The chemistry of the pedoderm – part 3: *Colophospermum mopane* shrublands and woodlands in the central Kruger National Park, South Africa

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The woody plant, *Colophospermum mopane*, occurs as either a shrub or tree in shrublands and woodlands, respectively, in the central Kruger National Park, South Africa. As a first step in identifying which soil properties potentially influence the structure of *C. mopane* in these landscapes, we investigated the soil chemistry of the pedoderm in shrublands and woodlands. A total of 39 composite pedoderm samples (0–2 cm) were analysed. Relative to the woodlands, the pedoderm of the shrublands had significantly lower mean concentrations of P, K, Ca, Mg, S, Mn, Cu, Na, B and C. Of the nutrients analysed, only B had a mean concentration likely to be constraining the growth of plants (0.16 ± 0.01 vs 0.69 ± 0.05 mg B kg⁻¹ in shrublands and woodlands, respectively). We suggest that the *C. mopane* shrubs do not establish as trees in the shrublands because deficiency of B limits their growth and increases the competitive strength of the grass sward relative to eudicot plants in the landscape.

**Keywords:** boron, grass-tree competition, nutrient deficiencies, soil chemistry, woody cover

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This paper is one of four research notes in this journal volume in which we explore the differences in soil nutrient status between treed and treeless areas in South African grasslands and savannas (Mills et al. 2021a, 2021b; Mills and Kellner 2021). Our rationale for focussing on soil nutrient deficiencies in the pedoderm is explained in the first research note of the series. Here we report on the results from a site in the central Kruger National Park, South Africa. The woody plant, *Colophospermum mopane*, known locally as mopane, occurs as a shrub less than one metre tall, as well as a tree up to 18 metres tall, in the central and northern regions of the park (Van Wyk 2008). In many shrublands and woodlands in these regions, *C. mopane* is abundant (Figure 1). Given that these vegetation types experience the same climate, it is likely that the marked differences in vegetation structure are ultimately because of differences in soil properties, with herbivory and fire potentially playing a modifying role.

As a first step towards identifying the soil properties underpinning the differences in structure of the *C. mopane* shrublands and woodlands, we investigated the chemistry of the pedoderm in both habitats. The shrublands and woodlands investigated were located on flat plains, with clayey topsoils derived from Timbavati gabbro and Letaba basalt parent materials, respectively (Council for Geoscience South Africa 2017). Based on global datasets, satellite imagery analysis and machine learning, soil types in the shrublands have been classified as Eutric Regosols and Ferralic Arenosols, and in the woodlands as Eutric Cambisols and Rhodic Nitisols (ISRIC 2008), with mean clay content of the two vegetation types ranging from 23% to 29% (Hengl et al. 2017) (Supplementary Figure S1). With respect to herbivory and fire, the data available indicates that there are no differences between the shrublands and woodlands in our study area (Supplementary Figures S2 and S3).

Composite pedoderm samples (0–2 cm), comprising six to eight subsamples within an area of approximately 100 m², were taken outside of the mopane canopies in both shrublands (n = 19) and woodlands (n = 20) (Figure 2). The samples were air-dried and sieved to <2 mm. pH (KCl) was determined using a 1:2.5 soil: 1 M potassium chloride solution. Inductively coupled plasma mass spectrometry was used to analyse extractable: phosphorus (P); potassium (K); calcium (Ca); magnesium (Mg); sodium (Na); sulphur (S); boron (B); manganese (Mn); copper (Cu); and zinc (Zn). Phosphorus, K, Ca, Mg and Na were extracted with 1% citric acid solution (Division of Chemical Services 1956; Du Plessis and Burger 1965). Sulphur and B were extracted using calcium phosphate and hot water, respectively (Beaton et al. 1968; Bingham 1982). Manganese, Cu and Zn were extracted using...
0.02 M di-ammonium ethylenediaminetetraacetic acid (Trierweiler and Lindsay 1969; Beyers and Coetzer 1971). The Walkley–Black method (Walkley 1935; Nelson and Sommers 1982) was used to determine organic carbon (C). Differences between the vegetation types were tested using independent \( t \)-tests in R (version 3.6.1).

The pedoderm of the shrublands had significantly lower concentrations of P (32 ± 2.3 vs 61 ± 4.4 mg kg\(^{-1}\); mean ± standard error), K (223 ± 17 vs 601 ± 37 mg kg\(^{-1}\)), Ca (821 ± 114 vs 6 255 ± 845 mg kg\(^{-1}\)), Mg (397 ± 54 vs 2 530 ± 347 mg kg\(^{-1}\)), S (3.3 ± 0.16 vs 4.4 ± 0.18 mg kg\(^{-1}\)), Mn (167 ± 24 vs 421 ± 27 mg kg\(^{-1}\)), Cu (4.7 ± 0.5 vs 8.7 ± 0.4 mg kg\(^{-1}\)), B (0.16 ± 0.01 vs 0.69 ± 0.05 mg kg\(^{-1}\)), Na (25 ± 1.2 vs 57 ± 4.8 mg kg\(^{-1}\)) and C (1.0 ± 0.1 vs 2.3 ± 0.1 mg kg\(^{-1}\)) than the woodlands (Figure 3). It is not known how individual plant nutrients affect the stature of mopane shrubs versus trees, but we suggest for two reasons that in this particular environment in the central Kruger National Park, B is of primary importance. This is firstly because plant growth is likely to have been constrained by the availability of B in the shrublands (mean concentration of 0.16 ± 0.01 mg kg\(^{-1}\)), but not in the woodlands (0.69 ± 0.05 mg kg\(^{-1}\)). None of

Figure 1: Examples of soil sampling plots in mopane shrublands (a) and mopane woodlands (b) in the central Kruger National Park, South Africa

Figure 2: The location (a), underlying geology (b) and vegetation types (c) of the study area (Mucina and Rutherford 2006; Council for Geoscience 2017). The position of the Kruger National Park within South Africa is shown in the map insert in (a). The sampling plots in mopane shrublands and woodlands are depicted as circles and triangles, respectively.
the other nutrients analysed had mean concentrations that would be expected to constrain plant growth (Peverill et al. 2005; Sims and McGrath 2011; Marschner 2012). Secondly, the relative scarcity of B in the pedoderm of the shrublands is likely to have increased the competitive strength of grasses relative to *C. mopane* seedlings. The reason for this is that grasses have a considerably lower requirement for B than eudicot plants (Bell 1997; Fleischer...
et al. 1999; Brown et al. 2002; Tariq and Mott 2007; Camacho-Cristóbal et al. 2008; Wimmer et al. 2015).

The potential importance of B on the growth of trees in South African savannas has previously been highlighted by a nursery experiment where the indigenous tree Vachellia karroo (Hayne) was grown in ten different toposols. Boron was found to be the nutrient most strongly correlated with growth (Wakeling et al. 2010). The results of this nursery experiment and the differences in chemistry of the pedoderm between mopane shrublands and woodlands at our study site suggest that further research on B is likely to be a fruitful avenue for investigating the effects of nutrient availability on vegetation structure in South African savannas.

The origin of the differences in soil chemistry between the shrublands and woodlands at our study site is potentially confounded by the effect of plants on soil nutrients. It is plausible, for example, that the greater stature of trees compared with shrubs caused the enrichment of nutrients in the woodland, given that trees are known to enrich soils beneath their canopies (Scholes and Archer 1997; Ludwig et al. 2001; Augusto et al. 2002; Reis et al. 2010; Ruwanza 2017). We suggest, however, that differences in geology between the shrublands and woodlands is a primary factor causing the difference in vegetation height, with soil texture and nutrient enrichment under tree canopies being secondary factors. Parent materials of the study site include gneiss and gabbro under the shrubland and basalt under the woodlands. Nutrient richer and more clayey soils would be expected to develop from the basalt parent material. The more clayey texture would result in reduced rates of nutrient leaching, further widening the difference in nutrient status between the basalt-derived and gneiss/ gabbro-derived soils. The presence of a woodland on the basalt-derived soils would also increase this difference in nutrient status because of inter alia the capture of dust in the tree canopy and importation of nutrients in dung and urine from animals using the tree canopy for shade. Notwithstanding the effects of clay and tree canopies, the extreme differences in mean concentration of nutrients such as Ca (521 ± 114 versus 6 255 ± 455 mg kg⁻¹) in shrublands and woodlands, respectively suggests that geology has had a primary role in determining the nutrient status of the soils in the study area. Slight differences in clay content and nutrient enrichment by tree canopies would not be expected to generate an eight-fold difference in nutrient status. We consequently conclude that variation in geology, resulting in a relative deficiency of B in the shrublands, is likely to be a primary underlying reason for the major differences in vegetation structure in the study site investigated.

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References

Augusto L, Ranger J, Binkley D, Rothe A. 2002. Impact of several common tree species of European temperate forests on soil fertility. Annals of Forest Science 59: 233–253. https://doi.org/10.1051/forest:2002020.
Beaton JD, Burns GR, Platou J. 1968. Determination of sulphur in soils and plant material. Washington, DC: Sulphur Institute.
Bell RW. 1997. Diagnosis and prediction of boron deficiency for plant production. Plant and Soil 193: 149–168. https://doi.org/10.1023/A:1004268110139.
Beyers CDL, and Coetzter FJ. 1971. Effect of concentration, pH and time on the properties of di-ammonium EDTA as a multiple soil extractant. Agrochimica 3: 49–53.
Bingham FT. 1982. Boron. Methods of Soil Analysis: Part 2 Chemical and Microbiological Properties. Madison: American Society of Agronomy.
Brown PH, Bellaloui N, Wimmer MA, Bassil ES, Ruiz J, Hu H, Pfeffer FD, Römheld V. 2002. Boron in Plant Biology. Plant Biology 4: 205–223. https://doi.org/10.1055/s-2002-25740.
Camacho-Cristóbal JJ, Rexach J, Gonzalez-Fontes A. 2008. Boron in plants: Deficiency and toxicity. Journal of Integrative Plant Biology 50: 1247–1255. https://doi.org/10.1111/j.1744-7909.2008.00742.x.
Council for Geoscience South Africa. 2017. Geology of South Africa. ArcGIS Web Map. Available online from: https://sageosscience.maps.arcgis.com/home/index.html.
Division of Chemical Services. 1956. Analytical methods. Pretoria: South African Department of Agriculture Technical Services.
Du Plessis RDT. 1965. A comparison of chemical extraction methods for the evaluation of phosphate availability of top soils. South African Journal of Agricultural Science 8: 1113–1122.
Fleischer A, O’Neill MA, Ehwald R. 1999. The pore size of non-graminaceous plant cell walls is rapidly decreased by borate ester cross-linking of the pectic polysaccharide rhamnogalacturonan II. Plant Physiology 121: 829–838. https://doi.org/10.1104/pp.121.3.829.
Hengl T, Mendes de Jesus J, Heuvelink GBM, Ruiperez Gonzalez M, Kilibarda M, Blagotić A, Shangguan W, Wright MN, Geng X, Bauer-Marschallinger B, et al. 2017. SoilGrids250m: Global gridded soil information based on machine learning. PLoS ONE 12: e0169748. https://doi.org/10.1371/journal.pone.0169748.
ISRIC. 2008. Soil and Terrain Database (SOTER) for South Africa. https://data.isric.org/geonetwork/srv/api/records/c3f7cfd5-1f25-4da1-bce9-cddcd8cf19a9. [Accessed 1 March 2021].
Ludwig F, Kroon H, Prins HHT, Berendse F. 2001. Effects of nutrients and shade on tree-grass interactions in an East African savanna. Journal of Vegetation Science 12: 579–588. https://doi.org/10.2307/3237009.
Marschner H. 2012. Marschner’s mineral nutrition of higher plants. Amsterdam: Academic Press.
Mills AJ, Strydom T, Allen J, Baum J. 2021a. The chemistry of the pedoderm – part 1: Grasslands and savannas in the central Kruger National Park, South Africa. African Journal of Range & Forage Science. https://doi.org/10.2989/10220119.2021.1938222.
Mills A, Strydom T, Allen J. 2021b. The chemistry of the pedoderm – part 2: Dichrostachys cinerea patches and adjacent grassland in the southern Kruger National Park, South Africa. African Journal of Range & Forage Science. https://doi.org/10.2989/10220119.2021.1938223.
Mills A, Kellner K. 2021. The chemistry of the pedoderm – part 4: Grasslands and savannas within Mokala National Park, South Africa. African Journal of Range & Forage Science. https://doi.org/10.2989/10220119.2021.1938221.

Mucina L, Rutherford M. 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. Pretoria: South Africa National Biodiversity Institute. pp 490–492.

Nelson DW, Sommers LE. 1982. Total carbon, organic carbon, and organic matter. In: Page A (Ed.). Methods of soil analysis. Part 2. Chemical and microbiological properties. Madison: American Society of Agronomy. pp 539–579.

Peverill KI, Sparrow LA, Reuter DJ. 2005. Soil analysis: An interpretation manual. (2nd edn). Clayton: CSIRO Publishing.

Reis G, Lana ÂMQ, Mauricio R, Lana RMQ, Machado RM, Borgeri TQ. 2010. Influence of trees on soil nutrient pools in a silvopastoral system in the Brazilian Savannah. Plant and Soil 329: 185–193. https://doi.org/10.1007/s11104-009-0144-5.

Ruwansa S. 2017. Invasion of abandoned agricultural fields by Acacia mearnsii affect soil properties in Eastern Cape, South Africa. Applied Ecology and Environmental Research 15: 127–139. https://doi.org/10.15666/aeer/1501_127139.

Scholes RJ, Archer SR. 1997. Tree-grass interactions in Savannas. Annual Review of Ecology and Systematics 28: 517–544. https://doi.org/10.1146/annurev.ecolsys.28.1.517.

Sims JT, McGrath J. 2011. Soil fertility evaluation. In: Huang PM, Li Y, Sumner ME (Eds), Handbook of soil sciences: Resource management and environmental impacts (2nd edn). Boca Raton: CRC Press. pp 1–36.

Tariq M, Mott CJB. 2007. The significance of boron in plant nutrition and environment – A review. Journal of Agronomy 6: 1–10.

Trierweiler JF, Lindsay WL. 1969. EDTA-ammonium carbonate soil test for zinc. Soil Science Society of America Journal 33: 49–54. https://doi.org/10.2136/sssaj1969.03615995003300010017x.

Van Wyk P. 2008. Field guide to the trees of the Kruger National Park. Cape Town: Struik Publishers.

Wakeling JL, Cramer MD, Bond WJ. 2010. Is the lack of leguminous savanna trees in grasslands of South Africa related to nutritional constraints? Plant and Soil 336: 173–182. https://doi.org/10.1007/s11104-010-0457-4.

Walkley A. 1935. An examination of methods for determining organic carbon and nitrogen in soils. Journal of Agricultural Science 25: 598–609. https://doi.org/10.1017/S0021859600019687.

Wimmer MA, Goldberg S, Gupta UC. 2015. Boron. In: Barker AV, Pilbeam DJ (Eds), Handbook of plant nutrition. Boca Raton: CRC Press. pp 305–346.