Mycorrhiza (2007) 17:375–393
DOI 10.1007/s00572-007-0130-9

REVIEW

Structural differences in arbuscular mycorrhizal symbioses: more than 100 years after Gallaud, where next?

S. Dickson · F. A. Smith · S. E. Smith

Received: 13 December 2006 / Accepted: 23 March 2007 / Published online: 3 May 2007

Abstract This review commemorates and examines the significance of the work of Isobel Gallaud more than 100 years ago that first established the existence of distinct structural classes (*Arum*-type and *Paris*-type) within arbuscular mycorrhizal (AM) symbioses. We add new information from recent publications to the previous data last collated 10 years ago to consider whether any patterns have emerged on the basis of different fungal morphology within plant species or families. We discuss: (1) possible control exerted by the fungus over AM morphology; (2) apparent lack of plant phylogenetic relationships between the classes; (3) functions of the interfaces in different structural classes in relation to nutrient transfer in particular; and (4) the occurrence of plants with both of the major classes, and with intermediate AM structures, in different plant habitats. We also give suggestions for future research to help remove uncertainties about the functional and ecological significance of differences in AM morphology. Lastly, we urge retention of the terms *Arum*- and *Paris*-type, which are now well recognised by those who study AM symbioses.

Electronic supplementary material The online version of this article (doi:10.1007/s00572-007-0130-9) contains supplementary material, which is available to authorized users.

S. Dickson (✉) · F. A. Smith · S. E. Smith
Soil and Land Systems (Waite Campus),
School of Earth and Environmental Sciences,
The University of Adelaide,
Adelaide, South Australia 5005, Australia
e-mail: sandy.dickson@adelaide.edu.au

S. Dickson · F. A. Smith · S. E. Smith
Centre for Soil–Plant Interactions,
School of Earth and Environmental Sciences,
The University of Adelaide,
Adelaide, South Australia 5005, Australia

Keywords Arbuscular mycorrhiza · AM morphology · *Arum* · *Paris*

Introduction

It has been more than 100 years since Isobel Gallaud published his dissertation that contained detailed descriptions and illustrations of different structures of what are now called arbuscular mycorrhizas (Gallaud 1904). This dissertation was subsequently published in sections in the *Révue Générale de Botanique* (Gallaud 1905), and it is this series that is now commonly cited in the literature. Gallaud's work has long been recognised as a very significant advance over the surveys of fungus–plant symbioses previously carried out in the middle to late nineteenth century (see Rayner 1927; Smith and Smith 1997; Koide and Mosse 2004). In terms of identification of mycorrhizal structures and their nomenclature, his paper was the most important since the term 'Mykorhizen' ('Pilzwurzel', i.e. 'fungus-root') was introduced by Frank (1885a, b; see Trappe 2005), with distinction between 'ectotropische' and 'endotropische' structures following soon afterwards (Frank 1887). It was Gallaud who introduced the term 'arbuscule' and by careful microscopy showed that the 'sporangioles' described by Janse (1897)—called 'protosporoidi' by Petri (1903)—were degenerating arbuscular structures in which were formed granular masses of fungal material that were apparently then digested. He also provided new information on the formation of the 'vésicules' described by Janse (1897) and others at the time.

The main aim of this review was to consider the extent to which Gallaud's findings have stood the test of time, especially in the context of research published since the long review by Smith and Smith (1997) which encouraged

many new studies. Many recent surveys of plants from different habitats now state their colonisation structures. We have collated this data to consider whether any patterns have emerged on the basis of different fungal morphology within those plant species or families. We discuss the possible influence of the arbuscular mycorrhizal (AM) fungus over AM morphology, the possibility of phylogenetic relationships among plants that form different structures, the functional effectiveness of different types of interface in relation to transfer of phosphate to the plant and the possible influence of plant habitat over the structures formed. We also suggest avenues for future research to help improve knowledge of the functional and ecological significance of the structural classes and urge that their names be retained both to give Gallaud ongoing recognition and to maintain consistency within the literature on AM symbioses.

Overview of Gallaud's work

Gallaud (1904, 1905) surveyed microscopically endomycorrhizas of many plant species and divided them into the following four classes based on types of internal fungal structures and named after plant species or plant taxa in which the 'type structures' were found.

1. *Arum maculatum* series ('*Arum*-type' hereafter), in which initial fungal penetration into epidermis and (where present) hypodermis is followed by development of hyphae along cortical intercellular airspaces and then penetration of cortical cells to form simple (individual) and terminal intracellular arbuscules. According to Gallaud, the arbuscules are not localised in definite layers of the root cortical cells.
2. *Paris quadrifolia* series ('*Paris*-type' hereafter), in which the fungus is entirely intracellular, with irregular coiled hyphae, on some of which are formed 'composite' (compound) arbuscules (i.e. more than one structure per cell) that are not terminal and (again according to Gallaud) are localised in definite layers. Following Yawney and Schultz (1990) and Cavagnaro et al. (2001a), we call these 'arbusculate coils' hereafter.
3. Hepatic (liverwort) series, resembling *Paris*-types but with arbusculate structures not organised in layers. Gallaud observed this type in gametophytes of *Pellia epiphylla* and *Conocephalum* (*Fegatella*) *conicum*.
4. Orchid series, in which the fungus is intracellular and tightly coiled, forming 'pelotons'.

In each of these series were included plants of different taxonomic affinities and from many habitats. For example, *Arum*-types and *Paris*-types each included monocotyledonous and dicotyledonous species, and *Paris*-types included *Angiopteris*, a fern. Although Gallaud did not strongly stress his observation of other structures, he did nevertheless record that three *Ranunculus* species had structures intermediate between those of *Arum*- and *Paris*-types. *Colchicum automnale* had some intracellular structures that did not match those of *Paris*-types generally. Some of Gallaud's illustrations of representative *Arum*- and *Paris*-type structures, with *Colchicum*, were reproduced by Smith and Smith (1997) and Smith and Read (1997). Gallaud (1904, 1905) recognised that lack of airspaces (or at least large continuous airspaces) in root cortices allows the other morphological types to be distinguished from *Arum*-types because in the absence of such spaces, the fungi can only be intracellular. Nevertheless, he believed that the difference between *Arum*- and *Paris*-types did not result only from the presence or absence of airspaces. For example, he pointed out that although roots of the pteridophyte *Ophioglossum vulgatum* have large cortical air spaces, the AM mycelium is always intracellular, and therefore, *Paris*-type. Accordingly, other properties of the root, or perhaps of the fungus, must also be important in determining the fungal growth pattern.

Gallaud's Hepatic series is not now recognised as distinct, and the structures can be considered as *Paris*-type because location of arbusculate coils in definite layers is not required as a defining feature, in comparison with the arbuscules of *Arum*-types. Not all *Paris*-type gymnosperms and angiosperms have their arbusculate coils in definite layers, while some A*rum*-types do (in the inner cortex only; e.g. Abbott 1982; Smith and Dickson 1991). It is also worth noting that not only liverworts, but also the gametophytes of pteridophytes (Read et al. 2000), are characterised by *Paris*-type structures. Although not known by Gallaud, all these structures, except those in orchids, are formed by members of the Glomeromycota (Schüβler et al. 2001). Orchid mycorrhizas are, of course, still considered a distinct class of mycorrhiza confined apparently only to the Orchidaceae. This follows much experimental work that soon went well beyond microscopic examination, starting with that of Noël Bernard at about the same time (1904) as Gallaud's publications. Bernard's research was described in some detail by Rayner (1927). Gallaud's Orchid series included non-orchids, such as the pteridophyte *Psilotum triquetrum* and *Tamus communis*, on the basis of the extensive hyphal coils. *Tamus* was ranked next to orchids, although vesicles and structures similar to arbuscules were observed. Detailed investigations by Peterson et al. (1981) give no reason to believe that *Psilotum* is also anything other than *Paris*-type, although this example apparently lacks arbusculate structures.

Gallaud found no reason to relate the different fungal structures to distinct taxonomic groups of fungi. He attempted to isolate the fungal partners of the symbioses

he studied but had no success with the endophytes: He recognised that those isolated by himself or others at the time were all from root surfaces. Likewise, his attempts to inoculate known fungi into seedlings grown aseptically were unsuccessful. This situation contrasts with that in orchids where the fungal partners are now known to belong to fungal groups other than the Glomeromycota. The isolation and culture of AM (glomeromycotan) fungi in vitro still remains a Holy Grail of AM research. Gallaud regarded the endophytes essentially as weak parasites that caused very limited damage in roots and could themselves be digested: There was no need to postulate a 'symbiose harmonique'. The seminal paper by Bernard (1904) that regarded colonisation of orchids as 'une maladie parasitaire chronique' was published too late to influence Gallaud's writings.

Acceptance and impact

Some confusion may have arisen over variation in fungal structures when Peyronel (1923, 1924) stated that it was *Rhizoctonia*-type fungi that produced the hyphal coils after initial colonisation by true AM fungi. He isolated such fungi from roots of a number of angiosperm species, including cereals. *Rhizoctonia* species are common (and sometimes weak) parasites on plant roots. Peyronel's work may have had a negative impact on the acceptance of Gallaud's findings during the prolonged period when the nature of many fungal infections of plant roots was uncertain. For example, Rayner (1927) found it difficult to believe that 'so heterogeneous a [structural] grouping has any real significance' and commented that it contributed little or nothing to resolving the main problem: 'the biological relation of fungus and host'. However, she acknowledged that it helped mark the beginning of a new period in relation to the need to identify endophytic fungi and showed the necessity for critical experimental investigations. It was not until later that it became clear that *Paris*-type hyphal coils are indeed AM structures formed by members of the Glomeromycota and that, depending on the plant species colonised, the same AM fungus was capable of producing either *Arum*- or *Paris*-type structures (Barrett 1958; Gerdemann 1965; Jacquelinet-Jeanmougin and Gianinazzi-Pearson 1983). Nevertheless, Gerdemann (1965) stated that AM morphology was not only influenced by the host plant but also by the fungal species.

Until the 1970s, only a scattering of research papers paid any attention to the existence of *Paris*-type AM structures (see Smith and Smith 1997). When the importance of AM in plant function started to be recognised in the 1960s and 1970s (see Koide and Mosse 2004), *Arum*-types came to be regarded as 'typical'. *Paris*-types were largely ignored or possibly (in field studies) not even recognised as AM. The reason was that most experimental studies were with cultivated herbaceous plants, with many AM fungi from the genus *Glomus*. *Arum*-type structures predominate in these combinations. However, by the mid-1990s a significant number of papers described, illustrated, or both, *Paris*-type structures; some did not refer to Gallaud, and others did. Research conducted in Canada, and especially the careful surveys of forest vegetation by Mark Brundrett and colleagues (Brundrett and Kendrick 1988, 1990a, b; Brundrett et al. 1985, 1990), led to a long review of available literature that mentioned or (more usefully) illustrated different AM structures (Smith and Smith 1997). The review included a compilation of plant families, with the type of AM structures observed in them, excluding vesicles. If an author did not give full details in the text, it was assumed that linear hyphae shown by light microscopy along longitudinal sections or squashes (the usual view) were intercellular (*Arum*-type), especially if arbuscules were visible and coils were not. The relation between hyphae and cell walls could not be resolved in such illustrations. Presence of hyphal coils, whether in the presence or absence of arbusculate coils, these being difficult to see, placed the plant into a family with *Paris*-type AM. In summary, the compilation showed that with very few exceptions, ferns and gymnosperms form *Paris*-type AM and that these predominate in wild angiosperms, whether herb, shrub or tree. In very small minorities of angiosperm families (out of about 90 in the list), there were both *Paris*- and *Arum*-types ('Both' types in the list) in different genera (e.g. in the Solanaceae), or AM with both intercellular hyphae and intracellular cortical coils. The latter were classified as 'Intermediate' types. An even smaller minority of families had plants classified as *Paris*-type, *Arum*-type and 'Intermediate' (e.g. Gramineae and Leguminosae). Despite some variations in detailed structure (as in *Colchicum*) and limitations discussed in the text, the survey seemed to support the earlier experimental evidence that the plant genome, and not the AM fungal genome, has main control over AM morphology. Nevertheless, cases were acknowledged where different AM fungi produced variations in structure in the same host, as in *Trifolium subterraneum* (Abbott 1982), *Gentiana* (Demuth et al. 1991) and *Petroselinium* (Söderström and Dickson, unpublished). There were also indications of developmental changes between *Arum*- and *Paris*-type structures in *Daucus* and *Petroselinium* (Söderström et al., unpublished).

Can the fungus influence the structures formed?

As will be shown, a number of recent papers that survey AM plants have classified colonisation as forming *Arum*- or

Paris-type morphology or, where the names have not been used, have described structures that can be so identified. Where the controlling factors have been considered, it has been generally assumed that which of the two classes formed is determined by the plant intercellular spaces within the root cortex, as emphasised by Brundrett and Kendrick (1988, 1990a). However, Cavagnaro et al. (2001b) showed that a cultivar of tomato (*Lycopersicon esculentum*, now reclassified as *Solanum lycopersicum*) formed *Arum*-type AM with three fungal species (*Glomus intraradices*, *G. mosseae* and *G. intraradices* isolate WFVAM23, then misidentified as *G. versiforme*; Fig. 1a), while another three (*G. coronatum*, *Gigaspora margarita* and *Scutellospora calospora*) produced *Paris*-type structures (Fig. 1b). Smith et al. (2004) showed that *Gigaspora rosea* formed *Paris*-type structures in the same tomato cultivar and that *G. caledonium* formed intermediate structures (Fig. 1c,e). These different structures shown in Fig. 1a–c are compared to *Paris*-type AM in *Medicago truncatula* (medic; Fig. 1d) also colonised by *Gi. rosea* and in *Callitris glaucophylla* colonised by an unknown AM fungus (Fig. 1f). Thus, in this tomato cultivar, fungal identity can indeed influence the class of AM produced, substantiating the views of both Gallaud (1905) and Gerdemann (1965). An experiment to measure the size of airspaces within the cortex of the same tomato cultivar, when grown in axenic or soil conditions, showed that they were discontinuous, but obviously this did not preclude formation of *Arum*-type AM with some fungi (J-P Toussaint et al., unpublished; Bago et al. 2006). Kubota et al. (2005) also showed, with a different tomato cultivar, that both types of colonisation could be produced in the same root system when the plants were grown in soil with a mixed fungal inoculum. However, in contrast to Cavagnaro

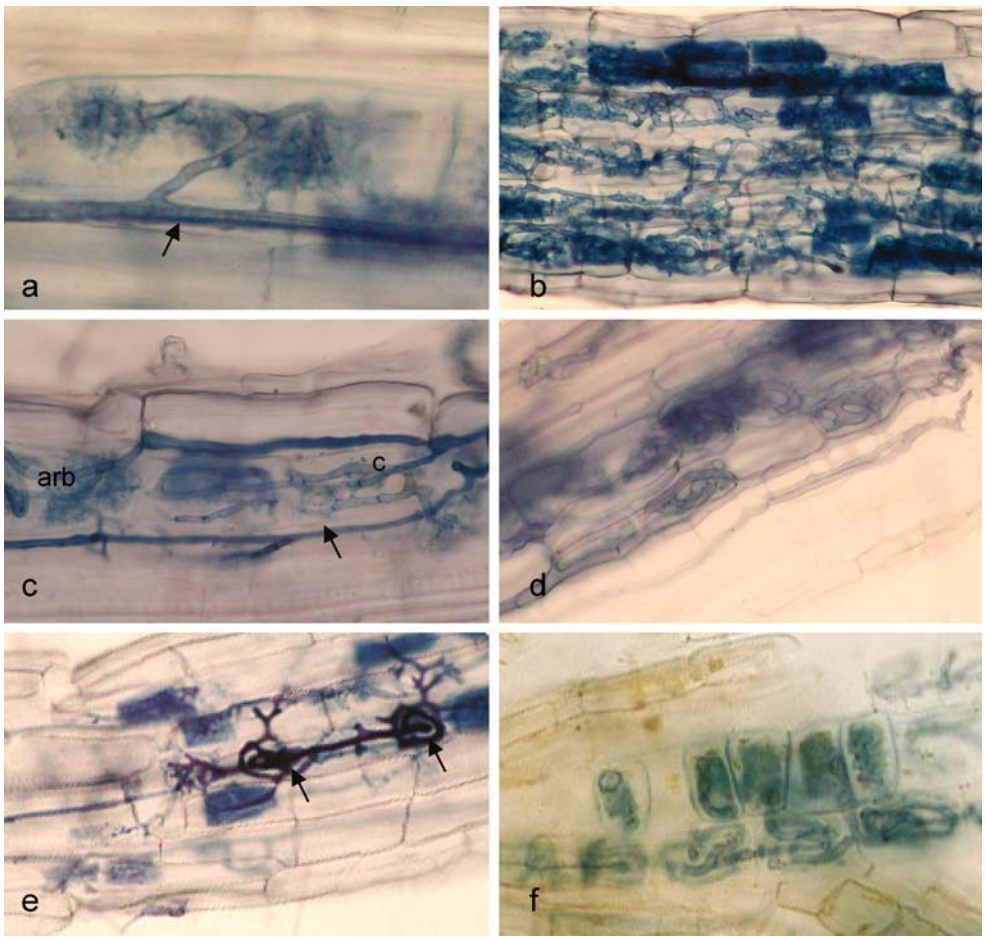

Fig. 1 Different morphological structures observed in arbuscular mycorrhizal roots. **a** Intercellular hypha (*arrowed*) of *Glomus intraradices* subtending an *Arum*-type arbuscule in the cortex of *Solanum lycopersicum* roots; **b** complex *Paris*-type hyphal coils of *Gigaspora rosea* in the cortex of *S. lycopersicum*; **c** intermediate mycorrhizal structures formed by *G. caledonium* in the cortex of *S. lycopersicum* L. roots. Longitudinal hypha (*arrow*), intracellular coils (*c*) and arbuscule-like structures (*arb*) can be seen. **d** *Paris*-type coils formed in the root cortical cells of *Medicago truncatula* by *Gi. rosea*; **e** well-developed 'entry coils' (*arrowed*) formed by *G. caledonium* in the hypodermal passage cells of *S. lycopersicum* and **f** typical *Paris*-type coils formed in the cortical cells of *Callitris glaucophylla* (white cypress pine) by an unknown fungus. **a**, **c** and **d**, reprinted from the New Phytologist, with permission; **b** and **e**, S Dickson and SE Smith; **f**, photo by SE Smith of material provided by N Warwick and R Kenny

et al. (2001b), they found that their isolate of *Gi. margarita* produced *Arum*-type colonisation. Whether this difference is due to differences in plant cultivar, fungal isolate or environmental factors such as soil and nutrient conditions is unclear, but it indicates that there is a need for further study. This is especially the case with plants from families such as the Solanaceae, which have considerable variation among species as to the type of AM formed.

Are *Arum*- and *Paris*-type morphologies clear-cut?

A study with different AM fungal species in *Gentiana lutea* showed that all six fungi tested produced *Paris*-type intracellular structures, although the size of hyphal 'loops' varied between fungi used (Jacquelinet-Jeanmougin and Gianinazzi-Pearson 1983). Differences in AM morphology that occur within plants 'normally' observed to form *Paris*-type structures have yet to be further investigated. Achlorophyllous plants in the Gentianaceae were once regarded as having a 'structurally incompatible' AM symbiosis, as the same fungus produced different structures in other plants (Weber et al. 1995; Imhof and Weber 1997). These members of the Gentianaceae were later shown to also form *Paris*-type colonisation, although *Voyria obconica*, like *O. vulgatum*, produces large intercellular spaces in the roots (Imhof and Weber 2000). Wubet et al. (2003b) studied the morphology of AM in wild and cultivated *Taxus baccata* (yew) and showed that two major types of *Paris*-type arbusculate structures were present: those that developed from hyphal coils and those that arose from extensions of linear intracellular hyphae.

It has become generally believed that most structures observed could be easily defined, and that therefore, the difference between *Arum*- and *Paris*-type morphology is always clear. The observations that other structural types are present (e.g. Widden 1996), also illustrated by Gallaud (1905), have largely been overlooked due to their rarity or the fact that they did not fit into the 'arbusculo-centric' definition of AM symbioses. Dickson (2004) examined the diversity of AM structures using 12 common commercially grown plant species colonised by six species of AM fungi. This survey showed that a range of structures was produced, depending upon the host plant and fungal species used. It was concluded that intermediate structures were clearly present and that there is a continuum of structures, making the identification of distinct *Arum*- and *Paris*-types more difficult to determine. Table 1 summarises the range of AM structures found by Dickson (2004) in some of the plants that were examined, although some of the 'intermediate' classes have been combined here for simplicity. It shows that in all these cases, there was a tendency for AM fungi other than *Glomus* species to form intermediate or *Paris*-type structures. In two reviews discussing the co-evolution of roots and mycorrhizal fungi and the diversity and classification of the symbioses, Brundrett (2002, 2004) proposed redefining *Arum*- and *Paris*-types as 'linear' and 'coiling', in relation to the appearance of longitudinal hyphae within the root. This new terminology can be misleading because it now appears that not all linear hyphae inside the root are intercellular (Dickson 2004). The use of root squashes, and failure to inspect transverse sections, obscures this inter- versus intracellular position and so possibly may also obscure functional differences between

Table 1 Plant species colonised by a range of AM fungi showing different AM structures modified from Dickson (2004)

Plant	Family	Fungi					
		Glomus coronatum	*Glomus intraradices*	*Glomus mosseae*	*Scutellospora calospora*	*Gigaspora margarita*	*Gigaspora rosea*
Monocots							
Allium porrum	Alliaceae	A	A	A	A	A	A
Hordeum vulgare	Poaceae	A	A	I	I	I-P	P
Sorghum bicolor	Poaceae	A	A	A	I-P	I	I-P
Lolium perenne	Poaceae	A	A	I	I	I	I
Triticum aestivum	Poaceae	I	I	I	I-P	I	P
Dicots							
Asterids							
Ocimum basilicum	Lamiaceae	A	A	A	I	I	I
Daucus carota	Apiaceae	I	I	I	I	I	P
Petroselium crispum	Apiaceae	I	I	I	P	P	P
Lactuca sativa	Asteraceae	A	A	A	A	A	A
Rosids							
Trifolium subterraneum	Leguminosae	A	A	A	A	A	I

A *Arum*-type, I intermediate, I-P intermediate but tending to *Paris* and P *Paris*-type

the structures. There is also the danger that hyphal loops or coils that underlie the fungal entry points and occur in the hypodermis of some plants (see Fig. 1e) might be interpreted as intermediate or even typical *Paris*-type structures. As originally shown by Gallaud (1904, 1905), these loops are distinguishable from the structures formed in the cortex that form the basis of *Arum*- and *Paris*-types (and also true Intermediate types). It might be thought that the large variability in structures formed along the *Arum–Paris* continuum renders the classification of doubtful utility. However, we consider that it is essential for researchers to recognise the variations, as only then will it be possible to reveal taxonomic, functional and ecological significance.

Distribution of mycorrhizas in land plants: are phylogenetic inferences possible?

Recently Wang and Qiu (2006) published an updated survey of the occurrence of different types of mycorrhiza in families of land plants. They used the DNA sequence-based phylogenies of both flowering plants (Stevens 2004) and non-flowering plants (Qui, unpublished) and greatly expanded records of the major groups of mycorrhizas (not just AM) in them to reach conclusions about the evolution of mycorrhizas. On the whole, these conclusions were satisfactorily similar to those reached earlier using much more limited information and the classification system of Cronquist (1981; Trappe 1987; Fitter and Moyersoen 1996; Zhao 2000; Brundrett 2002). The general conclusions are that arbuscular mycorrhizas were the first to evolve, that ericoid and orchid mycorrhizas evolved only once each, but that both non-mycorrhizal and ectomycorrhizal states are polyphyletic. Similarly, mycoheterotrophy of achlorophyllous plant species, apparently dependent on several different types of mycorrhizal fungal symbionts for their organic carbon (C) supplies, has arisen several times in divergent plant lineages (Leake 1994; Smith and Read 2007).

The previous phylogenetic analyses simply distinguished arbuscular mycorrhizas from the other major groups and probably focussed on *Arum*-types. Unfortunately, no attempts were made either to record or evaluate the occurrence of the two major AM classes or intermediate structures. Nevertheless, an increasing number of records of plant mycorrhizal status do include information about AM structures. We have used these, together with results from inoculation experiments, to examine a large number of plant species that form *Arum*-type, *Paris*-type or Intermediate structures. This information is given as an "Appendix" (electronic supplementary material). It expands the information presented by Wang and Qiu (2006) and greatly increases the data provided by Smith and Smith (1997). We have attempted to change taxonomic nomenclature where renaming of plant species has occurred. Data are based mainly on individual species except where, in a few cases, individual plants within a species have been shown to form different AM structures. Where there are different AM structures either within a genus or species, this has been recorded separately. Plant species showing characteristics of both *Arum*- and *Paris*-type structures have been recorded as Intermediate types. These features can be in the same field of view, same root system or roots of different plants within that species. This differs from the list in Smith and Smith (1997) which separated Intermediate or 'Both' types only within a family.

The data in "Appendix" are summarised in Table 2 which gives numbers of plant genera observed within each plant family, within the major groupings of pteridophytes, gymnosperms, monocots, magnoliids, basal eudicots, caryophylids and dicots. Table 3 is a further summary, with the numbers of families within the major plant groupings that show variations in structure. In Table 2, 'Intermediate' is used for families with characteristics of both *Arum* and *Paris* structures within the same genera, whereas 'Both' relates to the situation when *Arum*- and *Paris*-type morphologies, as strictly defined, have been observed within that family (as described by Smith and Smith 1997). The numbers given in brackets are the corresponding numbers previously recorded by Smith and Smith (1997). Plant families in the pteridophytes mostly form *Paris*-type or Intermediate AM, although there is one example of an *Arum*-type AM. Among the gymnosperms that form AM symbioses, the majority of families form *Paris*-types, although genera in the Cycadaceae, Zamiaceae, Auracariaceae and Cupressaceae have been recorded with *Arum*-type AM.

Among the angiosperms, the picture is much more complex than previously shown (Smith and Smith 1997). Both *Arum*- and *Paris*-types and their combinations occur frequently in the major taxa, although one type apparently predominates in many individual families. Many more angiosperm families can now be listed, especially those with *Arum*-type AM. Due to the increase in numbers of plant genera recorded within each family, there is also an increase in the number of families with more than one type of structure. For example, in the monocots families in the order Asparagales (families 10–16, Table 2) are predominantly *Arum*-type, and those in the Diascoriales (families 3 and 4) are mainly *Paris*-type. This last order includes the Burmanniaceae, which has achlorophyllous members typically forming *Paris*-types (Table 2). In general, nine families in the monocots have been recorded with only *Arum*-type, eight families with only *Paris*-type AM and eight families with Both or Intermediate types (Table 3). In the dicots, the picture is similar. The magnoliids and basal

Table 2 The numbers of plant genera observed within each plant family with different AM structures

Number of genera	Families	*Arum*–type structures only	Intermediates within plant/s of the same genera	*Paris*-type structures only	Both (A- and P-types) within the same genera	Smith and Smith (1997) I and B	Reference numbers
	Pteridophytes						
1	Selaginellaceae		1				87
2	Equisetaceae			1			87
3	Marattiaceae	1					28
4	Psilotaceae			1			61, 68
5	Ophioglossaceae			2			87, 94
6	Osmundaceae			1			87
7	Gleicheniaceae			1			87
8	Schizaeaceae		1				87
9	Pteridaceae			2			19, 87
10	Dennstaedtiaceae		2				87
11	Aspleniaceae		1	5			87
12	Thelypteridaceae		1	1			87
13	Blechnaceae		1				87
14	Dryopteridaceae		2				87
	Sum	1	9	14	0		
	Gymnosperms						
1	Cycadaceae	1					56, 94
2	Zamiaceae	1					25
3	Gingkoacaeae			1			9
4	Araucariaceae			2	1		10, 38, 52
5	Podocarpaceae			1			6, 33, 68, 93
6	Taxodiaceae			3			8, 27, 72, 84
7	Cupressaceae	3		3			1, 15, 38, 47, 49, 84, 93
8	Taxaceae			2			73, 83, 84
	Sum	5	2	12	1		
	Monocots						
1	Araceae	7 (5)		1 (1)			13, 14, 27, 38, 39, 57
2	Alismataceae	1					47
3	Burmanniaceae			3 (1)			38, 99, 100
4	Dioscoraceae			3 (3)			3, 27, 32, 38, 39, 53
5	Triuridaceae			1			38, 97, 98
6	Pandanaceae	1					38
7	Corsiaceae			1			22
8	Smilacaceae			3			7, 25, 27, 47, 49, 84
9	Liliaceae	7 (5)		9 (8)			13, 14, 27, 30, 38, 47, 81, 84, 94
10	Hypoxidiaceae	1 (1)					38, 57
11	Iridaceae	1		1			47, 85
12	Hemerocallidaceae	1					49
13	Asphodelaceae	4 (1)		1			17, 27, 49, 60
14	Alliaceae	1 (1)					11, 21, 27, 34, 55
15	Hyacinthaceae	4 (4)					27
16	Agavaceae	1 (1)					27
17	Ruscaceae	1 (1)					27, 47
18	Arecaceae	8	4	1	(3)		25, 38, 39, 58, 66
19	Cyperaceae	1		1	1		46
20	Poaceae	22	15	14	4	(>10 B, I)	3, 4, 21, 23, 29, 31, 39, 45, 46, 47, 49, 57, 59, 60, 66, 71, 84, 85, 89, 94
21	Commelinaceae	1					3
22	Musaceae			1			94
23	Heliconiaceae			1 (1)			39
24	Cannaceae			1 (1)			39

Table 2 (continued)

Number of genera	Families	*Arum*–type structures only	Intermediates within plant/s of the same genera	*Paris*-type structures only	Both (A- and P-types) within the same genera	Smith and Smith (1997) I and B	Reference numbers
25	Zingiberaceae	4 (1)	1	1 (1)			38, 39, 57, 94
	Sum	66 (20)	20	41 (16)	5 (3)	(>10 B, I)	
	Dicots						
	Magnoliids						
1	Myristicaceae	1					57
2	Magnoliacae			3 (2)			3, 38, 41, 57, 84, 94
3	Annonaceae			4 (1)			25, 39, 57, 94
4	Lauraceae	4	1	2			3, 25, 47, 57, 84
5	Aristolochiaceae			1 (1)			13, 14, 65
6	Piperaceae	1		1			57, 94
	Sum	6	1	11 (4)	0		
	Basal eudicots						
1	Menispermaceae			1			3
2	Ranunculaceae		1	3	1		27, 47, 71, 82
3	Proteaceae	1 (1)					38
	Sum	1 (1)	1	4	1		
	Caryophylids						
1	Dilleniaceae	1					49
2	Tamaricaceae	1					47, 66
3	Plumbaginaceae			1			66
4	Polygonaceae		1	1			3, 4, 82
5	Caryophyllaceae	1					47
6	Amaranthaceae		1	2			66, 94
7	Aizoaceae			1			66
	Sum	3	2	5	0		
	Asterids						
1	Santalaceae			1			94
2	Cornaceae	2 (1)		1 (1)			38, 71, 84
3	Balsaminaceae	1 (1)					38
4	Theaceae			3 (1)			3, 38
5	Ebenaceae		1				33, 57
6	Primulaceae	2		2	1		47, 49, 71, 85, 95
7	Myrsinaceae		1	3 (1)	1		33, 38, 57, 66, 84
8	Symplocaceae	1					38
9	Lecythidaceae			1(1)			39
10	Sapotaceae	1					93
11	Clethraceae			1			42, 84
12	Ericaceae	1					49
13	Icacinaceae	1					57
14	Boraginaceae	4 (2)		2			25, 27, 38, 39, 60, 66
15	Rubiaceae	13 (1)		10 (6)			3, 25, 33, 38, 39, 46, 47, 57, 71, 84, 85, 94
16	Gentianaceae		1	8 (7)			28, 36, 37, 38, 43, 47, 48, 49, 71, 84, 101, 102, 103, 104
17	Loganiaceae			1			74
18	Apocynaceae	13 (4)	3	4	2	(15BI)	27, 38, 66, 71, 75, 76, 79, 94
19	Oleaceae	5 (1)	1				3, 13, 15, 33, 47, 57, 71, 93, 94
20	Plantaginaceae	1					4, 47, 49, 60
21	Verbenaceae	5		7	1 (5)		39, 57, 66, 84, 91, 94
22	Lamiaceae	10	1	3	(7)		21, 27, 38, 39, 47, 49, 57, 71, 85, 94
23	Acanthaceae	5					57, 66, 85, 94
24	Scrophulariaceae	5	1	1	(2)		33, 39, 47, 49, 85, 94

Table 2 (continued)

Number of genera	Families	*Arum*–type structures only	Intermediates within plant/s of the same genera	*Paris*-type structures only	Both (A- and P-types) within the same genera	Smith and Smith (1997) I and B	Reference numbers
25	Convolvulaceae	2		1			24, 45, 60, 66, 94
26	Solanaceae	2	1	2	1 (4)		18, 38, 39, 42, 60, 70, 94
27	Aquifoliaceae			1			3, 84
28	Araliaceae			4 (2)	1		3, 39, 47, 80, 84, 105
29	Apiaceae	2	2	4 (6)	3		21, 27, 47, 49, 60, 71, 94
30	Campanulaceae	3 (1)		1			38, 49, 57, 71, 82
31	Menyanthaceae		2 (2)				78
32	Goodeniaceae	2			1		45, 49, 60
33	Asteraceae	49 (5)		1	1		3, 4, 21, 27, 39, 47, 49, 57, 60, 66, 71, 82, 85, 94
34	Adoxaceae				1		3, 38, 47, 71, 84
35	Caprifoliaceae		1 (I)				3, 47
36	Dipsacaceae	1					47
	Sum	131 (16)	15 (3)	62 (25)	13 (18)	(15)	
	Rosids						
1	Hamamelidaceae			2 (10)			38, 84
2	Haloragaceae	1					49
3	Grossulariaceae			1 (1)			38
4	Saxifragaceae	2		2 (1)			27, 39, 84
5	Vitaceae	4 (1)					3, 39, 85
6	Geraniaceae	1		1			60, 85, 94
7	Combretaceae	1 (1)					39
8	Onagraceae			1			57
9	Lythraceae	2		1			66, 94
10	Myrtaceae	5		1 (1)	3		38, 47, 49, 57, 66, 93, 94
11	Melastomataceae	1		1 (1)			25, 39
12	Celastraceae			1	1		3, 33, 71
13	Rhizophoraceae		1	2			66
14	Linaceae		1	(1)			21, 28, 70, 71, 92
15	Euphorbiaceae	10	2	2	3	(6BI)	25, 38, 39, 45, 47, 49, 57, 60, 66, 71, 77, 94
16	Violacaeae	1		1 (1)			27, 49, 71, 84
17	Salicaceae				2		13, 20, 38, 47
18	Turneraceae	1 (1)					39
19	Clusiaceae	1 (2)					39
20	Hypericaceae	1					71
21	Malpighiaceae			1			39
22	Oxalidaceae			1	1		4, 85, 94
23	Cunoniaceae			1 (1)			50, 51
24	Elaeocarpaceae	2 (2)					38, 57
25	Polygalaceae	2		1 (1)	1		25, 39, 47, 49, 57, 71
26	Fabaceae	31	4	7	7 (13)		2, 4, 5, 16, 21, 24, 25, 27, 33, 35, 38, 39, 45, 46, 47, 49, 57, 60, 64, 66, 70, 71, 85, 93, 94, 96
27	Rosaceae	7 (2)		1			3, 15, 27, 38, 47, 57, 71, 84, 85, 93, 94, 105
28	Rhamnaceae	3					49
29	Elaeagnaceae			1			3
30	Ulmaceae	1		2 (2)			3, 15, 25, 38, 57
31	Moraceae			2 (2)			38, 57, 69
32	Urticaceae	4 (2)					57, 71
33	Cucurbitaceae	3 (2)	1				42, 60, 63

Table 2 (continued)

Number of genera	Families	*Arum*–type structures only	Intermediates within plant/s of the same genera	*Paris*-type structures only	Both (A- and P-types) within the same genera	Smith and Smith (1997) I and B	Reference numbers
34	Begoniaceae	1 (1)					38, 57
35	Tetramelaceae	1					57
36	Juglandaceae	1					13
37	Betulaceae	1					47
38	Casuarinaceae	1		1 (1)			38, 45, 49, 66, 94
39	Moringaceae			1			94
40	Caricaceae			1 (1)			39, 94
41	Thymeleaceae	2 (1)					47, 49, 71
42	Malvaceae	5 (5)	4 (2)	3 (2)	1		39, 44, 45, 49, 57, 58, 60, 66, 69, 94
43	Rutaceae	9		1	1	(6BI)	33, 38, 39, 49, 54, 84, 94
44	Meliaceae	2	3 (1)	11	3		33, 38, 39, 57, 62, 66, 67, 69, 93, 94
45	Anacardiaceae	2 (1)	2	1			25, 33, 47, 84, 88, 94
46	Burseraceae		1 (1)				39
47	Sapindaceae	2		3 (12)			12, 13, 26, 38, 40, 57, 69, 71, 84, 86, 90, 94
48	Staphyleaceae	1					38, 94
	Sum	112 (21)	19 (4)	56 (38)	23 (13)	(12)	
	Total	325	69	201	43		

The numbers given in brackets are the numbers of genera previously recorded by Smith and Smith (1997) for that AM structure. Where they did not separate Both or Intermediate types this has been included in a separate column (Smith and Smith 1997; I and B).

I Intermediate types: characteristics of both *Arum*- and *Paris* structures within the same genera (as described by Smith and Smith 1997), *B* both: when strict *Arum*- and *Paris*-type morphologies were observed within that family.

Numbered references shown in table: 1, Abbas et al. (2006); 2, Abbott and Robson (1978); 3, Ahulu et al. (2005); 4, Antoniolli (1999); 5, Asai (1944); 6, Baylis et al. (1963); 7, Bedini et al (2000); 8, Böcher (1964); 9, Bonfante-Fasolo and Fontana (1985); 10, Breuninger et al. (2000); 11, Brundrett et al. (1985); 12, Brundrett and Kendrick (1988); 13, Brundrett and Kendrick (1990a); 14, Brundrett and Kendrick (1990b); 15, Brundrett et al. (1990); 16, Carling and Brown (1982); 17, Cavagnaro et al. (2001a); 18, Cavagnaro et al. (2001b); 19, Cooper (1976); 20, Dangeard (1900); 21, Dickson (2004); 22, Domínguez and Sérsic (2004); 23, Endrigkeit (1937); 24, Fisher and Jayachandran (2002); 25, Fisher and Jayachandran (2005); 26, Frankland and Harrison (1985); 27, Gallaud (1905); 28, Gay et al. (1982); 29, Gerdemann (1965); 30, Girard (1985); 31, Greny (1973); 32, Groom (1895); 33, Hawley and Dames (2004); 34, Hayman (1974); 35, Holley and Peterson (1979); 36, Imhof and Weber (1997); 37, Jacquelinet-Jeanmougin and Gianinazzi-Pearson (1983); 38, Janse (1897); 39, Johnston (1949); 40, Kessler (1966); 41, Kinden and Brown (1975); 42, Kubota et al. (2005); 43, Kühn and Weber (1986); 44, Laycock (1945); 45, Louis (1990); 46, Lovera and Cuenca (1996); 47, Maremmani et al. (2003); 48, McGee (1985); 49, McGee (1986); 50, McGee (1990); 51, McGee and Furby 1992; 52, McGee et al. (1999); 53, McLennan (1958); 54, McLuckie and Burges (1932); 55, Mosse (1973); 56, Muthukumar and Udaiyan (2002); 57, Muthukumar et al. (2003); 58, Nadarajah (1980); 59, Nicolson (1959); 60, O'Connor et al. (2001); 61, Peterson et al. (1981); 62, Redhead (1968); 63, Saif (1977); 64, Sannazzaro et al. (2004); 65, Schwartz (1912); 66, Sengupta and Chaudhuri (2002); 67, Shi et al. (2006); 68, Shibata (1902); 69, Smith et al. (1997); 70, Smith et al. (2004); 71, Stelz (1968); 72, Stockey et al. (2001); 73, Strullu et al. (1981); 74, Tiemann et al. (1994a); 75, Tiemann et al. (1994b); 76, Untch and Weber (1995); 77, Wastie (1965); 78, Weber and Krämer (1994); 79, Weber et al. (1995); 80, Whitbread et al. (1996); 81, Widden (1996); 82, Wu et al. (2004); 83, Wubet et al. (2003a); 84, Yamato and Iwasaki (2002); 85, Yamato (2004); 86, Yawney and Schultz (1990); 87, Zhang et al. (2004); 88, L Haugen and SE Smith, unpublished; 89, H. Henry (personal communication); 90, H. J. Hudson (personal communication); 91, P.J. O'Connor and F.A. Smith, unpublished; 92, B. Thomas and S.E. Smith, unpublished; 93, Wubet et al. (2003a); 94, Muthukumar et al. (2006); 95, Ruotsalainen and Aikio (2004); 96, Gross et al. (2003); 97, Yamato (2001); 98, Imhof (2003); 99, Imhof (1999a); 100, Imhof (2006); 101, Imhof (1999b); 102, Imhof (1997); 103, Imhof and Weber (1997); 104, Imhof and Weber (2000); 105, Ahulu et al. (2006)

eudicots, long regarded as primitive, have not been well explored, but the few records that exist indicate the presence of both *Arum* and *Paris* AM (Tables 2 and 3). In the asterids, one of the large dicot groups, about 22% of the 36 families with AM have only *Arum*-types, about 17% only *Paris*-types and the rest more than one type. The Asteraceae (Compositae; family 31, Table 2) have had most attention paid in this group, with records for 51 genera, 49 of them with *Arum*-type. The other large dicot group, the rosids, about 31% of the 48 families with AM, have been recorded as containing only *Arum*-types, 19% have only *Paris*-types, and the remainder have more than one type of structure. Individual families usually have one type predominating, including *Arum*-type in the Fabaceae (Leguminosae; family 26), which is a large family with many useful records. This all demonstrates that there is much more AM structural variation in different plant taxa than previously realised. However, the number of plant taxa

Table 3 The number of plant families within the major plant groupings that show large variation in their range of AM structures

Number of families having:	Strict *Arum*-type						Mixed structural types							Strict *Paris*-type
	A + I	A + I + B	A + B	A + B + P	A + P + I	A + I + B + P	I	A + P	B + I	B + P	B + I + P	P + I		
Pteridophytes	1						5					2		6
Gymnosperms	2							1		1				4
Totals in lower plants	3	0	0	0	0	0	5	1	0	1	0	2		10
Angiosperms														
Monocots	9			1	2	1		4						8
Magnoliids	2				1									3
Basal eudicots	1										1	2		2
Caryophylids	3											1		3
Asterids	8	1	1	3	2	3	3	6		1	1	1		6
Rosids	15	2		3	1	4	2	10		2		1		9
Totals in angiosperms	41	3	0	1	7	6	8	10	20	0	3	2	5	41

A *Arum*-type, I intermediate, B both, P *Paris*-type

forming strictly defined *Arum*- or *Paris*-types clearly outnumber those in which a range of different structures has been found, that is, there is a strong tendency towards the formation of structures at each end of the continuum from *Arum*-type to *Paris*-type (as also shown in Table 3).

From these data, it is not possible to conclude which structures are phylogenetically more advanced, and the fossil record is too limited to help. Arbuscules have been found in fossil protosteles of sporophytes of *Aglaeophyton major*, and in the gametophytes of the same plant (known as *Leonophyton rhynensis*) in the Rhynie Chert, from at least 400 million years ago (see Remy et al. 1994; Kerp et al. 2004; Taylor et al. 2005). This argues for very early appearance of *Arum*-types. Fossil records rarely include mention of hyphal coils, but these have now been clearly demonstrated in *Antarcticycas* and *Metasequoia* (Phipps and Taylor 1996; Stockey et al. 2001), and it is hoped that the lack of information on the diversity of AM structures in fossils will now be redressed.

Fossils aside, it remains true that the records of the AM status of plants, and of the structural variants in particular, have been biased by the '*Arum*-centric' view of the symbioses, the focus on herbaceous species and (in experimental studies) the use of *Glomus* species as the AM fungi of choice. Thus, *Paris*-types have frequently been ignored, and it is very possible that plants with this type of AM may have actually been recorded as non-mycorrhizal or of doubtful status. Secondly, it is frequently assumed that the type of AM formed is controlled solely by the identity of the plant. However, it is now known that fungal identity also plays a part in at least some plant taxa (Cavagnaro et al. 2001b; Dickson 2004). This dual control by plant and fungus is very likely to be the basis for records of both *Arum*- and *Paris*-types in single genera or species and must certainly complicate conclusions based on records from field studies with taxonomically unknown AM fungi—many of which are included in the data reviewed here. Thirdly, and given our second point, any specificity or even selectivity in choice of fungal partners might further blur any evolutionary inferences that can be made. Although it has been generally considered that host plants are non-specific in their preferences for AM associations, it is increasingly suggested (e.g. Klironomos 2003) that plants and AM fungi are locally adapted and that no plant does its best with all fungi on a site, indicating that there is some AM preference, if not absolute specificity. Lastly, it is also well established that roots of plants in the field can be colonised by several AM fungi. These last two points are now supported by the work of Ahulu et al. (2006). They used molecular probes to demonstrate that two plants from the field, *Rubus parvifolius* and *Hedera rhombea* (which form *Arum*- and *Paris*-type AM, respectively), had similar fungal genera present within their roots.

A total of 11 different phylogenetic clusters of AM fungi were identified in the roots, and both plants were colonised by *Glomus claroideum*, *G. etunicatum*, *Acaulospora longula* and *Scutellospora erythropa*. However, the assemblage of fungal species associated with each plant differed, indicating that although AM morphology was strongly influenced by the host plant identity, there was also preferential selectivity between the AM fungi and host. It is therefore possible that a root may contain both *Arum*- and *Paris*-type structures formed by different fungi. If a plant species associates preferentially with a fungus that has a tendency to form *Arum*- or *Paris*-type structures (or intermediate ones), then, any analyses based on plant phylogenetic relationships will be blurred or negated.

Does differentiation in mycorrhizal structures determine phosphate uptake efficiency and plant growth?

Positive growth responses and improved P nutrition have been shown in many plant species that form *Arum*-type AM, and this has been confirmed with measurements of uptake of radioactive phosphate (^{32}P or ^{33}P) via the external mycelium (e.g. Hattingh et al. 1973; Powell 1975; Jakobsen et al. 1992). Formation of *Paris*-type AM by *Liriodendron tulipifera* (tulip tree) and *Asphodelus fistulosus* has also been shown to promote positive growth responses via improved P uptake (Gerdemann 1965; Cavagnaro et al. 2003). This was confirmed in *L. tulipifera* with ^{32}P (Gray and Gerdemann 1967). There is now an increasing focus on the functioning of *Paris*-type AM. Different plant/fungal combinations can also provide varying efficiencies of P transfer to the plant. Smith et al. (2004) demonstrated that *Gi. rosea* transferred ^{33}P to *M. truncatula* (medic) via *Paris*-type coils (shown in Fig. 1d), although there was no net increase in the total P in the plant. Other fungal species used in this experiment (*G. caledonium* and *G. intraradices*), however, increased plant growth and promoted a positive P response in this plant. *S. lycopersicum* (tomato), a plant relatively unresponsive to colonisation, showed no positive responses in either plant growth or P uptake regardless of whether *Arum*- or *Paris*-type structures (see Fig. 1a,b) were produced. However, large amounts of ^{33}P were transferred by the *Arum*-type AM formed by *G. intraradices* and smaller but significant amounts by AM with intermediate structures formed by *G. caledonium*. With tomato, there was negligible entry by hyphae of *Gi. rosea* into the 'hyphal compartments' that contained ^{33}P.

Differences in characteristics of the interfaces between fungus and plant have been highlighted in relation to transfer of nutrients between the symbionts. An *Arum*-type arbuscule is formed by the repeated branching of a trunk hypha that penetrates through the cortical cell wall and invaginates the plant plasma membrane. Arbuscules, therefore, have large surface areas and, based on other evidence, are involved in P transfer to the plant. They may also be involved in carbon transfer to the fungus, although evidence is still limited. *Arum*-type AM (and also some Intermediates) have a second, intercellular interface formed by the longitudinal hyphae. These are highly metabolically active and are certainly involved in transfers in and out of arbuscules (i.e. with the fungus), but their role in transfer between symbionts is not clear (Smith and Smith 1990). Similarly, the role of coils is still uncertain. During formation of a *Paris*-type coil, a single hyphae penetrates the cortical cell wall and coils within the cell, again invaginating the plasma membrane and forming a symbiotic interface. Dickson and Kolesik (1999) compared a hyphal coil (*S. calospora* in *Lilium* sp.) with an arbuscule (*Glomus coronatum*, then called "City Beach", in *A. porrum*) and found that although a coil within an individual cell had a larger surface area and volume than an arbuscule, the surface area/volume ratio of the arbuscule was actually much greater. Thus, the rationale for highlighting the surface area of arbuscules as a factor likely to promote effective nutrient transfer, vis-a-vis coils, does not hold up. Arbuscular branches can be also formed on hyphal coils (i.e. producing arbusculate coils), and these structures have a large surface area, which may also be highly relevant when considering nutrient transfers via this morphological type. All of the aforementioned fungal structures remain separated from the cortical cell cytoplasm by a plant-derived periarbuscular (or peri-coil) membrane and interfacial matrix which forms an apoplastic compartment (Smith and Smith 1990; Bonfante and Perotto 1995; Armstrong and Peterson 2002). Enzyme activity has been investigated in structures produced by *G. intraradices* in *Arum*-type symbiosis with *Allium porrum* and *Paris*-type with *A. fistulosus* (Van Aarle et al. 2005). The two plants have similar patterns of root growth, and AM structures in them showed similar levels of metabolic activity. The percentage of structures with acid phosphatase (ACP) activity was greater in both cases than those with alkaline phosphatase (ALP) activity, indicating that ACP could be more important for fungal P metabolism than ALP. In the *Paris*-type, both hyphal and arbusculate coils showed high enzyme activity, and hence, are likely to be involved in P turnover.

Molecular techniques can now be used to highlight functional differences between the fungal morphologies. The expression of AM-inducible plant P transporters occurs in plants with *Paris*-type coils and arbusculate coils, as well as in transformed roots of several plant species which show intermediate AM morphology (Karandashov et al. 2004; Glassop et al. 2005). This again indicates that *Paris*-type symbioses can transfer P from fungus to plant as in the

more widely studied *Arum*-type symbioses. Defence reactions by the host towards the fungus can also be influenced by the AM structures. When tomato was colonised by *S. calospora* (forming *Paris*-type structures) expression of defence-related genes increased; however, when colonised by two isolates of *G. intraradices* that form *Arum*-type structures (including the isolate previously misidentified as *G. versiforme*), the genes were suppressed (Gao 2002; Gao et al. 2004). The authors suggested that higher expression might be related to extensive penetration of cortical cell walls in *Paris*-type AM. The fact that colonisation was extensive in all cases indicated that defence responses were unlikely to play suppressive roles in formation of either type of AM. Other experiments using *G. intraradices* or *G. mosseae* and *G. versiforme* have previously shown weak defence responses in *Arum*-forming *M. truncatula* (medic), *Glycine max* (soybean), *Nicotiana tabacum* (tobacco) and *Pisum sativum* (peas; Harrison and Dixon 1993, 1994; Lambais and Mehdy 1996; David et al. 1998; Ruiz-Lozano et al. 1999).

Can the recent surveys give more indication of the influence of different structural forms within communities or ecosystems?

Although Smith and Smith (1997) included many records from plants grown in the field, they did not address possible relationships between the structural classes and plant habitats. Inspection of the angiosperm families that they listed suggests common occurrence of *Paris*-type AM structures in tropical or subtropical species, especially woody ones. A better comparison can now be done to a very limited extent. Some of these surveys recorded the presence of hyphal coils (taken by us to indicate *Paris*-types except where we have supplementary information from the author), while others specified whether *Arum*- or *Paris*-types were present. Table 4 indicates that plants growing in desert, semi-desert, Mediterranean and savanna habitats mainly produce *Arum*-type structures—these records are predominantly (although not entirely) for herbaceous species. The possible predominance of *Paris*-types in tropical forest plants is not supported by the data of Muthukumar et al. (2003) from Xishuangbanna, southwest China, as the plants that they studied were predominantly *Arum*-types. However, as shown in Table 4, plants from woodland or forest communities elsewhere do include large numbers of *Paris*-type AM. The extensive study by Ahulu et al. (2005) is particularly interesting in that it showed that the proportion of *Arum*-type to *Paris*-type colonisation decreased in the order: pioneer group > early successional stage > late successional stage. There was also a decrease in the proportion of *Arum*-types in the order: annuals > perennials and deciduous perennials > evergreen perennials. Some of the surveys in Table 4 also identified the major AM fungi that were present (based on spore types), but no correlations with the formation of the two major structural classes can be drawn.

Conclusions—is the distinction between classes still important?

This question was asked previously (Smith and Smith 1997), and the answer must surely be the same—it depends on the context in which the question is asked. As it is established that both *Arum*- and *Paris*-type AM result in P transfer to the host, the detailed structure of the interface may not be important if the research focuses on growth responses or plant productivity. However, in terms of understanding development of colonisation, there remain intriguing issues. It is clearly not yet known what factors determine whether, after the initial colonisation through root hairs or epidermis and (where present) hypodermis, the spread of an AM fungus in the root cortex is primarily intercellular or intracellular (or, as in 'Intermediates', both) or whether there are developmental changes in individual roots. It is certainly true that lengthy, connected cortical intercellular spaces in some plants provide a pathway of low physical resistance to fungal growth, but obviously, they cannot be the sole determining factor. It is not yet known if cases where the individual AM fungal species control the outcome, rather than the plant, are exceptional—the problem here is that there have been few such detailed comparisons, especially with AM fungi other than *Glomus* species. In general, as with the phylogenetic approach, the broad-scale ecological approach sheds no light on the factors that determine formation of *Arum*- and *Paris*-types. It is still possible to accept the suggestion by Brundrett et al. (1990) that in general, *Arum*-type structures predominate in roots that grow rapidly, as in high light, while *Paris*-type structures are formed in slow-growing (and possibly longer lived roots) of plants such as understorey plants or many woody plants. Again, however, there are exceptions. One apparently firm conclusion (i.e. from evidence so far) is that interfaces through which mycoheterotrophic (achlorophyllous) AM plants receive organic C are always *Paris*-types, although presumably, the interfaces in the plant donating organic C via the fungus may be *Arum*-type (including both arbuscules and intercellular hyphae).

Figure 2 is our attempt to bring together the various factors that can (or might) determine which structural class is formed. As can be seen, we have given the plant genome most prominence, but have included a possible role for the AM fungal genome. We have included plant/AM fungal interactions via host/fungus preferences (i.e. partial selec-

Table 4 Herbaceous and woody species of plants and their associated observed AM structures within different ecosystems

	Arum-type		Intermediate		*Paris*-type		Reference
	Herbaceous	Woody	Herbaceous	Woody	Herbaceous	Woody	
Habitats with mainly *Arum*-types							
Australia							
Arid desert, dune and swales	27	11					O'Connor et al. (2001)
Open Mallee shrub	46	23			1	1	McGee (1986)
Ethiopia							
Dry Afromontane forest		10					Wubet et al. (2003a)
China							Muthukumar et al. (2003)
Slash and burn field, Xishuangbanna	3	1					
Primary tropical forest	17	18				4	
Secondary tropical forest	14	10			2	4	
Limestone forest	2	1				1	
Croatia: Brijuni National Park (mediterraean)	4	17				1	Maremmani et al. (2003)
Italy: Macchia Lucchese, Tuscany							Maremmani et al. (2003)
Woodland	11	15				1	
Backdunes	9	3					
Sanddune	17	3					
Japan:							
Vacant land, weedy vegetation	20		8		5		Yamato (2004)
Barren grassland and roadside weeds (pioneer species)	5	2			2		Ahulu et al. (2005)
Singapore: coastal reclaimed site	22				7		Louis (1990)
United States: South Florida							Fisher and Jayachandran (2005)
Coastal hammock		3		2		1	
Coastal hammock, pine rockland	1	6				1	
Pine rockland		5		1			
Venezuela:							Lovera and Cuenca (1996)
Natural savanna	5				2		
Revegetated savanna	7				1		
Old disturbed savanna	3				1		
Disturbed savanna	2						
West Indies:							Johnston (1949)
Seashore	1	2			1		
Roadsides and recent cultivation (weeds)	11				6		
Total	227	130	8	3	28	14	
Habitats with approximately equal numbers of *Arum*- and *Paris*-type							
S. Africa: Forest trees, Eastern Cape		9		7			Hawley and Dames (2004)
Canada: deciduous forest, Ontario	2	5			2	4	Brundrett et al. (1990)
Japan: mixed pine forest edge, sunny forest floor (early succession)	4	3			1	6	Ahulu et al. (2005)
West Indies:							Johnston (1949)
Orchard savanna	1	1			4		
Forest trees		3		4		6	
Total	7	21	0	11	7	16	
Habitats with mainly *Paris*-types							
China: pteridopytes, Duujiangyan			10		19		Zhang et al. (2004)
India:							Sengupta and Chauduri (2002)
Mangrove ecosystem, declined mangroves, crop agriculture							
Mangrove plants	1					1	
Non-mangrove plants	3	1	4	4	1	8	
Mangrove ecosystem, declining ridge mangroves							

Table 4 (continued)

	Arum-type		Intermediate		*Paris*-type		Reference
	Herbaceous	Woody	Herbaceous	Woody	Herbaceous	Woody	
Mangrove plants		1		3	4	7	
Non-mangrove plants	3	2	4		1	2	
Mangrove ecosystem, developed mangrove swamp							
Mangrove plants		6		3	4	11	
Non-mangrove plants	1					1	
Mangrove ecosystem, formative mangrove swamp							
Mangrove plants		3		1	1	9	
Japan: deciduous broadleaved forest, understory plants							Yamato and Iwasaki (2002)
St-M secondary forest			4		4	7	
St-K, primary forest	1	7			2	14	
St-O, secondary forest		8			7	5	
West Indies:							Johnston (1949)
Regenerating waste land	1	1			3	6	
Agricultural land, crop plants	4	3			11	7	
Total	14	32	22	11	57	78	

tivity). Although not discussed above, we have also included the possibility that soil properties may play a role insofar as they can influence rates of root growth and (via differences in soil aeration) extent of intercellular spaces. We have separated general environmental properties into 'above-ground' factors (e.g. light and temperature), which will affect plant growth and 'below-ground' factors (e.g. soil compaction, temperature, water-content, pH and nutrient supply), which will affect growth of both roots and AM fungi. Obviously, some above-ground factors can influence below-ground factors (e.g. temperature and rainfall). We have not shown influences of plant roots or AM fungi on soil properties (especially in the rhizosphere).

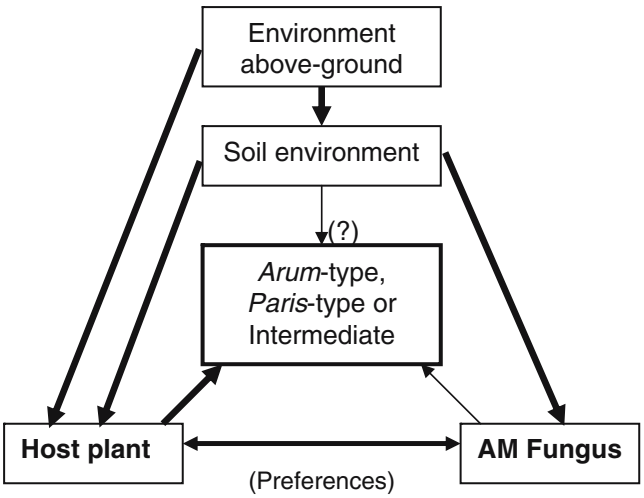

Fig. 2 Summary of the main factors that can or (in the case of the soil environment) might determine which AM structural class is formed. *Thickness of lines* indicates the possible importance of each factor. 'Preferences' indicates possible host fungus selectivity

Figure 2 gives some pointers towards future work. For example, there is a need to establish if control by AM fungi over the structures is in reality quite common—what is needed is more comparisons on individual plant species (or varieties) with AM fungi from different genera. It is possible that when roots are colonised by more than one AM fungus (as will be normal in the field) colonisation classified as 'Intermediate'—i.e. with features of both *Arum*- and *Paris*-types—might in fact result from colonisation by different AM fungi. This seems more likely where colonisation is distinctly different in spatially separated parts of a root system, as demonstrated for tomato by Kubota et al. (2005). To be attractive to researchers other than those who focus on development of interfaces in terms of chemical and enzymic factors, detailed studies of the different structures should extend to examining possible differences in P uptake efficiency and plant growth-related responses (see Peterson and Massicotte 2004). Manipulation of the soil environment to change size and extent of intercellular spaces in the root cortex is another possibility, e.g. by changing soil compaction or aeration. Changes during root development also require much more attention.

As previously (Smith and Smith 1997), we encourage those researchers who are surveying distribution of different types of mycorrhizal plants in plant ecosystems worldwide to record the AM structural classes. At the very least, it is essential that they do not look only for *Arum*-types as 'typical' AM structures and overlook *Paris*-types as possibly not even being AM (Illustrations in many textbooks

have much to answer for!). Likewise, given the popularity and success of using new molecular methods to identify AM fungi in roots from the field, it seems to us useful to record AM structural details and not just percent colonisation of the roots. Where possible, transverse sections, which provide information on location of hyphae (inter- or intracellular) should supplement root squashes. Preference by hosts for individual AM fungi may result in an AM fungal community underlying a plant community (and possibly forming a hyphal network) becoming dominated by fungi that form *Arum*-type or *Paris*-type structures. Mixed (artificial) communities of AM fungi are also used in laboratory experiments. Again, it could add value if the types of AM structures are recorded along with overall colonisation. Speculation and uncertainty aside, the occurrence of the two major structural classes, plus Intermediates within the continuum demonstrated by Dickson (2004), certainly argues for significant roles in enhancing fitness of the symbionts, and hence, their evolutionary success. We see a combination of molecular and microscopic methods as the best way of resolving uncertainty about the validity of structural groupings based on plant taxa (e.g. the "Appendix" and Tables 2 and 3). We will not learn the functional significance of the structural variations unless researchers investigating physiological and molecular aspects of the symbiosis take as much care to record mycorrhizal morphology as they do other aspects of the symbioses.

In conclusion, we believe that Gallaud's contribution still provides much food for thought and make a plea that the terms '*Arum*-type' and '*Paris*-type' be retained as the 'type structures'. Brundrett (2004) has suggested that AM symbioses be reclassified, using a mixture of terms that relate to the fungus ('linear' or 'coiling' AM), to the location of the interface ('inner cortex' AM: strangely restricted by Brundrett only to 'coiling' AM), to the root appearance ('beaded' AM) and to function ('exploitative' AM). We do not believe that these terms really help the researcher because they obscure what are actually quite distinctive pathways of fungal development within the root cortex.

Acknowledgements Our work is supported by the Australian Research Council.

References

Abbas Y, Ducousso M, Abourouh M, Azcón R, Duponnois R (2006) Diversity of arbuscular mycorrhizal fungi in *Tetraclinis articulata* (Vahl) Masters woodlands in Morocco. Ann For Sci 63:285–291

Abbott LK (1982) Comparative anatomy of vesicular–arbuscular mycorrhizas formed on subterranean clover. Aust J Bot 30:485–499

Abbott LK, Robson AD (1978) Growth of subterranean clover in relation to the formation of endomycorrhizas by introduced and indigenous fungi in a field soil. New Phytol 81:575–585

Ahulu EM, Nakata M, Nonaka M (2005) *Arum*- and *Paris*-type arbuscular mycorrhizas in a mixed pine forest on sand dune soil in Niigata Prefecture, central Honshu, Japan. Mycorrhiza 15:129–136

Ahulu EM, Gollotte A, Gianinazzi-Pearson V, Nonaka M (2006) Cooccurring plants forming distinct arbuscular mycorrhizal morphologies harbor similar AM fungal species. Mycorrhiza 17:37–49

Antoniolli ZI (1999) Arbuscular mycorrhizal community in a permanent pasture and development of species-specific primers for detection and quantification of two AM fungi. PhD, Soil and Water, The University of Adelaide, Australia

Armstrong L, Peterson RL (2002) The interface between the arbuscular mycorrhizal fungus *Glomus intraradices* and root cells of *Panax quinquefolius*: a *Paris*-type mycorrhizal association. Mycologia 94:587–595

Asai T (1944) Über die Mykorrhizenbildung der leguminosen Pflanzen. Jpn J Bot 13:463–485

Bago A, Cano C, Toussaint J, Smith S, Dickson S (2006) Interactions between the arbuscular mycorrhizal (AM) fungus *Glomus intraradices* and nontransformed tomato roots of either wild-type or AM-defective phenotypes in monoxenic cultures. Mycorrhiza 16:429–436

Barrett JT (1958) Synthesis of mycorrhiza with pure cultures of *Rhizophagus*. Phytopathology 48:391

Baylis GTS, McNabb RFR, Morrison TM (1963) The mycorrhizal nodules of podocarps. Trans Br Mycol Soc 46:378–384

Bedini S, Maremmani A, Giovannetti M (2000) *Paris*-type mycorrhizas in *Smilax aspera* L. growing in a Mediterranean scherophyllous wood. Mycorrhiza 10:9–13

Bernard C (1904) Le champignon endophyte des orchidées. C r Acad Sci Paris Sci 138:828–830

Böcher TW (1964) Morphology of the vegetative body of *Metasequoia glyptostroboides*. Dansk Bot Arkiv 24:1–70

Bonfante P, Perotto S (1995) Strategies of arbuscular mycorrhizal fungi when infecting host plants. New Phytol 130:3–21

Bonfante-Fasolo P, Fontana A (1985) VAM fungi in *Ginkgo biloba* roots: their interactions at cellular level. Symbiosis 1:53–67

Breuninger M, Einig W, Magel E, Cardoso E, Hampp R (2000) Mycorrhiza of Brazil pine (*Araucaria angustifolia* Bert. O. Ktze.). Plant Biol 2:4–10

Brundrett M (2002) Coevolution of roots and mycorrhizas of land plants. New Phytol 154:275–304

Brundrett M (2004) Diversity and classification of mycorrhizal associations. Biol Rev 79:473–495

Brundrett MC, Kendrick B (1988) The mycorrhizal status, root anatomy and phenology of plants in a sugar maple forest. Can J Bot 66:1153–1173

Brundrett M, Kendrick B (1990a) The roots and mycorrhizas of herbaceous woodland plants. I. Quantitative aspects of morphology. New Phytol 114:457–468

Brundrett M, Kendrick B (1990b) The roots and mycorrhizas of herbaceous woodland plants. II. Structural aspects of morphology. New Phytol 114:469–479

Brundrett MC, Piché Y, Peterson RL (1985) A developmental study of the early stages in vesicular-arbuscular mycorrhiza development. Can J Bot 63:184–194

Brundrett M, Murase G, Kendrick B (1990) Comparative anatomy of roots and mycorrhizae of common Ontario trees. Can J Bot 68:551–578

Carling DE, Brown MF (1982) Anatomy and physiology of vesicular–arbuscular and non-mycorrhizal roots. Phytopathology 72:1108–1114

Cavagnaro TR, Smith FA, Lorimer MF, Haskard KA, Ayling SM, Smith SE (2001a) Quantitative development of *Paris*-type arbuscular mycorrhizas formed between *Asphodelus fistulosus* and *Glomus coronatum*. New Phytol 149:105–113

Cavagnaro TR, Gao L-L, Smith FA, Smith SE (2001b) Morphology of arbuscular mycorrhizas is influenced by fungal identity. New Phytol 151:469–475

Cavagnaro TR, Smith FA, Ayling SM, Smith SE (2003) Growth and phosphorus nutrition of a *Paris*-type arbuscular mycorrhizal symbiosis. New Phytol 157:127–134

Cooper KM (1976) A field survey of mycorrhizas in New Zealand ferns. NZ J Bot 14:169–181

Cronquist A (1981) An integrated system of classification of flowering plants. Columbia University Press, New York, USA

Dangeard PA (1900) Le *Rhizophagus populinus*. Botaniste 7:285–287

David R, Itzhak H, Ginsberg I, Gafni Y, Galili G, Kapulnik Y (1998) Suppression of tobacco basic chitinase gene expression in response to colonisation by the arbuscular mycorrhizal fungus *Glomus intraradices*. MPMI 11:489–497

Demuth K, Forstreuter W, Weber HC (1991) Morphological differences in vesicular–arbuscular mycorrhizae of *Gentianaceae* produced by different endophytes. Flora 185:127–132

Dickson S (2004) The *Arum–Paris* continuum of mycorrhizal symbioses. New Phytol 163:187–200

Dickson S, Kolesik P (1999) Visualisation of mycorrhizal fungal structures and quantification of their surface area and volume using laser scanning confocal microscopy. Mycorrhiza 9:205–213

Domínguez LS, Sérsic A (2004) The southernmost myco-heterotrophic plant, *Arachnitis uniflora*: root morphology and anatomy. Mycologia 96:1143–1151

Endrigkeit A (1937) Beiträge zum ernährungsphysiologischen Problem der Mykorrhiza unter besonderer Berücksichtigung des Baues und der Funktion der Wurzel–und Pilzmembranen. Bot Arkiv 39:1–87

Fisher JB, Jayachandran K (2002) Arbuscular mycorrhizal fungi enhance seedling growth in two endangered plant species from South Florida. Int J Plant Sci 163:559–566

Fisher JB, Jayachandran K (2005) Presence of arbuscular mycorrhizal fungi in South Florida native plants. Mycorrhiza 15:580–588

Fitter AH, Moyersoen B (1996) Evolutionary trends in root-microbe symbioses. Philos Trans R Soc Lond B 351:1367–1375

Frank AB (1885a) Uber die auf Wurzelsymbiose beruhende Ernährung gewisser Bäum durch unterirdische Pilze. Ber Dtsch Bot Ges 3:128–145

Frank AB (1885b) On the nutritional dependence of certain trees on root symbiosis with belowground fungi (an English translation of A.B. Frank's classic paper of 1885). Mycorrhiza 15:267–275

Frank AB (1887) Ueber neue Mycorrhiza-formen. Ber Dtsch Bot Ges 5:395–409

Frankland JC, Harrison AF (1985) Mycorrhizal infection of *Betula pendula* and *Acer pseudoplatanus*: relationships with seedling growth and soil factors. New Phytol 101:133–151

Gallaud I (1904) Études sur les mycorrhizes endotrophes. Rev Gén Bot, Bigot Frerès, Lille

Gallaud I (1905) Études sur les mycorrhizes endotrophes. Rev Gén Bot 17:5–48; 66–83, 123–135; 223–239; 313–325; 425–433; 479–500

Gao L-L (2002) Control of arbuscular mycorrhizal colonisation: studies of a mycorrhiza-defective tomato mutant. PhD, Dept Soil and Water, The University of Adelaide, Australia

Gao L-L, Knogge W, Delp G, Smith FA, Smith SE (2004) Expression patterns of defense-related genes in different types of arbuscular mycorrhizal development in wild-type and mycorrhiza-defective mutant tomato. MPMI 17:1103–1113

Gay PE, Grubb PJ, Hudson HJ (1982) Seasonal changes in the concentrations of nitrogen, phosphorus and potassium, and in the density of mycorrhiza, in biennial and matrix-forming perennial species of closed chalkland turf. J Ecol 70:571–593

Gerdemann JW (1965) Vesicular–arbuscular mycorrhizae formed on maize and tuliptree by *Endogone fasciculata*. Mycologia 57:562–575

Girard I (1985) Écologie des mycorrhizes: caractère mycorhizien des espèces végétales se forêts climaciques et reflexion sur la relation humus—mycorrhize. MSc, Département de Science Forestière, France

Glassop D, Smith SE, Smith FW (2005) Cereal phosphate transporters associated with the mycorrhizal pathway of phosphate uptake into roots. Planta 222:688–698

Gray LE, Gerdemann JW (1967) Influence of vesicular–arbuscular mycorrhizas on the uptake of phosphorus-32 by *Liriodendron tulipifera* and *Liquidambar styraciflua*. Nature 49:106

Greny A (1973) Étude anatomo-morphologique des endomycorrhizes constitue par le Maïs, l'Avoine, le Blé, l'Orge et diverses Graminées prairiales et adventices. Mémoire presente au Conservatoire des Arts et Métiers pour obtenir le Diplome d'Ingenieur C.N.A.M

Groom P (1895) On *Thismia aseroe* Beccari and its mycorrhiza. Ann Bot 9:327–361

Gross E, Cordeiro L, Caetano FH (2003) Anatomical and ultrastructural aspects of root and mycorrhiza of *Anadenanthera peregrina* (L.) Speg. var. *falcata* (Benth.) Altschul (Leguminosae-Mimosoideae) Rev Bras Cienc Solo 26:515–523

Harrison MJ, Dixon RA (1993) Isoflavonoid accumulation and expression of defense gene transcripts during the establishment of vesicular–arbuscular mycorrhizal associations in roots of *Medicago truncatula*. MPMI 6:643–654

Harrison MJ, Dixon RA (1994) Spatial patterns of expression of flavonoid/isoflavonoid pathway genes during interactions between roots of *Medicago truncatula* and the mycorrhizal fungus *Glomus versiforme*. Plant J 6:9–20

Hattingh MJ, Gray LE, Gerdemann JW (1973) Uptake and translocation of ^{32}P-labeled phosphate to onion roots by endomycorrhizal fungi. Soil Sci 116:383–387

Hawley GL, Dames JF (2004) Mycorrhizal status of indigenous tree species in a forest biome of the Eastern Cape, South Africa. S Afr J Sci 100:633–637

Hayman DS (1974) Plant growth responses to vesicular–arbuscular mycorrhiza. VI. Effect of light and temperature. New Phytol 73:71–80

Holley JD, Peterson RL (1979) Development of a vesicular–arbuscular mycorrhiza in bean roots. Can J Bot 57:1960–1978

Imhof S (1997) Root anatomy and mycotrophy of the achlorophyllous *Voyria tenella* Hooker (Gentianaceae). Bot Acta 110:298–305

Imhof S (1999a) Subterranean structures and mycorrhiza of the achlorophyllous *Burmannia tenella* Bentham (Burmanniaceae). Can J Bot 77:637–643

Imhof S (1999b) Root morphology, anatomy and mycotrophy of the achlorophyllous *Voyria aphylla* (Jacq.) Pers. (Gentianaceae). Mycorrhiza 9:33–39

Imhof S (2003) A dorsiventral mycorrhizal root in the achlorophyllous *Sciaphila polygyna* (Triuridaceae). Mycorrhiza 13:327–332

Imhof S (2006) Two distinct fungi colonize roots and rhizomes of the myco-heterotrophic *Afrothismia gesnerioides* (Burmanniaceae). Can J Bot 86:852–861

Imhof S, Weber HC (1997) Root anatomy and mycotrophy (AM) of the achlorophyllous *Voyria truncata* (Standley) Standley and Steyermark (Gentianaceae). Bot Acta 110:127–134

Imhof S, Weber HC (2000) Root structures and mycorrhiza of the achlorophyllous *Voyria obconica* Progel (Gentianaceae). Symbiosis 29:201–211

Jacquelinet-Jeanmougin S, Gianinazzi-Pearson V (1983) Endomycorrhizas in the Gentianaceae. I. The fungi associated with *Gentiana lutea* L. New Phytol 95:663–666

Jakobsen I, Abbott LK, Robson AD (1992) External hyphae of vesicular–arbuscular mycorrhizal fungi associated with *Trifolium subterraneum* L. 2. Hyphal transport of ^{32}P over defined distances. New Phytol 120:509–516

Janse JM (1897) Les endophytes radicaux de quelques plantes Javanaises. Ann Jard Bot Buitenzorg 14:53–201

Johnston A (1949) Vesicular–arbuscular mycorrhiza in sea island cotton and other tropical plants. Trop Agric 26:118–121

Karandashov V, Nagy R, Wegmüller S, Amrhein N, Bucher M (2004) Evolutionary conservation of a phosphate transporter in the arbuscular mycorrhizal symbiosis. Proc Natl Acad Sci USA 101:6285–6290

Kerp H, Trewin NH, Haas H (2004) New gametophytes from the Early Devonian Rhynie chert. Trans R Soc Edinb Earth Sci 94:411–428

Kessler KJ (1966) Growth and development of mycorrhizae of sugar maple (*Acer saccharum* Marsh.). Can J Bot 44:1413–1425

Kinden DA, Brown MF (1975) Electron microscopy of vesicular–arbuscular mycorrhizae of yellow poplar. I. Characterization of endophytic structures by scanning electron stereoscopy. Can J Microbiol 21:989–993

Klironomos JN (2003) Variation in plant response to native and exotic arbuscular mycorrhizal fungi. Ecology 84:2292–2301

Koide RT, Mosse B (2004) A history of research on arbuscular mycorrhiza. Mycorrhiza 14:145–163

Kubota M, McGonigle TP, Hyakumachi M (2005) Co-occurrence of *Arum*- and *Paris*-type morphologies of arbuscular mycorrhizae in cucumber and tomato. Mycorrhiza 15:73–77

Kühn K-D, Weber HC (1986) Vesicular arbuscular mycorrhiza in *Gentiana asclepiadea* L. (Gentianaceae) on natural habitats. Angew Bot 60:427–439

Lambais MR, Mehdy MC (1996) Soybean roots infected by *Glomus intraradices* strains differing in infectivity exhibit differential chitinase and β-1,3-glucanase expression. New Phytol 134:531–538

Laycock DH (1945) Preliminary investigations into the function of the endotrophic mycorrhiza of *Theobroma cacao* L. Trop Agric 22:77–80

Leake JR (1994) The biology of myco-heterotrophic ('saprophytic') plants. New Phytol 127:171–216

Louis I (1990) A mycorrhizal survey of plant species colonizing coastal reclaimed land in Singapore. Mycologia 82:772–778

Lovera M, Cuenca G (1996) Arbuscular mycorrhizal infection in Cyperaceae and Gramineae from natural, disturbed and restored savannas in La Gran Sabana, Venezuela. Mycorrhiza 6:111–118

Maremmani A, Bedini S, Matoševic I, Tomei PE, Giovannetti M (2003) Type of mycorrhizal associations in two coastal nature reserves of the Mediterranean basin. Mycorrhiza 13:33–40

McGee PA (1985) Lack of spread of endomycorrhizas of *Centaurium* (Gentianaceae). New Phytol 101:451–458

McGee PA (1986) Mycorrhizal associations of plant species in a semiarid community. Aust J Bot 34:585–593

McGee PA (1990) Survival and growth of seedlings of coachwood (*Ceratopetalum apetalum*): effects of shade, mycorrhizas and a companion plant. Aust J Bot 38:583–592

McGee PA, Furby JH (1992) Formation and structure of mycorrhizas of seedlings of coachwood (*Ceratopetalum apetalum*). Aust J Bot 40:291–304

McGee PA, Bullock S, Summerell BA (1999) Structure of mycorrhizae of the Wollemi pine (*Wollemia nobilis*) and related Araucariaceae. Aust J Bot 47:85–95

McLennan EI (1958) *Thismia rodwayi* F Muell. and its endophyte. Aust J Bot 6:25–37

McLuckie J, Burges A (1932) Mycotrophism in the Rutaceae. I. The mycorrhiza of *Eriostemon Crowei* F.v.M. Proc Linn Soc N S W 57:291–312

Mosse B (1973) Plant growth responses to vesicular–arbuscular mycorrhiza. IV. In soil given additional phosphate. New Phytol 72:127–136

Muthukumar T, Udaiyan K (2002) Arbuscular mycorrhizas in cycads of southern India. Mycorrhiza 12:213–217

Muthukumar T, Sha LQ, Yang XD, Cao M, Tang JW, Zheng Z (2003) Mycorrhiza of plants in different vegetation types in tropical ecosystems of Xishuangbanna, southwest China. Mycorrhiza 13:289–297

Muthukumar T, Senthilkumar S, Rajangam M, Udaiyan K (2006) Arbuscular mycorrhizal morphology and dark septate fungal associations in medicinal and aromatic plants of Western Ghats, Southern India. Mycorrhiza 17:11–24

Nadarajah P (1980) Species of Endogonaceae and mycorrhizal association of *Elaeis guineensis* and *Theobroma cacao*. In: Mikola P (ed) Tropical mycorrhiza. Clarendon, Oxford, pp 233–237

Nicolson TH (1959) Mycorrhiza in the Graminae I. Vesicular–arbuscular endophytes, with special reference to the external phase. Trans Br Mycol Soc 42:421–438

O'Connor PJ, Smith SE, Smith FA (2001) Arbuscular mycorrhizal associations in the southern Simpson Desert. Aust J Bot 49:493–499

Peterson RL, Massicotte HB (2004) Exploring structural definitions of mycorrhizas, with emphasis on nutrient-exchange interfaces. Can J Bot 82:1074–1088

Peterson RL, Howarth MJ, Whittier DP (1981) Interactions between a fungal endophyte and gametophyte cells in *Psilotum nudum*. Can J Bot 59:711–720

Petri L (1903) Ricerche sul signifacto morfologica del prosporoidi (sporangiolo di Janse) nelle micorrize endotrofiche. Nuovo G Bot Ital 10:541

Peyronel B (1923) Fructification de l'endophyte a arbuscules et a vesicules des mycorhizes endotrophes. Bull Soc Mycol 39:119–126

Peyronel B (1924) Specie di "Endogone" produttrici di micorize endotrofiche. Boll Stan Patol Veg Roma 5:73–75

Phipps CJ, Taylor TN (1996) Mixed arbuscular mycorrhizae from the Triassic of Antarctica. Mycologia 88:707–714

Powell CL (1975) Plant growth responses to vesicular–arbuscular mycorrhiza. VIII. Uptake of P by onion and clover infected with different *Endogone* spore types in ^{32}P labelled soil. New Phytol 75:563–566

Rayner MC (1927) Mycorrhiza. An account of non-pathogenic infection by fungi in vascular plants and bryophytes. New Phytol Reprint No 15. Wheldon & Wesley Ltd, London

Read DJ, Duckett JG, Francis R, Ligrone R, Russell A (2000) Symbiotic fungal associations in 'lower' land plants. Philos Trans R Soc B 355:815–830

Redhead JF (1968) Mycorrhizal associations in some Nigerian forest trees. Trans Br Mycol Soc 51:377–387

Remy W, Taylor TN, Hass H, Kerp H (1994) Four hundred-million-year-old vesicular arbuscular mycorrhizae. Proc Natl Acad Sci USA 91:11841–11843

Ruiz-Lozano JM, Roussel H, Gianinazzi S, Gianinazzi-Pearson V (1999) Defence genes are differentially induced by a mycorrhizal fungus and *Rhizobium* sp. in wild-type and symbiosis-defective pea genotypes. MPMI 12:976–984

Ruotsalainen AL, Aikio S (2004) Mycorrhizal inoculum and performance of nonmycorrhizal *Carex bigelowii* and mycorrhizal *Trientalis europaea.* Can J Bot 82:443–449

Saif SR (1977) The influence of stage of host development on vesicular–arbuscular mycorrhizae and endogonaceous spore population in field-grown vegetable crops. I. Summer-grown crops. New Phytol 79:341–348

Sannazzaro AI, Ruiz OA, Albertó E, Menéndez AB (2004) Presence of different arbuscular mycorrhizal infection patterns in roots of *Lotus glaber* plants growing in the Salado River basin. Mycorrhiza 14:139–142

Schüßler A, Schwarzott D, Walker C (2001) A new fungal phylum, the *Glomeromycota*: phylogeny and evolution. Mycol Res 105:1413–1421

Schwartz EJ (1912) Observations on *Asarum europaeum* mycorrhiza. Ann Bot 26:769–776

Sengupta A, Chaudhuri S (2002) Arbuscular mycorrhizal relations of mangrove plant community at the Ganges river estuary in India. Mycorrhiza 12:169–174

Shi ZY, Chen YL, Feng G, Liu RJ, Christie P, Li XL (2006) Arbuscular mycorrhizal fungi associated with the Meliaceae on Hainan island, China. Mycorrhiza 16:81–87

Shibata K (1902) Cytologische studien uber die endotrophen mycorrhizen. Jahrb Wiss Bot 37:643–684

Smith SE, Dickson S (1991) Quantification of active vesicular–arbuscular mycorrhizal infection using image analysis and other techniques. Aust J Plant Physiol 18:637–648

Smith SE, Read DJ (1997) Mycorrhizal symbiosis, 2nd edn. Academic, San Diego

Smith SE, Read DJ (2007) Mycorrhizal symbiosis, 3rd edn. Elsevier (in press)

Smith SE, Smith FA (1990) Structure and function of the interfaces in biotrophic symbioses as they relate to nutrient transport. New Phytol 114:1–38

Smith FA, Smith SE (1997) Structural diversity in (vesicular)–arbuscular mycorrhizal symbiosis. New Phytol 137:373–388

Smith HF, O'Connor PJ, Smith SE, Smith FA (1997) (Vesicular) ± arbuscular mycorrhizas of durian and other plants of forest gardens in W. Kalimantan, Indonesia. In: Schulte A, Ruhiyat D (eds) Forest soils in the humid tropics: characteristics, ecology and management. Springer, Berlin Heidelberg New York, pp 192–198

Smith SE, Smith FA, Jakobsen I (2004) Functional diversity in arbuscular mycorrhizal (AM) symbioses: the contribution of the mycorrhizal P uptake pathway is not correlated with mycorrhizal responses in growth or total P uptake. New Phytol 162:511–524

Stelz T (1968) Mycorrhizes et vegetation des pelouses calcaires. Faculté des Sciences de l'Université de Rouen, France

Stevens PF (2004) Angiosperm phylogeny website: http://www.mobot.org/MOBOT/research/AP/ (Cited May 2004)

Stockey RA, Rothwell GW, Addy HD, Currah RS (2001) Mycorrhizal association of the extinct conifer *Metasequoia milleri*. Mycol Res 105:202–205

Strullu DG, Gourret JP, Garrec JP, Fourcy A (1981) Ultrastructure and electron-probe microanalysis of the metachromatic vacuolar granules occurring in *Taxus* mycorrhizas. New Phytol 87:537–545

Taylor TN, Hass H, Kerp H, Krings M, Hanlin RT (2005) Perithecial ascomycetes from the 400 million year old Rhynie chert: an example of ancestral polymorphism. Mycologia 97:269–285

Tiemann C, Demuth K, Weber HC (1994a) Zur VA-Mycorrhiza von *Gelsemium rankinii* und *G. sempervirens* (Loganiaceae). Beit Biol Pflanz 68:311–321

Tiemann C, Demuth K, Weber HC (1994b) Zur Symbiose von *Cynanchum vincetoxicum* (L) PERS., *Asclepias curassavica* L. and *Ceropegia woodii* SCHL. (Asclepiadaceae) mit mycorrhizapilzen (VAM). Flora 189:1–6

Trappe JM (1987) Phylogenetic and ecologic aspects of mycotrophy in the angiosperms from an evolutionary standpoint. In: Safir GR (ed) Ecophysiology of VA mycorrhizal plants. CRC, Boca Raton, pp 5–25

Trappe JM (2005) A.B. Frank and mycorrhizae: the challenge to evolutionary and ecologic theory. Mycorrhiza 15:277–281

Untch, Weber HC (1995) Strukturen der Mycorrhiza (AM) bei *Ceropegia dichotoma* Haw., *Ceropegia fusca* Bolle und *Periploca laevigata* Ait. (Asclepiadaceae). Beit Biol Pflanz 69:129–140

Van Aarle IM, Cavagnaro TR, Smith SE, Smith FA, Dickson S (2005) Metabolic activity of *Glomus intraradices* in *Arum*- and *Paris*-type arbuscular mycorrhizal colonization. New Phytol 166:611–618

Wang B, Qiu Y-L (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16:299–363

Wastie RL (1965) The occurrence of an *Endogone* type of endotrophic mycorrhiza in *Hevea brasiliensis*. Trans Br Mycol Soc 48:167–178

Weber HC, Krämer M (1994) VA ± Mycorrhiza bei Menyanthaceae. Beit Biol Pflanz 68:351–362

Weber HC, Klahr A, Marron-Heimbuch M (1995) Anatomical structures of the VA mycorrhiza in the Apocynaceae (Gentianales). Bot Acta 108:525–534

Whitbread F, McGonigle TP, Peterson RL (1996) Vesicular–arbuscular mycorrhizal associations of American Ginseng (*Panax quinquefolius*) in commercial production. Can J Bot 74:1104–1112

Widden P (1996) The morphology of vesicular–arbuscular mycorrhizae in *Clintonia borealis* and *Medeola virginiana*. Can J Bot 74:679–685

Wu BY, Isobe K, Ishii R (2004) Arbuscular mycorrhizal colonization of the dominant plant species in primary successional volcanic deserts on the Southeast slope of Mount Fuji. Mycorrhiza 14:391–395

Wubet T, Kottke I, Teketay D, Oberwinkler F (2003a) Mycorrhizal status of indigenous trees in dry Afromontane forests of Ethiopia. For Ecol Manag 179:387–399

Wubet T, Weiss M, Kottke I, Oberwinkler F (2003b) Morphology and molecular diversity of arbuscular mycorrhizal fungi in wild and cultivated yew (*Taxus baccata*). Can J Bot 81:255–266

Yamato M (2001) Identification of a mycorrhizal fungus in the roots of achlorophyllous *Sciaphila tosaensis* Makino (Triuridaceae). Mycorrhiza 11:83–88

Yamato M (2004) Morphological types of arbuscular mycorrhizal fungi in roots of weeds on vacant land. Mycorrhiza 14:127–131

Yamato M, Iwasaki M (2002) Morphological types of arbuscular mycorrhizal fungi in roots of understory plants in Japanese deciduous broadleaved forests. Mycorrhiza 12:291–296

Yawney WJ, Schultz RC (1990) Anatomy of a vesicular–arbuscular endomycorrhizal symbiosis between sugar maple (*Acer saccharum* Marsh) and *Glomus etunicatum* Becker and Gerdemann. New Phytol 114:47–57

Zhang Y, Guo LD, Liu RJ (2004) Arbuscular mycorrhizal fungi associated with common pteridophytes in Dujiangyan, southwest China. Mycorrhiza 14:25–30

Zhao Z-W (2000) The arbuscular mycorrhizas of pteridophytes in Yunnan, southwest China: evolutionary interpretations. Mycorrhiza 10:145–149