Commentary

Aromatic weapons: truffles attack plants by the production of volatiles

Truffles, fungal species belonging to the genus *Tuber*, include ectomycorrhizal species highly appreciated for their aroma. More than a hundred volatile organic compounds (VOCs) have been isolated from the fruiting bodies and mycelia of truffles (Zeppa *et al.*, 2004; Splivallo *et al.*, in press), and from ectomycorrhizal roots (Menotta *et al.*, 2004). In this issue of *New Phytologist*, Splivallo *et al.* (pp. 417–424) demonstrate the first biological activity for truffle VOCs. These volatiles cause rapid and efficient leaf bleaching and root inhibition of *Arabidopsis thaliana* and are therefore regarded as phytotoxic compounds. These findings suggest that truffle volatiles may play a role in 'burnt formation', inhibition of herbaceous plants by truffles (Pacioni, 1991).

> *'It can therefore be imagined that many more VOC-related inter- and intraorganismic interactions exist than previously thought.'*

The importance of volatiles was underestimated in the past, but recently a series of interesting new findings have focused attention on these low-molecular-weight compounds with high vapour pressure. They are necessary for inter- and intraorganismic communication. Apparent VOC producers and receivers (e.g. flowers and pollinators, and male and female animals) have been investigated. However, it is necessary to reconsider the fact that, in principle, all living organisms have the potential to synthesize, emit and receive volatile compounds. It can therefore be imagined that many more VOC-related inter- and intraorganismic interactions exist than previously thought.

Microbial volatiles modulating plant physiology

Plants produce and emit diverse mixtures of VOCs which play key roles in above-ground and underground plant development and in plant–microbe and plant–insect interactions. Extensively investigated volatile signals of plants include methyl esters of the phytohormones jasmonic acid and salicylic acid, ethylene, terpenoids, and six-carbon volatiles (Pichersky *et al.*, 2006; Tholl *et al.*, 2006). In contrast, the influence of microbial volatiles on plant physiology is only beginning to be understood. Ryu *et al.* (2003, 2004) demonstrated that 2,3-butanediol and acetoin synthesized and emitted by plant growth-promoting *Bacillus* strains enhance growth and induce systemic resistance of *A. thaliana*. In truffles, Splivallo *et al.* observed that, depending on the *Tuber* species, fungal volatiles caused bleaching of *A. thaliana* leaves, and/or inhibition of root and leaf development. The finding that the truffle host plant *Cistus incanus* was similarly inhibited to *A. thaliana* indicates a rather widespread action profile for the volatiles. More importantly, these results raise the question of what possible role(s) these volatiles play in ecosystems, and whether they are indeed responsible for the formation of plant inhibitory zones ('burnts'). That not only fungal, but also rhizobacterial volatiles can cause dramatic growth inhibitory effects on *A. thaliana* was recently demonstrated by Vespermann *et al.* (in press; Fig. 1). The volatile profiles of the rhizobacteria differ very much in qualitative and quantitative complexity; however, many compounds could not be identified, indicating that they comprise a new source of potential antibiotic compounds (Kai *et al.*, 2007). In contrast, many truffle volatiles could be identified and individual compounds such as *trans*-2-octenal, 3-octenol and 1-octen-3-ol induced bleaching and root growth inhibition (Splivallo *et al.*, in press). Interestingly when considering its biological activity, 1-octen-3-ol is responsible for the typical smell of fungi and thus is commonly found in the volatile blends of mushrooms. This compound together with *trans*-2-octenal led to a burst of hydrogen peroxide (H_2O_2) and to a significant increase of reactive oxygen species (ROS)-related enzyme activities in *A. thaliana*.

Before the current work of Splivallo *et al.* with truffles, the phytohormone ethylene was the only characterized fungal VOC with implications in fungus–plant interactions. *Botrytis cinerea* is able to produce ethylene *in vitro*, and the emission of ethylene follows the pattern that is associated with hyphal growth (Cristescu *et al.*, 2002). The possibility of 1-octen-3-ol–ethylene cross-talk would certainly be worth investigating in *A. thaliana*, as one of the functions of ethylene in plants is to adjust the release of H_2O_2 and other ROSs (Overmyer *et al.*, 2000).

Microbial volatiles and mycorrhizal symbiosis

The consequences of volatile production by bacteria for the target fungi are manifold; the volatiles affect the growth rate

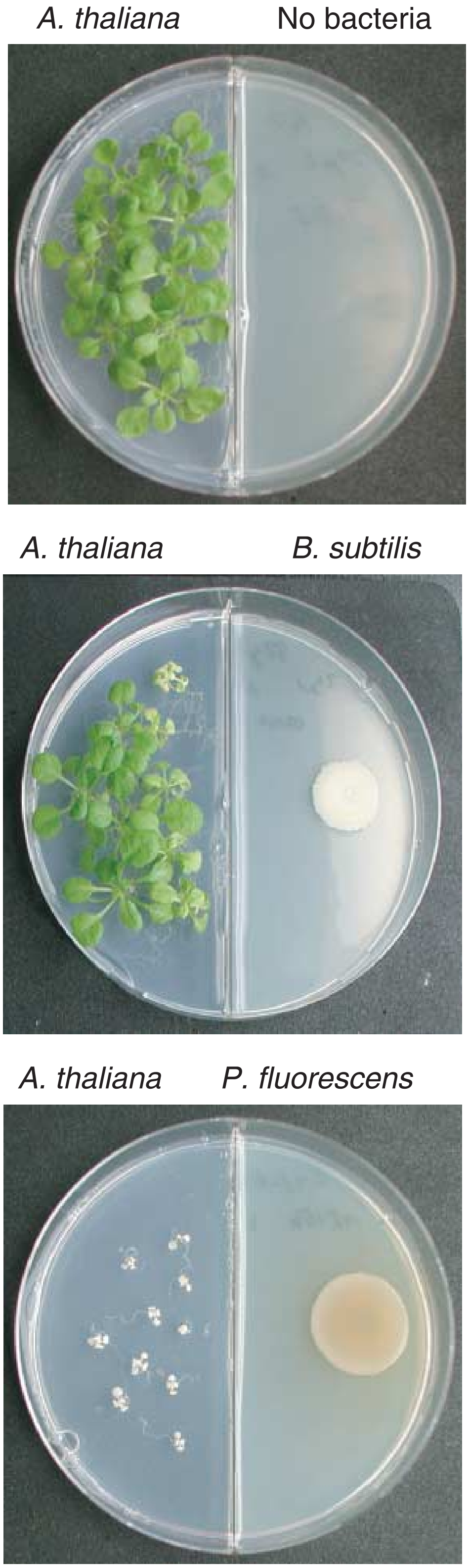

Fig. 1 Influence of rhizobacterial volatiles on the growth of *Arabidopsis thaliana* exposed to airborne chemicals released from growth-promoting *Bacillus subtilis* and growth-inhibiting *Pseudomonas fluorescens* strains. Figure courtesy of M. Kai, University of Rostock, Germany.

and the development of fungal mycelium and sclerotia, and lead to conidia deformation and discoloration (Wheatley, 2002; Kai *et al.*, 2007). Most interest has been focused on the influence of fungal and bacterial volatiles on the mycelial growth of mycorrhizal fungi. Saprophytic fungi may cause growth depression in mycorrhizal fungi; for example, *Trichoderma pseudokoningii* volatiles inhibit *Gigaspora rosea* spore germination and mycorrhiza establishment in soybean (*Glycine max*) (Martinez *et al.*, 2004). In contrast, spore germination and hyphal growth of *Glomus mosseae* were promoted by the volatiles of soil yeasts (Sampedro *et al.*, 2004). This positive effect of yeast volatiles warrants further investigation. Bacterial volatiles, for example from *Streptomyces* spp., have been shown to promote the germination of *G. mosseae* spores (Tylka *et al.*, 1991), and, depending on the fungal species, volatiles produced by mycorrhiza helper bacteria may either promote or inhibit mycelial growth (Garbaye & Duponnois, 1992). Direct contact among *Paenibacillus* sp. EJP73, *Lactarius rufus* and Scots pine (*Pinus sylvestris*) leads to accelerated mycorrhiza development. Using laboratory-based microcosms, Aspray *et al.* (2006) observed that volatile production by *Paenibacillus* sp. separated from plant roots led to inhibition of symbiosis development. These somewhat contradictory results reflect the general challenge of volatile application studies. Similarly, Barbieri *et al.* (2005) were able to analyse 65 volatiles produced by *Staphylococcus pasteuri*, an antagonist of *Tuber borchii*, while in *S. pasteuri–T. borchii* cocultures the spectrum of VOCs was distinct from that of the respective pure cultures. The terpenoid γ-pachoulene, a compound that was only produced in dual cultures, was linked to antifungal activity. Currently, no volatile profiles of the tri-trophic *S. pasteuri–T. borchii*–host plant interaction are known.

Perspectives

From the increasing evidence accumulating in the literature, it has to be concluded that multifunctional and multiorganismic volatile-based interactions exist in ecosystems, probably to a greater extent than has been envisioned. In the light of the observations of Splivallo, Vespermann, Ryu and colleagues showing that truffle or rhizobacterial VOCs directly influence plants (including host plants), one possible next step would be to expand investigations to other potential partners in the interaction; for example, to test how the truffle volatiles influence mycorrhiza development (Menotta *et al.*, 2004) or how rhizobacterial volatiles influence the soil ecosystem by studying volatile-dependent interactions between phytopathogenic fungi, plants, nematodes, etc. In this context, the volatiles of mycorrhiza helper bacteria and mycorrhiza-associated fungi can now be seen from a new perspective regarding symbiosis establishment. A more specific question relates to the ecological relevance of the truffle volatile–host plant interaction: are the bioactive volatiles responsible for the inhibition of herbaceous plants in nature? Such questions can now be addressed, for example, by relating VOC dose–plant responses to measurements within microcosms. The rapid development of analytical methods and the ever-increasing number of accessions in molecular mass databases, together with the use of model organisms, suggest that we have a realistic chance of taking a leap forward in our understanding of the role of volatiles in microbe–plant interactions in the near future.

Mika T. Tarkka[1]* and Birgit Piechulla[2]

[1]UFZ, Department of Soil Ecology,
Helmholtz-Centre for Environmental Research,
Theodor-Lieser-Str. 4, D-06120 Halle, Germany;
[2]Department of Biological Sciences, University of Rostock,
Albert-Einstein-Strasse 3, 18059 Rostock, Germany
(*Author for correspondence: tel +49 345 558 5414;
fax +49 345 558 5449; email mika.tarkka@ufz.de)

References

Aspray TJ, Jones E, Whipps JM, Bending GD. 2006. Importance of mycorrhization helper bacteria cell density and metabolite localization for the *Pinus sylvestris–Lactarius rufus* symbiosis. *FEMS Microbiology and Ecology* **56**: 25–33.

Barbieri E, Gioacchini AM, Zambonelli A, Bertini L, Stocchi V. 2005. Determination of microbial volatile organic compounds from *Staphylococcus pasteuri* against *Tuber borchii* using solid-phase microextraction and gas chromatography/ion trap mass spectrometry. *Rapid Communications in Mass Spectrometry* **19**: 3411–3415.

Cristescu SM, De Martinis D, Te Lintel Hekkert S, Parker DH, Harren FJ. 2002. Ethylene production by *Botrytis cinerea in vitro* and in tomatoes. *Applied and Environmental Microbiology* **68**: 5342–5350.

Garbaye J, Duponnois R. 1992. Specificity and function of mycorrhization helper bacteria (MHB) associated with the *Pseudotsuga menziesii–Laccaria laccata* symbiosis. *Symbiosis* **14**: 335–344.

Kai M, Effmert U, Berg G, Piechulla B. 2007. Volatiles of bacterial antagonists inhibit mycelial growth of the plant pathogen *Rhizoctonia solani. Archives in Microbiology* **187**: 351–360.

Martinez A, Obertello M, Pardo A, Ocampo JA, Godeas A. 2004. Interactions between *Trichoderma pseudokoningii* strains and the arbuscular mycorrhizal fungi *Glomus mosseae* and *Gigaspora rosea. Mycorrhiza* **14**: 79–84.

Menotta M, Gioacchini AM, Amicucci A, Buffalini M, Sisti D, Stocchi V. 2004. Headspace solid-phase microextraction with gas chromatography and mass spectrometry in the investigation of volatile organic compounds in an ectomycorrhizae synthesis system. *Rapid Communications in Mass Spectrometry* **18**: 206–210.

Overmyer K, Tuominen H, Kettunen R, Betz C, Langebartels C, Sandermann H, Kangasjärvi J. 2000. Ozone-sensitive *Arabidopsis rcd1* mutant reveals opposite roles for ethylene and jasmonate signaling pathways in regulating superoxide-dependent cell death. *Plant Cell* **12**: 1849–1862.

Pacioni G. 1991. Effects of *Tuber* metabolites on the rhizospheric environment. *Mycological Research* **95**: 1355–1358.

Pichersky E, Noel JP, Dudareva N. 2006. Biosynthesis of plant volatiles: nature's diversity and ingenuity. *Science* **311**: 808–811.

Ryu CM, Farag MA, Hu CH, Reddy MS, Kloepper JW, Pare PW. 2004. Bacterial volatiles induce systemic resistance in *Arabidopsis. Plant Physiology* **134**: 1017–1026.

Ryu CM, Farag MA, Hu CH, Reddy MS, Wei HX, Pare PW, Kloepper JW. 2003. Bacterial volatiles promote growth in *Arabidopsis. Proceedings of the National Academy of Sciences, USA* **100**: 4927–4932.

Sampedro I, Aranda E, Scervino JM, Fracchia S, Garcia-Romera I, Ocampo JA, Godeas A. 2004. Improvement by soil yeasts of arbuscular mycorrhizal symbiosis of soybean (*Glycine max*) colonized by *Glomus mosseae. Mycorrhiza* **14**: 229–234.

Splivallo R, Bossi S, Maffei ME, Bonfante P. (in press). Discrimination of truffle fruiting body versus mycelial aromas by stir bar sorptive extraction. *Phytochemistry.*

Splivallo R, Novero M, Bertea CM, Bossi S, Bonfante P. 2007. Truffle volatiles inhibit growth and induce an oxidative burst in *Arabidopsis thaliana. New Phytologist* **175**: 417–424.

Tholl D, Boland W, Hansel A, Loreto F, Rose US, Schnitzler JP. 2006. Practical approaches to plant volatile analysis. *Plant Journal* **45**: 540–560.

Tylka GL, Hussey RS, Roncadori RW. 1991. Axenic germination of vesicular–arbuscular mycorrhizal fungi: Effects of selected *Streptomyces* species. *Phytopathology* **81**: 754–759.

Vespermann A, Kai M, Piechulla B. (in press). Rhizobacterial volatiles affect the growth of fungi and *Arabidopsis thaliana. Applied and Environmental Microbiology.*

Wheatley RE. 2002. The consequences of volatile organic compound mediated bacterial and fungal interactions. *Antonie van Leeuwenhoek* **81**: 357–364.

Zeppa S, Gioacchini AM, Guidi C, Guescini M, Pierleoni R, Zambonelli A, Stocchi V. 2004. Determination of specific volatile organic compounds synthesised during *Tuber borchii* fruit body development by solid-phase microextraction and gas chromatography/mass spectrometry. *Rapid Communications in Mass Spectrometry* **18**: 199–205.

Key words: fungus, mycorrhiza, oxidative stress, plant, volatiles.

Drought and symbiosis – why is abscisic acid necessary for arbuscular mycorrhiza?

Plant hormones are prime targets when addressing the regulation of such an intimate plant–microbe interaction as arbuscular mycorrhiza (AM), which is found in nearly 80% of all plant species. Besides the most important feature of the mutualistic symbiosis – AM fungal provision of mineral nutrients in return for plant carbohydrates – the colonization of a plant root by AM fungi often improves growth and stress tolerance of the whole plant (Linderman, 2000). Alterations in the homeostasis of plant hormones have been implicated in this process and there are a large number of publications showing that the levels of plant hormones such as cytokinin, jasmonate (JA), auxin, auxin-related compounds and abscisic acid (ABA) actually change upon the establishment of AM (Hause *et al.*, 2007; Fig. 1). Although these findings suggest

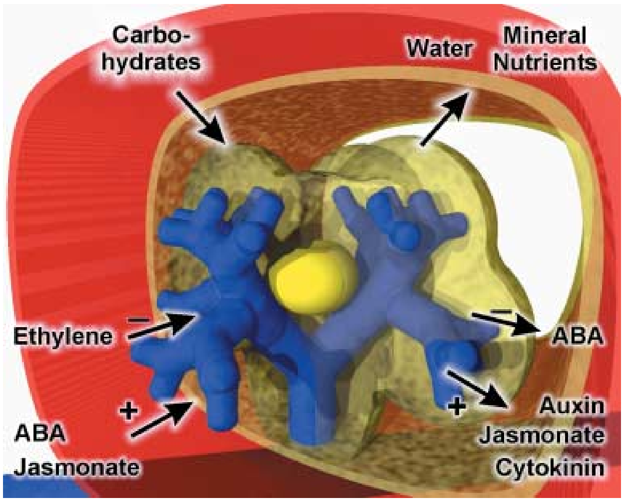

Fig. 1 Schematic summary of nutritional and hormonal changes upon colonization of plants by arbuscular mycorrhiza (AM) fungi and of hormonal effects on AM colonization. The picture gives a model of a colonized root cortical cell; the cell wall and cytosol have been partially removed. The plant cell nucleus is depicted in the center of the schematic arbuscule. Nutritional changes are given in the upper part of the scheme (the plant receives mineral nutrients and water while providing carbohydrates to the fungus) and the hormonal changes are given in the lower right part. Plants colonized by AM fungi have been described to contain lower levels of abscisic acid (ABA), but increased levels of auxin (and auxin-related compounds such as indolbutyric acid), jasmonate and cytokinin. The lower left part gives the observed effects of plant hormones on establishment of the AM symbiosis. Apart from the positive effect of jasmonate described by Isayenkov *et al*. (2005), the effects of ABA and ethylene are described by Herrera-Medina *et al*. (this issue; pp. 554–564).

that the beneficial effects of AM are not restricted to an improved nutrition of the plant, in most cases they do not provide clear functional proof regarding the importance of the changes in hormone levels observed. In addition, they only address the hormonal and physiological consequences of an established AM symbiosis. The question of a possible involvement of plant hormones in AM establishment is rarely in their scope. In this issue of *New Phytologist*, however, Herrera-Medina *et al.* (pp. 554–564) address exactly this question. By analyzing AM colonization of the tomato mutant *sitiens*, in which ABA levels are reduced to only 8% of those in wild-type tomato plants, they were able to show that ABA is necessary for the proper formation of arbuscules (the key symbiotic interface of AM) and for a sustained colonization of the plant root. The tomato mutant *sitiens* exhibits a reduced AM formation, which can be restored by the application of ABA, correlating with increased mycorrhization by treatment of wild-type roots with ABA. In addition, the data presented suggest an antagonistic role for the plant hormone ethylene (ET).

> *'Once the fungus has entered the root our knowledge on the molecular communication is only fragmentary'*

Molecular signals in the AM symbiosis

Despite the striking discoveries in recent years regarding the molecular communication between plants and AM fungi, it should be stressed that our knowledge of this communication is limited. It has been shown that a group of compounds (strigolactones) exude from the plant root and induce hyphal branching of AM fungi (Akiyama *et al.*, 2005). Moreover, a plant signal-transduction cascade, which is initiated by a receptor-like kinase, clears the way for the entry of AM fungi into the plant root (Parniske, 2004). Interestingly, this signaling cascade is partially shared in the plant–rhizobial and the plant–nematode interactions (Weerasinghe *et al.*, 2005). This initial signaling is followed by the formation of a highly specialized transient intracellular structure, designated the prepenetration apparatus, which is assembled by the epidermal cell with a novel cytoskeletal organization and plays a central role in the elaboration of the apoplastic interface compartment for fungal growth (Genre *et al.*, 2005). However, once the fungus has entered the root, our knowledge on the molecular communication is only fragmentary. The publication by Herrera-Medina *et al.* now adds a new piece to this puzzle. Similar experiments using a transgenic approach in *Medicago truncatula* have shown that the plant hormone jasmonic acid plays a comparable role for the establishment of a functional AM symbiosis (Isayenkov *et al.*, 2005). In addition, a number of plant mutants have been described to be disturbed in these later steps of the interaction.

ABA in plant–microbe interactions

ABA is well known for its important signaling and regulatory roles that enable plants to survive a variety of abiotic stresses, such as drought, salinity and cold stress (Finkelstein & Rock, 2002). In recent years, ABA has also been implicated in the regulation of a number of biotic stresses, such as pathogen attack. Its role, however, seems to depend on the interacting organisms. An increase in the level of ABA causes an increased resistance to the bacterial leaf pathogen *Pseudomonas syringae* or against viral infection in tobacco, explained by the induction of stomatal closure or by the inhibition of callose degradation (Adie *et al.*, 2007). This contrasts, however, with the reduced susceptibility (enhanced resistance) of ABA-deficient Arabidopsis or tomato mutants and soybean plants treated with an ABA biosynthesis inhibitor to various pathogens. The inverse relationship between the level of ABA and the induction of certain disease-resistance components led to the assumption that ABA has an antagonistic interaction with the JA/ET defense pathway that is necessary for resistance in Arabidopsis to the necrotrophic pathogen *Fusarium oxysporum* (Anderson *et al.* 2004). However, ABA also seems to interfere with signaling involving salicylic acid, leading to reduced plant resistance against biotrophic pathogens (Adie *et al.*, 2007). Along these lines, the effect of ABA treatment of Arabidopsis plants on the accumulation of two key resistance components after inoculation with an avirulent strain of *P. syringae* pv. *tomato* demonstrated that ABA is a suppressor of SA and lignin production and therefore the increase in ABA levels results in an increased susceptibility to infection (Mohr & Cahill, 2007). Regarding the AM symbiosis, it appears at least questionable if mechanisms observed in pathogenic interactions are applicable. Elements of plant defense reactions are observed only in a very reduced form during this interaction (Garcia-Garrido & Ocampo, 2002). Nevertheless, cross-talk with other hormones – at least with JA and salicylate – cannot be excluded. It will be a great challenge to establish how different hormones act in AM and whether their synergistic and/or antagonistic effects determine the outcome of the interaction.

Drought stress and AM

AM fungi not only improve the mineral nutrition of colonized plants, they also increase their resistance to abiotic stresses. In particular, drought stress can be alleviated by AM fungi; indeed, a number of cases have been reported where the beneficial effects of AM fungi on plant performance became apparent only under drought stress conditions (Augé, 2001). Although reports are not unanimous on this point, the beneficial consequences of AM colonization regarding drought stress seem to contribute not only towards a better mineral nutrition of plants, but encompass a more direct improvement of the plant water status. In addition, reduced levels of ABA and, accordingly, improved photosynthetic parameters have been described for above-ground parts of AM plants (Augé, 2001). Given this context, it makes sense that root ABA is necessary for a sustained colonization by AM fungi. This might ensure that roots become colonized particularly strongly when it is most needed (i.e. under drought stress conditions, when ABA levels are high). A similar regulatory mechanism has already been hinted at for phosphate, the main mineral nutrient provided by AM fungi to plant roots. In this case it has been shown that symbiotic structures unable to provide this nutrient are quickly degraded (Maeda *et al.*, 2006; Javot *et al.*, 2007). Many more experiments will be necessary to prove that plants in the field really use such mechanisms to engage only in AM interactions when they actually obtain benefits by these interactions.

Thomas Fester[1]* and Bettina Hause[2]

[1]Donald Danforth Plant Science Center,
975 North Warson Road,
St Louis, MO 63132, USA;
[2]Leibniz Institute of Plant Biochemistry,
Weinberg 3, D-06120 Halle (Saale), Germany
(*Author for correspondence: tel +1 314 5871653;
fax +1 314 5871753;
email tfester@danforthcenter.org)

References

Adie BAT, Perez-Perez J, Perez-Perez MM, Godoy M, Sanchez-Serrano JJ, Schmelz EA, Solano R. 2007. ABA is an essential signal for plant resistance to pathogens affecting JA biosynthesis and the activation of defenses in Arabidopsis. *Plant Cell* doi/10.1105/ tpc.106.048041.

Akiyama K, Matsuzaki K, Hayashi H. 2005. Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature* **435**: 824–827.

Anderson JP, Badruzsaufari E, Schenk PM, Manners JM, Desmond OJ, Ehlert C, Maclean DJ, Ebert PR, Kazan K. 2004. Antagonistic interaction between abscisic acid and jasmonate–ethylene signalling pathways modulates defence gene expression and disease resistance in Arabidopsis. *Plant Cell* **16**: 3460–3479.

Augé RM. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* **11**: 3–42.

Finkelstein RR, Rock CD. 2002. Abscisic acid biosynthesis and response. In: Somerville CR, Meyerowitz EM, eds. *The Arabidopsis book.* Rockville, MD, USA: American Society of Plant Biologists, 1–48. doi/10.1199/tab.0058. http://www.aspb.org/publications/arabidopsis/ (last accessed 30 September 2007).

Garcia-Garrido JM, Ocampo JA. 2002. Regulation of the plant defence response in arbuscular mycorrhizal symbiosis. *Journal of Experimental Botany* **53**: 1377–1386.

Genre A, Chabaud M, Timmers T, Bonfante P, Barker DG. 2005. Arbuscular mycorrhizal fungi elicit a novel intracellular apparatus in *Medicago truncatula* root epidermal cells before infection. *Plant Cell* **17**: 3489–3499.

Hause B, Mrosk C, Isayenkov S, Strack D. 2007. Jasmonates in arbuscular mycorrhizal interactions. *Phytochemistry* **68**: 101–110.

Herrera-Medina MJ, Steinkellner S, Vierheilig H, Ocampo Bote JA, García Garrido JM. 2007. Abscisic acid determines arbuscule development and functionality in tomato arbuscular mycorrhiza. *New Phytologist* **175**: 554–564.

Isayenkov S, Mrosk C, Stenzel I, Strack D, Hause B. 2005. Suppression of allene oxide cyclase in hairy roots of *Medicago truncatula* reduces jasmonate levels and the degree of mycorrhization with *Glomus intraradices. Plant Physiology* **139**: 1401–1410.

Javot H, Penmetsa RV, Terzaghi N, Cook DR, Harrison MJ. 2007. A *Medicago truncatula* phosphate transporter indispensable for the arbuscular mycorrhizal symbiosis. *Proceedings of the National Academy of Sciences, USA* **104**: 1720–1725.

Linderman R. 2000. Effects of mycorrhizas on plant tolerances to diseases. In: Kapulnik Y, Douds DDJ, eds. *Arbuscular mycorrhizas: physiology and function.* Dordrecht, the Netherlands: Kluwer Academic Publishers, 345–365.

Maeda D, Ashida K, Iguchi K, Chechetka SA, Hijikata A, Okusako Y, Deguchi Y, Izui K, Hata S. 2006. Knockdown of an arbuscular mycorrhiza-inducible phosphate transporter gene of *Lotus japonicus* suppresses mutualistic symbiosis. *Plant Cell Physiology* **47**: 807–817.

Mohr PG, Cahill DM. 2007. Suppression by ABA of salicylic acid and lignin accumulation and the expression of multiple genes, in Arabidopsis infected with *Pseudomonas syringae* pv. tomato. *Functional & Integrative Genomics* 7: 181–191.

Parniske M. 2004. Molecular genetics of the arbuscular mycorrhizal symbiosis. *Current Opinion in Plant Biology* 7: 414–421.

Weerasinghe RR, Bird DMcK, Allen NS. 2005. Root-knot nematodes and bacterial Nod factors elicit common signal transduction events in *Lotus japonicus*. *Proceedings of the National Academy of Sciences, USA* **102**: 3147–3152.

Key words: abscisic acid, arbuscular mycorrhiza, biotrophic interaction, drought tolerance, mutualistic interaction, plant hormones.

About *New Phytologist*

- *New Phytologist* is owned by a non-profit-making **charitable trust** dedicated to the promotion of plant science, facilitating projects from symposia to open access for our Tansley reviews. Complete information is available at **www.newphytologist.org**.
- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as-ready' via *OnlineEarly* – our average submission to decision time is just 30 days. Online-only colour is **free**, and essential print colour costs will be met if necessary. We also provide 25 offprints as well as a PDF for each article.
- For online summaries and ToC alerts, go to the website and click on 'Journal online'. You can take out a **personal subscription** to the journal for a fraction of the institutional price. Rates start at £131 in Europe/$244 in the USA & Canada for the online edition (click on 'Subscribe' at the website).
- If you have any questions, do get in touch with Central Office (**newphytol@lancaster.ac.uk**; tel +44 1524 594691) or, for a local contact in North America, the US Office (**newphytol@ornl.gov**; tel +1 865 576 5261).

© The Authors (2007). Journal compilation © *New Phytologist* (2007)