

Formation and functions of arbuscular mycorrhizae in coastal wetland ecosystems: A review

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ABSTRACT

Context: Coastal wetlands are ecotones interspaced by land and ocean and are among the most sensitive and vulnerable ecosystems worldwide. They are unique in hydrological, edaphic, atmospheric, and biological characteristics, and play important roles in maintaining the ecological security and ecosystem services of coastal zones. Arbuscular mycorrhizae (AM) are symbiont composed of plant roots and arbuscular mycorrhizal fungi (AMF), which are soil-borne microorganisms widely distributed in various habitats. Many previous studies on mycorrhiza have focused on terrestrial ecosystems while few on wetlands, especially coastal wetlands.

Method: We systematically reviewed previous relevant studies to explore the formation and functions of AM in coastal wetland ecosystems as well as the environmental factors that affect them. Habitat characteristics, morphological types, and species diversity of AMF in the coastal wetlands were summarized. Both responses of AMF to environmental factors during AM formation and the functions of AM in coastal wetlands were discussed.

Result: AMF are worldwide distributed in coastal wetland and are mainly limited by flooding, hypoxia, soil pH, salinity and the host plants identification. AMF play important roles in coastal wetlands, involving promoting nutrient uptake of host plants, improving the characteristics of rhizospheric soil, and enhancing plant resistance to salt and flooding stress.

Conclusion: More comprehensive studies of AMF in vitro in coastal wetlands would be helpful for the conservation and restoration of coastal wetland ecosystems in the changing world.

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Introduction

Coastal wetlands are located in transition areas between land and ocean, mainly developed in the estuaries of rivers (Schuerch et al. 2018; Li et al. 2021; Wang et al. 2021). Due to the influence of marine dynamics and river confluence, coastal wetland is one of the most vulnerable ecosystems (Kirwan and Megonigal 2013; Li et al. 2018; Bilal, Xie, and Zhai 2020), which is exposed to rapid changes in hydrological environment (Adam 1990), serious soil salinization (He et al. 2009) and vulnerability to exotic species invasion (Yang 2019). Firstly, coastal wetlands are affected by the cyclical fluctuation of tides and the seasonal role of the terrigenous water supply (Urish and McKenna 2004). Hydrological regimes are the basic and dominant ecological factors in coastal wetlands (Lee et al. 2006; Keddy 2010). Secondly, coastal wetlands are characterized by high soil salinization (Chi et al. 2021), mainly tidal flat saline and coastal saline soil, mostly muddy and silty tidal flats (Pennings, Grant, and Bertness 2005; Ma, Wang, and Wang 2014; Huang et al. 2015). Additionally, coastal wetland vegetation is zonally distributed, modified by tidal flooding depth. Only plants (*Scirpus mariqueter* and *Spartina alterniflora*) with

high saline-alkaline tolerance and waterlogging tolerance are distributed in low tide zone (Chen et al. 2004; He et al. 2009; Keddy 2010; He et al. 2011). With the increase of distance from the sea, the tidal effect weakened, and the soil salinity decreased. Some low-salt-tolerant plant species (*Phragmites australis*, *Imperata cylindrical*, and *Solidago canadensis*) gradually emerge (Bertness and Ellison 1987). The climate, soil, vegetation, and hydrology will influence coastal wetland environment and determine ecological succession trend (Schuerch et al. 2018).

Due to the unique geographical location, coastal wetlands are endowed with a variety of ecosystem services (Barbier et al. 2011; Liu et al. 2019). These services include: 1) regulating function: water purification, wave elimination and siltation promotion, climate regulation, coastal protection (Dierschke et al. 1999), sedimentary nutrients, and sequestration contaminant (McLeod et al. 2011); 2) supplying function: direct support of human welfare, as well as providing migration and wintering grounds for aquatic and swampy organisms (Dierschke et al. 1999); 3) supporting function: carbon fixation, oxygen release, and maintenance of

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ecosystem stability (Dierschke et al. 1999; He et al. 2020); 4) cultural function: tourism development, scientific research and education (He, Altieri, and Cui 2015). Fully understanding the ecological functions and disturbance factors of coastal wetlands would contribute to better maintaining and protecting their ecosystem health.

Coastal wetlands play an indispensable role in the global ecosystem (Sun et al. 2015), and their functions are inextricably linked to the microorganisms in the soil (Bai et al. 2012), among which arbuscular mycorrhizal fungi (AMF) are among the soil microorganisms most closely related to plants (Veresoglou and Rillig 2014). AMF are widely distributed in terrestrial ecosystems and play an important role in enhancing plant resistance to abiotic stress and promoting plant growth (Begum et al. 2019). Previous studies generally reported that AMF are aerobic microorganisms, which are limited by flooding in wetland ecosystems and cannot form a symbiotic association with plants (Ma, Wang, and Wang 2014). In recent years, with the increase of AMF investigation and research in wetland ecosystems, we have gradually had a preliminary understanding of AMF in wetland ecosystems. Existing studies provided evidence that AMF formed a near-ubiquitous mutualistic association with roots to help plants withstand harsh environments, and played a key role in the establishment of coastal beach plant communities (Wang et al. 2020a). However, there is still a lack of systematic understanding of the community structure, species composition and functional role of AMF in coastal wetland ecosystems. Based on the above background, we systematically reviewed the species composition of AMF, the environmental factors affecting the formation and function of AM (arbuscular mycorrhiza) in coastal wetland ecosystems in recent years. Also, we propose some prospects of AMF in coastal wetland ecosystem for future research.

Diversity of AMF in coastal wetland ecosystems

AM fungi belong to Glomales (Glomeromycota) (Rosendahl 2008) and are among the oldest terrestrial fungi (Simon et al. 1993), which were established between the Ordovician and Devonian periods (Pandey et al. 2019). Furthermore, AMF are the most important components of rhizosphere microflora and can form symbiotic associations with approximately 90% of vascular plant species (Read 1991; Nielsen et al. 2004; Genre et al. 2020). AMF help the host plant access to water and mineral nutrients from the soil (Begum et al. 2019), and in return, host plants provide photosynthesis-derived carbon for mycorrhizal fungi (Smith and Read 2010). Traditionally, AMF were thought to be aerobic or microaerophilic

microorganisms (Wang et al. 2010) and are limited by low oxygen content, which was not enough in wetland habitats (Ma, Wang, and Wang 2014). However, recent studies have found that AMF are ubiquitous and indispensable in wetland ecosystems (Wolfe et al. 2007; Fester 2013; Xu et al. 2016; Gaberščik et al. 2017; Huang et al. 2021). The abundance and diversity of AMF in wetland habitats are thought to be comparable to those in terrestrial habitats (Wang et al. 2011; Ramírez-Viga et al. 2018; Xu et al. 2021). AMF in coastal wetlands mainly belong to several genera including *Glomus*, *Acaulospora*, *Archaespora*, *Gigaspora*, *Appendicispora*, *Pacispora*, among which *Glomus* is dominant (Sengupta and Chaudhuri 2002; Wang et al. 2004; Kothamasi et al. 2006; Wilde et al. 2009; Wang et al. 2015; Ramírez-Viga et al. 2020; Wang et al. 2020a; Yu et al. 2021) (Table S1). By summarizing the distribution of AMF in coastal wetland habitats, it is found that AMF developed more in high intertidal zone where existed more abundant vegetation species and shorter flooding, as compared to in low intertidal zone. In addition, the number of AMF in coastal wetland habitats is relatively small than in terrestrial habitats, this may be due to the high-salt, low-oxygen and flooded environment of coastal wetlands, which may act as environmental filters that only allows salt-tolerant, hypoxia-tolerant and flood-resistant AMFs to survive normally (Deepika and Kothamasi 2021). AM may rely on plant aerenchyma to transport and secrete oxygen produced by photosynthesis from aboveground to rhizosphere, thus achieving gas exchange and selective symbiosis (Miller and Sharitz 2000). However, little is known about why AMF can survival in coastal wetland and further research is required to test it.

Generally, three major types of AM were identified: *Arum*-type, *Paris*-type (Cavagnaro et al. 2001), and their intermediate type, according to the morphological characteristics of their symbiotic interface (Dickson and Kolesik 1999). Field investigations have suggested that both *Arum*- and *Paris*-type mycorrhizal fungi exist in coastal wetlands (Sengupta and Chaudhuri 2002). The factors that determine the differences in AM morphology are not well understood (Ahulu, Nakata, and Nonaka 2005). AM morphology differed with family and genus of host plants (Brundrett and Kendrick 1988) as well as with fungal identities (Cavagnaro et al. 2001). *Paris*-type plants are more common found in wild plants, whereas *Arum*-type plants are mainly present in cultivated herbs (Smith and Smith 1997).

Environmental factors affecting formation of AM in coastal wetlands

In coastal wetlands, hydrologic characters, soil physical and chemical properties, oxygen content of rhizosphere as well as plant invasion are limiting factors

for AMF performance (Kothamasi et al. 2006; Zhang et al. 2019; Ramírez-Viga et al. 2020) (Figure 1).

Effects of hydrological fluctuation

Coastal wetlands are characterized by intermittent or prolonged inundation by saline water from the ocean or fresh water from land, such as river (Reed et al. 2018), leading to greatly variable water environments, particularly fluctuations in hydrological characteristics, such as soil moisture, flooding depth, and flooding duration. In the process of AM formation in coastal wetlands, mycorrhizal colonization may respond differently to fluctuations in hydrological characteristics (Oliveira, Dodd, and Castro 2000; Ma, Wang, and Wang 2014).

Flooding and higher soil moisture differently inhibited the mycorrhizal colonization in the roots of coastal wetland plants. Miller (2000) indicated that mycorrhizal colonization of two wetland plants, *Panicum hemitomon* and *Leersia hexandra*, grown in the Carolina Bay wetland of the southeast coast plain of the United States, decreased with increasing soil moisture. Oliveira, Dodd, and Castro (2000) reported that the roots of semi-aquatic *P. australis* could be colonized by AMF and that the magnitude of the colonization depended on the growth stage of the plant coupled with the apparent onset of water stress in the soil. Notably, mycorrhiza was more present at lower soil water content. In short, excessive soil moisture partially inhibits AMF colonization of coastal wetland plants. Compelling studies have found that an increase in water depth reduces the AMF colonization rate in host plants. Ipsilantis and Sylvia (2007) reported that

with an increase in water depth, the mycorrhizal colonization in the roots of *Typha latifolia* decreased greatly. The extraradical hyphae length of most fungi strains was restricted to 2.5 cm by flooding, but the length of extraradical hyphae differed among AMF strains, with a maximum of 16.5 cm observed. Miller (2000) also observed that AMF colonization was strongly negatively correlated with water depth in a field survey. In contrast, Bauer et al. (2003) found that AMF colonization was not significantly correlated with hydrological gradients in freshwater wetlands.

In addition, the response of AMF to flooding duration is more obvious, which is not only reflected in the AMF colonization rate, but also in the change in colonization structure of AMF with increasing flooding duration. For example, Ma, Wang, and Wang (2014) studied the root colonization of *Typha orientalis* with three AMF (*Glomus intraradices*, *G. versiforme*, and *G. etunicatum*) under flooding stress with different durations. Their results showed that different flooding durations changed the colonization rate, and moreover, the longer the flooding duration, the lower the colonization rate of *T. orientalis* with AMF. Furthermore, the change of fungal colonization structure was mainly manifested as the proportion of arbuscule formation decreased with the prolongation of the flooding duration, while the number of fungal spores produced between different AMFs increased or decreased. Wang et al. (2011) research also showed that flooding had an important effect on AMF diversity in the rhizosphere of mangroves, and its effects appear to depend on the degree (duration) of flooding. This also indicates that there are specific differences in the tolerance of different AMF strains to flooding stress,

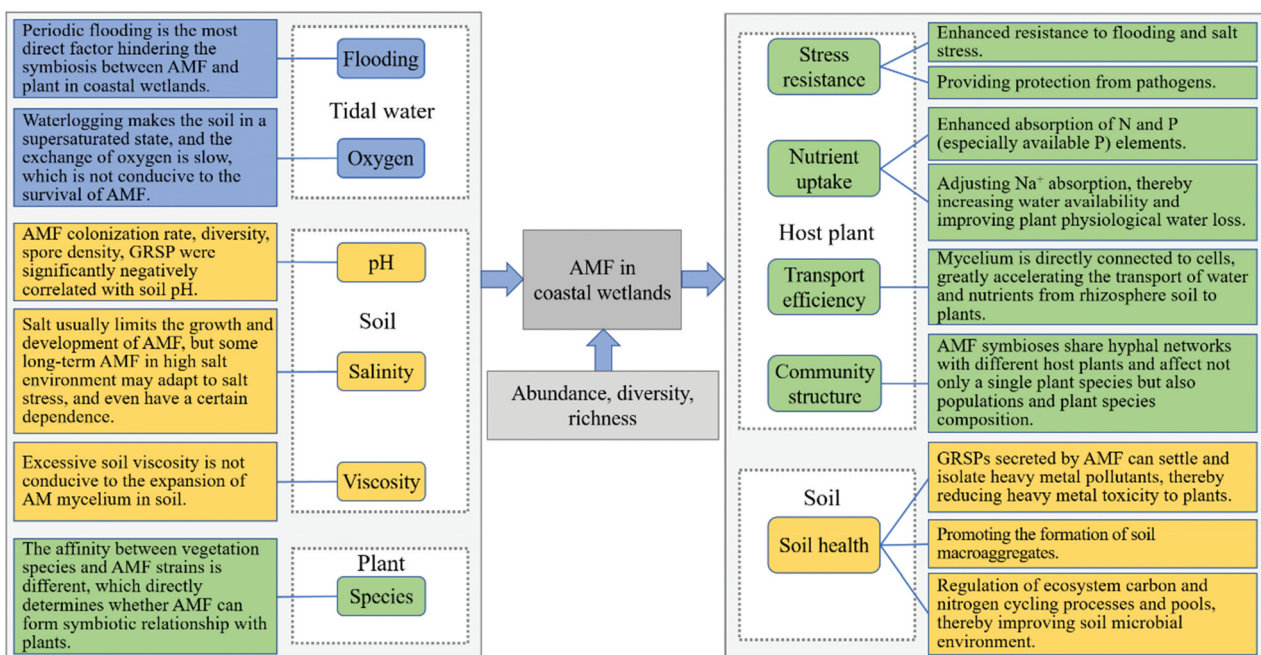


Figure 1. Conceptual framework for the factors affecting distribution of AMF and their ecological functions in coastal wetland ecosystems.

and the response patterns of different fungal strains to flooding stress are different.

As observed in previous studies, fluctuations in hydrological factors have varying effects on AMF colonization in coastal wetland plants (Oliveira, Dodd, and Castro 2000; Wang et al. 2011; Soudzilovskaia et al. 2015). However, hydrological conditions and water contents often fluctuate in coastal wetlands, resulting in large differences in water content, flooding duration, and flooding depth. It is obvious that most of the current studies are field observation and that few related studies are conducted under controlled environment with the underlying mechanisms still unknown.

Effects of soil physical and chemical properties

Tidal saline-alkali soils in coastal wetlands, which have a short history of formation and reclamation, are characterized by high viscosity, poor permeability, high salinity, poor nutrients, rare microorganisms, shallow groundwater burial, and a high degree of mineralization. Most of the soil characteristics affect the root colonization with AMF, and the main factors related to geographical environments, vary among regions (Soudzilovskaia et al. 2015). From a global perspective, soil characteristics that influence mycorrhizal colonization can be summarized as soil pH, salinity, nutrients, and dissolved oxygen (Delvian 2010; Ramírez-Viga et al. 2020; Wu et al. 2020).

Edaphic pH is one of the most important factors in determining AMF diversity, colonization and spore production (Alguacil et al. 2016; Eskandari et al. 2018; Ramírez-Viga et al. 2020). First, soil pH has an important impact on the community composition of AMF in coastal wetland habitats. Ramírez-Viga et al. (2020) investigated the relationship between rhizosphere soils and AMF in two mangrove plants (*Avicennia germinans* and *Conocarpus erectus*), and found that matrix pH was one of the main edaphic variables that determined changes in mangrove rhizospheres AMF, and pH had a direct negative impact on AMF species richness. Secondly, with the increase of soil pH, the colonization rate of AMF in plant roots and the number of spores produced generally decreased. Zhang et al. (2020) studied the spatio-temporal dynamic changes of AMF in the rhizosphere soil of halophyte of *Kosteletzkya virginica* in coastal saline wetlands through field investigation, and found that soil pH had an important impact on the distribution, species diversity and symbiosis process of plants and AMF, and the colonization, diversity, spore density and glomalin-related soil proteins (GRSP) content of AMF were significantly negatively correlated with soil pH. This is consistent with the research results in terrestrial ecosystems, and further indicates that soil pH is a key factor affecting the community structure and species

diversity of AMF in both terrestrial and wetland ecosystems. The mechanism of the effect of soil pH on mycorrhizal symbiosis can be summarized as the effect of pH on the availability of some ions and nutrients in soil to plants (Ramos, Façanha, and Feijó 2008). In addition, pH not only affects the symbiosis between AMF and plant roots, but also directly affects spore germination and mycelial growth (Corazon-Guivin et al. 2022), and indirectly affects mycorrhizal development by affecting the solubility of major substances and toxins in soil (Gong and Tian 2019).

The growth and development of AMF in terrestrial ecosystems are often inhibited by soil salinity (Juniper and Abbot 1993), which is also true for AM fungi in wetland. Delvian (2010) found that AMF diversity, activity, colonization rate, and spore density decreased with an increase in soil salinity. For the common mycorrhizal plant *P. australis*, AMF diversity and colonization rate in its roots decreased rapidly as soil salinity increased (Oliveira, Dodd, and Castro 2000; Wang et al. 2004). Some AMFs, which survived for a long time in high-salt environments, may have evolved with certain salt tolerance capabilities. For example, Carvalho, Correia, and Martins-Loução (2004) found that spore germination of two AM fungi (*G. geosporum* and *G. mosseae*) collected from the Pancas salt marsh was not affected by increased salinity compared to two non-marsh fungal strains. In the short term, the increase in soil salinity significantly reduced the colonization rate of AMF, which at least partly explained the inhibition of salt on the symbiosis of AMF and plants, and the formation of AMF-dependent dependence of some halophytes plants. Based on the previous studies on the effects of soil salinity on AMF in coastal wetlands, it is concluded salinity is the major environmental factor for the change of AMF community structure in sediments along vegetation succession sequences. Soil salinity not only affects the colonization rate, diversity, spore density and GRSP secretion of AMF, but also affects the community structure and species distribution of AMF (Delvian 2010). In these processes, AMF were mostly inhibited with the increase of soil salinity. However, different from the terrestrial ecosystems, some AMF strains living in high salinity environment for a long time in the coastal wetland ecosystems may have adaptability to the environment, showing a normal distribution phenomenon that the spore germination rate was low under salt-free or low salinity conditions, increased with the increase of salinity, and then gradually decreased with the increase of salinity (Carvalho, Correia, and Martins-Loução 2004). That suggested AMF had stronger salt tolerance in coastal wetland than in terrestrial habitats.

Soil nutrient also affect the growth and colonization of AMF, and is closely related to the diversity, colonization and spore density of AMF. Wu et al. (2020) showed that AMF species richness increased significantly with

increasing soil organic carbon. It was found that the availability of soil Fe, Cu, and Ca would reduce the mycorrhizal colonization or fungal spore density (da Silva et al. 2017). Additionally, Lovelock et al. (2010) suggested that available phosphorus and total phosphorus in the soil can affect the secretion of GRSP, which has been used as an indicator of fungal colonization in plant roots.

Effects of oxygen content in rhizosphere

AMF is considered as an aerobic or microaerobic microorganism (Wang et al. 2010). Due to the unique characteristics of wetland habitat, the oxygen content in the rhizosphere of plants varies greatly, which is one of the limiting factors affecting the colonization of AMF and plants in coastal wetland habitats. Daleo et al. (2007) found that the colonization rate of AMF in the roots of *Spartina anglica*, a constructive species on the Mar Chiquita coast of Argentina, was linearly and positively correlated with the density of caves excavated by the cave crab *Chasmagnathus granulatus*. Soil redox potential and soil oxygen availability are the main physical factors limiting the development of AMF in wetlands (Mukerji and Mandeep 1998). Kothamasi et al. (2006) reported the AMF mainly survived in the aeration cortex of the mangrove rhizosphere, which may be related to oxygen flow in the aeration cortex. In addition, Maricle and Lee (2002) found that the larger aeration tissue area of *S. alterniflora* under flooded conditions than that under non-flooded would be helpful for AMF colonization in *S. alterniflora* roots.

The periodic tidal rise and fall in coastal wetlands often cause the flooded state of soil. The transport of oxygen is controlled by molecular diffusion, so the diffusion of oxygen in wetland soil is very slow in a flooded state (Ramírez-Viga et al. 2018), which reduce the available amount of oxygen in the sedimentary matrix. During a certain period of time, some microaerobic soil microorganisms are sufficient to deplete most of the oxygen in the coastal wetland soil. Due to the slow gas diffusion rate in the wetland soil, oxygen cannot be fully replenished until oxygen is consumed again by the biota (Jackson and Armstrong 1999). However, even in such coastal wetland soil where oxygen exchange is not timely, many studies have shown that AMF can survive there and form symbiotic relationship with plants (Ramírez-Viga et al. 2020; Wang et al. 2020a; Yu et al. 2021). This may be due to the fact that the flooding environment in coastal wetlands is mainly dominated by the periodic fluctuation of tides. AMF in this habitat may have formed an adaptive mechanism to intermittent hypoxia caused by regular flooding. Some researchers suggest that the highly developed aeration organization of plant roots in coastal wetlands provides oxygen for AMF

(Kothamasi et al. 2006). In addition, some studies found that burrowing behavior of cave animals also promoted the gas exchange in the soil of coastal wetlands (Daleo et al. 2007). However, there is no clear and concise conclusion to explain how AMF in coastal wetlands adapt to anoxic environment. Obviously, oxygen is a factor limiting AM formation in coastal wetlands, but how AMF in coastal wetland habitats adapt to this anoxic environment needs further study.

Effects of biological invasion

At present, invasive plants seriously threaten the structure of native plant communities in coastal wetlands (An et al. 2007). However, up to now, there is still a lack of research on the impact of invasive plants on AMF in coastal wetlands, so there is little understanding of how biological invasion affects AMF in coastal wetlands.

On the one hand, the studies have shown that invasive plants can change the community structure and species richness. Wang et al. (2021) found that, with the *S. alterniflora* invasion, the species richness of AMF in rhizosphere soil of *S. alterniflora* community was higher than that in bare flats habitat, but lower than that in *P. australis* habitat. It also indirectly indicated that the species richness of AMF increased in the soil whose original habitat was a bare flat after *S. alterniflora* invasion, while the species richness of AMF decreased in the soil whose original habitat was a vegetation community of *P. australis*. Zhang et al. (2019) found that with the invasion of *S. alterniflora* into the native *Suaeda salsa* community, the relative abundance of soil fungi including AMF is generally enhanced. On the other hand, some studies suggest that the AMF community may play a positive role in the successful invasion of alien species. For example, Yang et al. (2016) reported that *S. alterniflora* invasion significantly increased the quantities of AMF phospholipid fatty acids by 1.47 to 6.70-fold compared to bare flat, *S. salsa*, and *P. australis* soils, which would be helpful for successful invasion of *S. alterniflora*.

Indigenous AMF can also directly or indirectly alter the interaction between native and invasive plants. When invasive and native plants with different AMF affinities grow together, they also affect AMF colonization rate (St-Arnaud et al. 1997). Although it may have a certain impact on the AMF community structure and species richness in the invaded areas, most of the current research results provide evidence that *S. alterniflora* is not easy to be colonized by AMF (Eberl 2011). Liang et al. (2016) found that the colonization rate of AMF in the root of *P. australis* under the condition of mixed *P. australis* and *S. alterniflora* was lower than that of AMF in the single community of *P. australis*, indicating that the invasion of *S. alterniflora* inhibited the colonization of AMF in the root of native

plant *P. australis*. The study further showed that the shorter the invasion time, the stronger the inhibition of AMF colonization rate.

However, the response of AMF to the interaction between invasive plants and native plants is still poorly understood. So far, the relationship between plant invasion and AMF has not yet reached a unified conclusion. On the interaction between invasive species and AMF, the results differed between different research areas, invasive species and AMF strains. Yang et al. (2016) showed that AMF could accelerate the successful invasion of invasive plants in coastal wetland habitats. Whereas, other study found that it was difficult to form a symbiotic relationship between invasive alien plants and AMF, so the establishment and strengthening of mycelium network contributed to the development of native plants, thus playing a role in hindering the invasion of exotic plants (Liang et al. 2016). In general, there are few studies on the relationship between invasive plants and AMF in coastal wetlands, and the results depend on the location of the study, the species of invasive plants and the length of the invasion time. Therefore, in order to clarify the relationship between AMF and invasive plants in coastal wetlands, more studies on the relationship should be carried out in the future.

Ecological functions of AM in coastal wetland ecosystems

Many studies have been conducted on the ecological effects and adaptability of mycorrhizal fungi in terrestrial ecosystems, and there is also strong evidence that

mycorrhizal fungi can play an irreplaceable role in promoting plant growth and fitness (Whipps 2001; Boruah et al. 2003), enhancing plant resistance to abiotic stresses (Noori, White, and Newman 2017), remediating polluted environments (Cicatelli et al. 2012), improving soil quality, maintaining biodiversity and ecosystem functions (Yang et al. 2014), and accelerating sustainable production in agriculture, forestry, and animal husbandry (Ryan and Graham 2002) (Figure 2). The ecological function of mycorrhizal fungi in coastal wetland habitats may be mainly manifested in the following aspects, though known very little currently.

Ecological functions in promoting plant growth

On the one hand, AM can regulate plant absorption of nutrients in the soil, especially soil available phosphorus to promote plant growth (Smith and Read 2010; Lagrange, Huillier, and Amir 2013; Latef et al. 2016). Numerous studies have shown that AMF can not only enhance plant uptake of mineral elements, such as P, Ca, Zn, and Cu in soil, but also the absorption of free NO_3^- and NH_4^+ in soil (Lagrange, Huillier, and Amir 2013; Ha et al. 2014). Although McHugh and Dighton (2004) found that AMF has a low colonization rate (5.5%) in the root of *S. alterniflora*, Khan and Belik (1995) also found that AMF significantly improved nutrient uptake in *S. alterniflora* under limited phosphorus availability.

On the other hand, AM can also enhance the host plant resistance to stress and help improve plant performance. Studies have shown that AMF plays an important role in improving the resistance of host plants to salinity,

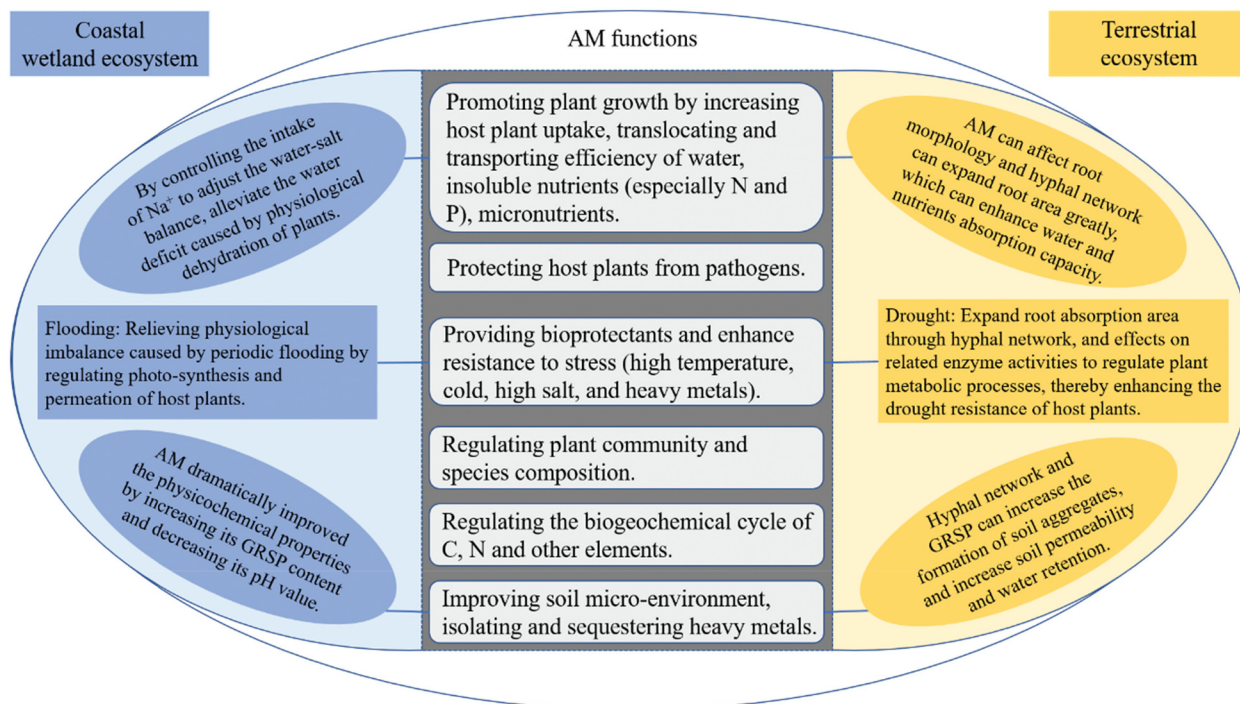


Figure 2. Ecological function differences of AMF between coastal wetlands and terrestrial ecosystems.

flooding, and heavy metal toxicity (Porcel, Aroca, and Ruiz-Lozano 2012). Studies by Wu et al. (2020) and You et al. (2021) have also shown that AMF can effectively promote the growth and physiological activity of *P. australis* under copper, zinc, and cadmium stress, thereby increasing *P. australis* biomass.

Ecological functions in coping with saline-alkali induced water deficit of plants

Coastal wetlands typically suffer from soil salinization caused by large and continuous supplementation of salts from the sea (Yu et al. 2014). The osmotic pressure of soil solutions is often high in coastal wetlands, which may lead to water deficits in coastal wetland plants (Ma et al. 2021). As a result, plants under osmotic stress weakened, and their growth was retarded (Porcel, Aroca, and Ruiz-Lozano 2012). Increasing evidence has shown that symbiotic fungi can significantly alleviate the detrimental effects of physiological drought through the following strategies. First, exposed to stressful environment, plant roots can detect the environmental signals and respond to them accordingly (Hodge 2009). When building mycorrhizal association with plants, AM fungi can change the root morphology and physiological functions of the host plants (Atkinson, Berta, and Hooker 1994). The extensive extraradical hyphal network of AMF helps roots explore more soil volume than non-mycorrhizal plants (Evelin et al. 2019). Zhang et al. (2020) reported that *Kosteletzkya virginica* grown in the coastal saline-alkali area of northern Jiangsu Province, China. Which can form a strong symbiotic relationship with the AMF, which confer benefits on absorption and transportation of water from the soil to the host. Second, AM improved the water transportation. The symbiosis of AM allows for a more flexible regulation of water transport according to the water storage and aboveground requirements of the host plant (Bárzana et al. 2012). As AM is a multinucleated non-diaphragm or a very thin septum mycelium, water can directly reach the arbuscular mycelium, and there is little resistance to water transport in the mycelium. After reaching the arbuscular structure at the top of the mycelium, water seeps into the root cells of the host, which shortens the water transport path in the root and may provide a special method of water absorption (Alexopoulos, Mims, and Blackwell 1996). Moreover, AM can also regulate the hydraulic conductivity of the roots (Kapoor, Sharma, and Bhatnagar 2008) and leaf stomatal conductance (Augé, Toler, and Saxton 2015) of host plants, which improves the lateral root pressure and vertical transpiration pull of host plants, and is conducive to smoother and more rapid water transport (Bárzana et al. 2012). Additionally, AM fungi can increase the accumulation of osmotic substances (i.e., soluble protein, soluble sugar, and proline) in plants, improves

ionic homeostasis, and reduces the tendency of water loss in plants (Huang et al. 2000). The GRSP secreted by AM can improve soil aggregates, permeability, and water retention and prevent plant dehydration (Holátko et al. 2021). Ma et al. (2021) reported that inoculation with three AM fungi (*Funneliformis mosseae*, *Rhizophagus intraradices*, and *Diversispora tortuosa*) with *S. glauca* plants grown in salinized wetland soils, the synergistic effects have been observed on nutrient absorption, ionic homeostasis, osmotic substance synthesis, and antioxidant enzyme activities in *S. glauca*, thus allowing the host plants to avoid physiological drought.

Ecological functions in meliorating of soil micro-environment

Soil microorganisms play an important role in the biogeochemical cycling of both inorganic and organic nutrients in the soil (Jeffries et al. 2003). AMF are essential components of soil microorganisms and play a significant role in improving and remediating soil (Meier et al. 2011), maintaining soil vitality, and sustainable productivity (Gianinazzi and Hannes 1994).

AMF can alter the microecological environment of the plant rhizosphere soil. Previous studies have shown that mycorrhizal colonization and microbial inoculation can change the morphological structure and ecological function of microbial communities (Khan et al. 2016; Xu et al. 2018). AMF, together with other soil microorganisms, would affect many biochemical cycle processes, such as organic matter decomposition, nutrient cycling, and ecosystem functions, thus improving the micro-ecological environment of plant rhizosphere soil (Marshall, McLaren, and Turkington 2011). Among them, Arfi et al. (2013) demonstrated that AMF plays a key role in detritus food web and nutrient cycling in mangrove ecosystems by promoting the degradation of organic matter, especially abundant lignocellulosic biomass.

On the other hands, in addition to AMF can directly improve soil microbiome, after AMF colonizes plant roots, AM can also secrete a class of thermostable glycoproteins, named glomalin-related soil protein (GRSP) (Rillig 2004), which are mainly produced on the surface of AM hyphae (Wright and Upadhyaya 1998). When hyphae die, they fall off and enter the rhizosphere, which can improve soil structure (Miller and Jastrow 2000) and the soil microenvironment (Rillig et al. 2010). GRSP is an important component of soil organic matter, which plays an important role in soil structure, physiology, and biochemical cycles (Holátko et al. 2021). Research has shown that GRSP can combine with soil particles to stabilize soil aggregates, thereby improving soil microhabitats (Wright and Upadhyaya 1998; Rillig 2004; Wright, Green, and Cavigelli 2007). It is also an important component of the soil carbon sink (Steinberg and Rillig 2003), which is beneficial for the accumulation

and circulation of soil organic carbon (Singh et al. 2017). The results showed that AMF inoculation not only significantly increased GRSP content and the number of water-stable soil aggregates (Jeffries et al. 2003) but also improved soil fertility, soil moisture, and soil spatial structure (Miller and Jastrow 2000). In addition, GRSP adsorbs organic pollutants and reduces heavy metal toxicity (Bedini et al. 2010), thereby mitigating the stress damage to plants in contaminated soils (Vodnik et al. 2008). Studies have shown that terrestrial GRSP can bind with heavy metals through functional group ligands and ion exchange to stabilize or remove heavy metals in coastal wetlands (especially in sandy sediments) (Wang et al. 2020b). Strong complexation and irreversible sequestration of GRSP reduce heavy metal mobility and bioavailability (Wang et al. 2020c). It not only alleviates the stress of heavy metal toxicity in plants but also reduces the health risks for human production and life.

Ecological functions in affecting plant community structure

Based on promoting plant growth, AMF can also play a role in affecting plant interspecific competition and community structure at a higher level (Mariotte et al. 2013; Lin et al. 2015). AMF may have different even opposite (positive versus negative) effects on symbiotic plants so that provide different benefits to different plant species, depending on nutrient environments and symbiotic species (Urcelay and Díaz 2003). AMF may thus affect the competitiveness of plants and have a greater impact on plant community structure as well (Daleo et al. 2008).

At low nutrient levels, nutrient uptake efficiency or resource allocation usually determines the competitive interaction of plants (Grime 1977; Tilman 1982). AMF is closely related to host plants, and they need to provide host plant with mineral nutrients in order to receive fixed carbon from the host plants in return. Because mycorrhizal symbionts can affect nutrient uptake and require carbon input (Smith and Smith 1997), they can potentially affect the competition level and community structure of vegetation species. Daleo et al. (2008) studied the community structure changes of two coastal wetlands dominated by *Spartina densiflora* and *S. alterniflora* under the action of AMF. The results showed that AMF colonization could promote the growth of *S. densiflora* at low nutritional level, while AMF colonization inhibited the growth of *S. densiflora* at high nutritional level. On the other hand, although *S. alterniflora* was not colonized by AMF, when nutrients or fungicides were applied, *S. alterniflora* migrated to higher marshes and even replaced *S. densiflora*. The results are consistent with the findings of Umbanhowar and McCann (2005), which stated that if a dominant species is more dependent on AMF, the removal of AMF may reduce its competitive ability, and then promote the coexistence of species in

the community, or even cause the species to suffer competitive exclusion and be replaced by other species. It also shows that under low nutrient level, AMF may have a positive impact on the competitiveness of the host plants, which is conducive to mycorrhizal plants to become dominant; in contrast, under high nutrient levels, mycorrhizal plants may have greater symbiotic costs than benefits, making them less competitive or even replaced (Olsson and Tyler 2004). The effect of AMF on this competitive outcome depends on both the dependence of plants on mycorrhiza and the level of competition (Daleo et al. 2008). Therefore, AMF can potentially regulate the community structure and succession trend of vegetation species by affecting the interspecific competition ability among species.

Although these evidences suggest that AMF have significant effects on plant interspecific competition, species diversity and community structure, the magnitude and direction of AMF effects and the underlying mechanisms remain unclear. Also little is known about the effects of AMF on plant coexistence, plant community dynamics, and ecosystem processes (Lin et al. 2015).

Discussion and conclusion

In this review, we focused on the adaptation of AMF to environmental factors when building symbiosis with host plants in coastal wetland habitats and the ecological effects of AM in coastal wetland ecosystems. Overall, although there is much less ecological understanding of AMF in coastal wetlands than in terrestrial ecosystems, it is clear that AMF are indispensable in ecosystem structure and functions of coastal wetlands just as them in terrestrial ecosystems. Furthermore, we draw the following conclusions: 1) AMF is widely distributed in coastal wetland ecosystem, mainly including *Glomus*, *Acaulospora*, *Archaespora*, *Gigaspora*, *Appendicispora*, *Pacispora*, among which *Glomus* is the dominant genus; 2) The distribution of AMF in coastal wetlands is mainly affected by flooding, hypoxia, matrix pH, plant species and other factors. The periodic flooding environment caused by tidal fluctuation is the most direct factor limiting the distribution of AMF. 3) The function of AM in coastal wetland habitat is mainly manifested in promoting plant nutrient absorption, improving soil microbial environment, and enhancing plant resistance to flooding and salt stress.

In future research, we suggest some open directions which deserved to be addressed to better understand ecological responses and effects of AMF in coastal wetlands. First, basic information about diversity and distribution of fungal strains should be strengthened since the number of well-studied AMF strains in coastal wetlands is still relatively small. Second, the adaptation mechanism of AMF to flooding, hypoxia and salt stress should be studied in order to mechanically understand their distribution, survival and symbiosis with plants in

coastal wetlands. Third, most of our understanding on the interactions between AMF and their host plant(s) were received from terrestrial ecosystems, especially from forest ecosystems and grassland ecosystems, and little is known in coastal wetland. This information could help to culture fungal species that can efficiently prevent the invasion of alien species and promote the recovery of coastal wetland ecosystem. Moreover, wetland ecosystems have become more vulnerable to global environmental change, including invasion of alien species, sea-level rising, global warming, ocean acidification, environmental pollutions, land use change (i.e., reclamation), etc. Future studies should thus assess whether AMF and their host plants could synchronously cope with those changing environment. Furthermore, interdisciplinary and multi-means comprehensive technologies should be used to facilitate studies on species diversity, structural characteristics, and functional characteristics of AMF in vitro in coastal wetlands, which would be helpful for the conservation and restoration of coastal wetland ecosystems. Meta-analysis should be adopted as well for more solid conclusion in overview for ecological research of AMF in coastal wetlands when relevant case studies have accumulated enough to meet the prerequisite.

Author contributions

Conceptualization, YS and MD; writing – original draft preparation, XW; writing – review and editing, XW, YW, YS and MD; funding acquisition, YS and MD; All authors have read and agreed to the published version of the manuscript.

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