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Life cycle specialization of filamentous pathogens — colonization and reproduction in plant tissues

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Filamentous plant pathogens explore host tissues to obtain nutrients for growth and reproduction. Diverse strategies for tissue invasion, defense manipulation, and colonization of inter and intra-cellular spaces have evolved. Most research has focused on effector molecules, which are secreted to manipulate plant immunity and facilitate infection. Effector genes are often found to evolve rapidly in response to the antagonistic host-pathogen co-evolution but other traits are also subject to adaptive evolution during specialization to the anatomy, biochemistry and ecology of different plant hosts. Although not directly related to virulence, these traits are important components of specialization but little is known about them. We present and discuss specific life cycle traits that facilitate exploration of plant tissues and underline the importance of increasing our insight into the biology of plant pathogens.

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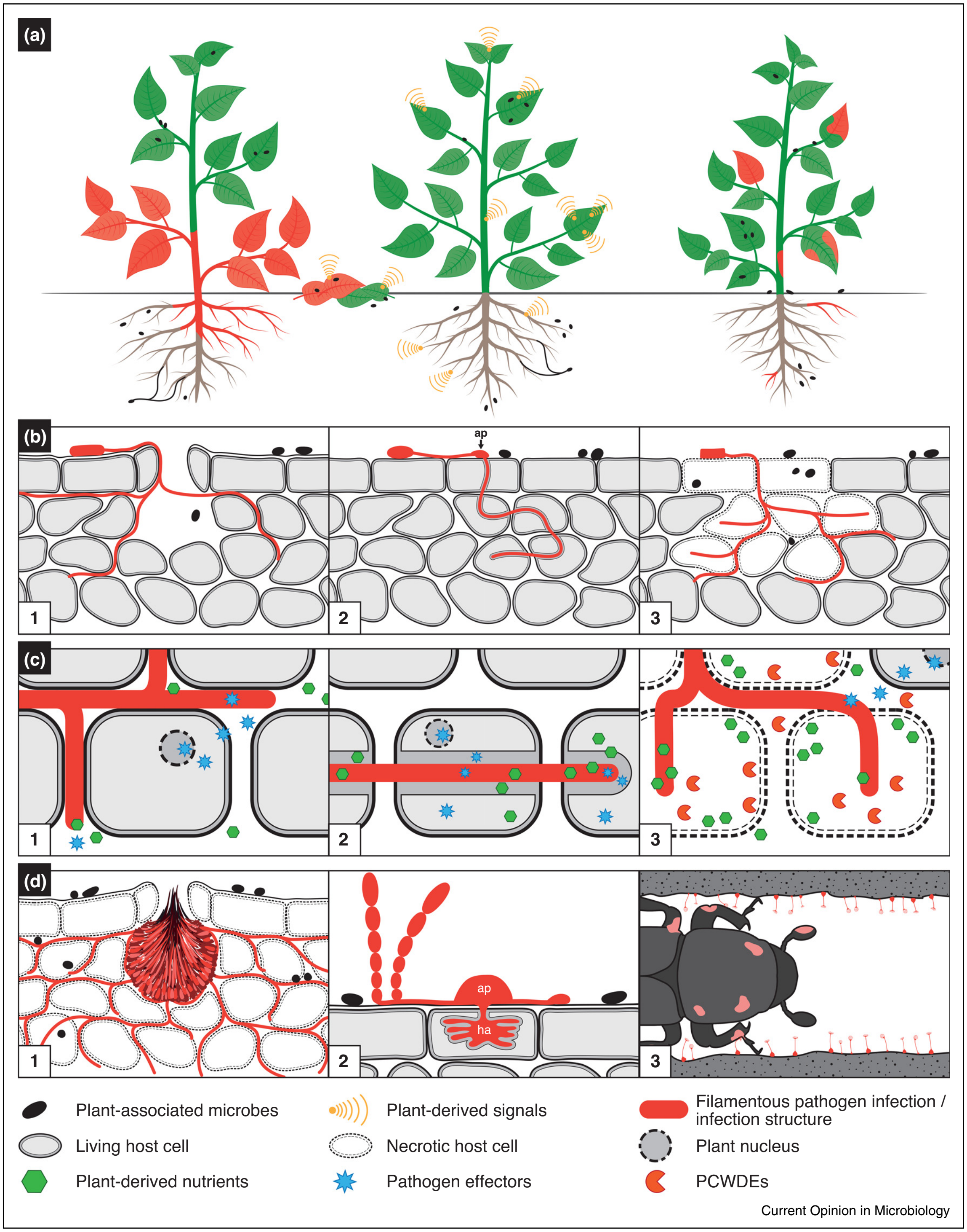
Introduction

Plants are habitats for a large diversity of microbial species colonizing the outside and inside of roots and all aerial tissues. Many microbes are harmless to plants and some even beneficial. Mycorrhizal symbionts are known to be strong enhancers of plant growth and health and are found in all plant-inhabited environments [1,2]. So are filamentous plant pathogens, which exploit plants as substrate for their growth and reproduction by inducing disease and thereby compromise host viability and reproduction. These fungal and oomycete species have evolved diverse strategies to infect and loot nutrients from the plant for their own growth and reproduction.

Theoretical and experimental approaches have shed light on the origin, diversity, and biology of a small number of well-studied pathogen species [3,4,5]. Most studies addressing host specialization have focused on recent micro-evolutionary changes related to host jumps or breakdowns of plant resistances [6••,7••]. A particular focus has been the fast evolutionary dynamic of genes encoding 'effectors' in many plant pathogens. Effectors are secreted molecules that interfere with plant defenses and in some cases act as determinants of host range [8,9•,10]. A general finding from a diverse range of pathogen species is that rapid evolution of many effector genes is enabled by compartmentalized genomes with particular repeat-rich regions where genes undergo an increased accumulation of mutational changes [3,11,12,13]. A number of reviews summarize and discuss studies focusing on such rapid adaptive changes in pathogens and the role of these in determining host specificities [14,15,16,17]. However, not only effectors with a direct role in the manipulation of host defenses are subject to adaptive evolution in plant pathogens [4,18]. In the wheat pathogen *Zymoseptoria tritici* genes encoding plant cell wall degrading enzymes and genes with functional relevance during late infection and asexual reproduction also show signatures of positive selection and species-specific adaptation [7••,19]. Likewise several genes involved in metabolism and signal transduction have evolved under positive selection during divergence of plant pathogenic species in the genus *Botrytis* [18]. These findings underline that host specialization of plant pathogens not only pathogenicity related traits but also affects a range of life cycle developmental stages and processes not directly related to virulence.

Our goal in this review is to address a broader perspective of host specialization of filamentous pathogens, considering, in addition to the molecular battlefield of host–pathogen interactions, also specialization to plant tissues as an ecological niche for growth and reproduction (Figure 1). We suggest that host specialization involves, across diverse lifestyles of plant pathogens: 1) the evolution of particular infection strategies to invade the inter- or intra-cellular spaces of plant hosts, 2) the production of an appropriate repertoire of effectors to suppress host defenses, 3) the expression of genes encoding an arsenal of enzymes and transporters for the uptake of available nutrients within or between plant cells, 4) the ability to co-exist or compete with other microbes inhabiting plant surfaces, and 5) an efficient reproduction program evolved to facilitate dispersal of spores to new uninfected hosts.

Figure 1



The host plant as an ecological niche of filamentous pathogens. **(a)** Plant rhizo-, phyllo- and endosphere are inhabited by different microbes (black ovals) ranging from beneficial to pathogenic. Specific plant signals (signal symbols) serve to recruit beneficial species but likewise attract pathogens [28]. Infection by filamentous pathogens (red areas) can be local or systemic and affect several organs up to whole plants. **(b)** Pathogens invade plant tissue by natural openings e.g. stomata **(b.1)** or form appressoria (ap) **(b.2)(d.2)** to break down plant cell walls. Many necrotrophic pathogens use toxins and enzymes to kill epidermal cells and enter by direct penetration **(b.3)**. Colonization of host tissues occurs by inter- (**b.1**) or intra-cellular growth **(b.2)**. **(c)** Pathogens take up host-derived nutrients and secrete effectors that are delivered to host apoplast, cytoplasma or nuclei to silence host defense and manipulate plant physiology [9•]. Biotrophic pathogens establish intimate host-pathogen interaction zones e.g. invaginations of host cell membrane **(c.2)** or haustoria (ha) **(d.2)**. Intercellular biotrophs have limited amounts of nutrients