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Review. Effects of arbuscular mycorrhizas on reproductive traits in sexually dimorphic plants

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Abstract

Most plant species grow in association with arbuscular mycorrhizal fungi in their roots forming arbuscular mycorrhizal (AM) symbiosis. The positive effects of this type of symbiosis on plant's performance are well known and established. However, relatively little is known about how AM symbiosis affects plant reproduction, even though reproduction is probably the most important component of life history. This review begins with a summary of the existing data on plants with monomorphic breeding systems, as most of the research has been performed using hermaphroditic and monoecious plants. Later, the limited number of studies examining mycorrhizal effects on plants with dimorphic breeding systems is detailed. Finally, several key areas for future investigations are highlighted. These include examination of the incidence of sex-specific interactions in other plant species with dimorphic systems, the influence of AM symbiosis in seed germination and establishment in plants with different gender, or the study of the mechanisms behind the AM effects seen on plant reproduction. Evidence suggests that AM symbioses are beneficial for plants with monomorphic and dimorphic breeding systems, as AM symbioses improve both sexual and asexual reproduction. However, the effects observed strongly depend on both the plant and the AM fungus species involved. Plant interactions with AM fungi and the outcome of these interactions may further depend on the gender of the host: sex-specific patterns of root colonization and sex-specific benefits from AM symbioses have been reported in several plant species. However, the incidence and the importance of sex-specific relationships between AM fungi and plants are still largely unexplored.

Additional key words: clonal growth, plant sexual dimorphism, plant-fungus interactions, sex-specific interactions, sexual reproduction.

Resumen

Revisión. Efecto de las micorrizas arbusculares en las características reproductivas de las plantas con dimorfismo sexual

La mayoría de plantas crecen en asociación con hongos micorrícicos arbusculares en sus raíces formando micorrizas arbusculares (MA). Los efectos positivos de este tipo de simbiosis para el desarrollo de plantas son bien reconocidos. Poco se sabe de los efectos de las MA sobre la reproducción; aunque sea probablemente el rasgo más importante de la estrategia vital de una planta. Esta revisión detalla los datos disponibles sobre los efectos de las MA en la reproducción de plantas con sistemas de reproducción monomórficos y dimórficos. Se presentan los datos existentes sobre los efectos en la reproducción en plantas con sistemas de reproducción monomórficos, dado que la mayoría de los estudios se han efectuado sobre plantas hermafroditas y monoicas; se detallan los estudios que examinan los efectos de las MA en plantas con sistemas de reproducción dimórficos; y se proporcionan líneas de investigación futuras. Los datos sugieren que las MA son mayoritariamente beneficiosas tanto para plantas con sistemas monomórficos cómo dimórficos, ya que mejoran la reproducción sexual y también la asexual. Los efectos observados dependen de la identidad de las especies de plantas y hongos MA involucrados en la simbiosis. Además, las interacciones entre plantas y hongos MA pueden también depender del sexo de la planta: se ha observado que los patrones de colonización de la raíz y los beneficios obtenidos pueden ser específicos para cada sexo. Todavía queda por explorar la incidencia y la importancia que puedan tener las relaciones específicas de sexo entre hongos MA y plantas.

Palabras clave adicionales: crecimiento clonal, dimorfismo sexual en plantas, interacciones específicas de sexo, interacciones planta-hongo, micorrizas arbusculares, reproducción sexual.

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Introduction

Most land plant species form some type of mycorrhizal association. Among mycorrhizal types, arbuscular mycorrhiza (AM) is the most common and widespread. In this association, symbiotic fungi of the phylum Glomeromycota (Schüβler *et al.,* 2001) colonise the roots of an enormously wide variety of plants (Wang and Qiu, 2006). The relationship is considered mutualistic (but see Johnson *et al.,* 1997; Jones and Smith, 2004), as the plant supplies the fungus with photosynthates whereas the fungus delivers nutrients from the soil in return. The result of this is a net movement of phosphorus, nitrogen and other nutrients to the plant and of carbon to the fungus (Smith and Read, 1997). Mycorrhizal plants are often more competitive and better able to tolerate environmental stresses than non-mycorrhizal plants through improved nutrient (Smith and Read, 1997) and water acquisition (Ruiz-Lozano and Azcón, 1995). The AM fungi are completely biotrophic and acquire all carbon necessary for fungal growth and nutrient uptake from the host plant (Smith and Read, 1997). Therefore, regardless of all the benefits the plant gains from AM symbiosis, there is also a cost in terms of the carbon allocated to the fungus. The amount of carbon allocated to mycorrhizal roots may be up 20% of the total photosynthate income (Jakobsen and Rosendahl, 1990).

According to the principle of allocation formulated by Cody (1966), limited resources must be shared among all plant functions. Therefore, trade-offs among growth, defence and reproduction may exist. The most important life history trait connected to fitness involves the pattern of resource allocation to reproduction. Reproductive allocation (defined as the proportion of the total pool of resources invested in reproduction) may constitute a great part of plant biomass and consequently, investment in reproduction may reduce future growth and survival (cost of reproduction, for a review see Obeso, 2002). Plants can reproduce sexually (through the production and fusion of haploid gametes), asexually via clonal growth, or both.

Despite the large body of research on AM effects of plant growth, relatively little attention has been given to the effects on plant reproduction. Most of the studies about the effects of mycorrhizas on plant reproduction have focused on monoecious and hermaphroditic species. The mycorrhizal effects observed are largely explained by the improved growth and nutrient uptake of colonised plants compared to non-mycorrhizal plants (Koide, 2000). Nevertheless, it is also possible that changes in host plant hormone levels due to AM symbiosis (Ludwig-Müller, 2000 and references therein) mediate the mycorrhizal effects on plant reproduction, as different hormones affect many plant functions related to reproduction (Davies, 1995).

Sexual dimorphism (differences between individuals of different gender in traits other than sex itself) is widespread in plants. Sexual dimorphism may be the consequence of sex-differential pattern of resource allocation, which is in turn caused by differences in requirements for disseminating pollen and maturing fruits (Geber, 1999 and references therein). In sexually dimorphic plants, reproductive allocation usually differs between the genders as a result of the different costs of the sexual functions and how the sexes achieve their fitness (reviewed in Case and Ashman, 2005). Sexual dimorphisms in life-history traits, physiology, morphology and biotic interactions have received extensive attention (Geber *et al.,* 1999 and references therein). However, whether the relationship between AM and its hosts can be gender-specific is a novel approach. Since the sexes differ in resource needs and allocation patterns, and AM impose both costs and benefits for the plant, one may hypothesize that the sexes may differ in their relationship with their mycorrhizal symbionts. For example, in dioecious species, reproductive allocation by female plants usually exceeds that of male plants (Obeso, 2002 and references therein) except when exceptionally large amount of pollen is produced (Lloyd and Webb, 1977). In gynodioecious species, female plants usually produce more seeds than hermaphrodites (Shykoff *et al.,* 2003) and therefore, females should invest relatively more in reproduction than hermaphrodites (Obeso, 2002). In other dimorphic breeding systems, empirical data is lacking.

In the present review, the current knowledge about the effects of AM on plant reproduction is summarized. Two excellent reviews are already available about the effects of mycorrhizal symbiosis on plant reproduction in monomorphic plants (Koide, 2000) and its implications for plant population dynamics (Koide and Dickie, 2002). In the present review, a new subject is added: the effect of AM on reproduction in plants with dimorphic breeding systems. First, a brief introduction to plant breeding systems is given. Then, the research done on the AM effects on plant reproduction on monomorphic and on dimorphic plants is reviewed. Finally, a list of gaps in the present knowledge is outlined as suggested key questions for future investigations.

Plant breeding systems

Most sexually reproducing plants belong to populations with monomorphic sexual systems (Yampolsky and Yampolsky, 1922; Richards, 1997), containing a single sexual phenotype in the population. Sexually monomorphic systems include hermaphroditic, monoecious, gynomonoecious and andromonoecious populations (Fig. 1). In hermaphroditic populations (found in about 72% of plants) individuals have only hermaphroditic flowers. In monoecious populations, plants have separated female and male flowers on the same individual (De Jong *et al.,* 2008). This condition is found in about 5% of plants. In gynomonoecious populations, female and hermaphroditic flowers are present on the same individual (2.8% of plants). Finally, andromonoecious populations are comprised by individuals with male and hermaphroditic flowers (1.7% of plants; Vallejo-Marín and Rausher, 2007). The rest of sexually reproducing plants belong to sexually dimorphic or polymorphic populations, where more than one type of individual can be recognized with regard to their sexual expression (Lloyd, 1980). Sexually dimorphic sexual systems include heterostyly, enantiostyly, dioecy, gynodioecy, androdioecy and subdioecy (Fig. 1). In heterostyly, populations with two (distyly) or three

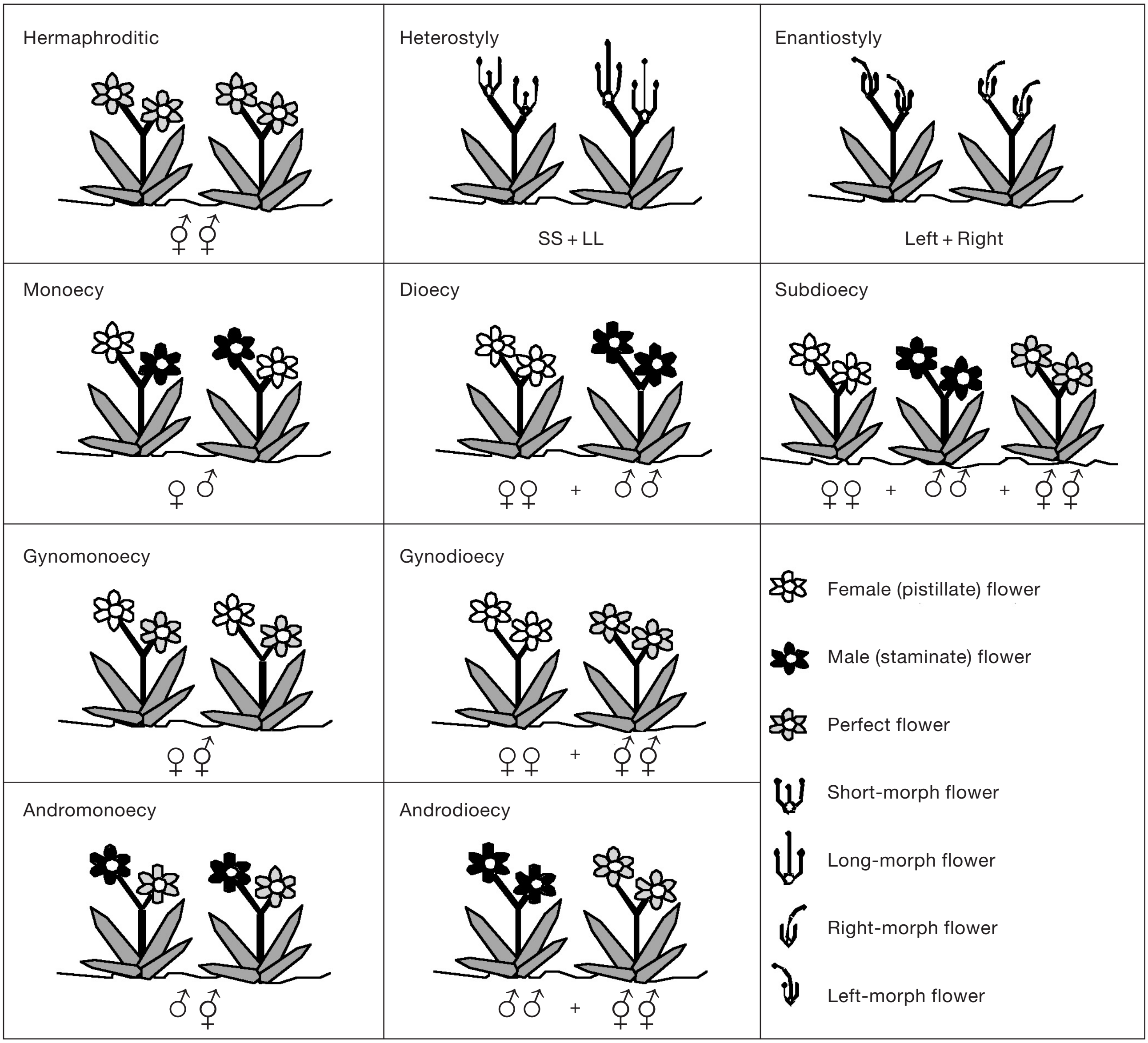

Figure 1. Sex breeding systems found in angiosperms populations.

(tristyly) floral morphs differing in morphological (anthers and stigmas positions within flowers) and physiological traits are recognized (Barrett *et al.,* 2009). In enantiostyly, sexual morphs differ in the style position on the flower (Jesson and Barrett, 2003). Dioecious populations contain female and male unisexual individuals. Approximately 4% of plants are dioecious and this sexual breeding system, together with gynodioecy, has been extensively studied to understand plant breeding system evolution (*e.g.* Charlesworth and Charlesworth, 1978; Freeman *et al.,* 1997). In gynodioecious populations, hermaphrodites coexist with females, which is the case in 7% of plants (see *e.g.* Jakobs and Wade, 2003). In androdioecy, hermaphrodites coexist with males, a rare breeding system found in less than 1% of plants (reviewed in Pannell, 2002). In subdioecy, populations contain female and male unisexuals and hermaphroditic or monoecious individuals (reviewed in Ehlrers and Bataillon, 2007).

Effects of AM on plant reproduction in sexually monomorphic plants

Vegetative (clonal) reproduction

Enhancement of clonal growth due to AM inoculation in agricultural species is well known and has an economic importance. For example, inoculation with *Glomus intraradices* increased runner production in *Fragaria* × *ananassa* (Varma and Schuepp, 1994) and *Glomus fistulosum* increased the runner number in *Fragaria vesca* (Mark and Cassells, 1996). Botham *et al.* (2009) also reported an increase in the number of plantlets produced by *Fragaria virginiana* in association with a commercial mixed inoculum containing *Entrophospora columbiana* and *Glomus intraradices*.

In a more ecological context, Streitwolf-Engel *et al.* (1997, 2001) observed that different co-occurring AM fungal species had a variable effect on the number of ramets and their spatial distribution in *Prunella grandiflora* and *P. vulgaris* (Lamiaceae), as some fungal isolates increased the number of ramets or the length of these ramets more than other isolates. The disparity of effects observed by different AM fungal isolates on clonal growth traits was later corroborated by Sudová and Vosátka (2008) and Sudová (2009), who reported a range of growth responses (from negative to positive) to AM inoculation. In these studies, a mixture of three AM native isolates (*Glomus intraradices*, *Glomus mosseae*, *Glomus microaggregatum*) was used to inoculate *Fragaria moschata* (Rosaceae), *Potentilla anserine* and *P. repens* (Rosaceae), *Galeobdolon montanum* and *Glechoma hederaceae* (Lamiaceae), *Ranunculus repens* (Ranunculaceae) and *Trifolium repens* (Fabaceae).

As Streitwolf-Engel *et al.* (1997) highlighted in their pioneer study, the importance of AM symbioses for clonal growth lies in its potential to affect plant population and plant community structure through affecting clonal reproduction of the host plants. However, after 12 years of research, our knowledge of the mechanisms involved and the consequences for plant population dynamics are far from being conclusive. Furthermore, as clonal and sexual reproduction may be linked through trade-offs (Ronsheim and Bever, 2000), whether mycorrhizal symbiosis may modify resource allocation and partitioning to both plant's function remains largely unexplored (but see *e.g.* Wilson *et al.,* 2001).

Sexual reproduction

Plants achieve their fitness through the male function, the female function, or both depending on the sexual breeding system considered. Fitness through the male function is the result of the plant's ability to disperse pollen and fertilize ovules. Fitness through the female function is the result of the plant's ability to mature seeds and the subsequent performance of these seeds.

Pollen production

In general, the amount of pollen produced by a plant and the probability to sire seeds are positively correlated (Schoen and Stewart, 1986; Devlin *et al.,* 1992). However, paternal success will also depend on the quality of these pollen grains. When the number of pollen grains deposited on the stigma exceeds the number of ovules to fertilize, pollen competition occurs between pollen grains (Mulcahy, 1979), and pollen vigour may become essential for seed sire success. Very few studies have investigated the relationship between AM symbiosis and pollen. AM symbioses have been reported to influence both pollen quality and quantity (Table 1). Both the number of flowers and the amount of pollen produced have been reported to increase due to AM symbiosis, even though the opposite effect or no effect

Table 1. Selected publications that have investigated the response of the male function to AM

Plant species	LF	BS	AM	# flowers	# pollen grains	Pollen quality	Pollen size	Authors
Cucurbita foetidissima	P	Mo	INT	M	M[1]		M	Pendleton, 2000
Cucurbita pepo	A	Mo	ETU	0	0[2]		M	Lau *et al.,* 1995
Cucurbita pepo	A	Mo	—			M[5]		Stephenson *et al.,* 1998
Geranium sylvaticum	P	G	CLA	0	M[2], 0[3]			Varga and Kytöviita, 2010c
Geranium sylvaticum	P	G	HOI	0	M[2], 0[3]			Varga and Kytöviita, 2010c
Lycopersicon esculentum	A	H	ETU	NM		0[4], M[5], M[6]		Poulton *et al.,* 2001a
Lycopersicon esculentum	A	H	ETU	M	M, 0[2]	0[4], M[5]		Poulton *et al.,* 2001b
Lycopersicon esculentum	A	H	ETU	M	M[1,2]		0	Poulton *et al.,* 2002
Lythrum salicaria	P	Het	AGR	0	0[1], M[2,3]			Philip *et al.,* 2001

[1] Per plant. [2] Per flower. [3] Per anther. [4] *In vitro* germination. [5] *In vitro* pollen tube growth. [6] *In vivo* siring success. LF: life form (A: annual species. P: perennial species). BS: breeding system (G: gynodioecious. H: hermaphroditic. Het: Heterostylous. Mo: monoecious). AM species (AGR: *Glomus aggregatum.* CLA: *Glomus claroideum.* ETU: *Glomus etunicatum.* HOI: *Glomus hoi*. INT: *Glomus intraradices*). M: mycorrhizal plants outperform non-mycorrhizal plants. 0: non-significant differences.

at all have also been reported (Table 1). As pollen production depends on resource availability during pollen development (see *e.g.* Delph *et al.,* 1997 and references therein), it is perhaps not surprising to find a beneficial effect of AM symbiosis on pollen production and performance. Pollen performance can be estimated as the growth rate of pollen tubes and the ability of pollen tubes to achieve fertilization in competition with pollen from other plants. Enhancement of pollen tube growth by AM symbiosis has been reported both *in vitro* and *in vivo* (Table 1). Possibly the most realistic study in this respect is that of Poulton *et al.* (2001a) who reported an increased *in vivo* siring success in *Lycopersicon esculentum*.

Mycorrhizal effects on pollen production and performance are largely the result of improved P acquisition, as AM inoculation and high soil P conditions have similar beneficial effects on the male function (Lau and Stephenson, 1994; Lau *et al.,* 1995; Poulton *et al.,* 2001b, 2002). Nevertheless, other mycorrhiza-mediated effects may play also a role.

Seed production

As with pollen production, seed production depends on resource availability. The number of seeds produced by a plant will be related to the amount of flowers produced, the proportion of flowers producing fruits, and the number of seeds produced per fruit. Mycorrhizal effects on seed production and performance are also largely the result of improved P acquisition, as AM inoculation and high soil P conditions have similar beneficial effects on the female function (*e.g.* Stanley *et al.,* 1993). Nevertheless, AM may alter resource allocation to reproduction (Koide *et al.,* 1988) and again the effects on the plant hormonal status or other mycorrhiza-mediated effects should not be neglected. Publications investigating the effect of AM symbiosis on this female function mostly report positive or neutral effects on flower, fruit and seed production, even though exceptions also exist (Table 2). Interestingly, the response observed seems to be dependent on the fungal species used (Jensen, 1982; Schenk and Smith, 1982; Oliveira *et al.,* 2006; Table 1), as when the same plant was inoculated with different AM fungal species, a range of responses was observed.

Offspring performance

The performance of a given seedling will be the result of its genotype, the environment where it grows as well as the result of the environment where its mother grew (maternal effects). Maternal effects can be broadly divided into genetic and environmental effects (reviewed in Roach and Wulff, 1987). Environmental factors such as temperature, photoperiod, carbon dioxide, light quality, water availability or nutrient levels experienced by the mother plants can affect germination, survival and performance of the resulting seeds (reviewed in Baskin and Baskin, 1998). Germination and seedling success are positively associated with seed mass (Jakobsson and Eriksson, 2000) and seed provisioning (Baskin and Baskin, 1998), even though the effects may be restricted to the very early stages (Saverimuttu

Table 2. Selected publications that have investigated the response of the female function to AM

Plant species	LF	BS	AM species	# flowers	# fruits	# seeds	Seed mass	Seed P	Authors
Abutilon theophrasti	A	H	ETU	M	M	M^{2}	M	M^{4}	Lu and Koide, 1994
*Abutilon theophrasti**	A	H	INT		M	0	M	M^{4}	Shumway and Koide, 1995
*Abutilon theophrasti**	A	H	INT	M	M	M^{3}	M, 0	M^{4,5}	Stanley *et al.,* 1993
*Achillea millefolium**	P	H	Field			Nm		Nm	Allison, 2002
Avena fatua	A	H	INT			M	M	M^{4,5}	Koide *et al.,* 1988
Avena fatua	A	H	INT					M^{4}	Koide and Lu, 1992
Avena sativa	A	H	INT			M	M	M^{4,5}	Koide *et al.,* 1988
Campanula rotundifolia	P	H	CLA + HOI + sp	M	0	0	0	M	Nuortila *et al.,* 2004
*Capsicum annuum**	P	H	FAS	M	M				Bagyaraj and Sreeramulu, 1982
Conyza bilbaoana	A	H	INT			0			Oliveira *et al.,* 2006
Conyza bilbaoana	A	H	MOS			M			Oliveira *et al.,* 2006
Conyza bilbaoana	A	H	GEO			0			Oliveira *et al.,* 2006
Conyza bilbaoana	A	H	CLA			M			Oliveira *et al.,* 2006
Cucurbita foetidissima	P	Mo	INT	M	0				Pendleton, 2000
Foeniculum vulgare	P	H	FAS	M	M^{1}				Kapoor *et al.,* 2004
Foeniculum vulgare	P	H	MAC	M	M^{1}				Kapoor et al., 2004
Glycine max	A	H	ETU			M	0	M^{5}	Bethlenfalvay *et al.,* 1997
Geranium sylvaticum	P	G	CLA	0	Nm	Nm			Varga and Kytöviita, 2010c
Geranium sylvaticum	P	G	HOI	0	0	0			Varga and Kytöviita, 2010c
Glycine max	A	H	MOS			M	M	M^{5}	Bethlenfalvay *et al.,* 1997
Glycine max	A	H	ROS			M	0	M^{5}	Bethlenfalvay *et al.,* 1997
Glycine max	A	H	CLA	0	M		0		Schenk and Smith, 1982
Glycine max	A	H	CLU	0	M		Nm, 0		Schenk and Smith, 1982
Glycine max	A	H	PEL	0	M		0		Schenk and Smith, 1982
Glycine max	A	H	GRE	Nm, 0	M		0		Schenk and Smith, 1982
Glycine max	A	H	MOS	M	M, 0		M, 0		Schenk and Smith, 1982
Glycine max	A	H	LAE	0	M		0		Schenk and Smith, 1982
Glycine max	A	H	CLA			M			Vejsadova *et al.,* 1993
*Holcus lanatus**	P	H	MOS	Nm					Wright *et al.,* 2000
*Hordeum distichon**	A	H	Field			Nm, 0	0	M, 0^{5}	Jensen, 1983
Hordeum vulgare	A	H	CON				M	0^{5}	Jensen, 1982
Hordeum vulgare	A	H	FAS				M	M, Nm^{5}	Jensen, 1982
Hordeum vulgare	A	H	MAR				0	0^{5}	Jensen, 1982
Lycopersicon esculentum	A	H	ETU	M, 0	M, 0	M, 0	0		Bryla and Koide, 1990a
Lycopersicon esculentum	A	H	ETU		M	M	0	M^{4,5}	Bryla and Koide, 1990b
Lycopersicon esculentum	A	H	ETU	M	M	M, 0^{2}			Poulton *et al.,* 2002
*Triticum durum**	A	H	MOS				0	0	Al-Karaki and Clark, 1999
*Vicia hirsuta**	A	H	Field	0	0				Ganade and Brown, 1997
*Vicia sativa**	A	H	Field	0	0				Ganade and Brown, 1997
*Vulpia ciliata**	A	H	Field			M			Carey *et al.,* 1992
*Vulpia ciliata**	A	H	Field			Nm, 0			Newsham *et al.,* 1994
Zea mays	A	Mo	INT			M, 0	M, 0	M, 0^{4}	Subramanian and Charest, 1997

^{1} Mass. ^{2} Per fruit. ^{3} Per pot. ^{4} Content. ^{5} Concentration. * When the species name is followed by an asterisk, the respective study employed fumigation or a fungicide for the non-mycorrhizal treatment, thus prudence in interpreting the results should be taken. The use of fumigation or fungicide applications have undesirable side effects as they kill not only mycorrhizal fungi but also other soil flora and fauna including other fungi (Hartnett and Wilson, 2002 and references therein). Furthermore, fungicides are not always effective in removing AM fungi (see *e.g.* Allison *et al.,* 2007 and references therein). LF: life form (A: annual species. P: perennial species). BS: breeding system (G: gynodioecious. H: hermaphroditic. Mo: monoecious). AM species (CLA: *Glomus claroideum.* CLU: *Glomus clarum.* CON: *Glomus constrictum.* ETU: *Glomus etunicatum.* FAS: *Glomus fasciculatum.* GEO: *Glomus geosporum.* GRE: *Gigaspora gregaria.* INT: *Glomus intraradices.* LAE: *Gigaspora laevis.* MAR: *Gigaspora margarita.* PEL: *Gigaspora pellucida.* ROS: *Gigaspora rosea*). M: mycorrhizal plants outperform non-mycorrhizal plants. Nm: non-mycorrhizal plants outperform mycorrhizal plants. 0: non-significant differences.

Table 3. Selected publications that have investigated the response of offspeing to AM colonization of the parents

Plant species	LF	BS	AM species	Seed mass	Seed P	Seed N	%	Survival	Growth	Repro-duction	Authors
Abutilon theophrasti	A	H	INT	M	M	M, 0	0		M		Shumway and Koide, 1994a
Abutilon theophrasti	A	H	INT				0		M	M, $0^{2,3}$	Shumway and Koide, 1994b
Abutilon theophrasti	A	H	ETU	M	M	M			M		Lewis and Koide, 1990
Abutilon theophrasti	A	H	INT	M	M	0	0	M^5	M	$M^{1,2,3}$	Heppell *et al.,* 1998
Abutilon theophrasti	A	H	INT	M, 0	M				M 4		Stanley *et al.,* 1993
Abutilon theophrasti	A	H	INT	M	M	M			M		Koide and Lu, 1995
Avena fatua	A	H	INT	0	M	M			M		Lu and Koide, 1991
Avena fatua	A	H	INT	0	M				M	0^3	Koide and Lu, 1992
Campanula rotundifolia	P	H	CLA + HOI + sp	0	M		0		M		Nuortila *et al.,* 2004
Medicago sativa	A	H	MAC				M			M^3	Srivastava and Mukerji, 1995
Medicago sativa	A	H	FAS				M			0^3	Srivastava and Mukerji, 1995

[1] Proportion of individuals reproducing. [2] Fruits. [3] Seeds. [4] Recruitment. [5] Number of survivors 94-98 days after plantin. LF: life form (A: annual species. P: perennial species). BS: breeding system (H: hermaphroditic). AM species (CLA: *Glomus claroideum.* ETU: *Glomus etunicatum.* FAS: *Glomus fasciculatum.* HOI: *Glomus hoi.* INT: *Glomus intraradices.* MAC: *Glomus macrocarpum.* sp: *Glomus* sp.). M: mycorrhizal plants outperform non-mycorrhizal plants. 0: non-significant differences.

and Westoby, 1996). If mycorrhizal colonization of the parental generation translates into a better provisioning of the seeds, it could theoretically also affect offspring performance. Indeed, AM symbioses have been reported to increase seed mass and seed provisioning (Tables 2, 3), and these responses have been translated into better growth and survival of the resulting seedlings (Table 3). The better performance of mycorrhizal offspring is likely to be related to the improved seed P concentration (Lewis and Koide, 1990; Heppell *et al.,* 1998), although inherent differences in growth unrelated to nutrient uptake have also been reported (Koide and Lu, 1995). Clearly, AM symbioses can have substantial consequences for plant populations dynamics (reviewed in Koide and Dickie, 2002).

Pollinator's attraction

About 9% of all flowering plants are animal pollinated (Linder, 1998). In animal pollinated plants, another important parameter linked with sexual reproduction is the ability to attract pollinators. Seed production in these plants depends on the plant's success at attracting pollinators for effective pollen transfer and ovule fertilization. Many floral adaptations have arisen in response to selection by pollinators (reviewed in Harder and Barrett, 2006). AM fungi are also reported to influence traits that may affect pollinator behaviour. Not only do mycorrhizal plants produce more flowers (Table 2) or flowers which produce more pollen (Table 1), but AM symbioses may also cause plants to flower for a longer period of time (Koide *et al.,* 1988); increase the quality as well as the quantity of nectar (Gange and Smith, 2005) or increase flower size (Sohn *et al.,* 2003; Gange *et al.,* 2005). Mycorrhizal symbiosis has also been shown to increase plant height (Lu and Koide, 1994; Gange *et al.,* 2005), and elevating the flowers higher above ground may influence insect visitation (Lortie and Aarssen, 1999). Regardless, few studies have investigated the interaction between AM and pollinators. These few studies show that the presence of AM fungi in plant roots increases pollinator visitation rates (Gange and Smith, 2005; Wolfe *et al.,* 2005; Cahill *et al.,* 2008; Varga and Kytöviita, 2010c). However, the mechanism responsible for AM symbiosis effects on pollinators seems to vary from one plant species to another and has been attributed to an increase in flower production and/or floral rewards (Gange and Smith, 2005; Wolfe *et al.,* 2005; Varga and Kytöviita, 2010c).

Effects of AM on plant reproduction in sexually dimorphic plants

Vegetative (clonal) reproduction

The only available evidence about mycorrhizal effects on clonal traits in dimorphic plants comes from *Antennaria dioica* (Asteraceae), a dioecious species (Varga and Kytöviita, 2008; Varga and Kytöviita, 2010a). Males of dioecious species are expected to have higher growth rates than females (Freeman *et al.,* 1976; Escarré and Houssard, 1991; Fujitaka and Sakai, 2007; but see Connor, 1984) and due to sex differential resource requirements, the effect on clonal growth by AM could be theoretically sex-specific. This possibility was investigated in two studies using *A. dioica* inoculated with or without *Glomus claroideum*. Water availability (Varga and Kytöviita, 2008) or soil pH (Varga and Kytöviita, 2010a) were manipulated under greenhouse conditions. Sex-specific benefits from AM symbiosis in terms of clonal growth were found in both studies. Males of *A. dioica* produced a greater number of ramets than females but only under certain environmental conditions (which included low-watering regime but which did not include soil pH). Under a moderate watering regime, females inoculated with *G. claroideum* benefited more from AM as they produced more (but lighter) ramets than males (Varga and Kytöviita, 2008). In the pH study, the mycorrhizal benefit was similar for both genders in the number of ramets produced but males benefited more from symbiosis as they produced heavier ramets when growing in a high pH compared to females (Varga and Kytöviita, 2010a). The mechanism responsible for the sex-specific responses to mycorrhiza reported for *A. dioica* remains still unknown but it seemed not to be linked to nutrition (Varga and Kytöviita, 2008).

As it was emphasized for monomorphic plants, the importance of AM symbioses may also have large consequences for clonal growth in populations of dimorphic plants, where the presence of both sexes is necessary to perpetuate the species. Clonal forms affect pollen donation and receipt through ramet distribution patterns (Charpentier, 2002). Furthermore, it has been recently shown that AM fungi can significantly modify the effects of clonal integration on the performance of clonal plants (Du *et al.,* 2009).

Sexual reproduction

The effects of AM symbiosis on reproduction in plants with dimorphic breeding systems have been investigated in a small number of species. Therefore, all the studies that have reported AM colonization levels or AM effects on plant growth for the different sexes in dimorphic plants are listed below. What seems clear from these studies is that the interactions with AM fungi may depend on the gender of the host. Variation in response to AM fungi have been reported for dioecious, gynodioecious and heterostylous plants. Additionally, the differences observed are most likely to be a consequence of the different resource patterns of the sexes.

Antennaria dioica (Asteraceae), dioecious

In the field, female and male roots of 40 arbitrarily selected genets growing in Oulanka National Park, northern Finland (66°22' N, 29°19' E) did not differ in AM colonization levels (Varga and Kytöviita, unpublished). The same result was observed in a greenhouse study manipulating water availability to the plants (Varga and Kytöviita, 2008). However, in a greenhouse experiment manipulating soil pH, *A. dioica* females had a higher proportion of roots colonized by hyphae than males (Varga and Kytöviita, 2010a).

Flowering was checked in both greenhouse studies even though the proportion of flowering plants was low. No significant AM effect on flowering was found in the pH study (Varga and Kytöviita, 2010a) but the proportion of flowering plants in the water study was the result of an interaction between AM inoculation, plant sex and water treatment (Varga and Kytöviita, 2008).

Carica papaya (Caricaceae), dioecious

Recently, Vega-Frutis and Guevara (2009) have shown different patterns of root colonization in *C. papaya*. Although females and males did not differ in size or growth rate in the field, root colonization was higher in females compared to males, presumably because of the higher resource demands in females. The authors claimed that the different resource demands of the sexes drive the AM interactions between *C. papaya* and its fungal symbionts in the field.

Distichlis spicata (Poaceae), dioecious

Eppley *et al.* (2009) analysed AM colonization in males and females of the wetland grass *D. spicata* in the field. They also found sex-specific interactions as females had higher root colonization than males and this difference in colonization level did not change during the reproductive season. Furthermore, in the greenhouse female plants were more likely to be colonized at all than were male plants, suggesting that differences in AM colonization between the sexes were explained by differences in sex-specific interactions rather than the growing conditions.

Geranium sylvaticum (Geraniaceae), gynodioecious

The response of female and hermaphrodite *G. sylvaticum* to simulated herbivory was investigated in the field (Varga *et al.,* 2009). Females and hermaphrodites had a similar proportion of root length colonized by AM fungi. However, the plants had a sex-specific relationship with their symbionts, as seed average was positively correlated with arbuscule frequency in females but not in hermaphrodites.

In another study, the effects of two different *Glomus* species on *G. sylvaticum* phosphorus acquisition and plant mass allocation were examined using a factorial greenhouse-common garden experiment (Varga and Kytöviita, 2010b). Results suggest that overall the plants benefited from the symbiosis with both AM fungal species tested, but that the benefits gained from the symbiosis depended on the sex of the plant and on the trait investigated. Hermaphrodites suffered most from the lack of AM symbiosis as the proportion of flowering plants was dramatically reduced by the absence of AM fungi. However, females benefited from the symbiosis relatively more than hermaphrodites in terms of phosphorus acquisition.

Lastly, the response of pollinating insects to sexual dimorphism and AM symbiosis was investigated by monitoring insect visitation rate using *G. sylvaticum* plants inoculated with *Glomus claroideum*, *Glomus hoi* or non-inoculated plants (Varga and Kytöviita, 2010c). The study revealed that AM increased several floral traits to which pollinating insects are known to respond (*e.g.* floral size, pollen amount per flower). Furthermore, AM inoculation had sex-specific effects on floral diameter, since sexual dimorphism in floral size between females and hermaphrodites was only significant when the plants were inoculated with *G. claroideum*. The results also showed that AM symbiosis may affect insect visitation rate to a gynodioecious plant.

Juniperus monosperma (Cupressaceae), dioecious

Gehring and Whitham (1992) reported similar AM colonization levels in both sexes of *J. monosperma* under low levels of parasitic mistletoe in the field. However, under high density of mistletoe, female plants had significantly lower levels of mycorrhizal colonization than males. Their results corroborated the hypothesis that severe mistletoe infestation suppresses mycorrhizas (as they both consume the plant's carbon) and that the suppression was more severe in female trees because of their greater energetic investment in reproduction.

Lythrum salicaria (Lythraceae), heterostylous

Philip *et al.* (2001) investigated the effect of *Glomus aggregatum* symbiosis on the sexual reproduction of the three floral morphs in this tristylous perennial plant. Even though the exact levels of colonization among the three morphs are not reported, AM fungi had contrasting effects on the plants: colonization decreased plant mass, did not affect flower production, number of days to anthesis, and number of ovules, but increased pollen production. There was also an interaction between AM and morph type in determining plant's mass (AM decreased biomass in the long- and short- morphs but increased in the mid-morph). Furthermore, AM changed flower distribution within an inflorescence: flowers were unevenly distributed in the long- and mid-morphs but appeared evenly distributed in the short-morph.

Future directions

By now, the importance of AM symbioses on plant reproduction and the huge implications AM symbioses may have on plant breeding systems have become obvious. However, many issues remain unresolved. In addition to the topics listed for future research suggested by Koide (2000) the next questions should also be addressed:

1) Too few plant and fungal species have been examined to draw any reliable conclusion. Moreover, molecular methods should be employed to identify the fungal communities colonizing the roots of the different genders in order to set up realistic experiments. AM species are functionally not identical (Munkvold *et al.,* 2004) and the hosts may vary in their response to inoculation by different AM fungi. Because of the differences in resource requirements by the sexes, is one sex morph more likely to be more mycorrhizal or to benefit more from mycorrhizal symbiosis than the

other morph? Is one sex morph more likely to be colonized by certain AM species than the other morph? How universal are sex-specific interactions between AM fungi and sexual morphs? Does mycorrhizal benefit differ between the sexes in other dimorphic breeding systems?

2) Most of the studies have been done using annual plants or evaluating the response of perennial plants in short-term experiments, even though changes in mycorrhizal functionality may vary across the season (Shumway and Koide, 1994a). Therefore, more meaningful and ecologically relevant experiments are certainly needed in order to build a proper picture of the mycorrhizal effects on dimorphic plants. What role (if any) do mycorrhizal fungi play in seed germination and offspring establishment? What is the effect of mycorrhizal fungi on the relative seed fitness for plants with different sexes? How do mycorrhizal fungi affect lifetime host reproduction in perennial plants?

3) The mechanisms behind the mycorrhizal effects seen on plant's reproduction are not completely understood. The effects have been largely attributed to the role of AM on nutrient uptake. However, other AM-mediated effects (such as effects on the host hormonal status) are largely unexplored. Moreover, greater tolerance to pathogens, parasites or herbivores mediated by mycorrhizal fungi may also help to explain differences in reproductive output between the sexes.

4) The consequences of mycorrhizal symbioses for plant population dynamics are far from conclusive. What effect does colonization by mycorrhizal fungi have on pollen production or pollen performance in dimorphic plants? What is the influence of AM symbiosis on pollinators in plants with different gender?

Conclusions

AM symbioses are widely distributed (Smith and Read, 1997) and their effects on plant reproduction and on plant population dynamics are relatively well established for plants with monomorphic breeding systems (Koide, 2000; Koide and Dickie, 2002; and references therein). However, relatively little is known for plants with dimorphic breeding systems, even though around 15% of angiosperms belong to populations with sexually dimorphic breeding systems (Sakai and Weller, 1999). Nevertheless, knowledge of the mycorrhizal effects on dimorphic plants is growing fast in recent years. The evidence suggests that AM symbioses may improve asexual and sexual reproduction on both monomorphic and dimorphic species. Furthermore, it seems that in both systems, growth responses strongly depend on both the AM fungal and plant species used. Most importantly, it seems that the sexes in dimorphic plants may gain sex-specific benefits from AM symbiosis. AM symbiosis may also affect inbreeding depression (Nuortila *et al.,* 2004; Botham *et al.,* 2009), which may have important consequences for plant breeding systems evolution. However, the mechanisms involved, the incidence, and the importance of sex-specific relationships between AM fungi and plants are still unknown.

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