an important role in ROS generation	[20]

2. Effector Proteins of Filamentous Microbes

Most of our knowledge on effector protein function, motifs, domains and structures derives from pathogenic species rather than beneficial and symbiotic species. Compared to oomycetes, identification of motifs and domains involved in delivering cytoplasmic effectors has been particularly challenging for fungi due to less clear sequence conservation. Nevertheless, fungi and oomycetes have been shown to translocate RxLR/RxLR-like effectors and CRNs into the host cell [10]. Oomycetes contain a particularly high number of RxLR effector proteins, which are likely to be secreted via the haustoria during plant–oomycete interaction [21]. RxLR effector proteins are composed of an N-terminal signal peptide responsible for effector secretion, followed by a highly conserved RxLR (Arg-Xaa-Leu-Arg) motif. This motif has been proposed to be in charge of the translocation of the effector protein into the host cell [22][23]. More recently, it has been hypothesized that the RxLR motif is cleaved before translocation into the plant cell and only a mature effector protein containing the C-terminal effector domain is delivered into the host cell [24]. The RxLR motif is often followed by a downstream (D)EER motif (Glu-Glu-Arg) located within 40 AA after the signal peptide, which is also linked to the effector translocation [22][25]. The effector proteins of *Phytophtora* species such as *P. infestans* (Avr3a and PexRD2), *P. capsici* (Avr3a11) and downy mildews such as *Hyaloperonospora arabidopsis* (Hpa; Atr1) also contain a WY or WL motif, which forms an alpha-helix [26]. The motif, identified by analyzing the crystal structure of PexRD2, is comprised of two hydrophobic residues buried inside the protein core that contribute to interactions with host target proteins. WY-containing effectors and their structures have been recently reviewed in detail by Mukhi, *et al*. 2020 [26]. Other RxLR effectors have been shown to interact with their targets in the cellular endomembrane system, including *P. infestans's* effector protein Pi03912 and *Bremia Lactucae's* effector proteins BLR05 and BLR09 that interact with NAC transcription factors located in endoplasmic reticulum [27][28].

Translocated CRN effector proteins are distributed in nearly all pathogenic oomycetes and have been shown to be translocated by fungi of pathogenic and beneficial lifestyle. CRN's share two conserved motifs in their N-terminal region, the LxLFLAK (Leu-Xaa-Leu-Phe-Leu-Ala-Lys) motif and the HVLVVVP (His-Val-Leu-Val-Val-Val-Pro) motif. The LxLFLAK motif is, comparable to the RxLR, associated with the translocation of the effector in to the host cell [29][30]. CRNs, initially identified through their ability to cause crinkling and necrosis upon expression in plant tissue are not typified by this characteristic. In fact, expression of CRNs leads to cell death only in a select few cases. So far, CRNs are less well studied than RxLRs [29][30].

Fungal species have further effector proteins with various effector motifs including but not restricted to, lysin (LysM), DELD, RSIDEDLD, RGD and the EAR (ethylene-responsive element binding factor-associated amphiphilic repression) motif.

Furthermore, most MAX effectors (Magnaporthe AVRs and ToxB- like effectors) so far have been identified to be translocated, contributing to the virulence of pathogenic fungi. These effectors contain a β-sandwich fold, showing similarities to the apoplast secreted *Pyrenapohora tritici-repentis* ToxB. This group of effectors have at least one disulfide bond with variable AA on their protein surface, which mediates their target interaction [31][32]. RALPHs (Rnase-like proteins expressed in haustoria) are another group of fungal translocated effectors discovered in pathogenic fungi, including the *Blumeria graminis* effector BEC1054. RALPHs block the function of the host's ribosome, inactivating proteins and suppress the host cell death [33]. The flax rust effector AvrP is considered an HESP (haustorial expressed secreted protein) that does not contain an RxLR and the translocation mechanisms in the host cell is not clear to date. Nevertheless, it is one of the few effector proteins with a known structure. It contains Zn-finger like motifs and three Zn- binding sites. The Zn-finger motifs are necessary for maintaining the integrity of the effector protein and cell death activity [34]. Other structurally resolved fungal and oomycete effector proteins are presented in **Table 2**.

Table 2. Summary of structurally resolved effector proteins available in PDB-deposited structures [35].

Effector Protein	Organism	Date of Release	Method	PDB Entry	Family
		Fungi			
Ecp11-1	*Passalora fulva*	4 August 2021	X-ray	6ZUS	LARS
APikL2A	*Magnaporthe oryzae*	24 March 2021	X-ray	7NLJ	MAX
APikL2F	*Magnaporthe oryzae*	24 March 2021	X-ray	7NMM	MAX
AVR-PikD	*Pyricularia oryzae*	17 Februrary	X-ray	7BNT	MAX

Effector Protein	Organism	Date of Release	Method	PDB Entry	Family
		2021			
AVR-PikF	*Pyricularia oryzae*	3 February 2021	X-ray	7B1I	MAX
AVR-PikC	*Pyricularia oryzae*	3 February 2021	X-ray	7A8X	MAX
SnTox3	*Parastagonospora nodorum*	4 November 2020	X-ray	6WES	MAX
Zt-KP6-1	*Zymoseptoria tritici*	4 March 2020	X-ray	6QPK	LysM
MLP124017	*Melampsora larici-populina*	18 December 2019	Solution NMR	6SGO	Cys knot, NTF2-like fold
Mg1LysM	*Zymoseptoria tritici*	16 October 2019	X-ray	6Q40	LysM
AVR-Pia	*Pyricularia oryzae*	10 July 2019	X-ray	6Q76	MAX
AvrPib	*Pyricularia oryzae*	5 September 2018	X-ray	5Z1V	MAX
MlpP4.1	*Melampsora larici-populina*	22 August 2018	Solution NMR	6H0I	Cys knot, NTF2-like fold
Avr4	*Passalora fulva*	22 August 2018	X-ray	6BN0	Chitin-binding
PIIN_05872	*Piriformospora indica*	2 May 2018	X-ray	5LOS	DELD
BEC1054	*Blumeria hordei*	20 June 2018	X-ray	6FMB	RALPH
AVR-PikE	*Pyricularia oryzae*	13 June 2018	X-ray	6G11	MAX
AVR-PikA	*Pyricularia oryzae*	3 June 2018	X-ray	6FUD	MAX
AvrP	*Melampsora lini*	30 August 2017	X-ray	5VJJ	Zn-binding
Avr2	*Fusarium oxysporum*	16 August 2017	X-ray	5OD4	ToxA/TRAF
PevD1	*Verticillium dahliae*	5 July 2017	X-ray	5XMZ	C2-like
Avr4	*Pseudocercospora fuligena*	29 June 2017	X-ray	4Z4A	Chitin-binding
AVR1-CO39	*Magnaporthe oryzae*	14 October 2015	Solution NMR	2MYV	MAX

Effector Protein	**Organism**	**Date of Release**	**Method**	**PDB Entry**	**Family**
Prp5	*Saccharomyces cerevisiae*	11 December 2013	X-ray	4LK2	DEAD-box
AvrLm4-7	*Leptosphaeria maculans*	11 December 2013	X-ray	2OPC	LARS
AvrM	*Melampsora lini*	16 October 2013	X-ray	4BJM	RXLR-like
AvrM-A	*Melampsora lini*	16 October 2013	X-ray	4BJN	RXLR-like
Ecp6	*Passalora fulva*	17 July 2013	X-ray	4B8V	LARS
AvrPiz-t	*Pyricularia oryzae*	12 September 2012	Solution NMR	2LW6	MAX
AvrL567-D	*Melampsora lini*	30 October 2007	X-ray	2QVT	RXLR-like
AvrL567-A	*Melampsora lini*	6 March 2007	X-ray	2OPC	RXLR-like
		Oomycetes			
Avr1d	*Phytophthora sojae*	17 March 2021	X-ray	7C96	RXLR
PsAvh240	*Phytophthora sojae*	6 February 2019	X-ray	6J8L	RXLR/WY
SFI3	*Phytophthora infestans*	5 December 2018	X-ray	6GU1	RXLR/WY
PcRXLR12	*Phytophthora capsici*	15 August 2018	X-ray	5ZC3	RXLR/WY
PSR2	*Phytophthora sojae*	16 August 2017	X-ray	5GNC	RXLR/WY
Avr3a	*Phytophthora infestans*	11 January 2017	Solution NMR	2NAR	RXLR/WY
PexRD54	*Phytophthora infestans*	3 August 2016	X-ray	5L7S	RXLR/WY
ATR13	*Hyaloperonospora parasitica*	18 January 2012	Solution NMR	2LAI	RXLR
AVR3a4	*Phytophthora capsici*	3 August 2011	Solution NMR	2LC2	RXLR
PexRD2	*Phytophthora infestans*	3 August 2011	X-ray	3ZRG	RXLR/WY

Effector Protein	Organism	Date of Release	Method	PDB Entry	Family
Avr3a11	*Phytophthora capsici*	3 August 2011	X-ray	3ZR8	RXLR/WY
ATR1	*Hyaloperonospora parasitica*	20 July 2011	X-ray	3RMR	RXLR/WY

Interestingly, even though filamentous effector proteins have been studied and defined extensively with genetic and molecular biology approaches, available protein structures are very limited (**Table 2**). Structural information is very valuable for elucidating the molecular mechanisms behind biological and biochemical functions. It is complimentary to genetic and molecular biology methods, giving a molecular explanation for observations seen in these studies and seeding hypothesis for further of these studies. In addition, the fundamental molecular level insights ultimately help link genome and sequence information to function and aiding improvements in effectome prediction. Considering the importance of effector molecules during infection processes of plants, but also of humans and animals, it is surprising that effector proteins have not been studied more intensively. This in part may be due to experimental challenges with structure elucidation, including the membrane-associated nature of many effector proteins and the potentially dynamic nature of their different molecular interactions along the infection/colonization cycle. Nonetheless, structures and their detailed molecular function, are a significant knowledge gap and that is true for oomycete as much as for fungal effectors.

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