THE ROLE OF FUNGAL SYMBIOSES IN THE ADAPTATION OF PLANTS TO HIGH STRESS ENVIRONMENTS

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Abstract. All plants studied in natural ecosystems are symbiotic with fungi that either reside entirely (endophytes) or partially (mycorrhizae) within plants. These symbioses appear to adapt to biotic and abiotic stresses and may be responsible for the survival of both plant hosts and fungal symbionts in high stress habitats. Here we describe the role of symbiotic fungi in plant stress tolerance and present a strategy based on adaptive symbiosis to potentially mitigate the impacts of global change on plant communities.

Keywords: adaptation, *Colletotrichum*, endophyte, fungi, mutualism, mycorrhizae, stress tolerance, symbiosis

1. Introduction

Throughout evolutionary time plants have been confronted with changing environmental conditions, forcing them to adapt or succumb to selective pressures such as extreme temperatures, insufficient water and toxic chemicals. Although it is difficult to determine the exact temporal dynamics of prehistoric climate changes, it is clear that climate change has accelerated in the last century (Murray 1997). This has resulted in elevated atmospheric CO2, temperature and ultraviolet radiation, which are predicted to increase plant stress by altering rainfall patterns, photosynthetic activity and water utilization, and increasing the incidence of plant disease and herbivory (Parry 1990). In addition, the increase and expansion of human populations during this same period has resulted in habitat degradation, decreased fresh water supplies and increased salinization of agricultural soils. Collectively, these continuing global changes constitute a significant threat to plants in natural and agricultural ecosystems and it is important to address fundamental questions such as: Will the temporal dynamics of global change allow plants the time necessary to adapt to increased environmental stresses?

Since plants lack any form of locomotion they have evolved complex biochemical/genetic systems to perceive stresses, transmit stress-activated signals to differ-

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ent tissues and activate cellular responses to avoid detrimental effects. Although there have been significant advances in understanding plant stress responses, much remains to be determined biochemically, genetically and ecologically. For example, all plants are known to initiate responses to elevated temperatures, yet few species are capable of tolerating environments that impose high temperature stress such as geothermal soils (Stout and Al-Niemi 2002). Is this due to differences in stress perception, stress-response timing or the magnitude of the response? Although the time frame necessary for plant adaptation to environmental stresses is unknown, the adaptive process is considered to be regulated by the plant genome (Smallwood et al. 1999). However, most plant studies do not consider the fact that plants in natural ecosystems have symbiotic associations with fungi. Symbiosis (from the Greek sumbiosis, living together) was first described by Anton de Bary (1879) and later interpreted by Hertig et al. (1937). Since that initial description, our understanding of biological organisms indicates that all plant life on Earth is symbiotic with fungi. These fungi are important to the structure, function, and health of plant communities (Bacon and Hill 1996; Clay and Holah 1999; Petrini 1986; Read 1999; Rodriguez and Redman 1997). In fact, symbiotic fungi contribute to and may be responsible for the adaptation of plants to environmental stresses (Clay and Holah 1999; Morton 2000; Redman et al. 2002a).

There are two major classes of fungal symbionts associated with plants: fungal endophytes reside entirely within plant tissues and may be associated with roots, stems and/or leaves; and mycorrhizal fungi that reside only in roots but extend out into the rhizosphere. Fungal symbionts express a variety of symbiotic lifestyles including mutualism, commensalism, and parasitism (Lewis 1985). Mutualistic symbioses confer host fitness benefits that can result in stress-tolerance, increased growth rates and/or nutrient acquisition. Commensal symbioses have no beneficial or detrimental effects on hosts. Parasitic fungi negatively affect host fitness by decreasing growth rates and/or fecundity, or inducing disease symptoms that may result in lethality (described here as a pathogenic lifestyle).

The genetic and biochemical processes responsible for the expression of different fungal symbiotic lifestyles are unknown. However, it is clear that lifestyle expression is regulated by the host genome and abiotic conditions (Graham and Eissenstat 1998; Johnson et al. 1997; Redman et al. 2001; Schulz et al. 1999; Smith and Goodman 1999). One approach to generating stress tolerant plants involves cloning genes from plants located in high stress environments into stress-sensitive species. Although this strategy will have some level of success, it does not consider symbiosis as an important factor in plant adaptation and survival. Since all plants are symbiotic with endophytic fungi, we began to investigate the potential role of symbionts in the adaptation of plants to high stress environments. Here, we describe examples of how mutualistic fungi confer stress tolerance to plants and how this may be used to mitigate the impacts of global change in this century.

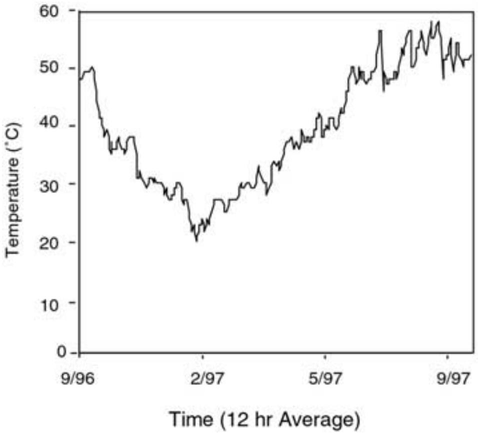

Figure 1. Annual soil temperatures at Amphitheater Springs in Yellowstone National Park Wyoming, USA. A data logger recorded temperatures in the root zone of *D. lanuginosum* (15 cm depth) every four hours for one year.

2. Stress Tolerance and Plant/Fungal Symbiosis

2.1. TEMPERATURE

All plants are known to initiate complex biosynthetic responses to elevated temperatures which involve the synthesis of heat shock proteins and antioxidant systems, and adjustments in osmotic potential and membrane lipids (Iba 2002). However, few plants are capable of thriving in geothermal soils that impose temperature and drought stress. For example, the plant species *Dichanthelium lanuginosum* grows in the geothermal soils of Yellowstone (YNP) and Lassen Volcanic National Parks (LVNP), and is located in soils that reach temperatures as high as 57 °C (Stout and Al-Niemi 2002). Geothermal soils of YNP have significant annual temperature fluctuations that are influenced by moisture (Figure 1). Winter snows melt on contact with geothermal soils to decrease temperatures and a lack of rainfall in summer results in dry hot soils. Therefore, *D. lanuginosum* is exposed to high temperatures and drought conditions on an annual basis.

Recently, we demonstrated that *D. lanuginosum* is symbiotic with a fungal species of the genus *Curvularia* (Redman et al. 2002a). All of the plants analyzed (N = 200) were colonized with *Curvularia* sp. Interestingly, the same *Curvularia* sp. was isolated from *D. lanuginosum* plants in geothermal soils of YNP and LVNP that are separated by 800 miles. Since all *D. lanuginosum* analyzed were symbiotic with *Curvularia* sp., we performed experiments to determine if the fungus contributed to host survival.

Laboratory and field studies indicate that *Curvularia* sp. confers thermotolerance to *D. lanuginosum* and this plant/fungal symbiosis is responsible for survival of both species in geothermal soils. When grown asymbiotically under controlled

Figure 2. Field performance of symbiotic (S) and non-symbiotic (NS) *D. lanuginosum.* S (colonized with *Curvularia* sp.) and NS (mock inoculated) plants were generated as previously reported (Redman et al. 2002a). Plants were grown for two months in the laboratory and planted into geothermal soils as two independent sets of five plants/set. Prior to planting, geothermal soil was removed from locations differing in soil temperatures and pasteurized twice in the laboratory (48 hr at 70 °C, 24 hrs at 25 °C, then 48 hr at 70 °C). The bottoms were removed from plastic containers which were inserted into the holes left after removing soil. Containers were filled with pasteurized soil and plastic barriers inserted to prevent cross-inoculation between S and NS plants. Seedlings were planted and watered with sterile water once/week for three weeks. Soil temperatures indicated on the left were recorded at 20 cm just before plants were removed for processing (May, 2002) and the biomass of plants (leaves and roots) is listed on the right.

conditions, the maximum growth temperature of *D. lanuginosum* and *Curvularia* sp. is 40 °C and 38 °C, respectively. However, when these organisms are grown symbiotically they are able to tolerate root temperature regimes of 70 °C for 10 hr followed by 37 °C for 14 hr (Redman et al. 2002a). We observed similar results with symbiotic and nonsymbiotic *D. lanuginosum* in geothermal soils of YNP. We chose six locations that ranged in soil temperature from 35 °C to 45 °C and placed plants into soil that had previously been removed, pasteurized to eliminate resident fungi and replaced. Twelve months after transplanting, symbiotic plants had greater biomass than nonsymbiotic plants at all temperatures (Figure 2). The difference between these plants increased with temperature with nonsymbiotic plants unable to survive 45 °C soil temperature. Although the mechanism of symbiotically conferred thermotolerance is not yet known, our data indicate that the symbiosis rather than the individual partners adapted to a habitat-specific stress.

TABLE I

Host range and symbiotic lifestyle expression of *Colletotrichum* species.

Fungus	Symptomatic hosts	Asymptomatic hosts	Symbiotic lifestyle(s) expressed
C. lindemuthianum	bean	none observed	P
C. graminicola	corn	none observed	P
C. coccodes	tomato, cucurbits, pepper, eggplant, strawberry	none observed	P
C. acutatum	strawberry	cucurbits	P, C
C. gloeosporioides	strawberry	cucurbits, tomato, pepper, eggplant	P, C
C. orbiculare	cucurbits, pepper, tomato*, eggplant*	tomato*, eggplant*	P, C, M
C. musae	banana	cucurbits, tomato, pepper, eggplant	P, C, M
C. magna	cucurbits	tomato, pepper, eggplant, bean, strawberry	P, C, M

Host range tests and pathogen bioassays were performed as previously described (Redman et al. 2001). P = pathogenic, C = commensal and M = mutualistic (based on the ability of the fungus to confer disease protection against fungal pathogens). * – depending on the plant variety fungi were either pathogenic or expressed non-pathogenic symbiotic lifestyles.

2.2. DISEASE

Filamentous fungal plant pathogens are responsible for tremendous annual crop and revenue losses throughout the world. Despite extensive investigations over the last 100 years to understand the basis of fungal pathogenicity and develop long term control strategies, fungal plant diseases remain a significant agricultural problem. Since the early 1920's the majority of plant disease control strategies use chemical fungicides and/or breeding specific pathogen resistance genes into plants. Plant species, and cultivars within a species, vary in resistance levels to fungal pathogens, and resistance correlates with a complex series of cellular responses (collectively known as host defense systems) that may be localized or systemic (Dangl et al. 1996; Ryals et al. 1996). Some researchers suggest that the difference between resistance and susceptibility is based on the ability of plants to perceive pathogens and the timing of defense system activation (Kuc and Strobel 1992). If plants are able to activate defense systems rapidly, then pathogen ingress will be terminated and the disease process thwarted.

Some fungal endophytes confer host resistance against several different fungal pathogens (Blee and Anderson 2000; Clay and Schardl 2002; Duchesne 1996; Freeman and Rodriguez 1993; Latch 1993). One of the more dramatic examples of this is represented by the behavior of plant pathogenic *Colletotrichum* spe-

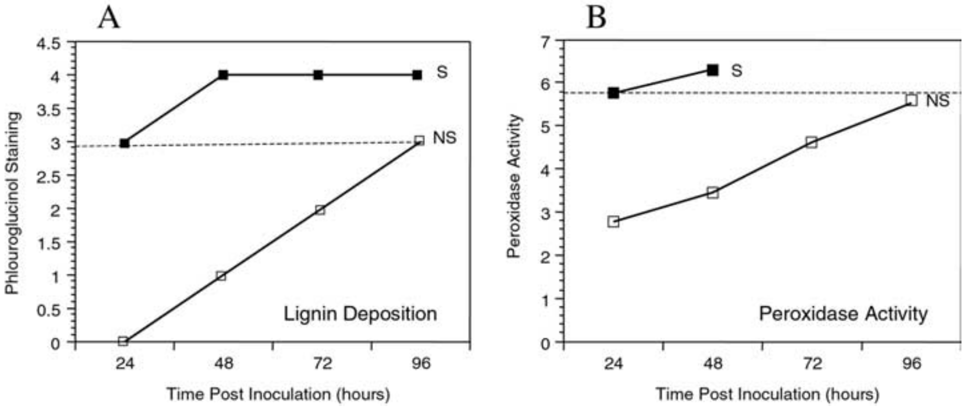

Figure 3. Biochemical response of symbiotic (S, colonized with a non-pathogenic mutant of *C. magna*) and non-symbiotic (NS, mock inoculated) watermelon seedlings to pathogen challenge. S and NS seedlings were prepared and biochemical assays performed as previously described (Redman et al. 1999). Ten plants were assayed for peroxidase activity and lignin deposition every 24 hours post inoculation with a virulent pathogen. Lignin deposition and peroxidase activity are correlated with disease resistance in watermelon plants (Hammerschmidt 1984; Hammerschmidt 1982).

cies in asymptomatic hosts (Redman et al. 2001). Historically, the host range of plant pathogenic fungi has correlated with disease symptoms and if there were no manifested symptoms (asymptomatic), the plant was not considered a host (Ulloa and Hanlin 2001). However, we observed that some pathogenic fungi have both symptomatic and asymptomatic hosts (Redman et al. 2001). Asymptomatic hosts are extensively colonized by fungi without the occurrence of disease symptoms and the fungi express either commensal or mutualistic lifestyles. For example, *Colletotrichum* species have one of three host range and symbiotic lifestyle expression patterns: 1) a narrow host range and a pathogenic lifestyle, 2) a wide host range and a pathogenic lifestyle, or 3) a wide host range and both pathogenic and commensal or mutualistic lifestyles (Table 1). All of these *Colletotrichum* species cause lethality on known symptomatic hosts and therefore, are defined as pathogenic.

The mechanism of how fungal endophytes confer disease resistance is unknown. However, we demonstrated that symbiotic and nonsymbiotic plants respond differently to pathogen challenge (Redman et al. 1999). This was determined by generating mutants of *Colletotrichum magna* that are no longer pathogenic but retain the ability to colonize cucurbit species such as watermelon and squash (Freeman and Rodriguez 1993; Redman et al. 1999a; Redman et al. 2001). Unlike the virulent wildtype from which they were derived, these non-pathogenic mutants express either commensal or mutualistic lifestyles in cucurbit hosts. One of the benefits conferred to hosts by the mutualistic mutants is protection against virulent fungal pathogens. Nonsymbiotic plants respond to pathogen challenge by slowly activating defense systems while plants symbiotic with mutualistic mutants respond by rapidly activating defense systems to high levels (Figure 3). This suggests

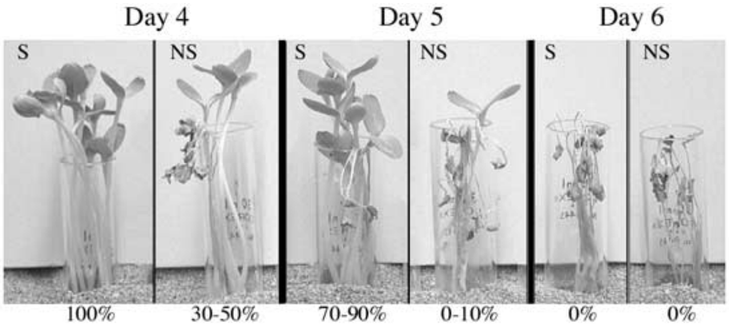

Figure 4. Desiccation tolerance of symbiotic (S, colonized with a non-pathogenic mutualistic mutant of *C. magna*) and non-symbiotic (NS, mock inoculated) watermelon seedlings. The ability of the mutant to confer drought tolerance was measured in 100 S and 100 NS watermelon seedlings (Sugar Baby cultivar). Ten plants were placed in separate 100 ml beakers containing 30 ml water. Every 24 hr, one of the beakers was emptied and the plants left dry. This process was continued for 9 days (the water in one of the beakers was maintained as a control) and all the beakers were re-filled with 30 ml water, the plants left to recover for 48 hours and assessed for mortality. The number of days without water is indicated above the plants and the viability (%) is indicated below.

that communication between host and symbiont increases the ability of plants to perceive a pathogen and rapidly activate defense systems.

It is clear that a single fungal isolate can express pathogenicity in some plant species, and commensalism or mutualism in others. In addition, some fungal endophytes express different symbiotic lifestyles (from mutualism to parasitism) based on host physiology, which changes in response to environmental conditions (Francis and Read, 1995; Graham and Eissenstat 1998; Johnson et al. 1997; Schulz et al. 1999). Therefore, global changes that alter plant physiology may also alter symbiotic communication such that native fungal symbionts express pathogenic rather than mutualistic lifestyles. This could have dramatic impacts on plant community structure and geographic ranges of individual species.

2.3. WATER

Plant responses to water deficits includes osmotic adjustments, production of antioxidants, altered transcriptional and translational regulation, and altered stomatal activity (Griffiths and Parry 2002; Shinozaki and Yamaguchi-Shinozaki 1998). Although all plants respond to water deficit, few species are drought-tolerant and avoid detrimental impacts of water stress (Bray 1993). However, there are numerous reports describing drought tolerance conferred to plants by fungal symbionts (Clay and Schardl 2002). The mechanism of symbiont conferred drought tolerance is not known, although it is thought to involve osmotic adjustments and/or altered stomatal activity (see Malinowski and Belesky 2000). This ability of fungal endophytes to confer drought tolerance has been studied in very few plant species. Fungal endophytes from the forage grass, tall fescue, significantly increase drought tolerance of this species under controlled and field conditions (see Clay and Schardl 2002). The mutualistic *Colletotrichum magna* mutants described above also confer significant drought tolerance to watermelon plants (Figure 4). Moreover, both the nonpathogenic mutants and wildtype *C. magna* asymptomatically colonize non-cucurbit hosts including tomato, and pepper (Redman et al. 2001). In tomato and pepper plants, the mutualistic mutants and wildtype *C. magna* confer drought tolerance that allows symbiotic plants to survive desiccation 24 (tomato) or 48 (pepper) hours longer than nonsymbiotic plants (Redman et al. 2001). This demonstrates the importance of the host genotype in expression and magnitude of benefits conferred by mutualistic fungi. More importantly, the host range of fungal endophytes is greater than previously thought and it is possible for endophytes to colonize distantly related plant species. Therefore, an endophyte responsible for conferring stress tolerance in one plant species could be used to colonize an unrelated asymptomatic host and confer similar benefits.

2.4. SALT

All plants are known to have salt sensitive metabolisms, whether they grow in salt marshes or temperate rainforests (Yeo 1998). However, plants that live in saline environments have developed several mechanisms to tolerate salt stress that include exclusion, compartmentalization or translocation of salt, cellular osmotic adjustments, and/or antioxidant systems (Gilbert et al. 2002; Sairam et al. 2002; Yeo 1998; Yoshida et al. 2003). Although salt stress adaptation by plants is biochemically and genetically complex, some mycorrhizal fungi confer salt tolerance through symbiosis (Al-Karaki et al. 2001; Ruiz-Lozano et al. 1996; Yano-Melo et al. 2003). The physiological basis of fungal-conferred salt tolerance has not been investigated but this appears to be a generalized phenomenon in several plant species including banana, tomato and lettuce. Like thermotolerance, the majority of research on plant salt tolerance focuses on isolated plant species rather than symbiotic partnerships that are more common in nature.

3. Mechanisms of Mutualistic Benefits

Mutualistic fungi may confer several benefits to plants such as tolerance to drought, metals (Read 1999), disease, and temperature, growth enhancement (Marks and Clay 1990; Redman et al. 2002b; Varma et al. 1999), and nutrient acquisition (Read 1999). Symbiotically conferred abiotic and biotic stress tolerance appear to involve two mechanisms: 1) rapid activation of host stress response systems after symbiotic plants are exposed to stress (Redman et al. 1999), or 2) synthesis of anti-stress biochemicals by the fungus (Bacon and Hill 1996). It is not known how endophytes activate host stress response systems or if there are additional mechanisms involved in symbiotically-conferred stress tolerance. The only known anti-stress biochemicals produced by endophytic fungi are alkaloids that decrease plant herbivory (Siegel and Bush 1997). Many of the endophytes that produce anti-herbivory alkaloids also confer drought tolerance to host plants (Bacon and Hill 1996). Although the mechanism of endophyte conferred drought tolerance is unknown, it is correlated with the activation of host stress response systems (Auge 2000). Therefore, we propose that, in addition to anti-stress chemicals, plant/fungal mutualisms have been maintained over evolutionary time by the ability of fungi to control the activation of host stress response systems and in essence, act as ‘biological triggers’. This is supported by the fact that symbiotic plants activate defense systems more quickly than non-symbiotic plants after pathogen challenge; all plants studied, including ancient lineages such as liverworts, ferns, and mosses are symbiotic with endophytic fungi; and symbiotic fungi (Auge 2000) have been associated with plants $\geq$400 mya (Pirozynski and Malloch 1975; Redecker et al. 2000; Remy et al. 1994; Simon et al. 1993). Although there are several potential biochemical mechanisms that the host may use to overcome stress, the symbiotic communication that leads to activation of host stress response systems is unknown.

4. Adaptive Symbiosis as a Strategy for Mitigating Global Change

As global changes continue to increase environmental stresses on plant communities, it is critical to begin developing strategies to mitigate detrimental impacts of these stresses on terrestrial and aquatic ecosystem health and agricultural productivity. More than 120 years after the first description of symbiosis, it is clear that all plants are symbiotic with fungi. In some high stress environments these symbioses are responsible for plant survival and although the universality of this observation is not known, it is possible that fungal symbionts are required for plant survival in all high stress environments. In addition, host range observations with *Colletotrichum* species indicate that fungal species expressing non-mutualistic lifestyles in specific hosts may establish mutualistic symbioses with genetically unrelated plant species and confer stress (disease and/or drought) tolerance. If this is common, it may be possible to use fungal endophytes from hosts thriving in high stress environments to confer desirable traits such as drought, temperature, disease, and salt tolerance to genetically unrelated stress-sensitive plant species. This would allow native plants and agricultural crops to be generated with new capabilities for tolerating specific environmental stresses brought about by global change.

5. Conclusion

The genetic and biochemical bases of plant/fungal symbiotic communication is not known. However, once the basis of symbiotic communication is elucidated it may be possible to develop predictive capabilities for establishing symbioses between specific fungi and plants to achieve desirable stress tolerance specific to geographic regions. In doing so, fungal symbiosis may provide an inexpensive and viable strategy for mitigating the impacts of global change on plants and plant communities.

References

Al-Karaki, G.N., Hammad, R. and Rusan, M.: 2001, ‘Response of two tomato cultivars differing in salt tolerance to inoculation with mycorrhizal fungi under salt stress’, *Mycorrhiza* **11**, 43–47.

Auge, R.M.: 2000, ‘Stomatal behavior of arbuscular mycorrhizal plants’, in Y. kapulnik and D.D. Douds (eds.), *Arbuscular Mycorrhizas: Physiology and Function*, Dordrecht, Kluwer Academic Publishers, pp. 201–236.

Bacon, C.W. and Hill, N.S.: 1996, ‘Symptomless grass endophytes: products of coevolutionary symbioses and their role in the ecological adaptations of grasses’, in S.C. Redkin and L.M. Carris (eds.), *Endophytic Fungi in Grasses and Woody Plants*, St. Paul, APS Press, pp. 155–178.

Blee, K.A. and Anderson, A.J.: 2000, ‘Defense responses in plants to arbuscular mycorrhizal fungi’, in G.K. Podila and D.D. Douds (eds.), *Current Advances in Mycorrhizal Research*, St. Paul, APS Press, pp. 27–44.

Bray, E.A.: 1993, ‘Alterations in gene expression in response to water deficit’, in A.S. Basra (ed.), *Stress-Induced Gene Expression in Plants*, Chur, Harwood Academic Publishers GmbH, pp. 1–23.

Clay, K. and Holah, J.: 1999, ‘Fungal endophyte symbiosis and plant diversity in successional fields’, *Science* **285**, 1742–1744.

Clay, K. and Schardl, C.: 2002, ‘Evolutionary origins and ecological consequences of endophyte symbiosis with grasses’, *The American Naturalist* **160, Supplement**, S99-S127.

Dangl, J.L., Dietrich, R.A. and Richberg, M.H.: 1996, ‘Death don’t have no mercy: cell death programs in plant-microbe interactions’, *Plant cell* **8**, 1793–1807.

De Bary, A.: 1879, ‘Die Erschenung Symbiose’, in K.J. Trubner (ed.), *Vortrag auf der Versammlung der Naturforscher und Artze zu Cassel*, Strassburg, pp. 1–30.

Duchesne, L.C.: 1996, ‘Role of ectomycorrhizal fungi in biocontrol’, in F.L. Pfleger and R.G. Linderman (eds.), *Mycorrhizae And Plant Health*, St. Paul, APS Press, pp. 27–46.

Francis, R. and Read, D.J.: 1995, ‘Mutualism and antagonism in the mycorrhizal symbiosis, with special reference to impacts on plant community structure’, *Can. J. Botany* **73**, S1301–S1309.

Freeman, S. and Rodriguez, R.J.: 1993, ‘Genetic conversion of a fungal plant pathogen to a nonpathogenic, endophytic mutualist’, *Science* **260**, 75–78.

Gilbert, G.S., Mejia-Chang, M. and Rojas, E.: 2002, ‘Fungal diversity and plant disease in mangrove forests: salt excretion as a possible defense mechanism’, *Oecologia* **132**, 278–285.

Graham, J.H. and Eissenstat, D.M.: 1998, ‘Field evidence for the carbon cost of citrus mycorrhizas’, *New Phytol.* **140**, 103–110.

Griffiths, H. and Parry, M.A.J.: 2002, ‘Plant responses to water stress’, *Ann. Botany* **89**, 801–802.

Hammerschmidt, R., Lamport, D.T.A. and Muldoon, E.P.: 1984, ‘Cell wall hydroxyproline enhancement and lignin deposition as an early event in the resistance of cucumber to *Cladisporium cucumerinum*’, *Physiol. Plant Pathol.* **24**, 43–47.

Hammerschmidt, R., Nuckles, E.M. and Kuc, J.: 1982, ‘Association of enhanced peroxidase activity and induced systemic resistance of cucumber to *Colletotrichum lagenarium*’, *Physiol. Plant Pathol.* **20**, 73–82.

Hertig, M., Taliaferro, W.H. and Schwartz, B.: 1937, ‘The terms symbiosis, symbiont and symbiote’, *J. Parasitology* **23**, 326–329.

Iba, K.: 2002, ‘Acclimative response to temperature stress in higher plants: approaches of gene engineering for temperature tolerance’, *Ann. Rev. Plant Biol.* **53**, 225–245.

Johnson, N.C., Graham, J.H. and Smith, F.A.: 1997, ‘Functioning of mycorrhizal associations along the mutualism-parasitism continuum’, *New Phytol.* **135**, 575–586.

Kuc, J. and Strobel, N.E.: 1992, ‘Induced resistance using pathogens and nonpathogens’, in E.S. Tjamos (ed.), *Biological Control of Plant Diseases*, New York, Plenum Press, pp. 295–303.

Latch, G.C.M.: 1993, ‘Physiological interactions of endophytic fungi and their hosts. Biotic stress tolerance imparted to grasses by endophytes’, *Agric. Ecosyst. & Envir.* **44**, 143–156.

Lewis, D.H.: 1985, ‘Symbiosis and mutualism: Crisp concepts and soggy semantics’, in D.H. Boucher (ed.), *The Biology of Mutualism*, London, Croom Helm Ltd, pp. 29–39.

Malinowski, D.P. and Belesky, D.P.: 2000, ‘Adaptations of endophyte-infected cool-season grasses to environmental stresses: mechanisms of drought and mineral stress tolerance’, *Crop Sci.* **40**, 923–940.

Marks, S. and Clay, K.: 1990, ‘Effects of CO2 enrichment, nutrient addition, and fungal endophyte-infection on the growth of two grasses’, *Oecologia* **84**, 207–214.

Morton, J.B.: 2000, ‘Biodiversity and evolution in mycorrhizae in the desert’, in C.W. Bacon and J.F.J. White (eds.), *Microbial Endophytes*, New York, NY, Marcel Dekker, Inc., pp. 3–30.

Murray, M.: 1997, *Carbon Dioxide and Plant Responses*, Somerset: Research Studies Press LTD., pp. 275.

Parry, M.: 1990, *Climate Change and World Agriculture*, London: Earthscan Publications Ltd., pp. 157.

Petrini, O.: 1986, ‘Taxonomy of endophytic fungi of aerial plant tissues’, in N.J. Fokkema and J. van den Heuvel (eds.), *Microbiology of the Phyllosphere*, Cambridge, Cambridge University Press, pp. 175–187.

Pirozynski, K.A. and Malloch, D.W.: 1975, ‘The origin of land plants a matter of mycotrophism’, *Biosystems* **6**, 153–164.

Read, D.J.: 1999, ‘Mycorrhiza – the state of the art’, in A. Varma and B. Hock (eds.), *Mycorrhiza*, Berlin, Springer-Verlag, pp. 3–34.

Redecker, D., Kodner, R. and Graham, L.E.: 2000, ‘Glomalean fungi from the Ordovician’, *Science* **289**, 1920–1921.

Redman, R.S., Ranson, J. and Rodriguez, R.J.: 1999a, ‘Conversion of the pathogenic fungus *Colletotrichum magna* to a nonpathogenic endophytic mutualist by gene disruption’, *Mol. Plant Micr. Int.* **12**, 969–975.

Redman, R.S., Dunigan, D.D. and Rodriguez, R.J.: 2001, ‘Fungal symbiosis: from mutualism to parasitism, who controls the outcome, host or invader? *New Phytol.* **151**, 705–716.

Redman, R.S., Sheehan, K.B., Stout, R.G., Rodriguez, R.J. and Henson, J.M.: 2002a, ‘Thermotolerance Conferred to Plant Host and Fungal Endophyte During Mutualistic Symbiosis’, *Science* **298**, 1581.

Redman, R.S., Freeman, S., Clifton, D.R., Morrel, J., Brown, G. and Rodriguez, R.J.: 1999, ‘Biochemical analysis of plant protection afforded by a nonpathogenic endophytic mutant of *Colletotrichum magna*’, *Plant Physiol.* **119**, 795–804.

Redman, R.S., Roossinck, M.J., Maher, S., Andrews, Q.C., Schneider, W.L. and Rodriguez, R.J.: 2002b, ‘Field performance of cucurbit and tomato plants colonized with a nonpathogenic mutant of *Colletotrichum magna* (teleomorph: Glomerella magna; Jenkins and Winstead), *Symbiosis* **32**, 55–70.

Remy, W., Taylor, T.N., Hass, H. and Kerp, H.: 1994, ‘Four hundred-million-year-old vesicular arbuscular mycorrhizae’, *Proc. Nat. Academy of Science* **91**, 11841–11843.

Rodriguez, R.J. and Redman, R.S.: 1997, ‘Fungal life-styles and ecosystem dynamics: biological aspects of plant pathogens, plant endophytes and saprophytes’, *Adv. Bot. Res.* **24**, 169–193.

Ruiz-Lozano, J.M., Azcon, R. and Gomez, M.: 1996, ‘Alleviation of salt stress by arbuscular-mycorrhizal *Glomus* species in *Lactuca sativa* plants’, *Physiologia Plantarum* **98**, 767–772.

Ryals, J.A., Neuenschwander, U.H., Willits, M.G., Molina, A., Steiner, H.Y. and Hunt, M.D.: 1996, 'Systemic acquired resistance', *The Plant Cell* **8**, 1809–1819.

Sairam, R.K., Rao, K.V. and Srivastava, G.C.: 2002, 'Differential response of wheat genotypes to long term salinity stress in relation to oxidative stress, antioxidant activity and osmolyte concentration', *Plant Sci.* **163**, 1037–1046.

Schulz, B., Rommert, A.K., Dammann, U., Aust, H.J. and Strack, D.: 1999, 'The endophyte-host interaction: a balanced antagonism? *Mycol. Res.* **10**, 1275–1283.

Shinozaki, K. and Yamaguchi-Shinozaki, K.: 1998, 'Molecular responses to drought stress', in K. Satoh and N. Murata (eds.), *Stress Responses of Photosynthetic Organisms: Molecular Mechanisms and Molecular Regulations*, Amsterdam, Elsvevier Science B.V., pp. 149–163.

Siegel, M.R. and Bush, L.P.: 1997, 'Toxin production in grass/endophyte associations', in G.C. Carroll and P. Tudzynski (eds.), *The Mycota*, Heidelberg, Springer-Verlag, pp. 185–207.

Simon, L., Bousquet, J., Levesque, R.C. and Lalonde, M.: 1993, 'Origin and diversification of endomycorrhizal fungi and coincidence with vascular land plants', *Nature* **363**, 67–69.

Smallwood, M.F., Calvert, C.M. and Bowles, D.J.: 1999, *Plant Responses to Environmental Stress*, Oxford, BIOS Scientific Publishers Limited, pp. 224.

Smith, K.P. and Goodman, R.M.: 1999, 'Host variation for interactions with beneficial plant-associated microbes', *Ann. Rev. Phytopathol.* **37**, 473–492.

Stout, R.G. and Al-Niemi, T.S.: 2002, 'Heat-tolerance flowering plants of active geothermal areas in Yellowstone National Park', *Ann. Botany* **90**, 259–267.

Ulloa, M. and Hanlin, R.T.: 2001, *Illustrated Dictionary of Mycology*, St. Paul, APS Press, pp. 448.

Varma, A., Verma, S., Sudha, Sahay, N., Butehorn, B. and Franken, P.: 1999, '*Piriformospora indica*, a cultivable plant-growth-promoting root endophyte', *Appl. Envir. Microbiol.* **65**, 2741–2744.

Yano-Melo, A.M., Saggin, O.J. and Maia, L.C.: 2003, 'Tolerance of mycorrhized banana (*Musa* sp. cv. Pacovan) plantlets to saline stress', *Agric. Ecosyst. & Envir.* **95**, 343–348.

Yeo, A.: 1998, 'Molecular biology of salt tolerance in the context of whole-plant physiology', *J. Exper. Botany* **49**, 915–929.

Yoshida, K., Kaothien, P., Matsui, T., Kawaoka, A. and Shinmyo, A.: 2003, 'Molecular biology and application of plant peroxidase genes', *Appl. Microbiol. & Biotechnol.* **60**, 665–670.