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Mercury Accumulation is Related to the Leaf Economics Spectrum

Håkan Pleijel · Jenny Klingberg · Henrik Sjöman · Göran Wallin

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Abstract Mercury (Hg) is a highly toxic metal with a complex biogeochemistry and the principles governing Hg uptake in different types of vegetation represent a knowledge gap. By combining published information from three sources with new data we investigated the rate of Hg accumulation in a wide range of leaf types from broadleaved and needle-leaved trees of evergreen or deciduous habit, in relation to leaf nitrogen concentration, and to specific leaf area (SLA) and leaf mass per area (LMA) using data from temperate trees in Europe and China. Leaf nitrogen, SLA and LMA are key traits along the resource conservation strategy continuum known as the leaf economics spectrum (LES), which has been shaped by evolutionary history of trees in different environments. We show, based on data from different geographical areas, that the rate of Hg accumulation by leaves and needles was significantly and linearly related to leaf nitrogen concentration, but more strongly so to SLA. The relationship of Hg accumulation with LMA was equally strong but non-linear. We conclude that leaf Hg accumulation rate of leaves and needles is connected to the LES. These results support the assessment and modelling of Hg accumulation in vegetation, including consequences of land use and climate change induced shifts in vegetation composition on Hg uptake by forest ecosystems. Importantly, the data from different geographical regions provided very similar results and conformed to general relationships with SLA and LMA. Further studies are needed to investigate if the results can be extrapolated also to other biogeographic regions.

Keywords Deciduous · Evergreen · Hg · Leaf mass per area · Nitrogen · Specific leaf area

H. Pleijel (✉) · J. Klingberg · G. Wallin
Biological and Environmental Sciences, University of Gothenburg, P.O. Box 463, 40530 Göteborg, Sweden
e-mail: hakan.pleijel@bioenv.gu.se

J. Klingberg · H. Sjöman
Gothenburg Botanical Garden, Carl Skottsbergs Gata 22A, 41319 Göteborg, Sweden

J. Klingberg
Gothenburg Global Biodiversity Centre, P.O. Box 463, 40530 Göteborg, Sweden

H. Sjöman
Department of Landscape Architecture, Planning and Management, Swedish University of Agricultural Sciences, 23053 Alnarp, Sweden

1 Introduction

In the biogeochemical cycling of the highly toxic metal mercury (Hg), the uptake by vegetation plays a crucial role (Obrist et al., 2018). In forest ecosystems 60–90% of Hg has been estimated to originate from uptake by vegetation from the atmosphere (Zhao et al., 2021). Most of this takes place as stomatal uptake of gaseous elemental mercury (Hg^0) into leaves or needles (Laacouri et al., 2013; Risch et al., 2017), but other pathways also exist. Deposition of Hg is a combination of Hg^0 (dry deposition) and oxidized species of Hg, including particulate Hg (both dry and wet deposition). Terrestrial surfaces also re-emit Hg, mainly as gaseous Hg^0 (Bishop et al., 2020). Dry deposition includes Hg^0 and oxidized Hg deposited on foliar surfaces, which can be washed off by throughfall (Graydon et al., 2008), and stomatal Hg^0 uptake (Risch et al., 2017). Hg accumulated in leaves eventually enter the soil through litterfall. Bishop et al. (1998) investigated the xylem sap as a pathway for Hg from the soil to the canopy in conifers, finding that only 11% of total Hg may originate from this pathway. Both Fleck et al. (1999) and Pleijel et al. (2025) reported much lower Hg concentrations in wood compared to conifer needles. Although several processes are in operation, there is consensus that net stomatal uptake of gaseous elemental Hg dominates vegetation uptake of Hg (Zhou et al., 2021). Due to its long residence time in the atmosphere (6–18 months), Hg^0 largely becomes globally distributed (Gworek et al., 2017), although with elevated concentration hotspots near large local emission sources (e.g., Baroni et al., 2023; Gworek et al., 2017). Jiskra et al. (2018) found that the seasonal amplitude in the background atmospheric Hg^0 concentration, like that of the atmospheric CO_2 concentration, increases with latitude and suggested that terrestrial vegetation acts as a global Hg pump, removing atmospheric Hg mainly during the growing season when plant gas exchange is large. The observed seasonality of atmospheric Hg^0 concentration in the Northern hemisphere (Zhou et al., 2023) can be explained by seasonal variation in the stomatal uptake by vegetation. However, important knowledge gaps exist with respect to the mercury uptake in different types of vegetation.

In a study synthesizing observations for broad-leaved and needle-leaved trees across Europe, Wohlgemuth et al. (2022) found indications of a positive association of growing-season average daily Hg uptake rate with leaf nitrogen (N) concentration based on data for seven species. The leaf concentration of the frequently limiting macronutrient N is a trait considered to be an indicator of physiological activity (Onoda et al., 2017). Results presented by Wohlgemuth et al. (2022) also suggested a negative relationship of Hg accumulation rate with LMA (leaf mass per area: LMA = LM/LA, where LM is leaf dry mass and LA is projected leaf area) based on data for six species. Pleijel et al. (2021), studying 13 tree species in south-west Sweden, similarly found a positive relationship of seasonal leaf Hg accumulation rate with SLA (specific leaf area, the reciprocal of LMA), but did not include an analysis of the association with leaf N concentration. Further, Zhang et al. (2025) reported a pronounced difference in Hg accumulation rate and LMA between four broadleaved deciduous and two evergreen conifers species in central China, suggesting a negative relationship between these variables. Leaf N, SLA and LMA are important and interrelated ecophysiological traits (Poorter et al., 2009) used to characterize growth and resource-conservation strategies of plants based on the so-called leaf economics spectrum (LES, Wright et al., 2004), where high SLA and leaf N concentration, and low LMA are associated with higher physiological activity, including higher stomatal conductance, net CO_2 assimilation and faster growth. In addition, leaf longevity is connected to LES, with leaves with a higher LMA (lower SLA) mostly becoming older, representing a resource conservation strategy (Reich et al., 1999, 2014). Since the characteristics of the LES are more or less correlated with each other (Osnas et al., 2013), the LES largely becomes a single axis of variation. Furthermore, the principles of the LES seem to apply to different biomes and plant functional types (Wright et al., 2004). If the variation in the uptake of Hg by leaves is controlled by interspecific variation in stomatal conductance, it can, based on LES theory, be assumed that there exists a corresponding relationship with leaf N concentration and SLA/LMA.

To test the generality of earlier observations in individual investigations, this study combines already published data with new data for a broad range of species with different leaf types to investigate the relationship of growing-season average daily Hg uptake rate with leaf N concentration, as well as with SLA and LMA, for 14 deciduous broadleaved species, eleven evergreen conifer species, one deciduous conifer species and one evergreen broadleaved species, thus representing a broad range of leaf functional types with respect to leaf form (broadleaved vs. needle-leaved) and leaf habit (evergreen vs. deciduous). It is based on the combination of information in Pleijel et al. (2021), for which leaf N concentration is added in this paper, Wohlgemuth et al. (2022), Zhang et al. (2025), and additional new data for four species as specified in the Methods section. Because long-term observations show that background atmospheric Hg^0 concentrations have declined over the last decades (Feinberg et al., 2024), leaf Hg accumulation reported from these studies were normalised over time to account for the sampling during different time periods.

Our hypothesis was that the average daily rate of Hg accumulation of leaves and needles is positively related to leaf N concentration and SLA, and negatively related to LMA, thus being connected to the LES. This has not been tested for a broad range of data to our knowledge. A second hypothesis was that the relationships between leaf Hg accumulation and LES would be similar in different geographical locations with temperate climates, which, if supported, would bring new light to the general understanding of the leaf accumulation of Hg.

2 Methods

2.1 Data

Data were obtained from four sources. The species covered by these sources are presented in Table 1. Firstly, information regarding daily Hg accumulation rate by leaves and needles during the growing season, as well as LMA and leaf N concentrations of deciduous tree species and current year needles of conifers were extracted from Wohlgemuth et al. (2022). These observations were made 2015–2017 within the United Nations Economic Commission for Europe (UNECE) International Cooperative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) network with a focus on Central and North Europe. For the association between daily Hg uptake rate and leaf N, data were obtained for seven species from Table 1 in the publication. Data for the association between daily Hg uptake rate and LMA for six species were taken from Table S3 in Wohlgemuth et al. (2022).

Secondly, leaf Hg uptake rates and SLA data for eight deciduous broadleaved species, one deciduous conifer and 1-year old needles of four evergreen conifers were obtained from Pleijel et al. (2021). The species selection of that study was made to cover a broad range of leaf functional types and included species both native and non-native to south-west Sweden, sampled in the Gothenburg Botanical Garden Arboretum.

In Pleijel et al. (2021) leaf Hg uptake rates of trees sampled 2018 were expressed on a per year basis. For the present study they were recalculated to average daily Hg uptake rates during the growing season to make them directly comparable with the per day data from Wohlgemuth et al. (2022) and Zhang et al. (2025). The development of new leaves of deciduous species was assumed to be complete by 15 May in line with local observations. For the evergreen conifers, represented by needles sampled early in their second year, the new flush of needles was assumed to be completely developed by 1 June, while the start of the second-year growing season was assessed to 15 April based on observed seasonal alteration in stomatal conductance and photosynthesis of Norway spruce in a neighboring area (Tarvainen et al., 2015). Also needed for the calculation of average daily Hg uptake rates are harvest dates. The evergreen conifers were sampled on 25 June 2018. Deciduous trees were sampled on 17 September 2018, except *Quercus palustris*, which was sampled on 19 September 2018. Data regarding leaf N concentrations used in the present study (analysis method described below) were not included in Pleijel et al. (2021).

A third source of data was Zhang et al. (2025), where the daily Hg accumulation rate during the growing season of 2022 was reported for four deciduous broadleaved species and current year needles of two evergreen conifers along with LMA (but not leaf N concentration) for two nearby sites in Central China. These data were reused (adapted to the format used in the present paper), with permission from the publisher, from Zhang et al. (2025). Comparative foliar atmospheric mercury accumulation across functional types in temperate trees. *Environ. Sci. Technol. 59*, 2084–2094, copyright 2025 American Chemical Society.

Fourthly, additional sampling in the Gothenburg region, south-west Sweden, was made for four species. To expand the leaf trait space, three individuals of the evergreen broadleaved *Trochodendron aralioides* were sampled in the Gothenburg Botanical Garden (N57.68, E11.95) on 21 September 2020. Six trees of Scots pine (*Pinus sylvestris*, the second most common tree species in Sweden) were sampled in a forest stand just north of the Gothenburg conurbation (N57.77, E11.88); sampling was

Table 1 Species included in the study with information on leaf habit (deciduous or evergreen) and leaf form (broadleaved or needle-leaved) and the data source

Data set: Plant functional type/Species	1 Wohlgemuth et al. (2022)	2 Pleijel et al. (2021)	3 Zhang et al. (2025)	4 New data
Deciduous – Broadleaved				
Betula pendula		X		
Carpinus betulus	X			
Fagus orientalis		X		
Fagus sylvatica	X			
Gleditsia sinensis			X	
Juglans ailanthifolia		X		
Populus tremula		X		
Prunus armeniaca			X	
Prunus cerasifera			X	
Prunus sargentii		X		
Quercus robur	X	X		
Quercus variabilis			X	
Qurecus palustris		X		
Sorbus commixta		X		
Evergreen – Broadleaved				
Trochodendron aralioides				X
Deciduos – Needle-leaved				
Larix decidua		X		
Evergreen – Needle-leaved				
Abies alba	X			
Abies pinsapo ssp. *marocana*				X
Abies sachalinensis		X		
Cedrus deodara			X	
Cryptomeria japonica		X		
Picea abies	X			X
Picea jezoensis		X		
Pinus bungeana			X	
Pinus nigra		X		
Pinus sylvestris	X			X
Pseudotsuga menziesii	X			

made on 19 August 2019. Three Norway spruce (*Picea abies*, the most common tree species in Sweden) trees in a forest stand of the Änggårdsbergens nature reserve next to the Gothenburg Botanical Garden were sampled (N57.66, E11.96). In addition, three trees of Moroccan fir (*Abies pinsapo* ssp. *marocana*) were sampled in the Botanical Garden Arboretum (N57.66, E11.96). These two species were sampled on 22 September 2020. All the new samples represent the first needle or leaf age class. Start of the growing season was defined as described above. The combined data from Sweden, in the following denoted "Swedish data", are available at https://doi.org/10.5878/hwa8-vn68.

2.2 Sampling, Preparation and Analysis

Sampling, sample treatment and analysis for the first data set is described in detail by Wohlgemuth et al. (2022), for the second data set by Pleijel et al. (2021) with the exception of the analysis of

N (see below), and for the third data set by Zhang et al. (2025). For the fourth data set, branches with leaves and needles in the outer part of the crown were selected. A minimum of three branches from each tree were sampled. The samples were packed in polyethylene plastic bags, transported in a cool bag and stored in a fridge until further handling. Samples were carefully collected to avoid contamination. Needles were separated from branch segments at the laboratory, dried in 70 °C in aluminium envelopes until constant mass (at least 48 h). Thereafter the samples were ground to a fine powder using a ball mill (model MM 301, Retsch, Haan, Germany) equipped with grinding jars and balls made of wolfram carbide. The grinding equipment was cleaned by a vacuum cleaner between each sample.

Samples were analysed for the content of 37 elements using inductively coupled plasma mass spectrometry (Dry Vegetation ICP-MS, 37 elements after digestion in HNO_3 and then aqua regia: Method VG101 by Bureau Veritas Mineral laboratories, Vancouver, BC, Canada). In this paper, only the Hg data are used. The laboratory has implemented an analytical quality management system meeting the requirements of ISO/IEC 17025 and ISO 9001. Further details on the analysis as well as on Quality Assurance and Quality Control, which includes the use of blanks, internal standards and repeated measurements of some samples, can be obtained here: https://publications.gc.ca/collections/collection_2024/rncan-nrcan/m183-2/M183-2-8837-1A-eng.pdf. The method detection limit for Hg was 1 ng g^{-1}. No sample had a Hg concentration below the detection limit.

The N concentrations of the samples from Pleijel et al. (2021) were determined by dry combustion using an elemental analyser (EA 1108, Fison Instruments, Rodano, Italy). N concentrations of the fourth, new data set were analysed with an elemental analyser (Automated Nitrogen Carbon Analyser ANCA TGII, SerCon Ltd., Crewe, UK). Specific leaf area (SLA, leaf area divided by leaf mass) and its reciprocal leaf mass per area (LMA) for *Trochodendron aralioides* and *Pinus sylvestris* in the third data set was determined in the same way as described in Pleijel et al. (2021). SLA of *Picea abies* and *Abies pinapo* var. *marocana* was determined using a LI-3100C Leaf Area meter calculating the ratio of one-sided area of fresh needles to its oven-dry mass.

Because of the shoot structure of *Cryptomeria japonica* it was difficult to sample needles in a way which permitted accurate estimation of SLA/LMA. This species was consequently excluded from the relationships with these leaf traits but included for relationship with leaf N concentration.

2.3 Accounting for Declining Background Hg Concentrations

The data used was based on sampling made in different years: Wohlgemuth et al. (2022) for 2015–2017, Pleijel et al. (2022) in 2018, 2019 and 2020, and Zhang et al. (2025) in 2022. An essentially linear declining trend of background atmospheric Hg concentrations has been observed over the Northern Hemisphere over the last decades (Feinberg et al., 2024). To account for this, Hg uptake rate values were normalized to represent 2022 by implementing a Hg concentration decline rate (based on Table S3 of Feinberg et al., 2024) of −0.019 ng m^{-3} yr^{-1} for Swedish data (representing Northern Europe) and −0.027 ng m^{-3} yr^{-1} for Wohlgemuth et al. (2022) data (representing Central Europe). No normalization was applied for Zhang et al. (2025) data since they were obtained in 2022.

2.4 Statistical Analysis

Linear regression was used to assess the relationships of daily Hg uptake rate with leaf N concentrations as well as SLA, while non-linear regression was used for the corresponding relationship with LMA. For the linear relationships the significance of the slope coefficient was estimated. Student´s t-test (assuming unequal variances) was used to test the significance of the difference in daily Hg uptake rate between evergreen conifers and deciduous broadleaved trees. Statistical analyses were made in Excel for Microsoft 365.

3 Results

3.1 Mercury Uptake Rate in Relation to Leaf Nitrogen Concentrations

Combining all available data resulted in a significant ($p = 0.0003$, $R^2 = 0.46$) linear relationship

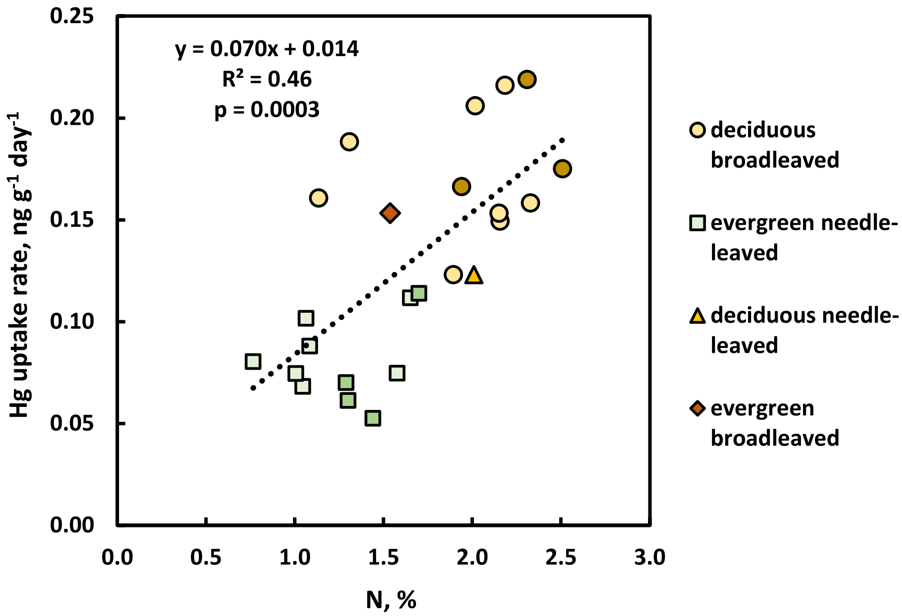

Fig. 1 The relationship of the average daily Hg uptake rate during the growing season with leaf nitrogen (N) concentration. For the deciduous broadleaved and evergreen needle-leaved species the lighter colour shades represent Swedish data while the darker shade data are from Wohlgemuth et al. (2022)

(Fig. 1) of daily Hg uptake rate during the growing season with the N concentration of leaves and needles. In general, broadleaved trees had higher Hg uptake rates and higher N concentrations, although this pattern was not completely unequivocal. A t-test comparing the Hg uptake rate of deciduous broadleaved trees and evergreen conifers showed a highly significant ($p < 0.0001$) difference between the two groups.

3.2 Mercury Uptake Rate in Relation to Specific Leaf Area (SLA) and Leaf Mass Per Area (LMA)

A stronger linear relationship than that with N was obtained when the daily uptake rate of Hg during the growing season was regressed with SLA ($R^2 = 0.77$, $p < 0.0001$; Fig. 2a). Plotting the daily Hg uptake rate with LMA resulted in an equally strong relationship ($R^2 = 0.77$; Fig. 2b), which was, however, strongly non-linear. It can be noted in the relationships of daily Hg uptake rate with SLA and LMA that broadleaved trees and evergreen conifers occupy different parts of the regressions, separating these groups more strongly than in the corresponding relationship with leaf N concentration (Fig. 1), with the deciduous needle-leaved *Larix decidua* in between the broadleaved trees and the evergreen needle-leaved trees, and the evergreen broadleaved *Trochodendron aralioides* in the lower end of daily leaf Hg uptakes rates observed for deciduous broadleaved species. Notably, the variability in daily leaf Hg uptake rate in relation to SLA was larger among deciduous broadleaved species compared to evergreen needle-leaved trees. It is worth noting that the normalization of Hg uptake rate data with respect to the decline in background atmospheric Hg^0 concentrations over the range of years during which the studies were conducted resulted in somewhat higher R^2 values: from 0.73 to 0.77 for the SLA relationship and from 0.74 to 0.77 for the LMA relationship (data not shown).

The residuals of the relationships presented in Fig. 2a and 2b were regressed with leaf N concentration, for the part of the data for which leaf N data was available, to investigate if any of the variation in leaf Hg uptake remaining unexplained by LMA or SLA could be related to leaf N. There were no significant relationships ($p = 0.12$ for SLA and $p = 0.08$ for LMA), but a weak indication of larger positive residuals at higher leaf N concentration (data not shown).

3.3 Comparison of the Data Sources

Comparing the three different data sources (Fig. 3) did not reveal any substantial difference between

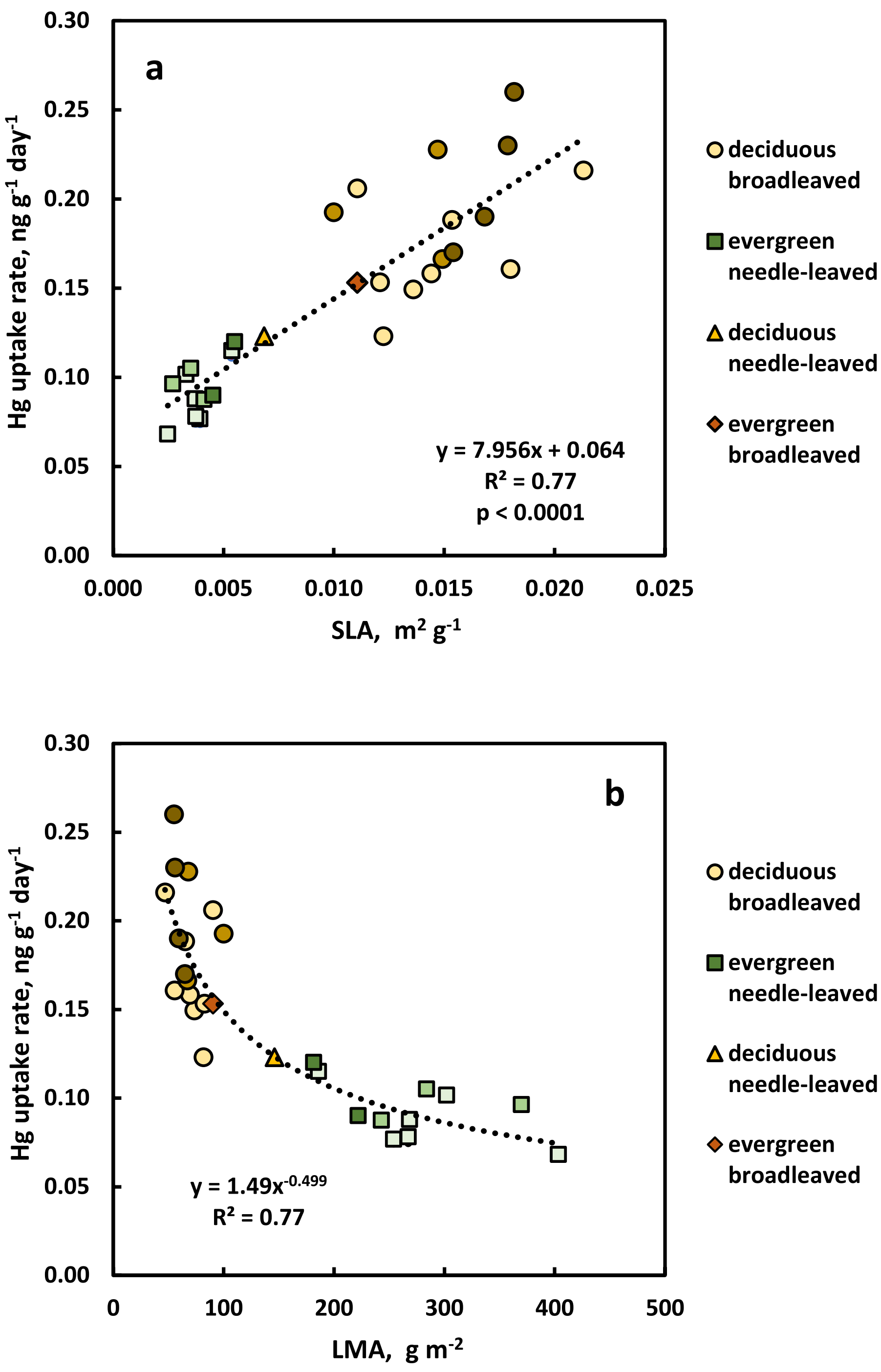

Fig. 2 The relationship between the daily average Hg uptake per unit leaf or needle mass during the growing season and **a** specific leaf area (SLA), **b** leaf mass per area (LMA). For the deciduous broadleaved and evergreen needle-leaved species the lightest colour shade represents Swedish data, the next darker shade data from Wohlgemuth et al. (2022) and the darkest shade the data from Zhang et al. (2025)

them. The relationships for the individual data sources were equally strong as, or stronger, especially for the LMA relationships (Fig. 3b), than for the combined relationships of Fig. 2. Thus, although different methods were used and the sites are biogeographically different (see Discussion), the relationships for the individual data sources are consistent internally and with each other.

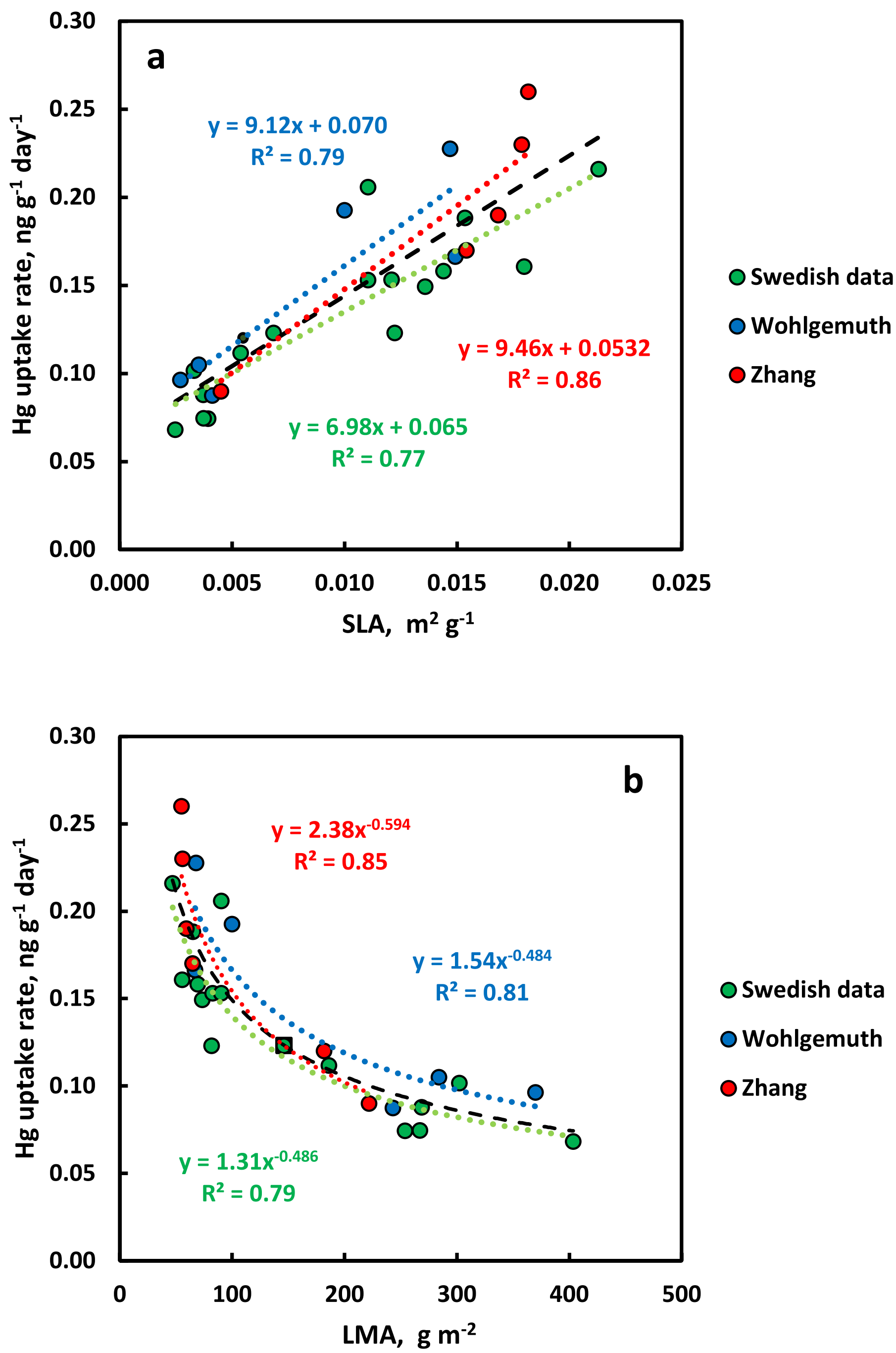

Fig. 3 The relationship between the daily average Hg uptake per unit leaf or needle mass during the growing season and a specific leaf area (SLA), b leaf mass per area (LMA), as in Fig. 2 but separate relationships for Swedish data, Wohlgemuth et al. (2022) and Zhang et al. (2025). The black broken line shows the general relationship representing all three data sources combined

4 Discussion

4.1 Linking the Leaf Hg Accumulation Rate to the Leaf Economics Spectrum

The novelty of our study involves several aspects. Firstly, the amount of data to study the relationship of the daily leaf Hg accumulation rate with the leaf N concentrations was substantially expanded by broadening the range of species and environments analysed compared to earlier studies. Secondly, it was shown that earlier, more general observations of higher leaf Hg accumulation rates in conifers vs. deciduous broadleaved trees, comparing a limited number of species, translated into consistent and strong quantitative relationships when using the LES relevant ecophysiological traits SLA, LMA and, although more weakly, leaf N concentration, when a broader range of data was used, in support of our first hypothesis. A final aspect of novelty is that data from three geographically different temperate regions were compared and shown to conform with each other to a large extent, which aligns with our second hypothesis.

The significant positive relationship of daily Hg uptake rate with the leaf N concentration, covering a broad range of trees species and representing a substantial variation in leaf form and habit, suggests an obvious link to the LES (Wright et al., 2004). The corresponding relationships of daily Hg uptake rate with SLA and LMA were, however, stronger and separated evergreen conifers from deciduous broadleaved species more distinctly than the relationship with leaf N concentration. The stronger linear relationship of daily Hg uptake rate with SLA as compared to leaf N concentration, can possibly be explained by SLA being a more conservative and genetically determined trait than leaf N concentration, which is more closely dependent on local environmental conditions in terms of N availability. SLA, however, also has an intraspecific variation which depends on environmental factors (Berzaghi et al., 2020; Poorter et al., 2009).

In modelling applications, the linear relationship of daily Hg uptake rate with SLA is more attractive than the non-linear association with LMA, since the uncertainty in modelling results is sensitive to non-linearities. A linear relationship is more robust and less sensitive to uncertainty in the x-variable. In contrast, in a non-linear relationship, the sensitivity of the y-variable to changes in the x-variable is larger where the slope is steeper. Since SLA = LA/LM, the linear relationship between unit leaf mass accumulation of Hg with SLA can be transformed by multiplying all terms of the linear regression of Fig. 2a with LM. This results in an expression where the total net leaf uptake rate (or flux) of Hg by an ecosystem, such as a forest stand, can be expressed as a linear combination of leaf mass and leaf area: $Hg_{flux} = 8.15*LA + 0.071*LM$ (unit: ng day^{-1}). This equation highlights the sensitivity of ecosystem Hg uptake to both leaf area and leaf mass but does not account for the decline in Hg uptake rate with leaf or needle aging in evergreen species discussed below (Pleijel et al., 2025). Leaf area, SLA/LMA, as well as leaf N concentration, are standard traits observed in many ecophysiological investigations, and have been extensively used in dynamic vegetation models. Examples of how they are implemented in this type of modelling can be found in White et al. (2000) and Sakschewski et al. (2015). A deeper analysis of the biogeochemical cycling of Hg would benefit from combining the modelling of atmospheric transport and conversion of Hg with dynamic vegetation modelling.

4.2 Mercury Accumulation and Forest Composition Dynamics

From the relationships of daily Hg uptake rate with leaf N, SLA and LMA it is obvious that the composition of the tree cover of forests with respect to leaf form and leaf habit plays a crucial role for the rate of Hg accumulation in ecosystems. This agrees with recent stand level observations of Hg fluxes to different forest types in North-East US, where the Hg flux to a deciduous forest was almost twice that of a conifer forest (Zhou et al., 2023). In our data set, the average daily Hg uptake rates of deciduous broadleaved species and evergreen conifers were 0.186 (0.200) and 0.087 (0.094) ng g^{-1} day^{-1}, respectively, using data normalised for 2022 (with non-normalised data within brackets), also close to a factor of two. Given a similar leaf area index, a shift in tree species composition can lead to a substantial change in the rate of deposition of Hg. Such changes in tree species composition can be the consequence of conscious decisions by the forestry sector, but also result from altered environmental conditions, such as climate change, which can trigger significant shifts in species composition with respect to leaf form and habit (Ma et al., 2023). Thus, in addition to effects of climate change on the stomatal conductance which controls leaf Hg uptake (Wohlgemuth et al., 2023), dynamic change of land cover following an altered climate can have profound effects on leaf Hg accumulation. Furthermore, leaf N concentration, also important for the Hg flux rate, depends partly on local N availability (Liang et al., 2020; Ordoñez et al., 2009), which is influenced by intrinsic soil fertility, the level of atmospheric N deposition from NO_x and NH_3 emissions (De Vries et al., 2024), as well as active forest N fertilization (Linder, 1995).

4.3 Limitations, Opportunities and Future Research

It should be noted that the Hg concentration of the plant material was analysed using different methods (extraction, chemical analysis, reference materials) in the data sources. Likewise, the methods for estimation of leaf N and SLA/LMA were not identical. A diversity in the methods is a persistent challenge for studies combining data from different investigations to provide general results based on a broad range of data. Although the application of relevant QA protocols should ensure that data from different sources are essentially comparable in meta-analyses or research syntheses, it cannot be neglected that the use of different methods is a source of systematic variation between studies.

Although the relationships of Hg uptake rate with SLA and LMA were strong, there are several factors which could have contributed to the unexplained variation in Hg accumulation rate among species. Stomatal uptake will depend on stomatal conductance, which, in turn, is sensitive to meteorological variables such as vapour pressure deficit (Wohlgemuth et al., 2022) and thus in a larger perspective to climate change (Wohlgemuth et al., 2023). We used observations made in fairly similar climates from a global perspective, but local environmental differences may have affected stomatal Hg uptake rate. Age of the trees and position in the canopy of sampled leaves (Wohlgemuth et al., 2020) are other potential sources of variation in leaf Hg accumulation. In addition, mercury pollution history at the different sites could be of importance.

Leaf N and SLA/LMA are among the most important of the different variables commonly used to represent LES, (Onoda et al. 2017). LES-relevant variables tend be more or less strongly correlated with each other (Osnas et al., 2013), but it cannot be excluded that LES-relevant factors not included in our data set, such as leaf phosphorus and leaf longevity, could provide further explanatory power to the relationship between leaf Hg uptake rate and the LES. To account for these uncertainties and sources of variation, future studies of the link between leaf Hg uptake and aspects of LES standardised protocols should be implemented. However, despite the influence of the mentioned sources of variation, the different data sources provided strikingly similar relationships between leaf Hg accumulation rate and SLA/LMA.

Accounting for the declining trend in background atmospheric Hg^0 concentrations strengthened the general relationships (Fig. 2) by making the response functions of different data sources becoming more similar. Although the improvements were not very large, it highlights the importance of considering the development of background Hg concentration in studies combining data based on observations made in different years.

Since dynamic ecosystem modelling can use leaf traits associated with the LES (Berzaghi et al., 2020), the connection of leaf Hg uptake to this analytic framework offers opportunities for the implementation of state-of-the-art modelling of the deposition of this element, and to understand the processes governing it in ecosystems of different types. Our data set represents a broad range of leaf functional types, with observations from temperate forests in north and central Europe as well as central China. Thus, different environmental conditions and a substantial number of species are included, but it would be of large importance to test the connection of leaf Hg accumulation with the LES for tree species adapted to and growing in a broader range climates and biogeographical regions. Further, the needles or leaves of evergreen conifers and broadleaved trees included in our investigation were up to just above 1-year old, although evergreen conifers can maintain their needles for much longer (e.g., *Pinus* up to 6 years, *Picea* up to 12 years and *Abies* up to 16 years; Niinemets & Lukjanova, 2003) and needle longevity is influenced by environmental conditions (Reich et al., 2014). Our study contained data for three *Abies* species and the average of the Hg accumulation rate for them was lower than for any other genus included. Since some genera are only represented by one species, and actual leaf longevity was not reported, this observation can only be taken as an indication in our study of the influence of leaf longevity on leaf Hg uptake rate.

There are observations clearly suggesting that the rate of Hg uptake by evergreen conifer needles declines over the needle life span (Pleijel et al., 2025; Wohlgemuth et al., 2022). This implies a dependence on needle age of the time-integrated Hg deposition, which needs to be considered to estimate Hg flux on an ecosystem scale and should be further investigated to improve our understanding of the significance of needle age for the assessment of uptake of Hg by vegetation. Based on the present study it can however be concluded that the LES is a theoretical framework for leaf strategy, which can explain a significant fraction of the variation in Hg uptake rate among leaves or needles of different leaf habit and leaf form.

Author Contributions *Håkan Pleijel*: Conceptualization, Field Sampling, Data Curation, Writing-Original Draft, Visualisation, Investigation, Funding Acquisition; *Jenny Klingberg*: Field Sampling, Laboratory Analysis, Writing-Review and Editing; *Henrik Sjöman*: Field Sampling, Writing-Review and Editing; *Göran Wallin*: Field Sampling, Laboratory Analysis, Writing-Review and Editing.

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Data Availability Swedish data used in this study are available here: https://doi.org/10.5878/hwa8-vn68.

Declarations

Ethics Approval Not applicable.

Consent for Publication All authors agreed with the content and have given their explicit consent to submit this manuscript.

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