Effects of Arbuscular Mycorrhizal Fungi and Intercropping with Bahiagrass on Growth and Anti-oxidative Enzyme Activity of Radish

Atsushi Matsumura*, Sachie Horii and Takaaki Ishii

Graduate School of Agriculture, Kyoto Prefectural University, Shimogamohangi-cho, Sakyo-ku, Kyoto 606–8522, Japan

Effects of bahiagrass (Paspalum notatum Flügge.) intercropping and arbuscular mycorrhizal fungi (AMF), Gigaspora margarita Becker and Hall, on the growth and activities of anti-oxidative enzymes (superoxide dismutase (SOD) and catalase (CAT)) in radish (Raphanus sativus L. ‘Midoribijin’), a non-host plant, was studied. Radish was grown with and without bahiagrass in a root box system divided into 5 compartments which allows AMF hyphae, but not roots, to enter between compartments. Pots without AMF inoculation were prepared as a control. G. margarita by itself had no significant effect on radish growth. Radish roots were colonized by G. margarita only when intercropped with bahiagrass; however, no arbuscule was observed and a lot of new spores were found on the radish root. Protein contents of radish roots were increased, but the plant biomass of radish, and the activities of SOD and CAT of roots were significantly decreased by AMF root colonization. These results suggest that the unavoidable invasion of hyphae into non-host plant roots due to intercropping with host plants, such as bahiagrass, that strongly promote AMF growth would result in the decline of non-host plants.

Key Words: anti-oxidative enzyme activity, arbuscular mycorrhizal fungi, bahiagrass, non-host, radish.

Introduction

More than 80% of land plants are colonized by arbuscular mycorrhizal fungi (AMF). AMF hosts normally show an improved nutritional state when inoculated with AMF, especially regarding soil nutrients with a low mobility, like phosphorus (Rhodes and Gerdemann, 1980). But some families of plants such as Cruciferae, Caryophyllaceae, Chenopodiaceae, and Polygonaceae, called ‘non-host’ or ‘non-mycorrhizal’ plants, do not form AMF symbiosis (Francis and Read, 1994). However, there are some reports of the AMF colonization of non-host roots when they are grown together with host plants (Allen and Allen, 1984; Byrne and Mitchell, 2004; Poole and Sylvia, 1990). These reports suggest that the non-host plants prevent the establishment of a functional AMF symbiosis. Allen and Allen (1984) reported that inoculation of Salsola kali with AMF, in the presence of mycorrhizal grasses, resulted in reduced stomatal conductance and survival compared with un-inoculated plants.

Generally, it is suggested that higher anti-oxidative enzyme activities such as superoxide dismutase (SOD) and catalase (CAT) involved in the elimination of active oxygen in cells are detected more in AMF-inoculated roots compared with un-inoculated roots (Arines et al., 1994; Blilou et al., 2000). These enzymes are involved in the detoxification of O₂ radicals and H₂O₂, thereby preventing the formation of OH radicals. SOD and CAT react with active forms of oxygen, keeping them at a low level (Smirnoff, 1993). Also, these anti-oxidative enzymes constitute an important primary defense mechanism of cells against superoxide free radicals generated under stress conditions (Bowler et al., 1992; Foyer et al., 1994; Tsang et al., 1991). However, there is little information on the effect of AMF and intercropping with a host plant on the anti-oxidative enzyme activities of non-host plants.

In this study, we used special pots divided into a compartment system that allows fungal hyphae to penetrate but not roots, which contained seedlings of a non-host plant to reveal the direct action of AMF on non-host plants. Bahiagrass (Paspalum notatum Flügge.) was used as the intercropping (companion) plant because of its strong ability to proliferate AMF (Cruz et al., 2000, 2004; Ishii et al., 1997). The effect of an AMF, G. margarita, on the growth and anti-oxidative enzyme activities of radish (Raphanus sativus L. ‘Midoribijin’) intercropped with bahiagrass was investigated to clarify
some mechanisms involving anti-oxidative enzyme activities induced by AMF hyphal invasion of non-host plant roots.

**Materials and Methods**

Acrylic boxes (4-cm wide, 55-cm long, and 15-cm deep) divided into five compartments were constructed. The two inoculation compartments (C: 4-cm wide, 5-cm long, and 15-cm deep), located 15 cm from both extremes of the root box, were separated from the lateral compartment by a barrier made of a nylon screen with a 41 µm mesh that allows the AMF hyphae but not the roots to penetrate. Each box was filled with a substrate mixture of vermiculite, zeolite, and perlite = 2 : 1 : 1 (v/v/v).

Four radish seeds were sown in the center compartment (A) of all boxes; then, after 1 week, radish plants were reduced to one plant. Bahiagrass seedlings were pre-germinated in trays containing sterile vermiculite, and transplanted into the two compartments (B) neighboring the center one of the half-root boxes (Fig. 1).

Inoculation was done with about 200 spores of AMF, *G. margarita*, collected from inoculum (unpublished data) in the compartments (C) (Fig. 1). The boxes were covered with an aluminum film to block light penetration and kept in a greenhouse without a temperature-controlling system. This experiment was started on 3 July.

All boxes were supplied with sufficient water daily. Each box was given 90 ml (30 mL per compartment except for inoculation sites) of macronutrients every 10 days, and 10 ml of micronutrients every 20 days using Hoagland solution. This experiment comprised a 2 × 2 factorial design consisting in total of 16 experimental units with 4 replications: inoculated with or without AMF, and radish only or radish intercropped with bahiagrass.

Three months later, the plants were harvested, and plant biomass, consisting of the total fresh weight (TFW), root fresh weight (RFW), and the number of leaves was measured. Chlorophyll was extracted in 80% acetone from leaf samples and the concentration was analyzed using a spectrophotometer (Shimadzu UV-120-02, Shimadzu Corporation, Kyoto, Japan) at 645 nm and 663 nm for chlorophyll a and b, respectively (Kirk, 1968). Apical parts of the fine roots of radish and bahiagrass were sampled for root colonization and scanning electron microscopic (SEM) observation. To determine root colonization, roots were stained by the technique of Phillips and Hayman (1970), and then the percentage of root colonization was determined according to Ishii and Kadoya (1994). Ten root segments, 1 cm in length, from each radish and bahiagrass plant in the AMF treatments were examined for the presence of arbuscules and spores formed inside and outside roots. Soil samples (20 g DW) from each plant’s compartment were taken to evaluate the number of spores according to the procedure of Ishii et al. (1996).

The remains of each plant root were preserved at −20°C for analyzing anti-oxidative enzyme activities. Roots (0.3 g FW) from each plant were homogenized with liquid nitrogen, and then homogenized again in 5 ml extraction medium (50 mM K-P buffer, pH 7.8). The homogenates were centrifuged at 15000 rpm for 20 min at 4°C. The supernatants were used for the determination of the protein content, SOD activity, and CAT activity. The protein content was determined by the method of Lowry et al. (1951), using bovine serum albumin as a standard. SOD activity was measured spectrophotometrically by the cytochrome c method using xanthine/xanthine oxidase as the source of superoxide radicals. One unit of activity was defined as the amount of enzyme necessary to produce a 50% inhibition of the cytochrome c reduction rate (McCord

![Fig. 1](image-url)  Design of a root box for intercropping with bahiagrass. Broken lines show nylon screens with a 41 µm mesh that allows AMF hyphae but not roots to penetrate.
and Fridovich, 1969). CAT activity was determined by the degradation of H$_2$O$_2$ according to Aebi (1984).

**Results**

**Effect of intercropping with bahiagrass on plant biomass and AMF root colonization**

TFW, RFW, and the number of leaves of radish were not affected by AMF inoculation alone. However, intercropping with bahiagrass without AMF slightly decreased TFW and RFW of radish, and this growth decline was significantly increased by AMF inoculation. The chlorophyll content was highest in un-inoculated treatment without bahiagrass. TFW and RFW of bahiagrass were not affected by AMF (Table 1).

**Table 1.** Effect of *Gigaspora margarita* and intercropping with bahiagrass on total fresh weight (TFW), root fresh weight (RFW), number of leaves, and chlorophyll content of radish and bahiagrass.

| Treatment $^a$ | TFW (g) | RFW (g) | Number of leaves (number/plant) | Chlorophyll content (mg·g$^{-1}$ FW) |
|---------------|---------|---------|---------------------------------|-------------------------------------|
| **Radish**    |         |         |                                 |                                     |
| − AMF R       | 70.8±8.1$^y$ | 41.9±6.7 | 12.0±0.7                        | 0.73±0.02                           |
| − AMF R+B     | 54.7±4.8 | 32.1±2.6 | 11.3±0.6                        | 0.64±0.02                           |
| + AMF R       | 73.2±7.5 | 32.1±3.9 | 12.5±0.6                        | 0.64±0.02                           |
| + AMF R+B     | 31.6±4.3 | 13.7±3.0 | 9.0±0.4                         | 0.64±0.03                           |
| **Bahiagrass** |         |         |                                 |                                     |
| − AMF         | 82.9±9.5 | 26.7±4.1 | —                               | —                                   |
| + AMF         | 85.8±7.7 | 26.0±2.8 | —                               | —                                   |

$^a$ Each treatment indicates radish only (R) and radish intercropped with bahiagrass (R + B) in the rootbox, along with AMF inoculation (+ AMF) or non-inoculation (− AMF).

$^y$ Mean ± SE (n = 4).

**Fig. 2.** Photomicrographs of *Gigaspora margarita*-inoculated radish roots intercropped with bahiagrass. a) Bahiagrass roots colonized with G. *margarita*; b) Arbuscule formation in an epidermal cell of a bahiagrass root; c) G. *margarita* hyphae and spores in/on radish roots; d) Spores formed on the surface of radish roots; e) Scanning electron micrograph of G. *margarita* hyphae invading radish roots. The arrow indicates the invasion site of hyphae; f) Scanning electron micrograph of new spore formation of G. *margarita* on radish roots. Scale bars = a) 500 µm, b) 20 µm, c) 500 µm, d) 100 µm, e) 20 µm, f) 50 µm. A: arbuscule, H: hypha, S: spore.
The rate of radish root colonization was very low, and few hyphae were observed on the surface of roots when the plants were grown alone with G. margarita, but hyphal presence was significantly increased to 57.1% when intercropped with bahiagrass and inoculated with G. margarita; however, no arbuscule was observed, as shown in the photomicrographs (Fig. 2). Bahiagrass roots were well colonized by G. margarita, the average rate of colonization was about 79.2% (Fig. 2). Arbuscules were abundant in all colonized roots of bahiagrass (Table 2). The number of spores formed inside and outside roots was higher in radish than in bahiagrass roots. But, contrary to what happened around the roots, the number of spores produced in bahiagrass compartment soil was higher than in that of radish when intercropped with bahiagrass. The number of spores in soil was very low when radish was grown alone.

**Table 2.** Effect of intercropping with bahiagrass on root colonization, number of arbuscules, number of spores in/on roots, and number of Gigaspora margarita spores in radish and bahiagrass soil.

| Treatment | AMF propagules in/around radish and bahiagrass |  |
|-----------|---------------------------------------------|---|
|           | Root colonization (%) | Arbuscule (number/cm) | Spore (number/cm root) | Spore (number/20 g DW soil) |
| Radish    |                             |                            |                         |                           |
| − AMF     | R                            | 0                           | 0                       | 0                          |
|           | R + B                        | 0.5 ± 0.3                  | 0                       | 12.0 ± 4.3                 |
| + AMF     | R                            | 57.1 ± 5.3                 | 0.57 ± 0.43             | 161.0 ± 24.7               |
|           |                             |                             |                         |                           |
| Bahiagrass| − AMF                        | 0                           | 28.4 ± 4.5              | 1.06 ± 0.29               |
|           | + AMF                        | 79.2 ± 1.8                 | 28.4 ± 4.5              | 1.06 ± 0.29               |

* Each treatment indicates radish only (R) and radish intercropped with bahiagrass (R + B) in the rootbox, along with AMF inoculation (+ AMF) or non-inoculation (− AMF).

**Table 3.** Effect of Gigaspora margarita and intercropping with bahiagrass on protein content, SOD activity, and CAT activity in radish and bahiagrass.

| Treatment | Protein content (mg·g⁻¹) | SOD (unit/mg protein) | CAT (µmol H₂O₂ destroyed/min/mg protein) |
|-----------|--------------------------|-----------------------|----------------------------------------|
| Radish    |                          |                       |                                        |
| − AMF     | R                        | 3.0 ± 0.2             | 50.7 ± 4.6                           |
|           | R + B                    | 2.5 ± 0.1             | 53.1 ± 2.4                           |
| + AMF     | R                        | 3.0 ± 0.3             | 47.5 ± 2.4                           |
|           | R + B                    | 3.8 ± 0.3             | 36.4 ± 1.7                           |
| Bahiagrass| − AMF                    | 4.2 ± 0.3             | 53.7 ± 5.4                           |
|           | + AMF                    | 5.5 ± 0.2             | 47.8 ± 3.7                           |

* Each treatment indicates radish only (R) and radish intercropped with bahiagrass (R + B) in the rootbox, along with AMF inoculation (+ AMF) or non-inoculation (− AMF).

The results showed the detrimental effects of the combination of AMF and intercropping with an AMF host plant on the growth and anti-oxidative enzyme activities of a non-host plant. Other studies involving incompatible AMF associations have been reported (Allen and Allen, 1984; Byrne and Mitchell, 2004; Francis and Read, 1994), and growth reduction was attributed to the inhibition of root growth either by the direct action of AMF or by inhibitory compounds.
released from AMF (Allen and Allen, 1984; Francis and Read, 1994). In this experiment, the growth reduction of radish by intercropping with bahiagrass without AMF would be due to competition for relatively mobile nutrients. But the root growth of radish was remarkably decreased by AMF root colonization. These results support previous research (Allen and Allen, 1984; Byrne and Mitchell, 2004; Francis and Read, 1994).

It is suggested that some AMF non-host plants lack signals essential for root colonization, whereas root exudates of AMF non-host plants contain inhibitory compounds for AMF (Giovannetti, 2000; Giovannetti and Sbrana, 1998; Vierheilig et al., 1998). In this experiment, however, radish roots were colonized by AMF when the plants were intercropped with bahiagrass. There are some reports of root colonization of non-hosts grown together with host plants (Allen and Allen, 1984; Byrne and Mitchell, 2004; Poole and Sylvia, 1990). It is reported that bahiagrass root extracts contain some AMF growth stimulants (Ishii et al., 1997), and intercropping with bahiagrass increases the AMF hyphal density in the rhizosphere (Cruz et al., 2000, 2002). Root exudates are the first stages of host recognition that govern signaling between AMF and their host plants, and would play an important role in the establishment of AMF symbiosis. Our results show that the exudates released from bahiagrass roots including a certain strong AMF growth stimulant may result in an improper hyphal invasion, as if the radish is a host plant.

In this experiment, a lot of arbuscules were observed in AMF-inoculated bahiagrass roots, but no arbuscule was observed in radish roots even when intercropped with bahiagrass. Meanwhile, AMF formed many spores inside and outside radish roots instead of forming arbuscules. Although the mechanisms of spore formation of AMF are not well known, it is thought that a certain stress is related to new spore formation (Ishii et al., 2003). In this experiment, we hypothesize that spore formation on the surface of radish roots was induced by certain chemical substances in radish exudates. It is suggested that root exudates from non-host plants significantly inhibited in vitro AMF hyphal growth (Cruz et al., 2002), and it is known that Brassicaceae species contain high levels of glucosinolates in their roots (Walker et al., 1937). These substances are known to inhibit microorganisms in soil (Lazzeri et al., 1993; Maniei et al., 1997). AMF might be stressed by non-host plant root exudates, and then form spores to tolerate such adverse conditions.

In this experiment, activities of SOD and CAT of radish roots were decreased by AMF root colonization. Arines et al. (1994) reported that a higher SOD activity was detected in AMF-inoculated pea roots compared with un-inoculated roots. It is suggested that increased SOD activity in AMF plants was directly correlated with enhanced plant production and drought resistance (Ruiz-Lozano et al., 1996). Induction of CAT activities was associated with the higher growth rates of the most infective mycorrhizal fungus at low P conditions, (Lambais et al., 2003). Garcia-Garrido and Ocampo (2002) also reported that anti-oxide enzyme activities would become stronger at later stages, such as arbuscule formation, compared to those in the early stage of root colonization, such as appressorium formation and hyphal penetration into roots. In this experiment, SOD and CAT activities in radish root were significantly decreased in radish inoculated by AMF with bahiagrass, whereas, these enzymes activities were not decreased in bahiagrass roots, and CAT activity was increased by AMF root colonization. These results indicate that arbuscule formation is the key event in the induction of these enzymes. Salzer et al. (1999) suggested that the induction of CAT activity in AMF-inoculated plants might be associated with higher levels of H₂O₂ observed in cells containing arbuscules. We suggest that the reduction of anti-oxidative enzyme activities in AMF non-host plants is due to compulsory AMF invasion into the roots. Gollotte et al. (1993) observed a stronger defense response characterized by the deposition of callose, PR-1 protein, and phenolics when non-host plants were challenged with AMF. The suppression of CAT activity has also been observed in incompatible plant-pathogen interactions (Ádám et al., 1995; Milosevic and Slusarenko, 1996). Therefore, these continuous defense responses to AMF hyphal invasion might reduce the growth and anti-oxidative enzyme activities of radish.

In conclusion, these results suggest that the enforced invasion of AMF hyphae into the roots of non-host plants would induce plant growth inhibition. This suggests that it would be deleterious for non-host plants to be cultivated in environments where AMF host plants have already been dominant and an AMF hyphal network has been established in the soil, resulting in a decreased yield of non-host plants. However, the abundant spore formation observed on the surface of non-host roots when intercropped with bahiagrass makes these results interesting. Further elucidation of this phenomenon would provide information on the mechanism of AMF spore formation.

**Literature Cited**

Allen, E. B. and M. F. Allen. 1984. Competition between plants of different successional stages: mycorrhizas as regulators. Can. J. Bot. 62: 2625–2629.

Ádám, A. L., C. S. Bestwick, B. Barna and J. W. Mansfield. 1995. Enzymes regulating the accumulation of active oxygen species during the hypersensitive reaction of bean to *Pseudomonas syringae* pv. *phaseolicola*. Planta 197: 240–249.

Aebi, H. 1984. Catalase in vitro. p. 121–126. In: L. Packer (ed.). Methods in enzymology. Academic Press, New York.

Arines, J., M. Quintela, A. Vilariño and J. M. Palma. 1994. Protein patterns and superoxide dismutase activity in non-mycorrhizal and arbuscular mycorrhizal *Pisum sativum* L. plants. Plant Soil 166: 37–45.
Bilou, I., P. Bueno, J. A. Ocampo and J. Garcia-Garrido. 2000. Induction of catalase and ascorbate peroxidase activities in tobacco roots inoculated with the arbuscular mycorrhizal Glomus mosseae. Mycol. Res. 104: 722–725.

Bowler, C., M. Van Montagu and D. Inzé. 1992. Superoxide dismutase and stress tolerance. Ann. Rev. Plant Physiol. Plant Mol. Biol. 43: 83–116.

Byrne, K. and D. T. Mitchell. 2004. Responses of mycorrhizal and non-mycorrhizal Erica cinerea and Vaccinium macrocarpon to Glomus mosseae. Mycorrhiza 14: 31–36.

Cruz, A. F., T. Ishii, I. Matsumoto and K. Kadoya. 2002. Network establishment of vesicular-arbuscular hyphae in the rhizosphere of trifoliate orange and Bahia grass seedlings under an intercropping system. J. Japan. Soc. Hort. Sci. 69: 237–242.

Cruz, A. F., T. Ishii, I. Matsumoto and K. Kadoya. 2004. Relationship between arbuscular mycorrhizal fungal development and eupalitin content in bahiagrass roots grown in a Satsuma mandarin orchard. J. Japan. Soc. Hort. Sci. 73: 529–533.

Foyer, C. H., M. Lelandais and K. J. Kunert. 1994. Photooxidative stress in plants. Physiol. Plant. 92: 696–717.

Francis, R. and D. J. Read. 1994. The contributions of mycorrhizal fungi to the determination of plant community structure. Plant Soil 159: 11–25.

García-Garrido, J. M. and J. A. Ocampo. 2002. Regulation of the plant defence response in arbuscular mycorrhizal symbiosis. J. Exp. Bot. 53: 1377–1386.

Giovannetti, M. 2000. Spore germination and pre-symbiotic mycelial growth. p. 47–68. In: Y. Kapulnik and D. D. Douds (eds.). Arbuscular mycorrhizae: physiology and function. Kluwer, Dordrecht.

Giovannetti, M. and C. Sbrana. 1998. Meeting a non-host: the behaviour of AM fungi. Mycorrhiza 8: 123–130.

Gollotte, A., V. Gianinazzi-Pearson, M. Giovannetti, C. Sbrana, L. Avio and S. Gianinazzi. 1993. Cellular localization and cytochemical probing of resistance reactions to arbuscular mycorrhizal fungi in a ‘locus a’ mutant Pisum sativum. Planta 191: 112–122.

Ishii, T. and K. Kadoya. 1994. Effects of charcoal as a soil conditioner on citrus growth and vesicular-arbuscular mycorrhizal development. J. Japan. Soc. Hort. Sci. 63: 529–535.

Ishii, T., Y. H. Shrestha and K. Kadoya. 1996. Effect of sod culture system of Bahia grass (Paspalum notatum Flügge.) on vesicular-arbuscular mycorrhizal formation of Satsuma mandarin trees. Proc. Int. Soc. Citriculture 2: 822–824.

Ishii, T., A. Narutaki, K. Sawada, J. Aikawa, I. Matsumoto and K. Kadoya. 1997. Growth stimulatory substances for vesicular-arbuscular mycorrhizal fungi in Bahia grass (Paspalum notatum Flügge.) roots. Plant Soil 196: 301–304.

Ishii, T., Y. Yachi, K. Oida, A. Matsumura and S. Horii. 2003. Improvement of axenic culture of arbuscular mycorrhizal fungi. ICOM 4: 696 (Abstr.).

Kirk, J. T. O. 1968. Studies on the dependence of chlorophyll synthesis on protein synthesis in Euglena gracilis, together with a monogram for determination of chlorophyll concentration. Planta 78: 200–207.

Lambais, M. R., W. F. Rios-Ruiz and R. M. Andrade. 2003. Antioxidant responses in bean (Phaseolus vulgaris) roots colonized by arbuscular mycorrhizal fungi. New Phytol. 160: 421–428.

Lazzeri, L., R. Taccconi and S. Palmieri. 1993. In vitro activity of some glucosinolates and their reaction products towards a population of the nematode Heterodera schachtii. J. Agric. Food Chem. 41: 825–829.

Lowry, O. H., N. J. Rosebrough, A. L. Farr and R. J. Randall. 1951. Protein measurement with the folin phenol reagent. J. Biol. Chem. 193: 265–275.

Manie, L. M., L. Lazzeri and S. Palmieri. 1997. In vitro fungitoxic activity of some glucosinolates and their enzyme-derived products toward plant pathogenic fungi. J. Agri. Food Chem. 45: 2768–2773.

McCord, J. M. and I. Fridovich. 1969. Superoxide dismutase: an enzyme function for erythrocyteopin. J. Biol. Chem. 244: 6049–6055.

Milosevic, N. and A. J. Slsarenko. 1996. Active oxygen metabolism and lignification in the hypersensitive response in bean. Physiol. Mol. Plant Pathol. 49: 143–158.

Phillips, J. M. and D. S. Hayman. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Br. Mycol. Soc. 55: 158–161.

Poole, B. C. and D. M. Sylvia. 1990. Companion plants affected colonization of Myrica cerifera by vesicular-arbuscular mycorrhizal fungi. Can. J. Bot. 68: 2703–2707.

Rhodes, L. H. and J. W. Gerdemann. 1980. Nutrient translocation in vesicular-mycorrhizae. p. 173–195. In: C. B. Cook, P. W. Pappas and E. D. Rudolph (eds.). Cellular interactions in symbiosis and parasitism. Ohio State University Press, Columbus.

Ruiz-Lozano, J. M., R. Azcón and J. M. Palma. 1996. Superoxide dismutase activity in arbuscular mycorrhizal Lactuca sativa plants subjected to drought stress. New Phytol. 134: 327–333.

Salzer, P., H. Corbiere and T. Boller. 1999. Hydrogen peroxide accumulation in Medicago truncatula roots colonized by the arbuscular mycorrhiza-forming fungus Glomus intraradices. Planta 208: 319–325.

Smimoff, N. 1993. The role of active oxygen in the response of plants to water deficit and desiccation. New Phytol. 125: 27–58.

Tsang, W. T., C. Bowler, D. Herouart, W. Van Camp, R. Villarroel, C. Gentillo, M. Van Montagu and D. Inzé. 1991. Differential regulation of superoxide dismutases in plants exposed to environmental stress. Plant Cell. 3: 783–792.

Vierheilig, H., B. Bago, C. Albrecht, M. P. Poulin and Y. Piché. 1998. Flavonoids and arbuscular-mycorrhizal fungi. p. 9–33. In: J. A. Manthey and B. S. Buslig (eds.). Flavonoids in the living system. Plenum, New York.

Walker, J. C., S. Moreill and H. H. Foster. 1937. Toxicity of mustard oils and related sulphur compounds to certain fungi. Amer. J. Bot. 24: 536–541.