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journal homepage: www.elsevier.com/locate/fbr

Review

The mechanism of ascus firing – Merging biophysical and mycological viewpoints

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ARTICLE INFO

Article history:
Received 4 November 2012
Received in revised form
19 March 2014
Accepted 17 July 2014

Keywords:
Apothecia
Ascospore
Locule
Paraphyses
Perithecia

ABSTRACT

The actively discharging ascus is the unique spore-bearing cell that is responsible to dispatch spores into the atmosphere. From a physical perspective, this type of ascus is a sophisticated pressure gun that reliably discharges the spores at an extremely high velocity, without breaking apart. We identify four essential steps in discharge of spores whose order and timing may vary across species. First, asci that fire are mature, so a cue must be present that prevents discharge of immature spores and signals maturity. Second, pressure within the ascus serves to propel the spores forward; therefore a mechanism should be present to pressurize the ascus. Third, in ostiolate fruiting bodies (e.g. perithecia), the ascus extends through an opening to fire spores into the air. The extension process is a relatively unique aspect of the ascus and must be structurally facilitated. Fourth, the ascus must open at its tip for spore release in a controlled rupture. Here we discuss each of these aspects in the context of understanding the process of ascus and fruiting body function. While there is great diversity among fungi, we focus on discharge in a few model species, and then discuss how this framework may vary in other fungi. Our goal is to tie the physiological and molecular studies of ascus function with concepts in engineering that dictate structure.

1. The problem of dispersal

As predominantly nonmotile organisms, fungi have evolved diverse ways to enhance their distribution. The more fascinating dispersal mechanisms involve forcible launching of spores into the air. Two groups of higher fungi, the Ascomycota and the Basidiomycota, have each taken a different approach to forcible spore discharge. Species of the Ascomycota form spores endogenously within cellular sacs called “asci”, which in many species function as cellular cannons, using turgor pressure to launch spores into the air. The Basidiomycota form their spores exogenously, on the tips of pointed cellular appendages. The basidiospores are then propelled from their appendages due to a sudden change in their center of mass resulting from the rapid motion of a fluid droplet, called ‘Buller’s drop, over the spore surface (Webster *et al.*, 1984; Pringle *et al.*, 2005; reviewed by Money, 1998). Despite the importance of spore release to fungal ecology and plant disease, the

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http://dx.doi.org/10.1016/j.fbr.2014.07.002
1749-4613/

mechanism of spore release remains largely undescribed. In this review, we will focus on the active mechanism of release of ascospores in the Ascomycota, orchestrating molecular processes with the physics of ascus deformation and we will discuss the accumulated literature in light of these concepts.

A fundamental mechanism of ascospore discharge appears common to all of the ascus-forming fungi that have forcibly discharging asci; however there is much variation, some of which affects how and when the spores are dispersed. New advances in high speed video microscopy have enabled close observation of the process of spore firing (Yafetto *et al.*, 2008; Roper *et al.*, 2008). However, asci are usually located within fruiting bodies (Fig 1) and hardly function in isolation; thus the microscopic dynamics of ascus expansion and discharge remain not readily experimentally accessible. In particular, how the structure of the ascus, including wall, cell membrane and cytoskeleton features permit unidirectional expansion and controlled release, are virtually unknown.

Asci are derived from a single cell, within which meiosis occurs. In many species, nuclei undergo an additional division following meiosis, and a double membrane bounding the ascospore wall forms around each nucleus, yielding eight spores in a tubular ascus (Fig 1; see Thompson-Coffe and Zickler, 1993; reviewed by Read and Beckett, 1996). The majority of asci have an opening (via a pore, slit or operculum) at their tip through which the spores are released along with the "epiplasmic fluid" in which they are suspended. Multiple (often hundreds) of asci are packaged together in a fruiting body. Ascomycete fruiting bodies are diverse in shape and structure (Fig 1), reflecting niche requirements. Fruiting body structure dictates whether asci within a single fruiting body fire singly or simultaneously. In flask-shaped fruiting bodies (locules and perithecia), asci fire one at a time in succession. In cup-shaped fruiting bodies (apothecia), asci commonly fire together, in a process called "puffing". Ascus structure reflects the difference in fruiting bodies in which they function.

Before uncontrolled rupture, the ascus opens up at its apex and forcibly releases its content. A variety of mechanisms and morphologies allow opening: asci can unseal through an apical pore or canal; or be released through an outer wall (Fig 1; see Schoch *et al.*, 2006). The ascus opening must be finely controlled, as a mismatch in timing may cause delays in firing, resulting in deterioration of the ascus, uncontrolled rupture of the ascus, or the dispatch of spores that are not mature.

2. Generalized model of ascus function

The ascus is an unusual cell that undergoes extreme morphological deformations perfectly orchestrated to reliably fire the spores. From a physical perspective, the ascus is a pressure gun that realizes accelerations of more than 10^5 g to discharge mature spores at an extremely high speed, without uncontrolled bursting. For the process to succeed, we identify four steps whose timing as well as molecular implementation may vary across species. We explore these four steps based on recent studies of ascus function:

A. *A signal for maturity and a signal to fire.* The process of maturation of spores and asci is diverse and can be very slow. For example, maturation of fruiting bodies of some plant pathogenic fungi occurs across seasons, while others can be initiated and mature within a few days. A signal must be produced upon maturation to prevent discharge of immature spores. In mature asci, the nuclei are embedded in the spores, which suggests that asci have limited ability to repair and regenerate. Thus, for some species it may be expedient to fire spores shortly after maturation is reached to prevent retention of mature spores until the ascus membrane degrades and firing is no longer feasible.

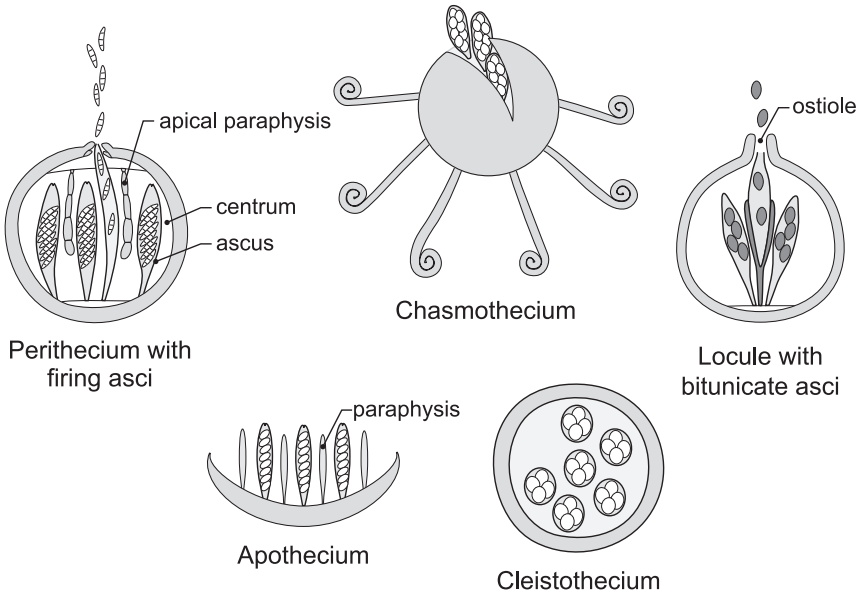

Fig 1 – Fruiting body types and structure among the Ascomycota. The fruiting bodies are associated with the following taxa: perithecia (Sordariomycetes), chasmothecia (Erysiphales); locules (Dothidiomycetes); cleistothecia (Eurotiomycetes); apothecia (Pezizomycetes and Leotiomycetes).