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Nutrition Status of Trees on Spoil Heaps After Coal Mining Can Be Inferred From Seasonal Dynamics of Foliar Nutrient Concentrations

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ABSTRACT

A stable vegetation cover on given habitat conditions can be one of the possible requirements for post-mining sites, as it can prevent erosion and dustiness of these anthropogenic surfaces and bring several practical future benefits, such as biomass production and microclimate improvement. The aim of this work was to evaluate nutrient sufficiency for trees in spoil heaps following coal mining in the Czech Republic, Central Europe. To achieve this aim, nutrient concentration dynamics in the foliage of deciduous trees common on spoil heaps was monitored during the 2024 growing season and compared to the nutrient content of the spoil heap substrates. The spoil heaps are indeed commonly poor in phosphorus (available and reserve) and magnesium (reserve). The goal was to assess whether nutrient insufficiency can be detected by (i) nutrient management by plants through resorption from leaves before senescence, and (ii) excessive uptake of indicator elements manganese and zinc far above plant needs. The autumn nutrient resorption is much smaller than the spring decrease after leaf emergence (for phosphorus and potassium) or the whole-season dynamics (potassium and magnesium). Uptake of indicator elements signifies low nutrient availability and/or low pH in species that facultatively accumulate excess Mn (alder, aspen, birch, hornbeam, lindens, Norway maple, poplar) and Zn (aspen, birch, poplar, willows). The low availability of phosphorus and magnesium is evidenced by low foliar concentrations of these macronutrients in summer (for phosphorus and potassium) and by a rapid decrease in nutrient content in summer (for phosphorus). The examined spoil heaps would not require amelioration unless high biomass production was desired; however, vegetation resilience to climatic extremes under nutrient stress might be weakened.

1 | Introduction

Mining has reshaped industrialised landscapes and changed hydrology and microclimate in many areas of the world (Krümmelbein et al. 2012; Macdonald et al. 2015; Guan et al. 2020; Spasić, Vacek, Vejvodová, Tejnecký, et al. 2024). In Central Europe, coal mining has been particularly extensive over the last century, but its complete cessation is expected in the coming years (Frantál et al. 2025). The areas of mining-impacted landscapes tended to grow during the 20th century, when thriving mining companies funded land reclamation from their profits. This rational economic scheme has been halted by regulations related to the European decarbonisation goals, which have made coal production and use increasingly uneconomical. In the subsequent years, rather large opencast and underground mines will be closed in the Czech Republic, Poland, and Germany, and the past reclamation strategies (Štýs 1981; Bradshaw 1997; Krümmelbein et al. 2012) will not be financially viable. Moreover, general attitudes towards post-mining sites have changed in recent decades (Spasić, Vacek, Vejvodová, Tejnecký, et al. 2024; Frantál et al. 2025). The former economic targets, such as expected gains from crop or wood production on the reclaimed spoil heaps (Štýs 1981; Krümmelbein et al. 2012; Spasić, Vacek, Vejvodová, Tejnecký, et al. 2024), have been gradually dismissed in favour of ecological targets (Řehounková et al. 2020, 2023). Natural succession has been promoted as the most cost-effective approach, potentially transforming post-mining sites into ecologically valuable hotspots of biodiversity (Prach and Hobbs 2008; Prach et al. 2019; Řehounková et al. 2020, 2023; Bakr et al. 2024).

Spontaneous succession (natural restoration) is currently presented as the only alternative opposed to technical reclamation, although natural and technical restorations represent endmembers on a continuum of possibilities (Štýs 1981; Bradshaw 1997, 2000; Prach et al. 2019). While early pedogenesis on spoil heaps can be facilitated by almost any plant cover or land use within the first decades of post-mining development (Vindušková and Frouz 2013; Guan et al. 2020; Spasić, Vacek, Vejvodová, Tejnecký, et al. 2024), the formation of a stable and dense vegetation canopy, which prevents sheetwash erosion and dust formation, can be hindered by a critical deficiency of total nutrients on newly exposed land surfaces (Štýs 1981; Bradshaw 1997; Jensen et al. 2010; Macdonald et al. 2015; Spasić, Vacek, Vejvodová, Tejnecký, et al. 2024; Rustowska et al. 2024). Low available or total phosphorus is typical of spoil heaps (Bradshaw 1997; Munford et al. 2021; Spasić, Vacek, Vejvodová, Tejnecký, et al. 2024; Spasić, Vacek, Vejvodová, Borůvka, et al. 2024), though this could be ameliorated by simple reclamation measures. Decisions regarding the management of post-mining sites should be holistic, as perspectives on these sites can be diverse or even contradictory (Štýs 1981; Krümmelbein et al. 2012; Řehounková et al. 2020, 2023; Spasić, Vacek, Vejvodová, Tejnecký, et al. 2024): economic (cost of reclamation versus potential gains from biomass production), ecological (biodiversity or other biological values versus sustainable plant cover to prevent surface erosion), and civic (recreational attractiveness). The sustainability of vegetation cover resilient to climatic stress has become increasingly valued (St.Clair et al. 2008; Jensen et al. 2010; Sitko et al. 2022; Spasić, Vacek, Vejvodová, Tejnecký, et al. 2024). Such resilience is especially desirable under the threat of meteorological extremes expected to intensify with ongoing climate change, which could particularly damage plants subjected to persistent nutrient stress (St.Clair et al. 2008; Lynch 2022).

Pioneer tree species such as birch or poplars can survive even in very nutrient-poor conditions within spoil heaps, but poor soil status causes variable growth rates among individual species (Štýs 1981; Macdonald et al. 2015; Spasić, Vacek, Vejvodová, Tejnecký, et al. 2024), or can lead to dieback even in reclaimed sites (Jensen et al. 2010). The aim of this work is to evaluate methods for assessing nutrient insufficiency in non-reclaimed spoil heaps. A literature review highlights two possible approaches for detecting insufficient soil nutrients in living trees: (i) enhanced nutrient resorption prior to senescence (Vergutz et al. 2012; Sohrt et al. 2018; Chen and Chen 2020), and (ii) excessive uptake of certain 'indicator' elements, such as Mn (Kogelmann and Sharpe 2006; Wen et al. 2021; Zhou et al. 2022; Bílková et al. 2024). The concept of nutrient resorption—a process whereby nutrients are partially recovered from mature leaves before senescence and redistributed to persistent parts of the plant—was introduced in the 20th century as a hypothetical evolutionary strategy for plants growing in nutrient-poor substrates (e.g., Woodwell 1974). Since then, it has been extensively examined quantitatively (Vergutz et al. 2012; Sohrt et al. 2018; Munford et al. 2021; Turpault et al. 2021). However, Aerts (1996) challenged this concept; Aerts and Chapin III (1999), and Sohrt et al. (2018) summarised some controversies surrounding it; and Munford et al. (2021) reported unexpected results from their case study on spoil heaps. Resorption can, in some cases, be hindered by nutrient imbalances (Sohrt et al. 2018; Lü et al. 2021). Therefore, this topic warrants further investigation.

The concept of indicator elements is based on the observation of excessive Mn or Zn uptake under conditions of low macronutrients—specifically, low soil P for Mn and Zn (Lambers et al. 2015; Wen et al. 2021; Yan et al. 2025), low Mg for Mn (Kogelmann and Sharpe 2006; Bílková et al. 2023), low K for Mn (Bílková et al. 2024), and low macronutrients in general for Mn (Salazar et al. 2021). This rationale is supported by the elevated exudation of low-molecular-weight complexing acids by plant roots, which mobilise both nutrients and indicator elements (Lambers et al. 2015; Wen et al. 2021). Elevated uptake of Mn and/or Zn is well-documented in species such as birch (Hrdlička and Kula 2004; Wildová et al. 2021; Sitko et al. 2022; Rustowska et al. 2024), willow (Matys Grygar et al. 2023), and alder (Matys Grygar et al. 2023; Hrdlička and Kula 2024), all of which are common on Central European spoil heaps (Štýs 1981; Spasić, Vacek, Vejvodová, Tejnecký, et al. 2024; Spasić, Vacek, Vejvodová, Borůvka, et al. 2024). Both nutrient resorption and excessive uptake of indicator elements can influence nutrient cycling, and initiating these processes is among the most desirable effects of early pedogenesis on spoil heaps.

The aim of this study was to evaluate nutrient sufficiency or other soil chemistry stress for trees growing on spoil heaps of hard coal mining in Ostrava and lignite mining in the Most Basin, both in the Czech Republic. This work tests the hypotheses that nutrient resorption or elevated uptake of Mn or Zn can serve as indicators of nutrient deficiency, which cannot be unequivocally evaluated by chemical analyses of spoil heap substrates. Nutrient insufficiency can represent stress to plants that could potentially be addressed through simple reclamation measures such as fertilisation if establishing a stable plant cover resilient to climatic stress or wood production would be desired for the spoil heaps. The hypotheses were tested on trees mostly originating from natural succession on technically non-reclaimed spoil heaps, which are now covered by trees of varying age and fitness, including sparsely vegetated areas with sandy substrates. The nutrient resorption hypothesis has yet to be evaluated controversially, perhaps because only a pair of foliage (summer and senesced leaves) has been examined. In this work, almost continuous seasonal monitoring was thus used as recommended by Munford et al. (2021) to shed more light on the hypothetical resorption phenomenon.

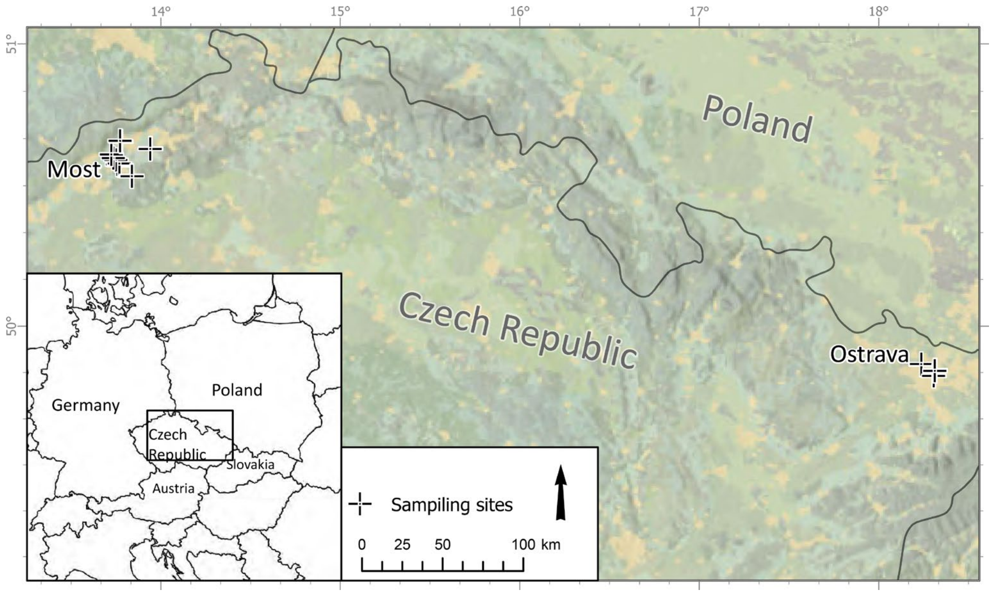

FIGURE 1 | Sampling sites in spoil heaps after coal mining in the Czech Republic. [Colour figure can be viewed at wileyonlinelibrary.com]

2 | Materials and Methods

2.1 | Study Areas

Sampling sites (Figure 1, Table S1) represent two examples of the most extensive spoil heaps resulting from coal mining in the Czech Republic: lignite in the Most Basin and hard coal in Ostrava. The sediments of the Most Basin include a 10–50 m thick coal seam of the Burdigalian (Lower Miocene) age (Matys Grygar et al. 2021). Coal mining in this region began in the Middle Ages, expanded during the Industrial Revolution, and reached its peak in the second half of the 20th century. The spoil heaps are composed mainly of sandy and silty fluviolacustrine deposits, and in some areas of silty lacustrine deposits, containing predominantly quartz, kaolinite, and illite (Matys Grygar et al. 2021). The overburden was deposited in freshwater lakes under a climate that was more humid and warmer than today, meaning the sediments originated from deeply weathered, relatively nutrient-poor catchment soils. Between 50 and 200 m of overburden was removed in certain 20th-century open-cast mines and deposited onto former agricultural landscapes of the flat basin floor (Štýs 1981). Consequently, the spoil heaps are characterised by flat, blanket-like shapes; for example, the Radovesice Spoil Heap covers an area of 12 km^2. Most samples were collected from sites where no technical reclamation had been carried out—for example, inner spoil heaps within the still active Bílina Mine, sites where further mining was originally planned but ultimately not realised, and small, steep remnants at the edges of reclaimed areas left to succession, including the edge of the Radovesice Spoil Heap. In some locations, trees were planted directly onto the spoil heap substrates.

The Ostrava spoil heaps were formed during the extraction of approximately 90 hard coal seams of Mississippian (Upper Carboniferous) age (Opluštil et al. 2024). The continental cyclothems containing these coal seams were deposited in a paralic basin under a very humid tropical climate (Opluštil et al. 2024). Consequently, the coal seams are embedded within clastic deposits derived from mature soils. Mining activity expanded during the 19th and 20th centuries, reaching its peak in the second half of the 20th century. The depths of the mines ranged from a few hundred metres to over 1 km. The spoil was piled into high, cone-shaped heaps; the most well-known of these is the Ema heap, which is 70 m high. The mines were located in densely populated areas of the rapidly growing city, limiting available space for the spoil heaps. The steep slopes of these heaps were unsuitable for reclamation by surface cover with soil (topsoiling) and tree planting. As a result, extensive areas left to natural succession are present on the heaps, and these areas were preferentially sampled in this study.

2.2 | Sampling

Tree leaves were sampled from 0.3 to 0.5 m long branches cut by 2.5 m long telescopic tree pruners. Leaves were sampled from the sun-exposed side of the tree crowns, following the methodology of Munford et al. (2021). One hundred to 200 g fresh leaves from entire cut-out branches were picked irrespective of their age and appearance, put into paper bags, and left to dry in those bags at ambient conditions. For each tree, 7 to 10 samples were collected during the growing season of 2024, between April and senescence in August and November, depending on the site.

Samples of spoil heap substrates were obtained from the top 20 cm using a soil auger or shovel. Preliminary analyses showed the spoil heap surfaces are rather homogeneous at metre scales, probably because of large-scale operations which produced them. It is known that early pedogenesis on similarly young spoil heaps mainly affects the uppermost several centimetres (Spasić, Vacek, Vejvodová, Tejnecký, et al. 2024) and thus the top 20 cm represented the entire spoil heap materials.

Sampled tree species are summarised in Table S1. The sampled trees included hornbeam (*Carpinus betulus* L.), lindens (*Tilia cordata* Mill.; *Tilia platyphyllos* ssp. *pseudo-rubra* C. K. Schneid.; *Tilia platyphyllos* ssp. *cordifolia* (Besser) C. K. Schneid.; *Tilia* × *vulgaris* L.), silver birch (*Betula pendula* Roth.), maples (*Acer pseudoplatanus* L.; *A. platanoides* L.), willows (*Salix caprea* L.; *S. alba* L.), aspen (*Populus tremula* L.), poplar (*Populus* × *canadensis* Moench), and alder (*Alnus glutinosa* (L.) Gaertn.).

2.3 | Leaf and Soil Analyses

Leaf samples were dried at 50°C, pulverised in a planetary mill, and analysed using an XRF spectrometer calibrated with reference materials, following the method described by Matys Grygar et al. (2023). The same procedure—drying, pulverisation and XRF analysis—was employed for the determination of total element contents in spoil heap surfaces, using a different set of certified reference materials, as described by Adamec et al. (2024).

Laboratory methods commonly used in Czech soil monitoring were employed for the analysis of extractable ions, particularly Mehlich III extraction and cold 2 M HNO_3 extraction, as these methods have established or reported limiting values for forest soils in the Czech Republic (Čechmánková et al. 2021). Monterosso et al. (1999) also recommended Mehlich III for evaluating nutrient availability on spoil heaps. Mehlich III extraction was carried out according to conventional protocols (Monterosso et al. 1999; Čechmánková et al. 2021), while the cold 2 M HNO_3 procedure was performed using an earlier Czech legislative protocol (Čechmánková et al. 2021; Adamec et al. 2024). In principle, this method approaches analysis of nutrient reserve similarly to other mineral acids (Štýs 1981). ICP-MS analysis of the extracts was conducted as described by Adamec et al. (2024).

3 | Results

3.1 | Content of Nutrients in Spoil Heap Substrates

Nutrient concentrations in the spoil heap surfaces are presented in Figure 2. The results of Mehlich III extraction (bioavailable nutrients) in Figure 2A are compared with the classification of nutrient status for Czech soils from Spasić, Vacek, Vejvodová, Borůvka, et al. (2024) and medians for Czech forest soils (Čechmánková et al. 2021). In some areas, bioavailable nutrients are insufficient for K, Mg and Ca, while P is low in the majority of sites (Figure 2A). The forestry classification of soils in Spasić, Vacek, Vejvodová, Borůvka, et al. (2024) is approximate, as certain tree species can grow in nearly any substrate, including spoil heaps (Krümmelbein et al. 2012; Woś et al. 2024). For pioneer species, the nutrient reserve (2 M HNO_3 extract) might be more relevant than bioavailable content, as this reserve can be converted to bioavailable forms through persistent rhizome activities. When assessing nutrient reserves, the results for spoil heaps (Figure 2B) were compared with medians for Czech forest soils (Čechmánková et al. 2021). Some spoil heap sites have lower reserve nutrient levels compared to forest soil medians. The fraction of stands exhibiting nutrient insufficiency on spoil heaps decreased in the order $P > Mg > K > Ca$, with phosphorus insufficiency being particularly pronounced. Critically low nutrient levels were mainly found in sandy substrates. The scale of stands examined in this work is suitable for assessing nutrient sufficiency.

The sediments surrounding coal seams, which now form the substrate of spoil heaps, were derived from deeply weathered continental weathering crusts (see Section 2.1) and primarily contain refractory primary minerals and secondary pedogenic minerals. As a result, nutrient concentrations in soil samples are intercorrelated due to the joint 'quartz dilution effect', typical of soils derived from sedimentary rocks. Table 1 shows that the concentrations of K, Mg and Ca are interrelated in the Mehlich III available fraction, and all analysed nutrients are interrelated in the reserve fraction (HNO_3). In Ostrava, total Ca also correlates with pH, possibly due to historical acid emissions; thus, low pH and low total Ca may indicate both acidification from emissions and Ca^{2+} leaching and a lack of buffering capacity in low-Ca soils. On the steep slopes of the Ostrava spoil heaps, nutrient leaching can be particularly intense. Those interrelated phenomena complicate the identification of the precise soil chemistry factor controlling the nutritional status of trees, as the soil chemistry variables are not independent.

3.2 | General Features of Seasonal Changes in Foliar Concentrations

Nutrient concentrations in leaves are detailed in Table S2, covering three parts of the growing season: spring (the first sampling), summer average from July to the 15th of September, and autumn (the last sampling). An overview of foliar element concentrations for individual species or genera is shown in Figure 3, with major seasonal trends summarised in Table 2. The trends of macronutrients are not highly species-dependent: phosphorus (P) decreases sharply after the first sampling and then remains relatively stable (Figure 4A); potassium (K) decreases stepwise throughout the season, although it stabilises in some months (Figure 4B); calcium (Ca) generally increases, and magnesium (Mg) either increases or remains stable at times (Figure 5).

Seasonal patterns in Ostrava were impacted by extreme rainfall in the second half of September 2024. Total precipitation for September 2024 was four times larger than the September monthly mean for the period of 2014–2023, resulting in total annual precipitation in 2024 being over 200 mm more than in the preceding decade. Some tree species afterwards exhibited a renewed increase in foliar P (notably birch, and to a lesser extent lindens) and K (birch, but not lindens) and a reversal of Ca or Mn accumulation, thus showing patterns opposite to those observed in autumn in the Most Basin, where no meteorological extremes occurred. This irregularity was not further addressed in this study, and autumn dynamics were primarily assessed using specimens from the Most Basin.

Considerable inter- and intraspecies variability was observed in micronutrient (Mn and Zn) uptake (Figure 3, Table 2). All sampled specimens of hornbeam and birch accumulated Mn, exhibiting high and seasonally increasing foliar Mn levels, typically exceeding 500 mg kg^{-1}. Similar accumulation was observed in some specimens of lindens, maples, aspens, and poplars. The majority of lindens, maples, aspens, and poplars, along with all sampled alders, Canadian poplars, and Norway maples, maintained foliar Mn within around ranges considered essential, generally in the order of tens mg kg^{-1}. The bimodality of foliar Mn is clearly illustrated for lindens (Figure 6). A bimodal pattern was

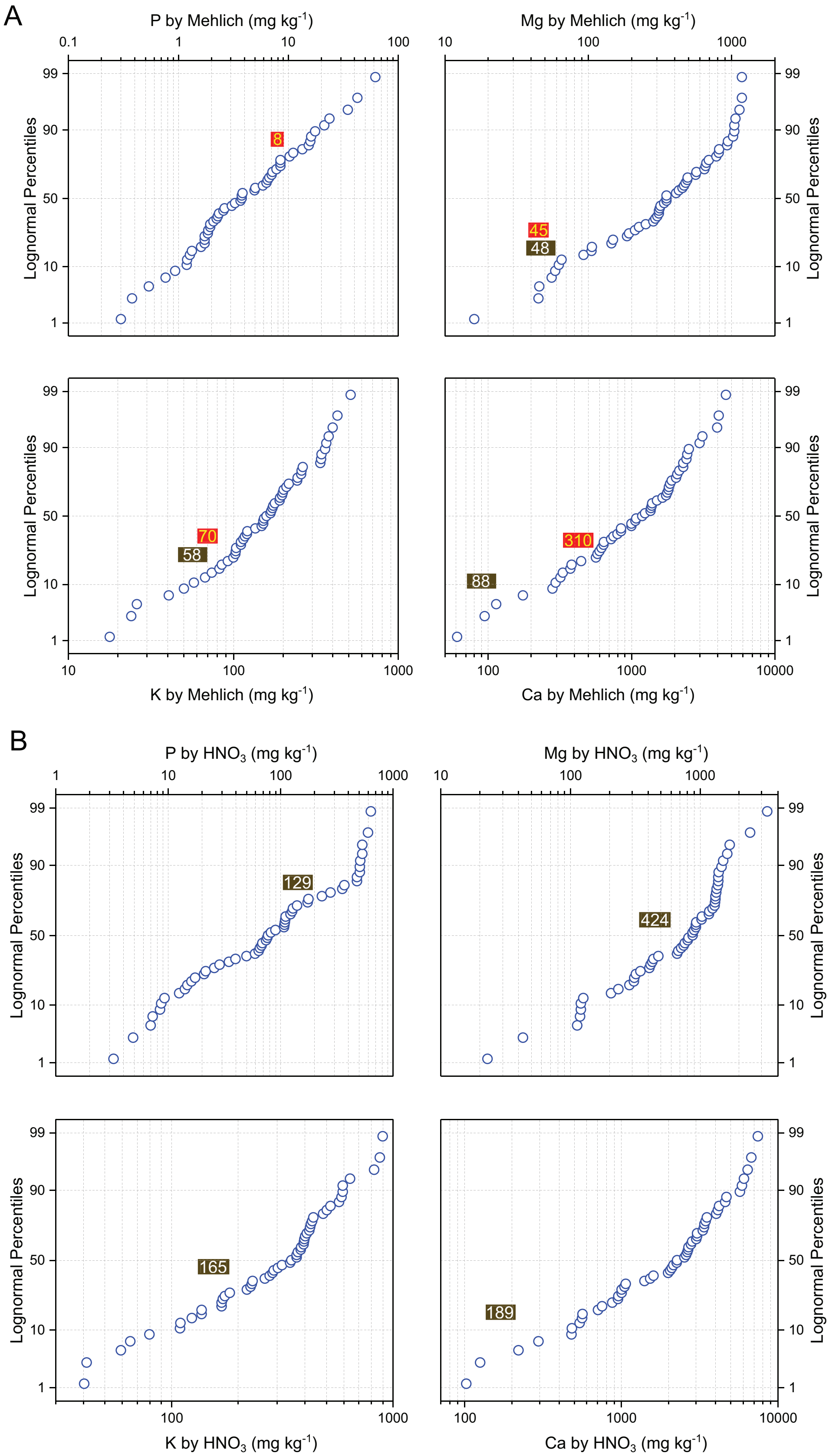

FIGURE 2 | Distribution of Mehlich III available (A) and HNO_3 extractable (reserve) nutrient concentrations (B) in spoil heap sbstrates. Nutrient sufficiency boundaries according to the Czech forestry standards (yellow letters on red background) were taken from Spasić, Vacek, Vejvodová, Borůvka, et al. (2024), medians for Czech forest soils (white letters on black background) are from Čechmánková et al. (2021). [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 | Spearman rank correlation (probability of null hypothesis in parentheses) of nutrients in spoil heap substrates for Mehlich III (upper right corner) and HNO_3 extracts of nutrients (lower left corner).

	P	Mg	K	Ca	Mn	Zn	
P	X	*−0.28 (0.05)*	*0.03 (0.85)*	*0.22 (0.12)*	0.39 (<0.001)	0.48 (<0.001)	Mehlich
Mg	0.43 (0.001)	X	0.72 (<0.001)	0.68 (<0.001)	*0.08 (0.56)*	*0.25 (0.07)*	
K	0.78 (<0.001)	0.64 (<0.001)	X	0.77 (<0.001)	*−0.07 (0.62)*	0.52 (001)	
Ca	0.70 (<0.001)	0.76 (<0.001)	0.75 (<0.001)	X	*0.22 (0.11)*	0.44 (0.001)	
Mn	0.62 (<0.001)	0.67 (<0.001)	0.72 (<0.001)	0.68 (<0.001)	X	*0.23 (0.10)*	
Zn	0.75 (<0.001)	0.43 (0.001)	0.77 (<0.001)	0.60 (<0.001)	0.65 (<0.001)	X	
			HNO_3				

Note: Insignificant correlations (probability of zero hypothesis > 10%) are in italics.

also observed for foliar Zn concentrations (Figure 3): median values between 200 and 300 mg kg^{-1} and consistent seasonal increases were found in birch, poplars, and willows, whereas Zn levels considered essential (tens of mg kg^{-1}) and relatively stable across seasons were found in lindens, hornbeam, and maples. Some species—and occasionally individual specimens—can thus accumulate excess Mn and Zn.

3.3 | Magnesium

Although Mg is a macronutrient and its content is typically regulated by homeostasis, foliar Mg concentrations in individual trees varied substantially, ranging from 0.1% to 0.5% (Figure 3), while the sufficiency range is generally considered to be between 0.15% and 0.35% (White and Brown 2010). The Mg reserve in spoil heap substrates is low in many stands (Figure 2B), indicating that plants growing there must be adapted to Mg insufficiency. Extremely low foliar Mg was observed in specimens growing on substrates with particularly high Mehlich-extractable Al, low soil Mg, low pH, and elevated soil arsenic (As) (Table 3). Five of seven specimens with summer foliar Mg below 0.15% (i.e., below the sufficiency limit as per White and Brown 2010) grew on substrates with > 0.5 mg kg^{-1} As in Mehlich III extract. Additionally, four of these seven low-foliar Mg specimens had substrates with less than 70 mg kg^{-1} Mg in Mehlich III extract, close to the boundary of deficiency (Figure 2A). Substrates with low Mg and high As generally exhibited relatively low soil pH, around 4.5. Woś et al. (2024) also reported on a negative correlation between foliar Mg and pH for alder and birch. The low foliar Mg appears to result from a complex response to soil chemistry stress.

Typical seasonal Mg patterns included stability or growth (Table 2, Figure 5), with growth often occurring in spring and late in the season. A decline after the first sampling was typical for specimens with low summer Mg (Figure 5). Autumn resorption of foliar Mg was observed rather infrequently, primarily in specimens with relatively high summer Mg (Figure 5A).

3.4 | Calcium

Foliar Ca was accumulated throughout the entire growing season, consistent with well-known general patterns (Tamm 1951; Turpault et al. 2021; Hrdlička and Kula 2024). Only a few tree specimens in Ostrava showed a temporal autumn decrease, which could be attributed to the extreme rains in September 2024 (Section 3.2). Foliar Ca increased from 0.5%–1% in spring to 1%–2% (or even higher in some individuals) before senescence (Figure 3). This Ca accumulation seemingly contrasts with both the adequate availability and reserve of Ca in the spoil heap substrate (Figure 2) and with the sufficiency interval of 0.05%–1% in plant leaves (White and Brown 2010). Elevated foliar Ca levels above the sufficiency threshold have also been observed in tree species growing in phosphorus-limited soils (Yan et al. 2024). The accumulation of Ca well above sufficiency levels (Figure 3) could therefore indicate a side effect of enhanced acquisition of other limiting nutrients. Alternatively, it might be part of a micronutrient detoxification strategy, as has been described for the sequestration of excess Cd in Ca-oxalate crystals (Blommaert et al. 2024).

3.5 | Potassium

Individual tree species did not differ substantially in early seasonal foliar K concentrations, which ranged from approximately 1% to 1.5%, nor in final concentrations at the end of the season, typically between 0.5% and 1% (Figure 3). Summer foliar K levels were generally within the lower part of the sufficiency interval (0.5%–4%) (Figure 3). A decrease in foliar K was observed in spring, with a weaker but persistent decline continuing through summer (Figure 4B), and a further decrease detected in autumn in species such as linden, some aspens, willows, poplars, and maples, but not birch (Table 2).

The spring decrease in foliar K (Figure 7A) was inversely proportional to the summer concentration (Figure 7B, green

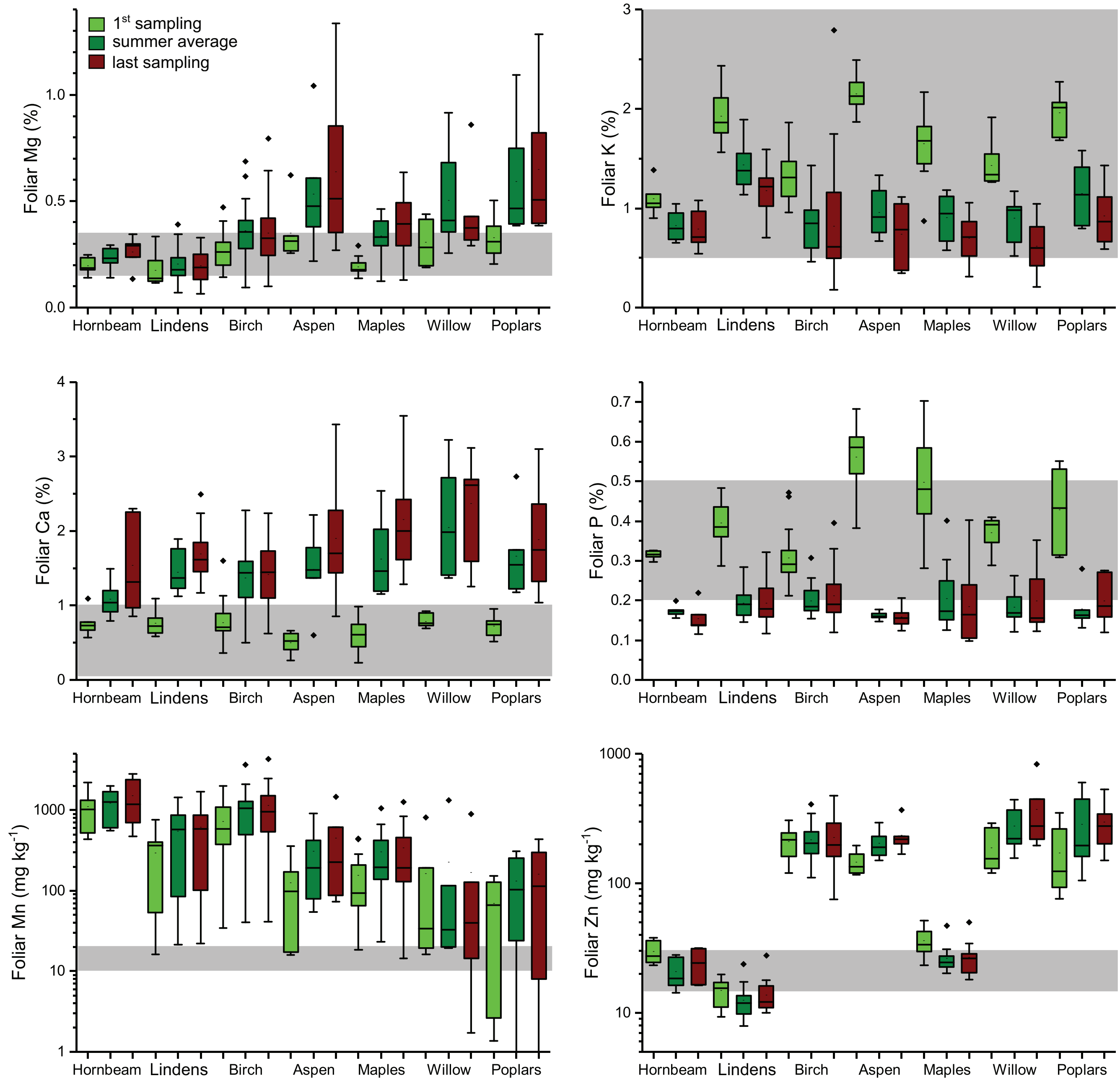

FIGURE 3 | Boxplots of foliar macronutrient concentrations in the 1st (spring) sampling (light green), summer average (dark green, July to middle of September), and the last (autumn) sampling (brown) for tree species/genera with at least six specimens. Sufficiency concentration intervals are shown by grey rectangles (White and Brown 2010). [Colour figure can be viewed at wileyonlinelibrary.com]

regression line), indicating that plants can focus K from internal reserves into young leaves even when overall uptake is low, as reflected by low summer foliar K content. This pattern was typical for birch, lindens, and poplars. However, the reserve for the young leaves is not formed by autumn resorption because a pre-senescence decrease in foliar K relative to summer levels was not observed at low summer foliar K. The decrease of foliar K before senescence (brown circles in Figure 7B) was scattered, but there was a cluster of points (brown ellipse in Figure 7B) showing resorption mainly under higher summer foliar K levels. This pattern is opposite to what would be expected if pre-senescence K resorption was an adaptation to low K uptake. The plant reserve for spring focus of K into young leaves, therefore, appears to be established earlier in the preceding growing season, not as late as before senescence. Nonetheless, foliar K concentrations in spring leaves of birch, aspen, poplars, some maples and willows tended to be higher under low pH and/or low available K (Mehlich III). This spring focus of K can be interpreted as an adaptive response to low nutrient uptake conditions.

3.6 | Phosphorus

Summer and autumn foliar P contents were not strongly species-dependent (Figure 3) and were mostly below the sufficiency threshold for plants (Figure 3). Achieving phosphorus (P) sufficiency appears limited to the first spring leaves. Trees

TABLE 2 | Seasonal changes in foliar element contents in three seasons separated by slashes (spring/summer/autumn).

Tree species	Mg	K	Ca	P	Mn	Zn
Hornbeam	X/G/S	D/S/S,D	S/G/G	**D**/S/S,D	**S/S/G,S**	D/S/S
Lindens	X/X/X	X/D/D	G/G/G	D/S,D/?	G/G/G	X/G,S/?
Birch	X/G,S/?	X/D/?	G/G/?	D/S,D/S,R	**G/G/G,S**	**X/S/S**
Sycamor (maple)	G/G/G,S	D/S/R	G/G/G	**D**/S/S,R	G,S/G/S	D/S/D,R
Norway maple	G/S/G	D/D,S/S,D	G/G,S/G,S	**D**/D,S/S	G,S/G/S	D/S/S,D
Willows	G/S/G,S	D/D/D	G/G,S/G,S	**D**/S/S,R	S/S/S	**G/G/G**
Aspen	G/G/G,S	D/D,S/D/S	G/G/G,S	**D**/S/D	G/G/G	**S/G/R**
Canadian poplar	G/S/S	D/D/D	G/G,S/G,S	**D**/S/S,R	G/G/G or S/S/S	**G/G/G**
Alder	S/S/D	D/D/?	S/G/S	**D**/S/D,R	S/S/G	S/S/S

Note: Bold font is used for accumulating patterns in Mn or Zn uptake.
Abbreviations: ?, variable; D, decrease; G, growth; R, resorption; S, stable; X, concentration dependent as a possible adaptation to nutrient insufficiency.

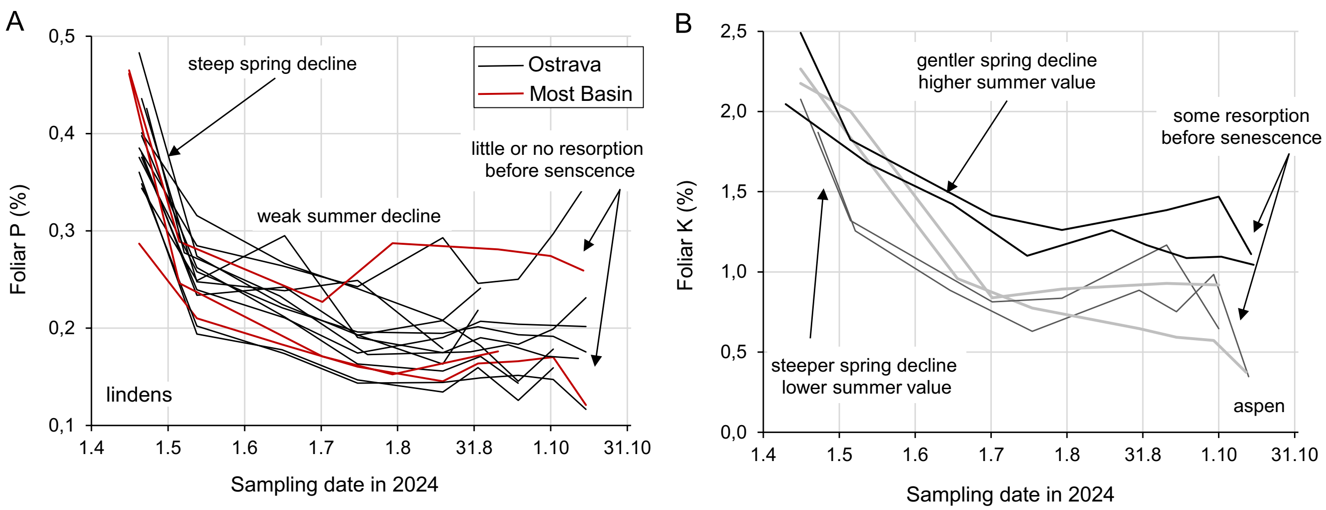

FIGURE 4 | Seasonally decreasing concentrations of P in lindens (A) and K in aspen (B). Resorption before senescence is minor beside spring decline and stable value in mature summer leaves. [Colour figure can be viewed at wileyonlinelibrary.com]

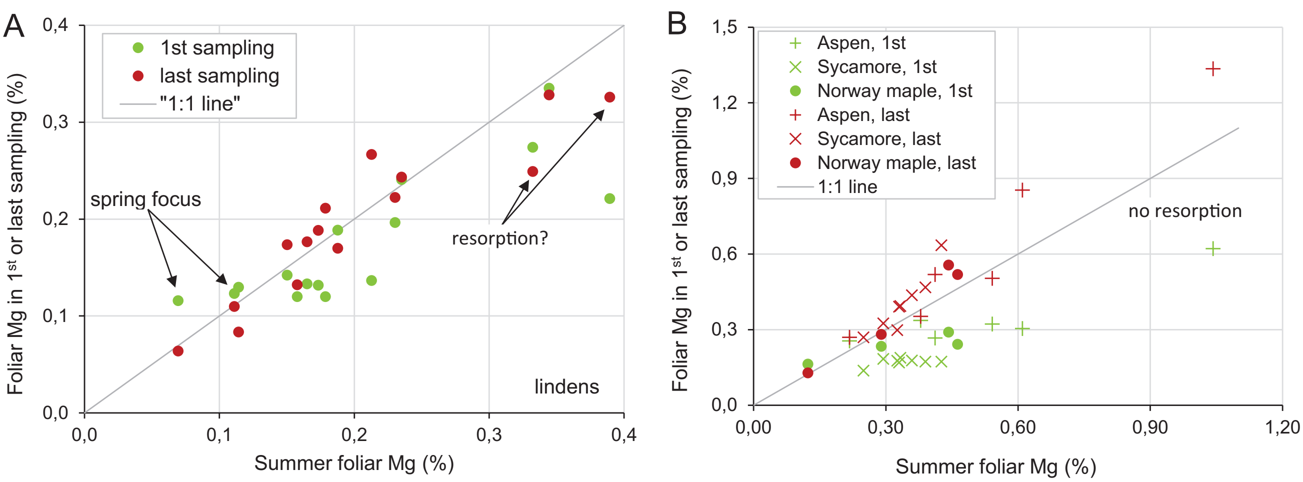

FIGURE 5 | The 1st (spring) and last (autumn) foliar Mg plot against mean summer Mg for lindens (A) and aspen and maples (B). Spring focus (Mg concentration maxima in the 1st sampling) is indicated in lindens (A). There is no significant Mg resorption at low foliar Mg. [Colour figure can be viewed at wileyonlinelibrary.com]

growing on spoil heaps thus evidently face insufficient P content, consistent with the low P levels found in soils (Figure 2). Foliar P showed the sharpest decline after the first sampling (Figures 3 and 4A), followed by a weaker decline during summer, with little (if any) resorption observed before the final sampling (Table 2, Figures 3 and 4A). Unlike potassium (K) (Figures 4B and 7B), in the case of P (i) the spring decrease was not dependent on the summer concentration, and (ii) summer P levels remained relatively stable. Similarly to K, the decline in foliar P after the first sampling was not compensated by autumn resorption; therefore, it is likely that plants store P for young leaves during the preceding summer rather than just before senescence. The absent or weak P resorption prior to senescence contradicts earlier studies (Tamm 1951; Vergutz et al. 2012; Hrdlička and Kula 2024) and could result from summer foliar P levels being below the minimal plant requirements. The spring concentration of P in leaves reflects an adaptive strategy of plants on spoil heaps to low nutrient availability (Figure 2), a pattern typical of P-impoverished environments (Yan et al. 2024).

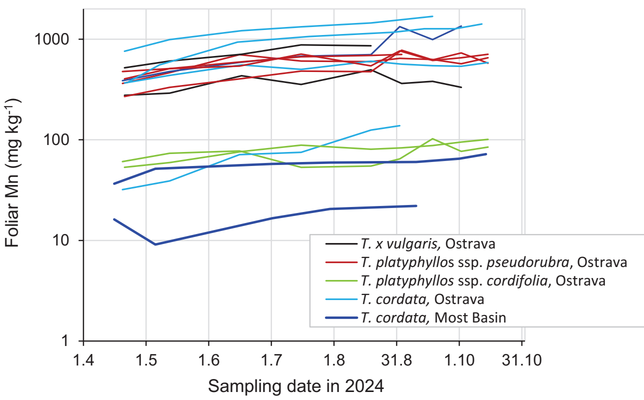

FIGURE 6 | Bimodality in foliar Mn in lindens documenting facultative Mn accumulation, 5 specimens showed stable summer foliar Mn $< 150\,mg\,kg^{-1}$ and 10 specimens showed Mn elevated far above the plant needs. [Colour figure can be viewed at wileyonlinelibrary.com]

The seasonal dynamics of P in leaves also include changes in P species during the growing season (Yan et al. 2024), with nucleoside phosphates like ATP, essential for tissue growth, being the most variable forms. Without sufficient spring P, plants could not produce leaves at all. In lindens and birch, the highest spring P concentrations were detected in leaves with low soil P extractable by Mehlich III or HNO_3, although this control was not very pronounced, suggesting that all plants preferentially focus P on the youngest leaves regardless of conditions. The most remarkable species-specific feature was the initial spring P concentration before its rapid decline to a summer plateau (Figure 3), reflecting the species' ability for a spring focus of P in young leaves. This order of P focus was aspen > maples > poplar > other species.

3.7 | Manganese

Consistent with known features of Mn uptake by trees, foliar Mn content was highly variable both between and within species (Table 2, Figures 3 and 6). Some individuals of maple, aspen, willow, and poplar had Mn contents as low as a few tens of $mg\,kg^{-1}$, close to the minimum essential level for plants (Figure 3). Conversely, hornbeam and most birch specimens exhibited Mn levels exceeding $500\,mg\,kg^{-1}$, with several thousand $mg\,kg^{-1}$ being not uncommon for species or specimens prone to Mn accumulation. Lindens displayed both ranges of concentrations, more or less stable essential levels or much higher with accumulation patterns (Figures 3 and 6). Foliar Mn was generally stable or increasing seasonally, with increases more frequently observed in lindens, birch, and individuals of other species with high summer Mn content (Figure 3, Table 2).

In particular, for aspen, birch in Ostrava, lindens and maples, summer foliar Mn was negatively correlated with soil pH (with foliar Mn increasing steeply below pH 6); in such acidic soils, Mn was also elevated when total calcium (Ca) in soils was below 0.6%. The negative correlation between foliar Mn and soil pH is a known feature for maples growing on acidified soils (Kogelmann and Sharpe 2006; St.Clair et al. 2008). For aspen, birch, hornbeam, lindens, and poplar, summer foliar Mn levels

TABLE 3 | Spearman rank correlation coefficients (and probabilities of zero hypothesis in parentheses) for foliar versus soil element contents.

	Aspen			Birch			Lindens
	Foliar Mg	Foliar Mn	Foliar P	Foliar Mg	Foliar Mn	Foliar P	Foliar Mn
Soil Mg (Mehlich)	0.37 (0.05)				−0.47 (0.02)		
Soil Mg (HNO_3)					−0.54 (0.007)		−0.45 (0.10)
Soil pH		−0.89 (0.05)	0.94 (0.005)		−0.37 (0.08)		
Soil Ca_{TOT}			−0.94 (0.02)	−0.46 (0.02)	−0.55 (0.006)		−0.70 (0.005)
Soil Al (Mehlich)				−0.53 (0.008)			
Soil P Mehlich							−0.75 (0.001)
Soil K (HNO_3)					−0.55 (0.007)		
Soil Pb (HNO_3)						−0.39 (0.06)	
Soil Cd (Mehlich)						−0.48 (0.02)	

Note: Only correlations with a probability of zero hypothesis < 10% are listed.

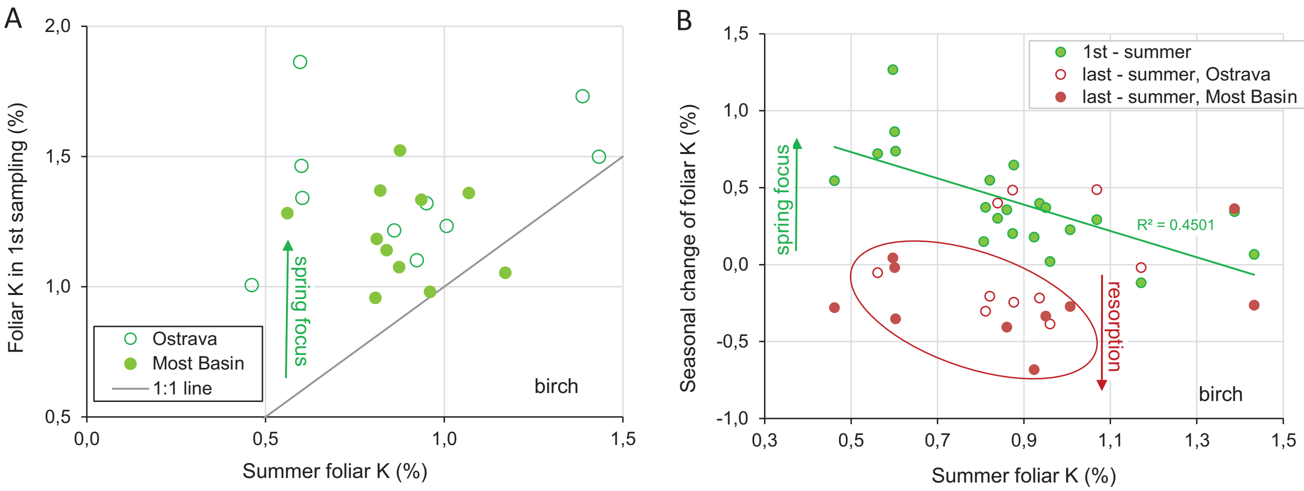

FIGURE 7 | Visualisation of K seasonal decline in birch. (A) Foliar K in the first spring sampling plot against mean summer (July—middle September) foliar K, the first K is in most cases higher than the summer concentration. (B) Differences between first and mean summer foliar K (green circles) and the last and mean summer foliar K (brown circles) plot against the mean summer foliar K. [Colour figure can be viewed at wileyonlinelibrary.com]

were negatively correlated with total soil Ca across all pH values. The results of regression analyses, presented in Table 3 for species with sufficient sample sizes and variable ranges, support these evaluations. Higher summer Mn levels were more likely when foliar and available Mg and P levels were low in lindens and birch, but the strong interrelation of nutrients and pH (see Table 1) complicates the identification of a single primary controlling factor.

3.8 | Zinc

The sampled tree species clearly fell into either a low-Zn group (foliar Zn in summer ranging from a few tens of mg kg^{-1} within the sufficiency range for plants) or a high-Zn group (around 100 mg kg^{-1}) (Figure 3). The low-Zn group includes hornbeam, linden, maple, and alder; these species exhibit a decline in foliar Zn during spring, followed by seasonal stability (Table 2). The high-Zn group displayed either seasonally stable or increasing concentrations, indicating an accumulative pattern (Table 2, Figure 3). Foliar Zn content was not directly controlled by Zn levels in soils, suggesting it may rather reflect soil chemistry stress, similar to Mn. In species that accumulate Zn, foliar Zn levels were elevated when nutrients, particularly calcium (Ca), were low, i.e., when Ca (HNO_3 extractable or total) was < 0.6% in the soils.

4 | Discussion

4.1 | Nutrient Resorption and Indicator Elements in Tree Leaves

Certain general patterns in seasonal dynamics (Figure 5) are broadly similar to earlier findings (Tamm 1951; Hrdlička and Kula 2024). The key differences from previously published patterns were: (i) a lack of clear signs of autumn resorption of P in the last sampling for most specimens, with only minor resorption observed in some individuals (e.g., Figure 4A), and (ii) no Mg resorption prior to senescence (Figure 5). A significant feature of Mg (Figure 5) and Ca is the variability among individuals of the same tree species, which is evidently concentration-dependent; the rate of seasonal growth was higher at higher concentrations, consistent with an overall accumulation regime. The behaviour of Mg (Figure 5A) contradicts the expectation that autumn nutrient resorption is an adaptive response to nutritional deficiency (Vergutz et al. 2012). The results in this work are thus not consistent with autumn nutrient resorption as adaptation to nutrient insufficiency, confirming scepticism of Aerts (1996) and Munford et al. (2021) about P resorption. In spite of those findings, Sohrt et al. (2018), Estiarte et al. (2023) and other authors still interpret their results in favour of autumn resorption as a response to low nutrients. Considerably more attention should be paid to the sharp spring decrease in P and K concentrations (Table 1, Figures 3–5 and 7). The spring focus of K (Figure 7) is particularly relevant for birch, lindens, and poplars with low summer K; i.e., this could represent adaptation to low available nutrients. The pattern is, however, not resorption—it documents internal storage of nutrients during the preceding growing season and their efficient focus on young leaves.

Nutrient insufficiency can indeed be revealed by elevated foliar Mn (Table 3), that can reach hundreds to thousands mg kg^{-1} in Mn-tolerant trees (aspen, birch, hornbeam, and lindens, birch and aspen, Figure 3). These trees appear to possess some adaptation mechanisms for accumulating and sequestering excess Mn internally (Alejandro et al. 2020), although these mechanisms are not always activated. Such facultative Mn accumulation does not seem advantageous for the studied species, and excessive Mn uptake is usually regarded as a cost of growing in unsuitable soils (St.Clair et al. 2008; Lambers et al. 2015; Salazar et al. 2021; Wen et al. 2021; Bílková et al. 2023, 2024; Yan et al. 2025). Species with high foliar Mn in spoil heaps are not necessarily Mn accumulators; for example, leaves of birch in central European lowlands typically range from a few tens to a maximum of 100 mg kg^{-1} (Tomašević et al. 2011; Rustowska et al. 2024), whereas Mn concentrations can reach 1000 mg kg^{-1} or more under harsh climatic conditions (Hrdlička and

Kula 2004; Bílková et al. 2024) or actually on some spoil heaps (Munford et al. 2021; Sitko et al. 2022; Rustowska et al. 2024). Facultative Mn accumulation and foliar Mn bimodality in lindens have not been reported previously.

Zinc cannot serve as an indicator element, although its uptake is associated with low soil Ca. Elevated foliar Zn was not associated with low P levels, as might have been expected based on the study by Wen et al. (2021).

4.2 | Trees and Nutrient Insufficiency on Spoil Heaps

Ecologists highly value species diversity on post-mining sites, which includes rare and endangered plant species that would not survive in stable climax forests or over-fertilised agricultural landscapes (Řehounková et al. 2020, 2023). Spoil heaps resulting from coal mining in the Czech Republic can thus be considered valuable, as they typically exhibit low available and reserve P (Figure 2) and correspondingly low foliar P (Figure 3). Additionally, summer foliar Mg and K levels often lie near the lower thresholds of sufficiency (Figure 3). However, trees—particularly pioneer species such as birch—are capable of growing even on the least fertile substrates on the studied spoil heaps after several years or decades of succession. Many tree species have evidently adapted to stress factors including low nutrients and low pH. Nonetheless, neither the Most Basin nor Ostrava spoil heaps typically suffer from extremely low pH: in the studied stands, the median pH was 5.5, with only four out of 53 stands having strongly acid pH values below 3.5, which is considered phytotoxic (Štýs 1981). If spoil heap substrates have such low pH, mainly due to pyrite oxidation, they cannot be left without amelioration through lime or ash additions (Schaaf and Hüttl 2005; Krümmelbein et al. 2012), because spontaneous neutralisation by soil minerals or H_3O^+ leaching is too slow under temperate climates (Bradshaw 1997, 2000).

Low nutrients and pH, which impose soil chemistry stress, can have several consequences. The senesced tree leaves tend to have low nutrient contents and elevated levels of accumulating elements such as calcium (Ca) and manganese (Mn), especially in birch, hornbeam, and some lindens. The element contents in senesced leaves are important for other plants, as trees are the major—and easiest manageable—factors influencing early pedogenesis, particularly the onset of nutrient cycling and the development of herbaceous undergrowth (Bradshaw 2000; Vindušková and Frouz 2013; Kompała-Bąba et al. 2020; Spasić, Vacek, Vejvodová, Tejnecký, et al. 2024; Spasić, Vacek, Vejvodová, Borůvka, et al. 2024; Woś et al. 2024). Excess foliar Mn, found in shrubs or trees growing on P-poor soils, can adversely affect undergrowth and seedlings (Gilliam et al. 2018; Staudinger et al. 2024; Yan et al. 2025), because not all plants are adapted to high Mn availability (White and Brown 2010; Alejandro et al. 2020; Skórka et al. 2023). Excess Mn has been reported to reduce Mg uptake (De Oliveira and de Andrade 2021; Skórka et al. 2023), which is particularly problematic in the studied spoil heaps, where soil and leaf Mg are indeed low (Figures 2 and 3). Some plants might require P for detoxification of excess Mn (Zemunik et al. 2020), but paradoxically, a deficiency in P can enhance Mn uptake by plants and thus amplify the P deficiency. Elevated Mn accumulation by birch and lindens can thus hinder undergrowth development and impede progression towards climax vegetation.

Although most studied spoil heaps in the Czech Republic are now mostly vegetated even without soil amelioration, some still show signs of low P and Mg, high acidity, and consequently elevated Mn uptake. This could jeopardise the stability of plant cover, especially if persistent nutrient deficiencies are combined with future climatic stresses. It is worrying because previous damage to forests impacted by acidification and nutrient depletion has demonstrated that trees with poor nutrition are more susceptible to abiotic stress and pathogens (St.Clair et al. 2008; Lynch 2022).

5 | Conclusion

Pioneer trees (birch, poplars, willows) that grow apparently well and spontaneously on spoil heaps without soil amelioration are typically species adapted to immature soils with low nutrient availability and limited nutrient reserves common in mine-waste substrates. However, low pH, low Ca, low P and high levels of risk elements such as As, Cd and Pb in spoil heaps can impede the attainment of sufficient foliar nutrient concentrations, particularly for P and, to a lesser extent, Mg, even in pioneer species like birch. Foliar nutrients are not resorbed immediately before senescence—as previously suggested in the literature—but primarily in the youngest leaves during spring (for P and K), with less resorption during summer (mainly for K). The insufficiency of P and K is more clearly evidenced by the decline in leaf nutrient contents between the first sampling in spring and summer, rather than by autumn resorption. Despite the low P availability in spoil heap substrates, plants seem able to acquire this element, though at the cost of enhanced uptake of excess Mn (in most species) and, to a lesser degree, Zn, of which excesses are known to require internal detoxification. Improper soil chemistry and low nutrient availability are largely responsible for elevated foliar Mn and Zn levels, with Mn in particular serving as an indicator of low soil nutrient status in species such as aspen, birch, hornbeam, and linden. The macronutrient-poor and Mn-rich litter will slow the development of climax plant communities by delaying early succession. This may be seen as beneficial for biodiversity; however, it raises concerns regarding plant cover stability on the spoil heaps, especially under meteorological extremes expected in the future.

Author Contributions

T.M.G. planned experiments and prepared the manuscript. G.B., M.K. and V.H. performed sampling. P.V. performed XRF analyses. M.K. and S.A. performed analyses of extractable elements in spoil heap substrates. M.K. prepared datasets for analyses.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** List of study sites with their positions and the sampled tree species. **Table S2:** Summary of foliar element concentrations in three parts of the growing seasons.