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Multi-interface Processes, Environmental Regulation, and Isotope Applications in Forest Mercury Cycling

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Abstract

Mercury (Hg), as a highly toxic heavy metal pollutant, poses a serious threat to ecosystems and human health worldwide. Forest ecosystems, as vital components of terrestrial ecosystems, serve not only as significant sinks for atmospheric Hg but also as key sites for Hg migration and transformation, playing a crucial role in the global Hg cycle. This paper reviews the Hg cycling processes in forest ecosystems. Starting from the global Hg cycle, it delves into the characteristics of Hg cycling within forest ecosystems, including Hg input pathways, vegetation uptake and fixation of Hg, as well as Hg transformation and re-release within plant bodies. Further summaries of Hg migration and storage mechanisms in forest soils elucidate the distribution, migration pathways, and reduction-re-release processes of Hg within these ecosystems. This paper also elaborates on the regulatory role of environmental factors in forest Hg cycling and the application of isotope techniques in forest Hg cycle research. Finally, it proposes future research directions and challenges, aiming to provide a theoretical basis for deepening the understanding of forest Hg cycling processes, accurately assessing the impact of Hg pollution, and formulating global Hg pollution prevention and control strategies.

Keywords

mercury, forest mercury cycle, transition and transformation

1. Introduction

Mercury (Hg) is a persistent toxic pollutant with global reach [1], continuously migrating and transforming within the atmosphere [2], water bodies [3], soil [4], and the biosphere, posing a serious threat to ecosystems and human health. Hg in the atmosphere primarily exists in three forms: gaseous elemental mercury (GEM), reactive gaseous mercury oxide (RGM), and particulate mercury (PBM) [5]. Forest ecosystems cover approximately 31% of the global land area [6] and play a crucial role in the global biogeochemical cycle of Hg [7]. Forest vegetation absorbs gaseous elemental mercury (Hg^0) from the atmosphere through leaves [8] and inputs Hg into soil via litterfall deposition, serving as a major atmospheric Hg sink [9]. Simultaneously, Hg stored in forest soils may be re-released back into the atmosphere through various physicochemical and biological processes, or transported via runoff into aquatic ecosystems [10].

However, the accumulation of Hg in forest ecosystems is not a unidirectional static process. Under the regulation of complex environmental factors such as light, temperature, and precipitation conditions, Hg present in the canopy and soil undergoes a series of physical adsorption, chemical redox reactions, and biotransformation processes. It may even be reduced back to Hg^0 and re-released into the atmosphere.This frequent migration and transformation across multiple interfaces—such as atmosphere-canopy, canopy-soil, and soil-water bodies—creates significant uncertainty in assessing whether specific forest ecosystems function as “sinks” or “sources” within regional and global Hg cycles [11]. Particularly within the complex matrix of forest environments, processes such as dark reduction mediated by soil organic matter or specific organic ligands, along with microbial reduction, further complicate the fate of Hg and the exchange fluxes at these interfaces. Therefore, accurately understanding the migration and transformation fluxes of Hg within forest ecosystems and the key interface processes is crucial for assessing environmental risks associated with Hg, predicting the impact of future environmental changes on the Hg cycle, and formulating effective Hg pollution control strategies.

Traditional research methods based on concentration gradients and flux measurements struggle to accurately quantify the proportion of Hg migration across interfaces within forest ecosystems and effectively disentangle multiple concurrent transformation mechanisms. In recent years, the rapid advancement of Hg stable isotope technology has provided a novel perspective for overcoming this methodological bottleneck. When Hg undergoes interfacial exchange or geochemical reactions in nature, it exhibits significant mass-dependent fractionation (MDF) and mass-independent fractionation (MIF) [12]. Leveraging these distinctive isotopic “fingerprint” signatures, researchers can not only quantitatively analyze Hg sources across forest multi-media but also unravel the underlying mechanisms of key processes—such as leaf uptake, soil accumulation, and reductive release—at the microscopic scale.

Based on this, this paper systematically reviews the migration and transformation processes of Hg across multiple forest interfaces and their environmental regulatory factors. It particularly summarizes the application progress of isotope techniques in elucidating forest Hg source-sink relationships and microscopic transformation mechanisms. The aim is to provide theoretical foundations for accurately assessing the Hg sequestration potential of forest ecosystems and refining global Hg mass balance models, while also outlining key future research directions and challenges in this field.

2. Characteristics of Hg Cycling in Forest Ecosystems

2.1 Input Pathways of Hg in Forests

Atmospheric Hg enters forest ecosystems through both dry deposition and wet deposition. During dry deposition, GEM can directly adsorb onto vegetation surfaces or soil particles; wet deposition refers to Hg entering forests via precipitation processes such as rainfall and snowfall, where RGM and PBM are washed by rainwater during rainfall events and subsequently deposited onto the ground.

Throughfall and stemflow play crucial transport roles in the entry of atmospheric Hg into forest soils. Throughfall refers to the portion of precipitation that reaches the forest floor after passing through the canopy. Its Hg content primarily originates from the adsorption of gaseous Hg^{2+} and the capture and oxidation of atmospheric Hg^0 by trees [13]. Research indicates that forest canopies intercept atmospheric Hg, with a portion being adsorbed by the canopy and subsequently leached into throughfall during rainfall [14]. For instance, in some forest ecosystems, Hg concentrations in throughfall are significantly higher than in atmospheric precipitation itself, suggesting that the canopy plays a role in Hg enrichment and redistribution [14, 15]. Trunk flow, the runoff formed as rainwater travels down branches and trunks, transports Hg adsorbed on the canopy surface to the ground, further increasing Hg input into the soil [16].

2.2 Absorption and Fixation of Hg by Forest Vegetation

Vegetation primarily absorbs GEM and methylmercury (MeHg) from the atmosphere through stomata [17]. Stomatal opening and closing are regulated by multiple factors, with photosynthesis (such as CO_2 uptake) and transpiration exerting synergistic control over stomatal conductance [18, 19]. During daylight hours when illumination is sufficient, stomata open, allowing atmospheric H_2O to enter the leaf interior via physical diffusion through the stomata. This diffusion flux is regulated by multiple leaf resistances, including stomatal resistance, cuticle resistance, and mesophyll resistance, with stomatal resistance playing the predominant role [20, 21]. However, multiple experiments indicate that vegetation can absorb Hg^0 even when stomata are closed (such as at night or under drought stress), suggesting that non-stomatal pathways may play a significant role in Hg^0 uptake [20, 22]. The non-stomatal pathway primarily refers to Hg diffusion through the cuticle into leaf tissue [23]. This occurs because the cuticle exhibits lipophilic properties [24], allowing elemental Hg to diffuse along its lipid channels and be absorbed and retained by mesophyll cells [20]. Studies indicate that under nocturnal conditions or high CO_2 concentrations, plant leaf uptake of Hg occurs predominantly via non-stomatal pathways [25]. Under these conditions, the majority of absorbed Hg becomes fixed within leaf tissues and is not subsequently released back into the external environment [20].

Different vegetation types also exhibit varying capacities for Hg uptake. For instance, conifers typically absorb Hg at a rate approximately 50%–80% lower per unit leaf area than broadleaved trees due to their thicker cuticle and lower stomatal density [26-28]. However, conifer leaves have longer lifespans (up to 3-5 years), endowing them with greater Hg accumulation potential over extended periods [26]. Regarding differences in atmospheric Hg uptake and release among plants with distinct photosynthetic pathways, previous studies have shown that C_4 plants typically exhibit lower stomatal conductance at night compared to C_3 plants. This implies weaker nocturnal gas exchange capacity in C_4 plants, which may affect their Hg release efficiency [29]. However, systematic studies on atmospheric Hg uptake and release in plants with different photosynthetic pathways remain scarce, and the underlying mechanisms require further investigation.

2.3 Transformation of Hg in Forest Plants

Hg entering leaves is oxidized and sequestered within the plant [30]. A portion is transported to and stored in tree trunk growth rings [31], while another portion may bind to substances within the leaves and be re-emitted to the atmosphere as Hg^0 [25]. Most Hg entering leaf tissue accumulates in cell walls, with only a small fraction distributed on leaf surfaces and in the cuticle [32, 33]. Hg in precipitation primarily exists as Hg^{2+} [34]. Studies have shown that following rainfall, concentrations of total mercury (THg) and MeHg in plant leaves significantly increase, indicating that plant leaves can effectively absorb Hg^{2+} from precipitation [35]. Furthermore, a portion of Hg^{2+} can react with reducing sulfur within plants to form HgS nanoparticles, which are stored in tissues such as leaves. High-energy-resolution X-ray absorption near-edge structure (Hg-XANES) spectroscopy indicates that over 50% of Hg in plant leaves exists as nanoparticles, with the remainder present as thiol complexes [36].

Stems not only serve as primary conduits for transporting water and nutrients, but also absorb Hg through surface lenticels. Hg captured by stomata on the stem surface can be further transported to the phloem and tree rings [37].Taking the halophytic plant purslane as an example, the sources of Hg in its stems include both direct uptake and uptake via root-to-stem translocation. Although Hg absorbed by the roots can be transported to the stems through the xylem by diffusion, the amount is relatively small. The primary source of Hg in the stems remains direct uptake [38].Additionally, sulfide ions in the stems can bind with absorbed Hg^{2+} to form stable sulfides, thereby contributing to Hg immobilization and accumulation.

Plant root systems accumulate atmospheric Hg primarily through indirect pathways. Research indicates that atmospheric Hg can be deposited directly onto the soil surface via wet and dry deposition or absorbed by plant aboveground parts and subsequently enter the soil through litter decomposition [39, 40]. Hg entering the soil undergoes chemical transformation in the soil solution to form soluble Hg ions (Hg^{2+}). These ions are then actively absorbed by plant fine roots via transporters on the root epidermal cell membranes [41], thereby completing the bioaccumulation of atmospheric Hg. Research on the subtropical forest ecosystem of the Ailao Mountains revealed that the $\Delta^{199}Hg$ values of shallow roots were similar to those of leaves and surface soil [42]. This further indicates that the source of root Hg is closely related to atmospheric Hg deposition, thereby validating the indirect accumulation mechanism of atmospheric Hg by plant roots. However, the accumulation of Hg in plant roots is constrained by multiple factors. Low soil Hg concentrations and limitations imposed by root barrier structures are key factors contributing to reduced Hg uptake by plant roots from the soil [40]. Additionally, Hg exhibits low migration efficiency within plant root systems. Absorbed Hg demonstrates weak vertical translocation capacity and is scarcely transported to the above-ground xylem. Vertically, Hg concentrations in roots show a marked decreasing trend from the surface downward [37, 42]. A small fraction of Hg^{2+} absorbed by roots enters cells, where it is primarily immobilized on cell walls and membranes. Plant cell walls are rich in negatively charged functional groups (such as hydroxyl groups -OH and ester groups -COO-), which exhibit strong affinity for metal ions. These groups form coordination bonds with Hg^{2+} to create stable complexes, thereby restricting its further inward migration [43]. Simultaneously, Hg^{2+} exhibits strong affinity for sulfur, enabling it to form stable complexes with other sulfur-containing compounds such as cysteine [44], glutathione [45], and plant chelators [33, 46], which are then immobilized within the cell wall. In contrast, organic Hg, particularly MeHg, exhibits higher bioavailability. In soil, organic Hg compounds can undergo active transmembrane transport via transporters by binding to sulfur-containing ligands such as sulfhydryl groups [47]. Additionally, organic Hg compounds can enter plant root systems via passive diffusion in the form of neutral complexes. For instance, studies on rice tissues have revealed that MeHg can combine with chloride ions to form CH_3HgCl. This compound possesses relatively small molecular dimensions and lipophilic properties, enabling it to pass through the lipid bilayer of plant root cell membranes via passive diffusion and subsequently enter the root system [48].

2.4 Forest Vegetation and the Resuspension of Hg

In fact, the exchange of Hg between vegetation and the atmosphere is a complex dynamic process. Vegetation can both absorb atmospheric Hg and release GEM through transpiration and photoreduction processes, thereby acting as a “source” of atmospheric Hg. Research indicates that under conditions of intense light and high temperatures during the day, Hg^{2+} within leaves can be converted to Hg^0 through a reduction reaction and released into the atmosphere via stomata.

Research indicates that under conditions of intense light and high temperatures during the day, Hg^{2+} within leaves can be converted to Hg^0 through a reduction reaction and released into the atmosphere via stomata [7]. Research on two typical subtropical forests in southern China [49], revealed that under conditions of high temperature and high radiation, vegetation exhibits enhanced photoreduction, promoting Hg release. Concurrently, increased transpiration also drives the release of GEM. This study indicates that during summer, under the combined effects of high temperature and high radiation, vegetation becomes a significant source of GEM emissions. Additionally, during nighttime when the boundary layer is stable and wind speeds are low, non-stomatal pathways can also promote Hg^0 deposition and storage on the cuticle surface, with subsequent release the following day. As leaves age and nutrients redistribute, Hg concentrations within leaf tissues exhibit an upward trend, and some Hg^0 may be released through desorption processes prior to physiological senescence [7]. The primary form of Hg in leaves is Hg^{2+}, whose formation is closely linked to the oxidation process of Hg^0. However, the oxidized and immobilized Hg^{2+} in leaves is not entirely stable. RGM and PBM deposited on leaf surfaces via atmospheric deposition may undergo photochemical reduction under light exposure, partially or entirely re-releasing Hg^0 back into the atmosphere [42, 50]. Light-induced reduction reactions convert Hg^{2+} bound within leaf tissues to Hg^0, thereby facilitating its re-emission into the atmosphere. Studies indicate that Hg volatilization fluxes correlate positively with leaf area. Larger leaves, by providing greater light-absorbing surface area, reaction sites, and opportunities for binding with thiol-containing compounds, are more conducive to the occurrence of photoreduction reactions [51, 52]. Studies based on stable Hg isotopes have also revealed that approximately one-third of Hg in leaves can be re-emitted into the air through photoreduction. As leaves age, heavier Hg isotopes are more readily photoreduced and re-released into the atmosphere, leading to the enrichment of lighter Hg isotopes within the leaves [52]. This implies that forest leaves continuously release Hg into the atmosphere during their growth process, making forests a significant “source” in the atmospheric Hg cycle.

3. Migration and Storage of Hg in Forest Soils

3.1 Input and Distribution of Hg in Forest Soils

Soil is one of the largest Hg reservoirs on Earth's surface, storing at least 90% of Hg in terrestrial ecosystems [53]. GEM primarily enters the soil through direct absorption by vegetation, leaching by rainwater permeating plant surfaces, and transfer via plant litter [9, 54, 55]. Studies both domestically and internationally indicate that the Hg input flux from litterfall significantly exceeds atmospheric wet deposition, accounting for approximately 50% of total forest Hg inputs [56]. Approximately 90% of soil Hg originates from litterfall deposition [10], indicating that plants absorb atmospheric Hg and primarily transfer it to the soil through leaf litter, making this the main pathway for vegetation to input Hg into the soil and surrounding environment. For example, on the forest surface of the Ailao Mountains, the stable isotope characteristics of Hg in litter highly correlate with those in soil Hg, strongly confirming that litter deposition is one of the primary sources of Hg accumulation in forest soils [57]. During the initial decomposition phase, Hg in litter undergoes photoreduction due to microbial reduction and light exposure, with some Hg released into the atmosphere as Hg^0. However, compared to Hg released during decomposition, the litter itself functions more significantly as a Hg "sink". For example, In the evergreen broad-leaved forests of Simianshan, Chongqing, THg concentrations in litter increased from an initial 78.4 $ng \cdot g^{-1}$ to 102 $ng \cdot g^{-1}$, representing an enrichment of approximately 30% [56]. This indicates that litter continues to accumulate Hg during decomposition. This enrichment effect makes the litter layer a significant source of soil Hg, with its contribution potentially exceeding that from rainfall input [7].

After litter deposition, Hg gradually accumulates in the soil organic layer, resulting in consistently higher THg concentrations in both the organic layer and mineral soil layer compared to the fallen leaves themselves [58]. As litter continues to decompose, Hg in the organic layer gradually decreases, while concentrations in the mineral layer remain relatively stable. This is primarily attributed to the mineral layer's strong adsorption capacity for Hg, along with the combined regulatory effects of soil thickness, bulk density, organic matter content, and iron-aluminum oxides [59]. Additionally, differences in plant species significantly influence the accumulation behavior of Hg in litter. The hydrophobicity of the waxy cuticle layer on leaf surfaces across different tree species, along with the aromaticity and content of internal dissolved organic matter (DOM), all affect Hg leaching behavior and its bioavailability [60]. Increased nitrogen deposition may influence the input patterns of Hg in forest soils by altering plant uptake capacity and the Hg sequestration effects of forest soils [61]. Concurrently, variations in rainfall also influence the accumulation of Hg in litter. Studies in southwest China reveal a significant negative correlation between litter decomposition rates and THg accumulation rates in evergreen Pinus massoniana forests and broad-leaved evergreen Cinnamomum forests. That is, faster decomposition leads to less Hg accumulation, while increased THg primarily stems from Hg accumulation in throughfall. This suggests that increased rainfall may inhibit litter decomposition, thereby promoting Hg accumulation in forest soils [57, 62].

Hg^{2+} can also enter soil through dry deposition and wet deposition, but its contribution to soil Hg accumulation is relatively minor compared to atmospheric Hg^0 deposition [63, 64]. GEM gradually accumulates in soil through deposition, with current global surface soil Hg concentrations ranging from 3.8 - 618.2 $\mu g \cdot kg^{-1}$. Primary sources include atmospheric deposition of Hg^0 and Hg^{2+}, plant uptake, and geological weathering processes [65]. Hg stable isotope signatures indicate that dry deposition triggered by vegetation uptake of atmospheric Hg^0 constitutes the dominant source of Hg in surface soils [66]. Although surface soil serves as the primary sink for atmospheric Hg deposition, studies indicate [67] that Hg accumulation rates in soil often increase significantly with depth. Hg concentrations in deeper soil layers frequently exceed expectations based solely on deposition flux accumulation, suggesting the presence of significant downward migration mechanisms. Water infiltration (such as rainfall and snowmelt) is a key driver of vertical Hg migration. Simultaneously, the decomposition of soil organic matter releases GEM, further promoting its downward leaching. Additionally, plants absorb atmospheric Hg and release it into the soil via litterfall or throughfall, forming a "soil-vegetation-atmosphere" cycle that enhances Hg redistribution within the soil. The physicochemical environment of deep soil horizons also favors Hg fixation and accumulation.

3.2 Reduction and Re-release of Hg in Forest Soils

In forest ecosystems, the reduction and release of soil Hg are primarily driven by three mechanisms: microbial metabolism, organic matter-mediated abiotic dark reactions, and light-induced photochemical reduction. Among these, microbial-dominated reduction serves as one of the key driving factors [68]. Some soil microbial genomes harbor the mer operon system, a fundamental unit of gene expression regulation in prokaryotes. This system encodes detoxification proteins that constitute a defense mechanism against Hg toxicity in bacteria. Among these functional genes, the most common include merA and merB. Specifically, merA encodes Hg^{2+} reductase, which utilizes reduced coenzyme II (NADPH) as an electron donor to catalyze the conversion of Hg^{2+} into volatile Hg^0 [69]; while merB encodes organic Hg cleaving enzymes capable of catalyzing the cleavage of C-Hg bonds in organic Hg compounds, disrupting their molecular structures and converting toxic organic Hg into Hg^{2+}. Subsequently, under the action of merA, this is further reduced to Hg^0, thereby achieving Hg volatilization and release [70-73]. Microbial-mediated reduction primarily induces Hg isotope mass fractionation (Hg-MDF), causing heavy isotopes to remain in the soil while light isotopes volatilize preferentially [74].

Beyond biological processes, abiotic reduction driven by soil organic matter (NOM) represents a significant mechanism, particularly in humus-rich forest soils near the surface. Such dark reactions induce Hg isotope non-mass fractionation (MIF) that can be more pronounced than biological reduction, with mechanisms closely linked to non-photochemical redox reactions of Hg and the nuclear volume effect (NVE) [61].

Furthermore, light-induced organic matter reduction is also one of the key processes for Hg^0 re-emission in forest soils, primarily achieved through photochemical reactions mediated by organic sulfur groups and dissolved organic matter (DOM) [75]. Among these, organic sulfur groups can form complexes with Hg, absorb light energy under illumination, and transfer electrons to Hg^{2+}, promoting its reduction to Hg^0 and subsequent release from the soil. DOM, meanwhile, facilitates the photoreduction of Hg^{2+} by generating reactive free radicals: under light exposure, DOM is excited to produce reactive species such as superoxide anion ($O_2•^-$), which efficiently catalyzes the reduction of Hg^{2+} [76]. This photocatalytic mechanism was validated in experiments involving the photoreduction of Hg^{2+} mediated by dissolved black carbon (DBC) [77]. Notably, DOM-mediated photoreduction processes are not only regulated by redox conditions but also exhibit potential coupling effects with microbial activity [78]. Stable Hg isotope analysis reveals the isotopic characteristics of these processes: within soil profiles, $\delta^{202}Hg$ values typically increase progressively from the litter layer downward, while $\Delta^{199}Hg$ decreases gradually. This indicates that over time and as decomposition progresses, processes such as microbial reduction, photoreduction of organically bound Hg, and dark reduction of organic matter promote Hg release from soil into the atmosphere. The isotopic fractionation resulting from these reactions differs from the initial characteristics observed after atmospheric Hg^0 absorption, exhibiting a “re-fractionation” pattern that aids in tracing the pathways of soil Hg re-release [7].

4. Regulation of Forest Hg Cycling by Environmental Factors

The exchange of Hg between the atmosphere and forests is influenced by various environmental factors, such as temperature, saturated vapor pressure difference, light intensity, solar radiation, and soil moisture. Studies indicate that Hg emission rates increase with rising temperatures, while elevated oxygen concentrations also promote Hg release [79]. MacSween et al. measured GEM fluxes using the aerodynamic flux gradient method and found that both soil temperature and air temperature positively correlate with Hg emissions. For every 1℃ increase in air temperature, Hg emission fluxes increase by 15% - 43%. This occurs because rising temperatures lower the activation energy required for Hg volatilization from the matrix, promoting the photoreduction of Hg^{2+} to Hg^0 and thereby enhancing Hg^0 volatilization rates [80]. High temperatures not only enhance Hg^0 volatilization by increasing vapor pressure, intensifying turbulent diffusion in the boundary layer, and promoting photoreduction of Hg^{2+}, but also indirectly facilitate Hg release by accelerating soil microbial respiration rates [81].

Vapor pressure deficit (VPD), as a key climatic factor influencing forest ecosystems, exerts potential effects on processes such as Hg cycling, transport, and accumulation within these ecosystems. VPD refers to the difference between the saturated vapor pressure and the actual vapor pressure in the air at a given temperature. It regulates vegetation uptake of Hg by altering stomatal conductance, reducing photosynthetic rates, and inhibiting vegetation growth and transpiration. In European forests, the Hg uptake rates of pine and spruce needles significantly decrease under high VPD conditions, exhibiting pronounced inhibition effects when VPD exceeds 1.2 kPa and 3 kPa, respectively [82]. Fabrizio Monaci's research also indicates that Hg uptake peaks under moderate VPD (0.8 - 1.2 kPa), while extremely low (<0.5 kPa) or high (>2.0 kPa) VPD values inhibit stomatal opening, reducing vegetation's Hg absorption efficiency [27]. VPD frequently interacts with other climatic factors to jointly influence Hg processes in forest ecosystems. Elevated VPD is often accompanied by rising temperatures and altered precipitation patterns. In certain regions, concurrent increases in VPD, temperature, and precipitation reduction lead to soil drying, suppressed vegetation growth, heightened Hg volatilization from soil, and diminished Hg uptake by vegetation. These changes alter the Hg budget within forest ecosystems [83].

Furthermore, light exposure and solar radiation also play crucial roles in the transformation and release of Hg. Solar radiation increases soil temperature, enhancing the photochemical reduction of Hg^{2+} in soil. This promotes the conversion of more Hg^{2+} into Hg^0, thereby increasing the release of Hg from soil into the atmosphere [84]. For instance, in the agro-pastoral transition zone of the Songnen Grassland, soil Hg release fluxes exhibit an upward trend as solar radiation intensifies [85]. Increased sunlight enhances DOM-mediated photoreduction reactions, thereby elevating Hg emission fluxes [77]. Different forest types exhibit varying degrees of solar radiation shading due to differences in canopy structure, which indirectly influences the amount of solar radiation reaching the soil and consequently affects Hg release. A comparative study of subtropical and temperate forest watersheds [86] revealed that in open areas of subtropical forests, the absence of canopy cover results in intense solar radiation and elevated soil temperatures, making these clearings the primary source of Hg release. The study further indicated that seasonal canopy changes—such as the leaf-fall period in deciduous forests—can also cause variations in radiation incidence, thereby indirectly regulating the exchange rate of Hg at the soil-atmosphere interface.

Solar radiation also exhibits synergistic effects with soil moisture, jointly regulating the migration and release behavior of Hg [87]. Soil moisture content exerts a dual effect on Hg emissions. Under moderately dry conditions, rewatering dry soil promotes upward migration of Hg through evaporation and increases emissions of surface Hg^0.Initially, Hg emissions peak as moisture evaporates; however, after multiple wet-dry cycles, Hg release gradually diminishes. When soil reaches saturation, the water layer may seal soil pores, inhibiting Hg release [88, 89]. Additionally, Hg^o can adsorb onto soil particle surfaces [90]. When water infiltrates the soil, Hg adsorbed onto particles desorbs into the soil pore gas. As soil moisture increases, Hg^0-containing air is displaced by water, simultaneously promoting Hg^{2+}-associated redox reactions in the aqueous phase [91], thereby enhancing the release flux of Hg^0 from the soil surface. Higher soil moisture may increase the diffusion rate of gases within soil pores, facilitating the release of Hg^0 into the atmosphere. In China's tropical rainforests, researchers employed stable Hg isotope techniques to investigate the deposition and re-release processes of Hg^0 in soil [92]. Results indicate that elevated soil moisture during the tropical forest rainy season leads to enhanced Hg^0 release, making it a source of atmospheric Hg^0. Furthermore, under conditions of ample soil moisture, temperature and light exposure further intensify Hg release.

5. Application of Isotope Techniques in Hg Cycle Research

5.1 Source Appraisal and Migration Pathway Tracking

Over the past decade, with continuous advancements in Hg stable isotope analysis technology, this technique has played a crucial role in investigating the sources, migration pathways, and transformation mechanisms of Hg. By analyzing the composition and fractionation characteristics of Hg stable isotopes, it is possible to more accurately trace the sources of Hg. For example, stable isotope techniques can determine whether atmospheric Hg originates from anthropogenic, natural, or re-emission sources, as well as the relative proportions of these sources in the atmosphere. Additionally, these techniques can reveal the migration pathways of Hg between different environmental media, elucidating how Hg enters vegetation and soil from the atmosphere and the migration processes occurring within vegetation and soil. Furthermore, by studying isotopic fractionation characteristics, we can gain deeper insights into the transformation mechanisms of Hg across various ecosystems and assess its accumulation and storage within these systems. This provides a novel perspective and powerful tool for investigating Hg cycling in forest ecosystems.

5.2 Conversion Mechanism and Fractionation Effect

The isotope fractionation effect of Hg provides crucial evidence for studying Hg transformation mechanisms, aiding in the elucidation of Hg transformation processes and mechanisms within forest ecosystems, as well as the kinetic characteristics of Hg re-emission processes. For instance, microorganisms typically induce MDF during Hg reduction and methylation processes [93], during Hg reduction and methylation processes, whereas MIF is commonly associated with photochemical processes [94]. Zhu et al. [95] demonstrated in their study of a decommissioned chlor-alkali plant site that photochemically driven Hg^0 releaching is typically accompanied by MIF characteristics, with the degree of fractionation primarily determined by the original chemical form of Hg in the contaminant source. Furthermore, due to differences in ligand selectivity, various forms of Hg^{2+} induce distinct isotopic fractionation effects during migration processes [96-98], a phenomenon particularly pronounced during Hg migration from salt sludge layers into deeper soil horizons. Furthermore, the study revealed that the reduction rate of Hg^{2+} exhibits significant species dependence, indicating that the reactivation process of Hg is not only influenced by thermodynamic stability but also regulated by kinetic factors.

6. Future Research Directions and Challenges

6.1 Filling Data Gaps

Current research has primarily focused on subtropical and temperate forests [99], while data on tropical rainforests remain extremely limited. Due to their high biomass, rapid nutrient cycling, and unique climatic conditions, tropical rainforests may exhibit Hg accumulation and release patterns significantly different from other ecosystems. However, their quantitative contribution to atmospheric-soil Hg exchange remains unclear [92]. Furthermore, research on Hg exchange characteristics in boreal and high-altitude forests remains largely unexplored. These regions may exhibit unique Hg cycling patterns due to factors such as low temperatures and snow cover influencing Hg release and deposition dynamics. However, systematic investigations into the underlying mechanisms and relevant data remain scarce.

6.2 Deepening the Absorption Mechanism

Regarding the mechanisms of vegetation uptake of Hg^0, numerous questions remain unanswered. For instance, the relative contributions of stomatal and non-stomatal pathways to Hg^0 uptake vary across species and environmental conditions, yet a universally applicable quantitative method is currently lacking. Regarding the mechanisms of vegetation uptake of Hg^0, numerous questions remain unanswered. For instance, the relative contributions of stomatal and non-stomatal pathways to Hg^0 uptake vary across species and environmental conditions, yet a universally applicable quantitative method is currently lacking. Furthermore, the oxidation mechanism of Hg^0 after entering plant cells remains unclear, particularly how plants convert Hg^0 to Hg^{2+} and immobilize it within tissues. The specific enzyme systems involved in this process have yet to be identified. These uncertainties in the mechanisms limit the model's ability to precisely quantify the contributions of the stomatal and non-stomatal pathways. Systematic studies on the differences in Hg^0 uptake among various vegetation types remain scarce. Differences in leaf surface characteristics (such as wax layer thickness and stomatal density) and photosynthetic metabolic pathways (C_3 vs. C_4) between broadleaf and coniferous trees may significantly influence Hg^0 uptake efficiency, yet existing comparative data remain insufficient.

6.3 Construction of Multi-factor Coupling Models

To achieve further breakthroughs in understanding Hg exchange processes and vegetation uptake mechanisms within forest ecosystems, in-depth research must be conducted across multiple critical areas. Future studies should focus on filling data gaps and strengthening investigations into Hg exchange characteristics in specialized ecosystems such as tropical rainforests, boreal forests, and high-altitude forests. Through long-term monitoring and multi-scale experiments, precise data on atmospheric-soil Hg exchange fluxes in these regions will be obtained to quantify their contributions to the global Hg cycle. To elucidate the mechanisms underlying vegetation uptake of Hg^0, multidisciplinary approaches are required. These include employing Hg isotope fingerprinting combined with high-resolution imaging to precisely quantify the relative contributions of stomatal and non-stomatal pathways across different species and environmental conditions. Furthermore, leveraging cutting-edge technologies such as gene editing and proteomics will enable in-depth analysis of the specific enzyme systems and associated metabolic pathways catalyzing Hg^0 oxidation within plant cells, thereby refining oxidation mechanism models. Regarding vegetation absorption variations, a comprehensive database of vegetation absorption differences has been established to provide fundamental support for elucidating the absorption characteristics of different vegetation types. Through the advancement of these studies, it is anticipated that current scientific bottlenecks will be overcome, offering a solid theoretical foundation for deepening the understanding of Hg cycling processes in forest ecosystems and accurately assessing the impact of Hg pollution on the ecological environment. This will in turn provide scientific basis for formulating global Hg pollution prevention and control strategies.

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Conflicts of Interest

The authors declare no conflict of interest.

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