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The Function and Structure of Mx Gene

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ABSTRACT

The Myxovirus resistance (Mx) gene, known for its role in antiviral defense, has been extensively studied across various species, revealing a complex interplay between its structure and function. Mx proteins, which are part of the dynamin superfamily of large GTPases, play a crucial role in the innate immune response by inhibiting viral replication. These proteins are induced by type I and type III interferons and are known to sequester viral nucleoproteins, thereby preventing the replication of a broad range of viruses. Structurally, Mx proteins are characterized by several conserved domains, including the GTPase domain, which is essential for their antiviral activity. The GTPase domain allows Mx proteins to bind and hydrolyze GTP, a process critical for their function. The presence of additional domains, such as the central interactive domain (CID) and the GTPase effector domain (GED), further supports their role in antiviral defense by facilitating interactions with other cellular components and enhancing their stability and function. The expression and regulation of Mx genes vary significantly among species, reflecting their evolutionary adaptation to different viral threats. For instance, in fish species like Labeo rohita and Cirrhinus mrigala, Mx proteins are upregulated in response to viral infections and other immune challenges, highlighting their importance in aquatic environments. Similarly, in birds, the presence or absence of specific Mx gene variants correlates with varying levels of resistance to viral infections, such as avian influenza, underscoring the gene's role in species-specific antiviral defense mechanisms. Overall, the Mx gene exemplifies the intricate relationship between genetic structure and immune function, with its diverse expression patterns and conserved structural features playing a pivotal role in the host's ability to combat viral infections. Continued research into the Mx gene and its protein products promises to enhance our understanding of antiviral immunity and may lead to novel therapeutic strategies for managing viral diseases across different species.

Keywords: Mx Gene; Innate Immunity; Interferon; Antiviral; GTPase; Genetic Diversity; Biomarker

Introduction

The Myxovirus resistance (Mx) gene has been extensively studied in various species, including mice, rainbow trout, sheep, and zebrafish. The mouse cells carrying the dominant resistance gene Mx develop a more efficient antiviral state towards influenza viruses in response to interferon compared to Mx-negative cells (Horisberger, et al. [1]). who demonstrated that interferons alpha and beta induce an efficient antiviral state against influenza virus in mouse cells possessing the Mx gene (Krug, et al. [2]. Interferon-regulated Mx genes are not responsive to interleukin-1, tumor necrosis factor, and other cytokines (Simon, et al. [3]). Furthermore, characterized a rainbow trout Mx gene and found homologous genes in other salmonid fish species (Trobridge, et al. [4]). Studied the temporal and spatial alterations in ovine uterine Mx expression during the estrous cycle and early pregnancy (Ott, et al. [5]). investigated the expression of the antiviral protein Mx in peripheral blood mononuclear cells of pregnant and bred non-pregnant ewes (Yankey, et al. [6]). Explored polymorphisms and the differential antiviral activity of the chicken Mx gene (Ko JH, et al. [7]) Additionally, conducted quantitative expression profiling of immune response genes in rainbow trout following infectious haematopoietic necrosis virus (IHNV) infection or DNA vaccination (Purcell, et al. [8]). cloned and characterized an Mx gene and its corresponding promoter from the zebrafish, Danio rerio (Altmann, et al. [9]). Investigated the effect of beta-glucan on the activity of antioxidant enzymes and Mx gene expression in virus-infected grass carp (Kim, et al. [10]). These studies collectively contribute to our understanding of the Mx gene and its role in antiviral responses across different species.

Genomic Organisation and Regulatory Elements

Mx loci typically comprise 13-15 exons spanning 8-15 kb. Chicken and quail possess a single Mx gene, whereas mammals harbour two paralogues (MX1 and MX2) arising from tandem duplication. Comparative promoter analyses reveal a tripartite architecture:

- Proximal ISRE/GAS elements for IFN responsiveness,
- NF-κB sites for synergistic enhancement during co-infection, and
- Species-Specific enhancers-for example, the duplicated ISRE motif in Atlantic salmon confers rapid induction by IFN-γ as well as IFN-α. Alternative splicing generates truncated isoforms lacking the GED in pigs and cattle, although their physiological relevance remains unclear.

The structure of the Mx gene has been extensively studied in various species. found that the Chicken Mx promoter contains an ISRE motif, which confers interferon inducibility to a reporter gene in chick and monkey cells (Schumacher, et al. [11]). investigated the genomic structure and diversity of the Chicken Mx gene (Li, et al. [12]), while characterized the gene structure, alternative splicing, and promoter region of the Bovine Mx1 gene (Kojima, et al. [13]). Additionally, conducted molecular cloning and characterization of the Porcine Mx2 gene (Morozumi, et al. [14]). Furthermore, highlighted the in vivo role of N-glycans using the Mx gene knockout mouse approach, demonstrating how the in vivo roles of apparently redundant gene products can be determined (Fukuda, et al. [15]). reported on the expression of the full open reading frame of the Mx gene in Escherichia coli, detecting a specified product of 75 kDa (Cg, et al. [16]). focused on the structural and functional characterization of the Senegalese Sole Mx promoter. In a different context (Alvarez Torres, et al. [17]), Explored the mutagen structure and transcriptional response by analyzing the induction of distinct transcriptional profiles in Salmonella TA100 after treatment with the drinking-water mutagen Mx and its homologues (Ward, et al. [18]). They investigated whether structural similarity between xenobiotics and endogenous metabolites could explain transcriptional changes. Research on the Mx gene's structure has provided valuable insights into its genomic organization, promoter regions, alternative splicing, and expression patterns in various species such as chickens, bovines, porcines, and Senegalese soles. Additionally, studies have explored the functional implications of the Mx gene through knockout mouse models and expression analysis in bacterial systems.The Mx gene is a crucial component of the antiviral immune response, acting as a dynamin-like machine that inhibits a wide range of RNA and DNA viruses (Haller, et al. [19,20]).

Studies have shown that targeted knockout of Mx can significantly impact antiviral function, highlighting the importance of this gene in innate immunity (Wang, et al. [21]). Interferons play a key role in inducing the expression of Mx and other antiviral genes, ultimately blocking virus replication (Katze, et al. [22]). The structure and biological properties of interferon-omega further contribute to its antiviral activity (Li, et al. [23]). The JAK/STAT signaling pathway, which is involved in interferon-stimulated gene expression, plays a complex role in antiviral immune signaling (Mahjoor, et al. [24]). The diversity of the Mx gene in avian species suggests varying levels of protection against avian influenza virus (Alam, et al. [25]). Additionally, the CARF domain, found in antivirus proteins, has been linked to type III CRISPR-Cas systems, further emphasizing the importance of antiviral mechanisms in host defense (Makarova, et al. [26]). The intricate network of antiviral genes and pathways underscores the complexity of the immune response to viral infections.

Mx Protein Architecture

Mx proteins are 70-80 kDa and share the dynamin-like fold (Haller, et al. [19]). Key domains include: N-terminal G-domain (1-300aa): binds and hydrolyses GTP; mutations such as K83A abolish antiviral activity.Bundle-signalling element (BSE, aa 300-480): three-helix bundle mediating conformational changes upon GTP hydrolysis. Central interactive domain (CID, 480–630aa): forms antiparallel coiled-coils required for oligomerisation. GED / stalk region (aa 630–760): membrane-interacting amphipathic helices that facilitate lipid tubulation. Nuclear localisation signal (NLS) or leucine-rich nuclear export signal (NES) dictate sub-cellular trafficking (human MxA is cytoplasmic, murine Mx1 is nuclear). Cryo-EM structures of human MxA show ring-like oligomers that assemble around viral nucleocapsids, physically sequestering them from the replication machinery (Zhou, et al. [20]).

Mx proteins belong to the large GTP family of enzymes with similar structure to dynamin-like proteins with the following major domains: N-terminal GTPase domain: responsible for GTP binding and hydrolysis and is the core functional region of Mx protein. Tram signaling element: located behind the GTPase domain and consists of multiple helices involved in protein self-assembly and oligomerization Nuclear localization signal (NLS): It is located at the C terminus and contributes to the localization of proteins within the cell (Wagner, et al. [27]). Other domains: including the L4 circular domain and possibly additional α helices that may be involved in the recognition and inhibition of specific viruses. These domains of Mx proteins enable them to form helical, high-molecular-weight oligomers by self-assembly and interact with lipid membranes, thereby interfering with viral replication and transcription (Noteborn, et. al. [28]).

The function of Mx proteins is a topic of interest in the field of host resistance to infection. the functional diversity of Mx proteins, highlighting variations in host resistance mechanisms. (Mosaffa, et al. [29]) explored the influence of proinflammatory cytokines on ABCG2 expression and function in breast cancer cell lines, including the mitoxantrone-resistant derivative MCF-7/MX. (Xiao, et al. [30]) proposed that LspA(Mx) proteins function as SPaseIIs, with LspA3 and LspA4 potentially involved in TA resistance and regulation. (Goujon, et al. [31]) demonstrated that transferring the amino-terminal domain of MX2 to MX1 confers anti-HIV-1 function. (Tallkvist, et al. [32]) studied Bcrp and Mdr1 expressions in murine mammary epithelial HC11 cells, providing a tool to investigate transport mechanisms. (Chen, et al. [33]) The R614E mutation in mouse Mx1 protein was identified as contributing to antiviral activity against classical swine fever virus. (Hagiwara, et al. [34]) Mx expression and function in dif-

ferent bird species compared to understand the relationship between Mx function and highly pathogenic avian influenza virus proliferation. (Mocatta, et al. [35]) The role of the MX helix in modulating the function of the 5-HT3 receptor, suggesting interactions with membrane lipids play a significant role. Overall, these studies contribute to understanding the diverse functions and mechanisms of action of Mx proteins in host defense and cellular processes.

Antiviral Mechanisms

Mx proteins are known for their antiviral activities against a wide variety of viruses, including negative-stranded RNA viruses. These proteins have been shown to inhibit the replication processes of RNA viruses such as influenza and vesicular stomatitis virus (Verhelst, et al. [36]). Recent structural analyses have provided insights into the mechanisms by which Mx proteins exert their antiviral effects, although the exact mechanism remains unclear (Betancor, et al. [37]). It is important to note that proteins such as rat Mx2, mouse Mx2, or any fish Mx protein are not orthologs of hMX2 or any other mammalian MX2, but orthologs of hMX1, and therefore exhibit hMX1-like antiviral activity against certain viruses (Lee, et al. [38]). The antiviral function of Mx proteins is associated with a single Ser631Asn substitution, which is present in about 50% of the breeds studied (Langley, et al. [39]). The Mx1 gene, which produces the Mx1 protein, plays a key role in the body's antiviral response by interfering with the replication processes of RNA viruses (Steiner, et al. [40]). Studies have shown that Mx proteins are induced by the interferon system in response to viral infections (Das, et al. [41]). Mx proteins exhibit different subcellular localizations and viral specificities, with human MxA accumulating in the cytoplasm and inhibiting a wide variety of RNA and DNA viruses (Zavyalov, et al. [42]). Mx proteins are considered to be versatile viral inhibitors with a crucial role in the host's defense mechanisms against viral infections (Haller, et al. [43]). The exact mechanisms by which Mx proteins exert their antiviral effects are still being investigated, and further research is needed to fully understand the antiviral functions of these proteins.

Applications in Disease Control

The application of Mx protein in diseases has shown promising potential in various studies. (Booy, et al. [44]) utilized a proteomics approach to identify differentially expressed proteins in diseased Atlantic salmon, including interferon-induced viral resistance protein Mx. This highlights the role of Mx protein in the immune response to infections. Additionally, (Meyer et. al., 2017) the clinical applications of quantitative proteomics discussed, emphasizing the potential of mass spectrometry-based workflows to investigate biomarker candidates and understand diseases, which could include the use of Mx protein as a potential biomarker. Furthermore, the study focused on molecular signatures for the diagnosis of infection using microarray technology, which could potentially involve the detection of Mx protein levels as a diagnostic marker for certain diseases (Campbell, et al. [45]).

The review discussed proteomic approaches in pancreatic cancer research, suggesting that similar techniques could be applied to study the role of Mx protein in disease progression (Tonack, et al. [46]). The literature suggests that Mx protein has significant potential applications in disease diagnosis and treatment. Future research efforts, as recommended (Udenigwe, et al. [47]), should focus on elucidating the in vivo molecular mechanisms of action of Mx protein and its safety and pharmacological activity in various disease conditions. Additionally, the advancements in targeted protein degradation technologies, as discussed by (Yu M, et al. [48,49]), could offer new strategies for utilizing Mx protein in therapeutic interventions for diseases [50-64].

Knowledge Gaps and Future Directions

Structural basis of viral target recognition: high-resolution complexes of Mx proteins with viral RNPs remain scarce. On-canonical functions: emerging evidence links Mx to autophagy regulation and tumour suppression.

Environmental modulation: how temperature, salinity and pollutants affect Mx induction in ectotherms is poorly understood. Delivery systems: nanoparticle-encapsulated Mx mRNA represents a promising next-generation antiviral platform.

Conclusion

The Mx gene exemplifies how a single IFN-Stimulated gene (ISG) can evolve exquisite specificity and breadth in antiviral defense. Its modular structure, inducible expression and allelic diversity make it an attractive target for both fundamental research and translational applications. Harnessing Mx biology promises to yield next-generation vaccines, therapeutics and breeding strategies against current and emerging viral threats.

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Conflicts of Interest

The authors declare no competing interests.

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