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REVIEW ARTICLE

Understanding the microbiome of ornamental plants: A comprehensive note

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Abstract

Ornamental plants are linked with a number of microbes present in rhizosphere, phyllosphere and endophytic region. Different plants host distinct microbiome communities. Many of these microorganisms are beneficial but some of them are pathogenic also. Beneficial microorganisms are engaged in putrefaction of organic matter, nutrient mineralization, nitrogen fixation, phosphate solubilization and development of plant-growth hormones. They also help the plants in restricting the development of pathogenic organisms and to withstand against various biotic and abiotic stresses. This review presents an extensive literature search on microbes of ornamental plants. The knowledge of microbiome and its beneficial effect on ornamental plants will be helpful in development of microbial formulations for sustainable flower production which will further lessen the utilization of agrochemicals and maintain ecological balance. Studies on microbiome-based sustainable practices in ornamentals, though promising, are poorly understood.

Keywords: ecosystem; microbiome; ornamental plants; plant nutrition; stress mitigation

Introduction

Plant microbiome is defined as an assembly of microorganisms which are interrelated with rhizosphere, phyllosphere and endosphere of higher plants. Interaction of these microbes with the plants constitutes the microbial ecosystem and play a vital role in plant nutrition as well as increased resilience to plant stresses, stress tolerance and productivity (1). The plant microbiome comprises not only fungi and bacteria, but also some microorganisms like viruses, algae, archaea and protozoa also exist. Microbial colonization in the plant rhizosphere is highly influenced and controlled by the composition of the host-specific exudates which further modify the physico-chemical properties of the soil and thus the microbiome. A few bacterial and fungal species have been isolated from ornamental plant tissues. Some of the microbes termed as “obligate symbionts” cannot survive without a host plant and includes fungi, viruses and some bacteria. The host plant plays its part by providing oxygen, space, carbohydrates and proteins to the microbes and the microbe in turn helps in improving the plant health by developing plant hormones, thus enhancing uptake of nutrients and solubilization of phosphate. Also, they help the plants in supressing the growth of plant pathogens by producing antibiotics, degrading fungal cell wall enzymes and supressing siderophores activity (2, 3).

Diversity in microbiome of ornamental plants

The microbiome of ornamental plant is vast and their habitats include the rhizosphere, phyllosphere as well as the endosphere where microbes engage in an associated, endophytic or epiphytic manner (Fig. 1). When microbes adhere to the plant tissues they are termed as epiphytes whereas when the microorganisms are positioned inside plant tissues then they are termed as endophytes. The rhizospheric microflora comprises of fungi, nematodes, algae, bacteria, protozoa and microarthrops (4). Although only about 2 % of soil microbes can be cultured under laboratory conditions, the remaining 98 % cannot be cultured. It is because identifying, characterizing and describing the role of these uncultured microbes is difficult. Recently, evaluation of molecules from soil samples by using nucleic acid based techniques which included analysis of DNA and rRNA have uncovered enormous heterogeneity in the rhizosphere dwelling microbial flora (5).

A total of twenty-three different species of arbuscular mycorrhizal fungi from rhizospheric soil of various ornamental plants pertaining to five genera i.e. *Acaulospora*, *Entrophospora*, *Gigaspora*, *Glomus* and *Sclerocystis* (6). Among all the genera, most dominant was *Glomus* followed by *Acaulospora.* Among different species of *Glomus*, the most profuse and frequent species reported in various ornamental flowering plants was *G. mosseae* and among the *Acaulospora* species, *Acaulospora laevis* was the most abundant.

Rhizospheric microbiome

The plant root system provides unprecedented ecological niches for soil microflora which inhabit the rhizosphere, roots and to some extent above ground parts. A broad range of bacterial

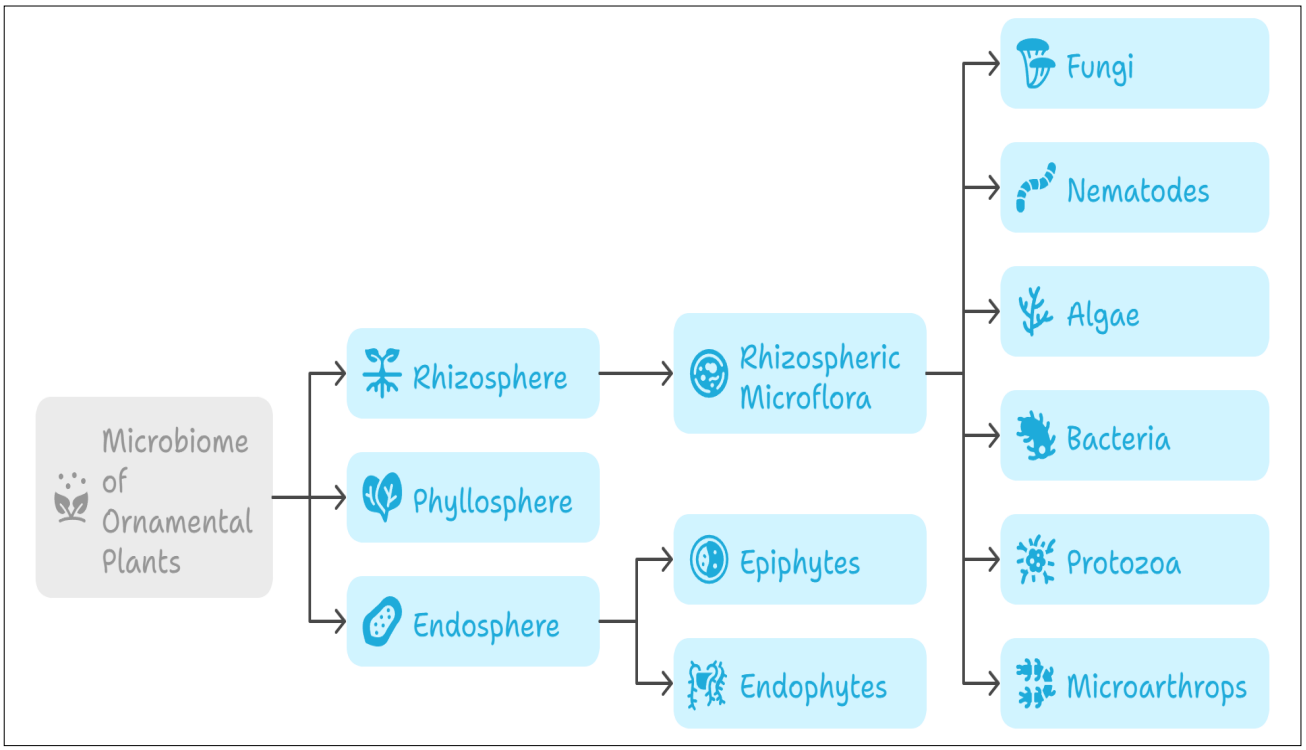

Fig. 1. Microbial habitats and interactions in ornamental plants.

endophytes colonize the root tissues of plants. Rhizobium bacteria, mycorrhizae, biocontrol microbes and plant growth promoting rhizobacteria (PGPR) are the most often studied rhizosphere organisms that are beneficial to the plants. Most profuse members of the rhizosphere population are mycorrhizal fungi, as they have been found in association with over 200000 species of plants i.e., over 80 % of all the plant species (7). Various rhizosphere bacterial taxa especially relating to *Pseudoxanthomonas* having significant divergent abundances among 30 plant species in angiosperms (8). Several authors described that the roots of *Rosa hybrida* were highly colonized by *Glomus intradices* (9-11).

High levels of phosphorus fertilization rates can lead to a decline in colonization rates of arbuscular mycorrhiza in rose plants (9). However, it was observed that mycorrhizal symbiosis in *Tagetes* and *Zinnia* plants is independent of changes in nutrient levels (12). Plants inoculated with *Glomus fasiculatum* showed higher percentage of colonization in chrysanthemum cultivars “Shyamal”, “Local Yellow” and “Bangalore White” than other species of mycorrhiza (13). When referring to the growth parameters such as number of laterals and plant height in all the cultivars, effect of VAM fungi viz., *Acaulospora laevis*, *Glomus fasiculatum* and *Glomus mosseae* were found to be stimulating in comparison to the control. Colonization by *Glomus fasciculatum* was also associated with the highest flower yield in chrysanthemum (14).

Phyllosphere microbiome

The phyllosphere of the ornamental plants provide exceptional habitat for both endophyte as well as epiphyte diversities. Endophytes usually move systemically through xylem to different parts of the plant like fruits, leaves, flowers and stem (15). These above-ground plant microbiome usually originates from soil, air and seed and are infamously known for their role in promoting disease resistance; alleviate stress tolerance and promoting plant growth. Population of fungal communities are significantly variable in the phyllosphere of the temperate regions and are usually diverse in tropical regions (16).

The exudations from pollen provide an attractive niche for microbial colonizers. These colonizers include both fungi (*Penicillium* and *Botrytis* molds) and bacteria (*Bacillus* sp.) (17). The primary site of infection for the pathogenic bacterium *Erwinia amylovora* is thought to be stigma; because of the numerous economic losses interrelated with floral infection caused by this pathogen (18).

Recent studies have recognized novel microbial taxa isolated from flowers, highlighting various ascomycetous yeasts belonging to *Wickerhamomyces* and *Candida* which signify that flowers might be an untapped reservoir of microbial diversity (19). Furthermore, the population densities of two epiphytic bacterial communities of petals and leaves of two ornamental plants, *Lotus corniculatus* L. and *Saponaria officinalis* L. were compared and reported that petals and leaves of both the plant species had different community formations (20). Communities from the petals were predominated by family Enterobacteriaceae which had lesser diversity as compared to the population of leaf communities. However, petal communities of two plants were reported to be similar and common taxa comprised the genus *Serratia*. In another study, culturable yeasts were examined from different parts of flowers and reported maximum number of yeast species found in the inner as well as outer corolla and the most abundant species on the surface of plant were reported to be basidiomycetous yeast species (21).

Endosphere microbiome

The endophytes invade and occupy the internal tissues of plants thus creating the endospheric microbiome. The arbuscular mycorrhiza as well as other endophytic fungi are the predominant dwellers of the endosphere. Bacteria are also important endophytes. The diversity and identity of the endophytic microbiome of both the above as well as below-ground tissues varies within the plant.

Factors influencing ornamental plant microbiome composition

Host factors

The host plant's identity plays a crucial role in shaping its unique microbial community. Plant species that are distantly related phylogenetically show greater variation in microbiome composition (22). When different plant species grow adjoining to one another they can harbour different microbiomes. All three factors i.e. host, environment and microbe are inter-linked and they together build the community of microbiome in plants.

Plant species that grow in closely resembling soil environment harbour distinct microbial communities in root compartments as well as rhizosphere. Different genotypes of plants behave differently in respect to interaction with microbiota that attract different microbiome members which confer resistance to biotic as well as abiotic stresses and may help for plant growth and nutrition (23).

Microbiome composition also varies with plant's age, health and surrounding soil environment. Sometimes different species of plants can harbour the same microbiome composition with variation in level of colonization. For instance, as mentioned in the earlier studies 71 % mycorrhizal root colonization was observed in snapdragon (24), 50 % in *Zinnia* and *Tagetes* (12) and 40 % in chrysanthemum (25).

In cases of relationship between pathogens and plants, age-related resistance (onto genic resistance) is highly expressed and correlated with developmental stage of the plant (26). Symbiosis research also indicated that the age and developmental stage of the plant are important factors that affect the microbial communities (27).

The arbuscular mycorrhizal fungal status of fifteen different ornamental flowering plants was investigated in 2012 (6). They observed that percent root colonization by the fungi varies from 14.28 % to 100.00 %. Maximum root colonization and spore count was observed in *Gladiolus grandiflorus* (172.00 ± 4.35) and *Senecio cineraria* (100.00 ± 0.0), respectively.

Some microorganisms produce antibiotics such as penicillin and polymyxin which increase the leakage, exudation of organic materials and altered cell permeability of roots (28) resulting in variable assembly of microbiome.

It is also documented that inoculation with arbuscular mycorrhizal fungi expressed varied colonized status in roots and production of biomass in *Hycinthus orientalis* L. Anna Marie. Only *Funneliformis mosseae* showed the greatest root colonization among other AM fungi species which confirmed that *Funneliformis mosseae* had the highest compatibility with the hyacinth plant species for greater efficiency (29).

Environmental factors

The formation of plant microbiome is highly affected by a range of abiotic and biotic factors. The rhizospheric microbiome is largely influenced by salinity, pH, structure, type, organic matter and moisture content of soil (30) whereas environmental factors like climate, presence of pathogen, geography and farming practices influence both rhizospheric and phyllospheric microbiota (31).

Land use activities and cultivation practices significantly contribute to the decline in microbial biodiversity (32). Change in the vegetation highly affects the structure and diversity of soil microbiomes. Continuous cultivation leads to the changes in soil properties mainly nutritional, which in turn affects the communities of soil microbiome directly. In prolonged field experiments, it was summarized in 2009 (33) that differently managed soils harboured distinct microbiomes.

In natural conditions, plants and their microbiota when exposed to different environmental conditions, such as changes in humidity, temperature, UV rays and pH, directly or indirectly affect the microbiome composition (34). A study in different ecosystems in Britain demonstrated that temperature and rainfall gradients are major climatic factors that shape the composition of bacterial community in plants (35). Drought is another factor that affects the microbiome composition due to altered oxygen availability and nutrient mobility in soil (36).

Role of microbiomes in ornamental plants

The microbiome of ornamental plant consists of harmful as well as beneficial microorganisms. Beneficial microorganisms of the rhizosphere are involved in disintegration of organic matter, primary productivity and nutrient mineralization (37). They are also involved in fixation of nitrogen (N_2), solubilization of phosphate and manufacturing of plant-growth hormones (38). Some of them help the plants to fight pathogen attack and withstand abiotic and biotic stresses. Exudates released in rhizosphere from plants or from microbes help the plants to communicate with microorganisms for assistance in environmental acclimation to mitigate stresses. The plant exudates are further utilised by microorganisms as a resource for carbon and other nutrients. The microbiome also modifies root architecture of plant (39), by releasing plant growth hormones. Harmful microbiota on the other hand acts as pathogens causing diseases on important crop plants leading to economical loss (Fig. 2).

Biofertilization and bio-stimulation

Biological modifications in soil leading to improving the efficacy of soil microbial community is known as "biofertilization". Biofertilizers are microbial inoculants or biologically active products comprising of one or more beneficial bacteria or fungal strains which conserve, add and mobilize crop nutrients in the soil (Table 1).

Excessive use of chemicals fertilizers in the cultivation system reduced soil microbial population which declines soil physico-chemical properties. Further, these applied fertilizers are lost through volatilization, denitrification, leaching and phosphorus fixation. Consequently, favouring the use of bio-fertilizers for sustainable farming.

Efforts in early 1970's were made to specify the microflora of English daisy, marigold and balsam (40, 41). The beneficial role played by biofertilizers in ornamental plants like jasmine, rose, marigold, chrysanthemum, aster, dahlia, gladiolus, tuberose and lilies (42).

Table 1. The most popular types of bio-fertilizers used in ornamental plants

Sl. No.	Biofertilizers	Examples
1.	Nitrogen (N_2) fixers	*Azotobacter* and *Azospirillum*
2.	Phosphorous solubilizers	*Bacillus* and *Pseudomonas*
3.	Phosphorous Mobilizers	*Gigaspora* sp. and *Acaulospora* sp.
4.	Zinc and silicate solubilizers	*Bacillus* sp.

Fig. 2. Unveiling the dual nature of microbiomes in plants.

Plant growth promoting rhizobacteria persistently colonize the roots of plants that augment plant growth through mineral solubilization. They also support establishment of other beneficial soil microbes, such as mycorrhizal fungi and help in supressing the growth of plant pathogens (43).

When phosphorus-solubilizing bacteria is used in combination with Arbuscular mycorrhiza it leads to synergistic effect because mycorrhizal exudations directly affect bacterial communities thus increasing water absorption by host plants (44). The synergistic effect of *Glomus fasciculatum* and *Bacillus subtilis* increased inflorescence numbers by 14-24 % and significantly higher fresh weight in *Tagetes erecta* cv. "Alcosa" compared to untreated plants (45). Similar reports on the combination of *Acaulospora laevis* and *Pseudomonas fluorescens* in enhancing root biomass, phosphatase activity and phosphorus uptake of *Chrysanthemum indicum* L. were documented in the earlier studies (46) and in *Gazania rigens* L. (47). A consortium of *Pseudomonas putida* and *P. fluorescens* strains improves growth and flowering in *Pelargonium peltatum*, *Chrysanthemum* sp. and *Dahlia variabilis* (48).

Some of the researches have highlighted the beneficial effect of *Azotobacter* in crops like *Tagetes erecta*, *Rosa hybrida* (49, 50). Yet others are of the opinion that the interaction of *Azotobacter* and phosphorus solubilizing bacteria are more beneficial in crops like *Gladiolus grandiflorus*, *Polyanthes tuberosa* and *Matthiola incana* than application of azotobacter alone (51-53).

Azospirillum is another important microbe used in ornamental crops which is reported to increase growth, early flowering and nutrient uptake in rose (54). A combination of *Azospirillum* and phosphate solubilizing bacteria in petunia and carnation improved flower quality and yield (55, 56).

Arbuscular mycorrhizal fungi live in symbiotic association with plants. The root colonization, spore count, dominant species and species diversity varies with the soil nutrient conditions and region (57). This symbiosis can enhance plant growth, flower production, reduce days to flower emergence (58, 59), increase size and weight of flowers (25) and flower longevity (24, 60) in different flower crops. It was observed in rose that there was marked reduction in the transpiration rate of leaves detached from plants that were inoculated with *Glomus* thus suggesting increased longevity for harvested flower stems (10).

The beneficial effect of arbuscular mycorrhizal fungi in improving growth and flowering of annual flowers such as *Zinnia elegans*, *Salvia splendens*, *Tagetes patula*, *Callistephus chinensis*, *Impatiens balsamina*, *Petunia hybrida* and *Antirrhinum majus* was reported by several workers (61-65). Low supply of NPK augmented with mycorrhizal fungi is particularly helpful in increasing phosphorous content in tissues of *Pelargonium hortorum* (66).

AMF inocula applied directly to cuttings of *Chrysanthemum morifolium* shows enhanced rooting rate to 99 % while it was 77 % in non-mycorrhizal inoculated plants (67) and resulted in improved fresh weight and size of flower (25, 68).

It was recommended that for better functioning and establishment of symbiosis, rhizobacteria plays important role in assisting arbuscular mycorrhizal fungi (69). A combination of *Aspergillus niger* and *Glomus fasciculatum* was proved to be economical for flower production of chrysanthemum (70). Application of phosphate-solubilizing bacteria, vesicular arbuscular

mycorrhizas and free-living nitrogen-fixing bacteria in *Eustoma grandiflorum* is also reported to produce more flowers per plant and advanced the flowering by 14 days than application of these microbes individually (71).

Zephyranthes bulbs inoculated with AMF during the storage period showed enhanced growth and flowering in the subsequent growing cycle (72). Likewise, corms produced from AMF-inoculated *Brodiaea* plants contained a greater proportion of non-reducing sugars compared to non-inoculated plants (60). Some microbes also release enzymes like, 1-carboxylic acid-1-aminocyclopropane (ACC) deaminase, which leads to the reduced level of ethylene production in the plants (15).

Some studies have documented earlier flowering (73) with the application of AM fungi whereas others have reported delayed flowering (66, 74), or non-significant effect on flowering (75) due to AM fungi. Prolonged flowering duration (76) as well as reduced flowering duration (77) with AMF application are also reported. Under greenhouse rose production system, inoculation of *Glomus mosseae* resulted in reduction of time needed for flowering for 80 % plants by one month and exhibited increased number of cut flowers (73). Application of *Glomus fasciculatum* in *Gerbera jamesonii* cv. "Bolus" leads to 50 days earlier flower initiation (78).

Pathogenic interactions and host resistance in plant microbiomes

The intricate relationship between plants and their associated microbiomes involves a dynamic interplay with both beneficial and detrimental microorganisms. Plant root exudates, for instance, attract not only advantageous microbes but also potential pathogens (79). While plants exist in close proximity to various bacteria, fungi and viruses, successful infections are frequently averted due to the plant's inherent "non-host resistance" or "horizontal resistance" (80).

However, environmental factors significantly influence fungal disease development, particularly temperature and moisture. For example, leaf blight of marigolds caused by *Alternaria dianthi* is strongly correlated with rainfall, temperature and humidity (81). Fungal mycelia require specific temperature ranges and moist surfaces to survive, though spores can overwinter in harsh conditions, germinating when favourable temperatures and moisture return (82). Upon successful infection, pathogens compromise plant productivity by disrupting physiology and growth. Common fungal diseases include damping-off caused by *Pythium* spp. and *Phytophthora* spp. in crops like carnation and poinsettia; *Ceratobasidium* sp. was newly reported to cause damping-off in marigold in India (83). *Botrytis* spp. is notorious for infecting propagation material and causing substantial post-harvest losses in flowers during transport and storage (84). Specific reports include *Alternaria tenuis* causing black spot-on *Rosa centifolia* (85) and *Septoria* leaf spot on marigold (86). *Fusarium oxysporum* is a widespread pathogen affecting many ornamentals like *Chrysanthemum* spp., *Dianthus* spp., *Gerbera* spp., *Gladiolus* spp. and *Lilium* spp., with specific forma specialis targeting different hosts (87, 88). Its coalition with *Pythium* sp. can cause root rot in gerbera (89) and it also impacts other ornamentals such as *Anoectochilus* spp. and *Ranunculus* sp. (90). Bacterial diseases, driven by phytotoxic proteins and phytohormones, are also devastating, with pathogens like *Erwinia* sp., *Pseudomonas* spp. and *Xanthomonas* spp. maintaining infection cycles via insect vectors, vegetative parts or seeds. Viral diseases lead to significant economic losses, with transmission primarily by insects (leafhoppers, aphids, whiteflies, thrips) and secondarily by nematodes, fungi and mites, as well as through infected plant parts or mechanical means.

Crucially, the plant microbiome plays an important role in inducing host resistance against these pathogens. Beneficial microbes, often existing in a dormant state, can be "reactivated" by pathogen attack to enhance resistance. This disease resistance, especially against soil-borne diseases, is influenced by the microbiome's composition, structure, functionality and assembly (91). Both rhizospheric and phyllospheric bacteria bolster host resistance through various biocontrol activities, including producing pathogen-inhibiting volatile compounds, siderophores, lytic enzymes and antibiotics (92). Some bacteria also enhance plant immunity by altering hormone levels and inducing systemic resistance (93). The plant microbiome further inhibits pathogen development by competing for resources, microenvironments and through antibiosis or parasitism (94).

Key bacterial genera known for protecting plants include *Pseudomonas*, *Streptomyces*, *Bacillus*, *Paenibacillus*, *Enterobacter*, *Pantoea*, *Burkholderia* and *Paraburkholderia* (94). Specific bacterial taxa like *Firmicutes*, *Actinobacteria* and *Acidobacteria* have been shown to control Fusarium wilt (95). For *Fusarium oxysporum*, effective biocontrol agents include *Bacillus*, *Fusarium*, *Glomus* and *Trichoderma* genera (96-98). *Pseudomonas fluorescens* is particularly significant, protecting roots from *Fusarium* sp. and *Pythium* sp. (99). Research indicates that healthy leaves of *Euonymus japonicus* harbour higher fungal and bacterial diversity compared to diseased ones, with powdery mildew altering the abundance of fungal (*Ascomycota*, *Basidiomycota*) and bacterial (*Proteobacteria*, *Firmicutes*) phyla (100).

Successful biocontrol examples abound: powdery mildew in rose can be controlled by *Ampelomyces quisqualis*, *Bacillus subtilis* and *Verticillium lecanii* (101), with *Gliocladium catenulatum* and *Bacillus subtilis* showing comparable efficacy to chemical treatment of mycobutanil (102). *Trichoderma viride* achieved 100% control of rhizoctonia stem rot in chrysanthemum (103) and *Trichoderma viride* and *Trichoderma harzianum* offered 63-73 % control of the same disease in carnation (104). *Trichoderma harzianum* and *Pseudomonas fluorescens* significantly inhibited fusarium wilt in carnation (105, 107, 108), with *Trichoderma asperellum* also reducing disease severity (106). *Pseudomonas fluorescens* and *Trichoderma viride* effectively reduced fusarium wilt in gerbera (109). Additionally, *Glomus mosseae*, *Trichoderma harzianum*, *T. viride* and *Bacillus subtilis* control Fusarium wilt in gladiolus (110-112). *Minimedusa polyspora* reduced the incidence of *F. oxysporum* f. sp. *narcissi* by 33% in narcissus (113). Botrytis cinerea sporulation was reduced by over 90 % using *Gliocladium roseum* FR136 and *Trichoderma inhamatum* (114) and leaf rot in cyclamen was mitigated by *Ulocladium atrum* and *Gliocladium roseum* (115). Furthermore, *Glomus mosseae*, *G. intraradices*, *Pseudomonas putida*, *Pseudomonas aureofaciens* and *Streptomyces* sp. delayed chrysanthemum yellows phytoplasma infection (116). Finally, *Streptoverticillium* sp., *Trichoderma* sp. and *Gliocladium virens* controlled collar rot in marigold (117) and *Trichoderma asperellum* successfully remediated *Phytophthora ramorum* infested nurseries (118) (Table 2).

Biocontrol of insect-pests

Intricate relationships exist among immune system and microbiome of plants which adds to the capability and versatility of the plant to deal with varying environments. The intrinsic immune system of the

Table 2. Biocontrol of diseases in ornamental plants

Disease in crop plant	Biocontrol agent	Beneficial effect	Reference
Powdery mildew of rose	*Ampelomyces quisqualis*, *Bacillus subtilis*, *Verticillium lecanii* and *Trichoderma harzianum*	Powdery mildew can be effectively control under the greenhouse conditions	(101)
Powdery mildew of rose	*Gliocladium catenulatum* and *B. subtilis*	Significant control of powdery mildew	(102)
Black spot incidence in rose	*Chaetomium globosum*, *T. harzianum* and *Bacillus subtilis*	Reduced disease index	(157)
Rhizoctonia stem rot in chrysanthemum	*Trichoderma viride*	No incidence of disease	(103)
Rhizoctonia stem rot in carnation	*Trichoderma viride* and *Trichoderma harzianum*	Disease control between 63-73 %	(104)
Fusarium wilt in carnation	*Trichoderma*, *Streptomyces*, *Pseudomonas* and *Bacillus* spp.	*Trichoderma harzianum* showed highest mycelial growth inhibition (87.78 %) followed by *Pseudomonas fluorescens* with 86.67 % growth inhibition of mycelia	(105, 106, 158)
Fusarium wilt in carnation	*Trichoderma viride* and *Trichoderma harzianum*	The beneficial effect of using *Trichoderma viride* and *T. harzianum* for disease control is reported	(107, 108, 159)
Fusarium wilt in gerbera	*Pseudomonas fluorescens* and *Trichoderma viride*	Significantly reduced the wilt incidence	(109)
Fusarium wilt in gladiolus	*Glomus mosseae* and *G. etunicatum*	Check the infection of *Fusarium* yellows	(110-112)
Anthracnose of cyclamen	AM fungi	Decrease the anthracnose incidence	(127)
Color rot of marigold	*Streptoverticillium* sp., *Trichoderma* sp. and *Gliocladium virens*	Effectively control collar rot of marigold caused *Rhizoctonia solani*, *Phytophthora* sp. and *Sclerotium rolfsii*	(117)
Phytophthora infested nnursery plants	*Trichoderma asperellum*	Infested nurseries were successfully remediated under greenhouse conditions	(118)

plant solitarily is usually not adequate to fight against the antagonists in the phyllosphere. The microbiome of ornamental plants can also contribute to naturally suppressing the pests. The communities of microorganisms in the endosphere, leaf surfaces and rhizosphere protect the plants against the various biotic stresses such as fungal pathogens and insect herbivory (119, 120).

Amelioration of abiotic stress

Plants undergoing various abiotic stresses engage advantageous microorganisms present in the environment by utilising a wide array of chemical stimulus to improve the capability of plants to ward off stresses. Abiotic stress such as salinity, drought, heat and mineral toxicity increases the population of specific microbial symbionts associated with plants by the following mechanisms viz., (i) change in immunity and plant physiology, which modifies the secretion profile of exudations from the plant roots and favour the growth of specific microbes associated (ii) directly alter the properties of soil properties viz., pH, O_2 and nutrient levels and communities of microbes by accumulation of specific microorganisms in the roots of the plants e.g., drought and flooding events favour betaproteobacteria and actinobacteria in soils (121) (iii) increase the population density of specific microorganisms due to nutritional interdependence (122).

Alterations in the microbiome of roots generally improve tolerance of plants during stress period. For example, when leguminous plants were grown in limited nitrogen (N), plants released higher proportions of flavonoids which attracted N-fixing bacteria (123). Studies also revealed that 1-aminocyclopropane-1-carboxylate (ACC), an amino acid present in the plants which ameliorates the stress conditions, could reorganize microbiome population which enhanced tolerance of plants to the salinity stress conditions (124).

Various exudations from the roots attract microorganisms during the stress period. Microbes retort swiftly to variations in root exudations. Abiotic stresses like metal toxicity, poor nutrition, drought and light limitation alters the microbial community and the plant root metabolism. In some instances, increase in the specific population of microorganisms during the stress-induced environments could improve the stress tolerance of plants (125). Drought increases the population of actinobacteria in the endosphere and/or rhizosphere of the plants. Likewise, limiting nitrogen/phosphate supply of improves the symbiosis of plants with advantageous microorganisms for acquisition of nutrients (8).

Temperature stress

Significant rise in temperatures could influence the plant physiology by increasing leaf transpiration rate and respiration and by varying the allocation of photosynthates. While, low temperature regimes reduce the metabolism of plants, which leads to reduction in the foliar growth, early senescence and reduced photosynthetic activity. Temperatures lower than freezing point hampers the development of buds because the growing and rehydrated buds get destroyed due to cold stress.

Microbial biostimulants boost the response of plants to heat stress. For instance, the production of ROS-damaging enzymes e.g. peroxidases, catalase, superoxide and dismutase, improve stress tolerance of plants to heat and it can be improved by colonizing with beneficial bacteria, such as *Pseudomonas* and *Bacillus* and mycorrhizal fungi such as *Septoglomus deserticola* and *Septoglomus constrictum* (126). For example, AM fungi enhance the growth under heat stress condition in cyclamen (127).

By utilizing microbes that inhibit ethylene synthesis helps the plants in escaping the damaging effects of heat stress (128). Specifically, bacteria which show activity of 1-aminocyclopropane-1-carboxylic acid (ACC), are known to be highly effective in surviving stress conditions such as *Bacillus subtilis* BERA 7, *Leclercia adecarboxylata* MO1, *Pseudomonas fluorescens* YsS6 and *Pseudomonas migulae* 8R6 (129).

For overcoming stress due to low temperatures, microbes which possess ice nucleating activity (INA^+), can encourage production of ice cores in plants and the first bacterial strain that was stated to wield ice nucleating activity was *Pseudomonas syringae* (130). Other microbes which show ice nucleating activity are *Erwinia herbicola* (syn. *Pseudomonas agglomerans*), *Xanthomonas campestris* and *Lysinibacillus* sp. (131).

Salinity and drought stress

Drought and salinity induce water stress in plants which takes place when water losses due to leaf transpiration surpass the water absorbed by roots, resulting in reduced turgor in plant tissues. Stress

caused by the drought conditions highly influences the plant morphology and physiology, leading to buildup of harmful ROS (132), ethylene emission and reduced availability of mineral nutrient, absorption and transport (133). Various direct and plant-mediated mechanisms involving microbial biostimulants improve plants tolerance to drought and salinity stress such as, *Pseudomonas* spp. PF23 and *Pseudomonas putida* GAP-P45 help in producing bacterial exopolysaccharides which improve structure of soil by creating micro and macroaggregates, which in turn improve the development of plants in water stressed conditions (134).

Mycorrhizal fungi increase root biomass, improves water retention, reduces leaching of mineral nutrients (135) and increase the tolerance of plants to soil salinity. The improvement in nitrogen uptake is considered as the major mechanism which induces salt tolerance in plants (136). *Glomus* sp. produces a glycoprotein known as glomalin, which helps in improving plant tolerance to drought (137). Arbuscular mycorrhizal fungi protects the plants from drastic effects of drought which might be due to an increase in hydraulic conductivity of roots, transpiration rate or stomatal regulation, increased uptake of water at lower levels soil moisture because of highly protruding hyphae (138), osmotic adjustment which helps in maintaining turgor pressure of plants even at lower tissue water potential (9), proline and carbohydrate accumulation, increased photosynthetic activity and nutrient availability (139).

Glomus constrictum Trappe was reported to induce drought stress tolerance in marigold (*Tagetes erecta*) (140). Similar report on mycorrhizal symbiosis improving the photosynthetic yield and water status of rose plants under drought stress have been documented (9). Enhanced plant growth as well as yield following AM inoculation in marigold due to improved uptake of P and Cu under water-stressed conditions was also reported (141).

The genus *Pseudomonas* is well known for its ability to increase plant growth in low-nutrient and drought conditions. Other genera like *Pseudomonas*, *Bacillus*, *Enterobacter*, *Agrobacterium*, *Streptomyces*, *Klebsiella* and *Ochromobacter* improves the production of wide range of crops under saline conditions (142). Increased number of flowers and biomass in *Petunia hybrida* and *Impatiens walleriana* plants grown under low-nutrient and drought conditions with the inoculation of *Pseudomonas poae* 29G9 and *Pseudomonas fluorescens* 90F12-2 was reported (143). Similarly, increase in plant growth, shoot biomass and growth index in greenhouse-grown zinnia and petunia at low fertility conditions was also reported with the inoculation of *Bacillus subtilis* QST 713 (144).

Some bacteria protect plants against different types of stress, which might be due to physiological-adaptive responses such as producing osmoprotective metabolic compounds; producing hormones which promote root growth of plants under stress; producing bioactive and antioxidant molecules. *Bacillus licheniformis* SA03 isolated from chrysanthemum plants grown in saline-alkaline soil of China conferred increased salt tolerance in chrysanthemum (145).

A previous study reported that *Crassula ovata* plants inoculated with *Glomus* spp. show more resistance to salt stress than non-inoculated plants by limiting sodium ion uptake at the cellular level (146). She further stated that the protective effect of microorganisms against salt toxicity is achieved through production of exopolysaccharide matrices, production of osmolytes, biostimulation of root development and production of ACC deaminase.

An earlier study reported that under high salinity levels (6 dS/m), *Entrophospora* sp. fungi could invade and inhabit the chrysanthemum plant roots effectively thereby significantly improving flowering and yield (147). Other mycorrhizal fungi like *Funneliformis mosseae* and *Diversispora versiformis* improve shoot and root dry weight, root length and root nitrogen concentration in *Chrysanthemum morifolium* plants cultivated for five months under moderate salinity conditions (50 mM NaCl). As salinity increased to 200 mM NaCl, mycorrhizal dependence and mycorrhizal colonization decreased due to the adverse effects of salinity on spore germination or impaired hyphal growth (136). A previous findings suggested that rhizosphere microbiome promote growth and germination of *Hibiscus hamabo* in salinity stress (148).

Preparation of microbial formulation and its application

The microbes thrive in their natural environments as compared to the ones introduced to new environments because they cannot compete with the indigenous microbes. The competitiveness of the introduced strain is affected by the physiological activity as well as concentration or quantity of the strain of the strain that is introduced (149). To secure that the cells are delivered at the appropriate positions with extended shelf-life appropriate solutions should be made. For example, for a specific microorganism to perform biocontrol functions, it is of utmost importance that the colonized strain establishes itself in the same niches as of pathogenic organisms and show antagonistic activities (150).

Combination of microbes with various characteristics are now commonly used as some microbes complement one another to cooperate various processes required for specific results such as biocontrol of pathogens and plant growth enhancement. Many a times, it has been observed that by combining bacteria that exhibit no, or very minute plant growth promotion impacts when used alone can exhibit plant growth promotion results when used in combinations, varying from combining three different species of bacteria that thrive in one biofilm (2) to applying of the whole microbiota (151). Efficiency of microbial inoculants relies on the inoculation characteristics and the capability of the inoculum to surpass the native microbiota competition and establish itself in the rhizosphere.

Formulations ensure that the cells remain viable during the storage period and are also available to the plants grown in fields. However, viability of these formulations depends on the capability of these microbes to tolerate low humidity (115).

The bioinoculants which have greater capability to invade, set up themselves in the rhizosphere of the host, they also create structural changes in the microbial community of native species (152). When arbuscular mycorrhizal fungi were introduced in salvia (*Salvia officinalis*), it was shown to alter the makeup of the bacterial community associated with the rhizosphere (153).

Pyrosequencing the 16S rRNA gene reveals variation in bacterial community in the rhizosphere of chamomile. The use of distinct bioinoculants where the bacteria related to phylum Verrucomicrobia existed when rhizosphere was treated with *Stenotrophomonas rhizophila* (154).

Table 3. Role of microbiome in crop productivity of flower crops

Crop plant	Microorganism	Beneficial effect	Reference
Zinnia elegans	AMF	Growth and overall yield	(61)
Crossandra	AMF	Increase in weight of flowers	(68)
Rose	*Glomus mosseae*	Time to flowering reduced by one month	(73)
Antirhinum majus	*Glomus deserticola*	Increase in flower size	(64)
Marigold	AMF	Increased the size of the flowers	(140)
Antirrhinum majus and *Hypericum perforatum*	AMF	Enhanced the number of flowers	(64, 65)
Rosa hybrida	*Azotobacter*	Increased leaf area and plant height	(50)
Tagetes erecta	*Azotobacter*	Maximize flower yield	(49)
Petunia hybrida	*Azospirillum* sp. + PSB	Improved flower quality and increase flower yield	(155)
Carnation	*Azospirillum* + PSB	Enhance flower fresh weight	(55)
Tagetes erecta cv. "Alcosa"	*Bacillus subtilis* and *Glomus fasciculatum*	Produced 14-24 % more inflorescences and flowers had higher fresh weight	(45)
Chrysanthemum indicum L.	*Acaulospora laevis* + *Pseudomonas fluorescens*	Increased plant height, fresh and dry root weight	(46)
Potted hyacinth (*Hyacinthus orientalis* L. Anna Marie) plants	*Funneliformis mosseae*	Greater raceme length and biomass production of single floret, raceme and flower stem	(29)
Gazania rigens (L.) Gaertn	*Funelliformis mosseae*, *Acaulospora laevis* and *Pseudomonas fluorescens*	Early flowering, improved flower head size, flower fresh and dry weight, total chlorophyll and carotene content	(47)
Tulip	*Azotobacter chroococcum* and *Azospirillum lipoferum*	Increased plant height, leaf area, tepal diameter, growth and quality of flower as well as bulb yield	(156)
Gladiolus grandifloras	*Azotobacter* + Phosphorus solubilizing bacteria	Early corm sprouting, increase in corm weight and number of corms/plants	(51)
Polyanthes tuberosa	*Azotobacter* + PSB	Increased bulb production	(52)
Pelargonium peltatum, *Chrysanthemum* sp.	*Pseudomonas putida* and *P. fluorescens* strains	Increases plant size and flower number of plants	(48)
Petunia × *hybrida*	*Azospirillum lipoferum*	Increases flower number	(56)
Matthiola incana	*Azotobacter chroococcum*	Increase plant growth and nutrient content	(53)
Eustoma grandiflorum	VAM + PSB + free-living nitrogen-fixing bacteria	Produced more flowers per plant, advanced flowering by 14 days	(71)

Conclusion

Microbiomes of the ornamental plants are highly diverse and several factors are responsible for their functioning. The microbes interact in an associated, epiphytic, or endophytic manner with the ornamental plants. These microorganisms possess high potential to increase productivity and plant growth (Table 3). Their abundance as well as composition in the environment are governed by abiotic as well as biotic factors. They also play a significant role in mitigation of abiotic and biotic stresses. The most common utilization of the plant microbiome finds place in biofertilization and disease control. Biofertilization improves the functionality and interaction of the plant microbiome. Moreover, the application of microbial formulations helps in maintaining the ecological balance by reducing the use of chemical fertilizers and pesticides for cultivating ornamental plants. For commercialization of beneficial microbes in cultivating ornamental plants, research on the suitability and functionality of specific microbe for specific crop is critical. Understanding the role of the plant microbiome in enhancing plant productivity by enhancing nutrient acquisition, biocontrol against pathogens and pests, stress tolerance enhancement and improved soil health is of paramount importance. Isolation, selection and quantification of efficient microbes with better performance in the field can contribute a huge in increasing the production potential of ornamental crops. Research on the factors influencing plant and soil microbiomes is progressing rapidly. However, a key challenge lies in translating microbiome composition and diversity into predictable functional outcomes because of the complexity of interactions of microbes and dependency on environmental factors too.

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Authors' contributions

NL and AS conceptualized the work. NL, AS, AS and SS prepared the original draft. NL and SS contributed to writing, review and editing. AS, SK and KMG handled visualization. and RK, SG and RM performed the editing. All authors have read and approved the final version of the manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

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