Introduction: Keylevels of Biocommunication in Fungi

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Abstract In contrast to former opinions, communicative acts are not restricted only to information exchange between a sender and a receiver, but designate a variety of social interactions mediated by signals according to syntactic (combinatorial), pragmatic (context dependent) and semantic (content-specific) rules. On one side, development and growth of fungal organisms depends upon successful communication processes within, and between, cells of fungal organisms. However, on the other side, sign mediated interactions are necessary to coordinate behaviour with the same, or related, fungal species and with non-related organisms such as bacteria, plants and animals. In order to generate an appropriate response behaviour, fungal organisms must be able to sense, interpret and memorise important indices from the abiotic environment and adapt to them appropriately. However, these communication and interpretation processes can also fail. In such cases the overall consequences could be disease-causing, or even lethal. Interestingly, certain rules of fungal communication are very similar to those of animals, while others more closely resemble those of plants.

1 Introduction

Currently it is estimated that there are at least 1.5 million fungal species, out of which about 300,000 are described in the scientific literature. It is estimated that fungi account for at least one-fourth of the global biomass. On an evolutionary time scale, the kingdom of fungi emerged approx. 300 million years after the

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appearance of the first animal species, although they descended from a common ancestor (Lang et al. 2002). In contrast to animal- and higher plant-life, mono-cellular representatives are fairly common among fungi, i.e., fungi are by no means mere multicellular organisms. This fact can be easily and coherently reconstructed through the lineages of Protoctista – in that coordinated behavioural patterns are found among single-celled eukaryotes, which closely resemble those of single-celled fungi. However, there are significant differences in protoctist structure (i.e. flagellated) and those of fungi (i.e. non-flagellated). Obviously, fungi have evolved out of protoctists, such as red and joch-algae (Margulis and Schwartz 1988).

As with plants, fungi are sessile organisms that can live for extremely long periods or extend over large areas: one example (*Armillaria gallica*) has been found which covers as much as 15 ha with an age of approx. 1,500 years (Casselman 2007). Endolithic fungi from the Antarctic are known to be among the most long-lived organisms on this planet (Villarreal 2005). Another example (*Armillaria ostoyae*) covers 900 ha with an estimated age of 2,400 years (Casselman 2007).

Higher fungi are modular hyphal organisms in that they reproduce by clonation or are parasexual. They establish interlocking networks. Like red algae they merge their cytoplasms to form a multi-nucleated cell. This holistically-merged body is also found among some plants. A spore germinates under appropriate environmental conditions and is followed by the formation of filaments called hyphae. The latter are characterised by nuclear division and spore formation, which develop into mono-karyotic filaments (tip-growing). As in other tip-growing organisms, this process requires a high density of tip-localised mitochondria (Levina and Lew 2006).

The embryological stage, a characteristic of higher plants and animals, is completely absent in fungi (Margulis and Schwartz 1988; Ingold and Hudson 1993). Hyphae formation is also found among certain bacteria, such as Streptomyces and Actinomyces. When hyphae are tightly packed together into a mat we term this a mycelium. Each filament of hyphae has tubular side walls made mostly of chitin, a feature that is also common in Arthropoda. The cell walls that seem to separate adjacent cells in a filament are called septa – however, their porous nature does not really give them separating properties. The merger of filamental tips of the same or different species triggers a self/non-self identification process. This process is sign-mediated and results either in repulsion or attraction. If the latter occurs, merger into a dikaryotic mycelium takes place and initiates the formation of a fruiting body.

Most fungi are saprobes and decompose and feed on non-living organic matter. They secrete powerful enzymes that enable the cells to digest organic matter from the nearby environment outside their body, in turn breaking this down to smaller molecules that can be absorbed in a dissolved form (Jennings 1995). To deter potential predators, a number of complex and highly efficient deterring substances are produced by fungi (Margulis and Schwartz 1988).

Fungi are known to utilise a broad variety of symbiotic interactions with animals, plants and eukaryotic protozoa for both mutual benefit as well as parasitic and even lethal associations (Lott et al. 2006). They also settle on specific types of tissue. Fungal diseases are known to affect both plant and animal life, in some cases inducing devastating effects on and also in organisms (Humber 2008),
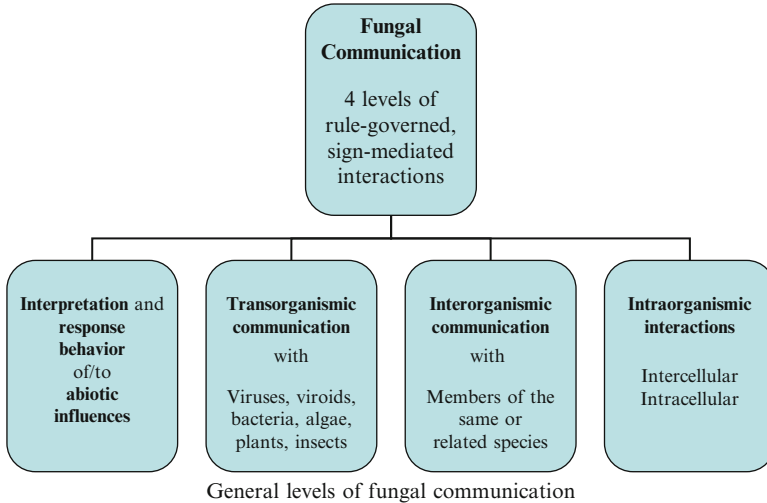
General levels of fungal communication

e.g. in agriculture. On the other hand, fungal activity has been actively exploited by humans for thousands of years in beer, wine, cheese and bread production. Since fungi are very simple organisms, sequencing and technical manipulation are relatively easy, making them ideal organisms for laboratory experiments (Weld et al. 2006), e.g. *Neurospora grassa* (Dunlap et al. 2004; FGSC 2011). Their application in the medical field as producers of various antibiotics is comprehensive and well-appreciated (e.g. penicillin).

Fungi communicate and therefore are able to organize and coordinate their behaviour. Coordination and organisation processes occur in all organismic kingdoms, and in fungi these are seen at the intraorganismic level e.g., during the formation of fruiting-bodies, between species of the same kind (inter-organismic) and between fungal and non-fungal organisms (trans-organismic). Without sign-mediated interactions, i.e. biocommunicative processes no coordination would occur (Witzany 2010). The semio-chemicals used are of biotic origin, in contrast to abiotic indicators that trigger the fungal organism to react in a specific manner.

2 Semiochemical Vocabulary

A variety of different primary signalling molecules have been shown to be involved in very different behavioural patterns such as filamentation, mating, growth, and pathogenicity (Adachi and Hamer 1998; Wang and Heitman 1999; Hemenway and Heitman 1999; Alspaugh et al. 2000; Borges-Walmsley and Walmsley 2000; Leeder et al. 2011). Behavioural coordination and the production of such

substances can only be achieved through interpretation of incoming information followed by appropriate response behaviour. Furthermore, there are numerous, less-investigated subunits that play an accompanying role as they are weaker in effect (Lengeler et al. 2000). Globally, these semio-chemicals serve to coordinate similar goals in different fungal species, yet species-variation among them cannot be ignored.

The roles of some of these signalling molecules are as follows: (i) Mitogen activated protein kinase signalling (MAPK) is involved in cell integrity, cell wall construction, pheromones/mating and osmo-regulation (Dohlman and Slessareva 2006; Yu et al. 2008), (ii) the cyclic adenosine monophosphate cAMP/PKA system is involved in fungal development and virulence, (iii) the RAS protein is involved in cross-talk between signalling cascades, (iv) calcium-calmodulin-calcineurin are involved in cell survival under oxidative stress, high temperature, membrane/cell wall perturbation and (v) rapamycin is involved in the control of cell growth and proliferation (Fernandes et al. 2005), (vi) aromatic alcohols tryptophol and pheny-lathylalcohol are used as quorum sensing molecules, (vii) a variety of volatiles (alcohols, esters, ketones, acids, lipids) and non-volatile inhibitory compounds (farnesol, H_2O_2) (Leeder et al. 2011).

To date, 400 different secondary metabolites have been documented. These are known to contain mycotoxins and are used both for defensive and aggressive behaviours.

3 Sensing, Interpretation, Memory and Coordination of Response to Abiotic Indices

Fungi differentiate varying contexts such as nutrient availability and nutrient fluxes, and react by organising appropriate intra-organismic communication. For example, in the case of carbon or nitrogen insufficiencies, the internal communication system of the organism responds adequately and is phenotypically expressed by a change in hyphal growth. To date, two specific signalling pathways have been found that coordinate such behaviour. These diverging pathways have also been documented among other fungi, including those that are pathogenic to plants and animals (Lengeler et al. 2000).

An abundance of nutrients for example, results in increased production of cAMP (Lee et al. 2003), which suppresses that of Ste11, itself a mating inhibitor. Such processes are sign-mediated processes that originate from cyclase-associated proteins (CAP) (Lengeler et al. 2000). Nutrient availability has to be communicated to induce cell growth (Dechant and Peter 2008).

As with animals and plants, seasonality is found in fungi as a part of the circadian rhythm (Dunlap et al. 2004; De Paula et al. 2008), e.g. light-regulated physiological processes that coordinate the internal fungal clock (Bell-Pederson et al. 1996). *Neurospora crassa*, for example, responds according to irradiance

patterns arising from the diurnal cycle. In such cases we can speak of a *Neurospora* chronotype (Dunlap et al. 2004; Tan et al. 2004). However, this responsiveness is not connected to photosynthetic activity, as this is only found in green algae, i.e. in the symbiotic association of lichens.

Fungi are capable to generate adaptive response behavioural patterns against environmental stress situations (Alonso-Monge et al. 2009) such as ROS reactive oxygen species (Moradas-Ferreira and Costa 2000) or in the case of varying osmotic conditions (Hohmann 2002; Santos and Shiozaki 2004; Krantz et al. 2006) which includes constant monitoring of cell wall integrity (Levin 2005).

Almost all fungi are saprobes and feed on dead organic matter. The excretion of extracellular digestive enzymes fragments larger biomolecules and makes them soluble, and more readily accessible for the fungal organism. This is particularly important for the digestion of cellulose, which is broken down by the enzymatic activity of exocellulase and endocellulase, and lignin (lignin peroxidase and manganese peroxidase). Enzymatic breakdown of organic matter yields simple sugars, amino acids, fatty acids and other smaller molecular components (Margulis and Schwartz 1988).

4 Remarkable Genomic Interactions Between Fungi and Viruses

Although prokaryotic ancestors of fungi were colonised mainly by large DNA viruses, in fungal populations they are missing but are commonly colonised by persistent double-stranded RNA viruses, single-stranded RNA viruses, double-stranded DNA viruses, retroviruses and even prions. They are the simplest organisms to be colonised by retroviruses, in the form of fungal retroposons. In contrast to all other eukaryotes, fungal mitochondria are infected by either double-stranded RNA or DNA viruses. Most fungus-infecting viruses are not pathogenic although they are associated with toxin genes that are pathologically dangerous, not for the infected host, but for non-infected fungal relatives and non-fungal organisms. This phenomenon has been used quite successfully by brewing industries, to protect useful yeasts from exogenous yeast genetic parasites by colonising the industrial yeast colonies with protective versions of killer viruses (Villarreal 2005). An example for mutually beneficial symbiosis is that of the black aspergillus species and dsRNA viruses, as in the case of mycovirus (van Diepeningen et al. 2006).

The interconnected filamentous fungi are a very attractive habitat for viruses because they allow rapid motility through the whole cellular network. Fungal networks also allow replacement of nuclei that are left behind in mitochondria. This may be an advantage if mitochondria are colonised by parasites, which is common (Villarreal 2005). It has been suggested that non-pathogenic viral colonisation of fungal mitochondria protects mtDNA from age-dependent degradation and is beneficial for the longevity of the fungal host. As a consequence, the growth radius of the fungal mats may increase up to tenfold (Villarreal 2005).

Interestingly, higher fungi lack repeat elements in DNA, whilst lower fungi can have up to 50% of their genomes colonised by repeat elements. Recent research shows that these repeat elements represent remnants of early retroviral genomic colonisation events. Fungi were the first organisms in evolutionary history to be colonised by viral RNA. This assumption is underlined by the presence of SINEs and LINEs. So far up to 15 SINE-families have been recognised (Whisson et al. 2005), a fact that supports the assumption that very early viral colonisation of the fungal genome must have taken place (Villarreal 2005; Rooney and Ward 2005).

Although plants and animals seem to be descendants of fungi, the relationship between fungi and viruses is different from virus–animal or virus–plant relationships (Villarreal 2005). The latter two lack linear plasmids, killer phenotypes, mitochondrial infections, distorted senescence and ubiquitous double-stranded RNA colonisation, which are all characteristics of the fungal virus–host relationship. This may be an indication of co-evolutionary interactions between fungi and viruses (Villarreal 2005).

Genomic studies show that most methylated regions of *Neurospora crassa* are derived from repeat-induced point mutations (RIP), which comprise a pre-meiotic homology-based genome defense system. This early immune system consists of a variety of inactivated transposons that include DNA modifications and chromatin modifications (Selker et al. 2003; Galagan and Selker 2004). As shown by comparative genomics, such inactivated transposons descended from viral infection events that reached a persistent status, providing the host with a new phenotype of an innate immune system in order to prevent similar infections (Villarreal 2005).

In yeast species this transposon is derived from an endogenous retrovirus, i.e. the characteristic Ty1 element, which encodes a functional reverse transcriptase, and a GAG gene, which encodes structural proteins. It is inserted into the silent regions of chromatin, which means that this is a good example of a beneficial situation for both the colonising virus and the host. Interestingly, yeasts also persistently harbour killer viruses that are lethal to related yeast species that are not infected persistently. Generally it is assumed that the high rate of different toxins in the organismic kingdom of fungi represents such toxin/antitoxin modules that are persistently integrated into the fungal host genomes (Villarreal 2009).

Interestingly RNAi that is lost in some yeast can be restored by introducing Argonaute and Dicer from close relatives. The reconstitutives silence endogenous transposons. Restoring RNAi affected maintenance of killer. This endemic viral system is inherited as a dsRNA virus (L-A) and its satellite dsRNA, M that encodes a toxin, that kills nearby cells and confers immunity to cells making the toxin. This clearly resembles a toxin/antitoxin addiction module provided by viral infection events to yeast hosts (Drinnenberg et al. 2011).

In comparison to animal or plant genomes fungal genomes are not highly populated by genetic settlers. Only one family of endogenous retroviruses is present in several full-length copies, some of them completely deactivated in specific fungal lineages. Such chromovirus sequences sometimes match with fungal host sequences. In Ascomycetes and Basidiomycetes these sequences are distinct but inactivated and not transcribed, which could be an indicator of several massive viral

colonisation events during which the previously integrated viruses were displaced. Interestingly, a small number of viral copies are highly conserved and transcribed, so we can assume that they are closely connected with fungal evolution (Villarreal 2009). The high infection rate by dsRNA viruses and endogenous retroviruses is coherent with the presence of a small interfering RNA system with the ability for post-transcriptional silencing. This new system for identifying RNA and repeated DNA sequences by double-stranded RNA sequences is able to silence RNA expression, its main purpose being to silence endogenous retroviruses (chromovirus) and retroposons (Villarreal 2009).

Interestingly, the mitochondria of fungi are highly colonised by persistent double-stranded RNA viruses, each of them from another lineage but present in the host genome as multiple interconnected settlers. Especially the oxidative competence of mitochondrial respiration which is essential for life span of fungal host share some antagonist which regulates its function. If regulation of this process is disturbed, the life span of the host can be interrupted abruptly (Villarreal 2009).

Generally the remarkable genomic interactions between fungi and viruses seems to be an indicator of the virus-driven evolutionary history of fungi in that the virus–host relationship, especially in the endogenous persistent status (represented by dsRNA and small linear dsDNA viruses), is linked to all immunity mechanisms in fungi, such as killer toxins in mitochondria or siRNA, i.e. dsRNA-based identification competence, with an important role in silencing endogenous retroviruses and limiting retroviral infections (Villarreal 2009). This would be coherent with the fact that most fungal genomes are small in comparison to other eukaryotic genomes that lack the ability to ward off RNA viruses and retroviruses.

5   Intraorganismic Communication of Fungi

The countless variety of fungal organisms represents a major challenge when establishing a homogeneous designation of the signalling processes employed. Research activities so far have predominantly focused on those fungal species that pose a serious threat to agriculture, are pathogenic to humans or possess antibacterial properties. Species of this kind are relatively well investigated, whereas species with obviously insignificant properties are little known.

Growth in *Saccharomyces cerevisiae*, for example, is entirely dependent on the final purpose of growth, i.e. its growth and behavioural patterns are correlated. Thus mating of haploid fungal cells is a completely different behavioural cycle than filamentous growth of diploid cells. The signals involved can be differentiated by four different signal-related production patterns (Lengeler et al. 2000).

There is new evidence that certain proteins that have been restricted to signalling pathways in animals so far are also common in fungal signalling pathways (Herranz et al. 2005). In addition, apoptotic processes, which have been considered to play important roles in the development of multicellular organisms of animals

and plants, have now been found to be important for regulating development, growth and aging processes in single-celled fungi (Hamann et al. 2008).

A very large family of transmembrane receptors is responsible for transducing extracellular signals into intracellular responses such as G protein-coupled receptors (Xue et al. 2008).

5.1 Intercellular Communication

Hyphal growth is a totally different behavioural pattern of conduct than normal cell growth: such cells change shape, become elongated, and re-orientate themselves into specific directions to physically come into contact or even merge with each other, only to colonise a potential growth resource.

Fungal hyphae simultaneously extend in a given direction only once nutritional resources are ideally distributed. However, this is a rare event. Usually the fungus propagates in the direction that is enriched with organic matter (carbon and its derivatives) just to halt growth once little or no resources are available; here the fungus coordinates its growth by establishing certain priorities. In order to do so, the fungus employs intercellular signals that enable it to comprehend the overall state of the organism. This includes an integrated ability to discriminate between self and non-self. Once the fungus encounters a resource-depleted substrate or even poisonous compounds, it responds by halting its growth cycle or by propagating in another direction. The protein signals involved in such processes are quite complex: the apex of hyphae houses specialised receptors that are able to respond to any environmental condition.

Any carbon-enriched substrate causes these receptors to become active, which in turn results in the production and release of protein signals into the hyphal cytosol where the corresponding signalling cascade is triggered. In turn, the mycelium responds with the mobilisation and translocation of resources into the activated area. In the absence of carbon-rich substrates, or at increasingly acidic pH levels, the hyphae respond by activating yet other receptors that slow down growth and eventually cause the organism to withdraw resources from the affected area. Since septa within the hyphae are perforated, they perform similar functions as the gap junctions in higher animals, micro-plasmodesmata in cyanobacteria and plasmo-desmata in higher plants (Belozerskaya 1998; Gessler et al. 2007).

An interesting example of intercellular communication in the sexual cycle of Saccharomyces cerevisiae. The sexual cycle of Saccharomyces cerevisiae begins by cells of the opposite type in producing a and alpha pheromones. The haploid cells possess receptors for pheromenes of the opposite mating type. They sense them and respond by stopping normal growth (G1) phase and develop cell outgrowth in the direction of the opposite cell. These outgrowths may fuse into a joint cell with two haploid nuclei that can fuse to produce a nucleus of an a/alpha diploid cell. This means that intercellular communication process initiates three subsequent

steps of internal coordination as appropriate response, G1 phase stop of the cell cycle, cell und nuclear fusion, and cell morphogenesis into direction of pheromone emitting partner (Shapiro 2011). This is clearly a concrete example of how cells communicate and trigger a genomic expression event to coordinate an appropriate response. Complex sensing and signalling are step by step coordination. Are these signalling pathways disturbed or damaged communication will not function appropriately.

5.2 Intracellular Communication

By investigating a great number of signal transduction events from the outside through the cell membrane into the cytoplasm it has been possible to decode some important intracellular communication processes. Thus, it was found that signal processes coordinate cell polarity, mating, pheromone control and cellular morphology. Some of these processes even adjust the cell cycle, cause polarised growth activity and modify the transcription profiles of fungal cells (Lengeler et al. 2000; Bardwell 2004; Fernandes et al. 2005).

By examining the fungal pathogen *Paracoccidioides brasilienus* it was realised that some signalling pathways are identical to those of other species such as *Saccharomyces cerevisiae*, *Cryptococcus neoformans*, *Candida albicans* and *Aspergillus fumigatus* (Fernandes et al. 2005).

The "protein cascades" that characterise production pathways of appropriate chemicals and messenger signals reflect the behavioural contexts, which are to some extent completely different (Fernandes et al. 2005):

- Cell integrity, cell wall construction, pheromone/mating, and osmo-regulation by mitogen-activated protein kinase signalling (MAPK)
- Fungal development and virulence by the cAMP/PKA system
- Cross-talk between cascades by the RAS protein
- Cell survival under oxidative stress, high temperature, membrane/cell wall perturbation by calcium-calmodulin-calcineurin
- Control of cell growth and proliferation by rapamycin

Combinatorial communication procedures such as those involving the MAPK and cAMP pathways are also part of the behavioural contexts (Lengeler et al. 2000). These in turn serve to multiply the semantic contents of the encoded messages.

Several signalling pathways have been found that sense extracellular stimuli and convert them into intracellular signals that regulate developmental and growth processes signalling. The guanine nucleotide-binding protein (G-Protein) is essential for extracellular detection of nutrients and sexual partners (Dohlman 2002; Kays and Borkovich 2004; Hoffman 2005). The TOR protein kinases, which are bound and inhibited by rapamycin, function as nutrient-sensing signals and regulate cellular responses like proliferation, transcription, translation, autophagy and ribosome biogenesis (Beck and Hall 1999; Cutler et al. 2001).
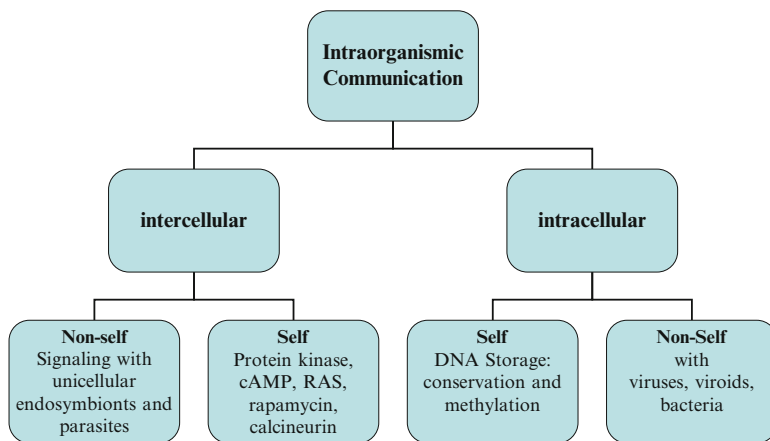
Levels of intraorganismic fungal communication

Levels of intraorganismic fungal communication

As with any signal-mediated interaction that can be achieved with molecules, the same components are employed for differing behavioural contexts and in varying messages. That is, different modes of behaviour can be achieved by syntactically identical signalling. The signalling pathways use identical proteins to coordinate different response patterns. Even if they are syntactically identical they semantically contain a completely different meaning: for example, activated cAMP

- triggers filamentous growth in *Saccharomyces cerevisiae*,
- regulates positive virulence in *Cryptococcus neoformans*,
- suppresses mating in *Schizosaccharomyces pombe* and
- inhibits filamentous growth in *Ustilago maydis* (Lengeler et al. 2000; D'Souza and Heitman 2001) or
- activates protein kinase for directly or indirectly induced developmental changes in *Magnaporthe grisea* during infection of rice (Mitchel and Dean 1995).

Another example is the *Ustilago maydis* pheromone response, which regulates both cell fusion and the pathogenicity programme for plant infection (Krüger et al. 1998; Hartmann et al. 1996, 1999).

These examples show that different behavioural contexts determine different meanings of identical signalling molecules. In such cases, biosemiotically identical signals can induce opposite responses in different organisms. It is interesting to note that fungi are not just capable of differentiating among varying messages and responding appropriately, but moreover are able to differentiate among molecules that are chemically identical to signalling molecules and obviously contain no relevant meaning ("noise"), i.e. are not parts of biotic messages.

Recent genome comparisons have provided new insights into the evolutionary aspects of fungi. The hypothesis that evolution happened by whole genome duplication events followed by selective gene-loss and stabilisation is strengthened

by analysis on *Saccharomyces cerevisiae* (Kellis et al. 2004). Interestingly the signal-to-noise ratio in yeasts is approximately 70% protein coding regions and 15% regulatory elements in the non-protein coding regions, in comparison to humans with ratios of 3% and 97% respectively (Kellis et al. 2003).

6 Interorganismic Communication of Fungi

Since there are both single and multi-cellular species, the communication processes between the same species and related fungal species cannot be distinguished unambiguously from intercellular communication (intra-organismic). Thus communication processes in the mono-cellular yeast (Banuett 1998), which resemble that of amoeba like *Dictyostelium*, must be considered as inter-organismic communication, whereas those within multi-cellular fungal species are truly intercellular. To verify whether cell-to-cell communication is inter- or intra-organismic, we have to consider intercellular processes on a case-by-case basis.

Herein we find another fundamental characteristic of biota, concerning the competence for identifying "self" and "non-self" (Muirhead et al. 2002). This competence was successfully demonstrated in *Neurospora crassa* (Glass et al. 2000; Glass and Saupe 2002; Glass and Kaneko 2003). It is obvious that this capacity to distinguish between oneself and others is vital for fungi, since the encounter of mycelia from the same species results in the merger of their fungal hyphae. However, such dikaryotic mycelia can also result from the merger of different fungal species.

While peripheral hyphae tend to avoid merging with hyphae of other species, the opposite is the case with those at the centre of the mycelium (Glass et al. 2000; Glass and Saupe 2002; Glass and Kaneko 2003). If one assigns mycelia the role of a wrapper within which the fungus is enveloped, so to speak, into a fluid-like continuum, then the nuclei of compatible but different species are "flowing" through the same mycelium. The overall result is an organism, which houses nuclei of different genetic origin in its cytoplasm (Wu and Glass 2001). However, if specific genetic sequences are incompatible, then repulsion sets in, forcing the approaching hyphae into an immune-like response, much like those found in plants.

Resource competition in fungi occurs directly, indirectly and via mechanical interaction. Indirect competition involves absorption of all available resources within the reach of the mycelium, thereby starving potential competitors by maintaining a nutritional deficiency gradient. Direct interaction on the other hand, involves secondary metabolites, which suppress growth or even induce death of the competing fungi. The antibiotics employed in such cases can be either volatile or non-volatile (Kettering et al. 2004). Mechanical interaction simply requires overgrowth of one fungal species by the other, in which the overgrowing species exerts its lytic action on the other. In some cases lysis is induced via antibiotic agents (Dix and Webster 1995; Griffin 1994).

Like bacteria, single-celled fungi also use quorum sensing to regulate and affect biofilm formation and pathogenesis (Reynolds and Fink 2001). This is mediated by small molecules that accumulate in the extra-cellular environment. If these reach a critical concentration a response regulator is activated within the local population of cells, leading to the coordination of gene expression (Hogan 2006).

In parasitic interactions between fungal organisms cytoplasmic fusion was found during infection processes, which indicated genetic transfer in the host–parasite relationship. The recognition pattern in this predator-prey relationship is mediated by trisporoids, which are also involved in a non-parasitic behavioural pattern, being responsible for sexual communication (Schultze et al. 2005).

Some fungi have drawn attention only as saprobes, ectomycorrhizal symbionts or parasites of plants, while their role as parasites of other fungi has not yet been mentioned e.g. basidiomycetes. Their role in a great variety of interactions is still being studied (Bauer and Oberwinkler 2008).

7 Transorganismic Communication of Fungi

Although viruses can be considered as essential agents of life they are lacking metabolism, that means they cannot be considered as organisms. In addition to the above outlined relationship to viruses, fungi are competent to generate a great variety of signalling processes with non-fungal organisms such as plants, animals (insects, nematodes) and bacteria. A typical example of this kind is the mutually beneficial symbiosis between bark beetles and quite a few different fungi (Sullivan and Berisford 2004). The fungal spores benefit from the locomotion provided by the beetles in several ways e.g. access to new hosts, while the beetle benefits from the availability of fungal nutrients and pheromones. Some fungi provide nitrogen, amino acids and sterols that are crucial for the development of beetle larvae – however, this takes effect only once the adult beetle has colonised a host. Many bark beetles have even evolved transportation pockets for fungal hyphae, a fact that points to their common evolutionary history (Kopper et al. 2004).

Another trans-organismic symbiotic signalling process happens between fungi and ants, and is derived from a co-evolutionary relationship that lasted over millions of years (Poulsen and Boomsma 2005). Interestingly some lignin-degrading fungi also produce semiochemicals that have effects on the feeding and foraging behaviour of a Formosan subterranean termite (Cornelius et al. 2004).

Some fungi live as both soprophytes and parasites. Nematode trapping fungi we can find in terrestrial and aquatic ecosystems. They play important symbiotic roles in maintaining nematode population density and therefore can control parasitic nematodes of plants and animals. They are capable of developing trapping devices such as adhesive networks and knobs, constricting rings to capture nematodes and then extract nutrients out of them. To organize this nematode trapping these fungi have to coordinate various steps intracellularly (Yang et al. 2011).

There is much evidence to suggest that the fungal and animal kingdom share common ancestors, such as protoctists, which have a true nucleus like choano-flagellates (Villarreal 2005). In this sense, fungi and animals are more related to each other than is the case with the plant kingdom. This is further strengthened by the sign-mediated processes, which regulate cellular functions. Yet another indicator of their common ancestry is found in a particular signalling pathway, termed the mitogen-activated protein kinase cascade (MAPK). This plays a crucial role in cell wall stabilisation of fungi and pheromone/mating interactions among mammalian cells. On top of that, MAPK is highly conserved (Lengeler et al. 2000).

Then there are fungi which parasitise plants. For example, they may colonise host tissues with an intercellular mycelium that forms haustoria, i.e. fungal mats within plant cells (Jakupovic et al. 2006) that penetrate the cell to utilise the nutrients of the plant. Studies on hazardous fungal infections on plants have revealed the crucial role of enzymes such as cutinase, pisatin, demethylase and HC-toxins (NIAID 1993).

Today, several hundred species of fungi colonise more than 100,000 different plant species. This type of cohabitation relies on and requires symbiotic signalling (Lammers 2004), e.g. the initiation of filamentous growth of fungi through plant hormones (Prusty et al. 2004).

Roots of plants provide better conditions for mycorrhizal fungi, which in turn supply plants with better nutrients (Witzany 2006). For the fungus, such a relationship is either balanced or predatory. Endophytic fungi, however, live in plants without triggering symptoms of disease (Brundrett 2002). Today, scientists consider the origin of the plant cell to be the result of the terrestrial activity of mycorrhiza, i.e. settlement on land was a co-evolutionary event that is comparable to that between flowering plants and insects (Villarreal 2005). The mutually beneficial relationship between subterranean fungi and plant roots is a fine-tuned network of sign-mediated interactions developed over millions of years (Besserer et al. 2006), whereby fungi excrete digestive enzymes into the surrounding soil, and convert nutrients into aqueous solutions that in turn can be readily absorbed by the plant. A staggering 80% of all terrestrial plants rely on the activity of mycorrhiza, especially trees (Schwarze et al. 2004).

Fungi that affect animals are usually dependent on the host's body temperature, i.e. host colonisation by the fungi is only possible if the body temperature is sufficiently high. *Aspergillus fumigatus* in particular colonises animal hosts if they are under thermal stress (Bhabhra et al. 2006). Although fungal disease is common in birds, the relative resistance of endothermic vertebrates to fungal diseases may be a result of immune responses connected with higher body temperature (Casadevall 2006).

A typical fungus cultivated in research laboratories is *Neurospora*. Several subspecies of this genus contain toxins that are pathogenic for animals and plants. However, they are essential components for the large-scale industrial production of antibiotics, chemicals, enzymes and pharmaceuticals (Dunlap et al. 2004).

One of the most striking trans-organismic communication processes between fungi and non-fungal species can be found in lichens (Sanders 2001, 2006). Lichens

are polyphyletic. They have been derived many times independently from different kinds of ascomycetes, so their nature of symbiosis doubtless varies (Raven 2001). In lichens, the algae provide the fungi with photosynthate, while the fungi provide the algae with nutrients. Lichens constitute one of the oldest known fungal members and are capable of resisting quite adverse environmental conditions. The symbiosis between fungi and algae or fungi and bacteria results in a mutual supply of nutrients and their associated competences. Through quorum sensing, the fungi benefit from the bacterial association (Hogan 2006). In turn, the bacteria utilise dissolved fungal metabolites to satisfy their nutritional requirements.

A similar co-dependence is observed with algae as symbiosis partners. But there is also a great variety of other sign-mediated interactions between fungi and bacteria that are beneficial for both and are based on reciprocal signalling (McAlester et al. 2008). Trans-organismic communication can be found in any interaction that involves fungi and viruses, bacteria, protoctista (algae), animals (insects) and plants.

8 Summary

An overview of all significant levels of fungal communication shows that identification of signal-mediated processes in signalling pathways are context dependent – both within and among fungal cells as well as between fungi and other organisms.

Depending on the context, semio-chemicals (molecular components) are integrated into unique signalling pathways where they are used to transport certain meanings. Such meanings are subject to change, i.e. they rely on various behavioural contexts, which differ under altered conditions. These contexts concern cell adhesion, pheromone response, calcium/calmodulin, cell integrity, osmotic growth, stress response or cell growth. The interactional context determines the semantic relationship, i.e., its meaning and the function of the chemical components, and forms a signal-mediated communication pattern in fungi. This is a common feature in all eukaryotic kingdoms: the context determines the meaning of trans-, inter- and intra-organismic (inter- and intracellular) communication, while differences in abiotic and biotic signal perception determine the content arrangement of response behaviour.

After recognising how versatile fungal communication competences really are we can see that one main principle is followed throughout all these signalling processes: fungal organisms coordinate all their behavioural patterns with a core set of chemical molecules. The interactional context and the different modes of coordinating appropriate response behaviour in e.g. development, growth, mating, attack, defense, virulence, etc. determines the combinations of signals that generate the appropriate meaning-function, i.e. informational content of messages. These generating processes normally function in a very conservative way but under certain circumstances may fail, or selective pressure may lead to changes that can be a driving force in fungal evolution.

Additionally it can be recognised that the persistent lifestyle of viruses is a driving force in fungal evolution in that they are the main resource for immunity, group identity and a large number of important secondary metabolites.

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