Plant Soil (2022) 480:213–226
https://doi.org/10.1007/s11104-022-05575-2

RESEARCH ARTICLE

Thallium accumulation and distribution in *Silene latifolia* (Caryophyllaceae) grown in hydroponics

Amelia Corzo Remigio · Philip Nti Nkrumah · Filip Pošćić · Mansour Edraki · Alan J. M. Baker · Antony van der Ent

Received: 6 January 2022 / Accepted: 20 June 2022 / Published online: 14 July 2022
© The Author(s) 2022

Abstract
Purpose Thallium (Tl) is one of the most toxic elements known and its contamination is an emerging environmental issue associated with base metal (zinc-lead) mining wastes. This study investigated the nature of Tl tolerance and accumulation in *Silene latifolia*, which has so far only been reported from field-collected samples.
Methods *Silene latifolia* was grown in hydroponics at different Tl concentrations (0, 2.5, 5, 30 and 60 μM Tl). Elemental analysis with Inductively coupled plasma atomic emission spectroscopy (ICP-AES) and laboratory-based micro-X-ray fluorescence spectroscopy (μ-XRF) were used to determine Tl accumulation and distribution in hydrated organs and tissues.
Results This study revealed unusually high Tl concentrations in the shoots of *S. latifolia*, reaching up to 35,700 μg Tl g^{-1} in young leaves. The species proved to have exceptionally high levels of Tl tolerance and had a positive growth response when exposed to Tl dose rates of up to 5 μM. Laboratory-based μXRF analysis revealed that Tl is localized mainly at the base of the midrib and in the veins of leaves. This distribution differs greatly from that in other known Tl hyperaccumulators.
Conclusions Our findings show that *S. latifolia* is among the strongest known Tl hyperaccumulators in the world. The species has ostensibly evolved mechanisms to survive excessive concentrations of Tl accumulated in its leaves, whilst maintaining lower Tl concentrations in the roots. This trait is of fundamental importance for developing future phytoextraction technologies using this species to remediate Tl-contaminated mine wastes.

Keywords Elemental distribution · Hyperaccumulator · Metal uptake · Phytoextraction · *Silene latifolia* · Thallium

Responsible Editor: Juan Barcelo.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-022-05575-2.

A. Corzo Remigio · P. N. Nkrumah · M. Edraki · A. J. M. Baker · A. van der Ent (✉)
Centre for Mined Land Rehabilitation, Sustainable Minerals Institute, The University of Queensland, Brisbane, QLD 4072, Australia
e-mail: a.vanderent@uq.edu.au

F. Pošćić
Molecular Genetics and Physiology of Plants, Ruhr University Bochum, Bochum, Germany

A. J. M. Baker
School of BioSciences, The University of Melbourne, Parkville, VIC 3010, Australia

A. J. M. Baker · A. van der Ent
Laboratoire Sols Et Environnement, Université de Lorraine – INRAE, UMR 1120 Nancy, France

Introduction

Thallium (Tl) is one of the most toxic elements known to mankind (Lennartson 2015) and recently, it has been considered as an 'emerging pollutant' (Antoniadis et al. 2019; Ma et al. 2022; Wang et al. 2021). Thallium toxicity is even greater than that of other well-known inorganic poisons such as arsenic (As), lead (Pb) and cadmium (Cd) (Liu et al. 2020; Viraraghavan and Srinivasan 2011), and the element is listed as one of the US Environmental Protection Agency's 13 Priority Pollutants (Keith and Telliard 1979). Thallium can exist in two different oxidation states (+1 and+3), although in the environment thallous (+1) is predominant (Lennartson 2015; Ma et al. 2022). Thallium toxicity in animals and humans is a consequence of its chemical similarity to K^+ (Mullins and Moore 1960). Even small doses of Tl can be lethal to humans (8 mg kg^{-1} body weight) (Moeschlin 1980). Thallium is readily taken up from the soil by plants (including some common vegetables), and transported internally using K^+ pathways (Scheckel et al. 2004). These properties make Tl readily available to biota, leading to bioaccumulation in crops such as *Sonchus oleraceus* and *Zea mays* (Antoniadis et al. 2019; Dmowski et al. 2014; Wang et al. 2021).

Thallium is generally present in nature at low concentrations although mining and processing activities release this element into the environment (Karbowska 2016). The background Tl concentration in the Earth's crust ranges from 0.85 to 1 µg g^{-1}, with increasing concentrations in acidic igneous and clay-rich sedimentary rocks (Kabata-Pendias and Mukherjee 2007). Geochemically anomalous areas, such as in the vicinity of base metal mines [notably Pb and zinc (Zn)], can contain elevated Tl concentrations (>5 µg g^{-1}) (Lis et al. 2003; Liu et al. 2020; Tremel et al. 1997). Some tailings materials originating from Zn-Pb mines have high Tl concentrations, *e.g.* up to 40 µg Tl g^{-1} at the mines sites near Saint-Laurent-le-Minier and Ganges in Southern France (Leblanc et al. 1999), and 424 µg Tl g^{-1} (average) at the Raibl (Cave del Predil) mine site in Italy (Fellet et al. 2012). Some subsoils in the Swiss Jura Mountains (at the Erzmatt site) which have developed from localized areas of mineralized carbonate rock contain up to 6000 µg Tl g^{-1} (Voegelin et al. 2015).

Hyperaccumulator plants can attain exceptionally high concentrations of potentially toxic metals and metalloids in their shoots without developing toxicity symptoms (Baker 1981; van der Ent et al. 2013). These plants are models for fundamental research in ecophysiology and biogeochemistry, and applied research such as their use in 'green technologies', *e.g.,* phytoextraction to clean-up soils, and phytomining to extract valuable metal(loid)s from unconventional resources for economic purposes (Corzo Remigio et al. 2020; Nkrumah et al. 2019; van der Ent et al. 2015). A notional threshold for Tl hyperaccumulation has been set at 100 µg Tl g^{-1} in above-ground tissues (dry weight) (Reeves et al. 2018; van der Ent et al. 2013). Thallium hyperaccumulators include two species from the Brassicaceae family: *Biscutella laevigata* with up to 32,700 µg Tl g^{-1} in its leaves (Fellet et al. 2012), and *Iberis linifolia* (synonym: *Iberis intermedia*) with up to 4000 µg Tl g^{-1} in its leaves (LaCoste et al. 1999). *Silene latifolia* (*S. latifolia* subsp. *alba*, synonym: *Melandrium album*) is another Tl hyperaccumulator which belongs to the Caryophyllaceae family. The populations of this species from the Saint-Laurent-le-Minier area can accumulate up to 1500 µg Tl g^{-1} in leaves from soils containing up to 32 µg g^{-1} total Tl (Escarré et al. 2011). Furthermore, three species from the Violaceae family, *Viola allcharensis*, *V. arsenica* and *V. macedonica,* have also been reported to accumulate 2190 µg Tl g^{-1}, 9090 µg Tl g^{-1} and 4290 µg Tl g^{-1} in their leaves, respectively, when growing in soils with 13.7–2140 µg g^{-1} Tl at the former As-Sb-Tl Allchar Mine in the Republic of North Macedonia (Bačeva et al. 2014).

The Caryophyllaceae family is known for numerous metallophytes that occur on copper (Cu) and Zn-Pb metalliferous gossans and mine wastes around the world (Baker and Brooks 1989). The genus *Silene* in particular has species with high tolerance to Cu, Zn and Cd, of which the European widespread species *S. vulgaris* is the best studied taxon (Schat et al. 2000). Other metallophyte species include *S. paradoxa* in Europe (Arnetoli et al. 2008), *S. burchelli* and *S. cobalticola* in Central Africa from Cu-cobalt (Co) metalliferous soils (Baker and Brooks 1989; Malaisse et al. 1983). *Silene paradoxa* behaves as an excluder by restricting the translocation of different metals, such as Cd, Cu, nickel (Ni) and Zn, from the root-to-shoot, displaying metal resistance at the cellular level (Colzi et al. 2014). In laboratory experiments, *S. cobalticola* was confirmed to be more tolerant to Cu and cobalt (Co) compared to *S. burchelli* (Baker et al. 1983). *Silene vulgaris* limits Cu translocation from its roots (~2000 µg Cu g^{-1}) to shoots (4–215 µg Cu g^{-1}) by efficiently binding the Cu in root cells (Song et al. 2004). *Silene vulgaris* is also tolerant to other metals such as chromium (Cr) (Pradas-del-Real et al. 2013), Cd and Zn (Ciarkowska and Hanus-Fajerska 2008; Ernst and Nelissen 2000). The resistance to Cu in *S. vulgaris* has been explained by an enhanced Cu efflux from the roots due to the increased SvMT2b gene expression, and its resistance to Zn by an enhanced tonoplast transport of Zn in the roots (Verkleij et al. 2001).

Silene latifolia is native to Europe and Western Asia and naturalized around the world (Barluenga et al. 2011; Castillo et al. 2014; Mikhaylova et al. 2021). *Silene latifolia* is well adapted to polluted areas along with other plant species in Southern Italy. It can accumulate up to 102.5 µg Tl g^{-1} in its shoots when growing in soils with 9.40 µg Tl g^{-1} (Visconti et al. 2018). This species thus has potential to extract Tl from polluted soils using phytoextraction (Corzo Remigio et al. 2020). Thallium phytoextraction could give an economic return, given that Tl metal is valuable, worth US$ 7500 kg^{-1} (USGS 2020). Despite this possibility, very limited research has been conducted on the development of commercial Tl phytoextraction (Robinson and Anderson 2018). In contrast to the other Tl hyperaccumulators which occur only in Europe, *S. latifolia* has been introduced to many other areas around the world (Blair and Wolfe 2004). Theoretical Tl yields have been calculated for *I. linifolia* which show that with a biomass of 10 t ha^{-1} and an average of 800 µg Tl g^{-1} in its biomass, it may yield a return of US$ 12,000 ha^{-1} yr^{-1} (Anderson et al. 1999). *Brassica juncea* can produce 15 t ha^{-1} and with an average of 500 µg Tl g^{-1} may yield ~ 7.5 kg of Tl ha^{-1} yr^{-1} (Rader et al. 2019). However, these potential Tl yields (and monetary returns) remain to be tested and proven under 'real-life' conditions.

To date, there are only data available for *S. latifolia* from Tl-polluted soils in the field (Duri et al. 2020; Escarré et al. 2011). No experimental trials have yet been conducted under controlled conditions to assess Tl accumulation and tolerance in *S. latifolia*. The present study was therefore devised to assess Tl (hyper)accumulation in *S. latifolia* grown hydroponically, and to determine the in situ distribution of Tl and other elements in hydrated plant organs.

Materials and methods

Hydroponics dosing treatments Seeds of *S. latifolia* originating from the ancient Zn-Pb mines near Saint-Laurent-le-Minier (43°55′54.8"N, 3°39′48.5"E) mining region in Gard, Southern France were germinated on Gelzan gel in 2 mL Eppendorf tubes (made up with 0.5-strength Hoagland's solution). The seeds were then vernalized for one week at 3 °C, and acclimatized for four days at 26 °C, making a total of 11 days of germination. The seedlings were then transferred to hydroponic cultures after the cotyledons had fully emerged. The hydroponics experiment was conducted in a temperature-controlled room with five containers (11 × 30 × 40 cm; capacity ~ 12 L). The nutrient solution was based on 0.5-strength modified Hoagland's formulation: K (3 mM as KNO_3), Ca (2 mM as $Ca(NO_3)_2 \cdot 4H_2O$), P (1 mM as $NH_4H_2PO_4$), Mg (0.5 mM as $MgSO_4 \cdot 7H_2O$), Fe (40 µM as Fe(K)-HBED), Cl (1 µM as KCl), B (25 µM as H_3BO_3), Mn (2 µM as $MnSO_4 \bullet 4H_2O$), Zn (2 µM as $ZnSO_4 \bullet 7H_2O$), Cu (0.1 µM $CuSO_4 \bullet 5 H_2O$), Mo (0.1 µM as $Na_2MoO_4 \cdot 2 H_2O$) and 2 mM MES (2-(N-morpholino)ethanesulfonic acid) buffer adjusted to pH 5.5 with KOH (van der Zee et al. 2021). When plants were sufficiently large (after 15 days), the nutrient solution was spiked with Tl (as $TlNO_3$) to yield five treatment levels: 0 (control), 2.5, 5, 30, and 60 µM Tl (corresponding to 0, 0.5, 1, 6, and 12 mg L^{-1} Tl, respectively). The solutions were aerated with air-stone diffusers at the base of each container. All plants were harvested after 16 days in the Tl treatment solutions.

Plant growth conditions Six seedlings for each treatment unit were transplanted to 3 cm circular retainer baskets with a foam holder to allow immersion in the nutrient solution and also to protect roots from the light. The experimental plants were grown on for 31 days in a growth cabinet with a 12/12-h light/dark cycle, using high-intensity photosynthetically active radiation (PAR) LED lights (Valoya, model B200, Finland) at a photosynthetic photon flux density of 350 µmol m^{-2} s^{-1} and a 26/20 °C day/night temperature regime. At harvest, plants were separated into young leaves, old leaves, and roots. The plant samples were rinsed three times with deionized water and were subsequently dried at 40 °C for 120 h in a drying oven.

Chemical analysis of plant samples Oven-dried samples were homogenized, weighed (~ 100 mg), and pre-digested using 2 mL of HNO_3

(70%, Ajax-Finechem, Univar) for 24 h. The samples were then digested on a heated block (Thermo Scientific™ Touch Screen Dry Bath/Block Heater) for 1 h at 70 °C followed by 1 h at 125 °C, cooled, and brought to volume (10 mL) with ultrapure water (Milli-Q, Merck). These digests were analyzed by inductively-coupled plasma atomic emission spectroscopy (ICP-AES, Thermo Scientific iCAP7400) for major and minor elements, as described earlier (Corzo Remigio et al. 2021).

Scanning electron microscopy with energy-dispersive X-ray spectroscopy Small leaflet fragments were excised from the plant with a razor blade and immediately shock-frozen by pressing quickly against a solid block of stainless steel with a high thermal mass (2 kg) that was cooled by liquid nitrogen (-196 °C). Subsequently, the whole block (with samples in thermal contact) was moved into the vacuum chamber of a lyophilizer (Thermoline) and immediately pumped down. Vacuum (0.004 millibar) was achieved < 5 min which ensured thermal insulation, and ensured that the metal block remained cold and very slowly warmed to the set temperature of the lyophilizer (-85 °C). After 24 h the freeze-drying was progressed in increments of 5 °C, and for another 24 h to room temperature (a total of 48 h). The samples were then sealed in a box with silica gel, mounted on stubs, sputter-coated with carbon and analyzed using scanning electron microscopy with energy-dispersive X-ray spectroscopy (SEM–EDS, Hitachi SU3500), as described previously (Corzo Remigio et al. 2021).

Laboratory micro-X-ray fluorescence elemental mapping The µ-XRF analysis was undertaken at the University of Queensland (UQ) Facility on fresh, hydrated leaves as described previously (Corzo Remigio et al. 2021). In summary, leaves were mounted between two layers of thin film immediately after excision from the plant in order to limit dehydration. The µ-XRF analysis used a 100 ms per pixel dwell time and took approximately 24 h for each scan. There were no visible signs of specimen degradation (*e.g.*, wilting or discoloration) at the end of the scans. The XRF data were exported into ImageJ as TIFFs and visualized with the built-in 'Fire' LUT (Schneider et al. 2012).

Statistical analyses The assumption of data normality was assessed using the Shapiro–Wilk normality test, and homogeneity of variances tested with Levene's test. However, biomass data and Tl concentrations in *S. latifolia* samples failed both assumptions and therefore non-parametric tests were conducted. The significance of differences in dry biomass subjected to different Tl concentrations in the nutrient solutions was assessed by a Kruskal–Wallis test. The significance of differences in Tl concentrations in the different parts of *S. latifolia* organs (roots, old leaves, and young leaves) resulting from the independent treatments were assessed with the non-parametric Scheirer-Ray-Hare test, equivalent to a parametric two-way ANOVA, followed by Dunn's pairwise post hoc tests. Spearman's rank correlation coefficient was used to estimate the association between Tl treatments and Tl concentrations in different plant organs. Statistical analyses were performed using R version 4.0.2 with RStudio 1.3.959 at a significance level of $p < 0.05$, or significance as indicated.

Results

Plant growth performance in the thallium dosing regimen *Silene latifolia* dry biomass yield in the different Tl treatments is shown in Table 1 and Fig. 1. A Kruskal–Wallis test showed that Tl treatment levels did not have a significant effect on biomass ($H_{(4)} = 8.83$, $p = 0.07$). However, the highest biomass was obtained in the 5 µM Tl treatment with 4820 mg (median) per plant, whilst the lowest was in the 60 µM Tl treatment (1950 mg per plant). The standard deviation of the biomass was relatively higher in the highest Tl treatment (Table 1) as some individuals (one in each of the 30 and 60 µM Tl treatments) showed signs of toxicity (necrotic leaves) with lower biomass.

Accumulation of thallium in roots and shoots Thallium concentrations in *S. latifolia* across the different Tl treatments are given in Table 1 and Fig. 2. A Scheirer-Ray-Hare test showed a significant effect of Tl treatments (nutrient solution) for Tl uptake, $H_{(4,\ 72)} = 62.167$, $p < 0.001$, and also statistically significant accumulation of Tl in different tissues (old leaves, young leaves and roots), $H_{(4,\ 72)} = 13.344$, $p = 0.001$. Thallium concentrations in shoots and roots increased with solution Tl concentrations (Fig. 2). Three significantly different groupings could be detected ($p < 0.05$, Dunn's test) (Fig. 2).

Table 1 Effects of Tl exposure in solution on Tl uptake and growth of leaves (young and old), and roots of *Silene latifolia* grown in hydroponics

	Treatment				
	0 µM Tl	2.5 µM Tl	5 µM Tl	30 µM Tl	60 µM Tl
[Tl] in young leaves (µg g^{-1})	<LOD	696 ± 333	705 ± 466	12,900 ± 4140	16,700 ± 2810
[Tl] in old leaves (µg g^{-1})	<LOD	504 ± 140	561 ± 322	13,800 ± 3370	9870 ± 4440
[Tl] in roots (µg g^{-1})	<LOD	40.8 ± 17.6	131 ± 15.9	329 ± 200	694 ± 158
Total biomass (mg)	3760 ± 459	4000 ± 529	4820 ± 528	2850 ± 658	1950 ± 792

Values are medians ± standard error ($n=6$). LOD is the limit of detection (0.176 µg Tl g^{-1})

The group with the highest Tl concentration included the 30 and 60 µM Tl treatments, and the group with the lowest the 2.5 and 10 µM Tl treatments; the group with an undetectable Tl concentration was the control (0 µM Tl) treatment (Table 1 and Fig. 2). The highest accumulation of Tl occurred in young leaves in the 30 µM Tl treatment with 35 700 µg Tl g^{-1} (median ± SE: 12 900 ± 4140), whereas the lowest concentrations were in the roots in the 2.5 µM Tl treatment (median ± SE: 40.8 ± 17.6 µg Tl g^{-1}) (Table 1). A post hoc test showed significant difference in Tl concentrations between leaves and roots ($p<0.05$), with leaf concentrations one to two orders of magnitude higher than in the roots (Table 1). Spearman's rank correlation revealed a strong significant relationship between Tl in the nutrient solution and the Tl concentrations in leaves and roots ($r_{s(88)}=0.763$, $p<0.001$). The translocation factors (TFs) in *S. latifolia* (based on the quotient of the shoot and root Tl concentrations in Table 1) are all > 1 and up to 42, typical of a hyperaccumulator (Lorestani et al. 2012).

Plant and tissue-level distribution of thallium The elemental maps of hydrated leaves of *S. latifolia* are shown in Figs. 3 and 4, and the microscopic analysis of freeze-dried leaflets in Table 2 and Figs. 5 and 6. Thallium concentrations in the leaves increased progressively with Tl concentrations in the solution (Fig. 3). Thallium is mainly enriched in the base of the midrib but depleted in the apex. Thallium is also present at higher concentrations in the veins compared to the blade (Fig. 3). Older leaves accumulated Tl differently to young leaves; Tl is higher in the base and depleted down to the apex in old leaves, whereas in young leaves Tl is most prominent in the veins (Figs. 3 and 4). In contrast to Tl, K distribution is more homogeneous throughout the leaf but relatively depleted in the midrib (Figs. 3 and 4). Potassium concentrations are also high in the trichomes, especially in the older leaves (Fig. 3). Calcium concentrations are higher at the base of trichomes (Figs. 3 and 4). Thallium is not localized in the trichomes (Fig. 3).

The SEM-EDS analysis of magnified images of *S. latifolia* shows its morphology (Figs. 5 and 6) and the composition of major constituents (Table 2). Brighter areas in the BSE mode show the presence of Tl, and so the point analysis was deliberately focused on these areas. Trichomes of *S. latifolia* are cylindrical and swollen at the base and have elongated and acuminate tips (Fig. 5a and c). Points 1 and 2 were focused in the trichome of a young leaflet, where K (24.5 and 23.7 wt%) is one of the major constituents after O (60.4 and 63.5 wt%). The same trichome had Tl concentrations of 13.2 and 11.1 wt%, respectively. Points 3 and 4, focused on epidermal cells, with relatively higher concentrations of K (28.3 and 28.9 wt%) and Tl (20.4 and 16.3 wt%), followed by P (1.2 and 1.3 wt%) and Mg (0.6 and 0.8 wt%). Point 5 focused on the base of the trichome of the old leaflet; Tl was below the limit of detection here, whereas K was highly enriched (64.2 wt%). Point 6 was focused on the vein, where major constituents were O (51.6 wt%) and K (40.2 wt%) and Tl was a minor constituent with 6.7 wt%. Points 7 and 8 were focused on epidermal cells, where the major constituent was O (45.4 wt% and 50.4 wt%) and K (43.1 wt% and 39.5 wt%), and Tl was a minor constituent with 9.6 wt% and 8.1 wt%, respectively. It can be seen from the BSE-EDS elemental maps that Tl distribution appears to mirror that of K, although being present at lower concentrations. The trichome itself does not appear to contain appreciable Tl, although a low concentration is visible in the basal area (Fig. 6).

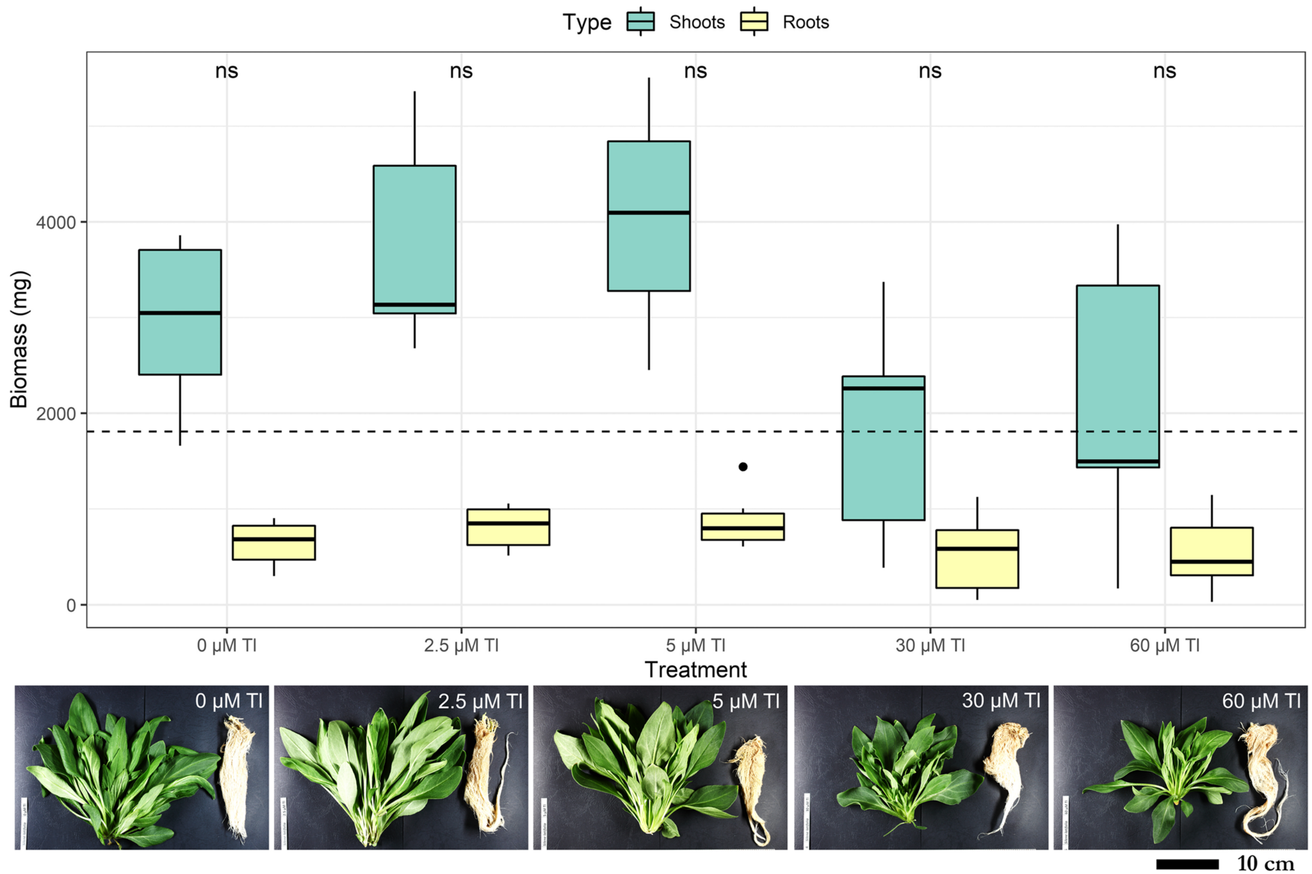

Fig. 1 Biomass graphs and images of *Silene latifolia* subjected to different Tl concentrations in the nutrient media (0, 2.5, 5, 30 and 60 µM Tl). For each treatment, median values (line inside the box), 25–75% inter-quartile range boxes and whiskers are displayed. The terminals of whiskers represent the lowest datum point still within 1.5 times inter-quartile range of the lower quartile, and the highest datum point still within 1.5 times inter-quartile range of the upper quartile. Outliers, data outside the whiskers, are shown as black circles. Data were analyzed by the non-parametric Kruskal–Wallis test ($p > 0.05$, ns = not significant). The dashed line represents the average biomass across all of the treatments

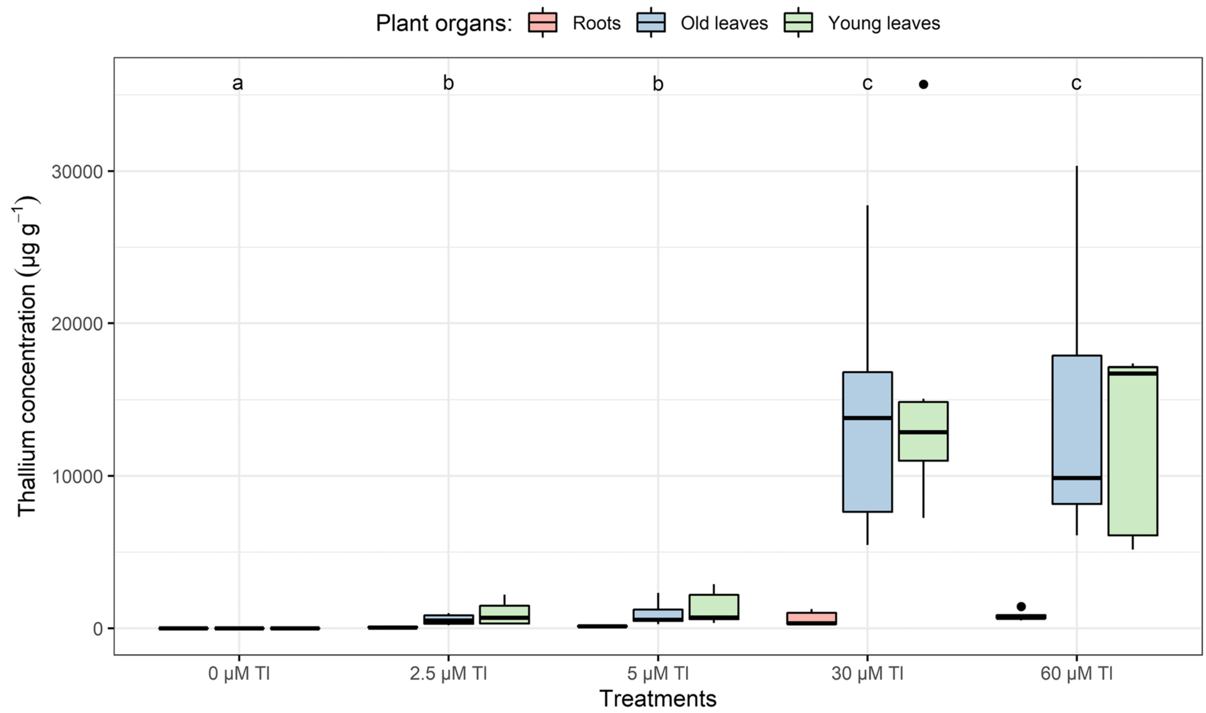

Fig. 2 Thallium concentration graphs of *Silene latifolia* grown in nutrient solution with different Tl concentrations (0, 2.5, 5, 30 and 60 µM Tl). For each treatment, median values (line inside the box), 25–75% inter-quartile range boxes and whiskers are displayed. The terminals of whiskers represent the lowest datum point still within 1.5 times inter-quartile range of the lower quartile, and the highest datum point still within 1.5 times inter-quartile range of the upper quartile. Outliers, data outside the whiskers, are shown as black circles. Whiskers are not represented if the 25% inter-quartile was equal to the lowest datum point (excluding the outliers), or if the 75% inter-quartile was equal to the highest datum point (excluding outliers). Data were analyzed by the nonparametric Scheirer-Ray-Hare test, followed by Dunn's test for the mean comparison. Different letters indicate statistically significant differences ($p < 0.05$) between treatments (the trend was the same for each organ)

Furthermore, Tl is not present in the stomata (Fig. 6). Subcellular analysis based on the SEM images was not considered as there is a high likelihood of metal redistribution at this level during the freeze-drying process (Siegele et al. 2007).

Discussion

Our hydroponic study confirms Tl hyperaccumulation in *S. latifolia* and reveals for the first time the distribution of Tl in its plant organs. Plant biomass increased in the 0–5 µM Tl treatment levels before decreasing in the 30–60 µM Tl treatments (Fig. 1), suggesting a stimulatory effect as observed for other toxic elements at low concentrations — a phenomenon known as hormesis (Agathokleous et al. 2019; Jalal et al. 2021; Salinitro et al. 2021). This has also been found in the Tl hyperaccumulator *B. laevigata* (Corzo Remigio et al. 2022). However, with exposure to higher Tl concentrations, some individuals developed necrotic older leaves. In nature, *S. latifolia* plants have been found to have highly variable Tl concentrations (up to 1500 µg Tl g^{-1}) that do not relate well with soil Tl concentrations (range 0–32 µg Tl g^{-1}), suggesting possible genetic variability in Tl uptake among individuals (Escarré et al. 2011). In our study, the experimental plants had variable Tl concentrations even within the same treatment, *e.g.,* the highest Tl concentration was 35,700 µg g^{-1} in young leaves exposed to 30 µM Tl, and the median ± SE was 12,900 ± 4140 µg Tl g^{-1} (Fig. 2; Table 1). Similarly, *B. laevigata* subsp. *laevigata,* from the Raibl/Cave del Predil (Italy) population was also reported to attain up to 32,700 µg Tl g^{-1}, growing in mine soils with an average Tl concentration of 400 µg Tl g^{-1} (Fellet et al. 2012).

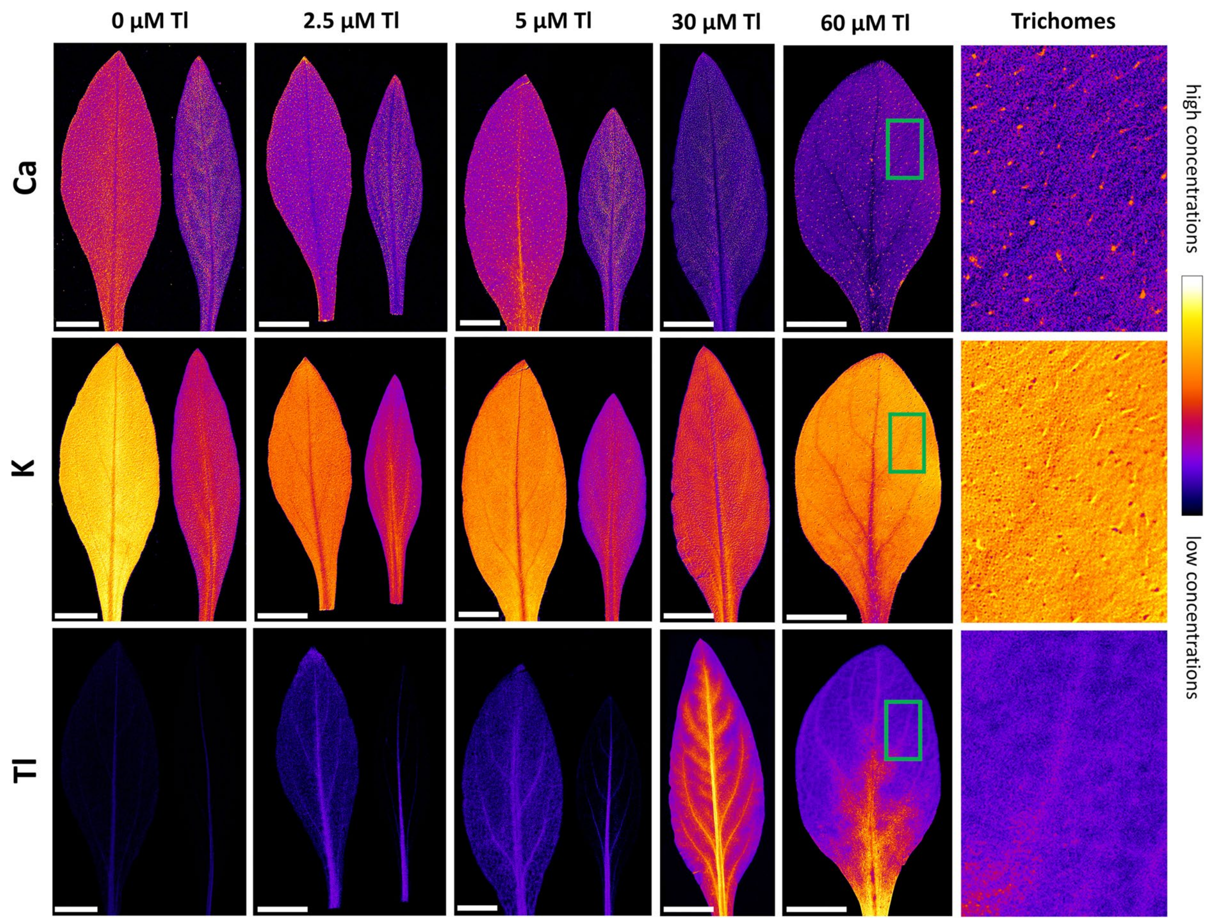

Fig. 3 Laboratory-based μ-XRF elemental maps of Ca, K and Tl of hydrated leaves of *Silene latifolia* grown in different concentrations of Tl in nutrient solution (0, 2.5, 5, 30 and 60 μM Tl). On the right end of the figure, trichomes are shown in a higher magnification of the old leaf from the 60 μM Tl treatment (green box). Scale bars denote 10 mm

The bioconcentration factor (BCF, the quotient of metal concentration in shoots:soil) of Tl hyperaccumulators is one of the highest reported compared to other non-essential metal(loid)s (Robinson and Anderson 2018); *e.g. B. laevigata* has a BCF of 27.3 (Fellet et al. 2012). In addition, Tl hyperaccumulators have high translocation factors. These traits make Tl phytoextraction applicable for a wide range of Tl-contaminated soils (Corzo Remigio et al. 2020). The potential Tl yields and market value of Tl make Tl phytoextraction potentially an economically attractive proposition. We estimate that *S. latifolia* can attain Tl yields of 5.88 kg Tl ha^{-1} yr^{-1} (based on the calculation of Tl concentration in plants × whole plant biomass), considering 16 plants m^{-2} and 0.46 t of biomass with 12,900 μg Tl g^{-1} from the 30 μM Tl treatment, suggestive of significant economic returns.

Thallium distribution in hydrated leaves of *S. latifolia* (Figs. 3 and 4) differs from that of *B. laevigata* (Corzo Remigio et al. 2022). In young leaves, Tl is predominantly localized in the mid-rib and the surrounding vascular bundles, whereas in *B. laevigata* Tl is localized at the foliar margins. In old leaves of *S. latifolia*, Tl is highest at the base and in the tip, whereas in *B. laevigata* it is across the surface and margins. Thallium enrichment in the basal and apical regions of old leaves of *S. latifolia* (Fig. 3) is similar to Mn distribution in the Mn hyperaccumulator *Gossia fragrantissima*, where the metal storage pattern is probably associated with transpiration (Abubakari et al. 2021). The SEM–EDS analysis of freeze-dried

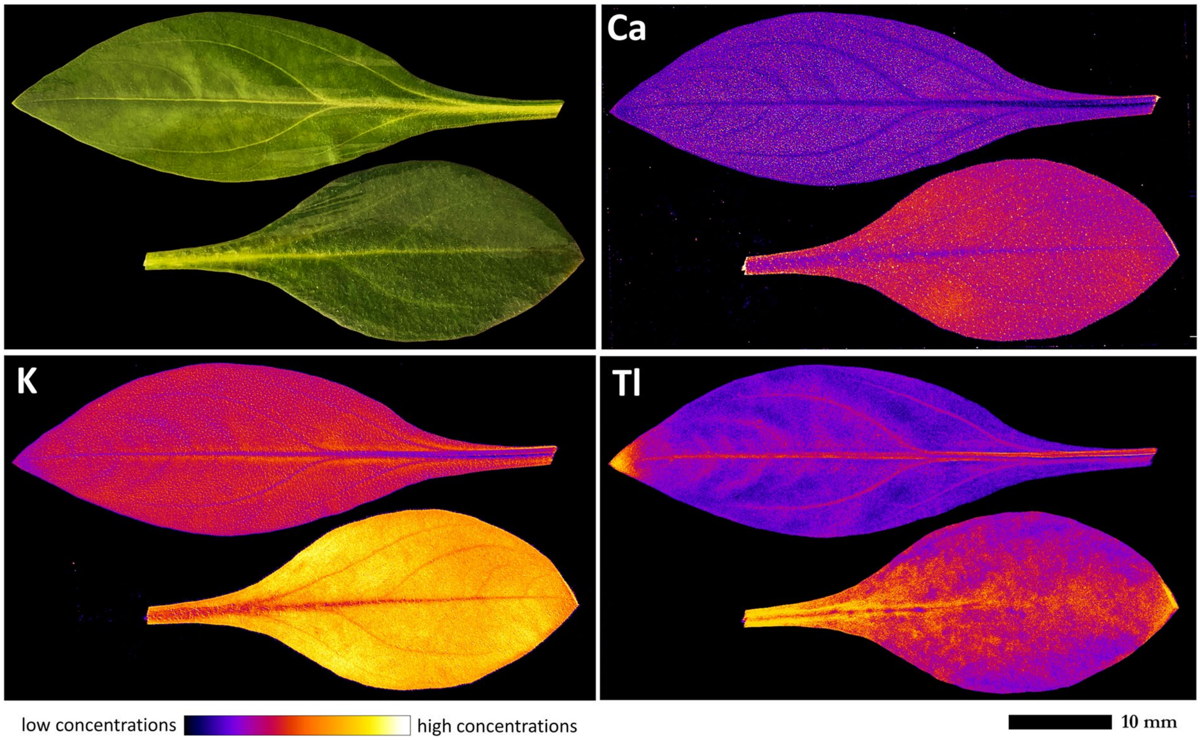

Fig. 4 Laboratory-based µ-XRF elemental maps of Ca, K, and Tl of hydrated leaves shown in the upper left corner of *Silene latifolia* grown in nutrient solution with 60 µM Tl; above: a young leaf, below: an older leaf

foliar fragments of *S. latifolia* revealed an uneven distribution of Tl across the epidermal cells (Figs. 5 and 6), which has been reported previously for other hyperaccumulators and suggested as a protection mechanism for photosynthetically-active mesophyll cells (Leitenmaier and Küpper 2013). Trichomes in *S. latifolia* were present on both the abaxial and adaxial surfaces (Figs. 3 and 4), and are abundant as expected from observations of leaves from European populations (Blair and Wolfe 2004). Similar to the *B. laevigata* population from Saint-Laurent-le-Minier (Corzo Remigio et al. 2022), Tl was not present in

Table 2 Energy Dispersive X-Ray Spectroscopy (EDS) point analyses in leaflets fragments of *Silene latifolia* from the 60 µM Tl treatment. The spots indicate the location of the point analysis as shown in Fig. 5

Specimen	Spot	Element (wt %)				
Silene latifolia		**Tl**	**O**	**K**	**P**	**Mg**
Young leaflet (Figs. 5a and 5b)	1	13.2 ± 0.3	60.4 ± 0.4	24.5 ± 0.2	1.1 ± 0.1	0.9 ± 0.1
	2	11.1 ± 0.3	63.5 ± 0.3	23.7 ± 0.2	0.9 ± 0.1	0.7 ± 0.1
	3	20.4 ± 0.3	48.8 ± 0.4	28.3 ± 0.2	1.2 ± 0.1	0.6 ± 0.1
	4	16 ± 0.3	53 ± 0.4	28.9 ± 0.2	1.3 ± 0.1	0.8 ± 0.1
Old leaflet (Figs. 5c and 5d)	5	< LOD	32.3 ± 0.4	64.2 ± 0.4	1.5 ± 0.1	1.4 ± 0.1
	6	6.7 ± 0.2	51.6 ± 0.3	40.2 ± 0.3	0.9 ± 0.1	0.4 ± 0.1
	7	9.6 ± 0.3	45.4 ± 0.4	43.1 ± 0.3	1.5 ± 0.1	0.4 ± 0.1
	8	8.1 ± 0.3	50.4 ± 0.3	39.5 ± 0.3	1.3 ± 0.1	0.6 ± 0.1

Values are concentrations in weight percent (wt%) ± error of analysis (σ uncertainty). LOD denotes the limit of detection (0.1 wt%)

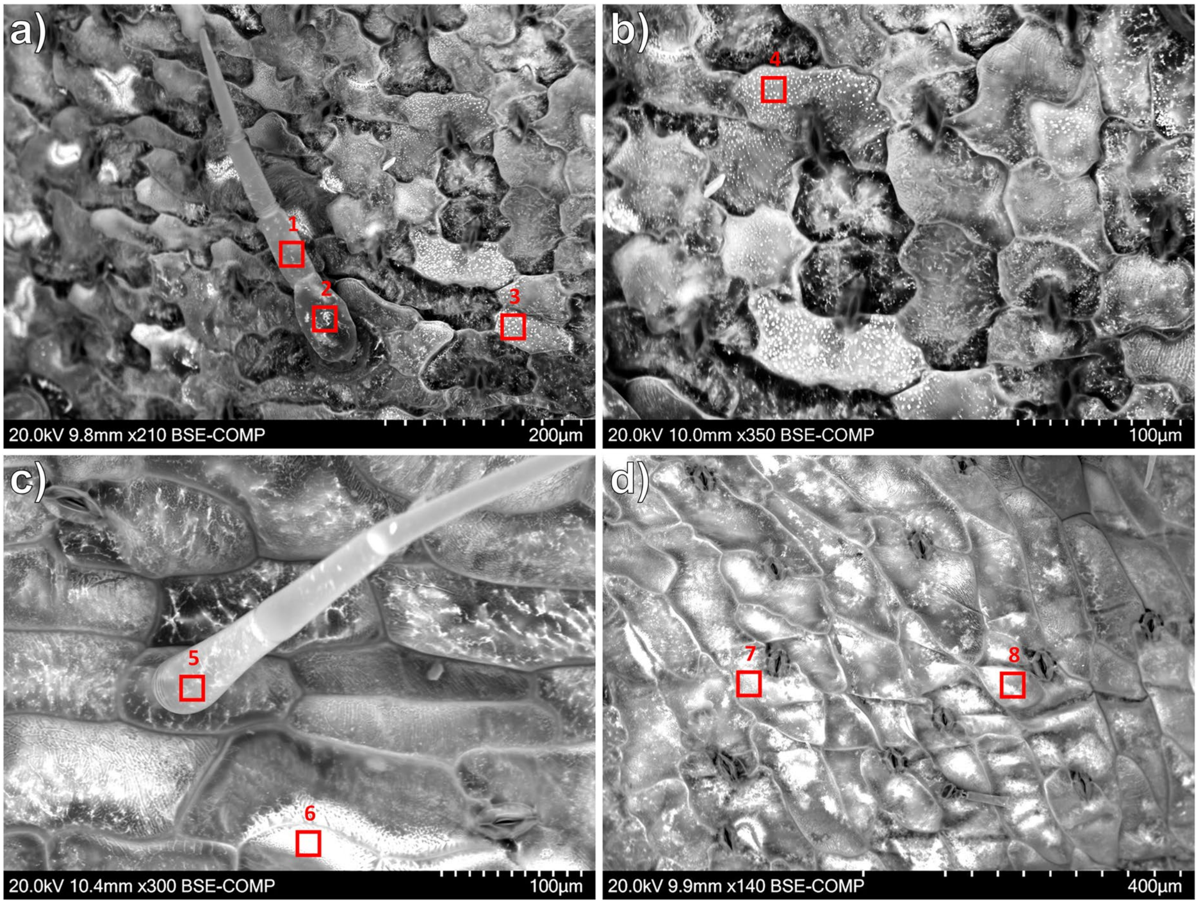

Fig. 5 Scanning electron microscopy—backscattered electron (SEM-BSE) images of a freeze-dried *Silene latifolia* specimen from the 60 µM Tl treatment: a) abaxial young leaflet with a trichome; b) a higher magnification of the abaxial young leaflet; c) a trichome growing in the vein of an old abaxial leaflet; d) lower magnification of the old leaflet abaxial surface showing stomata. Brighter areas represent higher Tl concentrations and the red boxes ticket by a number indicate the spots for the energy dispersive X-ray spectroscopy (EDS) point analysis, shown in Table 2

the trichomes themselves, but in the trichome bases (Fig. 6). Trichomes typically protect plants against physiological constraints, such as water loss/absorption and extreme temperatures, and from herbivory by making leaves unpalatable and/or excreting substances such as toxins (Werker 2000). Metal-enriched trichome bases have also been observed in other hyperaccumulators, *e.g.*, Mn in *Odontarrhena chalcidica* (synonym: *Alyssum murale*) (Broadhurst et al. 2009; McNear and Küpper 2014). To date, however, there remains no clear explanation of the role of trichomes in metal compartmentalization (Hopewell et al. 2021; McNear and Küpper 2014).

This study has shown that *S. latifolia* accumulates Tl in response to increasing Tl concentrations in a hydroponic system. In a similar Tl dosing trial with *Sinapis alba* exposed to 2 mg Tl L^{-1}, the highest Tl in shoots was 87.2 µg g^{-1} (Holubík et al. 2021), whereas in our experiment at 5 µM Tl (corresponding to 1 mg Tl L^{-1}) *S. latifolia* attains 705 ± 466 µg Tl g^{-1} in young leaves, and even more Tl is taken up in the higher Tl treatments, thereby showing that it is demonstrably highly Tl tolerant.

Conclusions

This study assessed *S. latifolia* tolerance and hyperaccumulation of Tl, an element of interest due to its extreme toxicity and high economic value. *Silene*

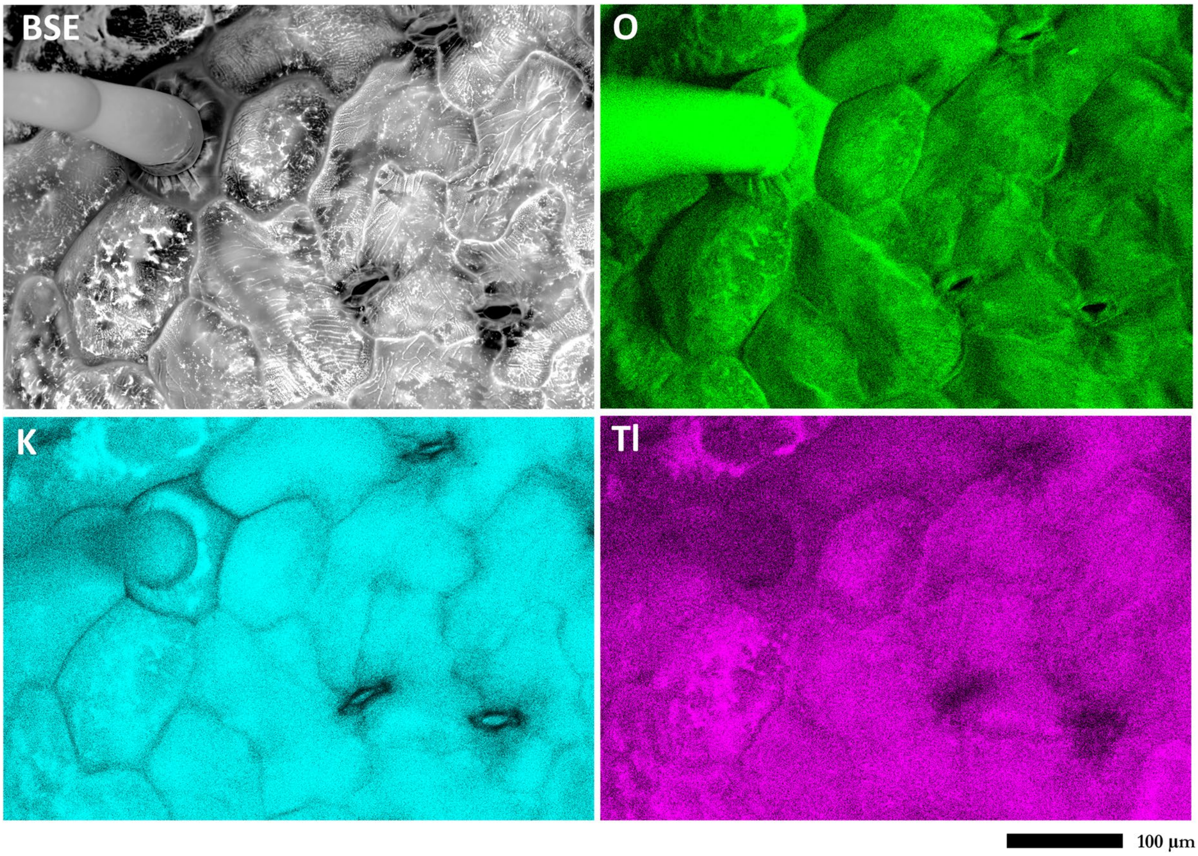

Fig. 6 Scanning electron microscopy—backscattered electron (SEM-BSE) coupled with energy dispersive X-ray spectroscopy (EDS) mapping of an old leaflet fraction of a freeze-dried *Silene latifolia* specimen, displaying BSE image, oxygen map, potassium map, and thallium map

latifolia possesses a strong capacity to accumulate Tl in its shoots, similar to *B. laevigata*, which implies that it has evolved ecophysiological mechanisms enabling it to survive in Tl-polluted environments. However, it is notable that the foliar Tl distribution in *S. latifolia* is different from that of *B. laevigata*. Further detailed analysis using synchrotron X-ray fluorescence microscopy is required to elucidate the (sub) cellular distribution of Tl in these two species, which could then provide more insights into the mechanisms underlying their Tl tolerance and hyperaccumulation. From both the ecophysiological and phytoextraction perspective, more research is required to evaluate the responses of *S. latifolia* to Tl-enriched substrates at the population level. As *S. latifolia* has been introduced to regions other than its native habitats in Europe and Western Asia (Mikhaylova et al. 2021), phytoextraction applications deserve full assessment of the (ecological) implications of any introduction into non-native areas. Considering the chemical similarity of Tl and K, and the relatively high Tl bioconcentration factors compared to other metals, it is very likely that there are other Tl (hyper)accumulators yet to be discovered. It would surely be worthwhile to search for more Tl hyperaccumulators in the field and by performinglarge-scale screening of herbarium collections using novel non-destructive methods based on portable X-ray fluorescence spectroscopy (pXRF) (Purwadi et al. 2021).

Acknowledgements A. Corzo Remigio is the recipient of a University of Queensland Research Training Scholarship, Australia. We kindly acknowledge Lachlan Casey (Centre for Microscopy and Microanalysis, The University of Queensland) for assistance with the laboratory-based µ-XRF analysis. We also thank the AMMRF at the Centre for Microscopy and Microanalysis at the University of Queensland for their support with the microanalysis. This work was supported by the French National Research Agency through the national program "Investissements d'avenir" (ANR-10-LABX-21 - RESSOURCES21).

Author contributions ACR, PNN and AVDE designed and conducted the experiment. ACR undertook the chemical analysis of the samples. ACR, PNN and AVDE performed data processing and analysis. AJMB, FP and ME provided critical insights to shape the research outcomes. All authors contributed to the writing of the manuscript.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions

Data availability The data generated during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no conflicts of interest relevant to the content of this article.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Abubakari F, Nkrumah PN, Fernando DR, Brown GK, Erskine PD, Echevarria G, van der Ent A (2021) Incidence of hyperaccumulation and tissue-level distribution of manganese, cobalt, and zinc in the genus *Gossia* (Myrtaceae). Metallomics 13 (4) https://doi.org/10.1093/mtomcs/mfab008

Agathokleous E, Kitao M, Calabrese EJ (2019) Hormesis: a compelling platform for sophisticated plant science. Trends Plant Sci 24(4):318–327. https://doi.org/10.1016/j.tplants.2019.01.004

Anderson CWN, Brooks RR, Chiarucci A, LaCoste CJ, Leblanc M, Robinson BH, Simcock R, Stewart RB (1999) Phytomining for nickel, thallium and gold. J Geochem Explor 67(1):407–415. https://doi.org/10.1016/S0375-6742(99)00055-2

Antoniadis V, Golia EE, Liu Y-T, Wang S-L, Shaheen SM, Rinklebe J (2019) Soil and maize contamination by trace elements and associated health risk assessment in the industrial area of Volos, Greece. Environ Int 124:79–88. https://doi.org/10.1016/j.envint.2018.12.053

Arnetoli M, Vooijs R, Gonnelli C, Gabbrielli R, Verkleij JAC, Schat H (2008) High-level Zn and Cd tolerance in *Silene paradoxa* L. from a moderately Cd- and Zn-contaminated copper mine tailing. Environ Pollut 156 (2):380–386 https://doi.org/10.1016/j.envpol.2008.01.044

Bačeva K, Stafilov T, Matevski V (2014) Bioaccumulation of heavy metals by endemic *Viola* species from the soil in the vicinity of the As-Sb-Tl Mine "Allchar", Republic of Macedonia. Int J Phytoremediation 16(4):347–365. https://doi.org/10.1080/15226514.2013.783551

Baker AJM (1981) Accumulators and excluders - strategies in the response of plants to heavy metals. J Plant Nutr 3(1–4):643–654. https://doi.org/10.1080/01904168109362867

Baker AJM, Brooks RR (1989) Terrestrial higher plants which hyperaccumulate metallic elements - a review of their distribution, ecology and phytochemistry. Biorecovery 1:81–126

Baker AJM, Brooks RR, Pease AJ, Malaisse F (1983) Studies on copper and cobalt tolerance in three closely related taxa within the genus *Silene* L. (Caryophyllaceae) from Zaïre. Plant Soil 73(3):377–385. https://doi.org/10.1007/BF02184314

Barluenga M, Austerlitz F, Elzinga JA, Teixeira S, Goudet J, Bernasconi G (2011) Fine-scale spatial genetic structure and gene dispersal in *Silene latifolia*. Heredity 106(1):13–24. https://doi.org/10.1038/hdy.2010.38

Blair AC, Wolfe LM (2004) The evolution of an invasive plant: an experimental study with *Silene latifolia*. Ecology 85(11):3035–3042. https://doi.org/10.1890/04-0341

Broadhurst LC, Tappero RV, Maugel TK, Erbe EF, Sparks DL, Chaney RL (2009) Interaction of nickel and manganese in accumulation and localization in leaves of the Ni hyperaccumulators *Alyssum murale* and *Alyssum corsicum*. Plant Soil 314(1):35–48. https://doi.org/10.1007/s11104-008-9703-4

Castillo DM, Kula AAR, Dötterl S, Dudash MR, Fenster CB (2014) Invasive *Silene latifolia* may benefit from a native pollinating seed predator, *Hadena ectypa*, in North America. Int J Plant Sci 175(1):80–91. https://doi.org/10.1086/673536

Ciarkowska K, Hanus-Fajerska E (2008) Remediation of soil-free grounds contaminated by zinc, lead and cadmium with the use of metallophytes. Pol J Environ Stud 17(5):707–712

Colzi I, Rocchi S, Rangoni M, Del Bubba M, Gonnelli C (2014) Specificity of metal tolerance and use of excluder metallophytes for the phytostabilization of metal polluted soils: the case of *Silene paradoxa* L. Environ Sci Pollut Res 21(18):10960–10969. https://doi.org/10.1007/s11356-014-3045-y

Corzo Remigio A, Chaney RL, Baker AJM, Edraki M, Erskine PD, Echevarria G, van der Ent A (2020) Phytoextraction of high value elements and contaminants from mining and mineral wastes: opportunities and limitations. Plant Soil 449(1):11–37. https://doi.org/10.1007/s11104-020-04487-3

Corzo Remigio A, Edraki M, Baker AJM, van der Ent A (2021) Is the aquatic macrophyte *Crassula*

helmsii a genuine copper hyperaccumulator? Plant Soil 464(1):359–374. https://doi.org/10.1007/s11104-021-04955-4
Corzo Remigio A, Pošćić F, Nkrumah PN, Edraki M, Spiers KM, Brueckner D, van der Ent A (2022) Comprehensive insights in thallium ecophysiology in the hyperaccumulator *Biscutella laevigata*. Sci Total Environ 383(155899):1–13. https://doi.org/10.1016/j.scitotenv.2022.155899
Dmowski K, Rossa M, Kowalska J, Krasnodębska-Ostręga B (2014) Thallium in spawn, juveniles, and adult common toads (*Bufo bufo*) living in the vicinity of a zinc-mining complex, Poland. Environ Monit Assess 187(1):4141. https://doi.org/10.1007/s10661-014-4141-7
Duri LG, Visconti D, Fiorentino N, Adamo P, Fagnano M, Caporale AG (2020) Health risk assessment in agricultural soil potentially contaminated by geogenic thallium: influence of plant species on metal mobility in soil-plant system. Agronomy 10(6):890. https://doi.org/10.3390/agronomy10060890
Ernst WHO, Nelissen HJM (2000) Life-cycle phases of a zinc- and cadmium-resistant ecotype of *Silene vulgaris* in risk assessment of polymetallic mine soils. Environ Pollut 107(3):329–338. https://doi.org/10.1016/S0269-7491(99)00174-8
Escarré J, Lefèbvre C, Raboyeau S, Dossantos A, Gruber W, Cleyet Marel JC, Frérot H, Noret N, Mahieu S, Collin C, van Oort F (2011) Heavy metal concentration survey in soils and plants of the Les Malines Mining District (southern France): implications for soil restoration. Water Air Soil Pollut 216(1):485–504. https://doi.org/10.1007/s11270-010-0547-1
Fellet G, Pošćić F, Casolo V, Marchiol L (2012) Metallophytes and thallium hyperaccumulation at the former Raibl lead/zinc mining site (Julian Alps, Italy). Plant Biosyst 146(4):1023–1036. https://doi.org/10.1080/11263504.2012.703250
Holubík O, Vaněk A, Mihaljevic M, Vejvodová K (2021) Thallium uptake/tolerance in a model (hyper)accumulating plant: effect of extreme contaminant loads. Soil Water Res 16(2):129–135. https://doi.org/10.17221/167/2020-SWR
Hopewell T, Selvi F, Ensikat H-J, Weigend M (2021) Trichome biomineralization and soil chemistry in Brassicaceae from Mediterranean ultramafic and calcareous soils. Plants 10(2):377. https://doi.org/10.3390/plants10020377
Jalal A, Oliveira Junior JCd, Ribeiro JS, Fernandes GC, Mariano GG, Trindade VDR, Reis ARd (2021) Hormesis in plants: physiological and biochemical responses. Ecotoxicol Environ Saf 207:111225. https://doi.org/10.1016/j.ecoenv.2020.111225
A Kabata-Pendias AB Mukherjee 2007 Trace elements from soil to human Springer Berlin, Heidelberg https://doi.org/10.1007/978-3-540-32714-1_20
Karbowska B (2016) Presence of thallium in the environment: sources of contaminations, distribution and monitoring methods. Environ Monit Assess 188(11):640. https://doi.org/10.1007/s10661-016-5647-y
Keith L, Telliard W (1979) ES&T special report: priority pollutants: I - a perspective view. Environ Sci Technol 13(4):416–423. https://doi.org/10.1021/es60152a601
LaCoste C, Robinson B, Brooks R, Anderson C, Chiarucci A, Leblanc M (1999) The phytoremediation potential of thallium-contaminated soils using *Iberis* and *Biscutella* species. Int J Phytoremediation 1(4):327–338. https://doi.org/10.1080/15226519908500023
Leblanc M, Petit D, Deram A, Robinson BH, Brooks RR (1999) The phytomining and environmental significance of hyperaccumulation of thallium by *Iberis intermedia* from southern France. Econ Geol 94(1):109–113. https://doi.org/10.2113/gsecongeo.94.1.109
Leitenmaier B, Küpper H (2013) Compartmentation and complexation of metals in hyperaccumulator plants. Front Plant Sci 4(374). https://doi.org/10.3389/fpls.2013.00374
Lennartson A (2015) Toxic thallium. Nat Chem 7(7):610–610. https://doi.org/10.1038/nchem.2286
Lis J, Pasieczna A, Karbowska B, Zembrzuski W, Lukaszewski Z (2003) Thallium in soils and stream sediments of a Zn−Pb mining and smelting area. Environ Sci Technol 37(20):4569–4572. https://doi.org/10.1021/es0346936
Liu J, Yin M, Xiao T, Zhang C, Tsang DCW, Za B, Zhou Y, Chen Y, Luo X, Yuan W, Wang J (2020) Thallium isotopic fractionation in industrial process of pyrite smelting and environmental implications. J Hazard Mater 384:121378. https://doi.org/10.1016/j.jhazmat.2019.121378
Lorestani B, Cheraghi M, Yousefi N (2012) The potential of phytoremediation using hyperaccumulator plants: a case study at a lead-zinc mine site. Int J Phytoremediation 14(8):786–795. https://doi.org/10.1080/15226514.2011.619594
Ma C, Cheng H, Huang R, Zou Y, He Q, Huangfu X, Ma J (2022) Kinetics of thallium(I) oxidation by free chlorine in bromide-containing waters: insights into the reactivity with bromine species. Environ Sci Technol 56(2):1017–1027. https://doi.org/10.1021/acs.est.1c06901
Malaisse F, Colonval-Elenkov E, Brooks RR (1983) The impact of copper and cobalt orebodies upon the evolution of some plant species from Upper Shaba, Zaïre. Plant Syst Evol 142(3):207–221. https://doi.org/10.1007/BF00985899
McNear DH, Küpper JV (2014) Mechanisms of trichome-specific Mn accumulation and toxicity in the Ni hyperaccumulator *Alyssum murale*. Plant Soil 377(1):407–422. https://doi.org/10.1007/s11104-013-2003-7
Mikhaylova YV, Gordon M, Maslova AR, Polev DE, Punina EO, Rodionov AV (2021) Chloroplast genome of native *Silene latifolia* subsp. *alba* from Fennoscandia shows high level of differences from invasive white campion. Plant Mol Biol Rep 39(1):226–239 https://doi.org/10.1007/s11105-020-01246-7
Moeschlin S (1980) Thallium poisoning. Clin Toxicol 17(1):133–146. https://doi.org/10.3109/15563658008985073
Mullins LJ, Moore RD (1960) The movement of thallium ions in muscle. J Gen Physiol 43(4):759–773. https://doi.org/10.1085/jgp.43.4.759
Nkrumah PN, Tisserand R, Chaney RL, Baker AJM, Morel JL, Goudon R, Erskine PD, Echevarria G, van der Ent A (2019) The first tropical 'metal farm': Some perspectives from field and pot experiments. J Geochem Explor 198:114–122. https://doi.org/10.1016/j.gexplo.2018.12.003
Pradas-del-Real AE, García-Gonzalo P, Alarcón R, González-Rodríguez Á, Lobo MC, Pérez-Sanz A (2013) Effect of genotype, Cr(III) and Cr(VI) on plant growth and

micronutrient status in *Silene vulgaris* (Moench). Span J Agric Res 11(3):685–694. https://doi.org/10.5424/sjar/2013113-3536

Purwadi I, Gei V, Echevarria G, Erskine PD, Mesjasz-Przybyłowicz J, Przybyłowicz WJ, van der Ent A (2021) Tools for the discovery of hyperaccumulator plant species in the field and in the herbarium. In: van der Ent A, Baker AJM, Echevarria G, Simonnot M-O, Morel JL (eds) Agromining: farming for metals: extracting unconventional resources using plants. Springer International Publishing, Cham, pp 183–195. https://doi.org/10.1007/978-3-030-58904-2_9

Rader ST, Maier RM, Barton MD, Mazdab FK (2019) Uptake and fractionation of thallium by *Brassica juncea* in a geogenic thallium-amended substrate. Environ Sci Technol 53(5):2441–2449. https://doi.org/10.1021/acs.est.8b06222

Reeves RD, Baker AJM, Jaffré T, Erskine PD, Echevarria G, van der Ent A (2018) A global database for plants that hyperaccumulate metal and metalloid trace elements. New Phytol 218(2):407–411. https://doi.org/10.1111/nph.14907

Robinson B, Anderson C (2018) Element case studies: thallium and noble metals. In: van der Ent A, Echevarria G, Baker AJM, Morel JL (eds) Agromining: farming for metals: extracting unconventional resources using plants. Springer International Publishing, Cham, pp 253–261. https://doi.org/10.1007/978-3-319-61899-9_15

Salinitro M, Mattarello G, Guardigli G, Odajiu M, Tassoni A (2021) Induction of hormesis in plants by urban trace metal pollution. Sci Rep 11(1):20329. https://doi.org/10.1038/s41598-021-99657-3

Schat H, Van Nathalie ALMH, Tervahauta A, Hakvoort HWJ, Chardonnens AN, Koevoets PLM, Verkleij JAC, Ernst WHO (2000) Evolutionary responses to zinc and copper stress in bladder campion, *Silene Vulgaris* (Moench.) Garcke. In: Cherry JH, Locy RD, Rychter A (eds) Plant tolerance to abiotic stresses in agriculture: role of genetic engineering. Springer Netherlands, Dordrecht, pp 343–360. https://doi.org/10.1007/978-94-011-4323-3_24

Scheckel KG, Lombi E, Rock SA, McLaughlin MJ (2004) In vivo synchrotron study of thallium speciation and compartmentation in *Iberis intermedia*. Environ Sci Technol 38(19):5095–5100. https://doi.org/10.1021/es049569g

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9(7):671–675. https://doi.org/10.1038/nmeth.2089

Siegele R, Kachenko AG, Wang YD, Ionescu M, Bhatia NP, Cohen DD (2007) Localisation of trace metals in hyperaccumulating plants using µ-PIXE. Paper presented at the 15th Australian Conference on Nuclear and Complementary Techniques of Analysis and 9th Vacuum Society of Australia Congress, Melbourne, Australia

Song J, Zhao F-J, Luo Y-M, McGrath SP, Zhang H (2004) Copper uptake by *Elsholtzia splendens* and *Silene vulgaris* and assessment of copper phytoavailability in contaminated soils. Environ Pollut 128(3):307–315. https://doi.org/10.1016/j.envpol.2003.09.019

Tremel A, Masson P, Sterckeman T, Baize D, Mench M (1997) Thallium in French agrosystems—I. Thallium contents in arable soils. Environ Pollut 95(3):293–302. https://doi.org/10.1016/S0269-7491(96)00145-5

U.S. Geological Survey (2020) Mineral commodity summaries 2020. U.S. Geological Survey, Reston, Virginia https://doi.org/10.3133/mcs2020

van der Ent A, Baker AJM, Reeves RD, Chaney RL, Anderson CWN, Meech JA, Erskine PD, Simonnot M-O, Vaughan J, Morel JL, Echevarria G, Fogliani B, Qiu R, Mulligan DR (2015) Agromining: farming for metals in the future? Environ Sci Technol 49(8):4773–4780. https://doi.org/10.1021/es506031u

van der Ent A, Baker AJM, Reeves RD, Pollard AJ, Schat H (2013) Hyperaccumulators of metal and metalloid trace elements: facts and fiction. Plant Soil 362(1):319–334. https://doi.org/10.1007/s11104-012-1287-3

van der Zee L, Corzo Remigio A, Casey LW, Purwadi I, Yamjabok J, van der Ent A, Kootstra G, Aarts MGM (2021) Quantification of spatial metal accumulation patterns in *Noccaea caerulescens* by X-ray fluorescence image processing for genetic studies. Plant Methods 17(1):86. https://doi.org/10.1186/s13007-021-00784-9

Verkleij JAC, Van Hoof NALM, Chardonnens AN, Koevoets PLM, Hakvoort H, ten Bookum WM, Schat H, Ernst WHO (2001) Mechanisms of heavy metal resistance in *Silene vulgaris*. In: Horst WJ, Schenk MK, Bürkert A et al. (eds) Plant nutrition: food security and sustainability of agro-ecosystems through basic and applied research. Springer Netherlands, Dordrecht, pp 446–447. https://doi.org/10.1007/0-306-47624-x_215

Viraraghavan T, Srinivasan A (2011) Thallium: environmental pollution and health effects. In: Nriagu J (ed) Encyclopedia of environmental health. Second edn. Elsevier, Oxford, pp 39–47. https://doi.org/10.1016/B978-0-444-63951-6.00643-4

Visconti D, Fiorentino N, Stinca A, Di Mola I, Fagnano M (2018) Use of the native vascular flora for risk assessment and management of an industrial contaminated soil. Ital J Agron 13(s1):23–33. https://doi.org/10.4081/ija.2018.1348

Voegelin A, Pfenninger N, Petrikis J, Majzlan J, Plötze M, Senn A-C, Mangold S, Steininger R, Göttlicher J (2015) Thallium speciation and extractability in a thallium- and arsenic-rich soil developed from mineralized carbonate rock. Environ Sci Technol 49(9):5390–5398. https://doi.org/10.1021/acs.est.5b00629

Wang J, Wang L, Wang Y, Tsang DCW, Yang X, Beiyuan J, Yin M, Xiao T, Jiang Y, Lin W, Zhou Y, Liu J, Wang L, Zhao M (2021) Emerging risks of toxic metal(loid)s in soil-vegetables influenced by steel-making activities and isotopic source apportionment. Environ Int 146:106207. https://doi.org/10.1016/j.envint.2020.106207

Werker E (2000) Trichome diversity and development. Adv Bot Res 31:1–35. https://doi.org/10.1016/S0065-2296(00)31005-9

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.