Soil and Biota of Serpentine: A World View
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Geoecology of a Forest Watershed Underlain by Serpentine in Central Europe

Pavel Krám[1,*], Filip Oulehle[1], Veronika Štědrá[1], Jakub Hruška[1],
James B. Shanley[2], Rakesh Minocha[3], and Elena Traister[4]

Abstract - The geoecology of a serpentinite-dominated site in the Czech Republic was investigated by rock, soil, water, and plant analyses. The 22-ha Pluhův Bor watershed is almost entirely forested by a nearly 110-year old plantation of *Picea abies* (Norway Spruce) mixed with native *Pinus sylvestris* (Scots Pine) in the highest elevations. It is mainly underlain by serpentinite, with occassional tremolite and actinolite schists and amphibolite outcrops. Tremolite schists and especially serpentinites are characterized by extremely high concentrations of Mg, Ni, and Cr and by negligible concentrations of K, creating an unusual environment for plants. The spruce growth rate is very slow, apparently as a result of K deficiency, Mg oversupply, and Ni toxicity. Foliar Ca is in the upper part of the optimum range because schists and amphibolites are important sources of Ca to the soil exchangeable pool and vegetation. Mineral weathering and atmospheric deposition generate near-neutral magnesium-bicarbonate-sulfate streamwater with a high concentration of Ni.

Introduction

Geologists refer to serpentine as a mineral with the ideal approximated chemical formula of $Mg_3Si_2O_5(OH)_4$, or a group of minerals like antigorite, chrysotile, and lizardite. Rocks composed mainly of serpentine minerals are called serpentinite. Serpentine minerals are formed from olivine minerals (and pyroxenes), usually in peridotite, that are exposed to water at high temperatures (Alexander et al. 2007, Wagner 1991). Peridotite is a coarse-grained rock composed chiefly of olivine with or without other mafic minerals such as pyroxene and amphibole. More specific forms of peridotite are dunite and harzburgite (Alexander et al. 2007, Coleman 1971). Serpentinite and peridotite are typical ultramafic rocks, defined as rocks composed of more than 90% magnesium-ferrous, dark-colored minerals and an SiO_2 content below 48%.

In many scientific disciplines, the term serpentine is broadly applied to all ultramafic rocks. For example, in pedology, botany, and ecology, the term serpentine rock or soil refers to rock or soil dominated by minerals with high Mg-silicate content (Alexander et al. 2007, Brooks 1987, Coleman 1971, Wagner 1991). Because this paper is part of a special serpentine ecology

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[1]Czech Geological Survey, Klárov 3, 11821 Prague 1, Czech Republic. [2]US Geological Survey, PO Box 628, Montpelier, VT 05601, USA. [3]USDA Forest Service, Northeastern Research Station, PO Box 640, Durham, NH 03824, USA. [4]University of New Hampshire, Department of Natural Resources and the Environment, Durham, NH 03824, USA. [*]Corresponding author - pavel.kram@geology.cz.

issue of the Northeastern Naturalist (Rajakaruna and Boyd 2009), we adopt the ecological use of the word serpentine throughout the paper.

Most of the serpentine in the world is derived from ultramafic mantle rocks through the process of serpentinization. In this process, water invades fractured mantle rock and alters it to serpentinite. Complete serpentinization of an ultramafic rock requires a dramatic influx of water that produces a large expansion of volume up to 33%, with a corresponding decrease in density from 3.3 to 2.5 Mg m^{-3}, as the newly formed serpentine minerals require much more volume than the primary minerals they replace. In this slow and complicated process, the rock changes from a brittle, strong, dense peridotite to a plastic, weak, light serpentinite. The serpentinite is easily deformed and often rises in the form of buoyant rock as a diapir, when orogenic folding forces the light and weak serpentinite to migrate upward (Alexander et al. 2007, Hostetler et al. 1966). Peridotite and serpentinite are chemically similar, but about 12–15% water is added to the crystalline structure in the conversion of peridotite to serpentinite. On the other hand, serpentinization is accomplished with no change in the relative amount of Si, Al, Mg, Cr, Mn, Fe, Co, and Ni. The only major component removed during serpentinization is Ca (Alexander et al. 2007, Sleep et al. 2004).

Ecosystems with serpentine soils are less productive than ecosystems with most other kinds of soils. Vegetation on serpentine soils is often sparser, smaller in stature, and atypical for its particular climatic zone, with an unusual plant species composition. Many endemic species are entirely or almost entirely restricted to serpentine areas (Alexander et al. 2007, Brooks 1987).

The first major objective of this paper is to summarize the geology and vegetation of the largest Czech serpentine body situated in the Slavkov Forest in the western part of the Czech Republic (Figs. 1 and 2). The second major objective, after introducing the occurrences of serpentine bodies in the Czech Republic (Fig. 1), is to discuss and interpret relevant facets of a long-term geoecology and biogeochemistry study on Pluhův Bor, a small, forested watershed from that area which is underlain by serpentine (Figs. 2 and 3). Only a limited number of serpentine watersheds in the world have been studied from the hydrologic and biogeochemical point of view (Table 1). We have previously published on three of these watersheds in the Czech Republic (Krám 2006), and in this paper, we build on our knowledge of the hydrology and biogeochemistry to analyze the geoecology of Pluhův Bor. It

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Figure 2 (opposite page bottom). Surficial geologic map of the central part of the Slavkov Forest with the location of the largest serpentine body (Vlčí Hřbet) of the Czech Republic. The elongated discontinuities within the major serpentine body are surficial quaternary deposits, mostly alluvial. Abbreviations used for the small protected areas: PB = Pluhův Bor; K = Křížky; V = Vlček; PV = Planý Vrch; M = Mokřady pod Vlčkem; D = Dominova Skalka. Three forested serpentine watersheds (Pluhův Bor, Vlčí Kámen and Císařský Les) were studied. Prepared using digital versions of the geologic maps 1:50,000 (after Schovánek 1997 and Tonika 1998).

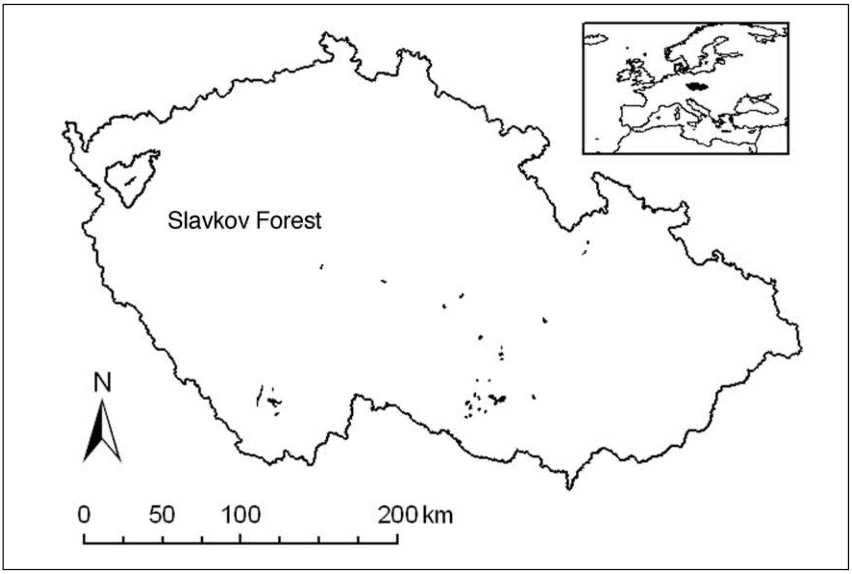
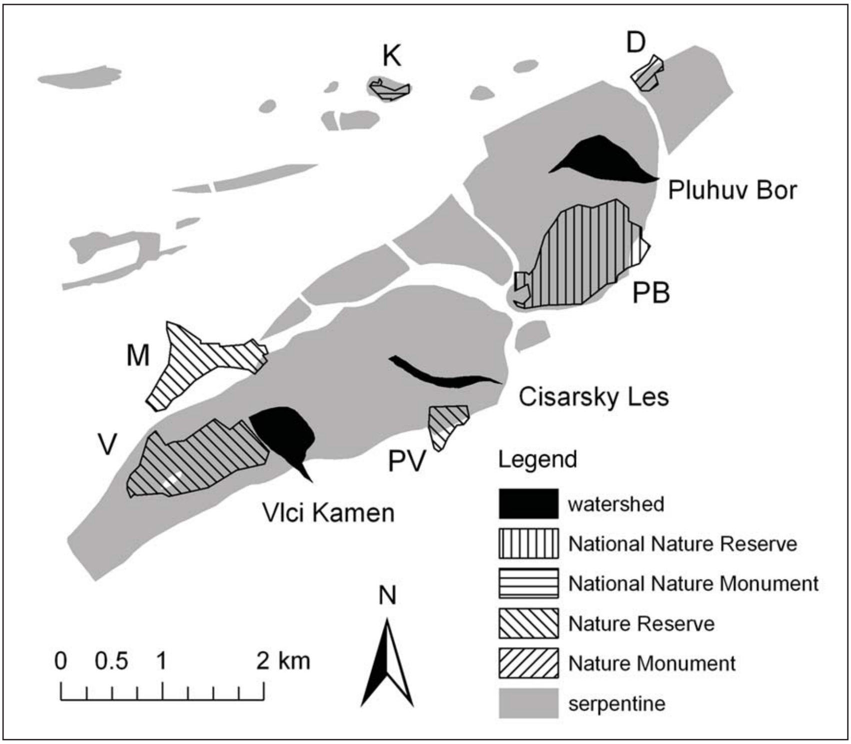


Figure 1. Upper–right panel: schematic map of Europe showing the location of the Czech Republic (in black). Lower panel: map of the Czech Republic showing occurrences of ultramafic rocks (serpentines). The largest Czech body of serpentine is situated in the Slavkov Forest Protected Landscape Area (CHKO Slavkovský Les).



is relevant to study this spruce-dominated, serpentine watershed because a very limited amount of research in such environments has been published, and in particular, the water fluxes of this watershed have been monitored continuously and quantitatively for a long period of time.

Site Description

One-third of the Czech Republic is forested, predominantly by managed stands of conifers. Damage to forest health by elevated atmospheric deposition of sulfur was severe in the northwestern part of the country mainly in the 1970s and 1980s (Hruška and Krám 2003). The Slavkov Forest (Slavkovský Les) is a Protected Landscape Area with an area of 610 km^2 (Majer et al. 2005) located in western Bohemia, western Czech Republic (Fig. 1). The highest elevations are in the southwest; Lesný at 983 m and Lysina at 982 m have the highest summits. There is no evidence of glaciation in the Slavkov Forest.

Serpentine geology of the Slavkov Forest

The most extensive accumulation (230 km^2) of metamorphic mafic and ultramafic rocks in the Bohemian Massif, the large craton of Central Europe, is situated in the Slavkov Forest. This accumulation has a triangular shape and is called the Mariánské Lázně Complex (MLC). It forms an independent unit (allochthonous body) of an ophiolite nature with foliations dipping mostly to the southeast. The rocks of the MLC contain mainly amphibolites (more than 60% by volume), and also eclogite lenses, gneisses, granulites, metagabbros, and partly or completely serpentinized peridotites. The MLC is associated with a first-order tectonic zone, interpreted as a subduction-related boundary between the Saxothuringian Zone (SZ) and the Teplá Crystalline Unit (TCU). Final configuration of the units was established during the Variscan collision about 390–370 million years ago in which the rocks of the MLC and TCU were thrust to the northwest over the SZ for a distance of at least 25 km. The thrust involved lower crustal and mantle rocks (Štědrá 2001, Štědrá et al. 2007).

Table 1. List of studied ultramafic (serpentine) watersheds in North America, South America, Europe, Asia, and Oceania.

Watershed	Area (km^2)	Elevation (m asl)	Reference
Clear Creek, California, USA	36.5	792–1579	Alexander et al. 2007
Soldiers Delight, Maryland, USA	0.567	140–213	Cleaves et al. 1974
Yaou, French Guiana	0.29	100–220	Freyssinet and Farah 2000
Vlčí Kámen, Czech Republic	0.24	756–849	Krám 2006
Císařský Les, Czech Republic	0.12	700–851	Krám 2006
Pluhův Bor, Czech Republic	0.216	690–804	Krám 2006
S1, in Nio watershed, Oe, Japan	0.073	170–430	Onda et al. 2001
S2, Oe, Japan	0.052	440–610	Onda et al. 2001
Couvelée, New Caledonia	40.5	0–1148	Trescases 1975, Alexander et al. 2007
Dumbéa Nord, New Caledonia	28.1	0–1250	Trescases 1975, Alexander et al. 2007
Dumbéa Est, New Caledonia	56.1	0–1046	Trescases 1975, Alexander et al. 2007

The ultramafic complex of the MLC spans approximately 9 km^2. The main strip of the ultramafic ridge, 8.1 km long and up to 1.6 km wide, is oriented in the northeast–southwest direction (Fig. 2) in the northwestern edge of the MLC. The dip of the main serpentine ridge is mostly very steep and varies between 60–90° southeast. Elevations reach up to 883 m on the highest summit named Vlčí Kámen. In addition, about ten smaller, elongated bodies of basal serpentinites occur as isolated pods or outliers of the MLC rocks further north and west on the SZ, forming small topographic highs (Fig. 2). They could be classified as immersed roof pendant relicts (Štědrá et al. 2007).

Serpentinized and retrogressed ultramafic rocks form the lowermost structural base of the MLC. They form sheets and pods of serpentinized peridotite several hundred meters thick, accompanied by minor tremolite, actinolite and chlorite schists, and metagabbros. In particular, the internal part of the main ultramafic ridge contains completely retrogressed spinel peridotite and bronzite harzburgite (Fiala 1958). Rather homogenous serpentinized peridotites include planar or elongated pale green tremolitite bodies a few decimeters in thickness and up to a few meters in length. The magmatic assemblage was replaced by products of metamorphism and hydration. The main ultramafic body corresponds to so-called alpine peridotites and island-arc harzburgites which equilibrated under temperatures of 850–900 ºC (Goliáš 1994). Complex segments with angular blocks of amphibolites, thin laminae and folded patches of actinolite schists, and relicts of segmented tremolitite veins were formed especially in the external parts of the main ultramafic body (Štědrá et al. 2007).

Serpentine vegetation of the Slavkov Forest

The rarest vegetation on serpentine is protected in five areas (Fig. 2), which cover an area of 1.7 km^2 and range in elevation from 662 to 883 m. The National Nature Reserve Pluhův Bor was declared in 1969 with an area of 87.2 ha and elevations of 662–766 m. The National Nature Monument Křížky was founded in 1962 and covers an area of 4.0 ha with elevations of 788–817 m. The three remaining areas have lower protection levels and include: Nature Reserve Vlček (1966: 62.3 ha, 784–883 m); Nature Reserve Planý Vrch (1966: 11.3 ha, 720–790 m); and Nature Monument Dominova Skalka (1989: 6.6 ha, 724–747 m).

A part of the Slavkov Forest which is underlain by ultramafic rocks belongs to the Serpentine Acidophilous Pine Woodland area, which includes the botanical association of *Asplenio cuneifolii-Pinetum sylvestris*. The overstory of this association on the main serpentine ridge is usually represented by semi-dense stands of old and stunted *Pinus sylvestris* L. (Scots Pine). Natural stands are often dominated by pine from the original local genotype, with a natural admixture of *Picea abies* (L.) Karsten (Norway Spruce) in wetter areas. At present, natural regeneration of pine is limited due to deer browsing (Neuhäuslová et al. 2001).

Several important understory species of this association are present on the main serpentine ridge. Shrubs form local heathland with dominant *Erica herbacea* L. (Winter Heath), *Calluna vulgaris* (L.) Hull (True Heather), and admixed *Polygaloides chamaebuxus* (L.) O. Schwarz (Creeping Evergreen). *Juniperus communis* L. (Common Juniper) sporadically represents the shrub layer, and the presence of *Rubus saxatilis* L. (Stone Bramble) is another feature (Zahradnický and Mackovčin 2004). In more open stands, large grassy areas have developed, mainly composed of *Calamagrostis arundinacea* (L.) Roth (Feather Reedgrass), *Festuca ovina* L. (Sheep's Fescue), *Deschampsia flexuosa* (L.) Trin. (Wavy Hairgrass), and *Calamagrostis villosa* (Chaix) J.F. Gmelin (Small Reed) (Neuhäuslová et al. 2001, Průša 2001).

The herb level contains the ferns *Asplenium cuneifolium* Viv. (Serpentine Spleenwort) and *Asplenium adulterinum* Milde (Adulterated Spleenwort). The largest Czech fern, *Pteridium aquilinum* (L.) Kuhn (Western Brackenfern), is also locally dense. The endemic herb *Cerastium alsinifolium* Tausch (Mouse-eared Chickweed) is very rare, and there is sparse occurrence of *Dianthus sylvaticus* Willd. (Carnation). Other species present at the main serpentine ridge, but also growing frequently outside the serpentine, are a tiny fern, *Botrychium lunaria* (L.) Schwartz (Moonwort), and the herbs *Huperzia selago* (L.) C.F.P. Mart. (Fir Club Moss) and *Anthericum liliago* L. (St. Bernard's Lily) (Neuhäuslová et al. 2001, Nevečeřal 1995, Zahradnický and Mackovčin 2004).

From the naturalist point of view, rock outcrops with associations of *Asplenietum serpentini* contain the most valuable vegetation. The association is formed by rare ferns such as *Asplenium cuneifolium*, *A. adulterinum*, and *Polypodium vulgare* (L.) *var. serpentiniti* (Common Polypody). The only known serpentine endemite of the area is the globally rare and endangered *Cerastium alsinifolium*. It is only present on the serpentines of the Slavkov Forest and it does not occur any other place in the world. This endemite was described in 1828 at Křížky as the very first Czech endemite (Neuhäuslová et al. 2001, Zahradnický and Mackovčin 2004).

Pluhův Bor watershed

The Pluhův Bor watershed (21.6 ha) is situated in the middle of the Slavkov Forest with an elevation range of 690–804 m (Fig. 3). Pluhův Bor watershed has a mixture of *Picea abies* (88%) and *Pinus sylvestris* (11%). Most stands were converted into even-aged *Picea abies* plantations between 1874 and 1894. The average age of trees in the watershed is 107 years. The major part of the watershed belongs to two altitudinal vegetation zones of the Czech forestry system (Průša 2001). Fifty-eight percent of the watershed is covered by waterlogged spruce-pine wood (0G category) and 34% is covered by serpentine pine wood (0C category) (Pavloňová et al. 2008). Pluhův Bor has been a research watershed since 1992 and belongs to the Czech GEOMON network of small forest watersheds (Oulehle et al. 2008).

Methods

All serpentine bodies of the Czech Republic were identified from the geodatabase of the Czech Geological Survey (CGS; Gürtlerová et al. 2002) based on archived 1:500,000 geological maps. The areal extent of serpentine bodies in the Czech Republic was evaluated (Fig. 1).

All rock outcrops in the Pluhův Bor watershed and its vicinity were mapped during the creation of a 1:1000 scale topographic map in 2002 (Hrdlička-Sokolov Ltd., Sokolov, Czech Republic, unpubl. data). Rocks were sampled at all major outcrops in the watershed and its immediate vicinity in autumn 2005. Rock samples were crushed and powdered in an agate mill. Prepared powders of 29 selected rock samples were dissolved in a mixture of H_2SO_4, HNO_3, and HF at 200 ºC and analyzed mostly by flame atomic absorption spectrophotometry (Flame AAS) and for FeO and SiO_2 by titration at the CGS, Prague.

Soils were sampled at four locations in the watershed, and the soil pool was estimated by excavating a quantitative pit with a surface area of 0.5 m^2 in June 1993 (Krám et al. 1997). Samples were taken from each organic and mineral soil horizon, and the mineral soil was also collected at 10-cm intervals from the surface of the mineral soil to a depth below 40 cm. The soil samples were air dried, weighed, and passed through either a 5-mm sieve for the organic soil or a 2-mm sieve for the mineral soil. Soil results are reported on an oven-dried (105 ºC) mass basis. Exchangeable base cations (Ca^{2+}, Mg^{2+}, K^+, Na^+) were determined by extracting 2.5 g of soil with 50 mL of a 1 M NH_4Cl solution for 12 hours using a mechanical vacuum

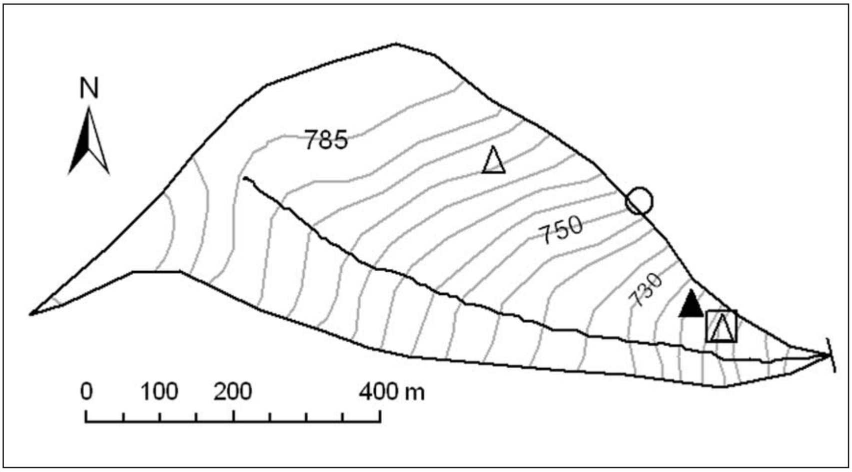


Figure 3. Topographic map of the intensively studied Pluhův Bor watershed showing the watershed boundary and the major stream channel. The contour interval is 5 m. Major sampling locations are shown: open triangle = throughfall plot; open circle = bulk precipitation plot; closed triangle = tree plot; open square = soil and soil water plot; line = weir.

extractor. Exchangeable acidity was determined with an identical procedure using a 1 M KCl solution. Individual base cations were analyzed by flame AAS in the laboratory at Syracuse University, Syracuse, NY, USA. Cation exchange capacity (CEC) was computed as the sum of the four exchangeable base cations and exchangeable acidity. Base saturation (BS) was calculated as the fraction of CEC occupied by base cations. Soil pH was determined in distilled deionized water using a glass combination electrode. The dilution ratios (solution mass:soil mass) were 5:1 for organic soils and 2.5:1 for mineral soils.

Spruce tissue samples were obtained in July 1994 from 4 felled trees at different altitudes of the watershed (Krám et al. 1997). One whole branch was collected from the upper, middle, and lower canopy, and twigs and foliage were separated after air-drying. The bole sample (circle shape) was sawn from the lowermost part of the felled tree. After air drying, its bark and wood were separated. Spruce samples and the Oi+Oe soil horizon samples were dried at 70 °C, ground, and dry-ashed. The ash was dissolved in concentrated HNO_3 plus 30% H_2O_2 and then in 10% HCl plus 10% HNO_3. Total cations were analyzed by inductively-coupled plasma (ICP) emission spectrophotometry at Cornell University, Ithaca, NY, USA.

In May 2003, foliar samples were collected from the mid-to-upper canopy with a pole pruner from 5 spruce trees situated at a plot in the lower part of the Pluhův Bor watershed (Fig. 3). Individual samples from six different foliage age groups were pooled together for chemical analyses of base cations. Unfortunately there was not enough sample collected for the third-year group because of technical difficulties. Total base cation concentrations of the 5 remaining age groups of foliage were determined by flame AAS after digestion with H_2SO_4 and HCl at the CGS.

The same pole-pruner technique was used at the identical plot in September 2004. Visually healthy needles for three age groups were collected from 15 trees. Samples were collected from each tree, placed in pre-weighed microfuge tubes, and 1 mL of 5% perchloric acid (PCA) was added to them in order to extract PCA exchangeable base cations (Minocha et al. 1994). Samples were transported to the laboratory on ice (Minocha et al. 2000) and stored at -20 °C until analyzed. They underwent 3 freeze-thaw cycles, then were centrifuged at 13,000 x *g* for 10 min (Minocha et al. 1994). Exchangeable cations were analyzed on fresh-weight basis using a simultaneous axial ICP emission spectrophotometer (Vista CCD, Varian, Palo Alto, CA, USA) and Vista Pro software (Version 4.0) at the USDA Forest Service, Durham, NH, USA. Sample supernatants were diluted 100x with deionized water prior to analysis.

Hydrochemical sampling of a watershed underlain by serpentine (Vlčí Kámen; Fig. 2) started in January 1988. In 1991, water sampling was transferred to the better hydrologically defined watershed of Pluhův Bor, and a V-notch weir was built there (Figs. 2 and 3). The outflow from Pluhův Bor was monitored continuously using a water-level recorder. Regular hydrologic and hydrochemical monitoring of the watershed has been conducted from 1992 to the present. Water monitoring consisted of measurements of bulk (open area) precipitation, spruce canopy throughfall, soil water in the organic and upper mineral soil, and streamwater (Fig. 3). Water was collected at monthly intervals with the exception of streamwater, which was collected weekly and more intensively during some high-flow events. Bulk precipitation and throughfall concentrations were multiplied by water quantities of individual samples to determine annual fluxes of chemical elements. Mass fluxes of individual solutes in streamwater were calculated using annual discharge-weighted average solute concentrations and annual water output. For detail description of the analytical procedures used, see Krám (1997) and Krám et al. (1997). Cations were analyzed by AAS or ICP methods at the CGS.

Above the V-notch weir, a 100-m reach was established and three replicate samples were collected from each major habitat type (pool, riffle, run) in June 2007, for a total of nine samples. Benthic macroinvertebrates were collected using a net and by scrubbing all rocks and disturbing sediment within 30 cm of the net frame. Specimens were usually identified to the family level (Krám et al. 2008).

Results and Discussion

There are 38 relatively large occurrences of serpentine rocks in the Czech Republic (Fig. 1). The area of these individual bodies is between 0.3 and 8.5 km^2. The total area covered by these serpentines is 67.8 km^2, which represents 0.09% of the country. The largest serpentine bodies are the Vlčí Hřbet (Fig. 2), the focus of this paper, between Prameny and Mnichov in northwestern Czech Republic (8.53 km^2), and the serpentine close to Mohelno (8.02 km^2) in southeastern Czech Republic (Fig. 1). Two other major serpentine bodies have an area between 4 and 5 km^2, and five bodies have an area between 1 and 3 km^2.

In total, 47 outcrops were described in the Pluhův Bor watershed and its immediate vicinity. Twenty-four (51%) outcrops were formed by serpentinite, seven (15%) by tremolite schist or tremolitite, six (13%) by actinolitic schist or actinolitite, and another six (13%) by amphibolite and other geochemically similar rocks. The remaining four outcrops were composed of other rocks (Table 2).

A geochemical comparison of serpentinites and other ultramafic and mafic rocks occurring in the watershed is shown in Table 3. The four major rock types differ markedly in chemical composition. Tremolite schists and serpentinites are characterized by extremely high concentrations of Mg, Ni, and Cr, and only negligible concentrations of K, Na, and Al. These rocks, therefore, create a very unusual environment for biota. It should be noted that the K concentrations are higher in actinolite schist and amphibolite, but the absolute values are still very low. Moreover, serpentinite contains negligible concentrations of Ca, but that is not the case for the tremolite and actinolite schists, nor for amphibolite. The lowest content of SiO_2 and the highest content of crystalline water (H_2O+) were found in serpentinite.

Serpentinite concentrations of the major oxides (SiO_2, MgO, and Fe_2O_3) and crystalline water (H_2O+) at Pluhův Bor (Table 3) are similar to average world serpentinite values calculated from the data in the review edited by Roberts and Proctor (1992). However, the serpentinite at Pluhův Bor contains lower amounts of K_2O (two thirds), CaO (one fifth), and especially NaO (one tenth of the global average value).

Soils in the Pluhův Bor watershed are moderately deep, roughly 1 m (Hruška and Krám 2003), and most soils are Eutric Magnesic Cambisols (Eutric Inceptisols). The mean documented depth of the upper mineral soil (to the C horizon) in the soil pits was 70 cm, and the mean depth of forest floor was 6 cm (Krám et al. 1997). Soils exhibited high base saturation, increasing with depth and reaching essentially 100% in the C horizon. Soil

Table 2. List of all rock types observed at outcrops of the Pluhův Bor watershed and its immediate vicinity within an area of approximately 0.3 km^2 in 2005.

Rock	Documented outcrops	Samples collected	Samples analyzed
Serpentinite	24	52	16
Tremolite schist, tremolitite	7	14	7
Actinolite schist, actinolitite	6	17	3
Amphibolite, amphibole gneiss, amphibolized mylonite	6	10	2
Derivate of ultramafics – deformed pegmatite	1	4	1
Gabbro	1	1	0
Calc–silicate rock	2	2	0
Total	47	100	29

Table 3. Elemental composition (mass percentage) of major rocks in the Pluhův Bor watershed. Abbreviations: n = number of rock samples; Md = median; SD = standard deviation; H_2O+ = crystalline water determined as loss on ignition at 1050 °C; H_2O- = moisture content determined by heating to 110 °C.

	Serpentinite (n = 16)			Tremolite schist (n = 7)			Actinolite schist (n = 3)			Amphibolite (n = 2)	
%	Mean	Md	SD	Mean	Md	SD	Mean	Md	SD	Mean, Md	SD
CaO	0.34	0.05	0.53	7.27	8.37	3.77	9.78	9.76	1.03	8.8	0.2
MgO	36.0	36.1	1.3	24.9	24.2	2.3	12.6	15.2	3.9	8.0	1.8
K_2O	0.018	0.020	0.008	0.024	0.020	0.014	0.15	0.16	0.02	0.23	0.02
Na_2O	0.022	0.020	0.015	0.087	0.080	0.046	2.8	2.1	1.1	4.5	0.7
Ni	0.197	0.197	0.029	0.131	0.122	0.030	0.023	0.028	0.012	0.007	0.002
Cr	0.241	0.252	0.048	0.255	0.217	0.163	0.055	0.042	0.044	0.010	0.003
Al_2O_3	1.21	1.00	0.73	2.60	3.12	1.15	14.5	13.5	1.8	16.4	0.2
Fe_2O_3	6.37	6.37	0.72	4.06	3.51	2.77	2.03	2.05	0.34	2.4	0.4
FeO	1.53	1.33	0.77	3.99	3.67	1.72	6.71	6.78	0.55	6.8	0.3
MnO	0.131	0.128	0.022	0.13	0.12	0.04	0.17	0.16	0.02	0.17	0.01
H_2O+	11.8	12.0	1.0	4.6	4.2	1.1	2.7	2.9	0.6	1.9	0.2
H_2O-	0.86	0.87	0.31	0.17	0.14	0.07	0.21	0.16	0.07	0.2	0.01
SiO_2	41.0	40.7	1.5	51.3	51.9	3.2	47.4	45.7	2.5	48.9	0.4

pH_{H_2O} increased steadily with depth from 3.8 (Oi+Oe) and 4.0 (Oa) to 5.0 (A) and 5.8 (B) and then to nearly neutral values (6.7) in the C horizon. Very high concentrations of Mg were observed in the soil exchange complex. Concentrations of exchangeable Mg increased from 0.7 g kg^{-1} in the litter (Oi+Oe) to 2.4 g kg^{-1} in the humus (Oa), decreased markedly in the uppermost mineral soil, and then increased steadily in the deeper mineral soils (Table 4). Pools of exchangeable Mg were high in the forest floor (12 g m^{-2}) and in the deepest mineral soil examined (60 g m^{-2}), but exhibited lower values (3 g m^{-2}) in the uppermost mineral soil, probably due to acidification and leaching by acidic throughfall fluxes and spruce litterfall (Krám et al. 1997).

Spruce tissue concentrations and pools of elements are summarized in Table 5. Among the base cations, Ca exhibited the highest concentrations and pools in tree tissue compartments with the exception of cones. The highest concentrations were found in bole bark. In contrast to non-serpentine stands, Mg concentrations and pools in spruce tissues were very high (Krám et al. 1997). The highest concentrations of K were found in the foliage, and concentrations of Na were very low in all compartments. Extremely high concentrations of Ni were observed, and Ni was especially concentrated in the bole bark (Table 5).

Elemental concentrations in foliage at Pluhův Bor were similar to values reported by Kaupenjohann and Wilcke (1995) at a serpentine site with a 120-year old *Picea abies* stand at Zell in the Fichtelgebirge, Germany. Total foliage concentrations at Pluhův Bor were 150% for Mg and 70% for Ni of the needle concentrations at Zell. Foliar concentrations of nutrient base cations and potentially toxic Ni were also compared with deficient and optimum concentrations proposed by several authors (Innes 1993, Zech et al. 1985, Zoettl et al. 1989). Foliar K appeared to be deficient at Pluhův Bor, with concentrations at only 70–85% of the published critical values. In contrast, foliar Ca was in the upper optimum range, and Mg exceeded the upper maximum by at least 90%. Concentrations of Ni in *Picea abies* at Pluhův Bor were about twice the upper critical concentration, representing the point at which yield starts to decline (5.8 g kg^{-1}; Burton et al. 1983, Innes 1993) for *Picea sitchensis* (Bong.) Carr (Sitka Spruce). Such a value is not directly available for *Picea abies*, but it is possible that the two *Picea* species are similar. The annual increment of bole wood biomass was only about one third of that in non-serpentine stands in the vicinity of Pluhův Bor (Krám et al. 1997).

At Pluhův Bor, total and exchangeable Ca and Mg concentrations increased with needle age (Table 6). However, an opposite trend of lower K concentrations was measured in older needles, suggesting that the deficient K may be retranslocated from the older to the current needles (Ende and Evers 1997, Kaupenjohann et al. 1989).

Net annual uptake of base cations fixed to above-ground tree biomass in the watershed (Pavloňová et al. 2008) was calculated from the tissue chemistry of bole wood and bole bark (Krám et al. 1997) which was divided linearly

Table 4. Mean values of chemical properties of the fine soil fraction (<2 mm for mineral soil, <5 mm for organic soil) in the Pluhův Bor watershed based on sampling in June 1993 (Krám 1997). The uppermost horizon Oi+Oe was analyzed for total (tot) and exchangeable (ex) fractions. All other horizons were only analyzed for the exchangeable fraction. Abbreviations: CEC = cation exchange capacity (in millimoles of charge); BS = base saturation; nd = not determined.

	Concentration ($g\ kg^{-1}$)					CEC		Concentration ($mmol_+\ kg^{-1}$)			
Soil horizon or stratum	Ca	Mg	K	Na	Ni	($mmol_+\ kg^{-1}$)	BS (%)	Ca^{2+}	Mg^{2+}	K^+	Na^+
Oi+Oe (tot)	1.310	1.39	0.360	0.025	0.099						
Oi+Oe (ex)	1.000	0.72	0.270	0.021	nd	236	48	51.0	60	6.90	0.9
Oa	0.760	2.41	0.300	0.025	nd	346	59	38.0	198	7.60	1.1
0–10 cm	0.048	0.08	0.041	0.008	nd	82	12	2.4	6	1.00	0.34
10–20 cm	0.027	0.17	0.013	0.007	nd	45	35	1.4	14	0.34	0.31
20–30 cm	0.068	0.42	0.007	0.006	nd	44	86	3.4	34	0.17	0.27
30–40 cm	0.098	0.69	0.006	0.006	nd	64	98	4.9	57	0.14	0.25

	Dry weight	Pool ($g\ m^{-2}$)					CEC	Pool ($mmol_+\ m^{-2}$)			
	pool ($kg\ m^{-2}$)	Ca	Mg	K	Na	Ni	($mmol_+\ m^{-2}$)	Ca^{2+}	Mg^{2+}	K^+	Na^+
Oi+Oe (tot)	3.1	4.0	4.4	1.10	0.076	0.31					
Oi+Oe (ex)	3.1	3.2	2.2	0.83	0.067	nd	730	158	184	21	3
Oa	4.1	3.1	9.9	1.21	0.101	nd	1420	156	812	31	4
0–10 cm	40.0	1.9	3.0	1.61	0.308	nd	3260	95	245	41	13
10–20 cm	68.0	1.9	11.4	0.90	0.490	nd	3100	93	935	23	21
20–30 cm	89.0	6.0	36.8	0.59	0.550	nd	3910	298	3030	15	24
30–40 cm	84.0	8.3	58.5	0.47	0.490	nd	5360	413	4810	12	21
Forest floor	7.2	6.3	12.1	2.00	0.200	nd	2150	314	996	52	7
Mineral soil	281.0	18.0	110.0	3.60	1.800	nd	15600	899	9020	91	80

by mean forest age (Pavloňová et al. 2008). The following net uptake of nutrient base cations was determined: Ca = 218 mg m^{-2} yr^{-1}, Mg = 50 mg m^{-2} yr^{-1}, and K = 27 mg m^{-2} yr^{-1}. The uptake of Na, the sole base cation that is not a nutrient, was only 1 mg m^{-2} yr^{-1}. The mean annual weathering rates of base cations were estimated by the biogeochemical MAGIC model (Cosby et al. 2001) calibration procedure. The fitted annual weathering rates were dominated by Mg (2800 mg m^{-2} yr^{-1}). Weathering release of Ca was much lower (200 mg m^{-2} yr^{-1}), but still significant, and the weathering releases of Na and K were negligible at 12 and 2 mg m^{-2} yr^{-1}, respectively (Hruška and Krám 2003). Long-term mean atmospheric deposition of K, apparently the most critical nutritional base cation, was 13 mg m^{-2} yr^{-1} in wet deposition and

Table 5. Mean total element concentrations and pools of *Picea abies* tissues in the Pluhův Bor watershed. Concentrations are based on sampling in July 1994 (Krám 1997). Pools of tree compartments are from calculations of Pavloňová et al. (2008).

	Concentration in g kg^{-1}				Ni
Spruce tissue	Ca	Mg	K	Na	(mg kg^{-1})
Foliage	6.53	2.71	3.27	0.027	11.4
Branches and twigs	3.67	1.00	1.80	0.017	10.0
Bole bark	8.37	1.57	2.03	0.010	20.0
Bole wood	0.53	0.16	0.14	0.010	0.70
Cones	0.16	0.47	1.10	0.022	10.9

	Dry weight	Pool in g m^{-2}				Ni
Spruce tissue	pool in kg m^{-2}	Ca	Mg	K	Na	(mg m^{-2})
Foliage	1.0	6.6	2.7	3.3	0.027	11.6
Branches and twigs	2.4	8.7	2.4	4.2	0.039	23.7
Bole bark	1.9	15.5	2.9	3.8	0.019	37.0
Bole wood	15.3	8.1	2.5	2.1	0.154	10.7
Total	20.5	38.8	10.5	13.4	0.240	82.9

Table 6. Mean total and exchangeable element concentrations in *Picea abies* foliage by age class in the Pluhův Bor watershed. The first set of samples was collected in May 2003 (J. Albrechtová and Z. Lhotáková, Charles University, Prague, Czech Republic) and analyzed at the Czech Geological Survey (Prague, unpubl. data). Samples from 2003 were pooled for each age class. The second set of samples was collected in September 2004 and analyzed at the USDA Forest Service (Durham, NH, unpubl. data). Samples from 15 individual trees per age class were analyzed. The data shown for exchangeable ions are mean ± standard error. nd = not determined.

	Total concentration in 2003			Exchangeable concentration in 2004		
Foliage	Dry weight (g kg^{-1})			Fresh weight (g kg^{-1})		
age (yr)	Ca	Mg	K	Ca	Mg	K
1	2.15	1.80	3.44	0.54 ± 0.05	0.35 ± 0.07	0.95 ± 0.04
2	2.89	2.29	3.00	0.97 ± 0.07	0.49 ± 0.12	0.78 ± 0.05
3	nd	nd	nd	1.21 ± 0.06	0.54 ± 0.10	0.72 ± 0.05
4	3.17	2.60	2.42	nd	nd	nd
5	3.90	2.70	2.08	nd	nd	nd
6	4.33	2.85	2.25	nd	nd	nd

4 mg m^{-2} yr^{-1} in dry deposition at Pluhův Bor. The difference between the K uptake of the trees (27 mg m^{-2} y^{-1}) and the deposition and weathering fluxes of K (19 mg m^{-2} y^{-1}) suggests that there is an additional source of base cation uptake by the trees which we are not accounting for and it is likely leaching from the soil exchangeable complex.

Serpentinite had the lowest Ca/Mg and K/Mg ratios of the four main rock types (Table 7). The ratios were higher in tremolite schist and especially in actinolite schist, and were greatest in amphibolite. Ca/Mg and K/Mg ratios in spruce foliage were much larger than in the soil. A serpentine soil sampled at Pluhův Bor exhibited a range of exchangeable Ca/Mg values from 0.1 in the deepest mineral soil to 0.6 in the shallowest mineral soil. The ratio was even higher in the litter (1.4). A similar pattern was apparent for the K/Mg values with the exception of the highest ratio, which was found in the uppermost mineral horizon. These two ratios were higher in surface horizons than in subsoils partially because Ca and K supplied by atmospheric deposition are retained near the surface by cycling in vegetation. Trees growing on serpentine take up and store more Ca and K, which are returned to the surface when the foliage falls to the ground and decomposes. Some nutrients are removed from senescent foliage before it falls. Similar Ca/Mg ratios in serpentine soils were reported in California, North Carolina, Maryland,

Table 7. Mean mass ratios (g g^{-1}) of nutrient base cations in different compartments of the Pluhův Bor watershed.

Compartment	Ca/Mg	K/Mg
Rock (total concentrations)		
Serpentinite	0.006	0.0003
Tremolite schist	0.4	0.0006
Actinolite schist	0.8	0.007
Amphibolite	1.3	0.02
Soil (exchangeable concentrations)		
Organic horizon Oi+Oe	1.4	0.4
Organic horizon Oa	0.3	0.1
Mineral soil 0–10 cm	0.6	0.5
Mineral soil 10–20 cm	0.2	0.08
Mineral soil 20–30 cm	0.2	0.02
Mineral soil 30–40 cm	0.1	0.009
Water (total concentrations)		
Bulk precipitation	5.7	0.7
Spruce throughfall	1.8	1.5
Soil water O horizon	0.2	0.2
Soil water A horizon	0.06	0.03
Streamwater	0.1	0.007
Picea abies (total concentrations)		
Foliage	2.4	1.2
Cones	0.3	2.3
Branches and twigs	3.7	1.8
Bole bark	5.3	0.6
Bole wood	3.3	0.9

Pennsylvania, New York, and Maine in the USA; Newfoundland, Canada (Rajakaruna et al. 2009); and France (Chardot et al. 2007).

Water Ca/Mg and K/Mg ratios (Table 7) declined steadily in the Pluhův Bor watershed from bulk precipitation and throughfall to the soil water in the mineral soil. An extremely low K/Mg ratio (0.007) was found in streamwater, which demonstrates convincingly the shortage of K in the watershed (Krám et al. 1997). Streamwater chemistry was also evaluated in 2001–2003 for a comparative study of Pluhův Bor with two other serpentine watersheds (Table 1). In that comparative study, higher values of K/Mg (0.013) calculated at Pluhův Bor were comparable to streamwater ratios at Vlčí Kámen (0.013) and Císařský Les (0.010) (Krám 2006).

According to some published results, highly deformed and sheared serpentines could act as an aquifer. Storage in this aquifer would delay stream runoff in such serpentine watersheds, and there would be more streamwater available later during the drier season. For example, a gradual release in stream runoff at the Clear Creek watershed in California, USA was attributed to fractures in tectonically sheared serpentine which retain precipitation and release groundwater gradually (Alexander et al. 2007). Slower runoff from sheared serpentine watersheds than from watersheds with more massive rock was also demonstrated in Japanese watersheds (Table 1); high flow was delayed, compared with flow from non-serpentine watersheds (Onda et al. 2001).

At Pluhův Bor, long-term mean annual precipitation and throughfall were 861 and 529 mm yr^{-1}, respectively, and mean streamwater runoff was 273 mm yr^{-1}. Long-term mean air temperature was 6 ºC, with the lowest mean monthly temperature in January (-3 ºC) and the highest in July and August (16 ºC). Mean lowest, median, and highest daily discharges of individual years were 0.03 L s^{-1} (0.014 mm d^{-1}), 0.52 L s^{-1} (0.21 mm d^{-1}), and 39 L s^{-1} (15.7 mm d^{-1}), respectively. Of the fourteen forested Czech catchments of the GEOMON network (Krám and Fottová 2007), Pluhův Bor had the largest percentage of runoff occurring during the wettest days of the year. These flow characteristics suggest a rapid or "flashy" hydrologic response, which is inconsistent with the development of an important aquifer within the serpentinite observed in the studies in California and Japan. Reasons for this discrepancy are unclear, but soil grain-size fraction (especially clay percentage and clay mineralogy) could contribute to the hydrologic differences.

Smectites are common secondary clay minerals in serpentine soils. Forces between layer complexes in smectites do not prevent entry of water, resulting in enormous expansion when the smectites are saturated with water. Smectites were detected at Pluhův Bor, and the areal masses of clay (<0.002 mm: 5 kg m^{-2}) and silt (0.002–0.063 mm: 110 kg m^{-2}) in the uppermost 40 cm of the mineral soil were considerably greater (almost one order of magnitude greater for clays) in comparison to the non-serpentine site nearby (Krám 1997). The clay fraction, particularly the swelling smectites, could lower the soil infiltration rate and increase the near-surface contribution to stream runoff, which may explain the flashy hydrology described above.

Pluhův Bor streamwater exhibited an extremely rapid decrease of sulfate concentrations in the 1990s (Hruška and Krám 2003, Majer et al. 2005). The relation of sulfate to flow shifted from positive in the early 1990s to negative in the 2000s, which indicates that the soil sulfate pool has become progressively depleted (Shanley et al. 2004). Magnesium-sulfate-bicarbonate streamwater (in equivalent units) dominated previously due to sulfur pollution. Streamwater shifted gradually to more natural magnesium-bicarbonate water where Mg^{2+} is the predominant cation and bicarbonate (HCO_3^-) is the dominant anion. Streamwater pH was usually in the range between 6.9 and 8.1 (Hruška et al., in press). Streamwater was partially acidified only during short-term hydrologic episodes when the runoff was dominated by flow through surface soil horizons. A typical feature of serpentine waters is an elevated concentration of Ni. The long-term mean streamwater concentration of potentially toxic Ni was 88 $\mu g\ L^{-1}$ at Pluhův Bor (standard deviation = 45 $\mu g\ L^{-1}$, range = 23–253 $\mu g\ L^{-1}$). These values were always above 20 $\mu g\ L^{-1}$, the European Union annual mean limit for inland surface waters (Anonymous 2008).

Benthic macroinvertebrates in the lowermost part of the serpentine stream at Pluhův Bor were examined (Krám et al. 2008). Nineteen taxons were identified in the bottom sediments, including sixteen families of *Insecta* (insects), and one taxon each of *Arachnida* (includes mites), *Oligochaeta* (worms), and *Turbellaria* (flatworms). Within the insects, there were 7 families of *Diptera* (flies), 3 families of *Coleoptera* (beetles) and *Trichoptera* (caddisflies), 2 families of *Plecoptera* (stoneflies), and 1 family of *Ephemeroptera* (mayflies). The most abundant individuals at Pluhův Bor were *Leuctridae* (roll-winged stoneflies) from *Plecoptera*, and *Simuliidae* (black flies) and *Chironomidae* (midges) from *Diptera*. The richness in biodiversity at Pluhův Bor was only slightly lower than expected from the regional relationship between the number of taxons and water pH. The described taxons were similar to taxons observed in other Czech streams with circum-neutral pH.

Conclusions

The total area covered by ultramafic (serpentine) rocks in the Czech Republic is 68 km^2, which represents almost 0.1% of the total land area. This study focused on field research at a small watershed on the largest serpentine body of the Czech Republic with an area of 8.5 km^2. The whole serpentine ridge originally belonged to the pine woodland area that includes the association *Asplenio cuneifolii-Pinetum sylvestris*. However, most of the forest stands in the Pluhův Bor watershed were converted into even-aged *Picea abies* plantations.

Serpentinites and tremolite schists in the watershed were characterized by extremely high concentrations of Mg and Ni and by negligible concentrations of K, creating an unusual environment for vegetation. Very slow *Picea abies* growth appears to be caused by K deficiency, Mg oversupply, and Ni toxicity. However, foliar Ca was well above the deficiency level probably because tremolite and actinolite schists and amphibolites in the watershed were important sources of Ca to the soil and vegetation. Mineral weathering and S from atmospheric deposition generated near-neutral magnesium-bicarbonate-sulfate streamwater with a high concentration of Ni. The stream was characterized by a relatively rich community of benthic macroinvertebrates.

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