



## Review

## Signal exchange and integration during self-fusion in filamentous fungi



André Fleißner\*, Stephanie Herzog

Institut für Genetik, Technische Universität Braunschweig, Germany

## ARTICLE INFO

## Article history:

Received 2 February 2016

Received in revised form 6 March 2016

Accepted 22 March 2016

Available online 23 March 2016

## Keywords:

Cell fusion

Cell communication

MAP kinase signaling

Filamentous fungi

## ABSTRACT

Growth and propagation of filamentous ascomycete fungi commonly involves vegetative cell fusion. In the red bread mold *Neurospora crassa* and many other ascomycete species, fusion occurs between germinating spores during colony formation and between hyphal branches in established mycelia. Both fusion processes promote the development and behavior of the fungal colony as a supra-cellular network. Germling and hyphal fusion in *N. crassa* rely on an unusual mode of cellular communication, in which the two fusion partners likely alternate between signal emission and reception, thereby establishing a kind of “cell dialog”. In recent years, numerous molecular factors mediating this unique cellular behavior have been identified, including several conserved signal transmission pathways, as well as proteins specific for ascomycete fungi. Analysis of their molecular interactions revealed the presence of an intricate signaling network, whose sophisticated interconnections are still unfolding. Despite this complexity, germling and hyphal fusion provide experimentally easily amenable model systems and might therefore advance as paradigms for signal transmission and cell fusion. In this article, we strive to highlight some of the recent advances in this field of research and to discuss the current working model of the “cell dialog”.

© 2016 Elsevier Ltd. All rights reserved.

## Contents

|   |    |
|---|----|
| 1. Introduction.....  | 77 |
| 2. Cell–cell fusion and the filamentous fungal lifestyle.....   | 77 |
| 2.1. Germling fusion.....                                       | 77 |
| 2.2. Hyphal fusion.....   | 77 |
| 3. Molecular basis.....   | 78 |
| 3.1. The “ping-pong signaling” or “cell dialog” model.....      | 78 |
| 3.2. What is the nature of the signal?.....                     | 79 |
| 3.3. Signaling complexes mediating cell–cell communication..... | 79 |
| 3.3.1. The MAK-2 MAP kinase cascade.....                        | 79 |
| 3.3.2. STRIPAK.....   | 80 |
| 3.3.3. The SO protein.....                                      | 80 |
| 3.3.4. Reactive oxygen species.....                             | 80 |
| 3.4. The model and open questions.....                          | 80 |
| 4. Conclusions.....   | 82 |
| Acknowledgements.....   | 82 |
| References.....   | 82 |

\* Corresponding author at: Institut für Genetik, Technische Universität Braunschweig, Spielmannstraße 7, 38106 Braunschweig, Germany.

E-mail address: [a.fleissner@tu-bs.de](mailto:a.fleissner@tu-bs.de) (A. Fleißner).

## 1. Introduction

Ascomycete fungi typically grow as unicellular yeasts or syncytial hyphae, which reproduce vegetatively or sexually. Both forms of propagation commonly involve cell fusion events, which serve various biological functions. The best-known example is mating partner fusion during the sexual reproduction of outcrossing species, which enables subsequent nuclear merger and recombination of the genetic material. In filamentous fungi, cell fusion is, however, also prevalent during the vegetative life cycle, where it promotes colony formation, growth and functioning [1–3]. Despite their different roles, all sexual and asexual fusion processes share common requirements, including communication and mutual recognition of the involved cells prior to plasma membrane and cytoplasmic merger [4]. The molecular basis of mating partner interaction has been extensively studied in bakers yeast, and the involved pheromone response pathway has advanced as a paradigm for MAP kinase mediated signaling processes [5]. In contrast, vegetative hyphal fusion has mostly been ignored until in recent years, when studies employing the red bread mold *Neurospora crassa* kindled broader interest in this subject. Since then, different experimental approaches identified numerous conserved and novel molecular factors mediating vegetative fusion in this fungus but also other ascomycete species, including *Sordaria macrospora*, *Fusarium oxysporum*, *Epichloe festucae*, and *Botrytis cinerea* (reviewed in Refs. [6,7]). As a distinctive feature of fungal vegetative fusion, no genetic or physiological differences are required in the fusion partners. In many fungal species, non-self fusion of genetically distinct individuals is even actively suppressed by vegetative incompatibility [8]. In contrast, most other eukaryotic cell–cell fusion events rely on developmental or genetic differences in the two merging cells. *Saccharomyces cerevisiae* employs, for example, the sophisticated system of mating type switching to create genetic distinction within clonal cell populations. Individuals of then different mating type achieve mutual attraction by the formation of two opposite gradients of mating type specific pheromones [9]. While during vegetative fusion, both cells similarly grow towards each other, the two partners are genetically identical and no evidence for the involvement of more than one chemoattractant exists. This raises the question how the two cells establish and read signal gradients while avoiding self-excitation. *N. crassa* solves this conundrum by an unusual mode of communication, in which the two partner cells coordinately alternate between two physiological stages, and probably take turns in signal emission and perception [10,11]. This so-called “ping-pong signaling” or “cell dialog” mechanism employs molecular elements homologous to parts of the yeast pheromone response pathway. However, these factors adopt unusual subcellular dynamics and are wired with other conserved and fungal-unique constituents into an intricate signaling network. Complete overviews of the involved genes and proteins have recently been provided elsewhere [6,12]. In this article, we strive to describe the main signaling hubs and their interactions within this network and to illustrate the current “cell dialog” working model.

## 2. Cell–cell fusion and the filamentous fungal lifestyle

While the need for cell fusion during mating is obvious, the role of non-sexual cell merger in fungal growth and development remains mostly elusive. Vegetative fusion primarily occurs at two different developmental stages: first, between germinating spores during colony development, and second, between hyphae in the inner parts of mature and established mycelia (Fig. 1) [13,14].

### 2.1. Germling fusion

Filamentous ascomycete fungi commonly propagate and disperse via vegetatively formed spores, so-called conidia. These cellular structures are well adapted to dissemination by wind, water, or biological vectors and are often produced in abundance. Colony formation commonly involves fusion of germinated and/or ungerminated conidia into a supracellular network, thereby merging numerous individuals into one functional unit (Fig. 1a–d) [1]. The cellular structures undergoing fusion are either the germ tube tips or specialized hyphal structures, so-called conidial anastomosis tubes, abbreviated as CATs. CATs are distinguished from germ tubes by characteristic features, including a smaller diameter, limited linear extension and the absence of septa [15,16]. It is still a matter of debate if fusing germ tube tips also require a prior differentiation into a CAT. In *N. crassa*, germ tubes undergoing cell–cell merger typically appear tapered, supporting this hypothesis [15]. However, since the molecular basis of germ tube and CAT fusion appear to be identical, this debate is mostly confined to the realms of terminology.

Germling fusion has been reported for numerous species covering all important genera, indicating that it serves conserved and important functions for the fungal life style [1]. Its biological role, however, is only poorly understood and mostly a matter of speculation. Consecutive fusion events within a spore population merge numerous individuals into one colony. Connecting into one functional unit allows propagation in a coordinated manner, thereby optimizing the use of available space and resources. In contrast, non-merged spores would form individual mycelia competing for these goods. Consistent with these theoretical considerations, the ability to undergo germling fusion correlates with increased fitness and competitiveness of *N. crassa* colonies [17,18]. This form of collaboration is, however, restricted to the early stages of colony development and does not take place between mature, established mycelia [19].

While germling fusion usually occurs between individuals of the same species, rare reports of interspecies interactions exist. An early study described positive tropic interactions between different species within the genera *Botrytis*, *Neurospora*, and *Fusarium*, and even weak reactions between the different genera. However, none of these interspecies pairings resulted in cell merger [20]. In contrast, successful CAT fusion between spores of the two plant pathogens *Colletotrichum gossypii* and *Colletotrichum lindemuthianum* has been observed under laboratory conditions. Interestingly, isolates originating from these mixed assays exhibited phenotypes different from the two parental strains, suggesting that germling fusion might potentially constitute one mechanism for horizontal gene transfer and the creation of genetic variability in fungi [21]. The prevalence of this phenomenon is nature is, however, unknown and presents a promising field for further research.

### 2.2. Hyphal fusion

Established mycelial colonies of *N. crassa* and other filamentous fungi comprise various hyphal types with different growth behaviors [22]. At the colony's periphery, fast growing leader hyphae extend the mycelium while actively avoiding mutual physical contact [13]. This negative tropism probably optimizes utilization of the available space and substrate. In the adjacent subapical and inner parts of the mycelium, the former leading hyphae become trunk hyphae, of which branches of different order emerge. These side branches fill in the remaining interhyphal space and frequently exhibit mutual attraction and subsequent fusion (Fig. 1e,f) [2]. Hyphal fusion or anastomosis therefore increases the interconnectedness within the mycelial colony. Similar to germling fusion, the biological role of this prevalent growth feature is only insufficiently

Download English Version:

<https://daneshyari.com/en/article/2202460>

Download Persian Version:

<https://daneshyari.com/article/2202460>

[Daneshyari.com](https://daneshyari.com)