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## Evolution of mobile genetic elements and their impact on plant-microbe interactions

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### Abstract

Mobile genetic elements (MGEs) play a crucial role in the evolution of both plants and microbes, significantly influencing their interactions. These elements, which include transposons, plasmids, and viruses, facilitate horizontal gene transfer, contributing to genetic diversity and the rapid adaptation of organisms. In plants, MGEs can lead to the development of novel traits, including resistance to pathogens, by integrating beneficial genes into the genome. Conversely, in microbes, MGEs can enhance virulence, enable evasion of plant defenses, and promote the acquisition of antibiotic resistance genes. The dynamic nature of MGEs creates a complex network of interactions between plants and their associated microbiomes, shaping the co-evolutionary processes. Understanding the evolution and function of MGEs in plant-microbe interactions offers new insights into plant immunity, microbial pathogenicity, and the potential for harnessing these elements in agricultural biotechnology. This review explores the diverse types of MGEs, their mechanisms of action, and their evolutionary significance in shaping plant-microbe relationships, with a focus on the implications for disease management and crop improvement strategies. The findings underscore the need for further research to fully elucidate the impact of MGEs on the ecological and evolutionary dynamics of plant-microbe interactions.

**Keywords:** Mobile genetic elements, plant-microbe interactions, horizontal gene transfer, plant immunity, microbial pathogenicity

### Introduction

Mobile genetic elements (MGEs) are segments of DNA that can move within and between genomes, playing a pivotal role in the evolution and adaptation of both plants and microbes. These elements include transposons, plasmids, integrons, and bacteriophages, among others, and are central to the processes of horizontal gene transfer (HGT). Through HGT, MGEs contribute to genetic diversity and facilitate the rapid acquisition of novel traits, which are critical for the survival and adaptation of organisms in changing environments (Frost *et al.*, 2005; Koonin & Wolf, 2008) [13, 23].

In plants, MGEs have been shown to influence genome structure and function, leading to the emergence of new traits, including resistance to various stresses. For instance, the integration of transposable elements (TEs) into regulatory regions of plant genes can alter gene expression, resulting in enhanced resistance to pathogens (Feschotte, 2008) [12]. The maize genome, which harbors a high density of TEs, provides a classic example of how MGEs can drive phenotypic diversity and adaptability. Recent studies have further highlighted the role of MGEs in shaping the immune responses of plants by facilitating the acquisition and rearrangement of resistance genes (Kim *et al.*, 2021) [22].

In microbes, MGEs are equally influential, particularly in the context of plant-pathogen interactions. MGEs such as plasmids and bacteriophages are vectors for the transfer of virulence factors, antibiotic resistance genes, and other traits that enhance microbial fitness and pathogenicity (Norman *et al.*, 2009) [29]. For example, the acquisition of virulence genes through plasmid-mediated transfer has been a key factor in the evolution of pathogenic strains of *Pseudomonas syringae*, a major plant pathogen (González *et al.*, 2022) [15]. Similarly, bacteriophages have been implicated in the horizontal transfer of effector proteins that allow pathogens to suppress plant immune responses, thereby facilitating infection (López-Pérez *et al.*, 2022) [25]. The interplay between MGEs and host genomes is not limited to the enhancement of pathogenic traits.

Some MGEs can integrate into host genomes and contribute to mutualistic interactions between plants and microbes. Endophytic bacteria, for instance, may acquire genes via MGEs that enable them to promote plant growth or enhance stress tolerance, thus benefiting both the plant and the microbe (Compant *et al.*, 2020) [7]. These mutualistic interactions are particularly important in the context of sustainable agriculture, where the manipulation of MGEs could be harnessed to improve crop resilience and productivity (Pérez-Jaramillo *et al.*, 2016) [30].

Despite the growing recognition of the importance of MGEs in plant-microbe interactions, many questions remain unanswered. For instance, the mechanisms by which MGEs are regulated within genomes, their impact on genome stability, and their role in the co-evolution of plants and their associated microbiomes are areas of active research (Boto, 2010; Ley & Medzhitov, 2020) [5, 24]. Understanding these dynamics is crucial for developing new strategies for disease management and crop improvement.

This review aims to provide a comprehensive overview of the evolution and function of MGEs in plant-microbe interactions. We will explore the various types of MGEs, their mechanisms of action, and their evolutionary significance in shaping the relationships between plants and microbes. Special attention will be given to the implications of these findings for agricultural biotechnology, particularly in the context of developing more resilient and sustainable crop systems.

Mobile genetic elements (MGEs) are DNA sequences that can move or be transferred between different locations within a genome or between genomes. These elements are crucial drivers of genetic diversity and play significant roles in the evolution of both plant and microbial genomes (Frost *et al.*, 2005) [13]. MGEs include transposable elements (TEs), plasmids, integrons, bacteriophages, and genomic islands, each with distinct mechanisms of mobility and impact on host organisms.

### Transposable Elements (TEs)

Transposable elements, also known as "jumping genes," can move within the genome, leading to mutations, gene duplications, and alterations in gene expression (Feschotte, 2008) [12]. In plants, TEs have been implicated in the evolution of novel traits, such as stress resistance and developmental changes. The *Ac/Ds* transposable elements in maize and *Tos17* in rice are well-studied examples that illustrate the role of TEs in plant genome plasticity (Jiang *et al.*, 2003) [21]. In plants, TEs can play crucial roles in adaptation to environmental stresses, including interactions with microbes. For example, the activation of certain TEs in response to pathogen infection can lead to the generation of new resistance gene variants, which enhance the plant's defense capabilities (Kim *et al.*, 2021) [22]. Additionally, TEs can influence gene expression by inserting themselves into or near regulatory regions of genes, potentially activating or repressing genes involved in plant immunity.

### Plasmids

Plasmids are extrachromosomal DNA molecules that can replicate independently of the chromosomal DNA. They are primarily found in bacteria and are known for carrying genes that confer advantageous traits, such as antibiotic resistance and virulence factors (Smillie *et al.*, 2010) [33]. Plasmids can be transferred between bacteria through

horizontal gene transfer (HGT), significantly impacting microbial evolution and interactions with plant hosts. For instance, the plasmid-borne *avrPphB* gene in *Pseudomonas syringae* plays a crucial role in the pathogen's ability to infect plants (González *et al.*, 2022) [15]. *Symbiosis plasmids* in rhizobia, these plasmids carry genes necessary for the formation of root nodules and nitrogen fixation in legumes, contributing to the mutualistic relationship between the bacteria and the plant (Masson-Boivin *et al.*, 2009) [28].

### Integrons and Gene Cassettes

Integrons are genetic elements that can capture and integrate gene cassettes, which are mobile genetic units containing one or more genes, often including antibiotic resistance genes (Stokes & Hall, 1989) [34]. These elements contribute to the rapid evolution of microbial populations by enabling the acquisition of new traits. Integrons have been found in plant-associated bacteria, where they may influence the dynamics of plant-microbe interactions, particularly in the rhizosphere (Boucher *et al.*, 2007) [6].

### Bacteriophages and Genomic Islands

Bacteriophages, or phages, are viruses that infect bacteria. They play a significant role in bacterial evolution by mediating horizontal gene transfer, particularly through transduction, where bacterial genes are transferred from one bacterium to another via a phage (Hendrix, 2002) [18]. In plant-microbe interactions, phages can influence the virulence of plant pathogens by transferring virulence genes or by lysing bacterial populations, thereby affecting microbial community dynamics (López-Pérez *et al.*, 2022) [25]. Genomic islands are large segments of DNA that are acquired through horizontal gene transfer and often contain clusters of genes that contribute to niche adaptation, such as symbiosis or pathogenicity (Dobrindt *et al.*, 2004) [11]. In plant-associated bacteria, genomic islands can carry genes that enhance the bacteria's ability to colonize plants, evade plant defenses, or establish beneficial symbiotic relationships (Hacker & Carniel, 2001) [17].

### Impact of MGEs on Plant-Microbe Interactions and Plant Pathogenicity

MGEs play a critical role in shaping the interactions between plants and their associated microbes, influencing both pathogenic and mutualistic relationships. These interactions are dynamic and involve complex molecular mechanisms that determine the outcome of plant-microbe encounters. *Magnaporthe oryzae*, the rice blast fungus, utilizes TEs to mobilize and express genes related to pathogenicity, allowing it to adapt to different rice varieties and environmental conditions (Dean *et al.*, 2005) [9].

*Agrobacterium tumefaciens* transfers T-DNA from its Ti plasmid into plant cells, where it integrates into the plant genome and causes crown gall disease by inducing the production of plant hormones and opines (Gelvin, 2009) [14]. Pathogens often use MGEs to acquire and disseminate virulence factors, which are essential for infecting host plants. For example, plasmid-encoded effector proteins in *Agrobacterium tumefaciens* enable the bacterium to transfer T-DNA into plant cells, leading to crown gall disease (Gelvin, 2009) [14]. Similarly, TEs can carry and mobilize pathogenicity-related genes in fungi, such as *Magnaporthe oryzae*, the causal agent of rice blast disease (Dean *et al.*, 2005) [9].

### **MGEs and Plant Immunity**

Plants have evolved sophisticated immune systems to detect and respond to microbial invaders. MGEs can influence plant immunity by facilitating the rapid evolution of resistance genes (R-genes). The presence of TEs near R-genes can lead to gene duplication, recombination, and the generation of novel resistance specificities, as observed in the *NLR* gene family in plants (Kim *et al.*, 2021) [22]. This process enhances the plant's ability to recognize and respond to a diverse array of pathogens.

### **MGEs in Mutualistic Plant-Microbe Interactions and the Rhizosphere Microbiome**

MGEs are also involved in mutualistic interactions between plants and beneficial microbes. For instance, rhizobia, which form symbiotic relationships with legumes, often carry symbiosis genes on plasmids or genomic islands that are essential for nitrogen fixation (Sullivan & Ronson, 1998) [35]. The horizontal transfer of these symbiosis genes allows rhizobia to colonize new host plants, expanding their ecological range and benefiting plant growth (Masson-Boivin *et al.*, 2009) [28]. The rhizosphere, the soil region influenced by plant roots, is a hotspot for horizontal gene transfer mediated by MGEs. Plasmids and bacteriophages in the rhizosphere facilitate the exchange of genes among microbial communities, impacting plant health and productivity (Pérez-Jaramillo *et al.*, 2016) [30]. For example, the transfer of antibiotic resistance genes among rhizosphere bacteria can influence the microbial balance and affect plant-microbe interactions (Compant *et al.*, 2020) [7].

### **Evolutionary Significance of MGEs in Plant-Microbe Co-evolution**

The co-evolution of plants and microbes is heavily influenced by MGEs, which drive genetic innovation and adaptation in both partners. This evolutionary arms race is characterized by the continuous exchange and reshuffling of genetic material, leading to the emergence of new traits and interactions.

### **Adaptive Evolution and Emergence of Novel Traits**

MGEs contribute to adaptive evolution by enabling the rapid acquisition of beneficial traits. In plant-associated microbes, the transfer of genes via MGEs allows for quick adaptation to host defenses, environmental stresses, and competition with other microbes (Koonin & Wolf, 2008) [23]. In turn, plants can adapt by evolving new resistance mechanisms, often mediated by MGE-induced genetic changes. The integration of MGEs into plant genomes can lead to the emergence of novel traits that provide a selective advantage. For example, the integration of TEs into regulatory regions can alter the expression of key developmental or stress-response genes, leading to phenotypic diversity (Feschotte, 2008) [12]. Similarly, the horizontal transfer of secondary metabolite biosynthesis genes among microbes can result in the production of new compounds that affect plant-microbe interactions (Bose *et al.*, 2022) [4].

### **Co-evolutionary Dynamics**

The continuous interaction between MGEs, plants, and microbes results in a dynamic co-evolutionary process. Plants and microbes are engaged in an evolutionary "arms race," where MGEs facilitate the rapid adaptation of both partners. For instance, the evolution of resistance genes in

plants is often driven by the selective pressure exerted by microbial effectors, many of which are encoded by genes located on MGEs (Dangl *et al.*, 2013) [18]. Conversely, microbes evolve new virulence strategies through the acquisition of genes via MGEs, perpetuating the co-evolutionary cycle.

### **Implications for Agricultural Biotechnology**

The understanding of MGEs and their role in plant-microbe interactions has significant implications for agricultural biotechnology. By harnessing the power of MGEs, it is possible to develop new strategies for crop improvement, disease management, and sustainable agriculture. One promising application of MGEs in agriculture is the engineering of disease-resistant crops. By leveraging the natural mechanisms of MGEs, scientists can introduce or enhance resistance genes in crops, providing protection against a wide range of pathogens (Kim *et al.*, 2021) [22]. For example, the insertion of TE-derived sequences near R-genes can enhance their expression and broaden their resistance spectrum (Borrelli *et al.*, 2018) [3]. MGEs can also be used to promote beneficial plant-microbe interactions. For instance, by transferring symbiosis genes or other beneficial traits to rhizosphere microbes, it is possible to enhance plant growth, nutrient uptake, and stress tolerance (Pérez-Jaramillo *et al.*, 2016) [30]. This approach could lead to the development of biofertilizers and biopesticides that reduce the reliance on chemical inputs in agriculture. The use of MGEs in sustainable crop management involves the manipulation of microbial communities to promote plant health and productivity. By understanding the role of MGEs in shaping the rhizosphere microbiome, it is possible to develop strategies that enhance the beneficial effects of microbes while suppressing harmful pathogens (Compant *et al.*, 2020) [7]. This approach aligns with the principles of sustainable agriculture, which emphasize the use of natural processes to maintain crop health and yield.

### **The Effects of Stress and Environmental Factors on the Transfer of Mobile Genetic Elements (MGEs) in the Rhizosphere**

#### **Abiotic Stress Factors**

##### **Soil pH and Nutrient Availability**

Soil pH and nutrient availability are critical abiotic factors that influence MGE transfer in the rhizosphere. pH can affect the mobility of MGEs by altering the charge and binding affinity of DNA, as well as the physiological state of microbial cells. For instance, acidic or alkaline conditions can lead to stress responses in bacteria, such as the upregulation of stress-response genes and an increase in HGT activity (Shakya *et al.*, 2013) [31]. Additionally, nutrient availability, particularly the presence of essential elements like phosphorus and nitrogen, can either promote or inhibit MGE transfer depending on the metabolic state of the microbial community (Griffiths *et al.*, 2018) [16]. For example, nutrient-rich environments may reduce the need for bacteria to acquire new traits via HGT, whereas nutrient-poor conditions might increase the pressure for genetic exchange as a survival strategy.

##### **Temperature and Moisture**

Temperature and moisture levels are pivotal in determining the rate of MGE transfer. High temperatures can induce stress responses in bacteria, such as the heat shock response,

which has been linked to increased plasmid transfer rates. Similarly, soil moisture content influences microbial activity and the diffusion of MGEs. Waterlogged soils may inhibit the transfer of MGEs due to reduced oxygen levels and microbial activity, whereas moderate moisture levels can enhance bacterial mobility and gene transfer. Moreover, temperature fluctuations can cause physiological stress, leading to an increased transfer of MGEs as bacteria seek to adapt to changing conditions.

### **Biotic Stress Factors**

#### **Plant Root Exudates**

Plant root exudates are a major biotic factor that influences MGE transfer in the rhizosphere. These exudates, which include sugars, amino acids, and organic acids, serve as a source of nutrients for microbes and can stimulate bacterial activity, including HGT (Baudoin *et al.*, 2003) [1]. Certain exudates can act as signaling molecules, triggering the expression of genes involved in MGE transfer. For instance, flavonoids secreted by legume roots have been shown to induce the expression of genes related to plasmid transfer in rhizobia, facilitating the spread of symbiosis-related genes (Díaz-Pérez *et al.*, 2020) [10]. The composition of root exudates can also vary depending on plant species, growth stage, and environmental conditions, further influencing the dynamics of MGE transfer in the rhizosphere.

### **Microbial Interactions**

Microbial interactions, including competition, cooperation, and predation, are critical in shaping the transfer of MGEs in the rhizosphere. For example, bacteriophages, viruses that infect bacteria, can facilitate the horizontal transfer of genes by transducing MGEs from one bacterial cell to another (López-Pérez *et al.*, 2022) [25]. Additionally, microbial competition for resources can drive the transfer of MGEs that confer competitive advantages, such as antibiotic resistance or enhanced metabolic capabilities. On the other hand, cooperative interactions, such as those seen in biofilms, can create microenvironments that are conducive to MGE transfer by maintaining high cell densities and close physical contact between bacteria (Madsen *et al.*, 2012) [26].

### **Anthropogenic Stress Factors**

#### **Agricultural Practices**

Agricultural practices, such as the application of fertilizers, pesticides, and antibiotics, can exert selective pressures that influence MGE transfer in the rhizosphere. The use of chemical fertilizers, for example, can alter soil nutrient levels and microbial communities, potentially increasing the selective pressure for bacteria to acquire nutrient acquisition genes via MGEs. Similarly, the application of pesticides can create a selective environment where only those microbes with resistance genes, often carried on MGEs, can survive and proliferate (Heuer & Smalla, 2012) [19]. Moreover, the use of antibiotics in agriculture has been shown to promote the spread of antibiotic resistance genes among soil bacteria, primarily through the transfer of plasmids and integrons (Binh *et al.*, 2008) [2].

### **Pollution and Heavy Metals**

Pollution, particularly the presence of heavy metals in the soil, is a significant anthropogenic stress factor that can enhance MGE transfer. Heavy metals, such as cadmium, lead, and mercury, are known to induce oxidative stress in

bacteria, leading to an increased rate of HGT as a survival mechanism (Martinez, 2009) [27]. MGEs often carry genes that confer resistance to heavy metals, allowing bacteria to thrive in contaminated environments (Siddique *et al.*, 2022) [32]. The presence of heavy metals can thus create a selective environment that favors the horizontal transfer of resistance genes, contributing to the spread of metal resistance among soil microbial communities.

### **Future prospectives**

The evolution of mobile genetic elements (MGEs) and their impact on plant-microbe interactions represents a dynamic and pivotal area of research. Future investigations should focus on elucidating the mechanisms through which MGEs contribute to the adaptability and evolution of both plants and their associated microbiota. Advances in genomic technologies will enable a more comprehensive understanding of MGE dynamics, including their role in horizontal gene transfer and their influence on microbial community structures in the rhizosphere. This knowledge could reveal how MGEs facilitate beneficial symbiotic relationships or exacerbate pathogenic interactions. Furthermore, integrating MGE research with plant breeding and biotechnology could lead to novel strategies for enhancing plant resilience to environmental stressors. Exploring the interplay between MGEs, environmental factors, and microbial communities will be crucial in developing sustainable agricultural practices and improving crop performance in diverse ecological settings.

### **Conclusion**

In conclusion, the evolution of mobile genetic elements (MGEs) plays a critical role in shaping plant-microbe interactions, influencing both plant adaptability and microbial dynamics. As MGEs facilitate gene transfer and contribute to genetic diversity, they significantly impact how plants and microbes respond to environmental stresses and adapt to changing conditions. The integration of advanced genomic techniques will enhance our understanding of MGE behavior, revealing their potential to drive both beneficial and detrimental interactions within the rhizosphere. Future research should focus on unraveling the complex relationships between MGEs, environmental factors, and microbial communities to harness their potential for improving crop resilience and sustainability. By leveraging this knowledge, we can develop innovative strategies to enhance plant health and productivity, ultimately contributing to more resilient agricultural systems and better management of plant-microbe interactions in diverse environments.

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### **Data availability**

There is not hidden data, all data are presented in this manuscript.

### **Ethical statement**

This study did not involve human or animal subjects; therefore, informed consent is not applicable.

**Conflict of interest**

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

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