Mechanisms and Research Advances of Horizontal Gene Transfer (HGT) in Plants and Microorganisms

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Abstract. It is becoming increasingly clear that horizontal gene transfer (HGT) serves as a key mechanism enabling the movement of genetic material across species during biological evolution. By extending beyond the constraints of vertical inheritance, HGT exerts substantial influence on the formation of biological diversity and ecological adaptation. Recent advances in genomics and phylogenetics have driven significant progress in understanding HGT in both plants and microorganisms. This paper summarizes the primary criteria and identification methods for HGT, including multidimensional assessments such as integration sequence characteristics, codon preference, colinearity patterns, and phylogenetic inconsistencies. Current knowledge of HGT in plants is also synthesized, including its discovery, functional consequences, gene characteristics, and underlying mechanisms, with particular emphasis on its contributions to terrestrial adaptation, metabolic pathway remodeling, and the evolution of stress resistance. In microorganisms, the principal routes of HGT—transformation, transduction, conjugation, and other non-classical modes—are reviewed, along with the ways in which host factors and environmental conditions jointly shape the frequency and direction of gene transfer. Potential mechanisms and evolutionary implications of Maverick/Polinton-like viroids acting as mediators of eukaryotic HGT are also highlighted.

Keywords: horizontal gene transfer, plant genome, microorganisms, Maverick.

1. Introduction

With advances in genome sequencing technology and bioinformatics, biological evolution is no longer viewed as a simple linear process of gradual differentiation from a common ancestor through vertical inheritance. Increasing evidence indicates that the flow of genetic information across species—known as horizontal gene transfer (HGT)—is widespread across all organisms and exerts significant influence on gene evolution and adaptive evolution. Initially, HGT was thought to occur primarily among prokaryotes, explaining the spread of resistance genes and the diffusion of bacterial metabolic capabilities. However, in recent years, deepening studies of eukaryotic genomes have revealed extensive HGT events in plants, fungi, and even animals. These transfers have played profound roles in the origin of land plants, the innovation of metabolic pathways, and environmental adaptation. The emergence of HGT research has not only transformed traditional phylogenetic tree models but also advanced our understanding of network-like evolution in life. This article systematically reviews HGT research across three dimensions: identification methods, advances in plants and microorganisms, and transposon-mediated horizontal transfer, aiming to provide comprehensive references and insights for future studies.

2. Identification of HGT Events

2.1. Identification criteria

Genomes exhibiting HGT adhere to a fundamental principle: when a gene transfers from one species to another, the donor and recipient initially possess identical sequences [1]. Therefore, based on the similarity of gene sequences, the developmental tree that contradicts species phylogeny, the scattered distribution of genes among species, and the results of colinearity analysis can all point to the existence of HGT events.

2.1.1 Sequencebased criteria

From the perspective of sequence characteristics, high sequence similarity is the primary signal for identifying HGT. When a plant gene exhibits nearly identical sequences with phylogenetically distant species (such as bacteria, fungi, or other plant groups) while showing significant differences from its closely related species, this abnormally high similarity often suggests the gene was acquired through horizontal transfer. Furthermore, if a gene in the target species exhibits high similarity in intron structure with its homolog in a distantly related species, this may indicate the gene was introduced via horizontal gene transfer. This is because introns typically evolve rapidly and are rarely shared between distantly related species.

2.1.2 Codonusage criteria

Secondly, codon usage preferences can also reflect gene sources. Different species exhibit characteristic differences in the usage of synonymous codons. If a gene's codon usage pattern significantly deviates from the host's overall characteristics but aligns more closely with the usage patterns of suspected donor species, this suggests the gene may have been acquired from an external source. However, since codon usage can also be influenced by gene expression levels and mutation preferences, it should be used as supplementary evidence for judgment.

2.1.3 Synteny analysis

Collinearity analysis provides crucial structural evidence for identifying HGT. When an exogenous gene integrates into the host genome, the surrounding gene arrangement often differs completely from that of the donor, exhibiting “non-collinearity.” This alteration in the genomic context indicates the gene has been inserted into a new location, supporting the hypothesis of horizontal transfer. Conversely, if the suspected exogenous gene retains the same adjacent gene structure as the donor in the genomic environment, it cannot corroborate the occurrence of an HGT event.

2.1.4 Phylogenetic analysis

From a phylogenetic perspective, phylogenetic incongruence between gene trees and species trees serves as key evidence for identifying HGT. If a gene's phylogenetic tree shows it clustering with distantly related species while diverging from its host species' paraphyletic clade, this indicates its evolutionary history conflicts with the host's phylogeny, suggesting potential horizontal gene transfer. To enhance reliability, methods like AU tests, support factor analysis, or gene-species tree reconciliation models (e.g., SpeciesRax, Ranger-DTL) can quantify and validate such incongruence.

Additionally, patchy distribution serves as a significant indicator of HGT. When a gene is present in phylogenetically distant species but absent in their close relatives, this discontinuous distribution pattern is often difficult to explain by vertical inheritance and more likely attributable to horizontal transfer.

2.2. Identification approaches

Identifying HGT genes typically involves extensive gene alignment, and multiple methods currently exist to detect the occurrence of HGT events.

As mentioned earlier, phylogenetic analysis compares gene trees with species trees to preliminarily determine the likelihood of HGT events. This approach is particularly useful for judging gene origins and estimating the direction or timing of HGT. However, factors such as gene loss, long-branch bias, variations in evolutionary rates, and post-transfer mutations during evolution can interfere with accurate assessment.

BLAST technology is also one of the methods currently used to identify HGT events. By searching for homologous sequences of genes in databases, it compares whether distantly related species within certain branches exhibit higher similarity than closely related species. Using BLAST yields relatively intuitive results and offers rapid comparison speeds, making it suitable for initial screening of large gene sets. However, BLAST technology is highly dependent on the database itself; if affected by sample bias in the database, it can lead to inaccurate judgments and a relatively high rate of false positives.

To address false positives, steps must be taken to exclude data contamination. During data screening, specific sources can be excluded as needed. For instance, studies investigating HGT events in terrestrial plants excluded cyanobacterial genes to eliminate interference from endosymbiotic origins [2]. Additionally, homologous verification among closely related species can be performed. Except in rare cases, once HGT genes integrate into a genome, they are typically retained across multiple closely related species within the same taxonomic group. If no homologous genes are found in any closely related species, this indicates the candidate gene lacks evolutionary continuity support, suggesting a high probability of false positives.

3. Research Advances on HGT in Plants

3.1. Discovery and identification of plant HGT

During the evolution of terrestrial plants, research has identified two major historical HGT events that played a crucial role in plants' successful colonization and adaptation to terrestrial environments. The first event occurred during the early evolution of Streptophytina, involving approximately 177 gene families of bacterial origin. These provided plants with vital tools for coping with stress and acquiring nutrients, such as drought tolerance, resistance to aluminum toxicity, and regulation of short-term nitrogen storage in bark and parenchyma cells.

The second one occurred during the origin of terrestrial plants, involving approximately 107 gene families. This event introduced pathways such as phenylpropanoid metabolism, enhancing plants' resistance to UV radiation and pest attacks, and conferred pollination-related proteins (POP2), which played a crucial role in adapting plants to terrestrial environments [2]. The distribution of recent HGT events among terrestrial plants exhibits significant unevenness. Analysis of 522 terrestrial plant genomes revealed that non-seed plants (e.g., mosses, hornworts, liverworts, lycophytes, ferns, gymnosperms, and angiosperms) averaged 5–15 recent HGT events, compared to 0.6 in gymnosperms and a mere 0.4 in angiosperms. The primary donors of HGT events are bacteria and fungi. Among bacterial phyla, Proteobacteria (18.6%) and fungal phyla, Ascomycota (21.4%) are the most common donor groups [3].

3.2. Functional impacts of plant HGT

Genes acquired through HGT may influence various plant functions, including but not limited to altering metabolic pathways, regulating gene expression levels, and modifying plant adaptability to the environment. HGT-acquired genes have endowed terrestrial plants with extensive metabolic capabilities, including but not limited to secondary metabolism, xenobiotic degradation, amino acid metabolism, carbohydrate metabolism, lipid metabolism, nucleotide metabolism, and energy metabolism. Taking the bacterial-derived guanine degradation pathway to xanthine as an example, studies reveal that in certain terrestrial plants, the acquisition of GuaD via HGT leads to the gradual loss of the original HGPRT gene, ultimately replacing the plant's native guanine degradation pathway (HGPRT) [3]. We can conclude that HGT plays a significant role in driving plant genome evolution and environmental adaptation.

In studying horizontal gene transfer (HGT) events occurring in seed plants, three genes transferred from bacteria to wheat were identified, encoding cold shock proteins (CSPs). Plants overexpressing these genes exhibit higher survival rates and photosynthetic efficiency under drought conditions. Among them, one CSP-H1 haplotype (*AetHap2*) discovered in the wheat D-genome ancestor *Aegilops tauschii*, when introduced into modern wheat, significantly enhances drought tolerance while boosting yield by approximately 20%. This clearly demonstrates that the HGT event contributed to improved drought adaptation in wheat.

3.3. Gene features of plant HGT

Although introns are almost entirely absent in prokaryotic genes, most genes acquired via HGT exhibit intron insertion after entering terrestrial plants. In gymnosperms, genes obtained through HGT contain an average of 3.2 introns, whereas their homologous genes in donor organisms contain only 0.2 introns on average. These introns can reach lengths of up to 82.9 kb, significantly exceeding the 0.16 kb average of donor genes. This strongly suggests that intron acquisition represents a common evolutionary outcome for HGT genes in terrestrial plants[3].

3.4. Mechanisms of HGT in plants

The mechanisms of HGT remain under investigation. Currently, identified plant HGT events primarily occur through three pathways at the microscopic level: organelle transfer, nuclear DNA transfer, and RNA transfer.

When plants engage in close interactions with other species—such as fungi, bacteria, etc.—through phenomena like parasitism, symbiosis, fungal coexistence, or grafting, genetic material has opportunities to transfer. Simultaneously, HGT events can also occur via vectors or mediators, including but not limited to pollen, fungi, bacteria, viruses, viroids, plasmids, transposons, and insects [4]. Taking bacteria as an example, Agrobacterium-mediated transformation—widely applied in numerous plant genetic engineering approaches—leverages precisely this type of mediated HGT event. In plant pathology research, Agrobacterium tumefaciens can insert T-DNA into plant genomes, causing crown gall disease. In some plants, such as *Nicotiana*, *Campsis*, and *Ipomoea batatas*, these T-DNA sequences have even been naturally integrated and inherited, potentially influencing plant evolution[5].

As mentioned earlier, although relatively rare, HGT events from fungi to plants do occur today. Not only do HGT events from fungi to plants take place, but instances of fungi acquiring plant genes also occur. By comparing the genomes of six plant species (*Arabidopsis thaliana*, *Oryza sativa*, *Populus trichocarpa*, *Selaginella moellendorffii*, *Sorghum bicolor*, *and Physcomitrella patens*) with sequences from 159 other organisms (including 46 fungi), combined with BLAST analysis, phylogenetic trees, and statistical topological tests, nine reliable HGT events have been confirmed: five with fungi as donors and four with plants as donors.

Research also indicates that transposable elements, first discovered by Mrs. McClintock, can drive horizontal gene transfer events in plants. For instance, highly similar MULE elements have been identified between *Setaria* (a close relative of sorghum) and *Oryza sativa*. The non-coding and synonymous sequence similarity between these elements far exceeds what could be explained by the evolutionary relationship between these two lineages over the past 30–60 million years. This excludes the possibility of vertical gene transfer and confirms that HGT occurred between them[7].

4. Research Advances on HGT in Microorganisms

4.1. Mechanisms of microbial HGT

HGT serves as a crucial driver for microbial genetic diversity and functional innovation, enabling genes to cross phylogenetic boundaries. It plays a central role in bacterial adaptive evolution, pathogenicity development, and resistance spread. Bacterial HGT primarily occurs through three classical mechanisms: transformation, transduction, and conjugation. Additionally, numerous non-classical transfer pathways mediated by mobile genetic elements exist[8].

During transformation, competent bacteria can absorb free DNA molecules from the environment and integrate them into their genome through homologous recombination. This mechanism does not rely on cell-to-cell contact and is widely present in natural communities. Strains such as Streptococcus pneumoniae and Bacillus subtilis can acquire exogenous genetic material through transformation. Transduction, on the other hand, is a phage-mediated method of gene transfer. When a bacteriophage infects a bacterium, some DNA from the host bacterium may be mistakenly packaged into the phage particle. This enables lateral gene transfer upon infection of a new host cell. Depending on the integration or replication mode of the phage, transduction can be classified into three types: generalized transduction, specialized transduction, and autotransduction[8]. Conjugation represents the most efficient and ecologically widespread mechanism of HGT. It relies on direct contact between donor and recipient bacteria and is mediated by plasmids or integrative and conjugative elements (ICEs). This process is typically accomplished through the coordinated action of the Type IV Secretion System (T4SS) and the relaxosome complex, enabling rapid transfer of large-molecule DNA. It is recognized as the primary pathway for the dissemination of resistance and virulence genes among bacteria.

Beyond these three primary pathways, recent research has uncovered multiple non-classical HGT mechanisms, such as Gene Transfer Agents (GTAs), Outer Membrane Vesicles (OMVs), and Intercellular Nanotubes. GTAs are particle structures derived from phage-like elements that can randomly package bacterial chromosomal fragments and mediate DNA dissemination within populations. OMVs facilitate transfer across species and even genera by encapsulating plasmids or chromosomal DNA fragments. Nanotubes form membrane channels connecting cells, enabling direct transfer of plasmids or cytoplasmic components between different strains. Although transfer frequencies via these pathways are typically low, they significantly enhance the diversity and robustness of gene flow within complex ecosystems, providing multi-tiered pathways for HGT [8].

From a macro perspective, HGT occurrence depends on the structural characteristics of mobile genetic elements and ecological connections between hosts. Through systematic analysis of over 10,000 plasmid genome sequences, Redondo-Salvo et al. revealed the central role of plasmids in HGT, constructing a “plasmidome network” that reflects global gene flow patterns among bacteria. Research indicates plasmids can spread through two mechanisms: conjugative transfer or mobilization. The former enables independent DNA transfer via self-contained transfer systems (e.g., tra gene clusters), while the latter relies on sibling conjugative plasmids—those co-residing with target plasmids within the same bacterial cell and possessing complete transfer systems—to facilitate transfer. This mechanism significantly broadens the host range of plasmids, enabling mobilizable plasmids to participate in gene flow and thereby enhancing genetic continuity between bacterial communities[9].

Building upon this foundation, phylogenetic analysis of plasmids revealed a hierarchical structure of HGT transmission. Researchers introduced the concept of “Plasmid Taxonomic Units” (PTUs) to describe groups of plasmids sharing common backbone structures and transmission characteristics. Lower-level PTUs typically confine transfer within the same genus or closely related bacteria, while certain higher-level PTUs (such as PTU-P1, PTU-C) can span multiple families or even phyla, forming “genetic transfer hubs” among bacteria. These broader host range plasmids play a pivotal role in HGT networks, bridging genes across different ecological niches and phylogenetic lineages, thereby driving the global dissemination of resistance and metabolism-related genes[9].

4.2. Host and environmental regulation of bacterial HGT

As a core driver of bacterial adaptive evolution and genomic reshaping, the frequency and scope of HGT are not random but are jointly regulated by host biological characteristics and environmental ecological conditions [10]. Host organisms provide the cellular physiological and genetic integration platform for gene transfer, while the environment shapes the spatial patterns, directionality, and selective pressures of gene exchange. The interaction between these two factors jointly determines the mechanisms, evolutionary pathways, and ecological effections of HGT.

At the host level, the physiological characteristics, metabolic activities, and ecological niche adaptations of different microbial groups directly influence the likelihood and stability of HGT. Protozoa (such as ciliates and amoebae) form digestive vacuoles during bacterial predation, concentrating donor and recipient bacteria within a microenvironment that significantly increases the probability of conjugation and transformation events [11]. The locally anaerobic, high-density, and nutrient-rich conditions within these vacuoles provide an ideal reaction environment for gene exchange. Furthermore, reactive oxygen species (ROS) generated during host metabolism activate bacterial DNA repair and conjugation systems, thereby inducing the expression of conjugative plasmids and mobile genetic elements (MGEs), indirectly increasing HGT frequency.

For bacteria, the host's genetic background and physiological structure determine whether exogenous DNA can effectively enter and stably integrate. DNA restriction-modification systems, membrane permeability, homologous recombination capacity, and natural DNA uptake competence are key intrinsic factors influencing HGT [10]. For instance, in soil-derived Listeria species, strains possessing intact transformation-related genes such as comK, comEC, and cinA acquire antibiotic resistance genes (ARGs) via natural transformation at a significantly higher rate than those lacking these genes. Furthermore, motile hosts equipped with flagella and chemotaxis systems more readily encounter donor cells or environmental DNA, thereby enhancing opportunities for gene exchange. Phylogenetic analysis revealed that resistance genes within the Listeria sensu stricto group are not only more complete but also subject to positive selection, whereas homologous genes in distantly related populations are predominantly inactivated. This indicates that host genetic compatibility and metabolic costs play crucial roles in gene retention following HGT[12].

At the environmental level, the driving forces behind HGT primarily stem from external physicochemical conditions and ecological structures. Nutrient-rich, high-density ecosystems such as wastewater treatment plants, biofilms, estuarine sediments, and agricultural soils are hotspots for HGT events, where conjugation and transformation occur far more frequently than in low-density or extreme environments [11]. These environments are typically rich in environmental DNA (eDNA) and are jointly influenced by antibiotic residues, heavy metal contamination, and organic carbon inputs, creating complex selective pressure fields. Under such conditions, bacterial communities not only acquire exogenous genetic material more readily but also achieve rapid adaptation by selectively retaining resistance, metabolic, or virulence-related genes[10]. Taking soil ecosystems as an example, the enrichment of metal elements (e.g., Al, Fe, Zn) shows a significant positive correlation with ARG abundance, indicating that heavy metal stress can promote resistance diffusion through both co-selection and HGT pathways [12]. Concurrently, land use types (forests, wetlands, or farmlands) and physicochemical factors (pH, organic matter content) alter community composition and the availability of exogenous DNA donors, thereby further regulating the ecological processes of HGT.

Biofilm environments are also a key ecological niche receiving extensive attention in HGT research. Within biofilms, cells aggregate at high densities, and the extracellular polysaccharide matrix (EPS) protects DNA from degradation while promoting the accumulation of quorum-sensing signals, significantly enhancing conjugation and transformation efficiency[10]. Furthermore, novel carriers such as microplastics adsorb bacteria and genetic material to form “mobile biofilms,” serving as important platforms for transmitting resistance genes across ecosystems[12].

It is noteworthy that the influence of hosts and the environment on HGT does not occur in isolation but forms complex eco-physiological coupling mechanisms. Host physiological activities determine the potential rate of HGT, while environmental selection pressures dictate which genes are retained and disseminated. In wastewater and natural water bodies, protozoan predation on bacteria simultaneously suppresses donor abundance and releases environmental DNA, exerting both inhibitory and promotional effects [11]. In soil systems, host motility and uptake systems jointly determine HGT frequency and direction alongside environmental heavy metal concentrations [12]. Furthermore, environmental stress induces host cellular stress responses and upregulates quorum sensing signals, triggering conjugative element activation and plasmid transfer[10].

It follows that hosts provide conditions for genetic integration and physiological pathways at the microscopic level, while the environment supplies energy and selective pressures at the macroscopic level. The host's uptake capacity, motility, and metabolic activity determine the entry and recombination of exogenous DNA, while environmental chemical stressors, ecological structure, and community density govern gene diffusion and fixation. The synergistic interaction between these factors positions HGT as a pivotal process linking individual physiology and community ecology, accelerating the flow and functional integration of resistance genes, metabolic pathways, and adaptive traits across ecosystems.

4.3. Viruslike transposons and HGT

Recent phylogenetic and genomic studies indicate that transposable elements in some eukaryotes exhibit characteristics of both viruses and transposons, forming a class of genetic units known as virus-like transposons. The most representative examples of these are Mavericks (Polintons). Maverick transposon elements were first identified in the early 2000s and are widely distributed across diverse eukaryotic genomes. Typically spanning 15–20 kb in length, they possess characteristic terminal inverted repeats (TIRs) and target site duplications (TSD). Structurally, Maverick genomes exhibit high modularity, incorporating both viral and transposable modules. The viral modules include core viral genes such as double-jelly-roll (DJR) capsid proteins, protein-initiated class B DNA polymerases (pPolB), and FtsK/HerA-type packaging ATPases. The transposable modules comprise RVE family integrases, transposases, and DNA repair proteins. This modular architecture enables Maverick to integrate into host genomes for vertical transmission while retaining the potential to assemble into virion-like particles under specific conditions, conferring potential cross-cell or cross-species transmission capabilities.

Phylogenetic analysis indicates that Maverick belongs to the PRD1–adenovirus lineage of eukaryotic large double-stranded DNA elements. It shares core gene modules with adenoviruses (Adenoviridae), iridoviruses (Iridoviridae), virophages, and giant viruses, suggesting a common ancestral origin [13]. Consequently, Maverick is regarded as a pivotal link connecting the evolutionary lineages of viruses and transposons, serving as a crucial model for studying the evolution of eukaryotic selfish genetic elements and the origins of viruses[14].

In studies of horizontal gene transfer (HGT) among eukaryotes, Maverick is considered one of the most likely known vectors. Comparative genomics reveal that Maverick is widely distributed across teleost fish, amphibians, reptiles, and invertebrates, while it tends to be degenerated in birds and mammals[15]. Its patchy distribution across species and inconsistencies in phylogenetic trees suggest multiple episodes of interspecies horizontal transmission. Molecular mechanism studies reveal that this process likely relies on virus-like functional modules acquired by Maverick, particularly the introduction of fusogen genes. These proteins mediate cell membrane fusion, enabling Maverick elements to form enveloped virus-like particles (VLPs) after replication. Through membrane fusion mechanisms, these VLPs infect heterologous hosts, facilitating the delivery and integration of exogenous DNA[16].

This infectious transfer mechanism endows Maverick with both the cross-host transmission capacity of viruses and the gene integration properties of transposons, forming a unique “transposon–virus chimera” capable of effectively breaching species barriers for genetic exchange. Experimental evidence confirms this mechanism occurs in animals. For example, the maternal toxin–antidote system (msft-1/tlpr-1) discovered in the nematode *Caenorhabditis briggsae* is embedded within the Maverick element and exhibits near-perfect sequence identity with homologous sequences in C. plicata, indicating that this gene underwent trans-species HGT mediated by Maverick[16]. Further systematic comparisons reveal that Mavericks in nematodes have facilitated multiple independent HGT events globally, indicating the mechanism's prevalence and persistence across the animal kingdom.

From an evolutionary perspective, Maverick's “dual lifestyle” not only ensures the long-term persistence of this intragenomic transposable element within its host genome but also endows it with the potential for gene transfer and interspecies exchange at ecological and evolutionary scales. Their virus-like replication and integration mechanisms provide the material basis for gene flow between eukaryotic cells, enabling the migration and fixation of foreign genes across species. This facilitates gene innovation, adaptive evolution, and even speciation on a macroevolutionary scale[17]. Furthermore, similar viral-like elements, such as the BovB retrotransposon, have been found to achieve transclass transfer via arthropod vectors [18], further demonstrating that viral-like mobile elements are significant drivers of horizontal gene transfer in nature.

Overall, the Maverick element represents an intermediate between viruses and transposons. Its modular gene structure, virus-like infectivity, and capacity to mediate horizontal gene transfer (HGT) not only reveal complex gene exchange networks among eukaryotic genomes but also provide crucial insights into viral origins, the evolution of eukaryotic selfish genetic elements, and mechanisms of eukaryotic gene innovation.

5. Conclusion

It is possible to tell that HGT is not an isolated phenomenon in both plants and microorganisms. Somehow it contributes to the supplementation of metabolic pathways, the enhancement of environmental adaptation capabilities, and changes in genomic structure. With the accumulation of more high-quality genomes, we can more accurately identify these cross-border transfer events and also gradually recognizing that the impacts of HGT are often more complex than previously imagined. However, many key questions regarding HGT remain unresolved. For instance, which ecological scenarios are more conducive to transfer, whether differences in transfer frequency between species follow some specific patterns, and how long these acquired genes can persist and play their role in real environments. All these questions require further data and experiments to support.

All in all, HGT has emerged as a crucial clue for understanding genomic evolution. Research on its practical applications will continue to advance as more data accumulates, helping us gain a more comprehensive understanding of the actual significance of gene flow between species.

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