Plant Soil (2023) 493:249–266
https://doi.org/10.1007/s11104-023-06228-8

RESEARCH ARTICLE

Edaphic and topographic gradients have differential influence on woody species assemblages on ultramafic and non-ultramafic soils in an African Savanna

**T. Nyenda · T. Musungwa · T. Piyo · P. Kowe ·
J. Muvengwi · E. T. F. Witkowski**

Received: 8 April 2023 / Accepted: 10 August 2023 / Published online: 23 August 2023

Abstract
Background and aims Understanding the determinants of plant species associations on unique ultramafic substrates is crucial for the study of restoration ecology. We investigated the influence of local edaphic and topographic gradients on woody species associations on ultramafic and non-ultramafic substrates along the Great Dyke of Zimbabwe.
Methods Vegetation attributes were assessed in 62 plots on ultramafic and adjacent non-ultramafic substrates at varying slope magnitude and orientation. Plant community comparisons and relationships with soil and topographic variables were analyzed using ANOVA and ordinations.
Results Aspect had more influence on woody composition, species associations and densities on ultramafic compared to non-ultramafic substrates. Lower species richness and tree/shrub densities were observed on ultramafic substrates. Soil Mg, Mg/Ca ratio, total Ni, Cr and Mn, and available Ni were significantly higher on ultramafic substrates. Most parameters (pH, Ca, Mg, Mg/Ca ratio; available Ni, Cr, Mn and total Mn) were similar between ultramafic east- and west-facing slopes, but only total Cr and Ni were higher on east-facing slopes. Only available Ni and Mn were higher on ultramafic piedmont than on slopes. Tree/shrub density and species richness were positively correlated with available Mn and Cr while negatively correlated with total and available Ni, pH, Mg/Ca ratio and herbaceous plant cover.
Conclusion Vegetation patterns on ultramafic substrates are partly driven by intra-site edaphic (metals and Mg/Ca ratios) and topographic gradients. Aspect has differential influence on woody vegetation assemblages on ultramafic and non-ultramafic substrates. Species associations and environmental determinants observed can be used in mine site rehabilitation planning.

Keywords Dyke · Endemic · Metallophytes · Metal levels · Mg/Ca ratio · Phytostabilisation · Serpentine

Introduction

Serpentine soils are scattered around the world covering around 1% of the earth's surface (Rajakaruna

Responsible Editor: Antony van der Ent.

T. Nyenda · J. Muvengwi · E. T. F. Witkowski
Restoration and Conservation Biology Research Group,
School of Animal, Plant and Environmental Sciences,
University of the Witwatersrand, Johannesburg,
South Africa

T. Nyenda · P. Kowe
Department of Geography, Environmental Sustainability
and Resilience Building Midlands State University, P. Bag
1020, Senga, Gweru, Zimbabwe

T. Nyenda (✉) · T. Musungwa · T. Piyo
Zimbabwe Mine Environment Research Network, No. 1
Adylin Road, Marlborough, Harare, Zimbabwe
e-mail: tatenyenda@yahoo.com

and Baker 2004). In some areas, they are located on off-shore islands, along continental margins and are derived from serpentine and other ultramafic rocks (Rajakaruna and Baker 2004). Approximately one third of the landmass in New Caledonia consists of ultramafic rocks (Coleman and Jove 1992; Rajakaruna 2004). Western North America is also characterized by both local and extensive occurrences of ultramafic rocks with areas of 520 km^2 in Washington, 1170km^2 in Oregon and 2860 km^2 in California (Kruckeberg 1985). Brazil has similarly large areas of ultramafic rocks, and Indonesia harbors 8000km^2 of ultramafic rocks (Baker et al. 2020; Brooks 1987). Ultramafic rocks are also found on the Great Dyke of Zimbabwe. The Dyke extends more than 550 km north-east to south-west of Zimbabwe, varying from 3 to 12 km in width (Wild 1965). However, the ultramafic region of Zimbabwe is one of the least-described and most poorly-explored serpentine regions of the world (but see Bangira 2010; Kativu et al. 2019; Wild 1965, 1974; Garnica-Díaz et al. 2023; Prendergast 2013; Werger et al. 1978).

Ultramafic soils have unique properties that usually support characteristic vegetation (Brooks 1987; Proctor and Woodell 1975; Whittaker 1954). At global scales they are reported to harbor high proportions of endemic plant species, with generally higher rates of endemism towards the equator (Kruckeberg 2002; Rajakaruna and Baker 2004). Ultramafic soils usually have stunted vegetation, extensive grasslands and unique plant communities often attributed to edaphic and other abiotic factors, including fire (Kativu et al. 2019; Wild 1965, 1974). Such soils have been reported to have high Magnesium/Calcium (Mg/Ca) ratios, generally low nutrient content, and often associated with high levels of Ni and other heavy metals (Bangira 2010; Oze et al. 2008; Wild 1965; Worst 1960). The soils are home to major mining activity and seldom used for agricultural purposes. Due to their low macronutrients such as N and Ca (Kumar et al. 2022) and high metal levels such as Ni and Cr, they are often viewed as “natural wastelands”, similar to mine tailings that are dumped after mineral processing (see Kumar et al. 2021; Ye et al. 2022; Wang et al. 2020).

Considerable attention to serpentine vegetation has been given outside of Africa (Garnica-Díaz et al. 2023). Serpentine flora is well studied not only for their taxonomic value, but also for their vitality in testing ecological and evolutionary scenarios, especially in California and other parts of Western-North America (Alexander et al. 2007; Harrison and Viers 2007; Safford and Harrison 2008; Harrison and Rajakaruna (2011), in tropical islands of Cuba and New Caledonia (Boyd et al. 2004; Kruckeberg 2002; Rajakaruna and Boyd 2009), and in Asia, Sri Lanka (Hewawasam et al. 2014; Galey et al. 2017). The studies in Asia mainly reported on endemism and the influence of rainfall gradients on plant communities (Hewawasam et al. 2014; Maas and Stuntz 1969), noting a high Mg/Ca ratio and Ni gradients as potential factors causing observed differences in plant assemblages on serpentine soils (Rajakaruna et al. 2009). While these studies provide insights into the general factors shaping vegetation communities on such substrates outside Africa, these findings have never been widely tested in Africa and in Zimbabwe, in particular, where topographic and climatic conditions markedly differ along the Great Dyke.

In Zimbabwe, only passing reference to serpentine vegetation was first made in the 1920s and 1930s (Blackshaw 1920; Henkin et al. 1998). Other studies described the grasslands of the Dyke with some contrasting findings, for instance, Rattray (1961) described them as *Andropogon gayanus* grasslands with *Panicum maximum* and *Themeda triandra* as surrogate species, while Rattray and Wild (1961) indicated the presence of *Andropogon Chirensis* and *Loudetia simplex* grasslands. More detailed descriptions were done in the northern Dyke where a general description of a small portion of the Horseshoe intensive conservation area was done (Barclay-Smith 1963). An extensive survey identified the species found across the Dyke more than 5 decades ago (Wild 1965) and another listed 30 endemic species (Mapaura 2002). These studies generated species lists which were neither linked to local microsite topographic and edaphic conditions nor species associations. In Zimbabwe, no studies have been done to investigate the role of topography and edaphic gradients in shaping woody vegetation occurrence patterns on serpentines and adjacent non-serpentine sites. Despite growing interest in the use of edaphically restricted plants for the study of ecology and physiology (Balkwill 2001), no attempt has been made so far to relate topographical and microscale edaphic influence to floristic composition, vegetation structure and the association of species on a serpentinic ultramafic substrate in the country.

Academic and industrial scientists have come together to explore how such plants can be used for both the phytoremediation of contaminated soils (Drozdova et al. 2019; Nascimento et al. 2021), and phytomining of toxic metals from metal-rich sites such as abandoned mine tailings (Brooks et al. 1998; Cerdeira-Pérez et al. 2019; Muthusamy et al. 2022; Reeves 2003; Walker et al. 1955). The study of plants growing under extreme soil conditions holds much promise, providing a model for both botanical studies as well a means for an alternative to environmental rehabilitation.

Natural topographic factors such as aspect and slope vary over space and this usually influences vegetation distribution (Cui and Zheng 2016; Malik et al. 2014; Woldu et al. 2020). Many studies observed significant influence of aspect on vegetation composition, species richness, production and structure due to its influence on solar radiation, air temperature and wind speed (Yang et al. 2006; Sternberg and Shoshany 2001; Woldu et al. 2020; Angessa et al. 2020; Yirdaw et al. 2015; Yuan et al. 2019), while slope magnitude has a similar effect due to its influence on water availability (Cui and Zheng 2016), with a few noting no effect (e.g. Gracia et al. 2007; Woldu et al. 2020). Slopes receiving lower solar radiation experience lower evapotranspiration rates and lower daily maximum temperatures in water stress periods, hence more favourable plant growing conditions, supporting the hypothesis that aspect influences vegetation. Some studies reported enhanced plant species richness, diversity and structure on steeper slopes compared to more gentle slopes, attributable to decreases in human disturbance regimes as slopes become steeper (Woldu et al. 2020), while some studies reported a negative relationship (Zhang et al. 2013) and no effect (Adhikari et al. 2022; Legendre et al. 2009; Song and Cao 2017). Despite contrasting reports about specific influences of aspect and slope on vegetation attributes, what is common is the mechanism of topographic effects on vegetation through varying solar radiation which in turn affects air and soil temperature, soil moisture, soil aggregation processes and nutrients (Ahmed et al. 2022; Kutiel and Lavee 1999; Sternberg and Shoshany 2001; Yang et al. 2020).

Understanding natural edaphic and topographic factors affecting woody plant distribution on botanically unique sites of high endemism such as the Great Dyke is key in crafting sustainable management plans on the site and for restoration purposes. Serpentinic ultramafic soils of the Zimbabwe Great Dyke present an opportunity for studies on plant–environmental relationships that are critical in reclamation of similar substrates such as mine tailings and rock waste dumps that continue to cover increasing areas of the landscape due to global surges in mining activities (Maus et al. 2022). While some attribute differences in vegetation composition and structure to local microsite edaphic and topographic conditions, little attention has been given to intensive description of the particular edaphic and topographic factors and their roles in shaping woody plant species composition and assemblages on these natural substrates. Studies that jointly investigate the influence of aspect, catena, total and bioavailable fractions of metals and Mg/Ca ratios on both ultramfic and non-ultramafic sites, including trees, shrubs and seedlings, are limited. Our study aimed to identify woody plant species, their associations, and densities, and relate them to topographic factors such as aspect and slope, as well as selected soil metals and Mg/Ca ratio. We posed the following questions: (1) What are the woody species growing on serpentinic ultramafic substrates? (2) How do their densities vary with aspect and catenal position? (3) How do their associations vary with aspect and catenal position? (4) How does species composition vary between ultramafic and adjacent non-ultramafic substrates? (5) What is the relationship between vegetation and aspect, heavy metal levels and Mg/Ca ratio?

Materials and methods

Description of study area

Location and climate

The study was carried out in the northern part of the Great Dyke, a unique linear geological feature that stretches about 550 km from the north-east to south-west across the center of Zimbabwe. The study region is centered on longitude 30° 54′ 28″ E and latitude 17° 09′ 35″ S on and around the Mutorashanga Pass (Fig. 1). Specific study sites were on

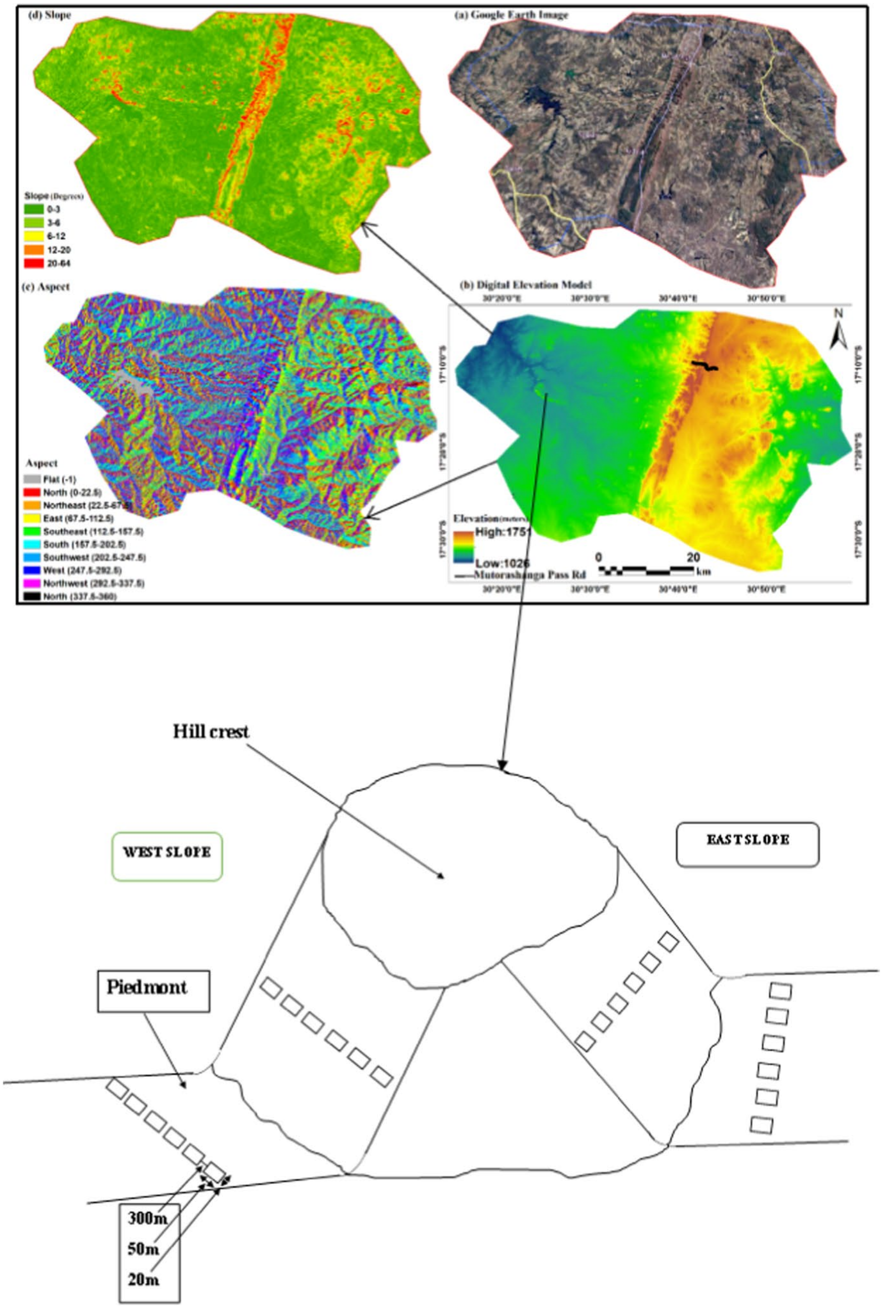


Fig. 1 Map of study sites and schematic diagram of layout of sampling plots

the hill slopes and piedmont at Mutorashanga pass. Twelve locations sampled include three Dyke west- and east-facing slopes of the hills, two flat grasslands at the piedmont (ultramafic substrates) and four reference (2-east facing and 2-west-facing) off-Dyke patches (non-ultramafic substrates) of similar exposures, all adjacent to the Dyke. The area receives a total annual rainfall of between 600 and 800 mm and a mean maximum temperature range of 19°-23 °C (Mugandani et al. 2012).

Geology, soils and flora

The Mutorashanga pass area is extensively covered by ultramafic rocks (Worst 1960). Serpentine is a mineral derived from dunite or other ultramafic rocks such as peridotite and serpentinite, which is composed of olivine, orthopyroxine, and about 3% chromite (Alexander et al. 2007; Wild 1965). The orthopyroxine is usually not present in the Dyke olivines. Both olivine and pyroxenite are magnesium rich silicates, which give serpentine soils their characteristic high Mg/Ca ratio. The area has minor intrusions of norite and pyroxenite. Generally, the upper layers are composed of mainly dunite, harzburgite and pyroxenite with lower strata containing serpentine, chromite and sulfide minerals (Worst 1960; Wilson and Prendergast 2001). The adjacent off-Dyke patches contain granite rocks. The soils of Mutorashanga are generally typical serpentines with high Mg/Ca ratio and nickel concentrations. The soils are rocky, gravelly and generally shallow on both hills and serpentine piedmonts characterizing the Dyke margins.

Vegetation on both hills and piedmont is typically grasslands to slightly wooded grasslands that are botanically unique and metal tolerant (Wild 1974). Typical woody species found in the area are dwarf, and dominant species include *Diplorhynchus condylocarpon* and *Ozoroa* insignis (Wild 1965). Dominant species in the grasslands are *Loudetia simplex*, *Themeda triandra* and *Andropogon gayanus* (Wild 1965). Typical succulents are *Eurphorbia wildii* (Wild 1974). The norite intrusions are reported to be dominated by typical Miombo co-dominants, namely *Brachystegia spiciformis* and *Julbernardia globiflora (*Wild 1965*)*. Vegetation of the off-Dyke patches is dominated by *Brachystegia spiciformis*, *Julbernardia globiflora* and *Uapaca kirkiana*.

Research design and sampling points layout

The field survey followed a stratified systematic sampling protocol. The study area was first stratified into two sites in accordance with location (Dyke and off-Dyke). In the Dyke and adjacent off-Dyke reference, the sites were further stratified in accordance with catenal position (i.e., hill foot, flat land-piedmont (0–5% slope) and hill bottom slopes (20–25% slope). The slopes of the hills were further stratified by aspect into west- and east-facing. These slopes were replicated three times for each aspect in the Dyke and twice for the adjacent reference site to eliminate the influence of chance in the vegetation and soil assessments (McKillup 2012). At each Dyke and adjacent off-Dyke site, six (6), 50 × 20 m plots (Campbell et al. 1995; Witkowski and Garner 2008) were systematically laid at 300 m intervals along a 1.5 km transect set at an approximate midpoint on the slope aligned along the contour, starting from a randomly chosen endpoint that was selected using a coin toss. The six plots were sufficient to capture 100% of the woody species found in the area as per the preliminary plot size testing exercise done during reconnaissance (Martinez-Ruiz and Marrs 2007). Total number of plots was 36 for the Dyke hills, 12 for Dyke piedmont and 24 for the adjacent off-Dyke hills. For woody seedling assessments, a 100 m line transect was marked on each of the sampling sites used for tree/shrub assessments, with five replicate 1 × 1 m quadrats at each point. The length of transect and number of quadrats were tested for sampling sufficiency in the preliminary survey and captured more than 95% of the species encountered. A total of 180 quadrats were laid in the Dyke hills, 60 for Dyke piedmont and 60 for the off- Dyke adjacent substrates.

Determination of species composition and density

In each plot all woody plant taxa encountered above 50 cm in height were identified to species and their abundance recorded, and density expressed per ha. Woody seedlings/juveniles (i.e., plants with height less than 50 cm) were identified and abundance determined in the 1x1m quadrats. Aerial covers of woody seedlings and herbaceous vegetation were each visually estimated as a percentage. Species richness for each sampling plot was determined following identification of each species.

Soil sampling and laboratory analysis

Soil sampling

To explore how the edaphic factors were related to observed vegetation patterns, 22 soil samples were taken at 0–15 cm depth from selected plots used for vegetation assessments. The sampling points were selected using woody vegetation densities and composition gradients. The 22 samples were collected from 2 to 3 points of each sampled face (i.e., 6 Dyke west-slopes, 6 Dyke east-slopes, 6 Dyke piedmont, 2 Dyke *Brachystegia spiciformis-Julbernardia globiflora* patches and 3 off-Dyke patches. At each point soil samples were collected from 5 quadrats laid at the center of the 50 × 20 m plot. In each quadrat samples were collected from the center using an 8 cm diameter bucket auger or a garden trowel where gravel and rocks were limiting. These were bulked and thoroughly mixed in the field before a 500 g homogenous sample was extracted and placed in a well labelled clean plastic bag. Samples were tied and appropriately stored in a plastic bag to avoid contamination before being transported to the laboratory at the Soil Chemistry Research and Specialist Services Department in Harare, Zimbabwe.

Laboratory analysis

All samples were air-dried before being passed through a 2 mm stainless steel sieve to remove non-soil particles (Anderson and Ingram 1993) before analysis. Care was taken to avoid sample contamination during sample preparation. Subsequently, soils were tested for pH, exchangeable Mg and Ca using standard laboratory methods (Okalebo et al. 2002). Soil pH was determined using the $CaCl_2$ method specified in Brady and Weil (2002). Exchangeable bases were determined by colorimetry following methods described by Anderson and Ingram (1993). Total heavy metal content was analyzed using the fusion method, following extraction with sodium peroxide and sodium carbonate (Zaranyika and Chirinda 2011). The samples were analyzed using the Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES SPECTRO ARCOS FHS12). Available metals were determined after sample extraction by EDTA followed by reading concentrations on an Atomic Absorption Spectrophotometer (Zaranyika and Chirinda 2011).

Data analysis

Data analysis was done using two-way analysis of variance (ANOVA) and multivariate ordination techniques. Firstly, before ANOVA, data were tested for normality using the Kolmogorov-Smirnov test in SPSS versions 20.0, and log-transformed before analysis when necessary. Two-way ANOVA ($P < 0.05$) was used to test differences of vegetation (woody densities, species richness) and soil (Ni, Cr, Mg, Ca, Mn levels and Mg/Ca ratios) among sampled sites using site (Dyke versus off-Dyke) and aspect as factors (Cañadas et al. 2010; McKillup 2012). In the event of a significant ANOVA test, a post hoc (LSD) test was done to see the pair of sites contributing to that (Cañadas et al. 2010).

Differences in plant communities among sampled sites and species-soil relationships were tested using ordination techniques in CANOCO-5. An unconstrained unimodal Detrended Correspondence Analysis (DCA) was used to test differences in plant communities among sites using species composition and abundance data. A DCA was used since the gradient length of the first axis was 6.2 (i.e. greater than 4 SD units), requiring the use of the unimodal DCA rather than linear PCA (Cañadas et al. 2010). This analysis was done in two ways, one down-weighting rare species to reduce potential distortion of the analysis, the other without down-weighting, but both presented similar results. A DCA scatterplot was used to display the separation of the 60 sites using woody species composition gradients. A DCA biplot was computed to show major species associations at particular sites. Canonical Correspondence Analysis (CCA) and Redundancy Detrended Analysis (RDA) were used to test the relationship between vegetation attributes, soil and aspect, which was computed as a dummy environmental variable. The techniques yield ordination monoplots, biplots and triplots that show samples and species as points, while environmental variables are displayed as vectors. Samples and species in closer proximity means high positive relationship, while acute angles between vectors depict a positive relationship, those at 90° unrelated, above 90° showing a negative relationship and with those at 180° strongly negatively related. For vegetation and soils data, there were only 2 off-dyke sites excluding the piedmont to eliminate distortions related to influence of agricultural activities at the off-Dyke piedmonts and restrictions due to lack of permission to extract soil samples by some landowners.

Results

General vegetation densities on- and off-Dyke substrates

The east-facing slopes of the Dyke had significantly higher woody tree/shrub density and seedling aerial cover than the west-facing slopes. However, both

Dyke sites had significantly lower woody densities than their corresponding off-Dyke sites (Fig. 2a). Woody seedlings aerial covers were similar for both aspects on- and off-Dyke, with Dyke sites having significantly higher cover than off-Dyke sites (Fig. 2b).

Woody species composition on- and off-Dyke hill slopes

A total of 19 woody species were observed on Dyke hills, while 32 were observed off-Dyke. On the Dyke, 12 species occurred on the piedmont, 20 on the east-facing slopes while only 6 species occurred on the west-facing slopes (Table 1). Of these species only 6 (*Combretum zeyheri, Combretum molle, Euphorbia wildii, Vangueria* sp., *Albizia* sp. *and Ozoroa insignis)* were common to both aspects (Table 1), while 13 species occurring on east-facing slopes were absent on the west-facing. All species had higher densities on east-facing slopes except for *Euphorbia wildii* which had higher density on west-facing slopes. DCA revealed that *Euphorbia wildii* was highly associated with west-facing slopes, while east-facing slopes and the piedmont patches were more associated with *Diplorhynchus condylocarpon*, *Ozoroa insignis*, *Protea welwitschii*, and *Albizia* sp. (Fig. 3a). In the adjacent off-Dyke matrix, 22 and 20 woody species were observed on east-facing and west-facing slopes respectively (Table 1). Off-Dyke sites were associated with key *miombo* dominants, *Brachystegia spiciformis*, *Julbernardia globiflora* and *Uapaca kirkiana.*

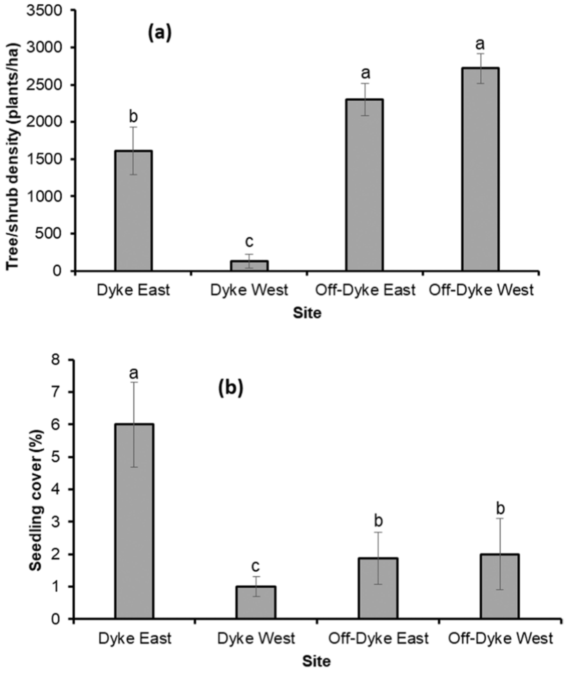


Fig. 2 Vegetation attributes (mean ± SE) on- and off- the Great Dyke sites. **a** Tree/Shrub densities, **b** Woody seedling cover**.** Different letters denote significant differences between sites ($P < 0.05$, LSD)

DCA showed separation of Dyke and off-Dyke plots while Dyke east-facing plots grouped with either the piedmont or west-facing plots, yielding 3 broadly distinct clusters represented by ellipses namely: (1) off-dyke plots (comprising all west and east-facing plots and a few Dyke east-facing plots), (2) largely Dyke west-facing along with a few east-facing plots and (3) a mixture of piedmont and east-facing plots (Fig. 3b). The first axis explained most of the variation (Eigenvalue = 0.941; explained variation = 13.64%) while the second axis explained less (Eigenvalue = 0.343; explained variation = 4.97%). Regardless of aspect, Dyke plots (E, W and Dyke Hill Foot) were on the right side of the diagram while off-Dyke plots were on the left side. Dyke west plots were more related to the first axis than the east and piedmont plots (Fig. 3b).

Soil chemical properties on- and off- Dyke

One-way ANOVA showed that pH ($F_{(4,17)} = 4.439$; $p = 0.01$), total Cr ($F_{(4,17)} = 3.154$; $p = 0.041$), total Ni ($F_{(4,17)} = 3.935$; $p = 0.04$); total Mn ($F_{(4,17)} = 3.682$; $p = 0.025$) and available Mn ($F_{(4,17)} = 3.55$; $p = 0.028$) generally significantly varied across sites. Most parameters (pH, Ca, Mg, Mg/Ca ratio; available Ni, Cr, Mn and total Mn) were similar between Dyke east- and west- facing slopes, with only total Cr and total Ni significantly higher on east-facing slopes. Only available Ni and Mn were significantly higher on Dyke piedmont than on Dyke slopes (Table 2). However, these elements varied significantly between Dyke and off -Dyke substrates (higher in Dyke substrates for Mg, Mg/Ca ratio, Total Ni, Cr and Mn, and available Ni and lower for available Mn).

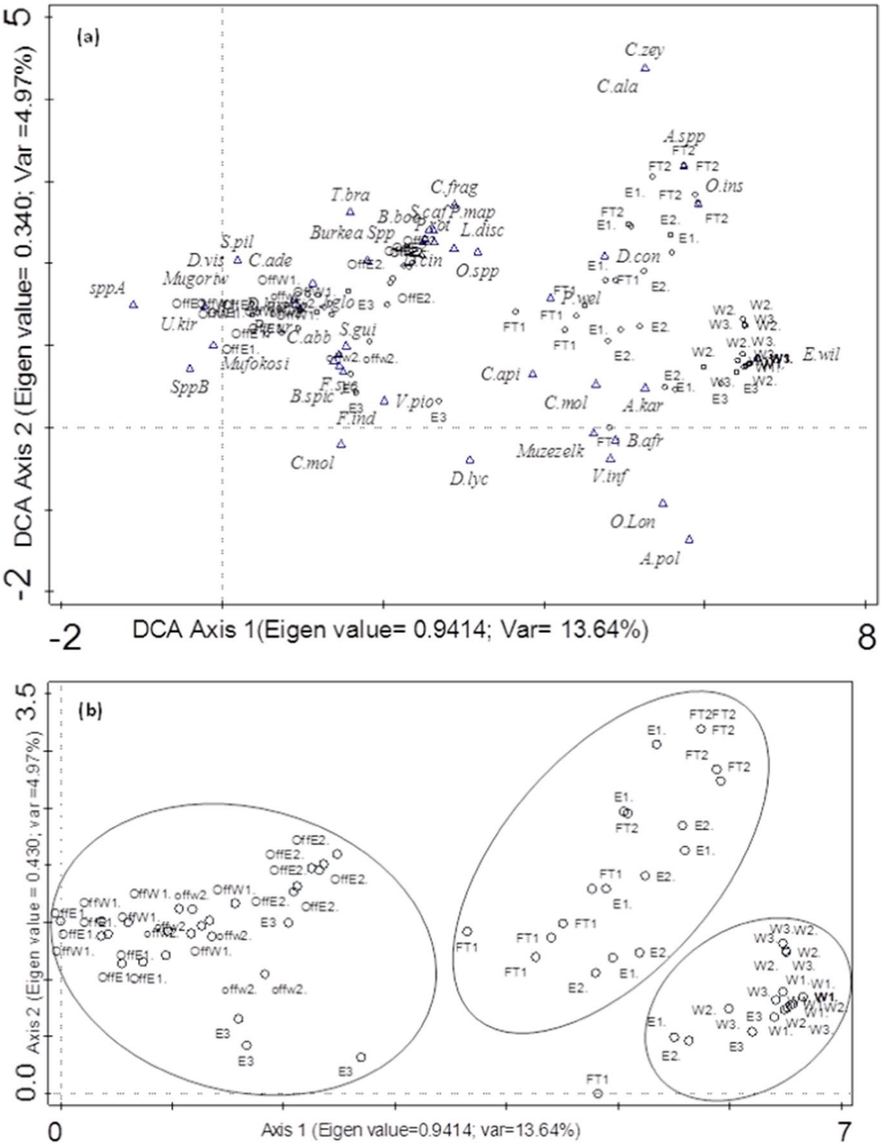
Correlations among vegetation attributes and between vegetation and soil

Redundancy Detrended Analysis (RDA) ($F = 2$; $p = 0.098$) showed that woody species density and

Table 1 Presence (+) and absence (−) of woody plant species on- and off- the Great Dyke patches. ND denotes not defined (unknown) family; * denotes Dyke endemic species

Family	Species	Dyke East	Off-Dyke East	Dyke Foot	Dyke West	Off-Dyke West
Anacardiaceae	*Lannea discolor*	+	+	+	–	+
	Ozoroa insignis	+	–	+	+	–
	*Ozoroa longipetiolata**	+	–	+	–	–
	Ozoroa reticulata	–	+	–	–	–
Apocynaceae	*Diplorhynchus condylocarpon*	+	+	+	–	–
Araliaceae	*Cussonia arborea*	–	–	–	–	+
Asteraceae	*Vernonia glabra*	–	+	–	–	–
Bignoniaceae	*Kigelia africana*	–	+	–	–	–
Celastraceae	*Gymnosporia senegalensis*	–	+	–	–	–
Chrysobalanaceae	*Parinari curatellifolia*	+	+	+	–	+
Combretaceae	*Combretum adenogonium*	–	–	–	–	+
	Combretum apiculatum	+	+	+	–	–
	Combretum elaeagnoides	+	–	–	–	–
	Combretum molle	+	+	–	+	+
	Combretum sp.	+	–	+	–	–
	Combretum zeyheri	+	–	–	–	–
	Terminalia brachystemma	–	–	–	–	+
Ebenaceae	*Diospyros* sp.	+	–	–	–	–
Euphorbiaceae	*Euphorbia wildii**	+	–	–	+	–
Fabaceae	*Albizia* sp.	+	–	+	+	–
	Baphia sp.	–	+	–	–	+
	Bauhinia petersiana	–	–	–	–	+
	Brachystegia boehmii	–	+	–	–	–
	Brachystegia glaucescens	–	+	–	–	–
	Brachystegia spiciformis	+	+	–	–	+
	Burkea africana	+	–	–	–	–
	Burkea africana-like sp.	–	+	+	–	+
	Dichrostachys cinerea	–	+	–	–	–
	Julbernardia globiflora	–	+	–	–	+
	Peltophorum africanum	–	+	–	–	–
	Pterocarpus angolensis	–	+	–	–	–
	Senegalia (Acacia) polyacantha	+	–	–	–	–
	Vachellia (Acacia) karroo	+	–	+	–	–
Lamiaceae	*Vitex payos*	–	–	–	–	+
Loganiaceae	*Strychnos caffra*	–	+	–	–	–
	Strychnos spinosa	–	–	–	–	+
Moraceae	*Ficus sycomorus*	–	–	–	–	+
Myrtaceae	*Syzigium guineense*	–	+	–	–	–
Phyllanthaceae	*Uapaca kirkiana*	–	+	–	–	+
	Pseudolachnostylis maprouneifolia	–	+	–	–	–
Polygalaceae	*"unique"*	–	–	–	–	+
Proteaceae	*Protea welwitschii*	+	–	+	+	–
Rhamnaceae	*Mzungu*	–	–	–	–	+
Rubiaceae	*Vangueria infausta*	+	–	–	+	+
	Vangueria apiculata	–	+	–	–	–

Fig. 3 Ordination plots showing separation of sites based on woody species composition. **a** DCA biplot showing species associations across sites, **b** DCA scatter plot showing separation of sites based on woody species composition (site symbols: Off = off-Dyke; E = Dyke East-facing slope; W=Dyke West-facing slope; FT = Dyke Hill Foot; number denotes slope replicate number. Full names of species in Table 1); ellipses delineate sites that clustered together



richness were positively correlated while both negatively correlated to herbaceous cover (Fig. 4a). Woody species richness and density were positively correlated to available Mn, Cr while negatively correlated to total Ni, available Ni, pH and Mg/Ca ratio (Fig. 4a). Most measured elements though differently related to vegetation attributes had comparable influence on vegetation structure (length of arrows were similar; Fig. 4a and b). Total Ni and Mn and available Ni were positively related to herbaceous aerial cover.

A CCA showed that *Diplorhynchus condylocarpon, Ozoroa longipetiolata, Ozoroa insignis, Combretum zeyheri, Combretum elaeagnoides, Vachellia (Acacia) karroo, Albizia* sp. *and Eurphorbia wildii* were positively correlated to Mg/Ca ratio, pH and total Cr while *Combretum apiculatum, Ozoroa insignis* and *Peltophorum africanum* and Muzeze-*like* were positively related to available Ni (Fig. 4b). *Combretum molle*, and *Lannea discolor* were positively correlated to available Cr while *Burkea africana-like* sp. was positively correlated to available Mn (Fig. 4b). *Brachystegia spiciformis* and *Julbernardia globiflora* were negatively related to most measured soil factors. Correlation analysis of vegetation data and soil variables using multivariate unconstrained unimodal CCA (F = 1.6; p = 0.004)

Table 2 Comparisons of soil properties (pH, exchangeable Ca, Mg and total and bioavailable Ni, Cr and Mn) (mean ± SE) among on- Dyke and off–Dyke substrates (results are in mg/kg for metals and me% for bases). Means with at least one same letter in superscript in same row are not significantly different (LSD, $P < 0.05$)

Soil parameter	Dyke East	Dyke West	Dyke piedmont	Off-Dyke East	Off-Dyke West
pH ($CaCl_2$)	5.74 ± 0.14^{a}	5.89 ± 0.11^{a}	5.26 ± 0.25^{a}	5.01 ± 0.06^{b}	5.05 ± 0.05^{b}
Ca	4.7 ± 0.76^{b}	5.25 ± 1.08^{b}	9.52 ± 3.27^{a}	7.38 ± 2.43^{a}	7.15 ± 3.65^{a}
Mg	10.3 ± 1.91^{a}	10.18 ± 2.13^{a}	14.74 ± 5.24^{a}	2.32 ± 0.34^{b}	2.65 ± 0.65^{b}
Mg/Ca ratio	2.4 ± 1.35^{a}	2.46 ± 1.66^{a}	1.57 ± 1.20^{a}	0.35 ± 0.23^{b}	0.37 ± 0.20^{b}
Total Cr	321.1 ± 69.44^{a}	132.6 ± 41.77^{b}	98.8 ± 6.23^{b}	46.60 ± 10.10^{c}	50.80 ± 11.00^{c}
Total Ni	533.6 ± 87.51^{a}	395.5 ± 71.63^{b}	669.2 ± 66.81^{a}	30.05 ± 6.16^{c}	33.05 ± 7.55^{c}
Total Mn	141.3 ± 20.11^{a}	108.6 ± 14.29^{a}	164.9 ± 15.30^{a}	58.4 ± 18.01^{b}	61.6 ± 20.40^{b}
Available Mn	7.1 ± 0.24^{c}	11.80 ± 2.38^{c}	22.30 ± 9.18^{b}	37.7 ± 6.90^{a}	35.9 ± 7.70^{a}
Available Cr	4.8 ± 0.45^{b}	4.7 ± 0.55^{b}	4.24 ± 0.470^{b}	5.80 ± 1.71^{a}	5.30 ± 1.50^{a}
Available Ni	53.2 ± 11.81^{b}	53.05 ± 16.04^{b}	98.0 ± 31.50^{a}	2.2 ± 0.13^{c}	2.10 ± 0.10^{c}

yielded 3 clusters namely (1) off-Dyke plots (2), Dyke *Brachystegia spiciformis–Julbernardia globiflora* patch (and 3) the largest cluster with the bulk of Dyke plots (2, 3 and 4; Fig. 4c). A CCA biplot of sites using composition data and soils attributes showed that most (Dyke east, west and foot) sites clustered around Mg/Ca ratio, total Ni, pH, available Ni, and total Cr, showing a positive relationship of their species assemblages with these soil elements (Fig. 4c). The Dyke *Brachystegia spiciformis-Julbernardia globiflora* plots were more positively related to available Cr while the off- Dyke plots were more positively related to available Mn with the rest of the Dyke piedmont, east and west-facing plots generally related to similar attributes (pH, total Cr and Mg/Ca ratio (Fig. 4d)). A forward selection analysis to identify significant explanatory soil variables picked total and available Mn and Ni, and pH.

Correlation of Dyke woody species with aspect

Higher abundances of *Protea welwitschii, Burkea africana-like* sp.*, and Ozoroa* sp. were obtained on plots from the piedmont while east-facing slopes were associated with higher densities of *Burkea africana, Combretum zeyheri, Combretum elaeagnoides, Ozoroa longipetiolata and Combretum molle* (Fig. 5). West-facing slopes were related *to Euphorbia wildii and Vangueria infausta. Albizia* sp., *Diplorhynchus condylocarpon and Combretum apiculatum* were more related to the piedmont.

Discussion

The study sought to answer the following questions: (1) What are the woody species growing on serpentinic ultramafic substrates? (2) How do their densities vary with aspect and catenal position? (3) How do their associations vary with aspect and catenal position? (4) How does species composition vary between ultramafic and adjacent non-ultramafic substrates? (5) What is the relationship between vegetation and aspect, heavy metal levels and Mg/Ca ratio? The study had five main findings: (1) Lower tree/shrub densities (Fig. 2 and species richness (Table 1) were observed on Dyke than off-Dyke, (2) Distinct compositional separation of Dyke and off-Dyke plots, clustering of off-Dyke plots, separation of the piedmont plots from the west–facing Dyke plots, while east plots overlapped with both Dyke piedmont, west-facing and some off-dyke plots (Fig. 3b). (3) Most soil parameters (pH, Ca, Mg, Mg/Ca ratio; available Ni, Cr, Mn and total Mn) were similar between Dyke east- and west-facing slopes except total Cr and total Ni which were significantly higher on east-facing slopes, while only available Ni and Mn were significantly higher on the piedmont than on slopes (Table 2), and (4) the following soil parameters: Mg, Mg/Ca ratio, total Ni, Cr and Mn, and available Ni were significantly higher in Dyke patches than off-Dyke except for available Mn which was lower on the Dyke. (5) Lastly, RDA showed that woody species density and richness were positively

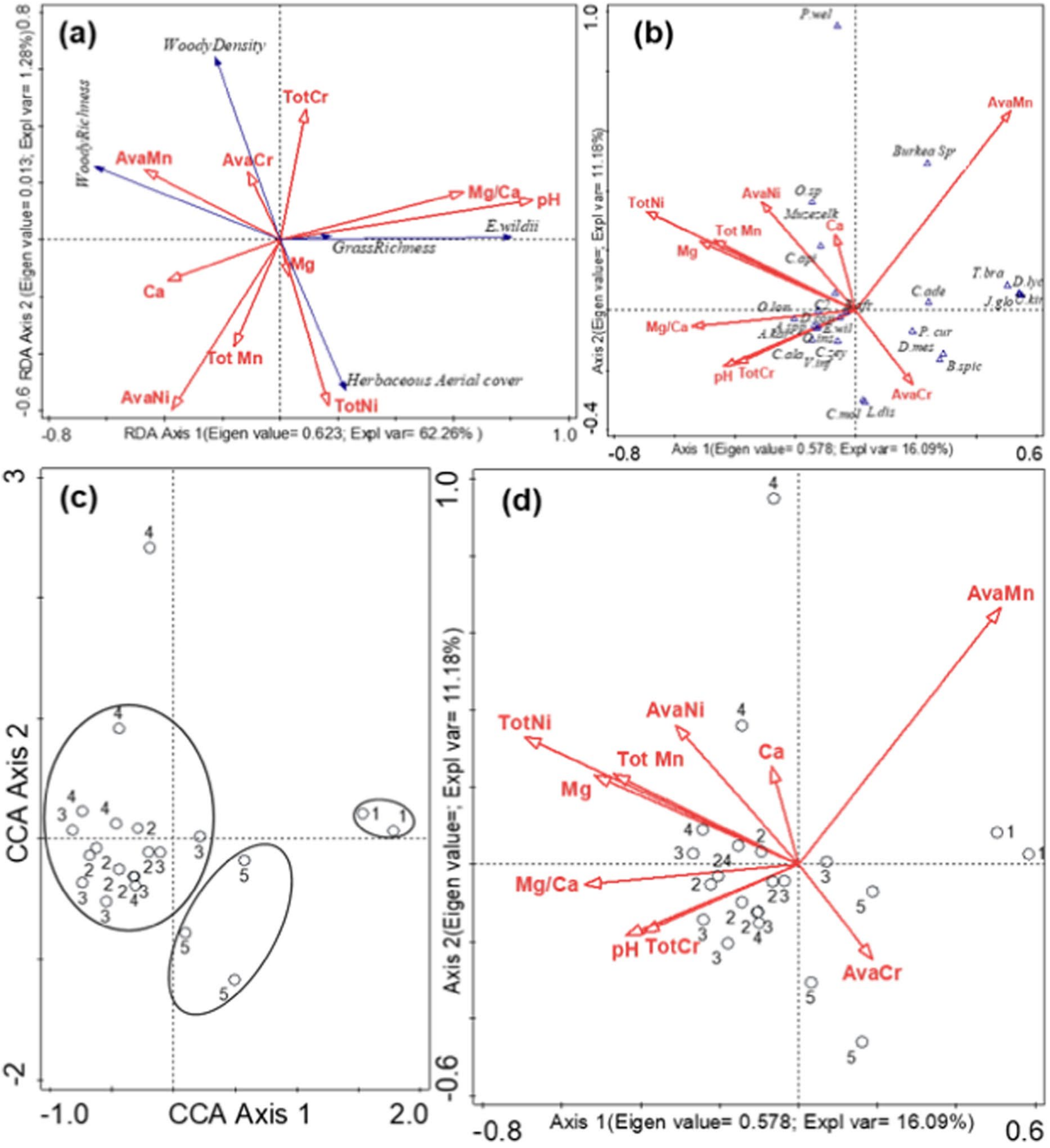


Fig. 4 Ordination diagrams illustrating relationships among woody vegetation composition, soil properties and sampled sites. **a** RDA ordination showing correlation between vegetation structural attributes and soil properties, **b** CCA plot for relationship of woody species and soils, **c** CCA scatter plot for sites similarity based on species composition, and (**d**) relationship between soils and sites [site symbols: 1 = Off Dyke; 2 = Dyke east-facing slope; 3 = Dyke west-facing slope; 4 = Dyke piedmont; 5 = Dyke east (Brachystegia-Julbernardia patch)

correlated to available Mn, and Cr, while negatively correlated to total Ni, available Ni, pH and Mg/Ca ratio and herbaceous cover (Fig. 4).

The observed vegetation patterns can be attributed to microsite variations between ultramafic and non-ultramafic substrates related to geology, microsite

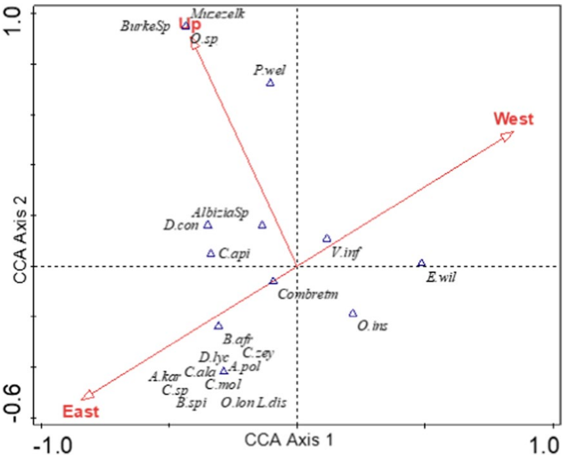


Fig. 5 CCA diagram showing correlation between Dyke woody species and aspect

variations related to slope, tree-grass interactions and availability of metals and differential responses of specific species to environmental gradients such as topography and edaphic factors. A forward selection analysis to identify significant explanatory soil variables picked total and available Mn and Ni, and pH, as explanatory variables for woody densities differences.

Variation of soil properties of ultramafic Dyke and non-ultramafic off-Dyke substrates

The observed higher Mg, Mg/Ca ratio, total Ni, Cr and Mn, and available Ni in Dyke patches than off-Dyke are due to differences in parent material forming the soils. The Dyke has serpentine ultramafic soils rich in magnesium and metals such as Ni, Cr and Mn (Whittaker 1954; Wild 1965) while adjacent soils are mafic of granite origin (Wild 1965). The ultramafic soils are basic while soils of granite origin are acidic sands (van Der Ent et al. 2018) and this may account for the differences in pH. In spite of high total metal levels, Dyke soils had low available metals most probably due to their slight alkalinity as they are derived from basic material. Heavy metals are less soluble at pH above 5 (Zaranyika and Chirinda 2011). The low available metals could also be due to the immobilization effect of adaptive plant species such as *Diplorhynchus condylocarpon, Ozoroa longipetiolata* and some herbaceous species that complex or precipitate the heavy metals into insoluble forms as a survival mechanism (Mendez and Maier 2008). The observed low Mg/Ca and lower metal levels in some patches of the Dyke especially the east-facing slopes dominated by *Julbernardia globiflora* may be because of norite and pyroxenes intrusions. Such geology has properties comparable to off-Dyke patches. Similarity in properties between west- and east-facing slopes generally show dominance of similar ultramafic substrates that is a natural occurrence independent of exposure or catenal position. The observed results concur with findings from similar studies (Lazarus et al. 2011; Oze et al. 2004) which report higher metals on ultramafic soils than surrounding matrix. The intra-Dyke variations concurred with findings from a similar study (Chiarucci et al. 2001).

Species composition and densities on the Dyke and surrounding matrix

The observed lower woody species richness, densities and seedling cover on the Dyke compared to the off-Dyke vegetation matrix can be attributed to the observed differences in soil properties between the two substrates (Table 2). Higher Mg/Ca ratios observed on the Dyke typical of ultramafic soils normally pose Mg toxicity to most plants (Rajakaruna et al. 2009). This toxicity is associated with suppressed nutrient uptake and below optimal plant metabolism (Rajakaruna and Baker 2004), yielding a feedback loop called the serpentine syndrome which is linked to Ca and Mg imbalances (Vlamis and Jenny 1948). The Dyke had very high Mg/Ca ratios which were above the 1.43 reported for normal soils (Werger et al. 1978; Wild 1965, 1974). Suppressed densities and richness can also be attributed to the observed higher Ni and Mn in the Dyke than the off -Dyke patches (Table 2; Fig. 4a). Though Ni and Mn are key plant micronutrients they exceeded normal soil levels in the Dyke (i.e., above 30 mg/kg and 50-100 mg/kg for Ni and Mn respectively). Such high metal levels inhibit germination of seeds, threaten survival of seedlings and suppress lateral root development, flowering and fruiting thus resulting in poor recruitment (Peralta et al. 2009; Naz et al. 2022). High Ni and Cr also inhibit nutrient uptake by forming insoluble compounds (Echevarria et al. 2006; Manzoor et al. 2020; Wani et al. 2022). This may leave only a few well adapted species that thrive here, and hence may account for the observed lower species richness and seedling cover in the Dyke. At pH < 5.5

as observed in off-Dyke patches, Mn bioavailability is high as Mn^{2+} while at higher pH, there is chemical auto-oxidation of Mn^{2+}, resulting in less available forms of Mn and this may explain suppressed bioavailable Mn in the Dyke patches that had average pH above 5.5 contrary to off–Dyke patches. Depressed Mn availability adversely affects plant growth as Mn is an essential plant nutrient (van Der Ent et al. 2018).

The existence of some woody species (e.g. *Diplorhynchus condylocarpon*, *Ozoroa longipetifolia*, *Combretum apiculatum, Protea welwitschii, Euphorbia wildii and Combretum zeyheri* (Table 1; Figs. 3 and 4) suggest their tolerance to Ni, Cr, Mn and Mg toxicity observed in the Dyke (Table 2). The survival of such species could be linked to rhizofiltration, metal exclusion and or phytoaccumulation (Mendez and Maier 2008). These species have been reported to occur in several serpentine soils in Shamva (Tiperrary hill), Bindura (Kingstone hill), Shurugwi and Shangani (Wild 1965, 1974). *Diplorhynchus condylocarpon,* for instance, has been reported to accumulate high levels of nickel into its above ground tissues (Wild 1965). These are dominant woody species of the Combretaceae, Euphorbiaceae and Proteaceae suggesting correlation between such families and substrate. The results are consistent with findings by Wild (1965) who reported 35.7%, 25% and 18.9% representation of Proteaceae, Euphorbiaceae and Combretaceae, respectively, on the Zimbabwe Great Dyke. The general absence of typical miombo species such as *Brachystegia spiciformis, Julbernardia globiflora, B. boehmii and Uapaca kirkiana* which characterized off-Dyke patches further suggests significant influence of edaphic factors.

The rare existence of *Brachystegia spiciformis*, and *Julbernardia globiflora* on one east-facing hill slope resulting in compositional overlap with off-Dyke patches could be due to observed higher Ca/Mg ratios when compared to the rest of the Dyke east-facing and west-facing slopes (Table 2). Such plots were on norite and pyroxenite intrusions which are known to be rich in silicates which improves the calcium content of the substrate hence the lower Mg/Ca ratios (Whittaker 1954; Wild 1974). The Ca/Mg ratios were near normal hence pose less toxicity to several plant species and may further account for the observed higher species richness on such plots than the bulk Dyke plots. The higher woody species richness and densities observed on east-facing than west slopes and flat piedmont can therefore be explained in terms of both influence of aspect and by chance due to a norite substrate coinciding with the eastern aspect.

Vegetation patterns on ultramafics and relationship with topographic factors

While Mg/Ca ratios and metal level gradients can account for differences in woody composition and densities between Dyke and off-Dyke substrates (Table 2) ("General vegetation densities on- and off-Dyke substrates" section), a few of these parameters may be accounting for intra Dyke- microsite differences. Considering the observed partial separation and overlaps of plots from Dyke-hill slopes and flatter piedmont and between west-facing and east-facing slopes, both slope orientation and magnitude appear to have partial influence on observed vegetation patterns.

The intra-Dyke variation between slopes and piedmont for some soil elements e.g. exchangeable Ca, available Ni and available Mn), is an example of influence of position or slope inclination on soil properties. Thanachit et al. (2006) reported the influence of catenal position on bases and metals dynamics related to hydrology, pH dynamics and degree of weathering. On serpentines there is a tendency of soils on slopes greater than 15 degrees to form shallow unstable soils with a high Mg/Ca ratio which in turn influence vegetation properties (Silva et al. 2007; Yang et al. 2022). Mechanisms accounting for this effect was beyond the scope of this study. Although generally aspect had an influence on woody vegetation communities, finer microsite sampling of soils and vegetation lumped the plots from all Dyke patches together, suggesting more influence of other factors beyond this study.

The relatively lower woody densities, species richness and herbaceous cover on the west-facing than east-facing slopes might be due to differences in solar irradiation received by the two opposing aspects. West-facing slopes in the southern hemisphere receive more irradiation in terms of intensity than east-facing slopes (Bennie et al. 2006). The higher irradiation on west-facing slopes might be mainly due to the fact that they face the sun in the hottest part of the day (i.e., 1–3 pm) whereas the east- facing aspects face the sun in cooler hours of the day (i.e., morning). This difference in irradiation influences soil moisture dynamics, creating drier conditions in the already shallow and rocky slopes, which in turn reduce seed germination, seedling recruitment and productivity on such west-facing slopes (Måren et al. 2015). Aspect markedly affects plant species composition, density and structure in low rainfall areas as radiation co-vary with many plants' physiological processes which inevitably affect species composition and forest structure (Bennie et al. 2006; Måren et al. 2015; Silva et al. 2007). The dominance of *Euphorbia wildii* and *Vangueria infausta* in the west-facing slopes (Fig. 5) therefore suggests these species are tolerant of lower soil moisture levels especially considering the two species have been reported to occur in dry and rocky areas (Van Wyk and Van Wyk 2013).

The distribution of individual species in the Dyke regardless of position or slope orientation tended to be highly related to exchangeable bases and heavy metal gradients, with some species thriving more in high Ni areas while others tolerating high Mg soils. Principal edaphic factors positively related to woody densities were total Ni and Cr, available Ni and exchangeable Mg. The positive correlation of vegetation species to high total metal content suggests the stabilization of heavy metals by the observed plants. Plants that survive high metals may be suppressing uptake of metals by roots through immobilizing them by their negative charges on their roots and their exudates, making the metals less soluble for uptake by plants and subsequent translocation to the shoots where toxicity is usually exhibited (Mendez and Maier 2008; Oze et al. 2008). Alternatively some plants may be hyperaccumulating metals such as Ni in their tissues (Wild 1965), a mechanism that was not tested in the present research but can be direction for follow-up research. Metal uptake discrimination and suppression in the roots could be the mechanisms for serpentine vegetation tolerance to the observed harsh soil chemistry (Oze et al. 2008). This together with high pH may account for uncharacteristically low bioavailale levels of Ni, Mn and Cr in the Dyke despite the observed high total metal levels related to the serpentine parent material. Our results are consistent with findings from several studies which highlighted that species richness and plant community composition are influenced by relief characteristics such as slope position and orientation (Cousins et al. 2014; Sternberg and Shoshany 2001; Silva et al. 2007; Yang et al. 2020) and in particular studies that reported differences in vegetation structure, composition and diversity between west- and east-facing slopes (Angessa et al. 2020; Yirdaw et al. 2015).

The fact that aspect seemed to have no effect on vegetation attributes on off-Dyke substrates suggests interactive influence of aspect and substrate on observed vegetation patterns on the Dyke. The grouping of plots of contrasting aspects off-Dyke while there was general separation on the Dyke suggests differential influence of aspect on woody species composition on ultramafic and non-ultramafic substrates. The off-Dyke substrates would be rescued from solar radiation by observed more woody vegetation cover giving a mulching effect from tree canopies and the litter from leaf fall and better soil water holding capacity compared to ultramafic dyke soils (Galey et al. 2017). This interactive influence of aspect and substrate was more pronounced for adult woody plants than seedlings, mainly driven by differences in total and available Ni and Mn and pH for woodies (Fig. 4). Overall, the edaphic and topographic attributes assessed partly and differentially influenced vegetation patterns on ultramafic and non-ultramafic substrates. Such gradients may also contribute to soil-plant metal relations (Adhikari et al. 2022). Other factors may be rockiness, fire regimes and other disturbances (Kativu et al. 2019). Consistent with our findings in summing the effects of topographic and edaphic factors on vegetation, Måren et al. (2015) postulated that plant diversity, composition and regeneration are affected by factors like topography, aspect, inclination of slope and soil type.

Conclusions and recommendations

We conclude that ultramafic substrates of the Great Dyke support unique species, mainly distinct from those of non-ultramafic substrates off-Dyke, with a few overlaps between off-Dyke non-ultramafic substrates and norite and pyroxenite intrusions on the Dyke. Compositional distinctiveness is mainly driven by *Ozoroa longipetiolata, Ozoroa insignis, Protea welwitschii and Euphorbia wildii*. Total Ni, Cr, Mn, Ca/Mg ratio and pH are the main determinants of differences in vegetation between ultramafic and non-ultramafic patches. Edaphic factors do not vary much with topographic gradients on the Dyke and that may account for compositional and structural overlaps. However, small differences in available Mn, Ni and exchangeable Ca and pH may account for the intra-Dyke vegetation differences.

We recommend further testing of the metal stabilization potential and drought tolerance of the plant species found on the serpentine Dyke patches (e.g. *Diplorhynchus condylocarpon, Combretum molle, Combretum zeyheri*, *Combretum apiculatum, Ozoroa* sp., *Protea welwitschii and Euphorbia wildii)* as they are candidate rehabilitation species for similar stressful and metalliferous sites such as mine tailings and waste rocks. We also recommend that use of such species be preceded by careful soil testing as different metals and bases affect different species differently. We also recommend that in rehabilitating different substrates, species be planted in associations, such as found in this current study. Future research may replicate such studies along climatic gradients to discover species that might universally thrive in harsh conditions under different climatic conditions, in order to establish a widely applicable set of rehabilitation species for metalliferous sites. Mechanisms of metal tolerance of dominant and rare species on serpentine Dyke must also be explored through future research.

Acknowledgements We are grateful to the International Foundation for Science (IFS) for partly funding this research under Grant Number D/5912-1 awarded to Tatenda Nyenda.

Author contribution Tatenda Nyenda and Tenderano Musungwa contributed to the study conception and design. Material preparation and data collection was performed by Tatenda Nyenda, Tenderano Musungwa and Tafadzwa Terrence Piyo. Data analysis and interpretation of results was performed by Tatenda Nyenda and Justice Muvengwi. The First draft was written by Tatenda Nyenda and reviewed by Ed. F.T Witkowski and Pedzisai Kowe. All Authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

The authors would like to declare the following:

Research involving human participants and/or animals There were no human participants and /or animals involved in this research.

Informed consent There was no conflict nor violation of informed consent in this research and it not include human participants.

Conflict of interest None of the authors has conflict of interest related to financial and non-financial relationships or support.

Competing interests The authors have no competing interests to declare.

References

Adhikari S, Marcelo-Silva J, Rajakaruna N, Siebert SJ (2022) Influence of land use and topography on distribution and bioaccumulation of potentially toxic metals in soil and plant leaves: a case study from Sekhukhuneland, South Africa. Sci Total Environ 806:150659

Ahmed S, Lemessa D, Seyum A (2022) Woody species composition, plant communities, and environmental determinants in Gennemar Dry Afromontane forest, Southern Ethiopia. Scientifica 2022:7970435. https://doi.org/10.1155/2022/7970435

Alexander EB, Coleman RG, Keeler-Wolfe T, Harrison SP (2007) Serpentine geoecology of western North America: geology, soils, and vegetation. OUP USA

Anderson JM, Ingram JSI (1993) Tropical soil biological and fertility: a hand book of methods. CAB International, Wallingford

Angessa AT, Lemma B, Yeshitela K, Fischer J, May F, Shumi G (2020) Woody plant diversity, composition and structure in relation to environmental variables and land-cover types in Lake Wanchi watershed, central highlands of Ethiopia. Afr J Ecol 58(4):627–638

Baker AJM, McGrath SP, Reeves RD, Smith JAC (2000) Metal hyperaccumulator plants: a review of the ecology and physiology of a biological resource for phytoremediation of metal polluted soils. In: Vangronsveld J (ed) Terry N, Ban˜uelos G. Phytoremediation of contaminated soil and water. CRC Press, Boca Raton, Fl, pp 85–107

Balkwill K (Ed.) (2001) Proceedings: third international conference on serpentine ecology. Part 2/Special Issue. South African J Sci 97

Bangira C (2010) Mineralogy and geochemistry of soils of ultramafic origin from the great dyke. Texas A&M University, Zimbabwe and Gillespie county, Texas

Barclay-Smith RW (1963) A report on the ecology and vegetation of the Great Dyke within the horseshoe intensive conservation area. Kirkia 4:25–34

Bennie J, Hill MO, Baxter R, Huntley B (2006) Influence of slope and aspect on long-term vegetation change in British chalk grasslands. J Ecol 94(2):355–368

Blackshaw GN (1920) Magnesia impregnated soils. S Afr J Sci 17(2):171–178

Boyd RS, Baker AJM, Proctor J (2004) Ultramafic rocks: their soils, vegetation and fauna. Proc. 4th International

Conference on Serpentine Ecology. Science Reviews 2000 Ltd., St. Albans, Herts

Brady NC, Weil RR (2002) The nature and properties of soils, 13th edn. Prentice Hall, New Jersey

Brooks RR (1987) Serpentine and its vegetation: a multidisciplinary approach. Discorides Press, Portland, p 454

Brooks RR, Chambers MF, Nicks LJ, Robinson BH (1998) Phytomining. Trends Plant Sci 3(9):359–362

Campbell BM, Cunliffe RN, Gambiza J (1995) Vegetation structure and small-scale pattern in miombo woodland, Marondera, Zimbabwe. Bothalia 25(1):121–126

Cañadas EM, Jiménez MN, Valle F, Fernández-ondoño E, Martín-peinado F, Navarro FB (2010) Soil e vegetation relationships in semi-arid Mediterranean old fields (SE Spain): implications for management. J Arid Environ 74(11):1525–1533

Cerdeira-Pérez A, Monterroso C, Rodríguez-Garrido B, Machinet G, Echevarria G, Prieto-Fernández Á, Kidd PS (2019) Implementing nickel phytomining in a serpentine quarry in NW Spain. J Geochem Explor 197:1–13

Chiarucci A, Rocchini D, Leonzio C, De Dominicis V (2001) A test of vegetation–environment relationship in serpentine soils of Tuscany, Italy. Ecol Res 16(4):627–639

Coleman RG, Jove C (1992) Geological origin of serpentinites. Pp. 1À17 in: The Vegetation of Ultramafic (Serpentine) Soils. In: Baker AJM, Proctor J, Revees RD (eds) Proceedings of the First International Conference on Serpentine Ecology. Intercept Ltd., Andover, United Kingdom

Cousins SR, Witkowski ETF, Pfab MF (2014) Elucidating patterns in the population size structure and density of Aloe plicatilis, a tree aloe endemic to the cape fynbos, South Africa. S Afr J Bot 90:20–36

Cui W, Zheng XX (2016) Spatial heterogeneity in tree diversity and forest structure of evergreen broadleaf forests in southern China along an altitudinal gradient. Forests 7(10):216

Drozdova I, Alekseeva-Popova N, Kalimova I, Bech J, Roca N (2019) Research of reclamation of polluted mine soils by native metallophytes: some cases. Geochem: Explor Environ Anal 19(2):164–170

Echevarria G, Massoura S, Sterckeman T, Becquer T, Schwartz C, Morel JL (2006) Assessment and control of the bioavailability of Ni in soils. Environ Toxicol Chem 25:643–651

Galey ML, van Der Ent A, Iqbal MCM, Rajakaruna N (2017) Ultramafic geoecology of south and Southeast Asia. Bot Stud 58:1–28

Garnica-Díaz C, Berazaín Iturralde R, Cabrera B et al (2023) Global Plant Ecology of Tropical Ultramafic Ecosystems. Bot Rev 89:115–157. https://doi.org/10.1007/s12229-022-09278-2

Gracia M, Montané F, Piqué J, Retana J (2007) Overstory structure and topographic gradients determining diversity and abundance of understory shrub species in temperate forests in Central Pyrenees (NE Spain). For Ecol Manag 242(2–3):391–397

Harrison S, Rajakaruna N (eds) (2011) Serpentine: the evolution and ecology of a model system. Univ of California Press, Berkeley

Harrison S, Viers JH (2007) Regional and local species richness in an insular environment: serpentine plants in California. Ecol Monographs Ecol 76:41–56

Henkin Z, Seligman NG, Kafkafi U, Prinz D (1998) End-of-season soil water depletion in relation to growth of herbaceous vegetation in the sub-humid Mediterranean dwarf-shrub community on two contrasting soils. J Plant Soil 202:317–326

Hewawasam T, Fernando GWAR, Priyashantha D (2014) Geo-vegetation mapping and soil geochemical characteristics of the Indikolapelessa serpentinite outcrop, southern Sri Lanka. J Earth Sci 25:152–168

Kativu S, Kunonga NI, Nhiwatiwa T, Tembani M (2019) Aspects of the population biology, life history and threats to aloe ortholopha Christian and Milne-Redh.: a serpentine endemic from the northern Great Dyke of Zimbabwe. Bothalia-African Biodivers Conserv 49(1):1–8

Kruckeberg AR (1985) California serpentines: flora, vegetation, geology, soils, and management problems. Univ of California Press, Berkeley

Kruckeberg AR (2002) Geology and plant life: the effects of landforms and rock types on plants University of Washington Press. Seattle, WA, USA

Kumar A, Maleva M, Borisova G, Chukina N, Morozova M, Kiseleva I (2021) Nickel and copper accumulation strategies in Odontarrhena obovata growing on copper smelter-influenced and non-influenced serpentine soils: a comparative field study. Environ Geochem Health 43:1401–1413

Kumar A, Ramamoorthy D, Kumar N, Verma R, Kumar A, Verma DK, Jaiswal KK (2022) Investigation on the potential of eco-friendly bio-char for amendment in serpentine soils and immobilization of heavy metals contaminants: a review. Biomass Convers Biorefinery 1–21

Kutiel P, Lavee H (1999) Effect of slope aspect on soil and vegetation properties along an aridity transect. Israel J Plant Sci 47(3):169–178

Lazarus BE, Richards JH, Claassen VP, O'Dell RE, Ferrell MA (2011) Species specific plant-soil interactions influence plant distribution on serpentine soils. Plant Soil 342:327–344

Legendre P, Mi X, Ren H, Ma K, Yu M, Sun IF, He F (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. Ecology 90(3):663–674

Maas JL, Stuntz DE (1969) Mycoecology on serpentine soil. Mycologia 61(6):1106–1116

Malik ZA, Hussain A, Iqbal K, Bhatt AB (2014) Species richness and diversity along the disturbance gradient in Kedarnath wildlife sanctuary and its adjoining areas in Garhwal Himalaya, India. Int J Curr Res 6(12):10918–10926

Manzoor MM, Goyal P, Gupta AP, Gupta S (2020) Heavy metal soil contamination and bioremediation. Bioremediation and Biotechnology, Vol 2: Degradation of Pesticides and Heavy Metals, 221–239

Mapaura A (2002) Endemic plant species of Zimbabwe. Kirkia 117–149

Måren IE, Karki S, Prajapati C, Yadav RK, Shrestha BB (2015) Facing north or south: does slope aspect impact forest stand characteristics and soil properties in a semiarid trans-Himalayan valley? J Arid Environ 121:112–123

Martinez-Ruiz C, Marrs R (2007) Some factors affecting successional change on uranium mine wastes: insights for ecological. Appl Veg Sci 10:333–342

Maus V, Giljum S, da Silva DM, Gutschlhofer J, da Rosa RP, Luckeneder S, McCallum I (2022) An update on global mining land use. Sci Data 9(1):1–11

McKillup S (2012) The soil resource. Origin and behaviour. Cambridge University Press, Cambridge

Mendez MO, Maier RM (2008) Phytostabilization of mine tailings in arid and semiarid environments—an emerging remediation technology. Environ Health Perspect 116(3):278–283

Mugandani R, Wuta M, Makarau A, Chipindu B (2012) Re-classification of agro-ecological regions of Zimbabwe in conformity with climate variability and change. Afr Crop Sci J 20:361–369

Muthusamy L, Rajendran M, Ramamoorthy K, Narayanan M, Kandasamy S (2022) Phytostabilization of metal mine tailings—a green remediation technology. In Phytoremediation Technology for the Removal of Heavy Metals and Other Contaminants from Soil and Water (pp. 243–253). Elsevier

Nascimento CWAD, Biondi CM, Silva FBVD, Lima LHV (2021) Using plants to remediate or manage metal-polluted soils: an overview on the current state of phytotechnologies. Acta Scientiarum Agron 43. https://doi.org/10.4025/actasciagron.v43i1.58283

Naz M, Ghani MI, Sarraf M, Liu M, Fan X (2022) Ecotoxicity of nickel and its possible remediation. In Phytoremediation Phytoremediation 297–322. https://doi.org/10.1016/B978-0-323-89874-4.00022-4

Okalebo JR, Gathua KW, Woomer PL (2002) Laboratory methods of soil and plant analysis: a working manual second edition. Sacred Africa, Nairobi 21:25–26

Oze C, Fendorf S, Bird DK, Coleman RG (2004) Chromium geochemistry in serpentinized ultramafic rocks and serpentine soils from the Franciscan complex of California. Am J Sci 304(1):67–101

Oze C, Skinner C, Schroth AW, Coleman RG (2008) Growing up green on serpentine soils: biogeochemistry of serpentine vegetation in the central coast range of California. Appl Geochem 23(12):3391–3403

Peralta JR, Gardea-Torresdey JL, Tiemann E, Gomez S, Arteaga E, Parsons JG (2009) Study of the effects of heavy metals on seed germination and plant growth on alfalfa plant (*Medicago sativa*) grown in solid media. In proceedings of the 2000 conference on hazardous waste research. University of Texas, Austin

Prendergast MD (2013) Landscape evolution, regolith formation and Nickel laterite development in the northern part of the Great Dyke. Zimbabwe. S Afr J Geol 116(2):219–240. https://doi.org/10.2113/gssajg.116.2.219

Proctor J, Woodell SR (1975) The ecology of serpentine soils. Adv Ecol Res 9:255–366

Rajakaruna N (2004) The edaphic factor in the origin of plant species. Int Geol Rev 46(5):471–478

Rajakaruna N, Baker AJ (2004) Serpentine: a model habitat for botanical research in Sri Lanka. Ceylon J Sc 32:1

Rajakaruna N, Boyd RS (2009) Advances in serpentine geoecology: a retrospective. Northeast Nat 16:1–7

Rajakaruna N, Harris TB, Alexander EB (2009) Serpentine geoecology of eastern North America: a review. Rhodora 111(945):21–108

Rattray JM (1961) Vegetation types of southern Rhodesia. Kirkia 2:68–93

Rattray JM, Wild H (1961) Vegetation map of the Federation of Rhodesia and Nyasaland. Kirkia 2:94–104

Reeves RD (2003) Tropical Hyperaccumulators of metals and their potential for Phytoextraction. Plant Soil 249:57–65

Safford HD, Harrison S (2008) The effects of fire on serpentine vegetation and implications for management1. In Proceedings of the 2002 Fire Conference on Managing Fire and Fuels in the Remaining Wildlands and Open Spaces of the Southwestern United States (pp. 321–28)

Silva WG, Metzger JP, Simões S, Simonetti C (2007) Relief influence on the spatial distribution of the Atlantic Forest cover on the Ibiúna plateau, SP. Braz J Biol 67:403–411

Song C, Cao M (2017) Relationships between plant species richness and terrain in middle sub-tropical eastern China. Forests 8(9):344

Sternberg M, Shoshany M (2001) Influence of slope aspect on Mediterranean woody formations: comparison of a semi-arid and an arid site in Israel. Ecol Res 16:335–345

Thanachit S, Suddhiprakarn A, Kheoruenromne I, Gilkes RJ (2006) The geochemistry of soils on a catena on basalt at Khon Buri, Northeast Thailand. Geoderma 135:81–96

van Der Ent A, Cardace D, Tibbett M, Echevarria G (2018) Ecological implications of pedogenesis and geochemistry of ultramafic soils in Kinabalu Park (Malaysia). Catena 160:154–169

Van Wyk B (2013) Field guide to trees of southern Africa. Penguin Random House South Africa

Vlamis J, Jenny H (1948) Calcium deficiency in serpentine soils as revealed by adsorbent technique. Science 107(2786):549–549

Walker RB, Walker HM, Ashworth PR (1955) Calcium-magnesium nutrition with special reference to serpentine soils. Plant Physiol 30(3):214

Wang YL, Tsou MC, Liao HT, Hseu ZY, Dang W, Hsi HC, Chien LC (2020) Influence of soil properties on the bioaccessibility of Cr and Ni in geologic serpentine and anthropogenically contaminated non-serpentine soils in Taiwan. Sci Total Environ 714:136761

Wani OB, Manzoor S, Molaei N, Shoaib M, Khan S, Zeng H, Bobicki ER (2022) Beneficiation of nickel from ultramafic ores: using sodium citrate as a green processing reagent. Resour Conserv Recycl 186:106496

Werger MJA, Wild H, Drummond BR (1978) Vegetation structure and substrate of the northern part of the Great Dyke, Rhodesia environment and plant communities. Vegetatio 37(2):79–89

Whittaker RH (1954) The ecology of serpentine soils. Ecology 35(2):258–288

Wild H (1965) The flora of the Great Dyke of Southern Rhodesia with special reference to the serpentine soils. Kirkia 5(1):49–86

Wild H (1974) Variations in the serpentine floras of Rhodesia. Kirkia 9(2):209–232

Wilson AH, Prendergast MD (2001) Platinum-group element mineralisation in the Great Dyke, Zimbabwe, and its relationship to magma evolution and magma chamber structure. S Afr J Geol 104(4):319–342

Witkowski ETF, Garner RD (2008) Seed production, seed bank dynamics, resprouting and long-term response to clearing of the alien invasive Solanum mauritianum in a temperate to subtropical riparian ecosystem. S Afr J Bot 74(3):476–484

Woldu G, Solomon N, Hishe H, Gebrewahid H, Gebremedhin MA, Birhane E (2020) Topographic variables to determine the diversity of woody species in the exclosure of Northern Ethiopia. Heliyon 6(1):e03121

Worst BG (1960) The Great Dyke of Southern Rhodesia; Bulletin 47; Southern Rhodesian Geological Survey: Salisbury, Zimbabwe

Yang Y, Watanabe M, Li F, Zhang J, Zhang W, Zhai J (2006) Factors affecting forest growth and possible effects of climate change in the Taihang Mountains, northern China. For: Int J For Res 79(1):135–147

Yang J, El-Kassaby YA, Guan W (2020) The effect of slope aspect on vegetation attributes in a mountainous dry valley, Southwest China. Sci Rep 10(1):1–11

Yang CY, Nguyen DQ, Ngo HTT, Navarrete IA, Nakao A, Huang ST, Hseu ZY (2022) Increases in ca/mg ratios caused the increases in the mobile fractions of Cr and Ni in serpentinite-derived soils in humid Asia. Catena 216:106418

Ye Z, Hong S, He C, Zhang Y, Wang Y, Zhu H, Hou H (2022) Evaluation of different factors on metal leaching from nickel tailings using generalized additive model (GAM). Ecotoxicol Environ Saf 236:113488

Yirdaw E, Starr M, Negash M, Yimer F (2015) Influence of topographic aspect on floristic diversity, structure and treeline of afromontane cloud forests in the Bale Mountains, Ethiopia. J For Res 26:919–931

Yuan ZQ, Fang C, Zhang R, Li FM, Javaid MM, Janssens IA (2019) Topographic influences on soil properties and aboveground biomass in lucerne-rich vegetation in a semi-arid environment. Geoderma 344:137–143

Zaranyika MF, Chirinda T (2011) Heavy metal speciation trends in mine slime dams: a case study of slime dams at a goldmine in Zimbabwe. J Environ Chem Ecotoxicol 3(5):103–115

Zhang JT, Xu B, Li M (2013) Vegetation patterns and species diversity along elevational and disturbance gradients in the Baihua Mountain reserve, Beijing, China. Mt Res Dev 33(2):170–178