

Is "weediness" and "invasiveness" of weeds a function of the plant microbiome?

Carmaleen U. Rodrigopulle^{1*}, James F. White^{1*} , Kurt P. Kowalski², Surendra K. Gond^{1,3}, Katheryn L. Kingsley¹ and Matthew T. Elmore^{1*}

¹ Department of Plant Biology, Rutgers University, New Brunswick, NJ 08901 USA

² US Geological Survey Great Lakes Science Center, Ann Arbor, MI 48105 USA

³ Dept. of Botany, MMV, Banaras Hindu University, Varanasi, UP. 221005 India

* Correspondence: cr992@scarletmail.rutgers.edu (Rodrigopulle CU); jwhite3728@gmail.com (White JF); matthew.elmore@rutgers.edu (Elmore MT)

Abstract

Over the past several decades, the extent to which microbes enhance plant development and health has become clearer; however, this has not been explored in terms of the aggressiveness and hardiness of weedy plants. In this review, we explore the hypothesis that many features of weeds and invasive plants are related to the activities of plant microbiomes. Microbes contribute to weed growth, fecundity, and fitness. They also play roles in soils, and in plants as endophytes, where they modulate plant development and protect the host from pathogens, insects, animals, and abiotic stresses. In addition, the adaptability and hardiness of weeds partly stem from the effects of endophytes on plant gene expression and genetic diversity. Weed control often involves multiple applications of herbicides or other treatments that can be costly and destructive. Weed and invasive plant control for agriculture and environment goes beyond monetary costs to negative impacts on people, animals and environment. However, with a more complete knowledge of the roles played by microbes, their symbiotic interactions may be altered to diminish aggressive traits less expensively and with fewer non target effects on environmental, human and animal health.

Keywords: Weeds, Invasive plants, Microbes, Stress tolerance, Endophytes, Anti-herbivory, Mutualism, Growth promotion, Disease protection

Citation: Rodrigopulle CU, White JF, Kowalski KP, Gond SK, Kingsley KL, et al. 2026. Is "weediness" and "invasiveness" of weeds a function of the plant microbiome? *Grass Research* 6: e020 <https://doi.org/10.48130/grares-0026-0017>

Impacts of weeds and invasive plants

Weeds can be characterized as plants that cause economical and/or ecological damage and are undesirable where they are growing^[1]. Invasive plants are a type of weed that persists and spreads widely, often destroying native plants and ecosystems^[1-3]. They grow rapidly and frequently cause environmental, ecological, and economical damage and may cause problems for human activities or health. Invasive plants are more problematic than other types of weeds, as they may be novel to the environment, and without natural hindrance to growth, they often outcompete native species. This may result in changes to ecosystem function and balance, leading to devastating effects on habitats^[1-3].

Both weeds and invasive plants may have negative consequences on the environment. Particularly, the aggressive growth of invasive species alters the balance in an ecosystem and changes community structure and composition, usually reducing biodiversity. While some flora may be locally extirpated, others may show diminished population sizes. According to the United States Department of Agriculture (USDA), invasive plants are the cause for the decline of 42% of U.S. endangered and threatened species^[2]. In addition, changes in vegetation affect the population structure of invertebrates and other animals that rely on native vegetation for their food and habitats, putting wildlife diversity in danger. Bateman and Ostojic^[4] reported changes in the composition of lizard and small mammalian communities in riparian woodland zones as a result of the invasion by *Tamarix* sp. These invasions can lead to changes in the ecological nutrient cycling processes and alter the structure and composition of soil. Control of weeds and invasive plants is expensive. In 2019, it was estimated that yearly, 137 billion

dollars were spent to manage invasive plants in the United States and 26 billion dollars for controlling weeds in agriculture^[3]. The use of toxic herbicides causes environmental pollution^[5]. This reduces the quality of water and soil resources available for humans, animals and agriculture^[6,7]. Weed invasions can also reduce the recreational value of properties^[8], cause blockage of water ways^[8], cause fire hazards, and sometimes can increase the risk of accidents due to the limited visibility caused by dense growth^[9]. Also, dense populations of some invasive plants become breeding places for mosquitos and other disease-vectoring insects^[10], increasing the risk of disease outbreaks.

Mechanisms of invasion

Invasive plants are introduced to a new area through international trade, human activities, climatic events, and through animal vectoring. It is still not very clear what characteristics mostly contribute to their invasiveness, but these plants often have certain phenotypic traits which may be drivers of their success. One such feature is the production of large quantities of pollen and seeds^[11]. Seeds can be easily spread by wind, water, or by attaching to the body parts of various animals. Seed structure facilitates dispersal. Many invasive plants also have extensive root systems^[2], which help them gain access to sufficient nutrients, water, and microbial resources in soils. Another important feature is their aggressive vegetative propagation^[12]. In addition to sexual reproduction through seeds, some invasive plants propagate through asexual methods. Stolons and rhizomes help them form large clonal populations that spread over hundreds of acres^[12]. Bulbs and tubers

can also contribute to invasiveness^[12]. In addition, allelopathy could contribute to the invasiveness of plants. Allelopathy is the phenomenon where some plants produce substances (known as allelochemicals) that inhibit the growth of other plants^[13]. Kalisz et al.^[13] reported the identification of potential allelochemicals from a significant portion of invasive plants they studied, and the ubiquitous presence of allelopathy among most invasive plant families. Further, the inherent ability of invasive plants to live in or adapt to a broader range of environmental conditions may be another feature that leads to their rapid growth and hardiness^[14]. All the above-mentioned features of weeds stem from weed genomes; however, all these features may be modified by the activities of microbes.

Weeds and microbes

Many definitions of weeds do not convey any of their properties that likely lead to their growth in unwanted areas^[15–17]. Weeds are often more competitive, stress-tolerant, and aggressive than crop plants^[15]. They may reduce or increase crop growth depending on the conditions^[16]. A weed may also be viewed as "a non-domesticated plant that has an intact and environmentally selected microbiome"^[17]. If one considers the ecologies of weeds vs. crop species it is clear why a naturally selected microbiome is an important feature of weedy plants. Weeds typically grow without human selection and management, and their seeds remain in nature or in soil where they are subject to colonization by soil microbes (bacteria and fungi, and perhaps other microbes). This leads to the development of a rich and growth-promoting microbiome that enables weeds to grow under stressful conditions without added nutrients^[17]. However, crops have been domesticated and managed by humans without consideration of their microbiomes in such a way that their selected microbiomes have been degraded. For example, during cultivation, seeds are gathered from crops soon after their development and stored under clean, dry, and often cool conditions where seed microbial communities do not continue to develop. Seeds may also be cleaned to remove or protect against pathogens. These are the conditions in which the living microbiomes on seeds are degraded over time, leaving the crop plants lacking in a microbiome that would enable seedlings to nourish themselves and defend themselves from pathogens and stresses^[17]. This point was illustrated in the domestication experiment done by Santhanam et al.^[18]. These authors began cultivation of coyote tobacco, *Nicotiana attenuata*, collecting seeds, storing them in cool, dry storage conditions, then planting in the following spring. After approximately eight seasons, the percentage of plants succumbing from a sudden-wilt disease caused by a *Fusarium–Alternaria* disease complex increased until crop failure. These investigators then transferred bacteria from the wild uncultivated tobacco onto the cultivated lines, and the wilt disease vanished^[18,19]. It is clear that the process of cultivation very quickly degraded the evolved microbiome in the wild tobacco. This same process has very likely occurred in domestication and cultivation of many of our crop plants. It is likely the degradation of plant and soil microbiomes in crop plants has increased their dependence on humans, resulting in the need to provide nutrients and various agrochemicals in their management. Also, application of nitrogen fertilizers can further alter plant endophyte communities^[20].

There is other evidence that the microbiomes of weeds are critical to their "weediness." Weediness here refers to the ability of a plant to grow rapidly and spread within any manmade or natural habitat. Some of the evidence is as follows. Rodrigues et al.^[21]

reported that plant invasions are associated with changes in the root zone microbial communities. Massensini et al.^[22] reported that weeds tend to show positive growth promotional responses to a diverse array of soil microbes, while crop plants may often show a neutral or negative response. This suggests that the presence of diverse and adapted microbiomes in plants enables weeds to associate positively with a range of soil microbes. Samad et al.^[23] found that weeds show a higher species richness in rhizospheres of roots than cultivated crop species, further reflecting a more developed microbiome. Rout and Chrzanowski^[24] found that the ability of Johnsongrass (*Sorghum halepense*) to grow in nutrient-poor tall grass prairie soils is related to its microbiome. Weeds have been found to contain more growth-promoting microbes than crop species^[25]. Taken in balance, it seems clear that one prominent feature of weed plants is a microbiome that contains numerous microbes that enhance growth and survival of the plant. Among hypothetical benefits of the microbiome include the following: modulation of host range, defense against herbivores and pathogens, increased nutrient acquisition, increased stress tolerance, increased fecundity, modulation of development and increased genetic and epigenetic diversity (Fig. 1).

Meng et al.^[26] showed possible evidence for the "enhanced mutualism hypothesis" in invasive plants. This hypothesis put forward the idea of the ability of invasive plants to enrich soil with beneficial microbes and establish intensified mutualistic associations to acquire microbial benefits for their success. Meng et al.^[26] found increased abundance of plant growth-promoting bacteria in soil with pokeweed (*Phytolacca americana*), a weed considered to be invasive. Further, this study found an increasing trend in microbial abundance, paralleling aging of the plant. This trend was prominent in early stages of invasion. Interestingly, high seed germination and biomass accumulation were observed when new plants grew in soil pre-conditioned with *P. americana* growth up to 5 years previously, while the effect was not observed when using soil aged

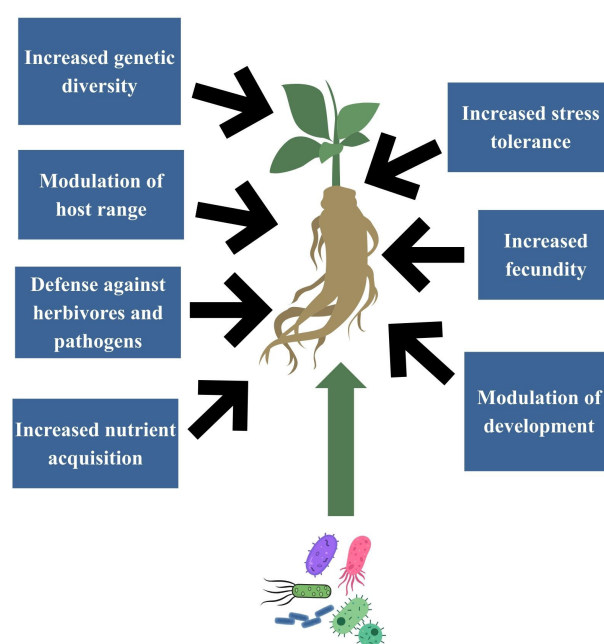


Fig. 1 Potential microbial contributions to weed and invasive plant growth. The benefits may include increased genetic and epigenetic diversity, modulation of host range, increased defense against herbivores and pathogens, increased nutrient acquisition, increased stress tolerance, increased fecundity, and modulation of development.

5–10 years. Thus, the plant–microbe interactions in early stages of development and invasions play a crucial role in the establishment of a particular weed in a new environment. Further, a study showed that invasive plants can act as reservoirs of pathogens of native plants, suppressing their growth^[27] and causing decline of native populations.

Roles of microbes in modulation of weed development

It is generally believed that eukaryotic organisms (including, animals, plants and fungi) are self-regulated in terms of their developmental programs, and their own genomes determine most or all aspects of development, rather than being modulated by microbes. However, there is growing evidence that this is not the case^[28]. Plants utilize microbes in their cells and tissues to modulate their development^[29,30]. This is particularly true in weedy and non-cultivated plants that tend to maintain healthy microbiomes^[31]. Jiang et al.^[32] examined the microbiome of the weedy plant *Stellera chamaejasme* and concluded that its weediness in part may stem from aspects of its microbiome that increase nitrogen and chlorophyll content in plant tissues. Irizarry and White^[33] showed that the addition of endophytic *Bacillus amyloliquefaciens* from a weedy tree (*Thespesia populnea*; Malvaceae) to the cotton microbiome resulted in increased expression of genes for nitrate metabolic processes and assimilation, membrane-bound vesicles, microtubule cytoskeleton and microtubule-based movement, and antioxidant and lignin synthesis, leaving plants hardier, healthier, and resistant to diseases. The density and length of root hairs and trichomes are largely determined by the numbers and kinds of microbes in the hair initials, with more microbes in root hair initials resulting in longer root hairs^[29,34,35]. Removal of all or most microbes from plants by surface disinfection of seeds results in seedling roots that do not develop root hairs^[29,34]. Figure 2a represents henbit (*Lamium amplexicaule*) showing an early-developing glandular trichome containing bacteria internally (black arrows), while Fig. 2b shows a more developed trichome containing abundant bacteria, with some emerging from openings in the trichome wall. Pečenková et al.^[36] found that intracellular bacteria in genus *Pseudomonas* promoted root hair elongation in *Arabidopsis thaliana* through ethylene signaling. Chang et

al.^[29] showed that bacteria at the tip of root hairs produced ethylene and nitric oxide, resulting in root hair elongation. Disrupting ethylene formation by bacteria using inhibitors, resulted in failure of root hairs to elongate. Similarly, scavenging nitric oxide in roots using methylene blue showed a reduction in root hair elongation. Thus, it seems clear that bacteria-produced substances like ethylene and nitric oxide play an important role in modulating plant cell development for particular cell types. In addition, Paungfoo-Lonhienne et al.^[37] showed that DNA is absorbed into *Arabidopsis thaliana* roots and triggers the expression of CLE (CLAVATA3/Embryo Surrounding Region-related) genes (coding for signaling peptides) that control root development. Thus, exposure of roots to DNA that is lost or extracted from microbes associated with roots is enough to alter root development through an unknown mechanism. Polar growth, in general in plant hairs, and elongated epidermal cells, fibers, and vascular tissues are associated with abundant bacteria early in their development, and thus their growth may be influenced by microbes within those elongated cell types^[29].

Growing evidence shows that plants cultivate bacteria in their meristematic tissues in both roots and shoots. The close interaction of endophytic microbes and developing plant cells makes this type of interaction important in plant tissue development. This close interaction was seen in Jerusalem artichoke (*Helianthus tuberosus*), where bacteria were observed within leaf margin meristem cells when tissues were stained for the presence of nitrate (Fig. 3). The development of plant organs such as root systems and stems is determined early in cell development in plant meristems^[29,30,33,37]. Endophytic interactions in meristem cells may well determine gene expression throughout the plant.

Nitrogen acquisition from the microbiome

Nitrogen is an essential nutrient required for plant growth and metabolism, but its presence is often limited. Invasive plants can alter ecosystem nitrogen cycling and soil nitrogen dynamics through various mechanisms^[38]. As an example, Kourtev et al.^[39] and Ehrenfeld et al.^[40] reported high nitrification and net nitrogen mineralization rates in soils invaded with Japanese stiltgrass (*Microstegium vimineum*) and Japanese barberry (*Berberis thunbergii*) compared to the soils beneath the native plant *Vaccinium* sp. Some invasions lead to high levels of bioavailable nitrogen in

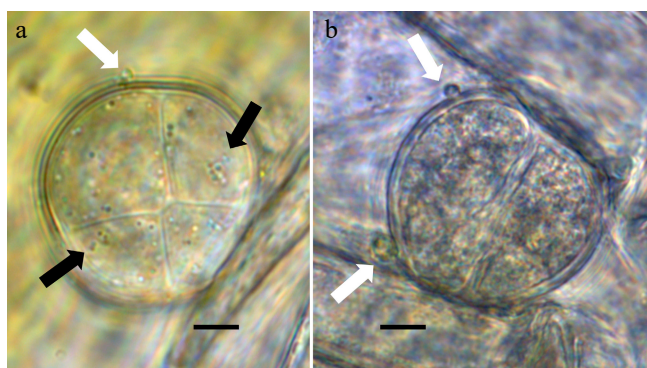


Fig. 2 Glandular trichomes of henbit (*Lamium amplexicaule*) showing endophytic bacteria within them. (a) Early-developing glandular trichome showing dividing trichome cells. Black arrows indicate bacteria within trichomes, while white arrows show bacteria emerging from the trichome (bar = 10 μm). (b) Late-developing trichome filled with bacteria, showing the escape of bacteria from the trichome (white arrows; bar = 10 μm). Images are original and are not previously published.

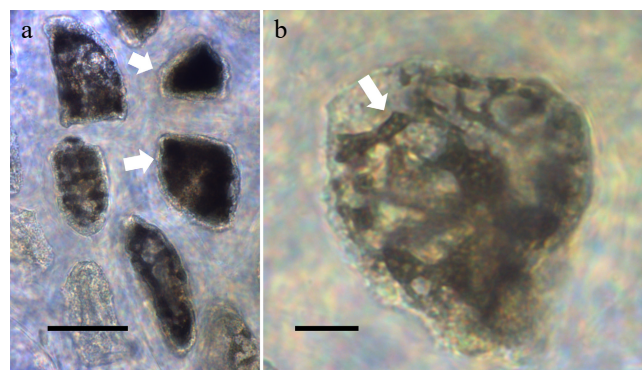


Fig. 3 Leaf margin meristem cells of Jerusalem artichoke (*Helianthus tuberosus*). (a) Several leaf margin meristem cells (white arrows) showing staining for nitrate (black color) using acidified diphenylamine stain (bar = 40 μm). (b) Single leaf margin meristem cell showing bacteria (arrow) inside the meristem cell (bar = 10 μm). Images are original and are not previously published.

soils^[24]. It was shown that tissues of some invasive plants have a higher nitrogen content than local plants^[40,41]. All these features suggest that invasive plants get more usable forms of nitrogen than local plants, thereby ensuring faster growth and establishment in new habitats, outcompeting natives. The superiority of invasive plants in terms of nitrogen content and nitrogen-related activities inside plant tissues and corresponding soils is due to several reasons as indicated below.

The interactions of plants with soil microbiomes play a key role in plant access to nitrogen. Even though the atmospheric air contains approximately 78% nitrogen, it must be converted to usable forms like ammonium ions or nitrates. This conversion is performed by some bacteria and archaea that are free living in soil or in a symbiotic relationship with plants. It is possible that invasive plants get the benefits from soil microbes and enrich their rhizospheres by selectively attracting microbes involved in the nitrogen cycle, thereby converting nitrogen compounds to bioavailable forms and helping in nutrient absorption. Kourtev et al.^[42] showed that invasive plants have distinct microbial communities in their rhizospheres compared to bulk soil. Evidence shows a greater difference in the rhizosphere microbial communities among the three plant species studied (two exotics, Japanese stiltgrass and Japanese barberry, and the native plant *Vaccinium* sp.). In addition, the bacteria-to-fungi ratio in the rhizospheres of both exotic plant species was significantly larger than the ratio of the native plant. Steer and Harris^[43] showed temporal changes in the rhizosphere microbial community of the invasive plant, creeping bent grass (*Agrostis stolonifera*). The plant likely modulates the microbial composition of the rhizosphere to meet different nutritional requirements at different growth stages of the plant.

Given the rich and distinct microbial structure of rhizospheres in exotic plants, it is possible that these plants have high rates of rhizophagy cycle which help them absorb more nutrients. Rhizophagy cycle is the process by which plants transfer nutrients from soil microbes to the roots by cultivating them close to the root tips, then absorbing them into root cells and tissues, and degrading them oxidatively to get nutrients^[34].

Nitrogen-fixing bacteria living inside plant tissues are also key for invasive plants to get access to nitrogen. Leguminous plants fulfill their nitrogen requirements by forming symbiotic relationships with bacteria that can fix atmospheric nitrogen. Even though not widely studied, plants have been shown to harbor endophytic bacteria that can fix nitrogen but not produce any specialized structures such as nodules. This is referred to as associative nitrogen fixation^[24]. These bacteria have been isolated from internal tissues of various plant parts such as roots, rhizomes, leaves, shoots, and seeds of economically important, non-leguminous crops, sugarcane, millet, corn, sorghum, rice, etc. Baldani et al.^[44] reported isolation of nitrogen-fixing bacteria from cereals.

Nitrogen-fixing or potential nitrogen-fixing endophytes have been identified from plants which are invasive, such as Johnsongrass^[24], *Phragmites* sp.^[45,46], elephant grass (*Pennisetum purpureum*)^[47], Bermuda grass (*Cynodon dactylon*)^[48], narrow-leaf cattail (*Typha angustifolia*)^[49], goosegrass (*Eleusine indica*)^[50], etc. The common microbial genera include *Herbaspirillum*, *Agrobacterium*, *Pseudomonas*, etc.^[24]. Some invasive plants, for example, Jerusalem artichoke, can grow well with low fertilizer inputs and in marginal soils^[51]. These plants may fulfil their nitrogen requirements through nitrogen-fixing endophytes living inside their tissues.

It may be hypothesized that nitrogen-fixing endophytes give invasive plants a competitive advantage over native plants by

increasing the availability of nitrogen for their growth. Endophytes can be seed-vectored, or plants can acquire them from the environment^[52,33]. It has been proposed that nitrogen-fixing bacteria entering plant cells form membrane-bound, vesicle-like structures termed "nitrosomes," where the nitrogen fixation is localized^[53]. Figure 4a shows bacteria associated with the seeds of *Typha latifolia*, while Fig. 4b shows nitrosome-like vesicles in root epidermal parenchyma cells. Invasive plants could fulfil the high nitrogen demand of meristematic cells by using nitrogen-fixing endophytes that make plants grow faster and denser in new habitats. Sher et al.^[54] reported the expression of the *nifH* gene in root elongation zones of *Populus trichocarpa*, which was inoculated with the nitrogen-fixing endophyte, *Burkholderia vietnamiensis*.

Plants maintain complex interactions with soil microbes and those in plant tissues^[55]. These microbial communities play crucial roles modulating the structure and function of plants and the ecosystem. Nitrogen fixation is an energy-demanding process^[56]. Therefore, all these communities may function as a consortium, towards the final goal of fulfilling nitrogen requirements of the plant(s) they associate with. With possible microorganisms genetically competent to perform all steps of the nitrogen cycling process, there may be different microbial groups contributing to different steps of the process. Signals from the environment, plant host, and different microbial groups may interact to alter the microbial community structure and composition. Chemical compounds in plant root exudates are signaling molecules that attract microorganisms from soil and incorporate them into the rhizosphere, or inside plant tissues as endophytes. Yan et al.^[57] modified the flavone biosynthesis pathway for rice plants to produce root exudates with more apigenin, a compound known to increase bio-film formation in nitrogen-fixing bacteria. They observed increased biofilm formation and plant tissue colonization of rice plants by nitrogen-fixing bacteria, which increased grain yield under nitrogen-limiting conditions.

Nitrogen fixers increase the activity of enzymes related to nitrogen metabolism^[58]. Among the enzymes upregulated are nitrate reductase, nitrite reductase, and glutamine synthetase, which are responsible for converting absorbed nitrogen into different forms that can be stored and used in metabolic pathways^[58]. It is also evident that the genes coding nitrogen transporter proteins are upregulated in the presence of nitrogen-fixing bacteria^[59]. While the exact reason is not clear, this may be because plants upregulate the expression of nitrogen transporters to manage the high nitrogen levels made available by bacteria within various plant parts and cell

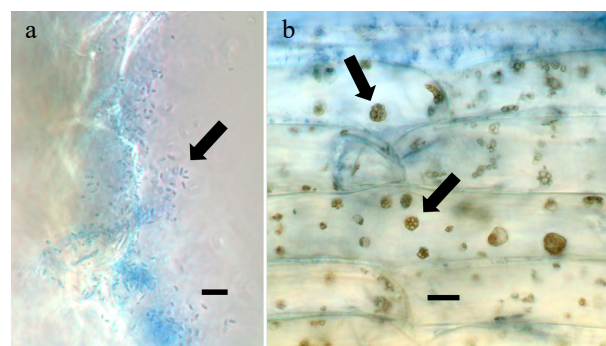


Fig. 4 Cattail (*Typha latifolia*) seed hairs and seedling tissues showing bacteria. (a) Seed hairs showing bacteria (arrow) vectored with the seed (Bar = 10 µm). (b) Root epidermal parenchyma showing hypothesized intracellular nitrosomes (arrows; bar = 10 µm). Images are original and are not previously published.

organelles. Also, there may be a direct effect of nitrogen-fixing bacteria on plants, where microbial signals trigger the expression of relevant plant genes.

Defensive mutualism endophyte symbiosis in weedy and invasive plants

Some microbes, especially fungi, establish symbioses with plants and benefit their host through production of compounds, principally toxins, that prevent animals from consuming the host plant. This contributes to the weediness of the host. This is frequently referred to as defensive mutualism^[60]. An example is wild grasses containing endophytic fungi belonging to genus *Epichloë* in the ergot family (Family = Clavicipitaceae)^[61]. These fungi fill their host plants with ergot alkaloids and other toxins that reduce the attractiveness of plants to animals. A concrete example is weedy grass called "sleepy grass," *Achnatherum robustum*, which contains endophytic fungus *Epichloë funkii* that produces alkaloids ergonovine and lysergic acid amide. This is commonly found in the mountainous regions of the west from Mexico to New Mexico^[62]. Lysergic acid amide causes prolonged sleep in horses, i.e., for 3 days, and they gradually recover. Another toxic grass, drunken horse grass, *Achnatherum sibiricum*, containing *Epichloë* spp. grows in China^[63]. Worldwide, grasses are known to contain endophytic fungi that reduce consumption by insects and animals^[61–63]. Generally, these grasses become locally abundant due to reduced herbivory. In the dicots, morning glories (*Ipomoea* spp.) often contain an endophytic fungus in genus *Periglandula* (Clavicipitaceae)^[64]. Ergot alkaloids produced by the endophytic fungus cause toxicity in morning glories. Another good example is locoweeds, e.g., *Astragalus* and *Oxytropis* spp., where fungal endophytes related to the fungal genus *Alternaria* (family Pleosporaceae) produce the toxin swainsonine that causes locoism in animals consuming the plant^[65,66]. The fungi involved in these mutualisms are from families known to produce toxins and thus may be pre-adapted for defensive mutualism. Little is known about how the host regulates toxin production in these symbiotic interactions. Fungal endophytes of many weeds produce substances that alter the herbivory of the host plant, thus effecting weediness.

Microbes and enhanced fecundity

Enhanced fecundity is a "weedy" and "invasive" attribute of weeds^[67]. Plant fecundity is the ability of a plant to produce new growth (if clonal) or to form seeds and seedlings. For a plant reproducing by seeds, the determinants of fecundity include the number of ovules per plant, the amount of pollen produced, and the success rate of ovule fertilization. The microbiome of plants typically increases the development of fruits and seeds on crop plants^[68–70]. Increase in flowering and fruiting in plants has been shown for crop plants where microbes have been explored for their plant growth promotional characteristics^[68,71,72].

Some weedy plants also attract and absorb microbes from soils, which could explain their high fecundity. The cause of increased flower production in plants treated with certain microbes (bacteria or fungi) is still unknown. It has been suggested that increased nutrients in plants as a result of microbial activities may be responsible for increased flowering^[68], in addition to other mechanisms. Development of more flowers or inflorescence branches may be compared to increases in branch root formation when plants are treated

with microbes. In roots, colonization of root tips by microbes is generally hypothesized to be concurrent with microbe-produced hormones (e.g., auxins) and other growth-promoting substances or signaling molecules (e.g., nitrogen, phosphorus, hydrogen peroxide) produced by rhizobacterial endophytes^[73]. Jones-Held and White^[74] found that endophytes trigger an oxidative burst in plants, resulting in the oxidation of ascorbate, which is required to propagate reactive oxygen species (ROS) signaling that leads to a plant response. Singh et al.^[75] found that ascorbate oxidation in a grass not only leads to increased expression of pathogen and stress defense traits but also positively stimulated root growth, suggesting a signal molecule effect on plant growth, which resulted in increased hormone production by the host. These signal molecules and direct hormone effects could be at play in both roots and shoots, where plants cultivate endophytic microbes.

Because endophytic microbes from the maternal plant are vectored in and on seeds, enhanced ovulate flower production results in increased dissemination of the endophytic microbes. Similarly, enhanced staminate flower formation due to microbial hormones or other signal molecules may result in more pollen and increased vectoring of endophytic microbes through pollen and increased fitness of the plant^[76]. This increased pollen production and release may even lead to increased rates of genetic change and adaptiveness of weedy and invasive plants. If endophytes are found to increase plant adaptation to the environment, then endophytic microbes may find applications in increasing gene variability in crop breeding programs.

Vertical transmission of endophytes has been recorded in a few species of weeds^[77], including in locoweeds (*Astragalus* and *Oxytropis* spp.) with the toxin-producing fungal endophyte *Undifilum oxytropis*, which enters the ovule and disseminates in seeds^[76]. This fungus appears to inhabit all tissues of the plant *Oxytropis sericea*^[78]. Hodgson et al.^[76] and Frank et al.^[79] reported that many fungal and bacterial endophytes are vectored in ovules and pollen grains. Madmony et al.^[80] showed that a bacterial endophyte, *Enterobacter cloacae*, of Mediterranean pines was vectored within pollen grains. Another proof of fecundity is the success rate of ovule fertilization—with more flowers corresponding to more ovule fertilization success. However, when pollen is vectored by an insect, endophytes also play a role in modulating the pollination by affecting the pollinators. Microbes have been shown to increase the attractiveness of floral nectar to bees and other pollinators^[81]. This greater attractiveness of flowers to pollinators results in increased rates of fertilization. In clonal plants, forming rhizomes, bulbs, or other propagating structures, plant microbes may be transmitted from the maternal plant to the offspring readily and efficiently^[82,83]. The clonal feature thus increases the ability of clonal communities to stabilize the microbiome^[83].

Endophytes modulate host range and niche in weeds

A range expansion effect was found for the grass tall fescue (*Schedonorus arundinaceus*) containing endophytic fungus *Epichloë coenophiala*^[84,85]. To reduce the toxicity of tall fescue, the fungal endophyte was removed, which resulted in the loss of persistence in many populations^[84]. Thus, the endophytes in tall fescue determined the persistence throughout a large geographical range. A similar host range extension phenomenon involves naturally occurring plants of *Dichanthelium* sp., where an endophytic fungus, *Curvularia* sp., enables the growth of grass individuals in

extreme thermic soils in contrast to those without the endophyte^[86]. This phenomenon gives rise to the "habitat adaptive symbiosis hypothesis" that plants engage in symbioses with microbes to adapt to their environment^[87]. Endophytes may also affect the particular niche of a plant. An extreme case is the tropical palm (*Iriartea deltoidea*) in Peru that contains a systemic fungal endophyte (*Diplodia mutila*) in leaves and seeds^[88]. This species is either an endophyte that protects the palm from insect feeding or a necrotrophic pathogen that destroys part or all the palm leaves. Interestingly, it is light that triggers the fungus to be a pathogen. Thus, the endophyte directly influences whether the plant can grow in forest gaps where light reaches, or in the dark understory.

Endophytes and abiotic stress tolerance

Invasive plants, when introduced to a new area, are exposed to a set of environmental conditions different from their native habitat. The variations are either biotic factors such as flora and fauna or abiotic factors such as climate and soil factors. Among new conditions may be biotic and abiotic "stresses" that affect plant growth. As an example, the new environment can harbor competitors, pathogens, and animals that reduce plant health. Also, the environmental conditions may be beyond the required or optimal range for growth. In addition, invasive plants are often subjected to chemical management practices such as treatment with herbicides, which are highly toxic. Some plants still thrive in new habitats and outcompete natives, becoming invasive in a specific region. Once established, invasive plants are difficult to control by physical and chemical means^[89]. They can thrive in a broader range of habitats and tolerate harsh conditions. As an example, there is a wide variation in the climatic and environmental conditions of the areas where the common reed (*Phragmites australis*) has invaded. Within North America, it is found in areas with little or no rain to humid and subtropical areas^[90]. Furthermore, it grows in a variety of soil conditions and even in deep waters and can tolerate high-salt conditions^[91]. The observed hardiness of invasive plants may be, in part, or completely the result of the endophytes they harbor. Over the past several decades, it has been shown that endophytic microbes may confer onto plants' increased ability to grow in stressful environments. This allows plants to acquire benefits from microbes during stress conditions.

Nutrient deficiency

Endophytes play a crucial role in nutrient acquisition in plants. They enhance plant nutrient status using various mechanisms. Chen et al.^[92] reported that the presence of *Epichloë* sp. in perennial ryegrass increased the growth and nutrient uptake of the host, thereby allowing it to survive in low-fertility soils. The endophyte-infected plants performed better than the controls and did not show signs of yellowing and withering for a period of 90 days. This demonstrates the increase in hardiness of plants containing endophytes. In low-fertility soils, the fungal endophyte improved grass health and survival by increasing root growth. This allows plants to uptake available nutrients more efficiently. Furthermore, increased root metabolic activity and plant biomass were also observed in endophyte-infected plants. Endophytes alter root architecture in a way to facilitate efficient nutrient uptake, as widely observed in endophyte-infected plants. The fungal endophyte *Epichloë coenophiala* has been reported to increase tolerance to low mineral

availabilities in soil, in tall fescue (*Schedonorus arundinaceus*)^[93]. Under phosphorus deficiency, the fungus triggered plants to produce long, thin root hairs. The production of long root hairs increases the surface area of the root system for the roots to reach soil particles far away from the plant. Also, production of root hairs under nutrient deficiency helps plants in several ways. This ensures efficient nutrient diffusion through the root cells and also benefits the rhizophagy cycle and increase nutrient extraction through microbes. In addition to modifying the root architecture, *E. coenophiala*-infected tall fescue had root exudates rich in phenolic compounds that help chelate aluminum compounds. As Malinowski and Belesky^[94] suggested, in this way, the endophyte helps plants mitigate aluminum deficiency.

Salt stress

Plants are exposed to salt stress when irrigated with high-saline water and/or when soils become saline due to natural and human activities. Invasive plants can survive in various habitats, and some can tolerate high-salinity conditions. Endophyte-mediated salt stress tolerance in plants has been widely documented^[95,96]. Gonzalez et al.^[96] reported a significant positive correlation between the colonization of dark septate endophytes in plant tissues with increasing salt concentrations in invasive *Phragmites* sp. This pattern was not observed in the native lineages of *Phragmites* sp. In addition, dark septate endophytes isolated from the roots of invasive species increased salt stress tolerance in both invasive and native lineages. This may be evidence for the "enhanced mutualism hypothesis," where invasive plants may associate more frequently with soil microbes, which helps them adapt better to the new environment and outcompete natives. In a study to evaluate the differences in the fungal endophyte communities in *Phragmites* sp. from low- and high-salinity areas, the researchers isolated endophytes that were tolerant to salt stress. At the same time, these endophytes increased salt tolerance of rice seedlings grown under salt stress^[95]. Some mechanisms by which endophytes increase salt tolerance in plants include increases in antioxidant enzyme activity, ion homeostasis, and increases in osmolyte levels^[97]. Any stress may induce the production of ROS. Accumulation of ROS is detrimental to cells, causing damage to cellular DNA and proteins. Plants use antioxidant enzymes to keep ROS at manageable levels. Under stress conditions, microbes increase the expression of plant antioxidant enzyme genes or secrete their own antioxidant enzymes. Fan et al.^[97] observed an increase in proline levels under salt stress. Proline acts as an antioxidant and an osmolyte, and helps prevent water loss from plant cells and maintains cell turgor. Gond et al.^[98] showed that the treatment with salt-tolerant bacterium, *Pantoea agglomerans*, enhanced salt tolerance in corn seedlings. Furthermore, the bacterium colonized the internal root cells, and a significant upregulation of the plasma membrane integral protein type 2 (PIP2-1) gene was observed. The gene codes for aquaporin proteins that regulate water flow through the plasma membranes. This helps regulate the water and ion (sodium) balance in and out of the cells and maintains cell turgor when exposed to salt stress.

Chemical stress

Invasive plants are often exposed to toxic chemicals in herbicides. Furthermore, some invasive plants can grow in heavy-metal-contaminated areas and absorb heavy metals into their tissues. As an example, the invasive plant *Typha angustifolia* grows in wetlands close to uranium mines^[99]. The plant is highly tolerant to heavy metals like cadmium, lead, and uranium. This ability of invasive

plants to tolerate toxic chemicals and metals can partly be attributed to the endophytes they harbor.

Microbes are chemical factories; some of them have evolved to metabolize toxic chemicals and metals and use them as energy for their growth or as components in their metabolic pathways^[100]. In the process, chemicals get converted into less toxic or non-toxic compounds^[100], which enables the plants to withstand toxic chemicals and grow under chemical stress^[101]. In addition, the chemical tolerance of microbes associated with plants may contribute to herbicide resistance in weeds^[102].

When considering microbial contribution to chemical stress tolerance in plants, detoxification of toxins by microbes is the most widely studied mechanism. Mesquini et al.^[103] reported detoxification of atrazine by *Streptomyces* sp., an endophyte from sugarcane. Feng et al.^[104] reported isolation of an endophytic bacterium (*Sphingomonas* sp.) from Chinese chives, which degrades chlorpyrifos (an insecticide used on plants to control pest attacks) by using it as the sole carbon source. The mechanisms involved in detoxification of herbicides and insecticides include oxidation, reduction, hydrolysis reactions, etc., mostly mediated by microbial enzymes. In addition to direct microbial detoxification, microorganisms regulate the expression of plant genes that can degrade toxins and other genes associated with metabolizing and/or e-fluxing them. Tétard-Jones and Edwards^[105] proposed that microbes are priming plants to chemical stresses, thereby making plants better tolerate downstream processing and subsequent negative consequences of toxins. Microbes are well known to induce defense responses in plants upon exposure to biotic and abiotic stresses. Early activation of these signaling pathways can alleviate stress perceived by the plant. Herbicides can cause the production of ROS as a result of their activities on plants. The ability of plants to keep ROS below detrimental levels is highly related to the plants' ability to withstand herbicide stress. Microbes can themselves produce ROS scavengers and/or work together with plant genes to produce sufficient amounts of antioxidants and exhibit tolerance to herbicides^[106]. As indirect effects, endophytes improve plant health in many ways and thus help plants better tolerate chemical stresses.

It is clear that plants are benefited by microbes during chemical stress. The contribution of microbes in plants to the development of genetic resistance to herbicides has not been sufficiently explored. Weedy plants can develop genetic resistance to herbicides through various mechanisms. Plant-associated microbes impact selection pressure and affect evolution of plants. Vila-Aiub et al.^[107] provide evidence for the effects of fungal endophytes on selection pressure and regulation of the evolution of resistance to diclofop-methyl in *Lolium multiflorum*. Microbes may have effects on the evolution of both major and minor genes governing chemical resistance. It is likely that the degree of microbial effects on genes contributing to chemical tolerance will affect the rate at which a particular plant population develops resistance to an herbicide.

Chilling and heat stress

Low temperature slows down plant growth by reducing photosynthesis and increasing cell ROS, and extreme cold may result in damage to cells due to the formation of ice crystals^[108]. In tomato, which is sometimes considered weedy, microbial endophytes (e.g., *Pararhizobium* sp.) counteract the effects of cold, enhancing plant growth and development, increasing antioxidants and other ROS management cellular systems^[108]. Subramanian et al.^[109] showed that psychrotolerant bacteria in several genera, including *Arthrobacter*, *Flavimonas*, *Flavobacterium*, *Massilia*, *Pedobacter*, and *Pseudomonas*, confer cold tolerance onto the host plant, resulting in

increased proline content. Proline is an amino acid that is associated with stress in plants and has been identified as an important amino acid for conferring cold tolerance. Cytosolic proline has been shown to be an osmo-protectant and necessary for freezing tolerance in *Arabidopsis thaliana*, an invasive weed and a model plant species^[110]. Even mycorrhizae and other fungal endophytes (*Epichloë* spp.) have been shown to result in increases in proline content in grasses and cold tolerance^[111,112].

Heat stress is a major factor affecting plants worldwide^[113]. Dastogeer et al.^[114] reviewed more than 30 articles on microbial endophyte-induced thermotolerance in plants and found that benefits from heat-tolerant microbes are not evident unless plants are under heat stress. Dastogeer et al.^[114] and Waqas et al.^[115] found that fungal endophytes increase the ability of rice to grow under prolonged heat stress, suggesting that fungal endophyte production of phytohormones and organic acids are responsible for heat tolerance. Khan et al.^[116] found that thermotolerant *Bacillus cereus* increased heat tolerance in soybean, and this involved increased levels of antioxidants and heat shock proteins. Redman et al.^[117] proposed that endophytes can be used to reduce the stress in crops at increasing temperatures as climate warms. Weeds and invasive plants are very likely to have, or have developed, microbiomes that protect them from excess chilling and heat stress due to their environmental adaptability and propensity to acquire new microbes.

Drought stress

Endophytes help plants alleviate drought stress in several ways. The mechanisms include production of osmolytes, changing root morphology in a way that plants can better absorb available water and nutrients, increasing exopolysaccharide production, production of antioxidants and balance plant hormones to reduce the damaging effects of drought stress, and changing the expression of plant genes involved in drought stress tolerance^[52,118–123]. Jeong et al.^[52] reported increased production of exopolysaccharides by *Kosakonia cowanii*, a seed-vectored endophytic bacterium of the invasive plant *Lactuca serriola*. Increased exopolysaccharide production helps plants retain soil moisture and reduce water loss. Furthermore, inoculation of *K. cowanii* into *Arabidopsis thaliana* plants under drought conditions resulted in growth promotion in plants. Li et al.^[121] proved that some of the dark septate endophytes isolated from the arid plant *Hedysarum scoparium* altered the root architecture under drought conditions. Researchers observed increased production of root biomass and root length under water-deficient conditions. These changes in root development help plants absorb water and minerals effectively and efficiently under limited water conditions and increase plant health and fitness. *Pseudomonas* sp.- and *Pantoea* sp.-inoculated barley showed increased antioxidant enzyme activity under drought stress, indicating reduced ROS damage^[123]. Furthermore, endophyte-treated plants accumulated more cations like Na⁺ and K⁺. Sodium and potassium play a critical role in osmoregulation in plants. Potassium levels affect stomatal open and closure, thereby a bacterial-induced increase in osmoregulators helps plants reduce water loss under drought conditions by controlling the water potential gradient. Yang et al.^[120] showed that several strains of endophytic *Colletotrichum* increased the biomass and chlorophyll content in the invasive plant *Ageratina adenophora* in response to drought stress. A transcriptomic study in tomato plants revealed that fungal endophytes change the expression of several plant genes involved in proline biosynthesis, ion homeostasis, and plant hormone signaling during drought stress^[122].

Light and radiation stress

Plants need light for various physiological processes, a major one among which is photosynthesis. Light levels must be in an optimal range for successful photosynthesis. Intense light conditions damage cell membranes and photoreceptors, and thereby decrease photosynthesis. Similarly, having shaded conditions with too little light is also disadvantageous for plants, reducing plant productivity by decreasing rates of photosynthesis. While the contribution of endophytes on plants tolerating light stress is largely unexplored, related studies show that endophytes have an effect. Abdolmaleki et al.^[124] showed that the application of fungal endophytes *Piriformospora indica* and *Trichoderma longibrachiatum* compensates the growth and yield reduction observed in wheat under reduced light. Similarly, Fadaei et al.^[125] showed that the application of *Chaetomium globosa* and *Bjerkandera adusta* increases the grain yield when the light intensity decreased from 100% to 70%. Though the exact mechanism remains unknown, this growth and yield compensation can be due to the endophytes enhancing overall plant health and/or by their direct actions on photosynthesis and stress tolerance. Under high UV-B irradiation, the presence of endophytes was shown to decrease lipid peroxidation and increase flower and biomass production in Antarctic pearlwort (*Colobanthus quitensis*), though the photochemical efficiency was not affected^[126]. The study showed that the endophytes modulated hormonal (salicylic acid, jasmonate, indole-3-acetic acid, abscisic acid) levels in plants exposed to high UV-B irradiation, elucidating one potential mechanism by which endophytes help plants tolerate high intensities of radiation. Barrera et al.^[127] reported increased photosynthesis efficiency and lower lipid peroxidation in *C. quitensis* in the presence of endophytes under high UV-B radiation^[127]. Furthermore, a reduced amount of ROS scavenger molecule, quercetin, was detected in endophyte-infected plants compared to non-infected plants. This can be because endophyte-infected plants are perceiving low amounts of radiation stress compared to non-infected plants. An increase in the number of inflorescences was seen in *Agrostis perennans* in the presence of endophytes under shaded conditions^[128]. Also, in *Poa autumnalis*, the presence of endophytes increased the specific leaf area under intense shaded conditions. Furthermore, the study shows a high density of fungal endophyte colonization in the leaves of *Agrostis perennans*, *Schedonorus arundinaceus*, *Poa autumnalis*, *Elymus villosus*, *Festuca subverticillata*, and *Poa alsodes* under shaded conditions.

Endopolyploidy and microbe-induced genetic and epigenetic change

From a recent study, it is hypothesized that endophytic microbes directly affect change in the plant genomes, resulting in more gene expression and genetic variation^[129]. A 20-year study comparing organically grown and conventionally grown barley showed that plants grown under organic and microbially rich conditions exhibited increased levels of gene expression compared to plants grown with chemical fertilizers and other agrochemicals^[129].

Over time, several mechanisms have been proposed to explain how microbes affect gene expression in plants. One such mechanism is the induction of endopolyploidy, also called "somatic polyploidy", which is a localized form of polyploidy that develops in vegetative plant cells and organs, where meristems typically may be diploid (or another ploidy level) and particular cells and tissues developing from meristems, including cells in leaves, stems, and

roots, may increase in ploidy level^[130,131]. Endopolyploidy is common in Angiosperms and mosses, but absent in Gymnosperms (except *Ginkgo biloba*), liverworts, ferns, and fern allies^[130]. Endopolyploidy develops cytologically in chromosome replication that is not followed by cell division, and plants show several orders more of chromosome replication ranging 4X to 64X, and higher, nuclear content. This process of generation of endopolyploids has been referred to as "endocycling"^[132]. Endopolyploidy develops in two ways, including through "endomitosis", where nuclei divide but cell division does not happen and cells become multinucleate, as is seen in plant epidermal cells, and through "endoreplication," where nuclei show internal replication of genetic material but do not divide and large mononucleate cells are produced^[133].

Endoreplication, part of root development, has been shown to lead to increased environmental stress tolerance in plants^[134]. Endoreplication is especially high in plants adapted to extreme and stressful environments^[134]. This process results in genome instability in the polyploids. During plant development, some cells show localized endoreplication and polyploidy effects. Glandular trichomes are cells that often show localized polyploids, which are often larger than diploid cells. Barkla et al.^[132] found that 70%–90% of Angiosperms show endopolyploidy in one or more cell types in halophyte plants in response to salt stress, another indication that endopolyploidy is a stress defense mechanism. Endopolyploidy is generally seen in enlarged cells (e.g., epidermal cells in roots and aerial parts of plants), as cell growth is associated with increases in endopolyploidy in those cells^[130].

Chao et al.^[135] reported that polyploid *Arabidopsis thaliana* plants showed increased salt tolerance compared to diploid plants. Yang et al.^[136] found that rice polyploids exhibited increased tolerance to drought and salt stress, which was proposed due to increased gene expression in stress and hormone response pathways. Oswald and Nuismer^[137] examined neo-polyploids (recently formed polyploids) and found increases in resistance to pathogens over diploids. Van de Peer et al.^[138] found that polyploid crops show increased resistance to fungal pathogens, nematodes, and insects. The invasive plants *Phragmites australis* and Japanese stiltgrass (*Microstegium vimineum*) show polyploidy^[139,140]. It is hypothesized that the invasiveness and environmental plasticity of these plants are related to polyploidy^[139,140]. Regardless of significant evidence, Rutland et al.^[141] noted that more must be learned about genomics of weeds to understand whether genome polyploidization in weed species is a significant process in evolution of weeds^[141].

Microorganisms influence plant gene expression and polyploidy. For example, Micci et al.^[35] observed a "nuclear symbiosis" present in many weedy plants, where bacteria colonize recently divided nuclei in the plant (Fig. 5). Using histochemical analysis, bacteria in and around plant nuclei were seen to produce ethylene and nitrate, and these substances have been shown to increase the formation of somatic polyploidy in plants^[29,142]. At present, it is clear that much more research is needed to understand how symbiotic bacteria cause changes in the host genome. Many microbial endophytes, bacteria and fungi, have been shown to produce phytohormones (e.g., auxin, ethylene, etc.) and other growth-promoting substances that induce endopolyploidy, thus potentially altering genetic expression in nuclei. Wildermuth et al.^[143] proposed and presented evidence that many biotrophic microbes symbiotic in plants induce somatic endopolyploidy to facilitate their own interaction with plants. Any effects of microbes in stimulating endoreplication in tissues of leaves, stems, and roots lead to epigenetic adaptation to the environment. Endopolyploidy via endocycling was evident in infections involving biotrophic microbes, including corn smut

(*Ustilago maydis*), powdery mildews (*Golovinomyces orontii*), bacterial spot (*Xanthomonas campestris*), Rhizobia (*Ensifer meliloti*), and arbuscular mycorrhizal fungi (*Glomus mosseae*)^[143]. With some frequency, the development of somatic endopolyploidy is induced by microbes where the plant cells show the most stress due to the nutrient exchange in the symbiosis. In plant leaves bearing powdery mildews, endopolyploidy is induced in mesophyll cells subtending the developing fungal fruiting bodies. Endopolyploidy develops within the root nodules of legumes induced by microbes that facilitates the symbiotic interactions with the plant^[143].

Aerial organs of plants are covered by epidermal cells, referred to as pavement cells, that are irregular in shape, often interlocking, and generally polyploid and multinucleate, with their size determined by the number of nuclei present^[133]. Root hairs form on root epidermal cells, with the overall length of hairs reflecting the degree of endopolyploidy present in the epidermal cells where generally a large endo-replicated nucleus develops^[144]. Epidermal cells on roots and shoots of weeds are frequently more colonized by microbes than the cells in the interior of the plant. This is because these tissues are colonized by microbes extracted from soils and cultivated on meristematic tissues of plants, where they are absorbed into plant cells, concentrating in surface layers (Fig. 6). The cells of outer tissues of weedy plants are thus microbially rich and constitute a stress resistance barrier. The microbes abundant in weeds may be critical to the development of stress tolerance, where cells with more microbes are higher in antioxidants and more reactive oxygen-tolerant. Further, the superficial presence of microbes is another type of biotic stress defense in plants, in that pathogen colonization of plants may be perturbed by superficial and endophytic microbes in a pathogen exclusion mechanism.

Another mechanism is described in the "nucleomodulin" hypothesis, according to which microbes that colonize nuclei, as is evident in many weedy plants, secrete effector proteins into plant nuclei that alter genetic expression in the plant to favor the microbe^[145]. Nucleomodulin effector proteins were found in *Agrobacterium* and *Xanthomonas* spp.^[145]. Thus, nucleomodulins are a mechanism by which microbes induce epigenetic modification of the host. Microbes also alter gene expression by repression of methylation of host genes^[146]. In a recent study of dandelion (*Taraxacum officinale*), Molina-Montenegro et al.^[147] reported that dandelion with intact microbiomes show enhanced competitiveness and increased gene expression related to stress response and DNA methylation compared to plants with reduced microbiomes, indicating

epigenetic effects that contribute to invasiveness. However, details of any interactions require further exploration.

Table 1 summarizes some published examples of weedy and invasive plants, their microbial partners, and specific benefits that they offer their hosts. These benefits range from defense against pathogens, herbivores, and abiotic stress to enhanced nutrient acquisition and growth promotion.

A reflection on crop plants

Unlike weeds, crop plants are consistently nurtured and thus have microbiomes that are not environmentally selected. Weeds benefit from a microbiome that is fortified every generation with fresh microbes absorbed from soils containing microbes adapted to the weed's environment. This does not imply that crop species lack a microbiome or that crops do not derive benefits from their microbiomes. The microbial endophyte communities of crop plants very likely play roles in the modulation of development, including roots and root hairs and other plant structures. Without these microbes in crops, plant development would be diminished. Rather than possessing an environmentally selected microbiome, crops possess whatever microbes can be obtained from agricultural soils—and often these are of limited diversity in soils with conventional management. Crop plants are thus dependent on humans to provide nutrients and for defense against stresses and disease, while weeds possess more agency to fend for themselves.

It is tempting to seek to "rewild" crop plants by re-establishing evolved microbiomes in plants by using microbes obtained from weedy relatives^[150]. However, this demands crops to be cultivated in ways more comparable to how weeds grow—without significant human intervention in terms of soil and plant management. Rewilding crop microbiomes could result in crop plants that are hardier and require fewer agrochemical inputs; however, plants also may in time develop more variability due to phenomena like endopolyploidy or the triggering of transposons that may affect the uniformity of crops needed for quality control and efficient harvesting. On the other hand, it may be possible to increase the use of microbes in plants to increase mutation rates to induce new variability and then remove microbes to regain genome stability and crop uniformity. It is also possible that selected microbes from weeds may be used as biostimulants to promote growth and protect crops in order to cope with very specific stressors in the environment, for example, to

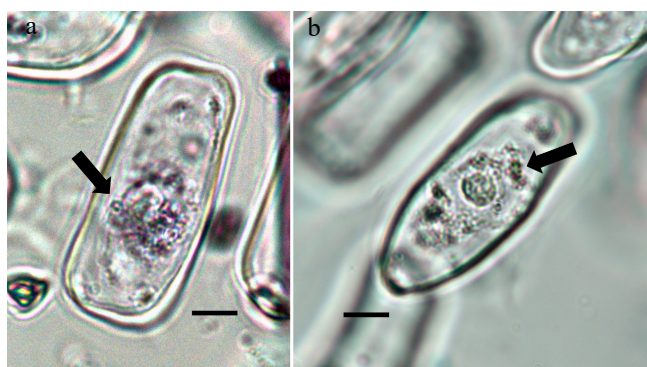


Fig. 5 Root cap cells of *Poa annua* showing bacterial endophytes around the nuclei after staining with Congo red indicator. (a) Arrow shows bacteria obscuring the nucleus (bar = 10 µm). (b) Arrow shows bacteria surrounding the nucleus (bar = 10 µm). Images are original and are not previously published.

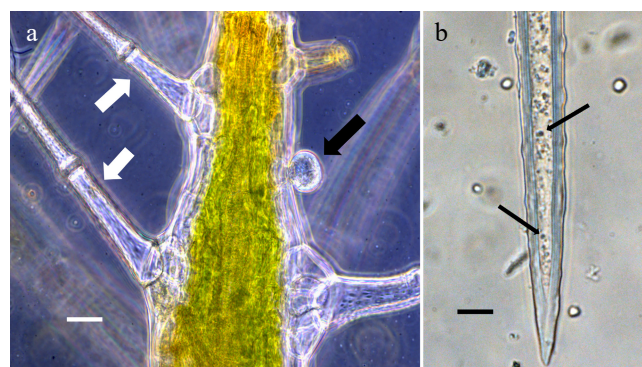


Fig. 6 Henbit (*Lamium amplexicaule*). (a) Henbit scale leaf tip showing large filamentous trichomes (white arrows) and a glandular trichome (black arrow; bar = 40 µm). (b) Trichome tip showing bacteria (arrows) within trichome cells stained with diphenylamine (bar = 10 µm). Images are original and are not previously published.

Table 1. Weeds/invasive plants-associated microbes and their proposed effects.

Weed/Invasive plant species	Microbes identified	Proposed effects	Ref.
<i>Achnatherum robustum</i>	<i>Epichloë</i> sp.	Defense against herbivorous animals	[62]
<i>Achnatherum sibiricum</i>	<i>Epichloë gansuensis</i> , <i>Epichloë sibirica</i>	Growth promotion	[63]
<i>Ageratina adenophora</i>	<i>Colletotrichum</i> spp.	Drought and nutrient stress tolerance, protection against pathogens	[120]
<i>Agrostis perennans</i>	<i>Epichloë amarillans</i>	Increased inflorescence formation in shade	[128]
<i>Argyreia</i> sp.	<i>Periglandula</i> sp.	Production of ergot alkaloids, anti-herbivory	[64]
<i>Astragalus</i> sp.	<i>Alternaria oxytropis</i>	Alkaloid swainsonine production, anti-herbivory	[65]
<i>Chromolaena odorata</i>	<i>Fusarium</i> sp.	Pathogenic effects on native plants (offensive mutualism)	[27]
<i>Cynodon dactylon</i>	<i>Desulfovibrio vulgaris</i>	Nitrogen fixation	[48]
	<i>Metabacillus indicus</i>	Potassium solubilization, nitrogen fixation, growth due to hormone production	[50]
<i>Dichanthelium lanuginosum</i>	<i>Curvularia</i> sp.	Thermotolerance	[86]
<i>Eleusine indica</i>	<i>Alcaligenes faecalis</i>	Phosphate solubilization, nitrogen fixation, growth due to hormone production	[50]
<i>Elymus repens</i>	<i>Acinetobacter</i> sp., <i>Bacillus</i> sp., <i>Stenotrophomonas</i> sp., <i>Pseudomonas</i> sp.	Generalized growth promotion	[25]
<i>Ipomoea</i> sp.	<i>Periglandula</i> sp.	Production of ergot alkaloids, anti-herbivory	[64]
<i>Jasione</i> sp.	<i>Rhodococcus rhodochrous</i>	Arsenic stress tolerance	[101]
<i>Lactuca serriola</i>	<i>Kosakonia cowanii</i>	Drought tolerance	[52]
<i>Leymus mollis</i>	<i>Fusarium culmorum</i>	Stress tolerance by habitat-adapted symbiosis	[87]
<i>Lolium multiflorum</i>	<i>Epichloë</i> sp.	Herbicide tolerance	[107]
<i>Lolium perenne</i>	<i>Epichloë</i> sp.	Growth promotion, increased nutrient content, increased metabolic activity	[92]
<i>Phragmites australis</i>	<i>Bacillus amyloliquefaciens</i>	Growth promotion under low nitrogen, growth due to hormone production, protection against pathogens by lipopeptide production	[45]
	<i>Alternaria tenuissima</i> , <i>Arthrinium arundinis</i> , <i>Bipolaris buchloes</i>	Salt stress tolerance	[95]
	Dark septate fungal endophytes	Salt stress tolerance	[96]
	<i>Microbacterium oxydans</i>	Growth promotion under low nitrogen, growth due to hormone production	[45]
<i>Phragmites karka</i>	<i>Mangrovibacter phragmitis</i>	Nitrogen fixation	[46]
<i>Phytolacca americana</i>	<i>Burkholderia</i> sp.	Increased germination rate, Increased biomass, Increased potassium availability	[26]
	<i>Phenylobacterium</i> sp.	Pathogen control	[26]
<i>Schedonorus arundinaceus</i>	<i>Epichloë coenophiala</i>	Production of ergot alkaloids, anti-herbivory, abiotic stress tolerance, range extension	[84]
<i>Schedonorus pratensis</i>	<i>Epichloë uncinata</i>	Drought avoidance through control of transpiration	[148]
<i>Sorghum halepense</i>	<i>Xanthomonas melonis</i> , <i>Agrobacterium tumefaciens</i> , <i>Herbaspirillum seropedicae</i> , <i>Sphingobium amiense</i> , <i>Pseudomonas jessenii</i> , <i>Caulobacter vibroides</i>	Nitrogen fixation	[24]
<i>Stellera chamaejasme</i>	<i>Acinetobacter</i> sp., <i>Pseudomonas</i> sp., <i>Alcaligenes</i> sp., <i>Lysinibacillus</i> sp.	Growth promotion, growth due to hormone production, potassium solubilization, phosphorus solubilization, nitrogen fixation	
<i>Taraxacum officinale</i>	Unidentified microbes	Increased production of allelopathic compounds, increased expression of stress response, and DNA methylation maintenance genes	[147]
<i>Thespesia populnea</i>	<i>Bacillus amyloliquefaciens</i>	Growth due to hormone production, nitrogen fixation, phosphorus solubilization, salt tolerance, protection against pathogens	[149]
<i>Turbina</i> sp.	<i>Periglandula</i> sp.	Production of ergot alkaloids, anti-herbivory	[64]
<i>Typha angustifolia</i>	<i>Staphylococcus</i> sp., <i>Pseudomonas</i> sp., <i>Bacillus</i> sp., <i>Micrococcus</i> sp., <i>Sphingomonas</i> sp.	Generalized growth promotion due to hormone production	[49]
<i>Wedelia trilobata</i>	<i>Sphingomonas</i> sp., <i>Pseudarthrobacter</i> sp.	Generalized growth promotion	[83]

protect against damage from extreme climate events like excess heat. This is an area of research that holds promise but demands more attention to understand the effects of microbes on plant growth, health, and genetics.

Conclusions

We conclude that "weediness" and "invasiveness", at least in part, is a function of the weed microbiome, although further research is needed to provide additional insights and understandings. The strongest evidence for microbial involvement in weed success is in abiotic and biotic stress tolerance, nutrient acquisition, and growth

promotion. The effects of microbes on plant gene expression or direct changes to the host genome require more investigation. Experiments involving comparative metagenomic and transcriptomic analysis of weeds and crop plants and their microbiomes may lead to a better understanding of the mechanisms of benefits of microbes to weeds. Furthermore, better knowledge of precisely how endophytes affect plant DNA expression, endopolyplidy, and DNA methylation will lead to a better understanding of potential epigenetic effects microbes have on weeds and invasive plants. The role of the weed microbiome in increasing invasiveness or aggressiveness poses the question, can the microbiome be manipulated to control weed invasiveness? This constitutes a novel and sustainable strategy for weedy and invasive plant management. Future work

will be needed to evaluate this strategy. Furthermore, the acquisition of biostimulant microbes from weeds is useful as a source of microbes to enhance crop productivity and hardiness.

Author contributions

The authors confirm their contributions to this study as follows: discussion and planning: Rodrigopulle CU, White JF, Elmore MT, Kingsley KL, Gond SK, Kowalski KP; original draft composition: Rodrigopulle CU, White JF; editing and corrections: Rodrigopulle CU, White JF, Elmore MT, Kowalski KP, Gond SK, Kingsley KL. All authors reviewed the results and approved the final version of the manuscript.

Data availability

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

Acknowledgments

Funding was provided to Rutgers University in agreement G21AC10139 "Truncating the Competitive Ability of *Phragmites australis* by Targeting Microbial Endophytes." We acknowledge support of the USDA Multistate Project #5147, Cooperative Ecosystem Study Unit focused on invasive plants, and the Dept. of Botany, Banaras Hindu University in India, for a teaching release that permitted SK Gond to work at Rutgers University from 10/1/2024 to 9/30/2025. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Conflict of interest

The authors declare that they have no conflict of interest.

Dates

Received 19 July 2025; Revised 3 April 2026; Accepted 21 April 2026; Published online 29 July 2026

References

- [1] Weed Science Society of America (WSSA). 2016. WSSA fact sheet: do you have a weed, noxious weed, invasive weed, or "superweed"? Public Awareness Committee of the Weed Science Society of America. <https://wssa.net/wp-content/uploads/WSSA-Weed-Science-Definitions.pdf>
- [2] United States Department of Agriculture (USDA), U. S. Forest Service. Invasive plants. www.fs.usda.gov/wildflowers/invasives/index.shtml
- [3] Middleton BA. 2019. Invasive plant species. In *Encyclopedia of ecology*, ed. Brian F. Vol. 1. 2nd Edition. Amsterdam, Netherlands: Elsevier. pp. 431–440 doi: 10.1016/B978-0-12-409548-9.11175-3
- [4] Bateman HL, Ostojia SM. 2012. Invasive woody plants affect the composition of native lizard and small mammal communities in riparian woodlands. *Animal Conservation* 15(3):294–304
- [5] Rashid B, Husnain T, Riazuddin S. 2010. Herbicides and pesticides as potential pollutants: a global problem. In *Plant Adaptation and Phytoremediation*, eds. Ashraf M, Ozturk M, Ahmad M. Dordrecht: Springer. pp. 427–447 doi: 10.1007/978-90-481-9370-7_19
- [6] Mendes KF, Régo APJ, Takeshita V, Tornisiello VL. 2019. Water resource pollution by herbicide residues. In *Biochemical Toxicology - Heavy Metals and Nanomaterials*, eds. Ince M, Ince OK, Ondrasek G. London: IntechOpen
- [7] Edwards CA, Pimentel D. 1989. Impact of herbicides on soil ecosystems. *Critical Reviews in Plant Sciences* 8(3):221–257
- [8] Halstead JM, Michaud J, Hallas-Burt S, Gibbs JP. 2003. Hedonic analysis of effects of a nonnative invader (*Myriophyllum heterophyllum*) on New Hampshire (USA) lakefront properties. *Environmental Management* 32(3):391–398
- [9] Marks M, Lapin B, Randall J. 1994. *Phragmites australis* (P. communis): threats, management and monitoring. *Natural Areas Journal* 14(4):285–294
- [10] Obiri JF. 2011. Invasive plant species and their disaster-effects in dry tropical forests and rangelands of Kenya and Tanzania. *Jàmbá: Journal of Disaster Risk Studies* 3(2):151–158
- [11] Moravcová L, Pyšek P, Jarošík V, Pergl J. 2015. Getting the right traits: reproductive and dispersal characteristics predict the invasiveness of herbaceous plant species. *PLoS One* 10(4):e0123634
- [12] van Kleunen M, Weber E, Fischer M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* 13(2):235–245
- [13] Kalisz S, Kivlin SN, Bialic-Murphy L. 2021. Allelopathy is pervasive in invasive plants. *Biological Invasions* 23(2):367–371
- [14] Sharma G, Barney JN, Westwood JH, Haak DC. 2021. Into the weeds: new insights in plant stress. *Trends in Plant Science* 26(10):1050–1060
- [15] Trognitz F, Hackl E, Widhalm S, Sessitsch A. 2016. The role of plant-microbiome interactions in weed establishment and control. *FEMS Microbiology Ecology* 92(10):fiw138
- [16] Rout ME, Callaway RM. 2012. Interactions between exotic invasive plants and soil microbes in the rhizosphere suggest that 'everything is not everywhere'. *Annals of Botany* 110(2):213–222
- [17] Pérez-Jaramillo JE, Mendes R, Raaijmakers JM. 2016. Impact of plant domestication on rhizosphere microbiome assembly and functions. *Plant Molecular Biology* 90(6):635–644
- [18] Santhanam R, Luu VT, Weinhold A, Goldberg J, Oh Y, et al. 2015. Native root-associated bacteria rescue a plant from a sudden-wilt disease that emerged during continuous cropping. *Proceedings of the National Academy of Sciences of the United States of America* 112(36):E5013–E5020
- [19] Santhanam R, Menezes RC, Grabe V, Li D, Baldwin IT, et al. 2019. A suite of complementary biocontrol traits allows a native consortium of root-associated bacteria to protect their host plant from a fungal sudden-wilt disease. *Molecular Ecology* 28(5):1154–1169
- [20] Miranda-Carrasco A, Navarro-Noya YE, Govaerts B, Verhulst N, Dendooven L. 2022. Nitrogen fertilizer application alters the root endophyte bacterial microbiome in maize plants, but not in the stem or rhizosphere soil. *Microbiology Spectrum* 10(6):e01785-22
- [21] Rodrigues RR, Pineda RP, Barney JN, Nilsen ET, Barrett JE, et al. 2015. Plant invasions associated with change in root-zone microbial community structure and diversity. *PLoS One* 10(10):e0141424
- [22] Massensini AM, Bonduki VHA, Melo CAD, Tótola MR, Ferreira FA, et al. 2014. Soil microorganisms and their role in the interactions between weeds and crops. *Planta Daninha* 32(4):873–884
- [23] Samad A, Trognitz F, Compant B, Antonielli L, Sessitsch A. 2017. Shared and host-specific microbiome diversity and functioning of grapevine and accompanying weed plants. *Environmental Microbiology* 19(4):1407–1424
- [24] Rout ME, Chrzanowski TH. 2009. The invasive *Sorghum halepense* harbors endophytic N₂-fixing bacteria and alters soil biogeochemistry. *Plant and Soil* 315(1):163–172
- [25] Sturz AV, Matheson BG, Arsenault W, Kimpinski J, Christie BR. 2001. Weeds as a source of plant growth promoting rhizobacteria in agricultural soils. *Canadian Journal of Microbiology* 47(11):1013–1024
- [26] Meng Y, Geng X, Zhu P, Bai X, Zhang P, et al. 2024. Enhanced mutualism: a promotional effect driven by bacteria during the early invasion of *Phytolacca americana*. *Ecological Applications* 34(1):e2742
- [27] Mangla S, Callaway RM. 2008. Exotic invasive plant accumulates native soil pathogens which inhibit native plants. *Journal of Ecology* 96(1):58–67

- [28] Frati F, Salvatori C, Incorvaia C, Bellucci A, Di Cara G, et al. 2018. The role of the microbiome in asthma: the gut–lung axis. *International Journal of Molecular Sciences* 20(1):123
- [29] Chang X, Kingsley KL, White JF. 2021. Chemical interactions at the interface of plant root hair cells and intracellular bacteria. *Microorganisms* 9(5):1041
- [30] Verma SK, Sahu PK, Kumar K, Pal G, Gond SK, et al. 2021. Endophyte roles in nutrient acquisition, root system architecture development and oxidative stress tolerance. *Journal of Applied Microbiology* 131(5):2161–2177
- [31] Lau JA, Funk JL. 2023. How ecological and evolutionary theory expanded the 'ideal weed' concept. *Oecologia* 203(3–4):251–266
- [32] Jiang Y, Li Q, Mao W, Tang W, White Jr JF, et al. 2022. Endophytic bacterial community of *Stellera chamaejasme* L. and its role in improving host plants' competitiveness in grasslands. *Environmental Microbiology* 24(8):3322–3333
- [33] Irizarry I, White JF. 2018. *Bacillus amyloliquefaciens* alters gene expression, ROS production and lignin synthesis in cotton seedling roots. *Journal of Applied Microbiology* 124(6):1589–1603
- [34] White JF, Kingsley KL, Verma SK, Kowalski KP. 2018. Rhizophagy cycle: an oxidative process in plants for nutrient extraction from symbiotic microbes. *Microorganisms* 6(3):95
- [35] Micci A, Zhang Q, Chang X, Kingsley K, Park L, et al. 2022. Histochemical evidence for nitrogen-transfer endosymbiosis in non-photosynthetic cells of leaves and inflorescence bracts of angiosperms. *Biology* 11(6):876
- [36] Pečenková T, Janda M, Ortmannová J, Hajná V, Stehlíková Z, et al. 2017. Early *Arabidopsis* root hair growth stimulation by pathogenic strains of *Pseudomonas syringae*. *Annals of Botany* 120(3):437–446
- [37] Paungfoo-Lonhienne C, Lonhienne TGA, Schmidt, S. 2010. DNA uptake by *Arabidopsis* induces changes in the expression of CLE peptides which control root morphology. *Plant Signaling & Behavior* 5(9):1112–1114
- [38] Jo I, Fridley JD, Frank DA. 2017. Invasive plants accelerate nitrogen cycling: evidence from experimental woody monocultures. *Journal of Ecology* 105(4):1105–1110
- [39] Kourtev PS, Huang WZ, Ehrenfeld JG. 1999. Differences in earthworm densities and nitrogen dynamics in soils under exotic and native plant species. *Biological Invasions* 1:237–245
- [40] Ehrenfeld JG, Kourtev P, Huang W. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* 11(5):1287–1300
- [41] Laungani R, Knops JM. 2009. Species-driven changes in nitrogen cycling can provide a mechanism for plant invasions. *Proceedings of the National Academy of Sciences of the United States of America* 106(30):12400–12405
- [42] Kourtev PS, Ehrenfeld JG, Häggblom M. 2002. Exotic plant species alter the microbial community structure and function in the soil. *Ecology* 83(11):3152–3166
- [43] Steer J, Harris JA. 2000. Shifts in the microbial community in rhizosphere and non-rhizosphere soils during the growth of *Agrostis stolonifera*. *Soil Biology and Biochemistry* 32(6):869–878
- [44] Baldani JL, Baldani VLD, Seldin L, Döbereiner J. 1986. Characterization of *Herbaspirillum seropedicae* gen. nov., sp. nov., a root-associated nitrogen-fixing bacterium. *International Journal of Systematic and Evolutionary Microbiology* 36(1):86–93
- [45] Soares MA, Li HY, Kowalski KP, Bergen M, Torres MS, et al. 2016. Functional role of bacteria from invasive *Phragmites australis* in promotion of host growth. *Microbial Ecology* 72(2):407–417
- [46] Behera P, Venkata Ramana V, Maharana B, Joseph N, Vaishampayan P, et al. 2017. *Mangrovibacter phragmitis* sp. nov., an endophyte isolated from the roots of *Phragmites karka*. *International Journal of Systematic and Evolutionary Microbiology* 67(5):1228–1234
- [47] Döbereiner, J. 1988. Isolation and identification of root associated diazotrophs. *Plant and soil* 110(2):207–212
- [48] Sapkota S, Harris-Shultz KR, Strickland TC, Anderson WF. 2023. Identification of cultured and diazotrophic bacterial endophytes in warm-season grasses. *PhytoFrontiers* 3(2):411–419
- [49] Saha C, Mukherjee G, Agarwal-Banka P, Seal A. 2016. A consortium of non-rhizobial endophytic microbes from *Typha angustifolia* functions as probiotic in rice and improves nitrogen metabolism. *Plant Biology* 18(6):938–946
- [50] Fatema K, Mahmud NU, Gupta DR, Siddiqui MN, Sakif TI, et al. 2024. Enhancing rice growth and yield with weed endophytic bacteria *Alcaligenes faecalis* and *Metabacillus indicus* under reduced chemical fertilization. *PLoS One* 19(5):e0296547
- [51] Long XH, Zhao J, Liu ZP, Rengel Z, Liu L, et al. 2014. Applying geostatistics to determine the soil quality improvement by Jerusalem artichoke in coastal saline zone. *Ecological Engineering* 70:319–326
- [52] Jeong S, Kim TM, Choi B, Kim Y, Klm E. 2021. Invasive *Lactuca serriola* seeds contain endophytic bacteria that contribute to drought tolerance. *Scientific Reports* 11:13307
- [53] Verma SK, White JF. 2025. From 'nitrosome' to 'nitroplast': stages in the evolution of nitrogen-fixing organelles from free-living diazotrophs. *Symbiosis* 95(1):29–34
- [54] Sher AW, Aufrecht JA, Herrera D, Zimmerman AE, Kim YM, et al. 2024. Dynamic nitrogen fixation in an aerobic endophyte of *Populus*. *The ISME Journal* 18(1):wrad012
- [55] Shelake RM, Pramanik D, Kim JY. 2019. Exploration of plant-microbe interactions for sustainable agriculture in CRISPR Era. *Microorganisms* 7(8):269
- [56] Rosenblueth M, Ormeño-Orrillo E, López-López A, Rogel MA, Reyes-Hernández BJ, et al. 2018. Nitrogen fixation in cereals. *Frontiers in Microbiology* 9:1794
- [57] Yan D, Tajima H, Cline LC, Fong RY, Ottaviani JL, et al. 2022. Genetic modification of flavone biosynthesis in rice enhances biofilm formation of soil diazotrophic bacteria and biological nitrogen fixation. *Plant Biotechnology Journal* 20(11):2135–2148
- [58] Qin Y, Xie XQ, Khan Q, Wei JL, Sun AN, et al. 2022. Endophytic nitrogen-fixing bacteria DX120E inoculation altered the carbon and nitrogen metabolism in sugarcane. *Frontiers in Microbiology* 13:1000033
- [59] Poole P, Ramachandran V, Terpolilli J. 2018. Rhizobia: from saprophytes to endosymbionts. *Nature Reviews Microbiology* 16(5):291–303
- [60] White JF, Torres MS. 2018. *Defensive mutualism in microbial symbioses*. Boca Raton, FL: CRC Press. 430 pp www.routledge.com/Defensive-Mutualism-in-Microbial-Symbiosis/WhiteJr-Torres/p/book/9781138372672
- [61] Schardl CL, Young CA, Hesse U, Amyotte SG, Andreeva K, et al. 2013. Plant-symbiotic fungi as chemical engineers: multi-genome analysis of the Clavicipitaceae reveals dynamics of alkaloid loci. *PLoS Genetics* 9(2):e1003323
- [62] Shymanovich T, Saari S, Lovin ME, Jarmusch AK, Jarmusch SA, et al. 2015. Alkaloid variation among epichloid endophytes of sleepygrass (*Achnatherum robustum*) and consequences for resistance to insect herbivores. *Journal of Chemical Ecology* 41(1):93–104
- [63] Zhou Y, Li X, Liu H, Gao Y, Mace WJ, et al. 2019. Effects of endophyte infection on the competitive ability of *Achnatherum sibiricum* depend on endophyte species and nitrogen availability. *Journal of Plant Ecology* 12(5):815–824
- [64] Leistner E, Steiner U. 2018. The genus *Periglandula* and its symbiont with morning glory plants (Convolvulaceae). In *Physiology and Genetics: Selected Basic and Applied Aspects*, eds. Anke T, Schüffler A. Cham: Springer International Publishing. pp. 131–147 doi: 10.1007/978-3-319-71740-1_5
- [65] Yang F, Li Y, Lu P, Wang Y, Gao F, et al. 2025. The effects of *P5CR* gene function of endophytic fungus *Alternaria oxypetris* OW7.8 on swainsonine biosynthesis. *Biomolecules* 15(4):460
- [66] Zhao M, Gao X, Wang J, He X, Han B. 2013. A review of the most economically important poisonous plants to the livestock industry on temperate grasslands of China. *Journal of Applied Toxicology* 33(1):9–17
- [67] Jelbert K, Stott I, McDonald RA, Hodgson D. 2015. Invasiveness of plants is predicted by size and fecundity in the native range. *Ecology and Evolution* 5(10):1933–1943

- [68] Bak GR, Lee KK, Clark IM, Mauchline TH, Kavamura VN, et al. 2024. The potato rhizosphere microbiota correlated to the yield of three different regions in Korea. *Scientific Reports* 14(1):4536
- [69] de Andrade LA, Santos CHB, Frezarin ET, Sales LR, Rigobelo EC. 2023. Plant growth-promoting rhizobacteria for sustainable agricultural production. *Microorganisms* 11(4):1088
- [70] Sharma I, Raina A, Choudhary M, Apra, Kaul S, et al. 2023. Fungal endophyte bioinoculants as a green alternative towards sustainable agriculture. *Heliyon* 9(9):e19487
- [71] Rho H, Van Epps V, Kim SH, Doty SL. 2020. Endophytes increased fruit quality with higher soluble sugar production in honeycrisp apple (*Malus pumila*). *Microorganisms* 8(5):699
- [72] Khan Z, Guelich G, Phan H, Redman R, Doty S. 2012. Bacterial and yeast endophytes from poplar and willow promote growth in crop plants and grasses. *International Scholarly Research Notices* 2012:890280
- [73] White JF, Kingsley KL, Zhang Q, Verma R, Obi N, et al. 2019. Endophytic microbes and their potential applications in crop management. *Pest Management Science* 75(10):2558–2565
- [74] Jones-Held S, White JF. 2024. Effects of endophytes on early growth and ascorbate metabolism in *Brassica napus*. *Frontiers in Plant Science* 15:1480387
- [75] Singh RR, Demeestere K, Kyndt T. 2023. Ascorbate oxidation stimulates rice root growth via effects on auxin and abscisic acid levels. *Plant Growth Regulation* 103(1):151–163
- [76] Hodgson S, de Cates C, Hodgson J, Morley NJ, Sutton BC, et al. 2014. Vertical transmission of fungal endophytes is widespread in forbs. *Ecology and Evolution* 4(8):1199–1208
- [77] Manirajan BA, Maisinger C, Ratering S, Rusch V, Schwiertz A, et al. 2018. Diversity, specificity, co-occurrence and hub taxa of the bacterial-fungal pollen microbiome. *FEMS Microbiology Ecology* 94(8):fyi112
- [78] Cook D, Gardner DR, Ralphs MH, Pfister JA, Welch KD, et al. 2009. Swainsonine concentrations and endophyte amounts of *Undulifilum oxytropis* in different plant parts of *Oxytropis sericea*. *Journal of Chemical Ecology* 35(10):1272–1278
- [79] Frank AC, Saldierna Guzmán JP, Shay JE. 2017. Transmission of bacterial endophytes. *Microorganisms* 5(4):70
- [80] Madmony A, Chernin L, Pleban S, Peleg E, Riov J. 2005. *Enterobacter cloacae*, an obligatory endophyte of pollen grains of mediterranean pines. *Folia Microbiologica* 50(3):209–216
- [81] Cullen NP, Fitters AM, Ashman TL. 2021. Integrating microbes into pollination. *Current Opinion in Insect Science* 44:48–54
- [82] Yenikalayc A. 2025. Impact of different strains of *Bacillus* spp. on the bulb production of *Tulipa sintenisii* Baker. *Frontiers in Plant Science* 15:1456919
- [83] Mei YH, Li X, Zhou JY, Kong FL, Qi SS, et al. 2022. Both adaptability and endophytic bacteria are linked to the functional traits in the invasive clonal plant *Wedelia trilobata*. *Plants* 11(23):3369
- [84] Ferguson TD, Vanzant ES, McLeod KR. 2021. Endophyte infected tall fescue: plant symbiosis to animal toxicosis. *Frontiers in Veterinary Science* 8:774287
- [85] Perez LI, Gundel PE, Parisi PG, Moyano J, Fiorenza JE, et al. 2021. Can seed-borne endophytes promote grass invasion by reducing host dependence on mycorrhizas? *Fungal Ecology* 52(3):101077
- [86] Redman RS, Sheehan KB, Stout RG, Rodriguez RJ, Henson JM. 2002. Thermotolerance generated by plant/fungal symbiosis. *Science* 298(5598):1581
- [87] Rodriguez RJ, Henson J, Van Volkenburgh E, Hoy M, Wright L, et al. 2008. Stress tolerance in plants via habitat-adapted symbiosis. *The ISME journal* 2(4):404–416
- [88] Álvarez-Loayza P, White Jr JF, Torres MS, Balslev H, Kristiansen T, et al. 2011. Light converts endosymbiotic fungus to pathogen, influencing seedling survival and niche-space filling of a common tropical tree, *Iriartea deltoidea*. *PLoS One* 6(1):e16386
- [89] Wan JZ, Wang CJ, Tan JF, Yu FH. 2017. Climatic niche divergence and habitat suitability of eight alien invasive weeds in China under climate change. *Ecology and Evolution* 7(5):1541–1552
- [90] Gucker Corey L. 2008. *Phragmites australis*. Fire effects information system. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). www.fs.usda.gov/database/feis/plants/graminoid/phraus/all.html
- [91] Chambers RM, Osgood DT, Bart DJ, Montalto F. 2003. *Phragmites australis* invasion and expansion in tidal wetlands: interactions among salinity, sulfide, and hydrology. *Estuaries* 26(2):398–406
- [92] Chen Z, Jin Y, Yao X, Chen T, Wei X, et al. 2020. Fungal endophyte improves survival of *Lolium perenne* in low fertility soils by increasing root growth, metabolic activity and absorption of nutrients. *Plant and Soil* 452(1–2):185–206
- [93] Belesky DP, West CP. 2009. Abiotic stresses and endophyte effects. In *Tall Fescue for the Twenty-first Century*, eds. Fribourg HA, Hannaway DB, West CP. Vol. 53. Madison, WI: American Society of Agronomy, Inc. pp 49–64 doi: 10.2134/agronmonogr53.c4
- [94] Malinowski DP, Belesky DP. 2000. Adaptations of endophyte-infected cool-season grasses to environmental stresses: mechanisms of drought and mineral stress tolerance. *Crop Science* 40(4):923–940
- [95] Soares MA, Li HY, Kowalski KP, Bergen M, Torres MS, et al. 2016. Evaluation of the functional roles of fungal endophytes of *Phragmites australis* from high saline and low saline habitats. *Biological Invasions* 18(9):2689–2702
- [96] Gonzalez MM, Baldwin AH, Maul JE, Yarwood SA. 2020. Dark septate endophyte improves salt tolerance of native and invasive lineages of *Phragmites australis*. *The ISME Journal* 14(8):1943–1954
- [97] Fan D, Subramanian S, Smith DL. 2020. Plant endophytes promote growth and alleviate salt stress in *Arabidopsis thaliana*. *Scientific Reports* 10(1):12740
- [98] Gond SK, Torres MS, Bergen MS, Helsel Z, White Jr JF. 2015. Induction of salt tolerance and up-regulation of aquaporin genes in tropical corn by rhizobacterium *Pantoea agglomerans*. *Letters in Applied Microbiology* 60(4):392–399
- [99] Ghosh UD, Singh PK, Ganguli S, Saha C, Chandra A, et al. 2019. Rhizospheric soil of *Typha angustifolia* L. from heavy metal contaminated and free sites: comparative profiling reveals selective abundance of γ -proteobacteria and β -proteobacteria. *Indian Journal of Experimental Biology* 57(10):733–740
- [100] Raab A, Feldmann J. 2003. Microbial transformation of metals and metalloids. *Science Progress* 86(Pt 3):179–202
- [101] González-Benítez N, Martín-Rodríguez I, Cuesta I, Arrayás M, White JF, et al. 2021. Endophytic microbes are tools to increase tolerance in *Jasione* plants against arsenic stress. *Frontiers in Microbiology* 12:664271
- [102] Lonkar K, Bodade R. 2021. Potential role of endophytes in weeds and herbicide tolerance in plants. In *Plant Growth-Promoting Microbes for Sustainable Biotic and Abiotic Stress Management*, eds. Mohamed HI, El-Beltagi HEDS, Abd-El salam KA. Cham: Springer. pp. 227–250 doi: 10.1007/978-3-030-66587-6_9
- [103] Mesquini JA, Sawaya ACHF, López BGC, Oliveira VM, Miyasaka NRS. 2015. Detoxification of atrazine by endophytic *Streptomyces* sp. isolated from sugarcane and detection of nontoxic metabolite. *Bulletin of Environmental Contamination and Toxicology* 95(6):803–809
- [104] Feng F, Ge J, Li Y, Cheng J, Zhong J, et al. 2017. Isolation, colonization, and chlorpyrifos degradation mediation of the endophytic bacterium *Sphingomonas* strain HJY in Chinese Chives (*Allium tuberosum*). *Journal of Agricultural and Food Chemistry* 65(6):1131–1138
- [105] Tétard-Jones C, Edwards R. 2016. Potential roles for microbial endophytes in herbicide tolerance in plants. *Pest Management Science* 72(2):203–209
- [106] Mohy-Ud-Din W, Chen F, Bashir S, Akhtar MJ, Asghar HN, et al. 2025. Enhancing maize yield and antioxidant capacity with glyphosate-resilient rhizobacteria in glyphosate contaminated soil. *BMC Plant Biology* 25(1):1255
- [107] Vila-Aiub MM, Martinez-Ghersa MA, Ghersa CM. 2003. Evolution of herbicide resistance in weeds: vertically transmitted fungal endophytes as genetic entities. *Evolutionary Ecology* 17:441–456

- [108] Díaz-Narváez L, Atanasov KE, Murillo E, Alcázar R. 2024. *Pararhizobium* sp. strains enhancing chilling stress tolerance and yield in tomato plants. *Plant Stress* 14:100587
- [109] Subramanian P, Kim K, Krishnamoorthy R, Mageswari A, Selvakumar G, et al. 2016. Cold stress tolerance in psychrotolerant soil bacteria and their conferred chilling resistance in tomato (*Solanum lycopersicum* Mill.) under low temperatures. *PLoS One* 11(8):e0161592
- [110] Hoermiller II, Funck D, Schönewolf L, May H, Heyer AG. 2022. Cytosolic proline is required for basal freezing tolerance in *Arabidopsis*. *Plant, Cell & Environment* 45(1):147–155
- [111] Chun SC, Paramasivan M, Chandrasekaran M. 2018. Proline accumulation influenced by osmotic stress in arbuscular mycorrhizal symbiotic plants. *Frontiers in Microbiology* 9:2525
- [112] Lee K, Missaoui A, Mahmud K, Presley H, Lonnee M. 2021. Interaction between grasses and *Epichloë* endophytes and its significance to biotic and abiotic stress tolerance and the rhizosphere. *Microorganisms* 9(11):2186
- [113] Shaffique S, Khan MA, Wani SH, Pande A, Imran M, et al. 2022. A review on the role of endophytes and plant growth promoting rhizobacteria in mitigating heat stress in plants. *Microorganisms* 10(7):1286
- [114] Dastogeer KMG, Zahan MI, Rhaman MS, Sarker MSA, Chakraborty A. 2022. Microbe-mediated thermotolerance in plants and pertinent mechanisms- a meta-analysis and review. *Frontiers in Microbiology* 13:833566
- [115] Waqas M, Khan AL, Shahzad R, Ullah I, Khan AR, et al. 2015. Mutualistic fungal endophytes produce phytohormones and organic acids that promote japonica rice plant growth under prolonged heat stress. *Journal of Zhejiang University-Science B* 16(12):1011–1018
- [116] Khan MA, Asaf S, Khan AL, Jan R, Kang SM, et al. 2020. Thermotolerance effect of plant growth-promoting *Bacillus cereus* SA1 on soybean during heat stress. *BMC Microbiology* 20(1):175
- [117] Redman RS, Kim YO, Woodward CJDA, Greer C, Espino L, et al. 2011. Increased fitness of rice plants to abiotic stress via habitat adapted symbiosis: a strategy for mitigating impacts of climate change. *PLoS One* 6(7):e14823
- [118] Liu Y, Wei X. 2019. Dark septate endophyte improves drought tolerance of *Ormosia hosiei* Hemsley & E. H. Wilson by modulating root morphology, ultrastructure, and the ratio of root hormones. *Forests* 10(10):830
- [119] West CP. 2018. Physiology and drought tolerance of endophyte-infected grasses. In *Biotechnology of Endophytic Fungi of Grasses*, eds. Bacon CW, White JF. Boca Raton, FL: CRC Press. pp. 87–99 doi: 10.1201/9781351070324-7
- [120] Yang A, Li Y, Zeng Z, Zhang H. 2024. Role of the foliar endophyte *Colletotrichum* in the resistance of invasive *Ageratina adenophora* to disease and abiotic stress. *Microorganisms* 12(12):2565
- [121] Li X, He C, He X, Su F, Hou L, et al. 2019. Dark septate endophytes improve the growth of host and non-host plants under drought stress through altered root development. *Plant and Soil* 439(6):259–272
- [122] González Ortega-Villaizán A, King E, Patel MK, Rodríguez-Dobrevá E, González-Teuber M, et al. 2025. Identification of a drought stress response module in tomato plants commonly induced by fungal endophytes that confer increased drought tolerance. *Plant Molecular Biology* 115(1):7
- [123] Abideen Z, Cardinale M, Zulfiqar F, Koyro HW, Rasool SG, et al. 2022. Seed endophyte bacteria enhance drought stress tolerance in *Hordeum vulgare* by regulating, physiological characteristics, antioxidants and minerals uptake. *Frontiers in Plant Science* 13:980046
- [124] Abdolmaleki AK, Pirdashti H, Yaghoubian Y, Abbasian A, Shiade SRG. 2023. Endophytic fungi improve growth and yield of wheat (*Triticum aestivum* L.) under limited light conditions. *Gesunde Pflanzen* 75(5):1517–1529
- [125] Fadaei A, Asghari H, Pirdashti H, Yaghoubian Y, Akandi ZN. 2024. Endophytic symbiosis enhances the growth, yield, and antioxidant defense in soybean (*Glycine max* (L.) Merrill) exposed to various light intensities. *Journal of Crop Health* 76(5):1167–1178
- [126] Ramos P, Rivas N, Pollmann S, Casati P, Molina-Montenegro MA. 2018. Hormonal and physiological changes driven by fungal endophytes increase Antarctic plant performance under UV-B radiation. *Fungal Ecology* 34:76–82
- [127] Barrera A, Hereme R, Ruiz-Lara S, Larrondo LF, Gundel PE, et al. 2020. Fungal endophytes enhance the photoprotective mechanisms and photochemical efficiency in the Antarctic *Colobanthus quitensis* (Kunth) Bartl. exposed to UV-B radiation. *Frontiers in Ecology and Evolution* 8:122
- [128] Davitt AJ, Stansberry M, Rudgers JA. 2010. Do the costs and benefits of fungal endophyte symbiosis vary with light availability? *New Phytologist* 188(3):824–834
- [129] Schneider M, Ballvora A, Léon J. 2024. Deep genotyping reveals specific adaptation footprints of conventional and organic farming in barley populations—an evolutionary plant breeding approach. *Agronomy for Sustainable Development* 44(3):33
- [130] Scholes DR, Paige KN. 2015. Plasticity in ploidy: a generalized response to stress. *Trends in Plant Science* 20(3):165–175
- [131] Darmasaputra GS, van Rijnberk LM, Galli M. 2024. Functional consequences of somatic polyploidy in development. *Development* 151(5):dev202392
- [132] Barkla BJ, Rhodes T, Tran KNT, Wijesinghe C, Larkin JC, et al. 2018. Making epidermal bladder cells bigger: developmental- and salinity-induced endopolyploidy in a model halophyte. *Plant Physiology* 177(2):615–632
- [133] Edgar BA, Zielke N, Gutierrez C. 2014. Endocycles: a recurrent evolutionary innovation for post-mitotic cell growth. *Nature Reviews Molecular Cell Biology* 15(3):197–210
- [134] Bhosale PM, Boudolf V, Cuevas F, Lu R, Eekhout T, et al. 2018. A spatiotemporal DNA endoploidy map of the *Arabidopsis* root reveals roles for the endocycle in root development and stress adaptation. *The Plant Cell* 30(10):2330–2351
- [135] Chao DY, Dilkes B, Luo H, Douglas A, Yakubova E, et al. 2013. Polyploids exhibit higher potassium uptake and salinity tolerance in *Arabidopsis*. *Science* 341(6146):658–659
- [136] Yang PM, Huang QC, Qin GY, Zhao SP, Zhou JG. 2014. Different drought-stress responses in photosynthesis and reactive oxygen metabolism between autotetraploid and diploid rice. *Photosynthetica* 52(2):193–202
- [137] Oswald BP, Nuismer SL. 2007. Neopolyploidy and pathogen resistance. *Proceedings of the Royal Society B: Biological Sciences* 274(1624):2393–2397
- [138] Van de Peer Y, Mizrahi E, Marchal K. 2017. The evolutionary significance of polyploidy. *Nature Reviews Genetics* 18(7):411–424
- [139] Ramachandran D, Huebner C, Daly M, Haimovitz J, Swale T, et al. 2021. Chromosome level genome assembly and annotation of highly invasive Japanese stiltgrass (*Microstegium vimineum*). *Genome Biology and Evolution* 13(11):evab238
- [140] Wang C, Liu L, Yin M, Eller F, Brix H, et al. 2024. Genome-wide analysis tracks the emergence of intraspecific polyploids in *Phragmites australis*. *NPJ Biodiversity* 3(1):29
- [141] Rutland CA, Hall ND, McElroy JS. 2021. The impact of polyploidization on the evolution of weed species: historical understanding and current limitations. *Frontiers in Agronomy* 3:626454
- [142] Dan H, Imaseki H, Wasteneys GO, Kazama H. 2003. Ethylene stimulates endoreduplication but inhibits cytokinesis in cucumber hypocotyl epidermis. *Plant Physiology* 133(4):1726–1731
- [143] Wildermuth MC, Steinwand MA, McRae AG, Jaenisch J, Chandran D. 2017. Adapted biotroph manipulation of plant cell ploidy. *Annual Review of Phytopathology* 55(1):537–564
- [144] Stetter MG, Schmid K, Ludewig U. 2015. Uncovering genes and ploidy involved in the high diversity in root hair density, length and response to local scarce phosphate in *Arabidopsis thaliana*. *PLoS One* 10(3):e0120604

- [145] Hanford HE, Von Dwingelo J, Abu Kwaik Y. 2021. Bacterial nucleomodulins: a coevolutionary adaptation to the eukaryotic command center. *PLoS Pathogens* 17(1):e1009184
- [146] Zimmermann SD, Gaillard I. 2023. Epigenetic control is involved in molecular dialogue in plant-microbe symbiosis. *New Phytologist* 238(6):2259–2260
- [147] Molina-Montenegro MA, Acuña-Rodríguez IS, Atala C, Ballesteros GI, Carrasco-Urra F, et al. 2026. The endomicrobiome and weed invasiveness in Mediterranean ecosystems worldwide. *Nature Communications* 17(1):3063
- [148] Malinowski D, Leuchtmann A, Schmidt D, Nösberger J. 1997. Growth and water status in meadow fescue is affected by *Neotyphodium* and *Phialophora* species endophytes. *Agronomy Journal* 89(4):673–678
- [149] Irizarry I, White JF. 2017. Application of bacteria from non-cultivated plants to promote growth, alter root architecture and alleviate salt stress of cotton. *Journal of Applied Microbiology* 122(4):1110–1120
- [150] Raaijmakers JM, Kiers ET. 2022. Rewilding plant microbiomes. *Science* 378(6620):599–600



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