SOME BIOLOGICAL ASPECTS OF THE ARBUSCULAR MYCORRHIZAL FUNGI (AMF)

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Abstract. The ecological mechanisms by which plant diversity (species richness and composition) is regulated and maintained are not well understood; so far, little attention has been paid to the effects of soil microbe-plant interactions, particularly mycorrhizal symbiosis. Hence, the aim of this paper is to review scientific literature relevant to arbuscular mycorrhizal fungi (AMF) biological aspects and the ecological mechanisms by which plant diversity is affected by AM fungal performance. Several studies show up that plant fitness, plant relative growth and abundance, and species competitive balance are affected by AMF. Therefore, AMF are one of the factors that determine plant diversity, and plant community structure. Discussion emphasizes on controversial aspects of AMF-plant diversity research.

Key words: arbuscular mycorrhizal fungi, mycorrhizal distribution, evolution and specificity, plant diversity, plant community structure

Resumen. El mecanismo ecológico por el cual la diversidad vegetal (riqueza y composición de especies) es regulada y mantenida, todavía no se comprende en su totalidad; asimismo, se le ha dado muy poca atención a los efectos que producen las interacciones entre los microorganismos del suelo y las plantas. El objetivo de este trabajo es llevar a cabo una revisión de la literatura científica relacionada con algunos aspectos de la biología de los hongos micorrizógenos arbusculares (HMA) en relación con los mecanismos ecológicos que afectan la diversidad vegetal. Varios estudios muestran que los HMA afectan a las plantas en su adecuación, crecimiento y abundancia relativos, y en su balance competitivo. Por lo tanto, los HMA son uno más de los factores que determinan la diversidad vegetal y la estructura de la comunidad. La discusión se centra en aspectos controvertibles de la investigación en HMA-diversidad vegetal.

Palabras clave: hongos micorrizógenos arbusculares, distribución, evolución y especificidad, diversidad vegetal, estructura de la comunidad vegetal

The ecological mechanisms by which plant diversity (species richness and composition) are regulated and maintained are not well understood. The ability of many plant species to co-exist, and thus to determine plant diversity, can be explained by competitive interactions, spatial or temporal resource partitioning, disturbance creating new patches for colonization, and interactions among different functional groups of organisms that constitute ecosystems (Van der Heijden *et al.*, 1998a). In this sense, little attention has been paid to the effects of microbe-plant interactions, particularly the mycorrhizal symbiosis, on plant diversity, and on ecosystem variability and productivity (Allen, 1980; Van der Heijden *et al.*, 1998a).

Arbuscular mycorrhizal fungi (AMF) are abundant in soils of most ecosystems, and can influence the coexistence of plants directly or indirectly (Zobel *et al.*, 1997). Direct ways include the modifications of plant traits by AMF and the interplant transfer of resources; both of these may have a direct influence on the outcome of competitive interactions and hence on plant coexistence. Indirect ways include the possible impact of AMF on ecological interactions between plants and other organisms (e.g. plant-herbivore or plant-pathogen interactions).

Arbuscular mycorrhizal fungi (AMF) are associated with ca. 80% of living terrestrial plants (Pirozynski, 1981), and are considered to be ecologically important for most vascular plants because they im-

prove the physical and chemical soil properties (Powell, 1980; Jakobsen, 1994), their beneficial effects on plant growth and survival by the improvement of nutrient uptake (Fitter, 1985, 1990; Koide and Elliot, 1989; Newsham *et al.*, 1995a; Merryweather and Fitter, 1996, 1998a, 1998b), limiting the uptake of toxic heavy metals from the soil (Gildon and Tinker, 1983), the improvement of plant water relationship (Allen *et al.*, 1981; Allen and Allen, 1986), defense against and/or altering the interactions against herbivores, increasing the resistance against pathogens (Carey *et al.*, 1992; West *et al.*, 1993a, 1993b; Newsham, 1994; Newsham *et al.*, 1995a, 1995b) and improving plant fitness (Carey *et al.*, 1992; Newsham *et al.*, 1995a; Johnson *et al.*, 1997; Merryweather and Fitter, 1998b), and the fact that mycorrhizal plant species have a different physiology and ecology than non-mycorrhizal plants (Fitter, 1985; Koide and Elliot, 1989; West *et al.*, 1993a; Newsham *et al.*, 1995a; Merryweather and Fitter, 1996; Johnson *et al.*, 1997; Wilson and Hartnett, 1997, 1998); even, affecting their clonal growth (Streitwolf-Engel *et al.*, 1997). Recently, it was found that AM fungal colonization delays nucleus senescence in leek root cortical cells (Lingua *et al.*, 1999).

Plant populations and plant-microorganisms relationships modify and are modified by the presence of AMF (Hayman, 1982; Carey *et al.*, 1992; Dhillon

and Anderson, 1993; West *et al.*, 1993a, 1993b; Francis and Read, 1994; Clapp *et al.*, 1995; Miller, 1995; Newsham *et al.*, 1995b; Streitwolf-Engel *et al.*, 1997; Titus and del Moral, 1998a, 1998b), suggesting that plant diversity is determined by AMF (Grime *et al.*, 1987, 1988; Gange *et al.*, 1990, 1993; Francis and Read, 1994; Turner and Fries, 1998; Van der Heijden *et al.*, 1998a, 1998b; Hartnett and Wilson, 1999).

The aim of this paper is to review and assess scientific literature relevant to arbuscular mycorrhizal fungi (AMF) biological aspects and the ecological mechanisms by which plant diversity is affected by AM fungal performance.

Arbuscular mycorrhizal fungi (AMF) evolution

The ancestor of the AMF is a Zygomycetes fungus; and Morton (1990a) places the origin of the symbiosis long after fungi and plants were mainly aquatic. Research on characteristics of the early terrestrial environment (e.g. atmospheric CO₂ concentrations, poor nutrient soils) has contributed to the hypothesis that mycorrhizas were important to the invasion-colonization of land by plants (Pirozynski, 1981; Fitter, 1985; Stubblefield *et al.*, 1987a; Allen, 1991; Hawksworth, 1991; Simon *et al.*, 1993).

Table 1. Evolution Model to Arbuscular mycorrhizal fungi (Morton, 1990a).

Evolution Model
1. The progenitor was an asexual saprobic zygomycete.
2. Ancient terrestrial plants became established on land either independent of a fungal symbiosis or with an association that was neutral or weakly mutualistic.
3. Symbiosis arose from contact between host and fungus that was not maladaptive to either, clonal reproduction in both partners insured replication and favorable gene combinations, thus, evolution of mutualism was gradual rather than saltational.
4. New fungal species arose during co-evolution of the mutualistic symbiosis and speciation stopped or greatly diminished after the fungus became obligately biotrophic.
5. Descendant arbuscular species originated from one or more clones in response to adaptations favoring fecundity, survival, and localized dissemination, thus, the geographic distribution of the new species might not correlate with that of the ancestral species.
6. Species have persisted from about the Cretaceous to modern times relatively unchanged in those spore phenotypes which delimit a species.
7. Clonal populations of species are the fundamental units of contemporary evolutionary processes, genetic change in clonal genotypes are directed by selection pressures optimizing fitness of both partners and this is expressed in mycorrhizal phenotypes.

Arbuscular mycorrhizal fungi (AMF) differentiated, from a monophyletic origin (Morton, 1990a, 1990b; Knoll, 1992), about 462 to 353 millions of years ago (Simon *et al.*, 1993). The fossil record shows that some Devonian fossil plants (e.g. *Aglaophyton*, *Rhynia* and *Asteroxylon* genus) bore vesicle-like structures similar to those of *Glomus* (Pirozynski, 1981). Stubblefield *et al.* (1987a, 1987b) reported the presence of arbuscules and other AM fungal structures in *Antarcticycas*, a common Carboniferous plant, and considered *Paleomyces asteroxyli*, a fungus from Rhynie chert, as the earliest AM fungal species. Hence, AMF were well established by the early Mesozoic (245-215 millions of years ago), and the wide array of mycorrhizal types found today had already arisen by late Cretaceous. However, AMF morphological stability has been established since early Paleozoic time (Pirozynski, 1981; Morton 1990a). Paleontological evidences and some phylogenetic and molecular data (DNA r genes sequences) also support this hypothesis (Simon *et al.*, 1993). It is important to realize that this record cannot delineate physiological interactions (Pirozynski, 1981; Morton, 1990a; Allen, 1991).

Pirozynski (1981) hypothesized that higher plants evolved vascular systems and an increase in height as a result of the efficient water and nutrient transport by the fungal symbiont from soil to plant. This hypothesis was confirmed since extant descendants of early land plants (e.g. *Psilotum*, *Equisetum*, cycads and ferns) are mycotrophic (Koske *et al.*, 1985; Dhillon, 1993; Simon *et al.*, 1993). Even though, a different point of view was expressed by Morton (1990a) by proposing an AM fungal Evolution Model to clarify the dimensions (space-time) of the AMF-plant symbiosis (table 1) Morton (1990a) pointed out that beneficial effects of the association in expanding the absorptive zone of rhizomes would have been slowed rather than increased selection pressures to differentiate new root architectures and vascularization; the seed development, one of the evolutionary innovations of the Devonian, would have been selected against if mycorrhizas would have been the major force in natural selection because soil-borne chlamydospores of the mycorrhizal fungi could not possibly have been kept pace with air-borne dispersal of seeds (or sporangia); and germinating seedlings greatly dependent on a mutualistic association would not have survived their new habitats.

Arbuscular mycorrhizal fungi (AMF) evolution trends suggest that once genes coding for specialized processes interfacing both organisms were widely distributed among most emergent plant lineages, speciation ceased to occur or slowed considerably, and only those characters responsible for co-adaptation-

al changes in mycorrhizal phenotypes continued to evolve in clonal subunits. Microevolution in clones of AM fungal species is uncoupled from processes of speciation and evolution of supraspecific taxa (macroevolution) because of differential selection pressures, and these processes resulted in co-adaptation between arbuscular clones and those hosts having compatible "symbiosis genes"; these processes are measurable in mycorrhizal phenotypes whose plasticity is regulated mostly by the host genotype, but the fungal contribution may be highly significant in mycotrophic hosts. Macroevolutionary processes led to emergence of the obligate AM symbiosis and more extensive speciation in host and fungal partners, and they are measurable by type and extent of change in spore phenotypes (Morton, 1988, 1990a, 1990b).

There are still numerous questions that can be examined relating to interactions between fungi and plants. For example, understanding the range of fungal diversity in the past may offer insights about the changing host and nutritional modes of certain groups. Together with data about the sedimentological environment occupied by the fungi, there are numerous questions that may be posed about the type and early distribution of mycorrhizas (Taylor, 1990).

Arbuscular mycorrhizal fungi (AMF) in natural systems

Factors influencing arbuscular mycorrhizal fungi (AMF) distribution. Arbuscular mycorrhizal fungi (AMF) are believed to be among the most abundant fungi in soil (Gerdemann and Nicolson, 1963; Brundrett, 1991). They are abundant in grasslands, savannas, scrub and open woodlands, rain forests, deserts and sand dunes; thus, on a global scale they are virtually ubiquitous (Hayman, 1982; Brundrett, 1991). As AMF are obligate root symbionts, it is important to understand the factors influencing AM fungal populations because species of these fungi differ greatly in their effects on plants, ranging from mutualistic to neutral to antagonistic (Hayman, 1982; Fitter, 1991; Francis and Read, 1995; Johnson *et al.*, 1997). Very little is known about their ecology; though, some insights have been gained by studying natural distributions of their spores (Johnson *et al.*, 1992; Hartnett and Wilson, 1999).

Arbuscular mycorrhizal fungi (AMF) distribution, activity and survival are related to several environmental factors (table 2) such as soil fertility, moisture, compaction, depth, water saturation and pH, topography, burning frequency, temperature, light intensity, altitude, latitude, plant susceptibility-phenology, AMF phenological variations and disturbance; physical movement by water, earthworms, and soil microfauna (Hayman, 1982; Abbot and Robson, 1991).

Table 2. Factors affecting arbuscular mycorrhizal fungi (AMF) distribution

Source	Factor	Research Site	Effect
Anderson <i>et al.</i> (1984)	Soil fertility and moisture	Tallgrass prairie	AM fungal species richness was positively correlated with percentage soil organic matter and negatively correlated with Ca, Mg, and P content of soil, while total spore number was positively correlated with N and organic matter content and negatively correlated with Ca, Mg and P content of soil.
Nadian <i>et al.</i> (1997, 1998)	Soil compaction	Greenhouse: pots	Total P uptake was significantly greater in mycorrhizal plants than in non-mycorrhizal ones; the response was smaller as soil compaction was increased. Soil compaction to a bulk density 1.6 Mg m^{-3} had no effect on the percentage of root length colonized, but total root length colonized decreased as soil compaction was increased. Soil compaction, which increased bulk density from 1.20 to 1.75 Mg m^{-3} , reduced O_2 content of the soil atmosphere from 0.16 to $0.05 \text{ m}^3 \text{ m}^{-3}$.
Jakobsen and Nielsen (1983)	Soil depth	Field grown crops	The proportion of root length infected decreased markedly below 40 cm soil depth; root density varied greatly between crops, whereas the absolute length of infected roots was similar.
Zajicek and Hetrick (1986)		Tallgrass prairie forbs	The degree of colonization varied with plant species and soil depth; spores of <i>Glomus fasciculatum</i> were found to a depth of 220 cm.
Virginia <i>et al.</i> (1986)		Californian Sonoran Desert	<i>Prosopis glandulosa</i> developed functional root symbiotic associations with N_2 -fixing nodules and AMF at depths greater than 4 m in moist soil above a seasonally stable water table.
Cooke <i>et al.</i> (1993)	Soil H_2O saturation	Salt marsh grasses	Roots were colonized by AMF to a depth of 42.5 cm, but none arbuscule was observed below 37.5 cm.
Miller (2000)		Semi-aquatic grasses along an hydrologic gradient	AM fungal colonization was strongly negatively correlated with water depth; colonization was lowest in plots that were consistently wet but rose as some plots underwent seasonal drying; soils that were wet for > 1 year had the same ability to form mycorrhizas in bait plants as those that had remained dry.
Green <i>et al.</i> (1976)	Soil Ph	Greenhouse: pot cultures	AMF spores germination was influenced by pH: <i>Glomus mosseae</i> germinated best at pH 7, <i>Gigaspora coralloidea</i> at pH 5, and <i>G. heterogama</i> at pH 6.
Porter <i>et al.</i> (1987a, 1987b)		Greenhouse: pot cultures	pH influenced the ability of infection, sporulation, and spore germination: <i>Acaulospora leavis</i> was distributed in soil samples ranging from pH 4.5-4.9, two species of <i>Gigaspora</i> from pH 4.5-6.4 and three different strains of <i>Glomus</i> at pH 5.5-8.4.
Johnson <i>et al.</i> (1992)	Diverse soil factors (composition, texture, structure, nutrients, pH, etc.)	Plots of monocultures of five successional grass species	Even closely related hosts (five grasses) may cause divergence in AM fungal communities on initially identical soils; fungal communities in the sandy end of the soil gradient diverged predictably from the fungal communities in the black soil end of the gradient.

Table 2.

Source	Factor	Research Site	Effect
Sylvia <i>et al.</i> (1993)	Diverse plant and soil systems	Greenhouse and growth chambers	AM fungal isolates exist which are effective in promoting plant growth over a range of edaphic and host conditions.
Gibson and Hetrick (1988)	Topography and burning frequency	Plots in a tallgrass prairie	Gradients of variation in AMF species were related primarily to topography and burning frequency and secondarily to original plot position within experimental plot rows.
Koske (1987)	Temperature	Plots on a latitudinal gradient along a barrier dunes	Average AM fungal species richness was positively correlated with distance south along the gradient and with temperature parameters.
Allen <i>et al.</i> (1995)	Latitudinal gradient of occurrence	Plots in the Mojave Desert	There were distinct northern, central and southern communities of fungi. <i>Glomus aggregatum</i> and <i>G. fasciculatum</i> occurred throughout the range of sagebrush, <i>G. deserticola</i> was restricted to the central and southern portions of its range, <i>Scutellospora calospora</i> occurred along the western and northern portions of the range, and <i>G. mosseae</i> was southern and central in distribution. AMF form their own specific community patterns regardless of the host plant (<i>Artemisia tridentata</i>).

It has been demonstrated that AM fungal distribution changes across a soil moisture-nutrient gradient (Anderson *et al.*, 1984), and that pH affects AMF infection, sporulation, and spore germination (Green *et al.*, 1976; Porter *et al.*, 1987a, 1987b). Hetrick and Wilson (1989) found out that low levels of phosphorus could regulate AMF spore germination.

Soil compaction can deplete AM fungal growth. Nadian *et al.* (1997, 1998) considered that the absence of any observable mycorrhizal growth response in highly compacted soil was attributed to the significant decrease in the O₂ content of the soil atmosphere, change in soil pore size distribution, and probably by ethylene production from impeded roots or by any combination of these factors.

The analysis of the influence of soil depth on mycorrhizal performance shows certain controversy. Jakobsen and Nielsen (1983) found that the proportion of root length infected decreased in relation to soil depth (>40 cm) and that the susceptibility to infection was independent of host species; while Zajicek and Hetrick (1986) observed that the degree of colonization varied with plant species and soil depth, and suggested that the deep-rooted growth trait of certain plants (e.g. forbs) probably is a survival mecha-

nism by which competition for water and nutrients with shallower-rooted, fast-growing plants (e.g. grasses) is avoided, since soil fertility generally decreases as soil depth increases. Another example is the woody legume *Prosopis glandulosa* that develops functional root symbiotic associations with N₂-fixing nodules and with AMF at depths greater than 4 m, and population densities of both symbiotic organisms are substantially greater at depth than near the surface (Virginia *et al.*, 1986).

In a marsh, Cooke *et al.* (1993) determined that the presence of infected roots at 42.5 cm depth and the lack of detectable oxygen at this depth suggested that sufficient oxygen transport occurs in host plants to sustain the growth of the AMF in roots; meanwhile, Miller (2000) found that AMF colonization was strongly negatively correlated with water depth and concluded that flooding was partially but not totally inhibitory to AM fungal colonization, such as it was concluded before by Søndergaard and Laegaard (1977), Koske *et al.* (1985), and Cooke *et al.* (1993).

Topographical gradients and burning frequency affect gradients of variation in AM fungal species; however, much of the AM fungal species compositional gradients may be an indirect consequence of topo-

graphic and fire effects on plant species distributions (Gibson and Hetrick, 1988).

Temperature can influence AM fungal species richness distribution along a latitudinal (north-south) gradient; though, temperature effects on the AM fungal communities may be separated into two components: a direct effect on the fungi and an indirect effect mediated through the host plant (Koske, 1987). Allen *et al.* (1995) found that AMF exhibited a latitudinal gradient of occurrence. There were three distinct communities of fungi within two sites indicating that AMF form their own specific community patterns regardless of the host plant.

Phenological variations occur in AM fungal populations, in saprophytic and in pathogenic fungi populations. AM fungal communities present differences in relative density, spore production and differential activities, correlated with the environment, the host plant species and other fungal species (Sanders and Fitter, 1992; Dhillon and Anderson, 1993; Gange *et al.*, 1993; Abbot and Gazey, 1994; Miller, 1995; Merryweather and Fitter, 1998a, 1998b; Titus and del Moral, 1998a, 1998b; Turner and Friese, 1998).

Interactions between different species of AMF have also been reported. In an early study, Koske (1981) reported that the presence of any AM fungal species did not reduce or increase the occurrence frequency of another AMF in the rhizosphere of dune plants. Though, competitive ability of AMF may be affected by the host plant species, environmental conditions, AM fungal phenology, inoculum frequency, time of harvest, differential incubation of the inoculum, spatial distribution of the interacting propagules (Koske, 1981; Wilson, 1984), by genetic traits (Sanders *et al.*, 1996), and by the presence of ectomycorrhizas (Moyersoen *et al.*, 1998). In a pragmatic sense, these findings illustrate the importance of selection of "efficient" AM fungal strains, native or introduced, into disturbed soils for restoration or agricultural purposes (Lambert *et al.*, 1980; Porter *et al.*, 1987b; Stahl *et al.*, 1988). Moreover, AMF do not colonize regions infected by endoparasitic nematodes, and nematodes rarely infect regions colonized by AMF; both organisms are often mutually inhibitory, each reducing the population of the other (Ingham, 1988). These studies further support the hypothesis that environment, soil and plant community influence more AM fungal distribution than the specific host-plant association (as it will be present later). However, other investigations (table 3) have demonstrated that there exists a functional relationship (e.g. seed germination, seedling establishment, plant growth, plant competitive ability) between AM fungal species selected and a particular host-plant species (Hayman, 1982; Carey *et al.*,

1992; Johnson *et al.*, 1992; Dhillon and Anderson, 1993; Hartnett *et al.*, 1993; Sylvia *et al.*, 1993; West *et al.*, 1993a, 1993b; Allen *et al.*, 1995; Clapp *et al.*, 1995; Miller, 1995; Newsham *et al.*, 1995b; Zobel *et al.*, 1997; Titus and del Moral, 1998a, 1998b; Van der Heijden *et al.*, 1998a, 1998b). Moreover, certain AM fungal species are able to provoke specific effects on plant performance (e.g. clonal growth, plant growth efficiency, differential rate in acquisition of soil phosphate) (Stahl *et al.*, 1990; Streitwolf-Engel *et al.*, 1997; Van der Heijden *et al.*, 1998b; Dickson *et al.*, 1999; Facelli *et al.*, 1999; Hartnett and Wilson, 1999; Koide *et al.*, 2000; Smith *et al.*, 2000); hence AM fungal species and/or communities may influence plant diversity and plant community structure through either stabilizing or destabilizing feedback mechanisms.

Plant mycotrophy and arbuscular mycorrhizal fungi (AMF) "ecological specificity". Stahl (1900) divided plants into non-mycotrophic, facultatively mycotrophic and obligately mycotrophic, and characterized plant families in terms of the prevalence of those mycotrophic groups. Recently, Wilson and Hartnett (1997, 1998) found that co-occurring plant species vary considerably in their germination, growth rate, and flowering responses to mycorrhizal infection along a continuum from highly responsive, obligately mycotrophic species to facultatively mycotrophic, non-responsive species.

It is accepted that "primitive" plants are arbuscular mycorrhizal (Koske *et al.*, 1985) and that some of the more "advanced" plant families develop mycorrhizal associations with more advanced fungi (ericoid, orchid and monotropoid mycorrhizae); the extant plants and their mycorrhizal association suggests that AM mycorrhizal association is the conservative condition with other mycorrhizal and non-mycotrophy plants evolving later (Allen, 1991).

Bellgard (1991) considers that mycotrophy/non-mycotrophy is an expression of ecological adaptation, hence it would be unwise to assume that because a plant belongs to a particular family, it would be non-mycorhizal or mycorrhizal (Newman and Reddell, 1987). However, non-mycotrophy appears to be restricted to a limited suite of colonizing annuals in few advanced families such as the Amaranthaceae, Brassicaceae, Chenopodiaceae and Zygophyllaceae, and many of the hemiparasitic plants (Pendleton and Smith, 1983; Allen, 1991; Bellgard, 1991).

Habitats conducive to most of the later evolving mycorrhizal (ericoid, orchid and monotropoid mycorrhizae) types and to non-mycotrophic plants tend to be specialized and to have come about late in the earth's evolutionary history; the only plants consistently found to be non-mycotrophic are annual weeds adapt-

ed to invasion of disturbed, fertile habitats (Pendleton and Smith, 1983; Allen and Allen, 1990).

In terms of host-endophyte preference or "ecological specificity", virtually, any AMF can associate with any vascular plant that forms arbuscular mycorrhizas. Low host specificity has been shown in greenhouse experiments (Francis and Read, 1994; Clapp *et al.*, 1995), and in field studies, several plant species have been shown to exhibit host-endophyte preference when associated with indigenous mycorrhizas (Allen, 1991; Dhillion, 1992a, 1992b; Francis and Read, 1994). For example, in a tallgrass prairie, indigenous mycorrhizal fungal isolates showed considerable amount of host preference (e.g. *Glomus geosporum* with *Schizachyrium scoparium*, and *Andropogon gerardi*) (Dhillion, 1992a). The degree of plant-AM fungal specificity (measured as colonization and sporulation levels and/or fungal morphology) has been related to plant dependence on native AM fungal species (Dhillion, 1992a, 1992b; Sanders and Fitter, 1992). It has been hypothesized that in native plant communities, endophyte preference and dependence suggest that selection favoring certain fungus-plant combinations occurs (Dhillion, 1992a, 1992b; Sanders and Fitter, 1992). Hence, the degree of specificity/preference or "ecological specificity" can only be adequately investigated under natural conditions when we are able to identify with certainty specific AMF within roots of plants (Dhillion and Zak, 1993); moreover, in natural systems the common situation is to find different genera of AMF coexisting in the same plant root (Sanders *et al.*, 1996), and both AMF and ectomycorrhizas growing together (Bellgard, 1991); in this sense, Moyersoen *et al.* (1998) suggested that both fungal groups are equally able to colonize the same niche.

Fungal diversity. Within the community, fungi possess a variety of heterotrophic roles that directly affect ecosystem variability and productivity (e.g. plant species richness, growth and relative abundance, ecosystem trajectories); thus, it is important to understand the effects of AM fungal diversity and AMF functional diversity on plant community structure and on ecosystem processes (Miller, 1995; Van der Heijden *et al.*, 1998a, 1998b), and to elucidate the mechanisms that control fungal diversity, and its various components; for example, how the large-scaled levels (e.g. abiotic environment) constrain the activities (e.g. growth rates, colonization patterns, species interactions) of the lower organizational levels (e.g. individual, population, community) (Zak and Visser, 1996).

Solbrig (1991) assumed that species diversity is comprised in three interrelated elements: genetic,

functional, and taxonomic. At present, the number of known fungi species is about 72 000 (Hawksworth, 1997), while in the world it is conservatively estimated at 1.5 million (Hawksworth, 1991, 1997); from them ca. 130-160 AM fungal species are recognized within class Zygomycetes, order Glomales, separated in three Families: Acaulosporaceae, Gigasporaceae and Glomaceae; with six genus: *Acaulospora*, *Entrophospora*, *Gigaspora*, *Glomus*, *Sclerocystis* and *Scutellospora* (Wejman and Meuzelaar, 1979; Morton, 1988; 1990a, 1990b; Montañó, 1999). These species colonize the roots of two-thirds of the plants on the planet, both aquatic (Søndergaard and Laegaard, 1977; Cooke *et al.*, 1993; Miller, 2000) and terrestrial (Newman and Reddel, 1987; Simon *et al.*, 1993; Newsham *et al.*, 1995a; Merryweather and Fitter, 1998a; Turner and Friesse, 1998).

In a tropical rain forest, fungal diversity values were determined by a very variable local species richness (between 30 and 90 species in zones of 1420 m²), but in general by high evenness of abundance and high overall richness (more than 500 species), indicating a considerable space-time heterogeneity, and implying that species richness has a temporal variation which suggests a permanent feed-back process in the community structure (Persiani *et al.*, 1998). Other study (Schultess and Faeth, 1998) documented the patterns of species richness, relative abundance, and associations of the fungal endophyte community inhabitant *Festuca arizonica*. More than 400 different fungi species were found, suggesting that the fungal endophyte communities of perennial grasses may be as diverse as fungal endophyte communities of woody shrubs and trees.

Allen *et al.* (1995) detected that exclusively AM fungal species richness is much lower (e.g. 20-25 species in a seasonal tropical forest in Mexico) than ectomycorrhizal fungi (e.g. more than 2000 EM fungal species associated with Douglas fir, *Pseudotsuga menziesii* (Trappe, 1977)).

In terms of functionality, a fungus may be present taxonomically within a given ecosystem, but if the fungus is not interacting within a given process, it is not a current contributor to the functional diversity of the system (Dobranic and Zak, 1999). In addition, although AM fungal diversity is low, AMF seem to have a high physiological diversity (Allen *et al.*, 1995; Wildman, 1995) due to a high genetic diversity (Sanders *et al.*, 1996).

Zak *et al.* (1994) defined functional diversity as the numbers, types and rates at which a range of carbon compounds can be utilized by microbial species occurring within a habitat, and (Zak *et al.*, 1995) the degree to which fungal species exhibit versatility in

Table 3. Effects of arbuscular mycorrhizal fungi (AMF) in plant diversity and plant community structure

Source	Research site	Analyzed factors	AM fungal effects
Allen <i>et al.</i> (1984), Allen (1987)	Mount St. Helens: Field	Plant establishment and community composition in a primary succession	Disturbed areas were new habitats open to invasion by mycorrhizal fungi where the immigration of these fungi influenced plant establishment and community composition. Small mammals, ants, and the exposure of old-soil by erosion were the dominant vectors for movement of AMF making inoculum available to plants colonizing in the area.
Titus and del Moral (1998a, 1998b)	Field microsites and greenhouse	Competition: different nutrient conditions in primary succession	AMF had significant effect on competition between facultative and non-mycotrophic species at low nutrient levels, and target species responded differently to AM fungal colonization under varying competitive scenarios; thus, AMF was one of many interacting factors determining competitive dominance and species change over successional time.
Grime <i>et al.</i> (1987)	Turfgrass microcosm	Competition among plant species and response to AM fungal colonization	Soil heterogeneity did not exert a significant effect upon floristic diversity, both grazing and mycorrhizal colonization were strongly influential. Micorrrhyzas reduced the yield of the canopy dominant <i>Festuca ovina</i> and stimulated strongly the yields of species such as <i>Scabiosa columbaria</i> , <i>Heracium pilosella</i> and <i>Plantago lanceolata</i> , all of which were found to have heavy AM fungal infection; moreover, the reduction of AM fungal infection, increased plant species diversity. The possible mechanism by which the presence of AMF affected the floristic diversity of plant communities was interplant transport of assimilates from the dominant species in the canopy via a common mycorrhizal hyphal network to subordinate plant species.
Gange <i>et al.</i> (1990, 1993)	Field early successional plant community	Plant response to AM fungal colonization	In an early successional plant community on poor soil, repeated applications of the fungicide iprodione reduced AM fungal infection in a number of annual forbs (e.g. <i>Tripleurospermum inodorum</i> , <i>Veronica persica</i> , <i>Vicia tetrasperma</i>) and one perennial legume (<i>Medicago lupulina</i>). In most of these species there was a significant reduction in growth as result of the fungicide treatment. This is the first demonstration that the reduction of mycorrhizal infection in the field can result in a decrease in plant species diversity.
Hartnett <i>et al.</i> (1993)	Greenhouse: native prairie soil in pots	Competition between two co-occurring prairie grasses under a range of neighbor densities, and plant dependency to AMF	AMF strongly influenced the patterns and intensity of both intraspecific density effects and interspecific competition between co-occurring prairie grasses that vary in their degree of mycorrhizal dependency, <i>Andropogon gerardii</i> (obligately mycotrophic) and <i>Elymus canadensis</i> (facultatively mycorrhizal-dependent), and the degree of host-plant benefit derived from AMF was strongly influenced by plant density. AMF can influence competitive hierarchies in tallgrass prairie such that patterns of species coex-

Table 3.

Source	Research site	Analyzed factors	AM fungal effects
			istence, richness and dominance may be mediated by mycorrhizal associations. However, other factors that influence local plant densities and size distributions such as fire, grazing, drought, or small animal disturbances may have not only direct effects on plant community, but also indirect effects mediated through changes in mycorrhizal benefits and mycorrhizal-mediated competitive relationships.
Hartnett and Wilson (1999)	Long term field experiment in a tallgrass prairie (5 years)	Competition between C ₃ and C ₄ plants and differential plant dependence to AM fungal colonization	Grasses, composites, legumes, forbs, and different AM fungal species, mainly of genus <i>Glomus</i> , were studied. AMF suppression resulted in decreases in abundance of the dominant obligately mycotrophic C ₄ tall grasses (e.g. <i>Andropogon gerardii</i> , <i>A. scoparius</i> and <i>Sorghastrum nutans</i>) and compensatory increases in abundance of many subordinated facultatively mycotrophic C ₃ grasses and forbs, but no changes in total aboveground biomass. Two mechanisms for mycorrhizal mediation of plant species composition and density were suggested: alterations in resources distribution among neighbors via hyphal connections, and differential host species responses to mycorrhizal fungal colonization in communities in which the competitive dominants were more strongly or more weakly mycotrophic than their neighbors. Active AM fungal associations decreased floristic diversity in tallgrass prairie. Mycorrhizal symbiosis and differential host plant species response to fungal colonization were the key factors explaining the dominance of C-4 perennial grasses in tallgrass prairie and limiting plant species evenness and diversity.
West (1996)	Greenhouse: pots	Influence of AMF on intra and interspecific competition	<i>Holcus lanatus</i> and <i>Dactylis glomerata</i> were grown in monocultures and mixtures. In monoculture, shoot biomass per plant of both species was increased over all densities by mycorrhizal infection. In mixed cultures, mycorrhizal infection enhanced shoot biomass of both species. Tiller production in <i>D. glomerata</i> was unaffected but reductions in leaf number were observed; infection had no effect on tiller production in <i>H. lanatus</i> . Relative yield totals suggested that mycorrhizal infection resulted in a reduction of resource complementarity: shoot biomass for each species in mixture was lower than that expected from growth in monoculture. Aggressivity indices suggested that <i>H. lanatus</i> was more aggressive than <i>D. glomerata</i> when present in equal or greater numbers; although, at very low densities, <i>D. glomerata</i> was more aggressive than <i>H. lanatus</i> when mycorrhizal.

Table 3.

Source	Research site	Analyzed factors	AM fungal effects
Watkinson and Freckleton (1997)	West (1996) data	Competition being dependent upon the density of the two plant species?	The relative crowding coefficient and the aggressivity index are influenced by density and do not distinguish between effects of changing environmental conditions on intra- and interspecific competition; consequently, in West (1996) analysis it is not possible to factor out the impact of AMF on the intra- and interspecific competition. The reinterpretation of the data differed from that presented by West (1996): a) no evidence for density-dependent competitive effects, and b) the intensity of both intra- and interspecific competition is increased following mycorrhizal colonization.
Wilson and Hartnett (1997, 1998)	Tallgrass prairie microcosm Greenhouse: pots	Plant dependence to AM fungal colonization	Suppression of mycorrhizas resulted in a reduction in total net aboveground plant production and changes in the relative production of C_4 (e.g. <i>Andropogon gerardii</i>) and C_3 plants (e.g. <i>Koeleria pyramidata</i>). C_4 produced less plant biomass, and had a greater ratio of reproductive to vegetative biomass. C_3 accumulated more biomass. There was a strong and significance relationship between phenology of prairie grasses and mycorrhizal responsiveness. Annuals were generally not responsive to mycorrhizal colonization and were lower in percentage root colonization than perennial species. There was a high mycorrhizal dependency of dominant prairie grasses, indicating that life history, taxonomic groups and phenologic guilds, differential growth and demographic responses to mycorrhizal colonization among species, might significantly affect plant productivity and species relative abundance, and therefore a significant influence on plant community structure.
Streitwolf-Engel et al. (1997)	Greenhouse: calcareous grassland soil pots	Plant dependence to AM fungal colonization and effect of AM fungal diversity	AM fungal species strongly determined the size and the clonal growth traits (stolon branching and length) of two plant species of <i>Prunella</i> , <i>P. vulgaris</i> and <i>P. grandiflora</i> . The effects of each AM fungal species were not the same in the two plant species, and the differential effects were independent of the differential colonization rates of the different AM fungal species. Different AMF in a natural community had the potential to influence the growth, number of ramets and distribution of ramets in <i>Prunella</i> populations. AM fungal diversity was potentially capable of determining plant population structure in ecosystems.
Van der Heijden et al. (1998a, 1998b)	Microcosms: European calcareous grassland Macrocosms: North American old-fields Greenhouse: calcareous grassland soil pots	Plant dependence to AM fungal colonization and effect of AM fungal diversity	Belowground diversity of AMF was a major factor contributing to the maintenance of plant diversity and ecosystem functioning; at low AM fungal diversity, plant species composition and the overall structure of the microcosms fluctuated greatly when the AM fungal taxa were changed. Plant diversity, nutrient capture and productivity in the macrocosms

Table 3.

Source	Research site	Analyzed factors	AM fungal effects
			<p>increased significantly with the increase of AM fungal species diversity. <i>Hieracium pilosella</i>, <i>Bromus erectus</i> and <i>Festuca ovina</i> were studied interacting with four different AM fungal strains of <i>Glomus</i>. Plant species differed in their dependency on AMF, thus varying in degree of benefit received. Specific AM fungal species and a mixture of these had significantly different effects on several plant growth variables, and these effects were not the same on each plant species. <i>H. pilosella</i> differed greatly in its growth response to several AM fungal species, <i>F. ovina</i> did not vary as much in its growth response as <i>H. pilosella</i>, while <i>B. erectus</i> did not exhibit much variation. Plant species responded differently to the mixed-AM fungal treatment, and these differential responses were even stronger than to those of the single-AM fungal species, indicating that a community of several AM fungal species may cause differences among the growth responses of plant species. Through their differential effects on plant growth, AM fungal species that co-occur as natural AM fungal communities have the potential to determine plant community structure.</p>

secondary metabolite production coupled with the range of enzymatic versatility.

For example, investigating the population variation among three geographic isolates of *Glomus mosseae*, Stahl *et al.* (1990) found significant differences between populations in terms of amounts of AM fungal colonization, spore production and their effect on biomass production, shoot phosphorus concentration and water relationship of *Melilotus officinalis*; it is clear that populations of *G. mosseae* from dissimilar environments are genetically different races or ecotypes. In addition to the significant genetic and physiological diversity, there is a functional diversity within morphologically defined taxa. Smith *et al.* (2000) give us another example, in a greenhouse experiment, they assessed the spatial differences in acquisition of soil phosphate between two AMF, *Scutellospora calospora* isolate WUM 12(2) and *Glomus caledonium* isolate RIS 42, in symbiosis with *Medicago truncatula*. They found that plants colonized by *S. calospora* preferentially obtained phosphorus from sites in the main "chamber-compartment" relatively close to the roots, compared with plants colonized by *G. caledonium*. Hence, formation of a highly beneficial mycorrhizal symbiosis did not necessarily depend on development of

hyphae at a distance from the roots or on large-scale translocation of phosphorus from distant sites, and concluded that differences in spatial abilities of individual AMF to acquire phosphorus might have strong ecological implications for plant growth in soils low in phosphorus.

Zak *et al.* (1995), and Zak and Visser, (1996) hypothesized that differences in large-scale patterns of fungal functional diversity (e.g. production and activities of exoenzymes), and fungal taxonomic diversity have been attributed to the degree of resource heterogeneity (carbon, nutrients and moisture) that exists both in time and space among ecosystems. Consequently, functional diversity should be the lowest at low levels of resource heterogeneity, and higher at a greater system heterogeneity; however, because of abiotic constraints, functional and taxonomic diversity should be the greatest at intermediate levels of resource heterogeneity.

Arbuscular mycorrhizal fungi (AMF) related to plant diversity

Arbuscular mycorrhizal fungi (AMF) related to plant diversity.
Arbuscular mycorrhizal fungi (AMF) are important

in determining the species composition of plant communities by three types of scale-time dependent interactions (Allen, 1991): 1] Direct contact between a hyphae of the mycorrhizal fungus and other organism, 2] Modifications of the environment by one organism (contact between one organism and the products of another), and 3] Indirect influence via a third organism, in this case the host plant. Several studies show up the effects of AMF on plant diversity (and on plant community structure) through processes such as competition, phenology, and interspecific nutrient transport through hyphal link (table 3).

Grime *et al.* (1987) determined that soil heterogeneity, grazing and mycorrhizal colonization were capable of promoting plant-species diversity in a turfgrass microcosms by raising the biomass of the subordinate species relative to that of the canopy dominant. On their side, Bergelson and Crawley (1988) made a reinterpretation of Grime's data, and demonstrated that although "diversity" increased in the mycorrhizal plots, species richness was identical under the treatments; thus the increase in diversity resulted from a reduction in dominance following mycorrhizal colonization, and the latest was detrimental to the growth of the dominant plant; likewise, there would be other cases in which the dominant plant benefited from mycorrhizal association and, in becoming more dominant, brought about a reduction in plant-species diversity. By his side, Newsham *et al.* (1995c) pointed out that both points of view were not incompatible because the response to mycorrhizas in terms of species richness will depend on the size of the pools of mycorrhizal and non-mycorrhizal species and their relative compatibilities and, in this case, there was a large number of non-mycorrhizal species present which were apparently able to profit from the loss of the AMF.

Gange *et al.* (1990, 1993), in an early successional plant community on poor soil, found out that repeated applications of a fungicide reduced AM fungal infection in a number of annual forbs and in one perennial grass, and a significant decrease in plant species diversity; and Van der Heijden *et al.* (1998a), using two independent, but complementary ecological experiments, demonstrated that belowground diversity of AMF was a major factor contributing to the maintenance of plant diversity and ecosystem functioning (e.g. nutrient capture, productivity).

Arbuscular mycorrhizal fungi (AMF) contribution to plant community structure. The role that mycorrhizas play in structuring plant communities is thought to be important through processes such as plant competition, and interspecific nutrient transport through hyphal links (Brundrett, 1991).

Arbuscular mycorrhizal fungi (AMF) benefits host plants by promoting a more efficient acquisition of phosphate ions from the soil, resulting in an increase in plant weight and a decrease in root: shoot ratio (Facelli *et al.*, 1999; Koide *et al.*, 2000), and these effects can be expected to increase the competitive ability of a plant (Zobel *et al.*, 1997).

Arbuscular mycorrhizal fungi (AMF) influence the patterns and intensity of both intraspecific density effects (Facelli *et al.*, 1999) and interspecific competition between different plant species (Hartnett *et al.*, 1993) altering the resource distribution among neighbors via hyphal connections, and favoring the competitive dominant mycorrhizal species and limiting plant species evenness and diversity (Hartnett and Wilson, 1999). Therefore, AMF may alter plant community structure by altering the competitive balance between plant species (Hartnett *et al.*, 1993; Newsham *et al.*, 1995c; West, 1996; Titus and del Moral, 1998a, 1998b; Facelli *et al.*, 1999; Hartnett and Wilson, 1999; Marler *et al.*, 1999).

On the other hand, within a community, the lack of mycorrhizas is a characteristic of early successional habitats (Nicolson, 1960). Ruderal plant species that colonize frequently disturbed sites are often facultative mycotrophs (Francis and Read, 1994), and early successional annuals are predominantly non-mycotrophic; thus, non-mycotrophy is hypothesized to be a derived character allowing a rapid exploitation of highly disturbed environments and, even if both arbuscular mycorrhizal infection and spore counts are reduced with disturbance, infection and spore density rapidly increased if mycotrophic plants start to be present (Allen and Allen, 1980).

For example, as a consequence of the eruption of Mount St. Helens, USA, in 1980, Allen *et al.* (1984) and Allen (1987) studied the process of AM fungal inoculum re-establishment, Carpenter *et al.* (1987) analyzed the role of fungi as a substrate for colonization by non-vascular plants and Titus and del Moral (1998a, 1998b) assessed the effect of AMF presence/absence in determining the plant species composition in primary succession, and concluded that AMF were one of many interacting factors determining competitive dominance and species change over successional time.

From this approach, it is no doubt that AMF can be considered as a non redundant functional group (Chapin *et al.*, 1992) with highly diverse combinations of specific functions (Allen *et al.*, 1995), and a "key-stone" species with an important mediation and modifying role between community structure and functioning (Hawksworth, 1991; Turner and Friese, 1998).

Discussion

Arbuscular mycorrhizal fungi (AMF) are capable of determining/modifying plant diversity, and plant community structure. Mycorrhizal symbiosis affects several plant traits and ecological processes: plant relative growth (e.g. Grime *et al.*, 1987) and abundance (e.g. Gange *et al.*, 1993), nutrient uptake and plant-plant nutrient interactions (e.g. Koide *et al.*, 2000), and the competitive balance between co-occurring plant species (e.g. Hartnett and Wilson, 1999). Likewise, these traits and processes can be altered by the presence/absence of AMF (rate of colonization, percentage of arbuscules, vesicles, spores) (e.g. Carey *et al.*, 1992; Dickson *et al.*, 1999), specific AM fungal species (e.g. Van der Heijden *et al.*, 1998a, 1998b), and ecotypes (e.g. Stahl *et al.*, 1990), degree of mycotrophy presented by the host plant (e.g. Wilson and Hartnett, 1997, 1998), and specific host plant species (e.g. Dhillon, 1992a, 1992b). According to Van der Heijden *et al.* (1998a) the ecological-functional range of AMF is also determinant to ecosystem variability and productivity. Though, some notes need to be pointed out.

Since AMF are obligated root symbionts, the context of mycorrhizal association studies must involve both partners (AM fungus-host plant) in terms of biological-ecological equal importance; any biotic/abiotic factor that affects one of the members of the association will affect the other as well. For instance, at the present, it is well known that the same environmental factors that affect AM fungal species distribution, establishment, and survival (e.g. soil pH, water content, temperature), affect the host-plant species distribution. Gianinazzi-Pearson *et al.* (1991) and Douds *et al.* (1998) state the complexity of this association in terms of plant and fungal "signals for specific responses" that may be based on genetically controlled substances.

It seems that these "symbiosis genes" (Morton, 1990a, 1990b), in spite of the environmental selection processes, are responsible of the diminish (or even stop) of AM fungal speciation processes that is reflected in the small number of AM fungal species reported at the present; however, other technical and laboral factors are also involved: difficulties in AM fungal identification in the field, the inability to grow AMF in pure culture (growth of fungi on whole plants or explants), reliance of subcellular morphological characters of spores that are difficult to see and interpret (Morton *et al.*, 1995), and the lack of basic information on the life histories of AMF (Sanders *et al.*, 1996), and an insufficient number of and well trained mycologists (Hawksworth, 1997).

The increase in interest on AMF ecological performance, and the differential effects provoked by different species/strains already identified on host plant performance (e.g. Smith *et al.*, 2000), has showed the importance of knowing the AM fungal symbiont species "identity". For example, the study of AMF functional diversity contributed to reveal the existence of AM fungal ecotypes with significant genetic (Sanders *et al.*, 1996), physiological and functional diversity within morphologically defined taxa (Stahl *et al.*, 1990), and the great complexity of the AMF-plant interactions. A practical approach was conducted by Montañño (1999) in a semi-arid region in central Mexico, where he studied the ecological function of AMF in relation to "fertility islands" where the "mesquite", *Prosopis laevigata*, was the dominant plant specie, and the aim of his study was the proposal of rehabilitation alternatives for the zone. He reported two species (*Acaulospora denticulata* and *Scutellospora gregaria*), seven morpho-species and 18 morphological types (color and forms), are they new species? He is still working on it, but it was clear that different AM fungal species have different effects on host plant species performance.

On the other hand, the majority of the AM fungal research in relation to plant diversity, has been made in tallgrass prairie vegetation, neglecting other vegetation types which could add interesting data. For instance, Carrillo-García *et al.* (1999) found that AMF helped to stabilize windborne soil that settled under dense plant canopies, enhanced the establishment of colonizer plants in bare soils of disturbed areas, and influenced plant associations through differences in the mycotrophic status of the associates in a "plant-soil" system of the Sonoran Desert in Mexico. Likewise, most of the experimental work have been done in greenhouse pots or microcosms (e.g. Grime *et al.*, 1987; Van der Heijden *et al.*, 1998b) and just some in the field (e.g. Gange *et al.*, 1990, 1993), very few plant species or/and taxonomic groups (mainly grasses and legumes), and AM fungal species or/and ecotypes (e.g. genus *Glomus*, *Scutellospora*) have been tested, and in addition, there has not been uniformity in the time scale of the studies (Zak and Visser, 1996) neglecting important temporal-biological aspects of both symbionts (e.g. development and growth processes, phenology), just Hartnett and Wilson (1999) have conducted a five years field experiment. Briefly, the overall of these factors make difficult the comparison and the generalization of the results and the data generated; hence an alternative could be the establishment of long-term ecological research sites (LTERS) for achieving the integration of both AMF and plant life history traits, and a better under-

standing of their ecological interactions.

Another process quite controversial is plant competition mediated by AMF. The influence of AMF in plant interspecific competition has been studied in species pairs where one species is strongly AMF dependent but the other is non-mycorrhizal (Allen and Allen, 1990). In some studies (e.g. Grime *et al.*, 1987; Hartnett *et al.*, 1993) the evidence of competition comes from simple comparisons of the performance (i.e. height growth and biomass production) of plants in monocultures and in mixtures at a single overall density that does not allow the impact of AMF on intra- and interspecific competition to be distinguished, whilst in others, although different densities are considered, and competition assessed (e.g. West, 1996), the use of a different mathematical approach can drive to a different interpretation of the data that, obviously, leads to different conclusions (Watkinson and Freckleton, 1997). Plant competition is, by itself, a wide subject and many questions are still in the air that need to be answer (e.g. the asymmetry or symmetry on plant populations competition, effects of habitat productivity on plant competition), first from the plant-plant approach and, second from AMF-plant interaction.

More studies are needed within this scientific field, but we must recognize that AM fungal research has an epistemological problem that is reflected on the opposed and controversial results, and conclusions found in the literature; therefore, it is of great importance to focus on the way questions are proposed, the methods that are chosen and developed to answer them (e.g. time-space scales), the interpretation of the results, and the feasible "generalization" of the conclusions obtained.

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