Review

***Botrytis* species: relentless necrotrophic thugs or endophytes gone rogue?**JAN A. L. VAN KAN^{1,*}, MICHAEL W. SHAW² AND ROBERT T. GRANT-DOWNTON³¹Laboratory of Phytopathology, Wageningen University, PO Box 8025, 6700EE Wageningen, the Netherlands²School of Agriculture, Policy and Development, University of Reading, Whiteknights, Reading RG6 6AR, UK³St. Peter's College, University of Oxford, New Inn Hall Street, Oxford OX1 2DL, UK**SUMMARY**

Plant pathology has a long-standing tradition of classifying microbes as pathogens, endophytes or saprophytes. Lifestyles of pathogens are categorized as biotrophic, necrotrophic or hemibiotrophic. *Botrytis* species are considered by many to be archetypal examples of necrotrophic fungi, with *B. cinerea* being the most extensively studied species because of its broad host range and economic impact. In this review, we discuss recent work which illustrates that *B. cinerea* is capable of colonizing plants internally, presumably as an endophyte, without causing any disease or stress symptoms. The extent of the facultative endophytic behaviour of *B. cinerea* and its relevance in the ecology and disease epidemiology may be vastly underestimated. Moreover, we discuss the recent discovery of a novel *Botrytis* species, *B. deweyae*, which normally grows as an endophyte in ornamental daylilies (*Hemerocallis*), but displays facultative pathogenic behaviour, and is increasingly causing economic damage. We propose that the emergence of endophytes 'gone rogue' as novel diseases may be related to increased inbreeding of hybrid lines and reduced genetic diversity. These observations lead us to argue that the sometimes inflexible classification of pathogenic microbes by their lifestyles requires serious reconsideration. There is much more variety to the interactions of *Botrytis* with its hosts than the eye (or the plant pathologist) can see, and this may be true for other microbes interacting with plants.

Keywords: endophyte, lifestyle, necrotroph.**INTRODUCTION**

Plant pathology has a long-standing tradition of classifying microbes as pathogens (causing disease), endophytes (colonizing internal plant tissues without causing disease symptoms) or saprophytes (decomposing dead plant matter). Among the pathogens,

lifestyles are usually distinguished as biotrophic (acquiring nutrition directly from living plant cells), necrotrophic (killing plant cells and feeding on the dead cells) or hemibiotrophic (an early biotrophic phase followed by a switch to necrotrophy). Biotrophic pathogens have an intimate and subtle interaction with their host, resulting from the co-evolution between host and microbe. However, necrotrophs have long been considered to be unsophisticated creatures ('Rambo') that kill host cells with the use of toxins and cell wall-degrading enzymes. This simplistic perception has changed drastically in the past decade.

The perception that necrotrophs 'simply' cause host cell death by the production of phytotoxic compounds was first challenged by studies showing that necrotrophs require the induction of an intricate host programmed cell death (PCD) machinery for successful infection. Transgenic plants expressing a PCD-inhibiting protein are resistant to *Sclerotinia sclerotiorum* and *Botrytis cinerea*, in spite of the fungi remaining capable of releasing phytotoxic molecules (Dickman *et al.*, 2001). One of the key regulators of PCD induction by *S. sclerotiorum* appears to be the simple dicarboxylic acid, oxalic acid (Cessna *et al.*, 2000; Kim *et al.*, 2008). Later studies have revealed that the balance between the induction of apoptotic cell death and autophagic cell death is crucial for successful infection by *S. sclerotiorum*, with apoptotic cell death promoting disease and autophagic cell death restricting pathogen outgrowth. In early stages of the interaction, the pathogen actively suppresses autophagic cell death by means of oxalate release, and in later stages the same compound initiates apoptotic cell death (Williams *et al.*, 2011). In the absence of oxalate production, autophagic cell death sets in and an effective resistance response is initiated in the host (Kabbage *et al.*, 2013). These studies imply that *S. sclerotiorum* is much more sophisticated than often appreciated, and the fungus must have a (brief) biotrophic phase prior to the onset of cell death that is typical for necrotrophs, such as *S. sclerotiorum*.

Sclerotinia sclerotiorum and *B. cinerea* are often considered as typical examples of indiscriminate broad-host-range necrotrophic pathogens, infecting most species of dicot plant on which they are inoculated. The family Sclerotiniaceae comprises species that display a complex intergradation of interactions with plants,

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ranging from necrotrophic to obligate biotrophic or endophytic interactions (Andrew *et al.*, 2012). However, the genus *Botrytis* was considered, until recently, to consist exclusively of pathogenic species with a necrotrophic infection mechanism. Most species have a very narrow host range, whereas only *B. cinerea* can infect a broad spectrum of dicots (Staats *et al.*, 2005). In this paper, we argue that there is much more variety to the interactions of *Botrytis* with its hosts than the eye (or the plant pathologist) can see, and that a trophic lifestyle reflects a dynamic physiological interaction, rather than a static tool to classify taxa of pathogenic microbes.

'LET'S PLAY HIDE AND SEEK'

A clear deviation from the common lifestyle of *Botrytis* species was first reported for *B. cinerea*, the grey mould, considered to be an archetypal necrotroph. The common perception among plant pathologists is that, 'if there is grey mould in a crop, you can clearly spot the infected plants; if you don't see grey mould, the fungus isn't there'. This perception was challenged by the discovery that *B. cinerea* can colonize plants without causing disease.

The initial surprise came when a glasshouse full of *Primula* × *polyantha* plants was inoculated with agar plugs of a single strain of *B. cinerea* and kept at 100% relative humidity for different times, in order to characterize the conditions needed for infection. No symptoms appeared for 3 weeks. When they came, multiple leaves were infected, both inoculated and uninoculated, and without relation to the site of inoculation. Many distinct genotypes were isolated, but not the inoculating isolate. On further investigation, it appeared that the inoculation of young plants, or seeds, with dry spores of marked isolates would produce symptoms weeks later, at the onset of flowering, on parts of the plant which had developed entirely since inoculation. The fungus appeared to be internal, as surface sterilization did not prevent the recovery of isolates. Although a single plant could host more than one genotype of the fungus and the population was genetically diverse, single genotypes were frequently distributed throughout individual plants. Roots were commonly infected. This is all consistent with endophytic growth for extended periods (Barnes and Shaw, 2003). A similar pattern was found for cyclamen (in which isolates could be recovered from the interior of the corn), and then for lettuce; in each case, there was evidence that infected seeds could give rise to systemically infected plants (Sowley *et al.*, 2010).

It appears that seeds are usually not infected directly from a systemic infection, but via flower infection originating from spores. In lettuce, seed-borne infection moved first to roots, and then stems; the lowest frequency of isolation was from leaves. *Botrytis*-specific monoclonal antibody labelling of whole mounts of lettuce root, stem and leaf sections detected internal hyphal spread within roots and above-ground parts (Sowley *et al.*, 2010).

These and other data suggest the following life cycle: young seedlings or seeds are infected by spores; the resulting mycelium grows actively for weeks or months in an association which is at least partly inside the host; when the host flowers, the lifestyle changes to an aggressive attack (Barnes and Shaw, 2002); abundant spores are produced which infect seed heads and/or seedling plants, and the cycle is repeated.

The evidence for fully connected internal spread is so far incomplete. It remains possible that the pattern is one of a system of seaports connected by ship routes. That is, there could be frequent local but quiescent presence of *B. cinerea* inside plant tissues, with hyphal extension on the phylloplane or rhizoplane. This remains very different from the spread of mycelia from the advancing front of a classic grey mould attack, or a lesion resulting from germinating spores supplied with nutrient. A small-scale survey of wild and glasshouse plants revealed other species from which it was easy to recover *B. cinerea* from all parts of symptomless plants after surface sterilization—for example, the perennial apomictic weed *Taraxacum vulgare* agg. (Asteraceae) (Rajaguru and Shaw, 2010) and wild-growing *Arabidopsis thaliana* (Brassicaceae) (Shafia, 2009). It is striking that in some species—such as lettuce and *T. vulgare*—root infection is very common. However, there are other species in which *B. cinerea* is recovered only from fruiting or flowering parts, including the small tree *Sorbus acuparia*, wild blackberry *Rubus fruticosus* agg. (B. A. P. Rajaguru, University of Reading, unpublished results) (all Rosaceae), glasshouse *Gerbera* × *hybrida* (A. C. Davies, University of Reading, Reading, UK, unpublished results) and the perennial flower *Bellis perennis* (Shafia, 2009) (both Asteraceae). Such endophytic growth is surprising only if *B. cinerea* is thought of as an obligate necrotroph. However, detailed study of infection processes in soft fruit (Bristow *et al.*, 1986; Coertze and Holz, 2002; McNicol and Williamson, 1989; Williamson *et al.*, 1987) demonstrates the ability of the fungus to grow endophytically over short distances in the environments of a flower. As plant defences are evaded in this setting, it does not seem far-fetched to suppose that more extended growth is possible.

A systemic, symptomless life cycle, producing infected tissue and spores at flowering, is similar in ecology to a smut fungus rather than the aggressive necrotrophic lifestyle familiar from a rotting strawberry. Isolates recovered from symptomless parts of plants produce aggressively spreading lesions of normal character when inoculated with nutrient on detached leaves of a range of hosts. The hypothesis was tested of the occurrence of genetic differentiation between *B. cinerea* isolates which can infect endophytically and those which cannot, but no evidence for this hypothesis was obtained (Rajaguru and Shaw, 2010). The difference between relentless necrotrophic infection behaviour and the internal, symptomless colonization by *B. cinerea* is therefore caused by a long-lived physiological switch, not a genetically determined difference in capacity.

'COME OUT, COME OUT, WHEREVER YOU ARE'

One might consider the facultative endophytic behaviour of a notorious pathogen, such as *B. cinerea*, as a freak incident, but several studies have unveiled the opposite. There are examples of members of the genus *Botrytis* behaving as nonpathogenic associates of various groups of photosynthetic organisms. Surprisingly, *B. cinerea* has been found to associate with healthy tissue of marine macroalgae (Zuccaro *et al.*, 2008), and undescribed *Botrytis* species have been identified as endophytes of pteridophytes and woody gymnosperms (Zhao *et al.*, 2010; Zhou *et al.*, 2010). Furthermore, *B. cinerea* has been reported to attack a range of different gymnosperm species (Mittal *et al.*, 1987). These studies demonstrate that *Botrytis* is not a genus that exclusively associates with angiosperms, but rather the current understanding of *Botrytis* diversity has been biased to the discovery of pathogens of flowering plants. Even amongst the flowering plants, our present knowledge of the genus remains inadequate. Sampling of endophytic fungi in knapweed (*Centaurea stoebe*) in both native and non-native, naturalized plant populations in North America revealed that *Botrytis* species may co-exist within angiosperms as endophytes (Shipunov *et al.*, 2008). Indeed, *Botrytis* was one of the most represented fungal genera amongst the endophytes in *C. stoebe*. At least six new species of endophytic *Botrytis* could be found in this host alone, in addition to *B. cinerea*, and at least two transitions from parasitism to endophytism were proposed within the genus (Shipunov *et al.*, 2008). *Botrytis cinerea* is also common in *Centaurea nigra* in the UK (Shafia, 2009). If a systematic survey in just one host from a highly diverse plant family (Asteraceae) can reveal so much diversity in the genus, it is hard to doubt that there is an abundance of undiscovered endophytic *Botrytis*. The apparent dogma that the genus *Botrytis* comprises only pathogenic fungi may well be reversed with wider sampling.

The versatility to switch between lifestyles is illustrated by the recent discovery of a novel *Botrytis* species in a genus of cultivated monocotyledonous plants. *Hemerocallis* (daylily) has been cultivated as an edible, medicinal and ornamental plant for many centuries in its natural Far Eastern range. In Europe and North America, introduced *Hemerocallis* have only received major horticultural attention in the past 120 years (Rodriguez-Enriquez and Grant-Downton, 2013). The first report of a mysterious foliar disease, 'spring sickness', appeared in the 1970s in the USA, and it became increasingly problematic in cultivated hybrids, yet no similar disease has been reported from the natural range of *Hemerocallis*. The disease is subtle, showing symptoms such as chlorosis, necrosis and distortion of emerging leaves in the spring. A causative agent had not been formally diagnosed until Grant-Downton *et al.* (2014) identified a fungus isolated repeatedly from infected leaf material as a member of the genus *Botrytis*. The new species is phylogenetically closest to *B. squamosa* and

B. elliptica (pathogens of onion and lily, respectively) and was named *B. deweyae*. Tests on *Hemerocallis* demonstrated that *B. deweyae* mycelium had the capacity to attack this genus specifically and cause tissue necrosis. Although *B. deweyae* isolates could produce macroconidia in culture, conidiation never occurred on infected plants. The mode of pathogenesis on leaf tissue without spread by conidia and typically without the development of mycelial outgrowth, as well as its sudden emergence in cultivated hybrids, suggest that *B. deweyae* is an endophyte 'gone rogue'. Cultivated *Hemerocallis* hybrids are based on a limited founder gene pool, and progressive selection and inbreeding of hybrid lines has resulted in reduced genetic diversity (Tomkins *et al.*, 2001). This may have been a significant factor in precipitating the emergence of necrotrophic *B. deweyae*.

This discovery might suggest that the over-representation of described *Botrytis* pathogens from cultivated monocotyledons itself may be a result of the conditions of cultivation tipping the balance in favour of pathogenic lifestyles. Most of the described *Botrytis* species that are specialist pathogens of monocotyledonous taxa infect groups that have been moved out of their natural range by humans and have become highly selected over a considerable period, including through interspecific hybridization. This is true for many ornamentals (for example *Tulipa*, *Hyacinthus*, *Gladiolus*, *Iris*), as well as edible *Allium* crops (Lorbeer *et al.*, 2004). Many *Botrytis* species were described in the 20th century from emergent diseases of cultivated material, whereas information on their presence in wild host populations is sparse or absent. In the case of *B. convoluta*, latent infections within *Iris* rhizomes appear to be frequent in cultivation (Maas and Powelsen, 1970) and this provides an interesting parallel to *B. deweyae*. This overall pattern may be a consequence of the bias towards the discovery of pathogenic fungi from economically important plants. It would thus be of interest to systematically survey wild *Botrytis* biodiversity, especially amongst the endophytes, because they may represent a pool from which new diseases may emerge during domestication and deliberate or accidental movement of plant material to new locations and environments.

OF TROJAN HORSES AND INVISIBILITY CLOAKS

The observation that *Botrytis* species are capable of endophytic colonization and could, under as yet undefined conditions, switch to necrotrophic development (the Trojan horse strategy) might be cause for concern, as it would be a potential risk of crop loss. However, endophytic *Botrytis* species might be beneficial to their hosts. There are numerous examples of endophytic fungi that (directly or indirectly) confer upon their hosts tolerance to abiotic stress and increased resistance to pests and pathogens (Rodriguez *et al.*, 2009). It is worthwhile exploring the balance between the risks and benefits of endophytic *Botrytis* colonization.

The fact that *Botrytis* species can switch between trophic lifestyles (using the 'invisibility cloak') implies that a mechanism must exist to induce or suppress the production of fungal phytotoxic metabolites and proteins, as well as cell wall-degrading enzymes, which can cause damage and death in host tissues (van Kan, 2006). The expression of many virulence factors requires functional signal transduction cascades, especially the heterotrimeric G protein cascade, mitogen-activated protein (MAP) kinase cascades and the calcineurin pathway (reviewed by Williamson *et al.*, 2007). It remains as yet unknown which chemical or environmental cues act upstream of these pathways to activate them. A major challenge for future research will be to study by which mechanism(s) the production of factors that cause damage to the host is suppressed during the endophytic colonization of host plants. One aspect worth exploring is whether small RNAs (sRNAs) generated in plant cells can modulate gene expression in the fungus. The recent observation that sRNAs produced in *B. cinerea* are able to silence plant genes that are key regulators of plant immune pathways (Weiberg *et al.*, 2013) implies that RNAs can be translocated from the fungus to the host in early phases of the interaction. The observation of host-induced gene silencing (HIGS) suggests the existence of an inverse machinery for translocating plant RNAs into hyphae in the interactions of powdery mildew, rust and *Fusarium* (Nowara *et al.*, 2010; Panwar *et al.*, 2013; Yin *et al.*, 2011). It will be interesting to search for sRNAs derived from the plant with a target in *B. cinerea*. The crucial timing for the occurrence of such sRNAs would be between the moment of host penetration and the induction of PCD leading to the onset of disease.

CONCLUSIONS AND PERSPECTIVES

The genus *Botrytis* currently contains approximately 30 recognized species, and its youngest member, *B. deweyae*, may be the first that does not display a classical necrotrophic behaviour, but rather combines an endophytic lifestyle with facultative necrotrophy. By contrast *B. cinerea*, despite being the best studied member of a genus that was considered to comprise only species with typical necrotrophic lifestyles, appears to display a facultative secretive endophytic behaviour ('hide and seek'). It seems plausible to propose that other *Botrytis* species (and who knows how many other pathogens) have similar potential to switch between lifestyles under appropriate conditions. The family Sclerotiniaceae comprises species that display a complex intergradation of interactions with plants, ranging from necrotrophic to obligate biotrophic or endophytic interactions (Andrew *et al.*, 2012). It is tempting to speculate how many new *Botrytis* species can be uncovered that do not conform to the archetypal necrotrophic behaviour. The phylogenetic tree of the genus *Botrytis* (Staats *et al.*, 2005) consists of two clades with long branch lengths between them. A search for novel *Botrytis* species might reveal

novel taxa that possibly close the phylogenetic gap between these two clades.

Finally, we suggest that the classification of plant-associated microbes as being endophytic, (hemi)-biotrophic, necrotrophic or saprophytic **organisms** is not useful. These terms should be restricted to describing the **lifestyle** of an organism. We must better recognize that pathogen lifestyle and behaviour are subject to phenotypic plasticity. The signals between fungus, host and environment that control the choice of lifestyle should be a rich source of future discovery.

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REFERENCES

- Andrew, M., Barua, R., Short, S.M. and Kohn, L.M. (2012) Evidence for a common toolbox based on necrotrophy in a fungal lineage spanning necrotrophs, biotrophs, endophytes, host generalists and specialists. *PLoS One*, **7**, e29943.
- Barnes, S.E. and Shaw, M.W. (2002) Factors affecting symptom production by latent *Botrytis cinerea* in *Primula × polyantha*. *Plant Pathol.* **51**, 746–754.
- Barnes, S.E. and Shaw, M.W. (2003) Infection of hybrid primula seeds by *Botrytis cinerea* and latent disease spread through the plants. *Phytopathology*, **93**, 573–578.
- Bristow, P.R., McNicol, R.J. and Williamson, B. (1986) Infection of strawberry flowers by *Botrytis cinerea* and its relevance to gray mold development. *Ann. Appl. Biol.* **109**, 545–554.
- Cessna, S.G., Sears, V.E. and Dickman, M.B. (2000) Oxalic acid, a pathogenicity factor for *Sclerotinia sclerotiorum*, suppresses the oxidative burst of the host plant. *Plant Cell*, **12**, 2191–2199.
- Coertze, S. and Holz, G. (2002) Epidemiology of *Botrytis cinerea* on grape: wound infection by dry, airborne conidia. *S. Afr. J. Enol. Vitic.* **23**, 72–77.
- Dickman, M.B., Park, Y.K., Oltersdorf, T., Li, W., Clemente, T. and French, R. (2001) Abrogation of disease development in plants expressing animal antiapoptotic genes. *Proc. Natl. Acad. Sci. USA*, **98**, 6957–6962.
- Grant-Downton, R.T., Terhem, R.B., Kapralov, M.V., Mehdi, S., Rodriguez-Enriquez, M.J., Gurr, S.J., van Kan, J.A.L. and Dewey, F.M. (2014) A novel *Botrytis* species is associated with a newly emergent foliar disease in cultivated *Hemerocallis*. *PLoS One*, **9**, e0089272.
- Kabbage, M., Williams, B. and Dickman, M.B. (2013) Cell death control: the interplay of apoptosis and autophagy in the pathogenicity of *Sclerotinia sclerotiorum*. *PLoS Pathog.* **9**, e1003287.
- van Kan, J.A.L. (2006) Licensed to kill: the lifestyle of a necrotrophic plant pathogen. *Trends Plant Sci.* **11**, 247–253.
- Kim, K.S., Min, J.-Y. and Dickman, M.B. (2008) Oxalic acid is an elicitor of plant programmed cell death during *Sclerotinia sclerotiorum* disease development. *Mol. Plant-Microbe Interact.* **21**, 605–612.
- Lorbeer, J.W., Seyb, A.M., de Boer, M. and van den Ende, J.E. (2004) *Botrytis* species on bulb crops. In: *Botrytis: Biology, Pathology and Control* (Elad, Y., Williamson, B., Tudzynski, P. and Delen, N., eds), pp. 273–294. Dordrecht: Springer.
- Maas, J.L. and Powelsen, R.L. (1970) Presence of latent *Botrytis convoluta* infections in rhizomatous irises. *Mycopathologia*, **41**, 283–286.
- McNicol, R.J. and Williamson, B. (1989) Systemic infection of blackcurrant flowers by *Botrytis cinerea* and its possible involvement in premature abscission of fruits. *Ann. Appl. Biol.* **114**, 243–254.
- Mittal, R.K., Singh, P. and Wang, B.S.P. (1987) *Botrytis*: a hazard to reforestation. *Eur. J. For. Pathol.* **17**, 369–384.
- Nowara, D., Gay, A., Lacomme, C., Shaw, J., Ridout, C., Douchkov, D., Hensel, G., Kunlehn, J. and Schweizer, P. (2010) HIGS: Host-Induced Gene Silencing in the obligate biotrophic fungal pathogen *Blumeria graminis*. *Plant Cell*, **22**, 3130–3141.

- Panwar, V., McCallum, B. and Bakkeren, G. (2013) Host-induced gene silencing of wheat leaf rust fungus *Puccinia triticina* pathogenicity genes mediated by the Barley stripe mosaic virus. *Plant Mol. Biol.* **81**, 595–608.
- Rajaguru, B.A.P. and Shaw, M.W. (2010) Genetic differentiation between hosts and locations in populations of latent *Botrytis cinerea* in southern England. *Plant Pathol.* **59**, 1081–1090.
- Rodríguez, R.J., White, J.F., Arnold, A.E. and Redman, R.S. (2009) Fungal endophytes: diversity and functional roles. *New Phytol.* **182**, 314–330.
- Rodríguez-Enriquez, M.J. and Grant-Downton, R.T. (2013) A new day dawning: *Hemerocallis* (daylily) as a future model organism. *AoB Plants*, **5**, pls055.
- Shafia, A. (2009) Latent infection of *Botrytis cinerea*. PhD Thesis, University of Reading.
- Shipunov, A., Newcombe, G., Raghavendra, A.K.H. and Anderson, C.L. (2008) Hidden diversity of endophytic fungi in an invasive plant. *Am. J. Bot.* **95**, 1096–1108.
- Sowley, E.N.K., Dewey, F.M. and Shaw, M.W. (2010) Persistent, symptomless systemic and seedborne infection of lettuce by *Botrytis cinerea*. *Eur. J. Plant Pathol.* **126**, 61–71.
- Staats, M., van Baarlen, P. and van Kan, J.A.L. (2005) Molecular phylogeny of the plant pathogenic genus *Botrytis* and the evolution of host specificity. *Mol. Biol. Evol.* **22**, 333–346.
- Tomkins, J.P., Wood, T.C., Barnes, L.S., Westman, A. and Wing, R.A. (2001) Evaluation of genetic variation in the daylily (*Hemerocallis* spp.) using AFLP markers. *Theor. Appl. Genet.* **102**, 489–496.
- Weiberg, A., Wang, M., Lin, F.M., Zhao, H., Zhang, Z., Kaloshian, I., Huang, H.D. and Jin, H. (2013) Fungal small RNAs suppress plant immunity by hijacking host RNA interference pathways. *Science*, **342**, 118–123.
- Williams, B., Kabbage, M., Kim, H.-J., Britt, R. and Dickman, M.B. (2011) Tipping the balance: *Sclerotinia sclerotiorum* secreted oxalic acid suppresses host defenses by manipulating the host redox environment. *PLoS Pathog.* **7**, e1002107.
- Williamson, B., McNicol, R.J. and Dolan, A. (1987) The effect of inoculating flowers and developing fruits with *Botrytis cinerea* on postharvest gray mold of red raspberry. *Ann. Appl. Biol.* **111**, 285–294.
- Williamson, B., Tudzynski, B., Tudzynski, P. and van Kan, J.A.L. (2007) *Botrytis cinerea*: the cause of grey mould disease. *Mol. Plant Pathol.* **8**, 561–580.
- Yin, C., Jurgenson, J.E. and Hulbert, S.H. (2011) Development of a host-induced RNAi system in the wheat stripe rust fungus *Puccinia striiformis* f. sp. *tritici*. *Mol. Plant-Microbe Interact.* **24**, 554–561.
- Zhao, J., Zhou, L., Wang, J., Shan, T., Zhong, L., Liu, X. and Gao, X. (2010) Endophytic fungi for producing bioactive compounds originally from their host plants. In: *Current Research, Technology and Education Topics in Applied Microbiology and Microbial Biotechnology*, Vol. 1 (Méndez-Vilas, A., ed.), pp. 567–576. Badajoz: Formatex.
- Zhou, X., Zhu, F., Liu, L., Lin, J. and Tang, K. (2010) A review: recent advances and future prospects of taxol-producing endophytic fungi. *Appl. Microbiol. Biotechnol.* **86**, 1707–1717.
- Zuccaro, A., Schoch, C.L., Spatafora, J.W., Kohlmeyer, J., Draeger, S. and Mitchell, J.I. (2008) Detection and identification of fungi intimately associated with the brown seaweed *Fucus serratus*. *Appl. Environ. Microbiol.* **74**, 931–941.