

UC Davis

UC Davis Previously Published Works

Title

Cryptic fungal infections: the hidden agenda of plant pathogens

Permalink

<https://escholarship.org/uc/item/6b24p4kw>

Journal

Frontiers in Plant Science, 5(SEP)

ISSN

1664-462X

Authors

Stergiopoulos, Ioannis
Gordon, Thomas R

Publication Date

2014

DOI

10.3389/fpls.2014.00506

Peer reviewed



Cryptic fungal infections: the hidden agenda of plant pathogens

Ioannis Stergiopoulos*[†] and Thomas R. Gordon[†]

Department of Plant Pathology, University of California Davis, Davis, CA, USA

*Correspondence: istergiopoulos@ucdavis.edu

[†]These authors have contributed equally to this work.

Edited by:

Benjamin Schwessinger, University of California Davis, USA

Reviewed by:

Eric Kemen, Max Planck Institute for Plant Breeding Research, Germany

Patrick Schäfer, University of Warwick, UK

Keywords: fungi, symbiosis, pathogenesis, virulence, disease, cryptic infection, plant

INTRODUCTION

Host-microbe interactions have traditionally been viewed primarily from the perspective of pathogenesis and disease. The principal assumption is that a susceptible host will support microbial growth inside host tissues, leading eventually to the development of symptoms and disease. Inversely, non-susceptible (resistant) hosts will block pathogen infection and the expression of disease (Casadevall and Pirofski, 2001; Hok et al., 2010). Compatible host-microbe interactions, however, do not always result in overt negative effects, and asymptomatic or cryptic fungal infections are increasingly recognized as a common feature of many symbiotic associations between fungi and their hosts (Rodriguez et al., 2009; Porrás-Alfaro and Bayman, 2011; Malcolm et al., 2013). It is now generally accepted that extensive intra (Stone, 1987; Bernardi-Wenzel et al., 2010) and intercellular (Schulz and Boyle, 2006) (Gómez-Vidal et al., 2006; Rodriguez et al., 2009) colonization of plants by endophytic fungi and other microorganisms (Thomas and Sekhar, 2014) is the norm, and that it would not be unusual for an individual host to sustain the growth and development of dozens of microbial taxa (Suryanarayanan et al., 2003; Ganley and Newcombe, 2006; Gazis and Chaverri, 2010; De Siqueira et al., 2011). Consequently, it should also not come as a surprise to discover that many of the fungi that we know only as pathogens have in fact a much broader repertoire of ecological interactions with their hosts,

which may include the capacity to infect and colonize them without inducing any visible damage (Malcolm et al., 2013). Despite this fact, we still largely regard these relationships as aberrations and not typical of the manner in which fungi interact with their hosts, often excluding them from the study of host-microbe interactions with potentially adverse consequences on disease control (Filipe et al., 2012). Here we use selected examples to emphasize how cryptic associations between fungi and plants can influence our capacity to manage plant diseases, while also providing insights into the origins of plant pathogens.

TIPTOEING ON THE SYMBIOSIS BALANCE BEAM

Fungi can participate in a diverse array of intimate symbiotic relationships with their hosts, ranging from harmful to beneficial (Newton et al., 2010). Broadly speaking, symbiotic relationships are categorized as parasitic, commensal or mutualistic. In parasitism, the parasite benefits from the association while the host is harmed. In commensalism, one partner benefits from the interaction while the other appears to be unaffected, whereas in mutualism, both partners benefit from the interaction (Casadevall and Pirofski, 2000). Although these categories are useful for conceptualizing relationships between hosts and microbes, they do not reflect the continuum that truly exists or the dynamic nature of the interactions, which can result in a single host-fungus combination displaying

features of parasitism, commensalism, and mutualism (Casadevall and Pirofski, 2003; Schulz and Boyle, 2005; Newton et al., 2010). It is thus not uncommon for the balance in a symbiotic interaction to shift depending on environmental conditions, the genetics of the host, the microbial species and the interaction stage (Casadevall and Pirofski, 2003; Kogel et al., 2006; Casadevall, 2007; Giauque and Hawkes, 2013; Iliev and Underhill, 2013). Consequently, fungi may adopt contrasting lifestyles, by completing their life-cycle as pathogens on some hosts, while living as commensals or mutualists on others (Schulz and Boyle, 2005; Malcolm et al., 2013). Disease in that perspective could be perceived as an unbalanced equilibrium between “supply-and-demand” in host-microbe interactions and a breakdown in the balanced and potentially (mutually) beneficial co-existence between hosts and microbes (Casadevall and Pirofski, 2000; Newton et al., 2010).

HIDDEN IN PLAIN SIGHT

Asymptomatic or cryptic plant infections by commensal or mutualistic fungi have been traditionally associated with endophytes (Rodriguez et al., 2009; Porrás-Alfaro and Bayman, 2011). The term was first coined in the mid-19th century by Anton de Bary (1879), the founding father of modern-day plant pathology, and was loosely translated as “any fungus or bacterium found inside plant tissues” (Bary, 1879). Today, however, endophytes are often categorized as “fungi or bacteria that invade tissues of living

plants and cause no apparent effect” (Wilson, 1995). Of course this definition specifically excludes microorganisms having a conspicuous beneficial effect, such as mycorrhizae and nodule-forming bacteria that maintain mutualistic associations with their hosts. It also excludes microorganisms with conspicuous negative effects, with the exception that pathogens may be included to the extent that they have an endophytic (or latent) stage (Wilson, 1995; Porrás-Alfaro and Bayman, 2011). Almost every vascular plant species examined to date has been found to harbor endophytic fungi. Consequently, there exists an enormous diversity both in species as well as symbiotic and ecological functions of endophytic fungi (Arnold, 2007; Arnold and Lutzoni, 2007; Rodríguez et al., 2009). Among the best studied endophytes are the so-called Clavicipitaceous endophytes of the genus *Neotyphodium* (teleomorph = *Epichloë*) and related genera, which form obligate biotrophic associations with temperate grasses and play an important role in host physiology by enhancing growth and conferring abiotic and biotic stress tolerance. Due to their agronomic importance, Clavicipitaceous endophytes have been extensively reviewed elsewhere (Saikkonen et al., 1998; Scharld et al., 2004, 2009; Rodríguez et al., 2009), and thus will not be considered further here.

THE SECRET LIFE OF PLANT PATHOGENS

Many fungi that establish symptomless associations with their hosts, however, are not obligate endophytes but rather may switch between pathogenic and commensal or mutualistic lifestyles, depending on environmental conditions and the host. This is well illustrated by strains of *Fusarium oxysporum*, which are regarded as host-specific because they cause disease on a narrow range of genotypes, but which also infect and grow asymptotically within the root cortex of crop plants (Gordon et al., 1989). The taxonomic breadth of species that host cryptic infections by *F. oxysporum*, suggests that this mode of existence may be the norm, whereas interactions causing conspicuous damage are an aberration. Consistent with this view is the widespread occurrence of *F. oxysporum* in native plant communities

as a benign colonizer of grasses and other plant hosts (Gordon and Martyn, 1997). Where grassland soils have been brought under cultivation, resident populations of *F. oxysporum* may persist (Gordon et al., 1992) and colonize whatever crops are made available to them. Over time, chance combinations of plant and fungal genotypes may result in interactions that are damaging to the host. This mode of origin could explain the emergence of *F. oxysporum* strains that cause wilt diseases on cotton (Wang et al., 2004; Chakrabarti et al., 2011). If such fungi with a potentially pathogenic lifestyle retain their ancestral capacity to exploit other hosts as endophytes, prospects for management through crop rotation will be diminished.

The significance of cryptic infections is not limited to agroecosystems, as may be seen in the example of *Fusarium circinatum*, a pathogen of pines in native forests, but now also known to colonize grass species as an endophyte (Swett and Gordon, 2012). Such grass isolates are virulent on pine and can potentially be dispersed asymptotically over multiple spatial and temporal scales, thus turning cryptically infected grasses into reservoirs of pathogen inoculum and accelerating disease transmission by facilitating horizontal grass-to-grass movement of the fungus between isolated stands of susceptible pines. Consequently, management strategies that are restricted to consideration of only symptomatic hosts without taking into account the pathogen's true host-range may not be effective. Acknowledging that plant pathogens can be dispersed in asymptomatic hosts over long distances is also of paramount importance when considering quarantine measures against invasive species such as *F. circinatum*.

“AVIRULENT” STRAINS: NOT SUCH LOSERS AFTER ALL

Whereas fungi such as *F. circinatum* adopt different symbiotic lifestyles on genetically distant host species, variation can also be found among fungal isolates infecting the same host species, thus challenging the concept of a species having a single symbiotic lifestyle on a particular host (Barrett et al., 2009). Although intraspecific variation in pathogenicity can be a consequence of quantitative host resistance,

cases in which endophytes represent seemingly avirulent (non-pathogenic) strains of known pathogenic species (Freeman and Rodriguez, 1993; Redman et al., 1999; Schulz and Boyle, 2006) in systems characterized by qualitative host resistance have been described as well. The hemibiotrophic ascomycete *Zymoseptoria tritici* (formerly known as *Mycosphaerella graminicola*), for example, is a notorious pathogen of wheat, whose interaction with the host conforms to the gene-for-gene relationship (Kema et al., 1996, 2000; Brading et al., 2002; Palmer and Skinner, 2002). Despite the expected race-specificity, host-pathogen incompatibility in this pathosystem does not necessarily restrict growth of the fungus inside the host, which nevertheless remains free of disease symptoms (Ware, 2006). Such isolates are non-pathogenic in the sense that they cannot complete a cycle of asexual reproduction on the host or induce any externally visible damage (i.e., necrosis and chlorosis), but they may still grow substantially inside plant leaves and engage in sexual recombination with virulent isolates colonizing the same host (Ware, 2006). Hence, their genes are not quickly removed from the gene pool, which consequently affects the disease transmission dynamics and the development of disease epidemics by maintaining virulence heterogeneity in the pathogen population. This could potentially moderate pathogen virulence at a population level and balance the overall cost of virulence, thus overcoming the risk of driving the host to extinction. For host-specific pathogens such as *Z. tritici*, which is known to have co-evolved as a specialized pathogen of wheat, the ability of some isolates to multiply asymptotically inside the host as non-destructive colonists could reflect an evolutionary adaptation at a population level that maintains allelic diversity at virulence-associated loci, thereby enhancing the prospects for long-term reproductive success of the pathogen (Vanbaalen and Sabelis, 1995; Frank, 1996; Read and Taylor, 2001; Rauch et al., 2003). Furthermore, retaining virulence heterogeneity at a population level could facilitate pathogen transmission by retaining a proportion of the host population alive for some time, thus prolonging the infectious period and enabling a higher

number of sexual cycles and consequently ascospores to be produced within a growing season. Ascospores of *Z. tritici*, in particular, are wind transmitted and have been reported to travel for hundreds of kilometers, in contrast to the rain-splash, locally dispersed asexual pycnidiospores. Thus, maintaining a parasitic continuum in a pathogen population between non-destructive endophytic colonizers and virulent isolates may reflect an evolutionary adaptation that increases the long-term reproductive success of the organism. More importantly, the ability of some isolates to grow asymptotically inside the host in a cryptic or latent manner could offer support to the idea that modern plant-pathogen interactions have arisen from the breakdown of past mutualistic interactions and a switch to a pathogenic lifestyle (Stukenbrock and McDonald, 2008; Eaton et al., 2010; Kiers et al., 2010).

CONCLUDING REMARKS

The majority of studies in host-microbe interactions have thus far followed a rather reductionist approach, focusing mostly on aspects of pathogenesis and disease. However, it is possible that all of our hard-won knowledge about the activities of some species as pathogens, in fact represents a vanishing small part of the full spectrum of ecological activities that constitute their life history. Thus, for a holistic understanding of host-microbe interactions, it is vital to understand and appreciate the true breadth and dynamic nature of the parasitic, commensal or mutualistic continuum that exists between microbes and their hosts. Failing to do so may compromise efforts to manage species normally perceived as pathogens, and increase the risk of introducing invasive species into new areas. We consequently stress the importance of determining the extent to which fungi with a potentially pathogenic lifestyle exploit host plants that manifest no symptoms, and incorporating this information into epidemiological models and disease management strategies. Future studies should also focus on identifying the genetic and environmental factors that trigger a transition in the trophic interactions between hosts and parasites, and subsequently the phenotypic state of an infection. By

studying in parallel the parasitic, mutualistic, and commensal lifestyles of traditional pathogens, key processes in the host-pathogen interplay and molecular communication can be identified that can be exploited for more sustainable disease control measures. Overall, we argue that a paradigm-shift in the study of host-microbe interactions is currently needed, to acknowledge the full extent of trophic interactions between parasites and hosts.

REFERENCES

- Arnold, A. E. (2007). Understanding the diversity of foliar endophytic fungi: progress, challenges, and frontiers. *Fungal Biol. Rev.* 21, 51–66. doi: 10.1016/j.fbr.2007.05.003
- Arnold, A. E., and Lutzoni, F. (2007). Diversity and host range of foliar fungal endophytes: are tropical leaves biodiversity hotspots? *Ecology* 88, 541–549. doi: 10.1890/05-1459
- Barrett, L. G., Kniskern, J. M., Bodenhausen, N., Zhang, W., and Bergelson, J. (2009). Continuum of specificity and virulence in plant host-pathogen interactions: causes and consequences. *New Phytol.* 183, 513–529. doi: 10.1111/j.1469-8137.2009.02927.x
- Bary, A. D. (1879). *Die Erscheinung der Symbiose: Vortrag*. Strassburg: Verlag von Karl J. Trübner.
- Bernardi-Wenzel, J., García, A., Celso Filho, J., Prioli, A. J., and Pamphile, J. A. (2010). Evaluation of foliar fungal endophyte diversity and colonization of medicinal plant *Luehea divaricata* (Martius et Zuccarini). *Biol. Res.* 43, 375–384. doi: /S0716-97602010000400001
- Brading, P. A., Verstappen, E. C. P., Kema, G. H. J., and Brown, J. K. M. (2002). A gene-for-gene relationship between wheat and *Mycosphaerella graminicola*, the Septoria tritici blotch pathogen. *Phytopathology* 92, 439–445. doi: 10.1094/Phyto.2002.92.4.439
- Casadevall, A. (2007). Determinants of virulence in the pathogenic fungi. *Fungal Biol. Rev.* 21, 130–132. doi: 10.1016/j.fbr.2007.02.007
- Casadevall, A., and Pirofski, L. (2001). Host-pathogen interactions: the attributes of virulence. *J. Infect. Dis.* 184, 337–344. doi: 10.1086/322044
- Casadevall, A., and Pirofski, L. A. (2000). Host-pathogen interactions: basic concepts of microbial commensalism, colonization, infection, and disease. *Infect. Immun.* 68, 6511–6518. doi: 10.1128/IAI.68.12.6511-6518.2000
- Casadevall, A., and Pirofski, L. A. (2003). The damage-response framework of microbial pathogenesis. *Nat. Rev. Microbiol.* 1, 17–24. doi: 10.1038/nrmicro732
- Chakrabarti, A., Rep, M., Wang, B., Ashton, A., Dodds, P., and Ellis, J. (2011). Variation in potential effector genes distinguishing Australian and non-Australian isolates of the cotton wilt pathogen *Fusarium oxysporum* f.sp. *vasinfectum*. *Plant Pathol.* 60, 232–243. doi: 10.1111/j.1365-3059.2010.02363.x
- De Siqueira, V. M., Conti, R., De Araújo, J. M., and Souza-Motta, C. M. (2011). Endophytic fungi from the medicinal plant *Lippia sidoides* Cham. and their antimicrobial activity. *Symbiosis* 53, 89–95. doi: 10.1007/s13199-011-0113-7
- Eaton, C. J., Cox, M. P., Ambrose, B., Becker, M., Hesse, U., Scharl, C. L., et al. (2010). Disruption of signaling in a fungal-grass symbiosis leads to pathogenesis. *Plant Physiol.* 153, 1780–1794. doi: 10.1104/pp.110.158451
- Filipe, J. A. N., Cobb, R. C., Meentemeyer, R. K., Lee, C. A., Valachovic, Y. S., Gilligan, C. A. et al. (2012). Landscape epidemiology and control of pathogens with cryptic and long-distance dispersal: sudden oak death in northern Californian forests. *PLoS Comput. Biol.* 8:e1002328. doi: 10.1371/journal.pcbi.1002328
- Frank, S. A. (1996). Models of parasite virulence. *Q. Rev. Biol.* 71, 37–78. doi: 10.2307/3037829
- Freeman, S., and Rodriguez, R. J. (1993). Genetic conversion of a fungal plant pathogen to a non-pathogenic, endophytic mutualist. *Science* 260, 75–78. doi: 10.1126/science.260.5104.75
- Ganley, R. J., and Newcombe, G. (2006). Fungal endophytes in seeds and needles of *Pinus monticola*. *Mycol. Res.* 110, 318–327. doi: 10.1016/j.mycres.2005.10.005
- Gaziz, R., and Chaverri, P. (2010). Diversity of fungal endophytes in leaves and stems of wild rubber trees (*Hevea brasiliensis*) in Peru. *Fungal Ecol.* 3, 240–254. doi: 10.1016/j.funeco.2009.12.001
- Giauque, H., and Hawkes, C. V. (2013). Climate affects symbiotic fungal endophyte diversity and performance. *Am. J. Bot.* 100, 1435–1444. doi: 10.3732/ajb.1200568
- Gómez-Vidal, S., Lopez-Llorca, L., Jansson, H.-B., and Salinas, J. (2006). Endophytic colonization of date palm (*Phoenix dactylifera* L.) leaves by entomopathogenic fungi. *Micron* 37, 624–632. doi: 10.1016/j.micron.2006.02.003
- Gordon, T. R., and Martyn, R. D. (1997). The evolutionary biology of *Fusarium oxysporum*. *Ann. Rev. Phytopathol.* 35, 111–128. doi: 10.1146/annurev.phyto.35.1.111
- Gordon, T. R., Okamoto, D., and Jacobson, D. J. (1989). Colonization of muskmelon and non-susceptible crops by *Fusarium oxysporum* f.sp. *melonis* and other species of *Fusarium*. *Phytopathology* 79, 1095–1100. doi: 10.1094/Phyto-79-1095
- Gordon, T. R., Okamoto, D., and Milgroom, M. G. (1992). The structure and interrelationship of fungal populations in native and cultivated soils. *Mol. Ecol.* 1, 241–249. doi: 10.1111/j.1365-294X.1992.tb00183.x
- Hok, S., Attard, A., and Keller, H. (2010). Getting the most from the host: how pathogens force plants to cooperate in disease. *Mol. Plant Microbe Interact.* 23, 1253–1259. doi: 10.1094/Mpmi-04-10-0103
- Iliev, I. D., and Underhill, D. M. (2013). Striking a balance: fungal commensalism versus pathogenesis. *Curr. Opin. Microbiol.* 16, 366–373. doi: 10.1016/j.mib.2013.05.004
- Kema, G. H., Verstappen, E. C., and Waalwijk, C. (2000). Avirulence in the wheat *Septoria tritici* leaf blotch fungus *Mycosphaerella graminicola* is controlled by a single locus. *Mol. Plant Microbe Interact.* 13, 1375–1379. doi: 10.1094/MPMI.2000.13.12.1375
- Kema, G., Sayoud, R., Annone, J., and Van Silfhout, C. (1996). Genetic variation for virulence and resistance in the wheat-*Mycosphaerella*

- graminicola* pathosystem. II: analysis of interactions between pathogen isolates and host cultivars. *Phytopathology* 86, 213–220. doi: 10.1094/Phyto-86-213
- Kiers, E. T., Palmer, T. M., Ives, A. R., Bruno, J. F., and Bronstein, J. L. (2010). Mutualisms in a changing world: an evolutionary perspective. *Ecol. Lett.* 13, 1459–1474. doi: 10.1111/j.1461-0248.2010.01538.x
- Kogel, K. H., Franken, P., and Huckelhoven, R. (2006). Endophyte or parasite - what decides? *Curr. Opin. Plant Biol.* 9, 358–363. doi: 10.1016/j.pbi.2006.05.001
- Malcolm, G. M., Kuldau, G. A., Gugino, B. K., and Jimenez-Gasco Mdel, M. (2013). Hidden host plant associations of soilborne fungal pathogens: an ecological perspective. *Phytopathology* 103, 538–544. doi: 10.1094/PHYTO-08-12-0192-LE
- Newton, A. C., Fitt, B. D., Atkins, S. D., Walters, D. R., and Daniell, T. J. (2010). Pathogenesis, parasitism and mutualism in the trophic space of microbe-plant interactions. *Trends Microbiol.* 18, 365–373. doi: 10.1016/j.tim.2010.06.002
- Palmer, C. L., and Skinner, W. (2002). *Mycosphaerella graminicola*: latent infection, crop devastation and genomics. *Mol. Plant Pathol.* 3, 63–70. doi: 10.1046/j.1464-6722.2002.00100.x
- Porrás-Alfaro, A., and Bayman, P. (2011). Hidden fungi, emergent properties: endophytes and microbiomes. *Ann. Rev. Phytopathol.* 49, 291–315. doi: 10.1146/annurev-phyto-080508-081831
- Rauch, E. M., Sayama, H., and Bar-Yam, Y. (2003). Dynamics and genealogy of strains in spatially extended host-pathogen models. *J. Theor. Biol.* 221, 655–664. doi: 10.1006/jtbi.2003.3127
- Read, A. F., and Taylor, L. H. (2001). The ecology of genetically diverse infections. *Science* 292, 1099–1102. doi: 10.1126/science.1059410
- Redman, R. S., Ranson, J. C., and Rodriguez, R. J. (1999). Conversion of the pathogenic fungus *Colletotrichum magna* to a nonpathogenic, endophytic mutualist by gene disruption. *Mol. Plant Microbe Interact.* 12, 969–975. doi: 10.1094/MPMI.1999.12.11.969
- Rodriguez, R. J., White, J. F. Jr., Arnold, A. E., and Redman, R. S. (2009). Fungal endophytes: diversity and functional roles. *New Phytol.* 182, 314–330. doi: 10.1111/j.1469-8137.2009.02773.x
- Saikkonen, K., Faeth, S. H., Helander, M., and Sullivan, T. J. (1998). Fungal endophytes: a continuum of interactions with host plants. *Ann. Rev. Ecol. Syst.* 29, 319–343. doi: 10.1146/annurev.ecolsys.29.1.319
- Schardl, C., Balestrini, R., Florea, S., Zhang, D., and Scott, B. (2009). “Epichloë endophytes: clavicipitaceous symbionts of grasses,” in *Plant Relationships*, ed H. Deising (Berlin; Heidelberg: Springer-Verlag), 275–306.
- Schardl, C. L., Leuchtman, A., and Spiering, M. J. (2004). Symbioses of grasses with seedborne fungal endophytes. *Ann. Rev. Plant Biol.* 55, 315–340. doi: 10.1146/annurev.arplant.55.031903.141735
- Schulz, B., and Boyle, C. (2005). The endophytic continuum. *Mycol. Res.* 109, 661–686. doi: 10.1017/S095375620500273X
- Schulz, B., and Boyle, C. (2006). “What are endophytes?” in *Microbial Root Endophytes*, eds B. Schulz, C. Boyle, and T. N. Sieber (Berlin; Heidelberg: Springer-Verlag), 1–13.
- Stone, J. K. (1987). Initiation and development of latent infections by *Rhabdochloa parkeri* on Douglas-fir. *Can. J. Bot.* 65, 2614–2621. doi: 10.1139/b87-352
- Stukenbrock, E. H., and McDonald, B. A. (2008). The origins of plant pathogens in agroecosystems. *Ann. Rev. Phytopathol.* 46, 75–100. doi: 10.1146/annurev.phyto.010708.154114
- Suryanarayanan, T., Venkatesan, G., and Murali, T. (2003). Endophytic fungal communities in leaves of tropical forest trees: diversity and distribution patterns. *Curr. Sci.* 85, 489–492.
- Swett, C. L., and Gordon, T. R. (2012). First report of grass species (Poaceae) as naturally occurring hosts of the pine pathogen *Gibberella circinata*. *Plant Dis.* 96, 908–908. doi: 10.1094/Pdis-02-12-0136-Pdn
- Thomas, P., and Sekhar, A. C. (2014). Live cell imaging reveals extensive intracellular cytoplasmic colonization of banana by normally non-cultivable endophytic bacteria. *AoB Plants* 6:plu002. doi: 10.1093/aobpla/plu002
- Vanbaalen, M., and Sabelis, M. W. (1995). The dynamics of multiple infection and the evolution of virulence. *Am. Nat.* 146, 881–910. doi: 10.1086/285830
- Wang, B., Brubaker, C. L., and Burdon, J. J. (2004). *Fusarium* species and *Fusarium* wilt pathogens associated with native *Gossypium* populations in Australia. *Mycol. Res.* 108, 35–44. doi: 10.1017/S0953756203008803
- Ware, S. B. (2006). *Aspects of Sexual Reproduction in Mycosphaerella Species on Wheat and Barley: Genetic Studies on Specificity, Mapping, and Fungicide Resistance*. Met lit. opg. - Met samenvatting in het Engels en Nederlands.
- Wilson, D. (1995). Endophyte - the evolution of a term, and clarification of its use and definition. *Oikos* 73, 274–276. doi: 10.2307/3545919

Conflict of Interest Statement: The Associate Editor Benjamin Schwesinger declares that, despite being affiliated to the same institution as Ioannis Stergiopoulos and Thomas R. Gordon, the review process was handled objectively and no conflict of interest exists. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 28 July 2014; paper pending published: 21 August 2014; accepted: 09 September 2014; published online: 26 September 2014.

Citation: Stergiopoulos I and Gordon TR (2014) Cryptic fungal infections: the hidden agenda of plant pathogens. *Front. Plant Sci.* 5:506. doi: 10.3389/fpls.2014.00506
This article was submitted to Plant-Microbe Interaction, a section of the journal *Frontiers in Plant Science*.
Copyright © 2014 Stergiopoulos and Gordon. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) or licensor are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.