Review

Role of Endophytes and Rhizosphere Microbes in Promoting the Invasion of Exotic Plants in Arid and Semi-Arid Areas: A Review

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Abstract: Endophytes and rhizospheric microorganisms support invasive species' adaptation to environmental stresses. Here, we review the impacts of endophytes, rhizospheric microbes (particularly symbiotic nitrogen-fixers), mycorrhiza and pathogens on plant invasion in arid and semi-arid areas. Endophytes and soil microorganisms either enhance nutrient acquisition for enhancing the invasive plant immune system and/or negatively affect native plants. In addition, the positive feedback between mycorrhizal fungi and invasive plants enhances the competitive ability of the aliens, providing them more opportunities for success, establishment, and dominance. The microbes and their secondary metabolites promote invasive plant species by changing soil microbial community structure and carbon biomass as well as enzyme activity, which improves soil properties and processes. The negative impact of invasive exotic plants on the associated biota and the role of allelochemicals are also discussed. It could be concluded that endophytes interact with rhizosphere microbes to promote invasive plant species in arid and semi-arid areas in a way similar to what happens in other ecosystems; the differences are in the pathways and reactions, which depend upon the prevailing abiotic factors. More interdisciplinary field experiments integrating microbial, biotechnological, and molecular approaches are needed to understand the role of symbiotic microbes in invasion biology.

Keywords: allelochemicals; arid lands; endophytes; ecological impacts; invasive plants; mycorrhiza; rhizosphere; *Rhizobium*; soil microorganisms

1. Introduction

High temperature and low rainfall are among the environmental stresses in arid lands, which occupy about one-third of the Earth's surface [1]. High temperatures coupled with low rainfall increase the water evaporation rate, which usually leads to soil salinization in arid lands [2]. Consequently, the high levels of toxic ions (Na^+ and Cl^-) hinder nutrient absorption and affect ion homeostasis, which upsets cell growth and associated metabolic activities, affecting pigment synthesis and reducing photosynthesis [3,4]. Additionally, rapidly growing international trade has significantly enhanced the introduction of many exotic plants into different parts of the world [5]. Although the introduction of some alien plants was accidental, it was intentional for many others for wildlife habitat improvement, greening landscapes, wood or fiber production, soil conservation, livestock forage production, or other crop uses [6–9]. Many of the exotic plants have become invaders in the new areas. For example, in the arid environment of the UAE, the invasive *Prosopis juliflora* has

been introduced for the afforestation and greening of the desert lands, but has escaped the forests and threatened the plant community of different ecosystems [10,11]. It is believed that the invasion of exotic plants is a major component of global change [12]. In addition, exotic plants are considered a major threat to the integrity and function of ecosystems and human health [13–17]. For example, invasive plants have potentially changed the ecosystems' geomorphology, hydrological cycles and biogeochemical properties [18–20].

Several invasive exotic plants have caused serious impacts on the associated biota in different parts of the world [21,22]. Invasive plants can change the composition and the diversity of the aboveground plant community structure [23,24] and the belowground soil microbial community of the invaded ranges [25]. Despite most of their harmful effects, some exotic plants have benefited the environment and the associated biota in the introduced range [26]. For example, the growth of invasive nitrogen-fixing leguminous plants can improve soil physical and chemical properties, which might positively affect the associated species. Moreover, the canopies of *Prosopis juliflora* improved soil physical and chemical properties by increasing the important macro-nutrients, such as K, N and P, as well as the organic matter contents [7]. Similar benefits were reported for *Acacia mangium* on the environment and associated flora [26]. As negative and beneficial impacts of exotic plants on native communities do not act in isolation of each other in nature, the relative importance of each impact type determines the community structure of a certain environment [27].

In addition to their major role in ecosystem functions [28], soil and rhizospheric microorganisms play important roles in plant adaptation to environmental stresses. Among the important soil microbes that help plants' adaptation to environmental stresses are plant growth-promoting (PGP) microbes, nitrogen-fixing microorganisms, and mycorrhizal fungi [29]. PGP microbes regulate the levels of important stresses-tolerance hormones, e.g., abscisic acid and ethylene, and growth promotion hormones, e.g., auxin, gibberellin (GA), cytokinins (CKs), brassinosteroids (BRs), and strigolactones (SLs) [30,31]. Generally, soil microbial communities have an important role in the success of invasive exotic plant species in their new range [32]. Moreover, soil biota can facilitate or limit the invasion of exotic plants in the new ranges [33]. It was suggested that encountering fewer soil-borne enemies could facilitate the invasion, but encountering fewer beneficial microbes limits the invasive ability of exotic plants [11]. In addition, other invasive plants might encounter novel but strong soil mutualisms, which enhance their invasive success [33,34].

Endophytes, which are special groups of bacteria and fungi surviving within tissues of a host plant, can form different kinds of relationships with the host. These relationships range from latent pathogens or saprotrophs to mutualistic associations [35]. Endophytes interact and cooperate with other microbes colonizing plant tissues, e.g., mycorrhizal fungi, pathogens, and saprotrophs, to produce useful secondary metabolites that affect plant growth and plant responses to other biotic (e.g., pathogens) and abiotic stresses [36]. Several invasive plants adopt pathogenic endophytes to protect them from several kinds of diseases [37]. Importantly, a pathogenic endophyte does not cause a disease or damage its host plant, but can do so for other native flora [38]. It has been reported that plants hosting pathogenic endophytes could more effectively protected from some of the dangerous pathogens than plants free from such endophytes [39]. For example, pathogenic endophytes hosted by *Dioscorea zingiberensis* did not cause any damage to this plant, but their secondary metabolites protected it against other pathogens [38].

The role of microbes in the invasion process and the mitigation of stresses in invasive plants is well explored in many climatic zones around the world [40–48]. However, few studies have assessed the role of soil microbes and endophytes in the invasion process in arid lands [37,49,50]. Therefore, this review aimed to explore and discuss the role of endophytes, rhizospheric symbiotic nitrogen-fixing organisms, mycorrhiza and pathogens, and their interactions with invasive plants, in arid and semi-arid areas.

2. Role of Microorganisms and Endophytes at All Life Cycle Stages of Invasive Plant

At all life cycle stages of the invasive plants in an arid ecosystem, endophytes and rhizospheric microorganisms together with root exudates and allelochemicals act in favor of invasion. The possible interactions of endophytes and rhizospheric microorganisms in facilitating the invasion of exotic plants in arid and semi-arid areas are shown in Figure 1. At the seedling stage, endophytes and allelochemicals improve seed germination and promote seedling growth. During earlier stages, the roots initiate symbiotic relationships with native mycorrhiza, nitrogen-fixing organisms, and other PGP microbes during plant growth. Meanwhile, the allelochemicals produced by invasive plants promote their growth but suppress some pathogens and native plants. At maturity, the different types of beneficial microorganisms, such as mycorrhiza, nitrogen-fixing organisms, and PGP microbes, form a network in the rhizosphere area, protecting against pathogens and diseases and suppressing native flora; they alter the belowground biodiversity of the ecosystem and consequently improve their competitiveness and antagonistic synergic effects over the native plants. All these mechanisms are affected by the prevailing abiotic factors in arid and semi-arid environments.

Figure 1. The possible interactions of endophytes and rhizospheric microorganisms in facilitating the invasion of exotic plants in arid and semi-arid areas. (a) Seedling stage, (b) vegetative and growth stage, (c) mature plant (for details see the text).

3. Endophytes: Are They Tools That Promote Plants' Invasion?

In arid and semi-arid environments, invasive and native plants harbor in their leaves, stems and roots large numbers and diverse communities of endophytic microorganisms [36,51–55]. Endophytes establish various types of symbiotic and mutualistic interactions with their host plant. They have an important ecological role in challenging arid environments [56]. Notably, some endophytes can facilitate plant invasion success [57,58]. Several reports presented the diversity of endophytes in various plant groups in arid lands. For example, Kulkarni and Nautiyal (1999) [59] isolated 44 fungal endophytes with significant antibacterial activity from the leaves of invasive *Prosopis juliflora*. Moreover, González-Menéndez et al., (2018) [55] isolated 349 fungal endophytes from leaves and stems of 63 invasive plant species; some of these isolates have high antifungal activities. In addition, Ratnaweera et al., (2015) [60] extracted equisetin, a compound with high

antimicrobial activities, from endophytic *Fusarium* sp. isolated from the arid zone invasive *Opuntia dillenii*. Invasive plants hosting antimicrobial endophytes are rarely harmed by these endophytes [36]. Interestingly, antimicrobial endophytes in an invasive host plant rarely cause a disease or harm the host, but can cause disease or damage for the associated native flora [38]. The possible roles of endophytes that favor the invasive plant species over native plant species in arid and semi-arid areas include: (i) ability to change microbial communities; (ii) influence microbial biomass carbon and enzymatic activity; (iii) change soil properties and processes and (iv) alter the aboveground vegetation (Table 1).

Table 1. Roles of endophytes in promoting invasive plant species in favor of native species in arid and semi-arid areas.

Roles of Endophytes	Invasive Plant	Reference
(i) Change microbial communities		
(a) Invasive species harbor more diversified bacterial communities compared to the bulk soil	<i>Prosopis juliflora</i> <i>Parthenium hysterophorus</i> <i>Acacia longifolia</i> <i>Prosopis juliflora</i>	[61,62]
(b) Alter the diversity and structure of native soil microbes in the rhizosphere	<i>Kalanchoe daigremontiana</i> <i>Pennisetum setaceum</i> <i>Schinus terebinthifolius</i>	[47,63–67]
(c) Increase the population of diazotrophs and total heterotrophs	<i>Prosopis juliflora</i>	[68]
(d) Modify and disturb the composition and structure of the mycorrhizal community in the rhizosphere	<i>Acacia dealbata</i> <i>Bromus tectorum</i>	[69–71]
(e) Encourage mycorrhizal association with invasive plant	<i>Prosopis juliflora</i>	[65]
(ii) Influence microbial biomass carbon and enzymatic activity		
(a) Increase the microbial biomass of carbon	<i>P. juliflora</i>	[65]
(b) Improve metabolic activity in the rhizosphere of invasive plant	<i>P. juliflora</i> <i>Pennisetum setaceum</i>	[64]
(c) Influence and modify the enzyme activity	<i>Prosopis juliflora</i> <i>Acacia dealbata</i>	[47,64,65,69]
(d) Increase urease and glucosaminidase activities	<i>Kalanchoe daigremontiana</i>	[66]
(iii) Change soil properties and processes		
(a) Change soil processes	<i>Acacia longifolia</i> <i>Kalanchoe daigremontiana</i>	[72]
(b) Influence the properties and processes of soils, increase nutrient availability	<i>Prosopis juliflora</i> <i>Acacia dealbata</i> <i>Prosopis juliflora</i> <i>Acacia dealbata</i>	[64–66,69]
(c) Increase soil N, C and organic matter under invasive species	<i>Atriplex</i> sp. <i>Tamarix</i> sp.	[64,65,69]
(d) Increase the salinity level in their rhizosphere of invasive species		[1]
(iv) Effect on above ground vegetation		
(a) Improve alien plant growth	<i>Prosopis chilensis</i> <i>Acacia longifolia</i>	[54]
(b) Alter the aboveground vegetation	<i>Prosopis juliflora</i> <i>Kalanchoe daigremontiana</i> <i>Acacia dealbata</i> <i>Bromus tectorum</i>	[62–66]
(c) Prohibit the establishment and growth of native species		[69–71]

Invasive plants in arid and semi-arid regions are most likely to harbor more tolerant and effective strains than native plants. They have different mechanisms for the mitigation of biotic and abiotic stresses in many introduced or invaded areas. It seems that, in their strategy to tolerate biotic and abiotic stresses, invasive plants harbor a large number of endophytic strains that produce diverse compounds. For example, Srivastava and Anandrao (2015) [73] isolated a total of 446 fungal strains from the leaves of the invasive *Prosopis juliflora*. All these strains have different ways to assist the tree in withstanding and tolerating harsh environments, such as drought, salinity, diseases, and heavy metal toxicity. Endophytes in a specific plant or its rhizosphere, irrespective of their type, seem

to coordinate their activities and functions in the host plant as an adaptive response to overcome biotic and abiotic stresses [74]. It is worth mentioning that all these strategies vary depending upon other abiotic factors, such as precipitation [75], drought and salinity [76], in addition to the effect of the soil microbial communities and extracellular enzymes in many terrestrial ecosystem processes.

Endophytes produce a wide range of secondary metabolites, which play direct or indirect roles in encouraging plant invasion. Among the roles of the secondary metabolites in invasive plants are: (i) regulation of antioxidant enzymes, such as ascorbic peroxidase, catalase, glutathione, superoxide dismutase, peroxidase, and polyphenol oxidase [77]; (ii) production of Jasmonic acid to defend the plant from biotic stress and damage [78]; (iii) production of salicylic acid, which causes systemic acquired resistance to mitigate pathogens, heat, salinity and drought stresses [79]; (iv) production of gibberellins to enhance plant growth and increase plant tolerance to stress [77]; (v) production of abscisic acid, which improves plant growth, promotes stomatal closure and mitigates stress damage [80] and (vi) improving plant resistance to pathogens [81,82].

However, the effects of secondary metabolites of endophytes varied greatly between invasive and native plants, and the endophytes of invasive species may be host-specific to facilitate plant invasion [83]. In general, invasive plants could benefit from association with endophytes to improve their competitiveness and sustain their invasiveness in two ways: (i) abundance of endophytes, such as mycorrhiza and PGP microbes, may improve plant growth, and the establishment and consequently the invasion of new areas [84,85], and (ii) they use endophytes as novel weapons to produce novel allelopathic compounds to inhibit the native species [60,86,87], and hence dominate in the new plant community. More explanations and examples are presented in Figure 2.

Figure 2. Examples of possible roles of endophytes that benefit the invader plant species, and harm native plant species in arid and semi-arid regions. References are: [88] Alcántara-Martínez et al., 2018; [89] Abdelmoteleb et al., 2017; [90] Mangla et al., 2008; and [91] Vilcinskis 2015.

Dark septate endophytes, for example, are recognized as good and promising candidate fungi in enhancing drought [92,93] and salinity tolerances [94], and increase plant biomass and nutrient concentration in invasive plants in arid environments [51,95]. Moreover, Knapp et al., (2012) [37] demonstrated that invasive grassland species could form associations with their roots' endophytic fungi in the invaded areas. They concluded that plants of semi-arid areas share common dominant members of the dark septate endophytes fungal present in their community [37]. Furthermore, the dark septate endophytes' colonization percentage and spore abundance depended on soil properties, type of host, and climatic factors [92,96]. As an example of a climatic factor in most arid lands, the high temperature significantly improved the mutual relationship between dark septate endophytes and the invasive *Cenchrus ciliaris* [92]. Interestingly, some dark septate endophytes were

reported to have melanized hyphae [97], which enable both partners to tolerate high heat and drought stresses [95].

4. Mycorrhiza: Multipurpose Roles for Invasive Plants

Mycorrhizas (endomycorrhiza and ectomycorrhiza) are known worldwide to establish symbiotic associations with vascular plants [3,28,85,98], where both partners exchange nutrients [99,100]. Among all the microbial–plant associations, mycorrhizal fungi are the preferable association for terrestrial plants [44]. It has been estimated that about 80% of vascular plant species are associated with mycorrhizal fungi [51,70,98]. For invasive plants, association with mycorrhiza is an adaptive strategy, particularly in arid and semi-arid ecosystems, where both partners benefit and increase their tolerance to biotic and abiotic environmental stresses [28]. Positive feedback between mycorrhizal fungal and invasive plants can contribute to a better chance for competition and more opportunities for success, establishment, and dominance of invasive plants [50,85].

In low-resource arid environments, invasive plants tend to form associations with rhizobia and mycorrhizal fungi to obtain enough N and P to survive, improve establishment, and tolerate adverse conditions [101,102]. Mycorrhizal symbioses, through extensive hyphal networks in soil, protect invasive plant communities against environmental stresses, pathogens, nutrient deficiency, salinity stress, drought, and soil disturbance [93,98,100,103,104]. Generally, the numerous advantages of mycorrhizal–plant symbiosis could be sub-grouped at the levels of (a) individual mycorrhizal–plant, (b) community, and (c) the ecosystem (Figure 3).

Ecological level	Benefits of mycorrhiza at different ecological levels	Reference(s)
(A) Individual level	- improves nutrient availability for the host, - increases dry biomass - improves tolerance of the host to environmental stress, and - protects the host against pathogens	[85, 105, 106]
(B) Community level	- improves the host competition - modify the density and abundance of fungal community and - influences plant community structure	[50, 98, 107]
(C) Ecosystem level	- promotes soil structure and aggregate stability, - improves soil biological properties and influence nutrient cycling by contributing to terrestrial carbon accumulation	[108]

Figure 3. Benefits of mycorrhizal symbiosis in invasive plants at individual, community and ecosystem levels in arid and semi-arid environments. References are: [85] Aslani et al., 2019; [105] Makarov 2019; [106] Lumini et al., 2020; [50] de Souza et al., 2019; [98] Jung et al., 2012; [107] Zhao et al., 2019; [108] Mahmoudi et al., 2020.

In arid and semi-arid areas, different invasive plant species can develop mycorrhizal association as a means of invasion. According to Yanfang et al., (2012) [109] and Dhar et al., (2015) [110], mycorrhizal symbiosis could be adopted to enhance the invasion of some invasive plants, such as *Asteraceae*, in arid regions. Moreover, different shrub species in semi-arid environments harbor numerous and diverse types of mycorrhiza in their rhizosphere [111]. In general, different hypotheses have been proposed

to explain mycorrhizal roles and mechanisms in supporting plant invasiveness: (a) Enhanced Mutualisms Hypothesis—favors the invader plant, [112]; (b) Degraded Mutualisms Hypothesis—negatively affects native plant [113]; and (c) Resistance Hypothesis—repels the invader plant [114].

According to Pringle et al., (2009) [115], many invasive plants can be associated with various types of endomycorrhizal or ectomycorrhizal species of fungi. Many reports [50,71,116] analyzed and/or compared the effect of arbuscular mycorrhizal fungi communities and soil characteristics of invasive and native plants in arid and semi-arid areas. For example, de Souza et al., (2019) [50] found that invasive plants such as *P. juliflora* modify the density and abundance of the fungal community and consequently enhance its root colonization, increase dry biomass and plant phosphorous, and consequently support the growth and invasiveness over the native *Mimosa tenuiflora*. Moreover, mycorrhiza positively boosted the growth of invasive plants in drylands, increased plant dry weight, and improved mycorrhizal colonization [85,117]. Furthermore, under salt stress, inoculation of *Acacia saligna* with mycorrhiza in the presence of *Rhizobium* significantly improved plant nutrition, enhanced nodulation, and consequently improved plant growth and tolerance to salinity [118].

The efficiency of mycorrhizal association with invasive plants seems to depend upon the geographical region [115], environmental condition [84,101], nutrient availability [101], host specificity, genetics of the species [84,92] and resource availability [119]. Moreover, the colonization levels and spore abundance of mycorrhiza were correlated with edaphic, host specificity and climatic conditions [96]. In addition, Silva et al. (2014) [120] concluded that in Brazilian semi-arid regions, the mycorrhizal diversity is affected by vegetation, season, and soil type. As shown in Table 2, studies of mycorrhizal-invasive species in arid and semi-arid regions showed positive feedback favoring alien species over native plants.

Table 2. Major studies depicting the role of mycorrhiza in plant invasion in arid and semi-arid areas.

Invasive Species	Growth Form	Invaded Habitat/Region	Main Findings	Reference(s)
<i>Cenchrus ciliaris</i>	Grasses	Sandy loam and alkaline soil, Pakistan	Mycorrhizal inoculation improved hyphal colonization rate up to 90%	[92]
<i>Cenchrus ciliaris</i>	Grasses	pasture in semi-arid regions, Brazil	31 mycorrhizal species were detected mainly from <i>Acaulospora</i> and <i>Glomus</i>	[121]
<i>Acacia farnesiana</i>	Trees	Alkaline soils, India	Spores of <i>Acaulospora foveata</i> , <i>Gigaspora albida</i> and <i>Glomus fasciculatum</i> , <i>G. geosporum</i> and <i>Sclerocystis sinuosa</i> were isolated	[96]
<i>Acacia saligna</i>	Trees	Different areas, Ethiopia	Highest species diversity of 19 species from 7 genera compared to 8 <i>Acacia</i> spp.	[122]
<i>Acacia saligna</i>	Tree seedlings	Giza, Cairo, Egypt	Mycorrhiza significantly increased plant height, stem diameter, leaf area, fresh and dry weights of stems and roots, chlorophyll content	[123]
<i>Acacia cyclops</i>	Tree seedlings	South Africa	Both Mycorrhiza and <i>Rhizobium</i> inoculation increased host biomass and relative growth rates. Dual inoculation significantly enhanced N and P acquisition and utilization rates	[124]
<i>Prosopis juliflora</i>	Tree seedlings	Semi-arid zones, Mexico	<i>Prosopis juliflora</i> inoculated with <i>Glomus aggregatum</i> showed 41.7% intensity of infection.	[125]
<i>Prosopis juliflora</i>	Trees	Arid zones, Saudi Arabia	<i>Prosopis juliflora</i> showed highest root colonization, spores, soil microbial biomass and number of nodules compared to the other 11 noninvasive plants	[126]
<i>Prosopis juliflora</i>	Trees	Arid zones, Saudi Arabia	<i>Prosopis juliflora</i> encouraged mycorrhiza, improved the microbial biomass carbon content and enzymes' activities in soils and inhibited the growth of other species under their canopy	[65]

However, in their review articles, in other ecosystems, Pringle et al., 2009 [115] and Shah et al., 2009 [127] reported some cases in which there was no clear benefit for the invasive plant from the mycorrhizal association. It is clear from the data in Table 2 that the role of mycorrhiza in plant invasiveness in arid and semi-arid regions was undertaken in single species or seedlings in pots and greenhouse experiments, rather than field studies or whole-system approach research. Similar observations were reported for grasslands, forests, and wetlands [127]. We suggest that more research should be directed towards direct field experiments and studies to stimulate real and natural environments.

5. Symbiotic Nitrogen Fixation: An Opportunity for Invasive Legumes

Rhizobia are a group of bacteria, well-known to promote plant growth and form endosymbiotic associations with most plant species in the Leguminosae, and to fix nitrogen through the transformation of atmospheric N_2 gas via nitrogenase enzyme [128] into bioavailable N [129–131]. Typically, the invasive plants secure nitrogen, one of the limiting nutrients in arid lands, from symbiotic nitrogen fixation [132,133]. Besides this, some nitrogen-fixing bacteria produce auxins, cytokinins, and gibberellins to enhance plant growth [134] and anti-microbial molecules to protect plants from diseases [135]. Despite the harsh conditions in the arid and semi-arid environments, which reduce the number and soil microbial diversity [136], different strains of rhizobia were reported to withstand severe and extreme conditions, such as salinity and osmotic stresses [130,137–140], temperature [141], drought and soil moisture deficiency [142], soil alkalinity and high pH [129]. The wide distribution of rhizobia is well documented in arid and semi-arid soils, [143,144] deserts [145], and sand dunes [146]. For instance, Chen et al. (1995) [147] isolated 20 different strains of root nodule bacteria, mainly *Rhizobium* and *Bradyrhizobium* species, from the arid saline deserts of China. Moreover, rhizobia could also be found in surface soils [148], and sometimes at a depth of up to 34 m [149]. The presence of nodules in the roots of invasive woody trees in the arid areas of countries, such as Australia [150,151], Morocco [132], China [147], Saudia Arabia [144,152] and UAE [153], indicates the natural presence of ineffective and effective indigenous rhizobia that nodulate invasive trees in arid environments (Table 3). Besides this, it was also proposed that invasive alien tree species may bring their own symbionts rather than entering into new associations with indigenous rhizobia [33].

Table 3. Studies depicted the role of rhizobia in plant invasion in arid and semi-arid regions.

Invasive Host Plant	Total Number of Genera or Strains Isolated	Rhizobial spp. Identified	Reference(s)
<i>Prosopis farcta</i>	50	<i>Ensifer</i> ; <i>Mesorhizobium</i>	[154]
<i>Prosopis juliflora</i>	274	<i>Achromobacter</i> ; <i>Ensifer</i> ; <i>Rhizobium</i> ; <i>Sinorhizobium</i>	[132]
<i>Prosopis juliflora</i>	150	<i>Rhizobium</i> spp. <i>Rhizobium leguminosarum</i>	[129]
<i>Acacia saligna</i>	133	<i>Rhizobium tropici</i> <i>Bradyrhizobium japonicum</i> <i>Bradyrhizobium</i> spp.	[150]
<i>Acacia saligna</i>	1	<i>Bradyrhizobium viridifuturi</i>	[155]
<i>Acacia saligna</i>	1	<i>Rhizobium</i>	[150]
<i>Acacia saligna</i>	5	<i>Rhizobium</i> ; <i>Sinorhizobium</i>	[156]
<i>Acacia saligna</i>	7	<i>Mesorhizobium</i> ; <i>Rhizobium</i> <i>Bradyrhizobium</i> ; <i>Ensifer</i>	[157]
<i>Acacia farnesiana</i>	1	<i>Sinorhizobium</i>	[158]
<i>Acacia Saligna</i>	28	<i>Rhizobium</i> ; <i>Phyllobacterium</i> <i>Bradyrhizobium</i> ; <i>Azorhizobium</i>	[159]
<i>Acacia longifolia</i> ; <i>Acaciacyclops</i> <i>Acaciamelanoxylon</i> <i>Acaciasaligna</i>	7	<i>Burkholderia</i> ; <i>Ensifer</i> <i>Methylobacterium</i> <i>Phyllobacterium</i>	[151]

Some invasive trees can cooperate with a wide range of nitrogen-fixing organisms for a successful and effective symbiotic relationship. For instance, the invasive *P. juliflora*

could be nodulated by bacteria of different strains, including α and β proteobacteria. According to Benata et al. (2008) [132], *P. juliflora* alone could establish nodulation with more than 274 different rhizobial strains in arid areas of Morocco, and most of these strains tolerate high concentrations of NaCl up to 500 mM. Interestingly, these strains include *Sinorhizobium* spp., *Rhizobium tropici*, *Rhizobium multihospitium*, and *Rhizobium giardinii*. Comparing rhizobial isolates from *Acacia saligna*, *Acacia seyal*, *Dalbergia sisso*, *Macarimum tipu*, *Leucaena leucocephala*, and *Sesbania sesban*, the isolate from invasive *Acacia saligna* showed the best performance in most of the following parameters: minimum inhibitory Na-azide concentration of 15 $\mu\text{g/ml}$, resistance to four different antibiotics, growth in high temperatures up to 40 °C, and tolerance of salt (NaCl) concentration up to 4%, compared to other non-invasive species [160].

The process of biological nitrogen fixation in invasive species was reported to be a significant factor in their invasion process [145,161], which assists in their growth and development and offers a competitive advantage over non- or slow-responsive nitrogen-fixing plants [162,163]. Moreover, Stock et al., (1995) [161] reported that the nodulation and nitrogen fixation of invasive *Acacia* species (*A. cyclops* and *A. saligna*) was a significant factor in their establishment, persistence, and successful competition with local flora. Furthermore, in arid and semi-arid lands, *Acacia farnesiana* (previously *A. smallii*) was identified as a serious invader [164] and was also reported to be a potentially high N_2 -fixer [158]. It has been reported that symbiotic rhizobia isolated from invasive plants introduced into hot tropical areas tolerate a wide range of stresses. For example, Otieno et al., (2017) [129] isolated 150 *Rhizobium* strains from the roots of *P. juliflora*, which showed wide diversity in their tolerance to NaCl (1–5%) and pH (4–10 units), and intrinsic antibiotic resistance. This wide diversity gives such invasive species some ecological and competitive advantages [165] due to the increase in the nitrogen content in plant tissues and the general improvement of soil health [166]. Such a large range of associations made by invasive species with microsymbionts may have a negative impact on the interaction networks of the indigenous species, whereby invasive species dominate in these areas. Interestingly, invasive plants tend to form an indeterminate type of nodules [129], giving them the ability to tolerate harsh stress conditions more than species with globose determinate types of nodules [167]. Comparing the invasive *A. saligna* with the other four *Acacia* spp. [157] determined that the invasive species were nodulated by a higher diversity of taxonomical groups, *Mesorhizobium mediterraneum*, *Rhizobium tropici*, *Rhizobium* sp., *Bradyrhizobium* sp., and *Sinorhizobium meliloti*. In general, invasive nitrogen-fixing plants influence soil nutrient dynamics; they increase soil organic matter, soil nitrogen mineralization, and nitrification rates, and consequently affect soil nutrient availability in their rhizosphere [168,169].

In the arid areas of Saudi Arabia, the invasive *P. juliflora* showed higher values for soil microbial biomass carbon (85.3 $\mu\text{g g}^{-1}$ soil), total number of spores (170 spores 100 g^{-1} soil), root colonization (65%), and the number of nodules (12 seedling $^{-1}$) in response to rhizobia and mycorrhiza compared to the other 11 noninvasive plants [170]. Moreover, it was reported that dual inoculation of *Acacia longifolia*, an invasive species in the Mediterranean region, significantly improved the growth of the plants [171]. The synergistic benefits of the dual inoculation of invasive legumes with both mycorrhiza fungi and rhizobia improved growth and increased the chances for invasion of alien leguminous species [124]. Furthermore, Ndoye et al., (2015) [172] suggested that co-inoculation with suitable strains of mycorrhiza and nitrogen-fixing bacteria is needed to ensure good plant growth and better P use efficiency so as to enhance atmospheric nitrogen fixation under limited phosphorus supply conditions.

6. Pathogens: Invasive Species Protection and Strong Weapon to Suppress Native Species

Soil pathogens often suppress the growth, productivity, and survival of plants, reduce the relative abundance of species in communities, mediate competitive interactions and affect succession [173,174]. In arid lands, the vast success of invasive species such as *Acacia dealbata* [175,176], *Prosopis juliflora* [7,62], *Ailanthus altissima* [177] and *Typha angustifo-*

lia [178] in the introduced ranges has been attributed to their ability to release allelopathic compounds that affect native plant species, and soil microbiota, which contribute to the process of invasion [176].

Invasive plants can escape from the inhibitory effects of soil pathogens by different strategies [87,174]; hence, invasive plants will have a better competitive chance through relief from the negative feedback carried out by the native species. Invasive species can harbor endophytes that improve immunity; for instance, in an arid land, the association between invasive *Acacia farnesiana* and *Methylobacterium* sp. improves the antioxidant defense and energy balance [88]. Another defense mechanism in invasive trees and shrubs of *Acacia* is the secretion of gum after natural or artificial injuries in the stem and branches [179]. Shehu et al., (2018) [180] found that Arabic gum significantly inhibited the growth of *E. coli* and *Pseudomonas aeruginosa*, and they suggested that it could serve as an antibacterial agent. Moreover, naturally synthesized nanoparticles of silver and copper in gum possessed antimicrobial activity against *E. coli*, *S. aureus*, and *Micrococcus luteus* strains, and have several potential therapeutic and pharmaceutical applications [181].

Prosopis juliflora is the most studied invasive species in the arid zone, with a very strong inhibitory effect on a wide range of microbes that cause diseases to plants, humans, and animals. For instance, extracts of leaves and flowers of *P. juliflora* were inhibitory for the following genera: *Botrytis*, and *Candida* [182], *Escherichia*, *Shigella*, *Salmonella*, *Proteus*, *Pseudomonas*, *Klebsiella*, *Enterococcus*, *Listeria*, and *Bacillus* [183], and *Escherichia*, *Staphylococcus*, and *Candida* [184]. In addition, Mazinani et al. (2017) [185] were able to isolate 32 strains from *Prosopis juliflora*, some of which were able to grow well at 25–50 °C, pH = 6–9, and could tolerate up to 10% NaCl. In addition, some of these strains showed very strong antimicrobial activities and inhibited the growth of *Aspergillus*, *Saccharomyces*, *Candida*, *Escherichia*, *Staphylococcus*, *Pseudomonas*, *Bacillus*, *Salmonella* and *Streptococcus* [185]. Moreover, eight endophytic fungi were isolated from the invasive *Opuntia dillenii*; seven showed antibacterial activities against at least one of *Bacillus*, *Escherichia*, *Pseudomonas* or *Staphylococcus*; the most active endophytes were identified as *Fusarium* and *Aspergillus* [54]. Furthermore, Mdee et al., (2009) [186] found that acetone extracts of invasive species *Solanum mauritianum* and *Lantana camara* significantly inhibited the growth of different phytopathogenic fungi—*Penicillium*, *Aspergillus*, *Colletotrichum*, *Fusarium*, *Trichoderma*, *Phytophthora*, *Pythium* and *Rhizoctonia*.

7. Allelochemicals: Promotion of Invasive Plants and Native Attack

In arid regions, several invasive tree species, such as *Acacia saligna*, *Acacia dealbata*, *Leucanea leucocephala*, *Prosopis juliflora* and *Salvia verbenaca*, produce allelopathic compounds that interfere with local flora [117,176]. It is well documented that the allelochemicals naturally produced by invasive plants such as *P. juliflora* [7,10,65,187,188], *Acacia saligna* [189], *Tamarix aphylla* [190] and *Acacia dealbata* [176] significantly inhibited the seed germination and/or growth of native plants. Moreover, in arid and semi-arid environments, allelochemicals of *Acacia dealbata* significantly modified soil bacterial activities and reduced the richness and diversity of the bacteria [176]. In addition, *P. juliflora* leaf extract revealed a significant antimicrobial activity [183,184].

The negative impacts of the toxicity of allelopathic compounds produced by invasive plants differ in effects on germination inhibition, seedling establishment, root elongation and cell division, length of shoots and roots, root volume, limitation of nutrients and/or water supply to shoots, and shoot growth, and they also change the morphology of the host plant, change the root structure, and may induce abnormal growth [10,126,184,188,191]. The damaging effect of allelochemicals of invasive plants is not confined to native plants, but it also negatively affects the native microbial community and other microbes, including beneficial microorganisms associated with native plants. For example, allelochemical compounds were reported to significantly reduce the performance of the mutualistic mycorrhizal fungi associated with native plants, hence reducing their growth [192]. As expected, invasive plants produce more allelopathic compounds than native species [33,193], and the

inhibitory effect of these chemicals vary depending on the part of the invasive plant, i.e., root, stem, leaf flower, or fruit [188,191].

Allelopathy is considered one of the key strategies for successful plant invasiveness [10,65,194]. The symbiotic relationship between invasive plants and mycorrhizae, rhizobia and fungal endophytes can stimulate or inhibit the interaction with consumers, pathogens, and competitors [126,195]. Several studies have reported that allelopathic compounds produced by invasive plants disrupt the mutualistic relationship between soil rhizobia and several leguminous species by reducing rhizobial population growth [196,197]. In general, allelochemicals significantly reduce the number and weight of developed nodules. However, Alford et al., (2009) [198] reported that the nodulation of some plants, such as *Astragalus bisulcatus*, *Psoralea tenuiflorum*, *Medicago sativa*, and *Sphaerophysa salsula*, were not affected by allelochemicals produced by the invasive *Acroptilon repens*. Moreover, they noticed that the rhizobia present in nodules are more protected from allelochemicals than those living free in the soils. Furthermore, in invasive plants, symbiosis improves the plant antioxidant system and provides the energy required for the host under stress conditions [111], and consequently affects allelochemical production in favor of the invasive plant [199]. Furthermore, Ma et al., (2009) [194] isolated two allelochemicals, namely, 3-3'-5-Trihydroxy-4'-7-dimethoxy flavone and 3-3'-5-Trihydroxy-4'-7-dimethoxy flavone-3-O-sulfate, from *Ipomoea cairica*, the most invasive alien species in China. The individual or joint application of these two allelochemicals inhibited the seed germination of four native plants. Moreover, the soil in the rhizosphere of *P. juliflora* was reported to contain higher levels of total phenolics and L-tryptophan than soils away from the rhizosphere [188]. In response to the allelopathic compounds produced by invasive species, native plants could be very sensitive, moderately sensitive, or tolerant [200]. When native plants fail to tolerate the new chemicals, the invasive plant species will quickly dominate in the invaded area [201].

Comparing the effects of extracts from invasive plant *P. juliflora* with non-invasive *P. cineraria*, Saadoun et al., (2014) [62] observed that extracts of *P. juliflora* significantly inhibited the growth of *Bacillus*, *Escherichia*, *Pseudomonas*, and *Staphylococcus*, as well as the seed germination of two desert plants, *Halocnemum strobilaceum* and *Halopogon perfoliatus*. Moreover, extracts of *Ailanthus altissima* have been proven to be used as an environmentally friendly and promising method to control harmful algal blooms caused by *Microcystis aeruginosa* [202]. In addition, Filippou et al., (2014) [76] isolated Ailanthone, a major plant inhibitor, from the invasive *Ailanthus altissima*, which significantly inhibited plant growth of *Brassica juncea*, *Eragrostis tef*, and *Lemna minor*.

8. Microbial Changes under Invasive Species: Self-Defense and Native Distraction

In arid lands, invasive plants can alter the structure of different native ecosystems and threaten native aboveground and underground biodiversity [69,203,204]. For example, invasion by the Australian *Acacia longifolia* [63], *Prosopis juliflora* [64,65], and *Kalanchoe daigremontiana* [66] significantly altered the characteristics of vegetation, as well as the diversity and structure of microbes, in their rhizosphere. Moreover, invasive plants can potentially modify the native soil environment and consequently influence the composition and density of the native microbes, which in turn influences the invasiveness of species in the invaded area [50,127,205,206]. Further, invasion of *Pennisetum setaceum* in semi-arid areas significantly modified the structure and composition of the native soil microbial community and the enzyme activity related to nitrogen cycling, which may potentially alter the function of the invaded ecosystem [47].

In their interactions with indigenous soil communities, invasive plant species can profoundly negatively affect native species [65,207]. To explore these interactions, Inderjit and Putten (2010) [208] proposed three pathways: plant–soil feedback interactions, manipulation of native soil biota by enhancing pathogens, and production of complex allelochemicals toxic to native plants and which cannot be degraded by local soil microbes. In their meta-analysis, Zhang et al., (2019) [46] found that invasive plants increased bacte-

rial biomass and microbivore abundance compared to native species. Moreover, a wide range of bacterial communities were reported in the rhizospheres of two invasive species, namely, *Prosopis juliflora* and *Parthenium hysterophorus*, where both species harbored more diversified bacterial communities from different phyla compared to the bulk soil [61]. The same authors found that the most predominant genera in the rhizosphere of *P. juliflora* were *Acidobacteria*, *Bacterioidetes* and *Gammaproteobacteria*, whereas *Acidobacteria*, *Betaproteobacteria*, and *Nitrospirae* dominated the rhizosphere of the *P. hysterophorus*.

The composition and structure of the mycorrhizal community in the rhizosphere of invasive species *Acacia dealbata* [69,70] and *Bromus tectorum* [71] were significantly modified and disturbed, and both invasive species prohibited the establishment and growth of native species. According to Phillips et al., (2019) [116], invasive grasses had an abundance of symbiotic mycorrhiza and other types of fungi compared to the native shrubs. They concluded that grass invasion might decrease the availability of beneficial symbionts that protect native species from pathogens. Moreover, the allelopathic effects of the invasive *P. juliflora* encouraged mycorrhiza, increased the microbial biomass carbon, inhibited the growth of other species under their canopy [65], and improved enzymatic activity in soils, as well as the nutrient status [64]. The consequences of these modifications may lead to further changes in the structure and function of other microbial species, and consequently, the invader plant can affect ecosystem function [47,209].

Changes in the structure and functions of microorganisms in the rhizosphere of invasive plants in arid lands could be attributed to different factors: (a) increase in the microbial biomass of carbon, (b) improved metabolic activity in the rhizosphere of invasive plants, (c) influence and modification of the enzymatic activity in the rhizosphere of invasive plants, and (d) increased urease and glucosaminidase activities (Table 1 (ii)). In addition, invasive plants can accelerate the change of microorganisms and promote their metabolic activity in the soil by modifying the microclimate. The dense covers and large amounts of litter produced by invasive plants improve soil physical and chemical properties, the quantity and quality of organic matter, and soil moisture, compared to the non-invaded sites [1,62,66,67]. In low-input agroecosystems such as arid and semi-arid soils, where both N and P content are typically low, the inoculum application of exotic and/or native PGP microorganisms is recommended to improve ecosystem productivity [65,210]. Applications of microbial inocula, such as biofertilizers, Phytostimulation and biological control agents, are encouraged to increase crop production and foster the restoration of degraded arid lands [139]. However, deliberate introductions of exotic plants for rehabilitation, and selected strains for improving productivity or to control pests and diseases, may lead to major positive or negative changes in the microbial composition and diversity [1,211]. The diversity and functions of microbes of native communities could be affected directly by competitions, antagonistic and synergic interactions with newly added microbes, or indirectly by the amount of the exudates secreted along the root with enhanced growth [212]. In addition, imported exotic PGP microbial inoculants might facilitate the invasion of new microbial species, and alter or suppress the resident microbial communities, hindering ecosystems' recovery [211].

9. Conclusions

In arid and semi-arid areas, invasive plant species harbor hundreds of endophytes and initiate positive interactions with rhizospheric microorganisms to ensure growth and increase tolerance to environmental stressors. In low-resource arid environments, invasive plants tend to form associations with mycorrhizal fungi to increase the absorption of nutrients and enhance plant tolerance to different environmental stresses. In addition, invasive leguminous trees can adopt a wide range of nitrogen-fixing organisms for successful and effective symbiotic relationships in order to survive, improve establishment, and tolerate adverse conditions. Endophytes, PGP microbes, and their secondary metabolites alter the aboveground and belowground ecosystem structure and function, encouraging invasive plant species to invade new areas. Moreover, invasive plants adopt allelopathic

mechanisms to enhance self-defense and distract native organisms. The allelochemicals significantly modify soil microbial activities and reduce the richness and diversity of native microorganisms and aboveground flora. Furthermore, invasive plants avoid the inhibitory effects of soil pathogens by harboring endophytes that improve immunity and gum production, in addition to their ability to release allelopathic compounds.

In arid and semi-arid areas, alien plant species contribute significantly to the diversity and numbers of autochthonous organisms and native flora. This, in turn, will significantly impact the ecosystem, which complicates and hampers the sustainability of these organisms and the processes in the whole ecosystem. It is well noted that most of the research carried out is sporadic and covers certain areas of interest, such as allelopathic effects, the role of specific microorganisms in plant nutrition or infection, and the extraction of novel antibacterial and antifungal products. Therefore, there is a real need for interdisciplinary research to explore the role of microbes in the invasion process and the mitigation of biotic and abiotic stresses in invasive plants across different climatic zones, to control and prevent the invasion into new areas. Moreover, the use of modern biotechnological and molecular tools, field experiments, and meta-analyses of data to attain high ecological validity that will sustain the integrity and function of arid and semi-arid ecosystems, are all needed too.

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