OOMYCETE PATHOGENESIS

Plant killers make the cut

Oomycete hyphae slice plant surfaces with a knife-like cutting action to invade underlying host cells.

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As the world's population grows, safeguarding food supplies is a key challenge of the twenty-first century. Harvests are frequently lost owing to plant diseases caused by fungi and oomycetes[1], two large classes of eukaryotic microbial plant pathogens that have similar morphologies and infection strategies[2]. Pathogens of both classes can breach obstinate plant surface barriers during infection, so understanding this crucial step in the infection process might identify weaknesses that could be targeted to reduce the toll of these pathogens on crops. However, whereas fungi have evolved specialized infection cells — true appressoria — that develop on host surfaces from germinating spores, are melanized, and generate enormous internal turgor pressures to puncture host cuticles using penetration hyphae that emerge from the appressorial base[3], the biomechanics of oomycete plant invasion are poorly understood. Oomycetes often form appressorial-like swellings, but these are small and unmelanized, and likely do not generate high turgor pressures[4,5]. How, then, do oomycetes breach host plants? In this issue of *Nature Microbiology*, Bronkhorst and colleagues describe how three important *Phytophthora* species of oomycetes (*P. infestans*, *P. palmivora* and *P. capsici*) dispense with appressorial structures entirely and rely instead on a remarkable invasion strategy involving hyphae that slice through plant surfaces like a knife[6].

Fungal appressoria[3] are best understood in the devastating rice pathogen *Magnaporthe oryzae*[7]. After spores adhere to surfaces and germinate, a dome-shaped appressorium develops at the tip of the germ tube in response to surface cues. This highly programmatic process involves signal transduction pathways[8], cell cycle checkpoints and spore cell death. Melanin deposition in the appressorial cell wall traps 3 M glycerol and generates enormous hydrostatic turgor pressures of up to 8 MPa. Appressorial adhesion to the surface substrate maintains turgor build-up[9], and a septum seals the appressorium from the germ tube. When sufficient turgor is detected by a sensor kinase, septin GTPases are recruited to the appressorial base to facilitate F-actin remodelling, leading to force generation and polarized growth of the protruding penetration hypha[10]. In addition to colossal turgor, a defining feature of appressorial formation is that a switch from polarized germ tube growth to non-polarized isotropic growth of the nascent appressorium is followed, in turn, by septin-mediated repolarized growth of the penetration peg at a 90° angle to the germ tube (Fig. 1, left).

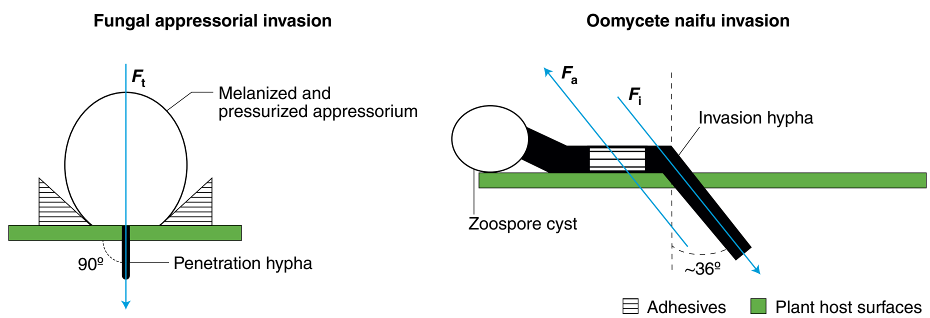

Fig. 1 | Biomechanics of contrasting host invasion strategies. Dome-shaped fungal appressorial cells are melanized and generate enormous internal turgor when tightly adhered to the host surface. This force (F_t) is directed onto a slender penetration hypha emerging from the appressorial base, leading to penetration that is perpendicular to the surface. In contrast, *Phytophthora* species of oomycetes dispense with appressoria and instead slice the host surface at oblique angles using invasion hyphae with polar mechanical geometry. Spatially distinct but mechanically coupled adhesion and indentation sites together generate balanced adhesion forces (F_a) and indentation forces (F_i) that fracture the surface. This naifu-invasion mechanism concentrates stresses at the indentation site to create tensile stresses directed along the surface plane, resulting in cracks that are advanced with penetrating hyphal growth and conclude in devastating plant diseases. Blue arrows denote force direction.

Oomycetes — which infect a wide range of hosts and include one of the most notorious plant killers, *P. infestans*, which caused the Irish potato famine and is still a global threat to potato and tomato crops — were long considered to be fungi. In addition to forming appressoria-like structures, both grow as a network of filamentous, branching hyphae and disperse via spores[2]. However, these are convergent traits, and oomycetes are now taxonomically grouped with stramenopiles including diatoms and brown algae. Unlike fungi, oomycete hyphae are diploid, and their cell walls contain cellulose instead of chitin. Notably, they neither make melanin nor carry septins, which therefore precludes the formation of highly pressurized appressoria.

How do oomycetes invade hosts in the absence of melanin and septins? By addressing this question, Bronkhorst and colleagues describe an entirely new mechanism of plant invasion. They inoculated etiolated stems of potato plantlets with a strain of *P. infestans* expressing GFP and monitored host invasion using three-dimensional confocal imaging. After spore germination and a period of germ tube growth, the hyphal tip indented and then invaded host surfaces at an oblique angle of attack, without forming distinct appressoria, in a manner that was recapitulated on artificial polydimethylsiloxane (PDMS) substrates (facilitating mechanical analysis) and conserved in the wide-host-range pathogens *P. palmivora* and *P. capsici*. The oblique angle of attack suggested a 'slicing' mechanism of invasion, which would fracture substrates by concentrating forces at the surface. Fracture imaging, using the molecular mechanosensor spiropyran, confirmed that oblique indentation propagated surface cracks in front of the growing hyphae, into which the pathogen could invade.

Surface deformation profiling and contact-mechanics modelling demonstrated that the oblique application of force required for hyphal slicing resulted in polarized, non-concentric surface deformations that were not expected for appressoria but were consistent with a geometry of hyphal adhesion and indentation. Upward surface deformations resulted from an adhesive force near the spore, whilst downward deformations manifested from oblique indentation pressure at the hyphal apex. These opposing, spatially distinct but mechanically coupled pressures were balanced, and grew in amplitude until the surface fractured (Fig. 1, right). After fracture, hyphae penetrated the substrate at relatively constant pressures, growing the cracks sufficiently to facilitate invasion.

The authors name this striking, previously undocumented slicing infection strategy 'naifu invasion', after the Japanese knives that similarly use polar force application under an oblique angle to concentrate stresses and fracture surfaces.

Naifu invasion of PDMS substrates required actin-mediated polarized hyphal growth, adherence and modest pressure generation. Are these processes physiologically relevant? The authors showed that they are, because cytoskeletal disruption, or blocking adhesion, reduced infectivity on host leaves, perhaps pointing to molecular targets that could be exploited to prevent plant infection.

Because naifu invasion involves polarized hyphal growth and polar force application, but not isotropic expansion of the hyphal tip and re-establishment of polar growth, the authors argue that the term 'appressoria' is not appropriate for the hyphal tip swellings of oomycetes. Rather, the hypha itself, undergoing changes in the angle of polar growth to fracture the host surface, is the invasion organ.

This study establishes a vastly improved understanding of oomycete invasion biology, and raises fascinating questions for future research. What is the molecular basis of the adhesive sites that balance hyphal tip forces as they slice surfaces? What triggers the switch from surface growth to penetration? Which signalling pathways coordinate the process? How is the hyphal apex shaped to enhance stress localization? To find answers, it may be necessary to classify other microorganisms as naifu invaders, but only if they can make the cut. ❐

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Competing interests

The author declares no competing interests.