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Review Paper

Hyperaccumulator plant discoveries in the Balkans: accumulation, distribution, and practical applications

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ABSTRACT:
Hyperaccumulator plants are able to tolerate extremely high concentrations of metals/metalloids in the soil in which they grow and to accumulate high concentrations in their shoots. To date, a total of 31 hyperaccumulator plant species have been identified in the Balkans, the centre of diversity and speciation in the European flora which is particularly rich in ultramafic areas. A further 8 species have yet to be confirmed through additional studies. Most of the 31 hyperaccumulator taxa (13 taxa or 41.9%) are species of the genus *Odontarrhena*, all hyperaccumulating Ni, but concentrations of this element above the hyperaccumulation threshold were also found in the genera *Bornmuellera* and *Noccaea* (all Brassicaceae), *Orobanche* (Orobanchaceae), *Centaurea* (Asteraceae) and *Viola* (Violaceae). The existence of hyperaccumulators of Tl and Zn is of particular interest because very few species worldwide hyperaccumulate these elements. Multiple metal hyperaccumulation was found in *Noccaea kovatsii*, as the hyperaccumulation of Zn was found in this species in addition to Ni, the primary accumulated element. Metal hyperaccumulation is discussed in terms of phylogenetic relationships and species distributions, with special attention to their systematics, the detection and recognition of new hyperaccumulating species and the possibilities for their future practical applications in phytotechnologies.

Keywords:
hypertolerance, metallophyte, flora, ultramafics, nickel, thallium

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INTRODUCTION

Essential and non-essential trace elements are inseparable components of nature found in varying concentrations in all its parts. However, at elevated concentrations, these elements can be toxic to organisms and more generally, the environment. According to their origin, trace metals and metalloids can be divided into those from natural and anthropogenic sources. Whereas anthropogenic sources are numerous and highly diverse (industrial activities such as mining and smelting, fuel combustion, transportation, agriculture through fertilizers, pesticides, sewage sludge and livestock manure, etc.), natural sources are primarily of geological origin whereby metals and metalloids are released as products of the weathering process, i.e. the decomposition of minerals (Alloway 2013). Not all types of parental rock contribute equally to increasing the concentrations of trace metals in soil. Of particular importance in this regard are ultramafics, the type of ferromagnesian rocks which are also rich in Ni, Cr, Mn and Co (Bani *et al.* 2014; Echevarria 2021). Soils formed on ultramafic bedrock share similar unique chemical characteristics, e.g. elevated concentrations of certain trace metals, but also an unfavourable Ca/Mg quotient and low nutrient status. In addition, because ultramafic soils are typically dry and skeletal (at least in the Mediterranean region), they can provide a physically stressful environment for plants, thus harbouring a very specific and specially adapted flora. The combined effect of these factors is referred to as the 'serpentine syndrome' (Kazakou *et al.* 2010), and the visible plant responses to it include morphological adaptations such as nanism, plagiotropism, glaucescence, and purpurescence, etc. (Kruckeberg & Kruckeberg 1989).

Plants adapted to a substrate rich in metals and/or metalloids, on which they can grow and reproduce without showing significant toxicity symptoms, are called metallophytes and may be obligate or facultative, depending on whether they also occur on metal-poor substrates (Pollard *et al.* 2014; Lange *et al.* 2017). Depending on the strategy used to tolerate excess trace elements in the substrate, they can be classified as excluders, indicators or accumulators (Baker 1981). At the most extreme end of accumulators are hyperaccumulators which are species able to accumulate certain potentially toxic elements in their leaves under field conditions at concentrations above a nominal threshold, without showing symptoms of toxicity (or without significant effects on plant reproduction and survival). Hyperaccumulation thresholds are specific for each element and are usually determined as values 10–1000 fold higher than the mean foliar concentration in plants growing in non-metalliferous soil (van der Ent *et al.* 2015a). Earlier proposed thresholds (Baker & Brooks 1989) have been subsequently modified as follows: 100 mg kg^{-1} for Se, Tl, and Cd; 300 mg kg^{-1} for Co, Cr, and Cu; 1000 mg kg^{-1} for Pb, Ni, and As; 3000 mg kg^{-1} for Zn; and 10,000 mg kg^{-1} for Mn (van der Ent *et al.* 2013; Reeves *et al.* 2018). However, the nominal threshold criteria should be applied with caution, and other factors in addition to absolute concentrations of metals in above-ground plant parts may also be considered. A bioconcentration factor (BF) >1 (but often >50) and a shoot-to-root translocation factor (TF) >1 are indicative, taken together with demonstrable hypertolerance to concentrations of trace metals which are toxic to most plants (Baker & Whiting 2002; van der Ent *et al.* 2013, 2015a).

There are several hypotheses regarding the evolution of hyperaccumulation in plants (Boyd & Martens 1992). The accumulated metals may serve as protection against herbivory or phytopatogenes and depends not only on the type of element hyperaccumulated, its concentration and chemical form, but also on the sensitivity of the target organism (Cappa & Pilon-Smits 2014). Moreover, some elements act independently, whilst for others the effect is manifested only when they act together (joint effect hypothesis) (Boyd 2012). In some species, hyperaccumulation has been shown to be beneficial for drought resistance, and some species may accumulate for the purpose of metal deposition (Boyd 2007; Cappa & Pilon-Smits 2014). Hyperaccumulation of metals may also be merely fortuitous, i.e. the result of inadvertent uptake of trace metals chemically similar to essential elements (Cappa & Pilon-Smits 2014). Tolerances to high metal concentrations in the substrate can develop at different rates. The colonisation of metalliferous substrates is usually a long-term process, taking thousands (or even millions) of years and leading to the development of a specific flora rich in endemic taxa, but can also be very rapid, even within one generation under extreme habitat conditions (Baker 1981).

In most species, the hyperaccumulation of metals/metalloids is found in plants from metalliferous habitats where the habitat conditions exert selection pressures resulting in such a phenomenon (Baker *et al.* 2010). However, in a number of species, hyperaccumulation can be considered to be a constitutive trait found in populations from both metalliferous and non-metalliferous habitats. Examples include Zn hyperaccumulation in *Noccaea caerulescens* which can accumulate Zn at concentrations of 8890 mg kg^{-1} on soils containing only 139 mg kg^{-1} of this element (Reeves *et al.* 2001a) and *Arabidopsis halleri* (Manara *et al.* 2020) with a foliar concentration of Zn from non-metalliferous soils reaching a value of 53,900 mg kg^{-1} (Stein *et al.* 2017).

To date, the ability to hyperaccumulate one or, much more rarely, multiple elements has been confirmed in 721 taxa from 130 genera and 52 families (Reeves *et al.* 2018). The largest number of hyperaccumulator species was found in the families Brassicaceae (104 taxa; Reeves *et al.* 2018), especially in the genera *Noccaea* (formerly *Thlaspi*) and *Odontarrhena* (formerly *Alyssum*), with the predominant hyperaccumulation of Ni and Zn (Drozdova *et al.* 2019). Nickel is the element most frequently accumulated at concentrations above the nominal threshold. Its hyperaccumulation has been detected in 532 taxa from more than 40 families (Reeves *et al.* 2018; Purwadi *et al.* 2021). With respect to the distribution of Ni hyperaccumulators, two basic groups can be distinguished: one main group comprising taxa with tropical and subtropical distribution (predominantly New Caledonia, Cuba, and Indonesia, etc.), and the other with a distribution in the Mediterranean and Eurasian regions (extending from Portugal eastward across the Apennines and the Balkan Peninsula to Turkey) (Reeves *et al.* 2021), indicating the multiple, independent evolution of hyperaccumulation of this element (Cappa & Pilon-Smits 2014).

Where ultramafic rocks are the main natural source of Ni, it is the element that most frequently accumulates above the hyperaccumulation threshold. However, ultramafic rocks occupy only 3% of the Earth's surface (Guillot & Hattori 2013), with the largest areas located in New Caledonia, Cuba, Malaysia, Indonesia, Turkey and Iran (van der Ent 2015b). In Europe, the largest are located on the Balkan Peninsula, extending more or less continuously from Western Bosnia through W, C, and SW Serbia to Albania, in North Macedonia and Greece to the south, with smaller isolated areas in Bulgaria and the European part of Turkey (Stevanović *et al.* 2003). The high proportion of ultramafic areas contributes to the great diversity of metallophytes found on the Balkan Peninsula, an important centre of diversity and speciation in the European flora (Španiel *et al.* 2017). It has led to the emergence of a large number of edaphic endemics, species associated with a particular type of geological substrate, in this case ultramafics. Endemic metallophytes can be paleoendemics or neoendemics. Paleoendemics were once widespread species which are now restricted to metalliferous habitats due to environmental pressures. Neoendemics, on the other hand, have evolved in metalliferous habitats and developed traits which now distinguish them from their relatives (Baker 1981, 1987; Reeves *et al.* 2021).

The peculiarities of the Balkan Peninsula have made it a centre of speciation and richness of European flora, and due to its geological features, especially the abundance of ultramafics, a considerable richness of hyperaccumulator taxa can be expected in this area. Therefore, this review provides an overview of the hyperaccumulator plant species in the Balkans, but also guidelines for future research on this particular group of plants.

HYPERACCUMULATORS ON THE BALKAN PENINSULA

Previous studies as well as unpublished data indicate that the phenomenon of hyperaccumulation occurs in at least 31 taxa from the Balkan Peninsula (Table 1), whilst a further 8 can be considered as possible hyperaccumulators and their status remains to be confirmed. The largest number (24 taxa; 77.4%) belong to the Brassicaceae family, which is known to be particularly rich in hyperaccumulator species (Reeves *et al.* 2018). A total of 23.1% of hyperaccumulators from the Brassicaceae family have been found in the study area. Hyperaccumulation has also been detected in three members of the family Violaceae, as well as two taxa from the family Orobanchaceae, and one each from the families Asteraceae and Caryophyllaceae.

Nickel hyperaccumulators

On the Balkan Peninsula, hyperaccumulation of this element has been recorded in 27 taxa (87.1%), whose distribution is primarily related to an ultramafic geological substrate, one of the most important natural sources of this element. A comprehensive account of early studies of the flora of the ultramafics of the Balkan Peninsula was provided by Brooks (1987). Further discussion of the history of the botanical studies and ecological aspects of the Balkan ultramafic flora, and a list of obligate Balkan serpentinophytes, were presented by Tatić & Veljović (1992). Extreme Ni accumulation was first found in several species of *Alyssum* sect. *Odontarrhena* (now the genus *Odontarrhena*) in *O. bertolonii* in Italy (Minguzzi & Vergnano 1948), *O. muralis* in Armenia (Doksopulo 1961) and *O. serpyllifolia* in Portugal (Menezes de Sequeira 1969). Although the extensive studies of Bosnian ultramafic flora carried out by Ritter-Studnička included some analyses of plants for Fe, Ni and Cr (Ritter-Studnička & Dursun-Grom 1973), it was not until the research carried out by Brooks & Radford (1978), analysing fragments of herbarium specimens, that Ni hyperaccumulation by the species of the Balkan Peninsula was established. This survey of all 64 European species of *Alyssum* listed in *Flora Europaea* found 11 Ni hyperaccumulator species (all from sect. *Odontarrhena*) and confirmed this behaviour in the three species reported earlier. Of the 11 species, eight were from the region covering the former Yugoslavia, Albania, and Greece (including the Greek islands of Crete, Tinos and Euboea). The worldwide survey of nearly all 170 *Alyssum* species known at that time (Brooks *et al.* 1979) increased the total to 45 including many species from Turkey, four species from Cyprus and *A. lesbiacum* (*O. lesbiaca*) from the Greek island of Lesbos.

Odontarrhena species

The largest number of a total of 27 taxa which hyperaccumulate Ni on the Balkan Peninsula belong to the Brassicaceae family (24 taxa), mainly to *Odontarrhena*, a taxonomically very complex genus with the largest number of representatives in the temperate regions of Eurasia

Table 1. List of hyperaccumulator plant species on the Balkan Peninsula with maximum detected concentrations in the plant tissues

	Taxon	Element	Shoot	Reference	Leaves	Reference
Brassicaceae	*Bornmuellera baldaccii* (Degen) Heywood	Ni	12,170	1	27,300	2
Brassicaceae	*Bornmuellera dieckii* Degen	Ni	9713	3	24,290	3
Brassicaceae	*Bornmuellera emarginata* (Boiss.) Rešetnik	Ni	9109	4	34,890	4
Brassicaceae	*Bornmuellera tymphaea* (Hausskn.) Hausskn.	Ni	7100	5	31,200	2
Brassicaceae	*Noccaea boeotica* F.K. Mey.	Ni			23,400	6
Brassicaceae	*Noccaea epirota* (Halácsy) F.K. Mey.	Ni			2930	6
Brassicaceae	*Noccaea graeca* (Jord.) F.K. Mey.	Ni			4450	6
Brassicaceae	*Noccaea kovatsii* (Heuff.) F.K. Mey.	Ni	21,500	7	21,550	7
Brassicaceae	*Noccaea kovatsii* (Heuff.) F.K. Mey.	Zn	4920	8		
Brassicaceae	*Noccaea ochroleuca* (Boiss. & Heldr.) F.K. Mey.	Ni	13,000	9	23,400	7
Brassicaceae	*Noccaea praecox* (Wulfen) F.K. Mey.	Ni	11,100	8	21,530	10
Brassicaceae	*Noccaea tymphaea* (Hausskn.) F.K. Mey.	Ni	6652	4	16,540	6
Brassicaceae	*Odontarrhena baldaccii* (Vierh. ex Nyár.) Španiel	Ni	13,150	11	17,670	12
Brassicaceae	*Odontarrhena chalcidica* (Janka) Španiel & al.	Ni	19,300	13	24,000	14
Brassicaceae	*Odontarrhena decipiens* (Nyár.) L.Cecchi & Selvi	Ni	14,600	13	17,300	15
Brassicaceae	*Odontarrhena diffusa* Jord. & Fourr.	Ni			9350	12
Brassicaceae	*Odontarrhena euboea* (Halácsy) Španiel & al.	Ni	3876	4	15,410	4
Brassicaceae	*Odontarrhena heldreichii* (Hausskn.) Španiel & al.	Ni	6650	11	32,040	16
Brassicaceae	*Odontarrhena lesbiaca* P. Candargy	Ni	6898	17	23,650	18
Brassicaceae	*Odontarrhena moravensis* (F.K.Mey.) L.Cecchi & Selvi	Ni			16,390	19
Brassicaceae	*Odontarrhena muralis* (Waldst. & Kit.) Endl.	Ni	7564	20	34,690	16
Brassicaceae	*Odontarrhena rigida* (Nyár.) L. Cecchi & Selvi	Ni	17,000	13	17,100	15
Brassicaceae	*Odontarrhena serpentinicola* (F.K. Mey.) Španiel & al.	Ni	14,500	13	14,000	15
Brassicaceae	*Odontarrhena smolikana* (Nyár.) Španiel & al.	Ni	2780	4	13,540	4
Brassicaceae	*Odontarrhena stridii* L.Cecchi, Španiel & Selvi	Ni	16,380	11		
Orobanchaceae	*Orobanche nana* Noë ex Rchb.	Ni	1737	21		
Orobanchaceae	*Orobanche nowackiana* Markgr.	Ni	1335	21		
Asteraceae	*Centaurea thracica (Janka) Gugler*	Ni	2156	4	11,410	4
Caryophyllaceae	*Minuartia recurva* (All.) Schinz & Thell.	Cu	1960	22		
Violaceae	*Viola allchariensis* Beck	Tl			4013	23
Violaceae	*Viola arsenica* Beck	Tl			10,400	23
Violaceae	*Viola tricolor* subsp. *macedonica* (Boiss. & Heldr.) A. F. W. Schmidt	Tl			4292	23

References: 1. Bani *et al.* 2013; 2. Reeves *et al.* 1983; 3. Paçarizi *et al.* 2020; 4. Konstantinou & Kyrkas, unpublished data; 5. Zhang *et al.* 2014; 6. Reeves & Brooks 1983; 7. Bani *et al.* 2010; 8. Mišljenović *et al.* 2020; 9. Lopez *et al.* 2019; 10. Dimitrakopoulos & Reeves, unpublished data; 11. Cecchi *et al.* 2020; 12. Reeves *et al.* 1997; 13. Bettarini *et al.* 2019; 14. Bani *et al.* 2015a; 15. Cecchi *et al.* 2018; 16. Reeves, unpublished data; 17. Adamidis *et al.* 2017; 18. Kazakou *et al.* 2010; 19. Bani & Echevarria, unpublished data; 20. Salihaj *et al.* 2018; 21. Dimitrakopoulos *et al.* 2021; 22. Jakovljević *et al.* 2022; 23. Bačeva *et al.* 2014.

(POWO 2022). A total of 13 representatives of this genus were found to have concentrations in their aerial parts exceeding the nominal threshold for hyperaccumulation of 1000 mg kg^{-1} (van der Ent *et al.* 2013).

Odontarrhena muralis (Waldst. & Kit.) Endl. is the most widespread species of this genus among the hyperaccumulators of the Balkan Peninsula. It occurs throughout almost the entire region, except in the western parts, as well as in Bulgaria, Turkey, and Armenia (POWO 2022). It is found predominantly, but not exclusively, on ultramafic soils, and in some regions acts as a reliable indicator of ultramafics. The ability to hyperaccumulate Ni has been confirmed in a large number of samples, both in the shoots and in separate individual above-ground plant tissues such as the leaves, seeds, and flowers, etc. (Table 1). However, the concentrations found vary widely, confirming that Ni concentration in plant tissues depends not only on plant characteristics, but also on Ni in the soil and the environmental conditions (climate, altitude, soil properties, pH) at different sites. A comparison of the Ni concentrations in the shoots as a whole and in specific above-ground plant parts such as the leaves, flowers, seeds, etc. (if these concentrations are available for the same sample) shows that the highest concentrations are found in the leaves, indicating that they are the main site of deposition. *Odontarrhena muralis* can be considered as a hypernickelophore, in the sense used by Jaffré *et al.* (2013), having been found in many cases with >1 wt% Ni in its dry matter. It has been found with 21,300 mg kg^{-1} Ni near Osmaniye, Turkey (Reeves & Adigüzel 2008), and with >1 wt% in many places in Greece and other parts of the Balkans: 19,240 and 10,320 mg kg^{-1} at Valia Kalda and Voras, respectively, in Greece (Babalonas 1984; Konstantinou & Kyrkas, unpublished data); 15,100 mg kg^{-1} from Kazak, Bulgaria (Bani *et al.* 2010), and 13,160 mg kg^{-1} from Mt. Maljen in Serbia (Tumi *et al.* 2012). A collection of 13 samples from Prrenjas, Albania, exhibited a mean Ni concentration of 18,520 mg kg^{-1}, and ranged from 9650 to 34,690 mg kg^{-1} (Reeves, unpublished data). It is interesting to note that even in a limestone sample, the Ni concentration in the leaves of *O. muralis* can reach 5145 mg kg^{-1}, with 2056 mg kg^{-1} Ni in the shoot and only 10 mg kg^{-1} available Ni in the soil, indicating the constitutive ability of a species to absorb Ni regardless of its content in the substrate (Konstantinou & Kyrkas, unpublished data). This behaviour is not invariable, however, and some specimens from ultramafics in Greece and Turkey contained only 500–1000 mg kg^{-1} Ni, whereas others from non-ultramafic substrates contained <200 mg kg^{-1} Ni (Reeves, unpublished data). In Kosovo, the highest Ni concentrations in shoots (>7000 mg kg^{-1}) were found in samples from Mušutište, Goleš and Kišna Reka, with most samples having values >1000 mg kg^{-1} (Salihaj *et al.* 2018). Analyses of Ni concentrations in fruits and seeds have shown that in general, significantly higher concentrations can be found in these plant organs than in the shoots, albeit lower than in the leaves. For example, concentrations of up to 11,520 mg kg^{-1} Ni were found in these parts of *O. muralis* from Trigona in Greece, whereas 2337–7787 mg kg^{-1} were measured in other samples of this species (Konstantinou & Kyrkas, unpublished data). Concentrations in the roots are much lower, although they very often exceed 1000 mg kg^{-1}, which has been established as the hyperaccumulation threshold for above-ground material.

Since the range of this species on the Balkan Peninsula overlaps with that of *O. chalcidica* which was only occasionally recognised as a separate species (treated usually as an *O. muralis* subspecies) and since according to Bettarini *et al.* (2021), *O. muralis* occurs mainly in non-ultramafic sites and is often confused with *O. chalcidica* in ultramafic areas, some of these data should be taken with a degree of caution. Indeed, Bianchi *et al.* (2022) point out that most populations of *O. muralis* are not hyperaccumulators and that hyperaccumulators are not so common and are mainly associated with ultramafics, which is consistent with some of our results (Reeves, unpublished data). However, at the same time, the hyperaccumulation of this species in the Balkans has been confirmed by numerous authors and *O. muralis* is considered a fairly reliable ultramafic indicator plant in regional areas (Bani *et al.* 2010; Salihaj *et al.* 2016, 2018; Cecchi *et al.* 2018; Konstantinou & Kyrkas, unpublished data). It is almost impossible to determine with certainty to what the literature data refers, as well as to revise all the herbarium material, now that *O. chalcidica* has attained the status of a valid species. New findings (such as 2n = 16 in *O. muralis* and 2n = 32 in *O. chalcidica*, or differences in morphology; Cecchi *et al.* 2018) may help us to identify the plant material more precisely in the future and thus eventually extrapolate the known data and gradually remove doubts about the previously published concentrations. Being one of the most taxonomically complex species of the genus *Odontarrhena*, many species are synonymous with *O. muralis* (e.g. Euro+Med 2006–; BrassiBase 2022; POWO 2022). For example, *Alyssum decipiens* is considered synonymous with *O. muralis* according to the BrassiBase (BrassiBase 2022) and Euro+Med (2006–) checklists, although it is accepted under the name *O. decipiens* (Nyár.) L.Cecchi & Selvi according to more recent data (Cecchi *et al.* 2018; POWO 2022). In the leaf samples of this hypernickelophore from Albania, Ni was detected at concentrations up to 17,300 mg kg^{-1}, with a minimum of 7900 mg kg^{-1} (Cecchi *et al.* 2018).

The native range of *O. chalcidica* (Janka) Španiel & al. includes the Balkan Peninsula and the Asian part of Turkey (POWO 2022). The analyses of a large number of samples have shown that Ni concentrations in the leaves and stems vary considerably, reaching very high values in some samples. Indeed, Ni concentrations in the leaves were found to range from 1000 to 24,000 mg kg^{-1} (Bani *et al.* 2010, 2015a; Bani & Echevarria, unpublished data), whereas in the stems they varied from 3000 to 19,300 mg kg^{-1} (Bani *et al.* 2013; Konstantinou & Tsiripidis 2015; Bettarini *et al.* 2019). Bianchi *et al.* (2022) confirmed that this species regularly accumulates exceptional Ni concentrations when growing on ultramafic substrates, both under experimental and natural conditions. High Ni concentrations in above-ground tissues were found even in non-ultramafic areas, indicating the strong potential of the species for Ni uptake. Similar to other samples, Ca and Mg concentrations in plants and soils indicate typical characteristics of those from ultramafics and associated flora, with a Ca/Mg quotient <1 in the soil and >1 in most of the plant samples.

Hyperaccumulation of Ni has also been demonstrated in *O. baldaccii* (Vierh. ex Nyár.) Španiel, an obligate serpentinophyte from Crete. The leaves of this species from two herbarium specimens (under the earlier name of *A. fallacinum*) were reported to contain 3810–3960 mg kg^{-1} (Brooks & Radford 1978), while a subsequent collection of 7 specimens from the field from soils with 349–2336 mg kg^{-1} Ni showed a range from 1430–17,670 mg kg^{-1} (Reeves *et al.* 1997). Concentrations in the shoots, with a mean value of 13,150 mg kg^{-1} have also been reported (Cecchi *et al.* 2020). This species is incorrectly treated as a synonym of *O. fallacina* in the BrassiBase Species Checklist (BrassiBase 2022). However, recent studies (including analysis of type material) indicate that this taxon is distinct from *O. fallacina* and should therefore be considered a new species (Hartvig 2002; Španiel 2019). Additional analyses indicated that populations from ultramafic mainland Greece should be further isolated from *O. baldaccii* s.l. and considered as a new species – *O. stridii* L. Cecchi, Španiel & Selvi. With mean shoot concentrations of 16,380 mg kg^{-1} (significantly higher than those found in the roots and soil) in the sample from Kedhros in Greece (Cecchi *et al.* 2020), this species represents another hypernickelophore and is consistent with the related species *O. baldaccii* in terms of Ni concentrations. As with *O. baldaccii*, the taxonomic status of this species has not yet been accepted by all nomenclatural sources.

Nickel hyperaccumulation was also noted in *O. rigida* (Nyár.) L. Cecchi & Selvi, an obligate endemic serpentinophyte from Albania (POWO 2022), previously incorrectly synonymised with *O. bertolonii*, a species endemic to Italy. Very similar Ni concentrations were found in the leaf samples of this species collected from three sites in Albania, with maximum values of 17,100 mg kg^{-1} (Cecchi *et al.* 2018). The particularly high potential of this taxon for Ni uptake, in addition to >1 wt% Ni in the shoots, is also determined by the pH of the habitat (>7), even though the highest availability of this element stands at pH ~ 5 (Villen-Guzman *et al.* 2019). High pH could be one of the reasons for the extremely low value of available Ni in the soil (79 mg kg^{-1}), despite a relatively high total concentration of >4000 mg kg^{-1} Ni. A similar pH effect (increased Ni uptake at higher pH values) was reported for *O. muralis* and *O. corsica* grown under controlled conditions (Li *et al.* 2003).

Nickel concentrations above the hyperaccumulation threshold have also been detected in the above-ground plant tissue of *Alyssum tenium* Halácsy, now accepted as *O. diffusa* Jord. & Fourr. (Euro+Med 2006–; Brassibase 2022) from the ultramafic area of the island of Tinos (one of the Cyclades islands, Greece). The nickel concentrations in its leaves were found to be in the range 730–9350 mg kg^{-1}, with concentrations in the soil of 244–5940 mg kg^{-1} (Reeves *et al.* 1997).

In the case of *O. euboea* (Halácsy) Španiel & al. (formerly *Alyssum euboeum* Halácsy) a wide range of Ni concentrations has been found. The initial report of Brooks & Radford (1978) was based on just two herbarium specimens from the collections of K.H. Rechinger, with 26 mg kg^{-1} and 4550 mg kg^{-1}, suggesting its occurrence on both serpentinitic and non-serpentinitic soil. A further example of the low-Ni collection of Rechinger, from "the shore, S of Limni" showed 38 mg kg^{-1} Ni (Reeves *et al.* 1983). The records of Brooks and Radford include another herbarium specimen of unrecorded origin (omitted from their publication) with 8814 mg kg^{-1} Ni. A specimen collected by Reeves in 2002 from 2 km E of Mandoudhi had 752 mg kg^{-1}, whilst another from the University of Athens herbarium (ATHU) collected by Georgiadis in 1978 from 1 km N of Vasiliká, Euboea, was found to contain 14,000 mg kg^{-1} Ni (Reeves, unpublished). Concentrations as high as 15,410 mg kg^{-1} have now been recorded (Konstantinou & Kyrkas, unpublished data). More detailed plant and soil data on individual plant sites may be helpful in establishing the relationship between plant Ni and the range of soil chemical and physical properties.

The eight specimens of *O. heldreichii* (Hausskn.) Španiel & al. (*Alyssum heldreichii* Hausskn.) analysed by Brooks & Radford (1978) contained 1440–12,500 mg kg^{-1} Ni. Collections from Milea and Malakasi in Northern Greece by Reeves in 2002 (unpublished) showed 10,400 and 32,040 mg kg^{-1} Ni, respectively, whilst Bani *et al.* (2010) reported concentrations of 11,800 and 5400 mg kg^{-1} from the Katara Pass and Malakasi, respectively. Concentrations of 5800 and 6650 mg kg^{-1} Ni were found in shoot samples from Kteni and the Katara Pass in Northern Greece, respectively (Konstantinou & Tsiripidis 2015; Cecchi *et al.* 2020). Moreover, in the soil sample from Kteni, the pseudo-total Ni concentrations were several times lower than those in the aerial parts of the plant (Konstantinou & Tsiripidis 2015), whereas in the sample from the Katara Pass, similar values were found for the extractable Ni concentrations, with significantly lower concentrations in the root (Cecchi *et al.* 2020).

From Lesbos, four specimens of *O. lesbiaca* P. Candargy [*Alyssum lesbiacum* (Candargy) Rechinger f.] were found to have 7920–22,400 mg kg^{-1} Ni (Brooks *et al.* 1979), and multielement analysis of various plant parts from a collection of 10 specimens from Vaterá, Vasiliká and Megali Limni showed that the highest Ni concentrations were in the leaves, ranging from 4300 to 19,560 mg kg^{-1} Ni (Kelepertsis *et al.* 1990; Reeves *et al.* 1997). Recent research has shown that concentrations of this element increase over time in both the stems and leaves, with a maximum of 22,240, 6898 and 10,610 mg kg^{-1} in the leaves, stems and flowers, respectively (Adamidis *et al.* 2017). pH values in the range of 5.9 to 6.4 and total soil concentrations of up to 3740 mg kg^{-1} Ni further contribute to the uptake of this element in plant tissues. Somewhat higher Ni concentrations in the leaves (23,650 mg kg^{-1}) were found by Kazakou *et al.* (2010). A detailed analysis of the accumulation of Ni in some plant parts showed that the concentrations of this element occur in the following order: leaves > flowers > petals > seeds > fruits > anthers > pollen. Whereas the highest concentrations in the leaves were measured at 18,410 mg kg^{-1}, in the pollen they were only 1588 mg kg^{-1}. Moreover, Ni concentrations lower than 1000 mg kg^{-1} were detected only in some pollen samples, while in all the other aerial plant parts the Ni concentrations were higher than the Ni hyperaccumulation threshold (Stefanatou 2020).

Notably high Ni concentrations have also been observed in *O. serpentinicola* (F.K. Mey.) Španiel & al. and *O. smolikana* (Nyár.) Španiel & al., two endemic hypernickelophores from Albania and Greece, respectively (Cecchi *et al.* 2018; Bettarini *et al.* 2019; Bani *et al.* 2021; Konstantinou & Kyrkas, unpublished data). Nickel concentrations in the range of 7700–14,000 mg kg^{-1} in the leaf samples of *O. serpentinicola* (Cecchi *et al.* 2018) and 8200–14,500 mg kg^{-1} in the shoot samples (Bettarini *et al.* 2019) were found at a total of 24 sites investigated in Albania. Nickel concentrations in the leaf samples of *O. smolikana* reach 13,540 mg kg^{-1}, but in the shoots they are much lower (up to 2780 mg kg^{-1}; Konstantinou & Kyrkas, unpublished data). Analyses of herbarium specimens of *O. smolikana* revealed 1700–6600 mg kg^{-1} Ni in the leaves (Brooks & Radford 1978). The closely related species *O. moravensis* (F.K.Mey.) L.Cecchi & Selvi (formerly known as *Alyssum smolikanum* subsp. *moravense*) is another hypernickelophore within the genus *Odontarrhena*. In the leaf samples of this species endemic to Albania, nickel concentrations were in the range from 10,190 to 16,390 mg kg^{-1} (Bani & Echevarria, unpublished data).

Nickel concentrations of 2700 mg kg^{-1} were found in the leaves of *O. albiflora* (F.K. Mey.) Španiel & al., a stenoendemic species from the Thatë Mountains in the Korçë region of Albania (Cecchi *et al.* 2018). Considering the unknown concentrations of this element in the underground tissues and the lack of any evidence of active Ni uptake, the hyperaccumulator status of this species could be considered doubtful. However, as a species which exclusively inhabits calcareous substrates, it is evident that the species has an extremely strong potential for Ni uptake, which has most likely been preserved as a relic feature of the ancestors from which *O. albiflora* evolved.

The (hyper)accumulation of Ni is a phenomenon occurring in almost all representatives of the genus *Odontarrhena* which inhabit ultramafic substrates (Kidd *et al.* 2018). A unique response has been observed in *O. sibirica* (Willd.) Španiel, Al-Shehbaz, D.A.German & Marhold (*Alyssum sibiricum* Willd.), a facultative serpentinophyte which seems generally incapable of extreme Ni accumulation from ultramafic soils: it has been found on this substrate with up to 8810 mg kg^{-1} in several populations in Kütahya province, Turkey (Reeves *et al.* 2001b; Reeves & Adigüzel 2008). This unusual feature of *O. sibirica* could be the consequence of active evolution in habitats with different Ni contents, but could also be related to the loss of Ni uptake capacity observed in other serpentinophytes of the genus *Odontarrhena* (Cecchi *et al.* 2010; Bettarini *et al.* 2020). Further detailed studies of such hyperaccumulating populations are needed.

Noccaea species

In the genus *Thlaspi* s.l. zinc accumulation by the species previously listed variously as *T. alpestre, T. calaminare* and *T. caerulescens* (among other names, valid or otherwise), and now known as *Noccaea caerulescens*, has been known since the report by Sachs (1865), as discussed in detail in Reeves & Baker (2000). However, Reeves & Brooks (1983) and Reeves (1988) also recorded Ni hyperaccumulation by species of this genus from various parts of the world, following the analyses of more than 500 specimens. Many of the species in this genus, including Ni hyperaccumulators, have subsequently been assigned to *Noccaea*. Due to the significant challenges evident from disagreements among botanical experts relating to both the nomenclature and species discrimination relating to herbarium specimens, the number of Ni hyperaccumulating taxa in this genus could only be estimated from the above publications as approximately 22 (9 from Europe, 9 from Turkey, 3 from the US and one from Japan).

In terms of recently accepted nomenclature (Euro+Med 2006–; Brassibase 2022; POWO 2022), the high Ni specimens from Reeves & Brooks (1983) can be summarised as follows: *N. boeotica* F.K. Mey. from Mt. Gerania, Greece (23,400 mg kg^{-1}); *N. tymphaea* (Hausskn.) F.K. Mey. from 3 sites in the Pindus Mts., Greece (7120–11,800 mg kg^{-1}) and an additional specimen originally misidentified and reported as *Thlaspi goesingense* (with 16,540 mg kg^{-1}); *N. epirota* (Halácsy) F.K. Mey. from Milea, N. Greece (1720–2930 mg kg^{-1}); *N. kovatsii* (Heuff.) F.K. Mey. (previously known as *N. aptera*) from near Kačanik, Kosovo (13,600 mg kg^{-1}); *N. graeca* (Jord.) F.K. Mey. from Mt. Panachaikon near Patras, Greece (4450 mg kg^{-1}); *N. ochroleuca* (Boiss. & Heldr.) F.K. Mey. from Mt. Timfristos, Greece (2000 mg kg^{-1}). The last two, from areas of dominant limestone, were somewhat surprising, but the specimens may have come from associated schistose soil which would probably have higher Ni. Among the 88 specimens from the Balkans in this paper, there were many lower-Ni concentrations in species such as *N. boeotica, N. kovatsii* and *N. praecox* (Wulfen) F.K. Mey. Concentrations above the hyperaccumulation threshold were also found in the sample of the species *N. bulbosa* (Spruner ex Boiss.) Al-Shehbaz, endemic to Greece (1590 mg kg^{-1} of Ni; Reeves & Brooks 1983). However, this observation needs to be supported by additional studies, especially considering that high Zn concentrations were found in the same samples.

As a result of more recent work (Bani *et al.* 2010; Kazakou *et al.* 2010; Salihaj *et al.* 2018; Lopez *et al.* 2019; Šinžar-Sekulić *et al.* 2019; Mišljenović *et al.* 2020) several *Noccaea* species can be regarded as hypernickelophores with >1 wt% Ni in their above-ground tissues. The three most abundant among them on the Balkan Peninsula are *N. kovatsii*, *N. ochroleuca*, and *N. praecox*, making them the species with the widest distribution among hyperaccumulators on the Balkan Peninsula. The highest concentrations of Ni in leaf tissue were found in the specimens collected in Bulgaria by two of the present authors (Dimitrakopoulos & Reeves) in 2005: 21,550 mg kg^{-1} in *N. kovatsii* (reported under the synonym *T. apterum* in Bani *et al.* 2010) from Fotinovo, and 21,530 mg kg^{-1} in *N. praecox* (unpublished) from Kazak. The pseudo-total concentrations of soil Ni at the Bulgarian sites were 2333–3278 mg kg^{-1}. Lower Ni concentrations have been found in samples of *N. kovatsii* from Serbia and Bosnia and Herzegovina, ranging from 2090 (Mišljenović *et al.* 2020) to 12,500 mg kg^{-1} (Šinžar-Sekulić *et al.* 2019) in the shoots, with pH having a clear influence on the Ni concentrations accumulated.

The nickel concentrations observed in the shoot samples of *N. ochroleuca* are somewhat lower than those of *N. kovatsii*, ranging from 1100 mg kg^{-1} (Bani *et al.* 2009) to 13,000 mg kg^{-1} (Lopez *et al.* 2019), as found in the samples from Pishkash and Memelisht in Albania with 92 and 322 mg kg^{-1} extractable Ni in the soil, respectively, indicating the importance of environmental factors and microbial community composition for Ni uptake capacity. Similar to *N. kovatsii*, the highest Ni values were found in the leaf concentration analysis of herbarium samples from Albania, Bulgaria, and Greece (15–23,400 mg kg^{-1}; Bani *et al.* 2010). In the leaf samples from the field (sites in Greece and Bulgaria), the Ni concentrations were significantly lower (3330 and 3400 mg kg^{-1}, respectively; Kazakou *et al.* 2010; Salihaj *et al.* 2018).

Noccaea praecox has been studied intensively in Serbia and Bulgaria with respect to its potential for Ni hyperaccumulation (Bani *et al.* 2010; Mišljenović *et al.* 2020). In addition to unpublished data from Bulgaria (21,530 mg kg^{-1}; Dimitrakopoulos & Reeves, unpublished data), the foliar concentrations of Ni in the samples from Bulgaria recorded by Bani *et al.* (2010) ranged from 1100 to 13,600 mg kg^{-1}, with a very similar pseudo-total Ni concentration in the soil. Hyperaccumulation was confirmed in several shoot samples from Serbia, with values ranging from 3470 to 11,100 mg kg^{-1}, and a general positive correlation was found between these concentrations and extractable concentrations in the soil, and also with concentrations in the root dry matter at circum-neutral pH values (Mišljenović *et al.* 2020).

Noccaea tymphaea, an endemic species from Albania and Greece, was reported with 8140–16,540 mg kg^{-1} Ni (Reeves & Brooks 1983). It has also been found with 10,850 mg kg^{-1} in a leaf sample and 6652 mg kg^{-1} in a shoot sample from Greece (Konstantinou & Kyrkas, unpublished data), whilst for the leaf samples from Albania these concentrations were in the range of 7932–15,630 mg kg^{-1} (Bani & Echevarria, unpublished data).

Bornmuellera species

From the genus *Bornmuellera* (Brassicaceae), Reeves *et al.* (1983) analysed the leaves of herbarium specimens of 8 taxa (3 from Turkey, 5 from Greece and Albania), finding Ni concentrations >10,000 mg kg^{-1} in all except two Turkish species (not from ultramafic soils). At that time, no specimen of *B. dieckii* Degen from Kosovo was available (see below). Two more recent additions to *Bornmuellera* have been made: a distinctive new Turkish species, *B. kiyakii* Aytaç & Aksoy was discovered (Aytaç & Aksoy 2000) and found to be a Ni hyperaccumulator (Reeves *et al.* 2009), and the species from northern Greece and Euboea formerly known as *Peltaria emarginata* (Boiss.) Hausskn. and then as *Leptoplax emarginata* (Boiss.) O.E.Schulz has been transferred to *Bornmuellera* [accepted as *B. emarginata* (Boiss.) Rešetnik; Fig. 1b]. The Balkan species are endemic to the region (POWO 2022). A tabulation of the analytical results for all the taxa from 51 herbarium and field specimens with the exception of *B. dieckii* and *B. emarginata* was provided by Reeves *et al.* (2009), who predicted that *B. dieckii* would also prove to be a Ni hyperaccumulator.

Reeves *et al.* (1980) recorded Ni hyperaccumulation by *B. emarginata* under the name *Peltaria emarginata* which was generally accepted at that time. No other species of *Peltaria* behaved in this way. The 17 specimens analysed showed Ni in the range of 4800–34,400 mg kg^{-1}. Four additional specimens collected by Reeves in 2002 (including one from Euboea) had 2040–24,500 mg kg^{-1} (unpublished data). This gave an overall range of 2040–34,400 mg kg^{-1} with a mean of 16,690 mg kg^{-1}. Very high foliar concentrations have been found in other field samples of *B. emarginata*, with Ni concentrations ranging from 21,760–34,890 mg kg^{-1} (Konstantinou & Kyrkas, unpublished data), whereas much lower levels, ranging from 1100 (van der Ent *et al.* 2019a) to 9109 mg kg^{-1} (Konstantinou & Kyrkas, unpublished data) were found in the shoots. In the flowers of *B. emarginata*, 3641 mg kg^{-1} Ni were detected (van der Ent *et al.* 2019a), while in the fruits concentrations reached levels as high as 12,180 mg kg^{-1} (Konstantinou & Kyrkas, unpublished data).

The highest Ni concentrations in three subspecies of *B. baldaccii* (Degen) Heywood, an endemic species from Albania and Greece, were found in the leaves of her-

Fig. 1. Hyperaccumulator plant species in the Balkans: a) *Bornmuellera tymphaea*; b) *B. emarginata*; c) *Centaurea thracica*; d) *Viola allchariensis* (photo A. van der Ent)

barium specimens (up to 27,300 mg kg^{-1}; Reeves *et al.* 1983), whereas much lower concentrations were detected in samples from the field (Bani *et al.* 2010; Konstantinou & Kyrkas, unpublished data). In the shoot sample from Gramsh in Albania 12,170 mg kg^{-1} Ni was detected, where the extractable concentration of Ni in the soil was only 285 mg kg^{-1} (Bani *et al.* 2013). Significantly lower concentrations (3193–3574 mg kg^{-1}) were found in the shoot samples of *B. baldaccii* from Mt. Smolika (Greece), while the leaf Ni concentrations exceeded 10,000 mg kg^{-1} (10,220–13,710 mg kg^{-1}), at notably lower extractable Ni concentrations in the soil (81 mg kg^{-1}; Konstantinou & Kyrkas, unpublished data). *Bornmuellera dieckii* is known only from Mt. Šar Planina in Kosovo (the village of Mušutište). The nickel concentrations in the soil and different plant tissue samples of this species showed a significant increase from the soil to the leaves. Whilst 2062 mg kg^{-1} extractable Ni was found in the soil and 4102 mg kg^{-1} Ni in the root, these concentrations are significantly higher in the shoot and leaves with 9713 and 24,290 mg kg^{-1} Ni, respectively (Paçarizi *et al.* 2020).

Nickel concentrations in the range 1590–31,200 mg kg^{-1} were found by Reeves *et al.* (1983) in the leaves of herbarium specimens of *B. tymphaea* (Hausskn.) Hausskn. (Fig. 1a), a species endemic to Greece. Additional specimens collected from the Katara Pass and Malakasi by Reeves in 2002 contained 11,130 and 23,640 mg kg^{-1}, respectively. These were included in the summary by Reeves *et al.* (2009) and gave a mean of 14,820 mg kg^{-1} for the total of 11 specimens analysed up to that time. More recent specimens from the Katara Pass and Vovoussa sites (Zhang *et al.* 2014), showed that the Ni concentrations varied considerably in the shoot, leaf, and seed samples. The highest concentrations were found in the leaves (13,900–21,800 mg kg^{-1}), with lower levels in the seeds (9400–11,600 mg kg^{-1}), and the lowest in the shoot samples (4500–7100 mg kg^{-1}) (Zhang *et al.* 2014).

Other species

Hartvig (1991) observed that *Orobanche rechingeri* Gilli (now regarded as conspecific with *O. nowackiana* Markgr.) is "apparently parasitic only on ultramafic species of Brassicaceae which are hyperaccumulators of nickel, in Greece found on *Bornmuellera baldaccii, B. tymphaea, Alyssum heldreichii, A. murale* and *A. smolikanum*". Reeves (1992) added *Alyssum lesbiacum* (from Megali Limni, Lesbos) to this list noting that *Orobanche* alone contained more than 600 mg kg^{-1} Ni. A detailed study of the parasitic behaviour of *O. nowackiana* on the host *Alyssum murale* in Albania was published by Bani *et al.* (2018). The average Ni concentrations in *O. nowackiana* were 299 mg kg^{-1} Ni in the leaves and 601 mg kg^{-1} in the tubercules and roots. The parasitism caused a small reduction in the Ni concentrations in the host plants, but strongly affected plant growth (biomass yield). It was concluded that this was a significant issue for the use of *A. murale* for any application of phytoextraction.

Recent studies from Lesbos (Dimitrakopoulos *et al.* 2021) showed that *Orobanche nana* Noë ex Rchb. and *O. nowackiana* parasitising *Odontarrhena lesbiaca* may reach the Ni hyperaccumulation threshold. Nickel concentrations in the shoot samples of *O. nana* were found in the range of 343 to 1737 mg kg^{-1}, while the Ni concentration in the shoots of *O. nowackiana* was 435–1335 mg kg^{-1}. These values were similar or slightly higher in the tubercles, ranging from 460–1670 mg kg^{-1} in *O. nana* and 631–2562 mg kg^{-1} in *O. nowackiana* (Dimitrakopoulos *et al.* 2021). The analyses showed that in this case not only does the theory of the evolutionary development of hyperaccumulation in response to herbivory not hold, and that hyperaccumulation does not prevent infection, but also that parasitic species reduce the host plant's ability to hyperaccumulate nickel. Again, parasitism reduces the host's potential for use in phytoremediation/phytomining. In this case, lower Ni concentrations were found in the infected individuals of *O. lesbiaca* than in the uninfected ones (Dimitrakopoulos *et al.* 2021). The importance of the interactions between *Orobanche* species and hyperaccumulative hosts of the genus *Odontarrhena* is evidenced by the fact that significantly lower Ni concentrations were found in the plant tissues of *Orobanche pubescens*, a serpentinophyte from the same region but not associated with *O. lesbiaca*, with a maximum of 25 mg kg^{-1} Ni in the flowers (Dimitrakopoulos *et al.* 2021).

Nickel concentrations above the nominal threshold have also been found in a *Centaurea* species from Greece (Asteraceae) and potentially in one *Viola* species (Violaceae). In *Centaurea*, Ni hyperaccumulation has been well established in a number of species from Turkey (Reeves & Adigüzel 2004, 2008). On the Balkan Peninsula Ni hyperaccumulation occurs in *Centaurea thracica* (Janka) Gugler (Fig. 1c), for most of the area studied here, with an extension to the Asian part of Turkey (POWO 2022). Nickel concentrations in the leaves reached 11,410 mg kg^{-1}, with slightly lower concentrations found in the rosettes (7884 mg kg^{-1}), shoots (up to 2156 mg kg^{-1}) and flowers (2346 mg kg^{-1}) (Konstantinou & Kyrkas, unpublished data). Levels above and below the nominal hyperaccumulation threshold were found in the inflorescences, and Ni accumulation was observed in seeds from Trigona, Greece, but without hyperaccumulation (203 mg kg^{-1}; Konstantinou & Kyrkas, unpublished data). The potential of the species to accumulate Ni is confirmed by the lower concentrations of this element in the roots compared to those in the aerial parts, and by the fact that extractable Ni concentrations in all the soil samples were <300 mg kg^{-1} (Konstantinou & Kyrkas, unpublished data). The analysis of herbarium specimens and field samples confirmed the hyperaccumulation capacity of this species, showing Ni concentrations in the leaves between 2688 and 4771 mg kg^{-1} (Psaras & Constantinidis 2009). In the same study, Ni concentrations were analysed in the leaves of *Viola vourinensis* Erben, also in herbarium specimens and in field samples. The results (Ni concentration in the range of 748–1208 mg kg^{-1}; Psaras & Constantinidis 2009) showed concentrations above the hyperaccumulation threshold. However, since the concentrations of this element in the root and in the soil were not determined simultaneously, *V. vourinensis* can only be considered as a possible hyperaccumulator and its capacity should be verified by additional studies.

Thallium hyperaccumulators

Thallium hyperaccumulation is generally a very rare phenomenon and has only been observed in a few taxa belonging to two main groups. In the family Brassicaceae, high Tl concentrations have been observed in species of *Iberis* and *Biscutella* in Southern France (LaCoste *et al.* 1999; Leblanc *et al.* 1999; Corzo Remigio *et al.* 2022). High Tl concentrations have also been recorded in *Viola* species within the borders of the Balkan Peninsula near the Allchar mine on Mount Kožuf in North Macedonia (Bačeva *et al.* 2014). The peculiarity of the mineral composition of this mine is mainly reflected in the extremely rich Tl deposits, considered the largest in the world (Rieck 1993), together with relatively large deposits of As and Sb (Bačeva Andonovska *et al.* 2021). The potential for hyperaccumulation of these three elements was examined in species spontaneously overgrowing the mine area and was confirmed in *Viola allchariensis* (Fig. 1d), *V. arsenica*, and *V. tricolor* subsp. *macedonica*. In all three taxa, Tl concentrations in the above-ground parts exceeded the nominal hyperaccumulation threshold of 100 mg kg^{-1} (van der Ent *et al.* 2013), but at the same time, there is a marked potential for the accumulation of this element in the above-ground organs, i.e. a higher concentration in the aerial tissues compared to those below-ground. Moreover, the highest concentrations were found in the leaves, up to 10,400 mg kg^{-1} in *V. arsenica*, but in the flowers and seeds these concentrations were slightly lower, still > 2000 mg kg^{-1} in all the samples (Bačeva *et al.* 2014). In *V. allchariensis* and *V. tricolor* subsp. *macedonica* similar concentrations of Tl were found (4013 and 4292 mg kg^{-1}, respectively), considerably higher than the hyperaccumulation threshold (Table 1). Concentrations of Tl above this level were also found in the species *Thymus allchariensis* (104 and 131 mg kg^{-1} in the leaves and flowers, respectively; Bačeva *et al.* 2015; Bačeva Andonovska *et al.* 2021), although even higher concentrations were reported in the roots. Further studies are clearly needed to confirm the hyperaccumulator status of this species.

Zinc and lead hyperaccumulators

Hyperaccumulation of Zn occurs much less frequently in nature compared to Ni and has so far been confirmed in only 30 taxa, mainly representatives of the family Brassicaceae (Jakovljević & Mišljenović, unpublished data). Within the Balkan Peninsula *Noccaea kovatsii* from the chlorite schists in Suvo Rudište on Mt. Kopaonik (Serbia) can be considered a hyperaccumulator of this element, with a mean Zn concentration of 4920 mg kg^{-1} in the shoots and a strong accumulation tendency (Mišljenović *et al.* 2020). The extremely strong accumulation potential is evidenced by the fact that only 142 mg kg^{-1} pseudo-total and 25 mg kg^{-1} extractable Zn were detected in the soil, whilst the concentrations in the roots (958 mg kg^{-1}) were intermediate between the values in the soil and in the shoots. High foliar concentrations of Zn (up to 4850 mg kg^{-1}) were also found in the analysis of dry leaf material from European herbaria (Reeves & Brooks 1983).

In contrast to the hyperaccumulation of Zn, which has also been found at uncontaminated sites, the potential hyperaccumulation of Pb in plant tissues is mainly associated with sites near Pb (or Zn-Pb or Zn-Pb-Cd) mines and smelters (van der Ent *et al.* 2013). This is also true for the species *Noccaea ochroleuca*, *Minuartia greuteriana* Kamari and *Cistus creticus* L., where Pb concentrations above the hyperaccumulation threshold were observed at several sites in Greece, with the highest detected in the leaves of *C. creticus* (2300 mg kg^{-1}; Konstantinou & Tsiripidis 2015). However, despite the high concentrations reported in the shoots, the status of hyperaccumulation in these species may be considered doubtful. It is noted that some earlier claims of metal hyperaccumulation, especially in small compact members of the Caryophyllaceae family, have not been supported by subsequent studies. Further studies are needed in light of the problems discussed by van der Ent *et al.* (2013). Such studies may include the investigation of the intercellular location of the accumulated element and its concentration in localised areas of plant organs.

Arsenic hyperaccumulators

Arsenic hyperaccumulation is a phenomenon most common in ferns, particularly in the Pteridaceae family (Xie *et al.* 2009), where concentrations of up to 22,630 mg kg^{-1} (Ma *et al.* 2001) in some specimens of *Pteris vittata* L. growing on anthropogenically-contaminated and spiked soils significantly exceed the nominal hyperaccumulation threshold (1000 mg kg^{-1}; van der Ent *et al.* 2013). Notable As deposits are located on the Balkan Peninsula in the region of the Allchar mine in North Macedonia, where Tl and Sb also occur in high concentrations (Bačeva Andonovska *et al.* 2021). Unlike Tl, whose hyperaccumulation concentration has been observed in several species, As occurs in concentrations above the hyperaccumulation threshold only in *Viola arsenica* and then only in its seeds (in the range of 6–2776 mg kg^{-1}; Bačeva *et al.* 2014). However, since As concentrations in other plant organs are much lower (<70 mg kg^{-1} in the shoots, leaves, and flowers; Bačeva *et al.* 2014), this species cannot be considered a hyperaccumulator of As but only of Tl, strictly in accordance with the definition of van de Ent *et al.* (2013). Arsenic concentrations in the shoots of these three species far below the hyperaccumulation threshold were also found by Stevanović *et al.* (2010), confirming the uncertain accumulation capacity of the *Viola* species studied.

Copper hyperaccumulators

Copper is an essential trace element usually present in plants at low concentrations in the shoots, mostly <20 mg kg^{-1}, and concentrations between 20 and 100 mg kg^{-1} are already considered as excessive (Kabata-Pendias 2011). The potential for Cu hyperaccumulation has been identified to date in approximately 50 taxa, most of which occur in the DR Congo region (Lange *et al.* 2017). However, their status is uncertain due to the high potential for significant soil Cu contamination confounding the results of foliar analysis of ostensible Cu hyperaccumulating plants (van der Ent *et al.* 2019b). Until recently, Cu hyperaccumulation was not known for any plant species on the Balkan Peninsula. However, Jakovljević *et al.* (2022) showed that *Minuartia recurva* (All.) Schinz & Thell. from Suvo rudište, near an abandoned Fe-Cu mine on Mt. Kopaonik (Serbia), accumulates Cu in the shoots at concentrations of 1960 mg kg^{-1}, several times higher than the nominal hyperaccumulation threshold (300 mg kg^{-1}; van der Ent *et al.* 2013). The high concentrations of Cu in the plants here are due to the high Cu content of the substrate. However, higher concentrations of Cu in the above-ground plant parts compared to the roots and the exchangeable concentrations in the soil clearly indicate the potential for hyperaccumulation of this element (Jakovljević *et al.* 2022).

Co-accumulation of trace elements

Most hyperaccumulator plant species take up only one element and accumulate concentrations above the particular hyperaccumulation threshold. The simultaneous hyperaccumulation of several different elements is an extremely rare phenomenon only observed in a small number of taxa. Similarly, on the Balkan Peninsula, the hyperaccumulation of more than one element has so far been observed only in *N. kovatsii*, while in *N. ochroleuca* and *V. arsenica* (hyperaccumulators of Ni and Tl, respectively) the hyperaccumulation of both Pb and As remains to be confirmed. Different patterns of co-accumulation are observed in these taxa. On the one hand, some species grow on polymetallic substrates and co-accumulate multiple (usually geochemically-related) elements at the same time (such as Co and Cu, Zn, Pb and Cd, As and Tl, etc.; Reeves & Baker 2000; Xing *et al.* 2013). On the other hand, however, certain species hyperaccumulate more than one element, but not simultaneously on the same type of substrate. This is the case, for example, with the hyperaccumulation of Ni and Zn, for which antagonistic effects in accumulation have been demonstrated several times (Kozhevnikova *et al.* 2021), although there is also evidence of positive correlations in the uptake of these two elements (Xing *et al.* 2013). Previous studies have shown that *N. kovatsii* hyperaccumulates Ni (up to 21,550 mg kg^{-1}; Bani *et al.* 2010) in most cases, but Zn hyperaccumulation (with concentrations up to 4920 mg kg^{-1} in the shoots) has also been reported on chloritic schist as the geological substratum (Mišljenović *et al.* 2020). Since both the Ni and Zn concentrations are extremely low in such cases, it is obvious that the ability of the species to absorb Zn can be expressed in the absence of high Ni concentrations. Zinc hyperaccumulation is not an uncommon phenomenon in *Noccaea* species (Martos *et al.* 2016). However, to date, no species in this genus has been found to accumulate Zn exclusively, i.e. the hyperaccumulation of Zn has been observed in species which also hyperaccumulate another element, usually Ni (Peer *et al.* 2006). The potential for co-accumulation in hyperaccumulator species in the Balkans is probably also present in *N. ochroleuca*. Indeed, this species, a Ni hyperaccumulator (with 13,000 mg kg^{-1} Ni in the shoots and 23,400 mg kg^{-1} in the leaves; Reeves & Brooks 1983; Lopez *et al.* 2019), probably has the ability to hyperaccumulate Pb, as indicated by the levels above the hyperaccumulation threshold in the fruit samples from Vouves in Greece (1345 mg kg^{-1}). However, considering the extreme Pb loading of the site (111,100 mg kg^{-1} soil total Pb; Konstantinou & Tsiripidis 2015), the excessive Pb concentration is likely the result of excessive levels of this element in the soil rather than the species' ability to actively take it up.

Viola arsenica, a hyperaccumulator of Tl, was found to have As concentrations above the hyperaccumulation threshold (As-Sb-Tl) at sites near the Allchar mine. Whereas Tl is taken up and transported to all the above-ground parts at concentrations considered to be hyperaccumulating (up to 10,400 mg kg^{-1} in the leaves), true hyperaccumulation of As was observed only in the seeds of this species (2776 mg kg^{-1}). Considering that the concentrations in the leaves and shoots were much lower (Bacheva *et al.* 2014), this species is not formally recognized as a hyperaccumulator of arsenic despite the high concentrations of this element found in the seeds.

THE DISTRIBUTION OF BALKAN HYPERACCUMULATORS

Specific edaphic features are one of the main causes for endemism (edaphic endemism) and the floristic richness of a given area in general (Isnard *et al.* 2016). Since the known hyperaccumulators to date are dominated by species which hyperaccumulate Ni, which is primarily associated with ultramafic bedrock, the location of this type of substrate has had a major influence on the distribution of hyperaccumulator species. For example, the distribution of most *Odontarrhena* species is closely associated with the distribution of ultramafic areas in S Europe, the eastern part of the Mediterranean region, as well as in Asia Minor (Brooks *et al.* 1979).

Most of the hyperaccumulators from the Balkan Peninsula analysed to date are species endemic to Greece (10 taxa, e.g. *B. emarginata*, *B. tymphaea*, *N. epirota*, *N. graeca*, *O. euboea*, etc.), which is consistent with the overall high degree of endemism (15.6%; Georghiou & Delipetrou 2010) and the generally high diversity (>7000 native plant taxa; Kougioumoutzis *et al.* 2021) in this country. A considerable proportion of these endemic taxa have close relatives which are not so distant, but the metalliferous characteristics of the habitat and the distribution on the islands have led to the evolution and development of specific morphological traits clearly distinguishing these species from their relatives. Nine species have a slightly wider distribution and are endemic to the Balkan Peninsula, whilst 8 species occur outside the Balkans, most of them in the Asian part of Turkey, such as *O. chalcidica*, *C. thracica, Orobanche nowackiana*, etc. (POWO 2022). In Albania, a total of four species analysed are endemics, all belonging to the genus *Odontarrhena* (*O. albiflora*, *O. moravensis*, *O. rigida*, *O. serpentinicola*). The lowest number of hyperaccumulators are found in Kosovo, but one of them (*Bornmuellera dieckii*) is a local ultramafic endemic.

THE POTENTIAL APPLICATION OF HYPERACCUMULATOR SPECIES

Due to the strong tendency to transport and (hyper)accumulate metals into above-ground organs, hyperaccumulator species can play an important role in the process of phytoremediation by phytoextraction, i.e. the uptake of metals into above-ground plant parts and the simultaneous and progressive reduction of their accessible content in the soil. These elements can be removed by harvesting, after which the plant material is available to be disposed of in various ways, or the material is ashed to recover metals and generate energy (Corzo Remigio *et al.* 2020). The recovery of metals from the biomass of hyperaccumulator species is one of the most important steps in the agromining process, which involves growing plants specifically to extract metals from the soil in an environmentally-sound manner and provide an alternative to conventional mining in places where it is not cost-effective, whilst also recovering a significant amount of energy (Chaney *et al.* 2021). Agromining practices have already been used with great success in the Balkans in recent years, at sites in Albania and Greece (Bani *et al.* 2015a, b, 2021). Significant Ni yields per ha were obtained with *O. chalcidica* at ultramafic sites in Pojskë (Eastern Albania), after appropriate intensive agromining practices had been applied (with 112 kg ha^{-1} as the maximum yield in 2013; Kidd *et al.* 2018; Bani & Echevarria 2019). *Odontarrhena chalcidica* meets several criteria making it a suitable candidate for this practice: it is a hypernickelophore (accumulating up to 2.4 wt% Ni), it is an autochthonous species, it is well-adapted to the local edaphic and climatic conditions, its seeds germinate readily, and it is easy to establish and grow (Bani *et al.* 2007; Nkrumah *et al.* 2021). There is also the potential for the use of *O. decipiens* in agromining, mainly due to its large biomass, ploidy level, and >17,000 mg kg^{-1} Ni accumulated in its aerial parts (Cecchi *et al.* 2018). Satisfactory Ni concentrations were also obtained by *O. lesbiaca* with levels higher than 23,000 mg kg^{-1} in the leaves, and it also has a relatively large biomass (Kazakou *et al.* 2010; Bani *et al.* 2021). In addition to employing *O. chalcidica* in agromining in Greece, two *Bornmuellera* species (*B. emarginata* and *B. tymphaea*) have also been cultivated in an area around the Pindus Mountains. Nickel yields of 106.3 kg ha^{-1} Ni for *O. chalcidica*, 151 kg ha^{-1} Ni for *B. emarginata* and 88.3 kg ha^{-1} Ni for *B. tymphaea* were obtained in 2019 (with biomass yields of 13.5, 8.1 and 6.1 t ha^{-1}, respectively) (Kyrkas *et al.* 2019 a, b).

However, the use of hyperaccumulator species in the phytoextraction process does have some limitations. Namely, the most common disadvantage is their low biomass, which makes the extraction process less or even unprofitable. An additional problem is that metalliferous habitats are usually co-enriched with several metals/metalloids at the same time, and hyperaccumulators usually take up only one element above the hyperaccumulation threshold, as the hyperaccumulation of several elements is a much rarer phenomenon (Jakovljević *et al.* 2021).

Significant Ni concentrations have also been reported in the aerial parts of several *Noccaea* species on the Balkan Peninsula. Moreover, some of these *Noccaea* representatives are capable of hyperaccumulating more than one element, which makes them particularly attractive for the phytoextraction process. However, most of these species are characterised by extremely low biomass, which makes their use in the remediation/agromining process largely unviable (Jakovljević *et al.* 2021).

THE DISCOVERY OF NEW HYPERACCUMULATOR SPECIES

The classical method for detecting new hyperaccumulator species begins with the search for metalliferous areas in and around orefields (using geographic and geological maps), the flora of which is then intensively researched. In addition to this time-consuming method, which involves determining potentially high concentrations of certain elements by conventional laboratory analysis of specimens, there are several methods for rapidly detecting the potential hyperaccumulating capacity of target species. In recent years, for example, X-ray fluorescence (XRF) instruments have been increasingly used (and developed) because of their ability to analyse large numbers of soil and plant samples for elemental composition in a short time, and to reveal their concentrations non-destructively. The particular importance of this tool is shown in the systematic analysis of herbarium samples of entire families, or the flora of a given area to search for potential new hyperaccumulators (van der Ent *et al.* 2019c, d). Although the results obtained with this hand-held instrument are not fully quantitative (sometimes even after calibration), they reliably indicate those concentrations which represent hyperaccumulation thresholds. This method was also used in the Herbarium of the Institute of Botany (BEOU) and in the Herbarium of the Museum of Natural History (BEO) in Belgrade, Serbia, and on this occasion representatives of the family Brassicaceae, known for the largest number of hyperaccumulator species, were analysed. This device confirmed hyperaccumulation in some previously known hyperaccumulator species, mainly from the genera *Noccaea* and *Odontarrhena*. However, a new hyperaccumulator species was also discovered in this way - *Cardamine waldsteinii* Dyer, where XRF instrumentation detected Zn hyperaccumulation with concentrations of 3300 mg kg^{-1} in samples from non-metalliferous soil. However, further analysis of material from the field is needed to confirm this potential for hyperaccumulation. A very rapid but far less accurate method for detecting Ni hyperaccumulation, used primarily in the field, is the use of a qualitatively indicator paper treated with dimethylglyoxime (DMG) (Reeves *et al.* 1996), which turns deep rose-pink when very high Ni concentrations are present in a fresh leaf sample pressed against the test paper (see for example, Baker *et al.* 1992, Plate 7).

CONCLUSIONS

The potential for hyperaccumulation has so far been confirmed in 31 taxa from the Balkan Peninsula and remains to be confirmed in 8 taxa by additional studies. Most of these hyperaccumulator taxa belong to the Brassicaceae family, mainly to the genus *Odontarrhena*, and Ni is the metal predominantly hyperaccumulated. The concentrations of the elements differ considerably between plant tissues, with higher concentrations observed in most cases in the leaves, especially from the analyses of herbarium materials. Almost all the Ni hyperaccumulator species have shown some specimens with >1 wt% Ni, while >3% Ni was detected in the leaves of *Bornmuellera emarginata*, *B. tymphaea* and *Odontarrhena heldreichii*. In addition to Ni, Balkan Peninsula hyperaccumulators also take up Zn, Cu, and Tl and accumulate them to above the hyperaccumulation threshold, but the hyperaccumulation of Pb and As remains to be confirmed. The hyperaccumulation of Zn and Tl is of particular importance as it has been confirmed in only a very low number of species in Europe and worldwide. Unusually, *Noccaea kovatsii* has been shown to have the capacity to hyperaccumulate more than one element (for *N. ochroleuca* and *Viola arsenica* the ability to co-accumulate has yet to be confirmed), which is of particular importance given the polymetallic nature of most metalliferous soils.

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REZIME

Botanica SERBICA

Otkrića hiperakumulatorskih biljaka na Balkanu: akumulacija, distribucija i potencijalna primena

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Hiperakumulatorske biljne vrste mogu da tolerišu ekstremno visoke koncentracije metala/metaloida u zemljištu na kome rastu i da ih u visokim koncentracijama akumuliraju u svojim nadzemnim delovima. Do danas je 31 hiperakumulatorska biljna vrsta konstatovana na Balkanu, kao centru diverziteta i specijacije evropske flore, a koji je naročito bogat ultramafitskom geološkom podlogom. Dodatnim studijama je potrebno potvrditi hiperakumulatorski status još 8 vrsta. Najveći broj ovih hiperakumulatorskih taksona (13 taksona ili 41.9%) pripada rodu *Odontarrhena*, pri čemu svi hiperakumuliraju Ni, a koncentracije ovog elementa iznad praga za hiperakumulaciju su zabeležene još i u okviru rodova *Bornmuellera* i *Noccaea* (Brassicaceae), *Orobanche* (Orobanchaceae), *Centaurea* (Asteraceae) i *Viola* (Violaceae). Od posebnog značaja je prisustvo hiperakumulatora Tl i Zn, budući da je hiperakumulacija ovih elemenata zabeležena globalno kod malog broja vrsta. Hiperakumulacija više elemenata zabeležena je kod vrste *Noccaea kovatsii*, koja uz Ni, kao primarni element, hiperakumulira i Zn. Hiperakumulacija metala je diskutovana u smislu filogenetskih odnosa i distribucije vrsta, sa posebnim osvrtom na njihovu sistematiku, otkrivanje i prepoznavanje novih hiperakumulatorskih vrsta i mogućnosti njihove buduće praktične primene u fitotehnologijama.

Ključne reči: hipertolerancija, metalofite, flora, ultramafiti, nikl, talijum