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Secretomics of Plant-Fungus Associations: More Secrets to Unravel

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The versatility of fungi allows them to associate with plants in many ways. When interacting with a live organism, a fungus will invade its plant host and manipulate its metabolisms either detrimentally or beneficially, depending on whether the fungus is a pathogen or a symbiote. Many crop diseases originate from fungal pathogen attacks targeting above and belowground plant organs, which cause massive yield losses. The majority of tree species develop symbiotic relationships with Arbuscular Mycorrhizal (AM) fungi, widening their root network, thus enhancing nutrient absorption and growth. These beneficial soil fungi are also present in agricultural crops, increasing tolerance against unfavourable biotic or abiotic conditions thereby positively impacting yields. When growing off dead plant tissue, fungi contribute to the general carbon cycling. Saprophytic fungi such as the white-rot basidiomycetes use lignocellulosic compounds for their own development as they are able to biochemically break it down.

Secretomics describes the global study of proteins that are secreted by a cell, a tissue or an organism [1], and has recently emerged as a field for which interest is rapidly growing. The term secretome was first coined by Tjalsma et al. [2] at the turn of the millennium and was defined to comprise not only the native secreted proteins but the components of machineries for protein secretion as well. Greenbaum et al. [3] narrowed down the definition of secretome to "the population of gene products that are secreted from the cell". More recently, Agrawal et al. [4] refined secretome as "the global group of secreted proteins into the extracellular space by a cell, tissue, cell, organ or organism at any given time and conditions through known and unknown secretory mechanisms involving constitutive and regulated secretory organelles". Two secretory pathways have been described in fungi: i) the canonical pathway through which proteins bearing a N-terminal peptide signal can traverse the endoplasmic reticulum and Golgi apparatus, and ii) the unconventional pathway for proteins lacking a peptide signal [5]. To this day, more than a hundred secretomic studies have been published on all taxa and the number of publications is increasing steadily (Figure 1). Noteworthy, the number of publications investigating secretomes of fungal species interacting or associating with plants represents only a small fraction of total secretomic studies (Figure 1). Secretory pathways have been described in various species of fungi and/or their plant hosts, yet the functions of proteins secreted outside the cell remain to be fully grasped.

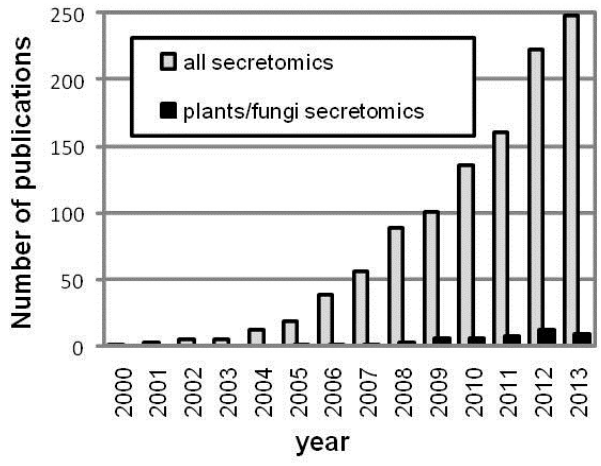

Figure 1: Number of publications listed in PubMed per year using "(((secretome[Title/Abstract]) OR secretomic[Title/Abstract]) OR secretomics[Title/Abstract])" keyword for all secretomics studies in grey, and "((((secretome[Title/Abstract]) OR secretomic[Title/Abstract]) OR secretomics[Title/Abstract]) AND fung*[Title/Abstract]) AND plant[Title/Abstract]" keyword for plant/fungi secretomics in black. Searches performed on 30 October 2013.

Deciphering secretomes became a crucial biological question when an increasing body of evidence indicated that secreted proteins were the main effectors initiating interactions, whether of pathogenic or symbiotic nature, between fungi and their plant hosts (reviewed in [6] and [7]). Moreover, the particular activities of some secreted enzymes allow saprophytic fungi to live off dead plant mater [8]. Secretomics may help to contribute to the global food security and to the ecosystem sustainability by addressing issues in i) plant biosecurity, with the design of crops resistant to pathogen fungi [9], ii) crop yield enhancement, for example driven by AM fungi helping plant hosts utilise phosphate from the soil hence increase biomass [10], and iii) renewable energy, through the identification of fungal enzymes able to augment the bio-conversion of plant lignocellulosic materials for the production of second generation biofuels that do not compete with food production [8,11].

Several technical challenges are restricting our understanding of the molecular factors driving the interaction between fungi and their plant hosts.

The way the fungi are cultured, with or without its natural host, will consequently generate different secretomic patterns. The great majority of the studies are performed using culture media containing synthetic carbon sources and sometimes plant-based elicitors from which fungal secreted proteins are recovered and identified by mass spectrometry (MS). As informative as a list of secreted protein identities obtained from such *in vitro* systems can be in terms of general secretory mechanisms, it does not genuinely reflect the secretomic signature that would have occurred *in planta*. Furthermore this signature will be highly dependent upon the culture media used (e.g. [12,13]). Finally

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the plant response to the invasion of fungal secreted proteins is not being explored in such experimental designs.

Tackling *in vivo* studies of plant-fungal interactions is much more relevant, particularly because obligate biotrophes can then be considered, yet much more challenging. The hurdles are i) the recovery of secreted proteins from infected plant tissues (e.g. plant apoplastic fluids), ii) the MS-based analytical workflow which must follow several separation steps in order to identify low abundant proteins, and iii) the searched protein databases which might not include sequences from the organisms studied.

The identification of secreted protein strongly relies on protein databases that need to be accurately predicted from gene models based on protein domain knowledge (example of secreted protein databases for fungi [14] and plants [15]). Algorithms such as SignalP, TargetP or SecretomeP can putatively sort successfully identified proteins into canonical and unconventional secretory pathways.

The completion of several genome sequencing projects in various species is a promising step towards unravelling genome organization and gene function. It is therefore possible to predict *in silico* all the proteins potentially secreted by an organism and, afterward, experimentally observe their presence, thereby validating gene models. These exhaustive genomic sequencing programs pave the road for comparative secretomics. It remains that the genetic differences occurring between cultivars or strains may still decrease the ability to efficiently identify secreted proteins. Scientists now face the overwhelming task of designing relevant *in vivo* experiments endeavoured at identifying the secretomes underpinning plant-fungal associations.

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