
Horizontal Gene Transfer in Soil and the Rhizosphere: Impact on Ecological Fitness of Bacteria

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Abstract

The ecological fitness of soil- and root-associated bacterial communities is a key element for soil fertility and plant health as well as plant stress tolerance. Genetic variability in bacterial populations is maintained through mutation and gene acquisition. Horizontal gene transfer (HGT) is accomplished by conjugation, transformation, and transduction both in vitro and under natural conditions. Mobile genetic elements (MGEs) play a significant role in gene dissemination in bacterial communities and increase their adaptability, survival, and ability to colonize different environmental niches. In this context, bacterial conjugative plasmids encoding resistance genes, degradative genes, and tolerance to stress conditions are of much significance. The biofilm mode of bacterial growth further enhances gene exchange and increase the fitness and competitiveness of bacteria. Microcosm studies reveal a number of factors influencing the HGT process in soil. Considering the importance of HGT, a better understanding of genetic processes in the rhizosphere will further help in effective exploitation of naturally engineered bacteria for sustainable agriculture.

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6.1 Introduction

Horizontal gene transfer (HGT) refers to the transfer of genetic material between prokaryotes. The process occurs in one of three ways: (1) transformation (the uptake of free DNA by competent bacteria from the surrounding environment), (2) transduction (gene transfer mediated by bacteriophages), and (3) conjugation (gene transfer by means of plasmids or integrative conjugative elements). Conjugation is the process by which a DNA molecule (i.e., plasmid or conjugative transposon) is transferred from a donor cell to a physically attached recipient cell via some conjugation apparatus (Zechner et al. 2000). Although most conjugative plasmids shared common mechanistic principles, e.g., synthesis of conjugative pili, there is a remarkable diversity of conjugative systems in Gram-negative and Gram-positive bacteria, depending on the shape and other characteristics of the plasmid-encoded pili. Nonconjugative plasmids are transferred to recipient cells by mobilizing/helper plasmids (Heuer and Smalla 2007). Transfer of conjugative plasmids or transposons has been demonstrated to occur in various ecological habitats, for example, the plant surface, rhizosphere, surface water, and human and animal intestines (Aminov 2011; Madsen et al. 2012; Huddleston 2014; Juhas 2015; Pinto-Carbo et al. 2016; Sun et al. 2016). In contrast to conjugation, transduction provides a means of DNA acquisition in which nonviral DNA is transferred from an infected host bacterium to a new host via infectious or noninfectious virus particles (Meena et al. 2013a; Bahadur et al. 2014; Maurya et al. 2014; Jaiswal et al. 2016; Jha and Subramanian 2016; Kumar et al. 2016a, b).

Defective phage particles released from lysed host cells attach to new host cells and deliver their DNA into the new host. The injected bacterial DNA is subsequently integrated into the recipient genome. Unlike conjugation, transduction does not require cell-to-cell contact; however, most bacteriophages infect only a narrow range of hosts (Wommack and Colwell 2000). Evidence for the importance of transduction as an HGT process in the natural environment arises from studies on the abundance of bacteriophages in different settings, primarily soil (Ashelford et al. 2003) and from bacterial genome sequences (Canchaya et al. 2003). The role of bacteriophages in contributing various genes to bacterial genera of medical and ecological significance is well documented (Weitz et al. 2013; Broszat and Grohmann 2014; Dalmaso et al. 2014; Chen et al. 2015; Obeng et al. 2016).

Horizontal gene transfer plays an important role in formulating bacterial genomes, promoting intra- and interspecies variability and distributing functional genetic modules within communities. HGT provides a means for enhanced understanding of ecological adaptation and bacterial evolution in the biosphere. Extensive gene exchange during bacterial evolution is made evident by the marked similarity

of genes among distantly related species, variation of gene content between closely related strains, and incongruent phylogenetic trees. Horizontal gene transfer is a major force in bacterial evolution; a well-documented example of HGT is the spread of antibiotic resistance genes among pathogenic and nonpathogenic bacteria (Barlow 2009; Boto 2010; Davies and Davies 2010; Abulreesh 2011, 2012; Baltrus 2013; Wellington et al. 2013). The driving force for the acquisition of foreign genes via HGT is believed to be the need for bacteria to overcome environmental stresses for survival and to compete successfully in their ecological niches (Hacker and Kaper 2000).

Mobile genetic elements (MGEs) such as plasmids, bacteriophages, integrative conjugative elements, transposons, insertion sequences (IS) elements, integrons, gene cassettes, and genomic islands are the key vehicles among HGT mechanisms. In many species, a high proportion of horizontally transferred genes can be attributed to plasmid-, phage-, or transposon-related sequences, as remnants of these mobile elements have been located adjacent to genes identified as horizontally transferred (Ochman et al. 2000; Brussow et al. 2004; Frost et al. 2005; Gyles and Boerlin 2013). It has been suggested that MGEs add some metabolic burden to their host, and adaptation occurs to minimize this impact (Dahlberg and Chao 2003; Heuer et al. 2007). The prevalence of plasmids, however, indicates that they benefit bacteria and compensate for any burden they might impose on the cell. Plasmids persist because bacterial communities and their environments are continuously changing; the variability carried by these genetic elements increases the speed at which adapted strains arise, and the adapted strains retain the MGE so they can propagate rapidly (Jat et al. 2015; Kumar et al. 2015; Ahmad et al. 2016; Meena et al. 2015f, 2016a; Dominguez-Nunez et al. 2016; Dotaniya et al. 2016).

The MGEs that enhance an organism's adaptability evolve and survive at the expense of those that do not. Thus, MGEs confer an improved fitness to the bacterial community and its ability to colonize different environmental niches. MGEs additionally increase the possibility of new strains arising with novel or increased selective advantages over neighboring communities. Metagenomic approaches have revealed a large and untapped diversity of resident MGEs in soil- and plant-associated bacteria. Approximately 18% of bacterial isolates from the phytosphere of sugar beets was found to contain plasmids (Powell et al. 1993), and a large proportion were able to mobilize non-self-transferable but mobilizable Inc-Q plasmids (Kobayashi and Bailey 1994). The extensive presence of plasmid-related sequences in soil DNA (directly extracted) indicates a significant abundance of plasmids in soil (Heuer et al. 2009). The abundance of transferable plasmids in soil is believed to be related to the presence of contaminants (e.g., antibiotics, xenobiotics). Several studies have indicated that genes encoding the enzymes involved in catabolism of environmental pollutants are present on plasmids (Smets and Barkay 2005; Kopmann et al. 2013).

Different methods involving various molecular techniques have been employed to detect and study soil plasmid structure, organization and function (Heuer and Smalla 2012). Moreover, metagenomics methods such as pyrosequencing of soil DNA have proved to be highly sensitive and have led to the discovery of novel

plasmid sequences (Kristiansson et al. 2011). Genome sequencing data have revealed the modular character of conjugative plasmids, where different modules (e.g., a compactly arranged gene) are dedicated toward carrying out specific functions (de la Cueva-Méndez and Pimentel 2007; Norman et al. 2009). The overall genetic makeup of conjugative plasmids can be divided into four distinct categories of modules: (1) modules affecting plasmid replication and copy control, (2) modules affecting plasmid stability, (3) modules affecting plasmid propagation, and (4) modules affecting plasmid host adaptation, along with numerous other subcategories (Norman et al. 2009). The first three categories are considered “plasmid core” or plasmid “backbone” genes. Sequence analysis of plasmid backbone genes is considered a consistent and reliable foundation for plasmid classification, as opposed to traditionally used methods (Heuer and Smalla 2012). Apart from plasmid backbone genes, a highly diverse, accessory, or flexible set of genes within soil plasmids occurs as a fourth module which carries genes responsible for environmental adaptation. These accessory genes often differ greatly among plasmids with identical plasmid backbones and impart the ability to adapt to varied environmental conditions such as exposure to antibiotics, heavy metals, and xenobiotics (Dennis 2005; Schluter et al. 2007; Heuer et al. 2009).

Degradative genes resident on MGEs have been isolated successfully from soil treated with the herbicide 2, 4-D but not from untreated control soil. Similarly, self-transferable plasmids which confer resistance toward antibiotics have been isolated from animal manures used for soil fertilization (Heuer and Smalla 2007; van Overbeek et al. 2002). Sequencing of plant-associated bacteria reveal that many phytopathogenic and symbiotic bacteria carry plasmids (Zhao et al. 2005; Bardaji et al. 2011), pathogenicity islands (Gardiner et al. 2014), or integrons (Gillings et al. 2005). These studies reveal the significance of horizontal gene transfer in bacterial adaptation and evolution under changing environmental conditions (Parewa et al. 2014; Prakash and Verma 2016; Meena et al. 2015e, 2016b; Teotia et al. 2016; Bahadur et al. 2016b; Das and Pradhan 2016).

In recent years, the importance of biofilm formation and its relationship to gene transfer has received significant attention (Burmolle et al. 2014; Stalder and Top 2016). It is well recognized that horizontal gene transfer via plasmids occurs more effectively on surfaces, e.g., in biofilms than among planktonic cells. Biofilms are highly structured bacterial communities embedded in a self-produced matrix composed of exopolysaccharides (EPSs), proteins, and DNA. These films adhere to biological and non-biological surfaces (Hall-Stoodley et al. 2004) and provide a favorable environment for genetic elements to be transferred horizontally. Rhizobacterial biofilms associated with plant roots support bacterial survival and host plant colonization, reduce biotic and abiotic plant stress, and enhance agricultural productivity (Lopez et al. 2010; Yadav and Sidhu 2016; Meena et al. 2016d; Saha et al. 2016b; Verma et al. 2014, 2015b). All these advantages conferred by biofilms are directly or indirectly associated with a high frequency of horizontal gene transfer in the biofilm mode of growth. In this chapter, we focus on horizontal gene transfer in soil- or plant-associated (rhizosphere) bacteria that contribute to

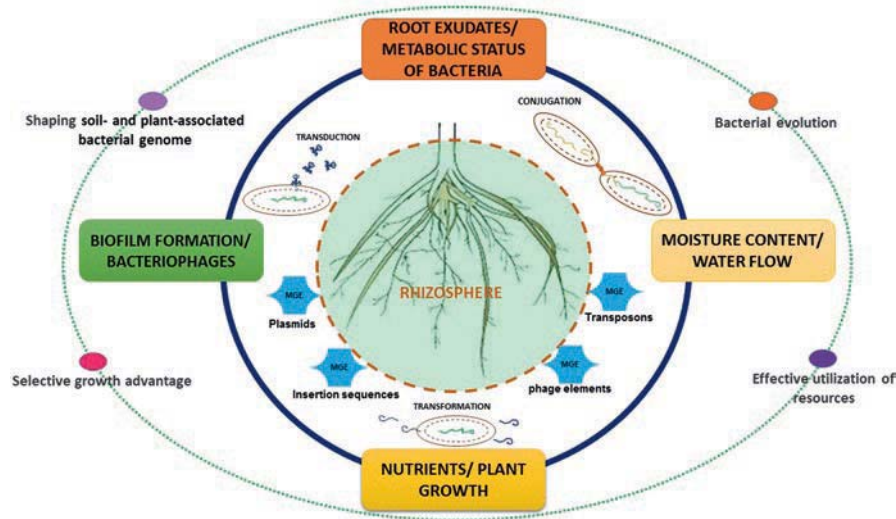


Fig. 6.1 Gene transfer in the rhizosphere: mechanisms, factors, and outcomes

genetic variation in microbial populations and ultimately broaden their range of environmental niches by increasing their fitness and competitiveness (Fig. 6.1).

6.2 HGT in Environment and Its Role in Evolution of the Bacterial Genome

Discovery of the transferable nature of multidrug resistance by Watanabe in 1963 resulted in the recognition of horizontal gene transfer. Since then, HGT has become a topic of extensive investigation worldwide, particularly in medical microbiology. The occurrence of HGT among bacteria in the natural environment was subsequently recognized; such processes are believed to relate to the risk of genetically modified bacteria released into the environment (Heuer and Smalla 2012). In view of the use of genetically modified (GM) crops and microbes in agricultural settings, the role of mobile genetic elements (MGE; plasmids, transposons, bacteriophages, etc.) associated with plant and soil and factors influencing this mobility has received attention from many scientists (Smalla et al. 2000; van Elsas and Bailey 2002). Studies have demonstrated that HGT is a major, if not the dominant force in bacterial evolution (Frost et al. 2005; Davies and Davies 2010; Wiedenbeck and Cohan 2011; Dutta and Sarkar 2015; Navarre 2016). Up to 20% of a typical bacterial genome acquired from other species and MGE acts as a vector for HGT (Ochman et al. 2000).

HGT affects only those bacteria that readily exchange genes, and members of such rapidly exchanging communities have shown similar characteristics such as genome size, GC content, carbon utilization, and oxygen tolerance (Jain et al. 2003).

On the other hand, considerable evidence indicates that HGT is an ongoing process that plays a primary role in real-time ecological adaptations of prokaryotes (Smets and Barkay 2005). MGEs play an essential role in the process by shaping the bacterial genome, promoting intraspecies variability, and distributing functional genetic modules among communities. Consequently, HGT of genetic modules that allows adaptation to rapidly changing biotic interactions has frequently been observed (Smets and Barkay 2005). The interactions include:

1. Antibiotics production by microorganisms
2. Dissemination of antibiotic resistance
3. Release of xenobiotics or new secondary metabolites
4. Dissemination of degradative gene and pathway assemblies (McManus et al. 2002; Top and Springael 2003; Larrain-Linton et al. 2006)
5. Symbiotic or pathogenic interactions and speed of the spread of genomic islands (Arnold et al. 2007; Heuer and Smalla 2012)

The most widely studied examples of genetic exchange through HGT in natural environments is the dissemination of multiple antibiotic resistance via MGE, which allows bacterial populations to adapt rapidly to strong selective pressures (Cordero et al. 2012; Wellington et al. 2013; Ojala et al. 2014). MGEs involved in transmission of antibiotic resistance include combinatorial genetic evolution of MDR facilitated by transposons, IS elements, and integrons. Transposable elements like ISCRs (insertion sequence common regions) mobilize DNA adjacent to their insertion site via rolling circle replication (Toleman et al. 2006). ISCRs are closely associated with antibiotic resistance genes on conjugative plasmids (Priyadharsini and Muthukumar 2016; Kumar et al. 2017; Masood and Bano 2016; Meena et al. 2016).

It is interesting to observe that under natural conditions, especially in wastewater and soil, the presence of several toxic pollutants (e.g., metals and pesticides) may increase selective pressure and co-selection of resistant strains. These pollutants may further increase the ecological fitness and survivability of bacterial strains (De Liphay et al. 2008; Imfeld and Vuilleumier 2012). Various degradative plasmids have been characterized from bacteria which degrade PCBs, chloroaniline, and other recalcitrant molecules (Merlin et al. 1999; Boon et al. 2001; Springael and Top 2004). Many self-transferable plasmids participate directly in active gene transfer. Russell et al. (2011) reviewed the evolutionary trends of enzymatic machinery involved in the degradation of xenobiotics and concluded that horizontal gene transfer among bacteria is one of the major determinants in the acquisition of new and efficient enzymatic functions. New enzymatic pathways have emerged from a wide variety of enzyme families.

Metagenomic mapping studies for two discretely located hexachlorocyclohexane (HCH)-degrading strains of *Sphingobium japonicum* (*Sphingobium japonicum* UT26 from Japan and *Sphingobium indicum* B90A from India) have shown that the previous common ancestor was unable to degrade HCH isomers, but descendants acquired degrading genes by transposon-mediated HGT (Sangwan et al. 2014). Likewise, Pearce et al. (2015) showed that different HCH-degrading bacteria

yielded a distinct set of metabolites during degradation of HCH isomers. The analysis confirmed the role of horizontal transfer mediated by an insertion sequence in the acquisition of the pathway.

6.3 Gene Transfer in the Rhizosphere

Among the conditions occurring within the phytosphere, the rhizosphere is optimally suited for the growth and intensive interaction among microbial communities. The availability of essential elements (C, N, P, K), moisture, and other critical constituents (e.g., organic acids) in the vicinity of plant roots make the rhizosphere the preferred site for gene transfer, such that it is referred to as a “hotspot” for genetic evolution (van Elsas et al. 2003). The rhizosphere provides an ideal environment for HGT processes and may support rapid adaptation of bacteria against environmental changes as compared with bulk soil. Conjugative plasmid transfer frequency between bacterial species is enhanced under high nutrient availability and water movement (Kroer et al. 1998). Bacterial colonization and adherence to the root surface in response to the presence of root exudates impart significant effects on gene transfer.

Due to intimate contact among cells and higher metabolic activity in response to the presence of an ample nutrient supply, elevated plasmid transfer in the rhizosphere has been observed (Kroer et al. 1998; van Elsas et al. 2003). Musovic et al. (2006) demonstrated the exceptionally broad host range of the pKJK10 plasmid in the barley rhizosphere. They describe the potential of mobile genetic elements, crossing large phylogenetic distances, i.e., gene swapping between Actinobacteria and Proteobacteria, in bacterial evolution. Organic acids and other constituents of root exudates stimulate the transformation in *Acinetobacter* sp. BD413 (pFG4) in sterile soils. The organic acids, acetate, lactate, and alanine, resulted in the highest transformation frequencies (Nielsen and van Elsas 2001). Molbak et al. (2007) studied conjugal transfer in the rhizospheres of pea and barley. The experiments showed that a higher rate of root exudation and root growth rate in pea was responsible for higher conjugal frequency. The distribution pattern of donors on pea roots was shown to affect genetic transfer. Transfer of the plasmid RP4 derivative between *Pseudomonas fluorescens* and *Serratia* sp. was studied in a sand microcosm and found to be related to the availability of root exudates and bacterial metabolic activity (Kroer et al. 1998). Regardless, however, the direct relationship between the metabolic activity of transforming bacteria and gene transfer is in need of further investigation (Meena et al. 2013c, 2015a; Raghavendra et al. 2016; Zahedi 2016; Singh et al. 2015; Bahadur et al. 2016a).

Genetic transfer of various contaminant-degrading genes has also been shown to take place effectively in the rhizosphere and is concurrently responsible for enhanced plant growth (Wang et al. 2007, 2014a, b; Jia et al. 2013). Using an in silico metagenomic prediction method, Cabezon et al. (2015) and Lopes et al. (2016) revealed a significantly higher abundance of predicted genes associated with HGT in the rhizosphere compared with bulk soil. The pilus assembly protein CpaE and type IV

pilus assembly protein PilV as well as genes involved in transformation/conjugation, such as the type IV secretion system proteins VirB4, VirB5, VirB6, and VirB9, among other transduction and transformation stimulating genes, were prevalent in the rhizosphere.

Bacteriophages present in the rhizosphere serve as another important agent responsible for genetic variation and evolution of indigenous bacterial communities. Because phage DNA is often packaged in relatively resilient phage coats, it is possible that transducing phages provide a reservoir of bacterial genes under localized conditions where the host may not survive (Van Elsas et al. 2003). Studies have shown that soil conditions affect the burst size of the lytic phage thus indirectly affecting the frequency of gene transfer and lysogeny (Burroughs et al. 2000). One of the mechanisms responsible for interspecies gene transfer in the rhizosphere is the overlapping susceptibility to phages among bacterial communities (Ashelford et al. 2000). Ashelford et al. (2003) highlighted the importance of soil bacteriophages in controlling bacterial populations and in mediating gene transfer in soil. Moreover, studies have shown that the lysogenic mode is preferable and common under different soil environments (Williamson et al. 2007; Ghosh et al. 2008).

Biofilm development and succession of microbial communities are now recognized as an important arena of rhizosphere biology. Different rhizospheric factors are known to influence bacterial biofilm formation. The beneficial effects of root exudates on biofilm development have been extensively investigated and reviewed (Bais et al. 2006; Zhang et al. 2014; Yuan et al. 2015).

6.4 Gene Transfer in Biofilms

Genetic variability among bacterial populations occurs via mutation and acquisition of new genes through various genetic exchange mechanisms. Gene transfer in a single species results in the propagation of specific traits. Interspecies gene transfer may result in an entirely new genetic combination which may be of significance to human health and the environment. The relationship between biofilms and HGT has been investigated by numerous workers (Ghigo 2001; Tormo et al. 2005; Antonova and Hammer 2011; Madsen et al. 2012; Cook and Dunny 2014). In general, HGT rates are higher in biofilm communities compared with those in the planktonic state. Biofilms are also implicated in the promotion of plasmid stability and may enhance the host range of MGEs that are being transferred (Madsen et al. 2012; Broszat and Grohmann 2014).

Several authors have reported enhanced HGT in biofilms via conjugation (Sorensen et al. 2005; Maheshwari et al. 2016); however, certain spatial constraints within biofilms may hinder the dispersal of plasmids (Krol et al. 2011; Merkey et al. 2011). Lili et al. (2007) indicated that plasmids which are maintained through high transfer frequencies may only be able to persist in biofilms. Interestingly, other mechanisms of gene transfer, for example, transformation, occur at higher rates in biofilms. Gene transfer via both small DNA fragments as well as plasmid transformation has been documented (Maeda et al. 2006; Etchuuya et al. 2011). It has been

reported that competence of cells in the biofilm mode is triggered by extracellular DNA (eDNA) molecules within the biofilm matrix (Molin and Tolker-Nielsen 2003; Meena et al. 2014a, 2016c; Saha et al. 2016a; Sharma et al. 2016). Thus, transformation triggers and stabilizes biofilms and vice versa.

Conjugative pili formation is best studied among other biofilm-associated factors encoded by backbone genes of plasmids. There is much evidence in support of greater effectiveness of conjugative plasmids, compared to deficient strains, in biofilm formation (Reisner et al. 2006; Burmolle et al. 2008; Roder et al. 2013; Madsen et al. 2016). Other factor encoded by plasmid accessory regions includes different types of fimbriae and conjugative pili. These adhesions play a significant role in cell surface adherence and cell-to-cell contact, mainly in members of family Enterobacteriaceae. Three pathways in enteric bacteria are known for synthesis of surface-associated fimbriae: (1) the type IV pili pathway, (2) the nucleation pathway, and (3) the chaperone/usher pathway (Clegg et al. 2011; Madsen et al. 2012). These fimbriae perform a number of functions, and genes are located both on plasmids and on chromosomes. Several such plasmid-encoding cell surface adhesion factors are known in Gram-negative and Gram-positive bacteria, for example, *Pseudomonas putida* TOL plasmid, *Lactococcus lactis* pAMb1, and *Azospirillum brasilense* plasmids (D'Alvise et al. 2010; Petrova et al. 2010). Thus, the plasmid's role as a social evolutionary platform has been described in accordance to plasmid functions including (a) host fitness, (b) multicopies of gene present on the plasmid, (c) high gene expression rate, (d) mobility of gene, and (e) high turnover of plasmid-encoded gene (Madsen et al. 2012).

The interconnection between biofilm formation and gene transfer has been a topic of investigation in recent years. Madsen et al. (2012) published an excellent article on this issue and concluded that plasmid biology and biofilm community structure and related functions are interconnected through various interactions at both community and genetic levels. Biofilms provide an excellent environment for bacterial interaction due to their high cell density and extensive communication network within the biofilm matrix. Since bacterial communities within biofilms are heterogeneous and often multispecific, variations within specific bacterial lineages have been recorded (Stewart and Franklin 2008). These variations provide recipients that are more accessible for plasmid transfer than in planktonic culture. Thus, bacterial genetic heterogeneity is maintained and promoted by HGT and mutation provided via the biofilm mode of growth (Jefferson 2004; Conibear et al. 2009; Rankin et al. 2011).

6.5 Gene Transfer in the Soil System

Most of our knowledge of gene exchange, however, comes from investigations of the planktonic mode. The study of gene transfer under complex natural conditions such as bulk and rhizosphere soil remains a challenging task. Many factors are known to affect gene transfer occurring in the soil system; therefore, careful investigation using soil microcosms is suggested. Hill and Top (1998) reviewed gene

transfer in soil using microcosms with special focus on transfer of broad host range plasmids and catabolic soil plasmids. The importance of gene transfer in soil and other natural habitats has been recognized due to (a) interest in the possible spread of genetically modified microorganisms, (b) spread and exchange of antibiotic resistance, (c) the role of HGT in the evolution of new bacterial traits, and (d) the possible role of introducing catabolic genes to enhance bioaugmentation strategies to enhance bioremediation of soil contaminants.

Laboratory microcosms are used to assess gene transfer for a number of potential benefits as mentioned above. Although microcosms are not exact replicas of the soil system, they possess many of the same chemical and physical attributes. Microcosms must be calibrated to ensure that they reflect natural conditions (Bolton et al. 1991). Microcosms can be used to obtain vital information on (1) survival and dispersal of bacterial strains, (2) ability to compete with indigenous microflora, (3) capacity to exchange genetic information, and (4) stability of heterogeneous DNA in soil. Most of the well-studied examples mainly comprise various conjugative plasmids and their exchange by conjugation using suitable recipient strains. Some of the widely used plasmids described by Hill and Tops (1998) are RP4, RP4p (RP4::pat), pBLK1-2 (pRK2073::Tn5), RP4::Tn4371, pJP4, pEMT3k (pEMT3::mini Tn5), pEMT1k (pEMT1::miniTn) R57.b, R388::Tn1721, pLF40, pFT30, pJB5JI::Tn5, and pIJ673. Other plasmids studied include fluorescent marker-tagged plasmids such as pB10 (De Gelder et al. 2005), pKJK10 (Musovic et al. 2006; Claudia et al. 2013), gfp-tagged IncP-1 α plasmid RP4 (Musovic et al. 2010), pBP136, pCAR1, NAH7 (Shintani et al. 2014), and low GC-type plasmid pHHV216 (Jechalke et al. 2013).

Soil microcosms utilized in gene transfer studies vary in complexity from simple closed vessels containing a few grams of soil in a conical flask or falcon tube to more complicated systems including vertical soil columns. Other microcosms include continuous flow reactors through which water or nutrients are percolated. Microcosms for studying bacterial interactions in the rhizosphere/rhizoplane were elaborated by Hill and Top (1998). The microcosm system adopted depends upon the objectives of the study. Care should be taken to assess the desired factors affecting gene transfer in the soil/rhizosphere (Meena et al. 2013b, 2014b, 2015b, c, d; Rawat et al. 2016; Yasin et al. 2016; Verma et al. 2015a; Shrivastava et al. 2016; Velazquez et al. 2016; Sindhu et al. 2016; Singh et al. 2016). Important factors include inoculum treatment and mode of application, concentration and sampling methods, soil temperature, soil depth, concentrations of media, and types and amounts of degradable chemicals (Hill and Top 1998; Wang et al. 2014a, b). Table 6.1 shows the various soil factors affecting gene transfer studies in microcosms.

Table 6.1 Soil factors affecting gene transfer

Factors	Effects/explanation
Drying and sieving	Disturbing the soil results in poor survivability of strains and ultimately poor conjugation
Earthworm activity	Varying influence, depending upon the depth at which earthworms are present
Nutrient availability	Nutrient availability enhances survival and therefore gene transfer
Plant rhizosphere	High concentrations of root exudates and nutrients in the rhizosphere positively affect gene transfer
Selective pressure such as heavy metals or recalcitrant organics	In most of cases, heavy metals/recalcitrant organics enhance the number of transconjugants
Soil type	Soil variables such as types and amounts of clay, organic matter, pH, moisture, and incubation temperature influence gene transfer
Spatial separation between donor and recipient strains	Moisture content helps in movement and survivability of strains thus directly affecting gene transfer
Sterilization	Sterilization of soil increases transfer frequencies
Temperature	Higher transfer frequency observed at environmentally relevant soil temperatures

Adopted and modified from Hill and Top (1998)

6.6 Conclusions

The current state of understanding of HGT in soil and other natural environments demonstrates that HGT is a mechanism of bacterial chromosomal evolution which provides real-time adaptation among bacteria. HGT also provides genetic diversity through its gene pool, which helps bacteria adapt to changing environmental conditions. The availability of nutrients in the plant rhizosphere attracts bacteria, thus offering a greater opportunity for HGT compared to bulk soil. Microcosm and bio-film studies demonstrate that bacteria receive advantages and long-term ecological benefits for survival and adaptation through HGT. However, the exact mechanisms and magnitude of HGT in unsterile soil and in the rhizosphere must be explored further, as factors influencing gene transfer in such situations are complex and multifactorial.

Considering the untapped diversity of MGEs in soil- and plant-associated microbiomes, the impact of HGT on influencing plant-microbe interactions must be further explored for possible exploitation in sustainable agriculture.

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