Potential geochemical constraints on tree seedlings in northern Kruger National Park grasslands

In the northern Kruger National Park (KNP), South Africa, there are extensive areas of treeless grassland interspersed within treed savannas (Figure 1) (Pienaar 1963). To the authors’ knowledge, there have been no investigations into the factors preventing trees from establishing in these grasslands.

There are many potential factors that could lead to poor recruitment of tree seedlings in these grasslands relative to the savanna matrix. Such factors, including for example competition from grass and herbivory pressure (Morrison et al. 2019; Porensky & Veblen 2012; Riginos 2009; Van Auken & Bush 1988), warrant further investigation. Soil nutrients are likely to interact with herbivory and grass competition in the tree constraint given that sub-optimal availability of any particular nutrient will adversely affect a recently germinated tree seedling’s rate of growth as well as recovery from herbivory (Cohn, Van Auken & Bush 1989; Kambatuku, Cramer & Ward 2011; Vadigi & Ward 2012). Consequently, the soil surface of the grasslands and adjacent savannas was sampled as a first step in assessing the potential influence of nutrition on grass competition as well as tree seedling growth immediately after germination.

Forty composite soil samples (0 cm–2 cm) were taken from an extensive treeless grassland and adjacent savanna north of Letaba Rest Camp in the KNP, South Africa with permission from the South African National Parks. The dominant tree in the savanna is Colophospermum mopane. The underlying geology of both vegetation types is Letaba basalt. The study did not include excavation of soil pits and consequently the researchers did not classify the soils. However, a study by Venter (1990) near the study site found that the two most common soil forms were Oakleaf and Valsrivier. The Oakleaf soil form is a cumulic soil characterised by young, unconsolidated sediment, either colluvial, alluvial or aeolian in origin (Fey 2010) with A horizons ~10 cm–20 cm deep (SCWG 2018). The Valsrivier soil form is a clay-enriched duplex soil (Fey 2010) with A horizons ~15 cm–25 cm deep (SCWG 2018). Each composite sample comprised 8–10 sub-samples taken from 100 cm2 within a plot of 100 m2. The samples in savannas were taken outside of tree canopies. The influence of land use on the geochemistry of the 0 cm–2 cm surface layer of the soils sampled is likely to be insignificant because no agriculture has taken place in the area for at least one century.

Soil samples were air-dried and sieved to < 2 mm. pH was determined using a 1:2.5 soil:1M KCl solution. Inductively coupled plasma mass spectrometry was used to analyse: (1) potassium; calcium; magnesium and sodium (1% citric acid extract) (Division of Chemical Services 1956); (2) phosphorous (1% citric acid extract) (Du Plessis & Burger 1965); (3) sulfur (calcium phosphate extract) (Beaton, Burns & Platou 1968); (4) boron (hot water extract) (Bingham 1982); and (5) manganese, copper, zinc (0.02M di-ammonium ethylenediaminetetraacetic acid extract) (Beyers & Coetzter 1971; Trierverweiler & Lindsay 1969). Organic carbon was determined using the Walkley-Black method (Nelson & Sommers 1982; Walkley 1935).

The results showed that relative to the savanna the soil surface in the grassland was enriched in phosphorous, magnesium and zinc, impoverished in boron and more alkaline (Figure 2). The only nutrient that emerged from this study as potentially constraining tree seedlings shortly after germination in the grassland was boron, with a mean concentration of 0.4 mg kg–1. Assessing whether a concentration of 0.4 mg B kg–1, extracted using hot water from a specific soil, will impede growth in a particular plant species is complex, as multiple soil properties such as pH, clay mineralogy, soil water content and phosphate concentration influence boron uptake by roots (Bell 1997; Shorrocks 1997). Notwithstanding this complexity, on finding such concentrations of B and
assuming that the goal (at any given site, regardless of soil properties, climate, or plant species involved) was to optimise plant growth, it would be prudent, based on the existing literature (see e.g., Bell 1997; Tariq & Mott 2007), to experimentally determine whether boron is limiting plant growth. Particularly relevant studies in this context include those by Li et al. (1978), Rashid, Rafique and Bughio (1994), Rafique et al. (2002) and Yadav et al. (2017), which found that concentrations of 0.4, 0.5, 0.6 and 0.5 mg B kg\(^{-1}\), respectively, restricted the growth of the plants under investigation. It is noteworthy that boron requirements of dicotyledonous plants, such as the tree seedlings at the study site, are likely to be considerably greater than those of the grass species (Bell 1997; Tariq & Mott 2007). Scarcity of boron would consequently be expected to constrain the tree seedlings more than the competing grasses. It is also noteworthy that within fertilisation experiments in the Brazilian Cerrado, plant growth was constrained by deficiencies of boron more than deficiencies of any other nutrient (Lannes et al. 2020), and that a pot experiment in South Africa, using a wide range of soils from natural ecosystems, found that boron was the nutrient most strongly correlated with growth of indigenous tree seedlings (Wakeling, Cramer & Bond 2010). Pot experiments with a wide range of local grass and tree species are likely to be of value for further investigation into the hypothesis that a relative scarcity of boron in the northern KNP grasslands enhances the competitive strength of grasses more than recently germinated tree seedlings. Given that nutrient deficiencies in plants are usually identified most effectively using foliar nutrient analyses, the authors suggest that such pot experiments should include nutrient analyses of foliage as well as soil.

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**Competing interests**

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

**Authors’ contributions**

A.J.M. conceived and carried out the study and acquired funding. J.B. and T.S. provided administrative assistance and

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**FIGURE 1:** Study site location and habitats within the Kruger National Park (KNP), South Africa, showing (a) the distribution of treeless grasslands in the northern Kruger National Park, photographs of (b) grassland and (c) adjacent treed savanna and (d) the location of sampling plots (~100 m\(^2\)) in grassland (squares) and savanna (triangles).
T.S. facilitated access to the field site where J.B. and A.J.M. conducted field work. J.B. and J.L.A. conducted a literature review for this study. With A.J.M., J.L.A. conducted the statistical analyses. J.L.A. prepared the figures. A.J.M. wrote the manuscript, with all authors approving its contents.

**Ethical considerations**

Ethical clearance to conduct this study in the Kruger National Park was obtained from South African National Parks (permit reference number MILA1364).

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**Data availability**

The raw data from this study are available at the Stellenbosch University Institutional Research Data Repository ‘SUNScholarData’: https://doi.org/10.25413/sun.23659920.

Note: Asterisks denote significant differences between grassland and savanna plots according to independent t-tests. The lower and upper bounds of the boxes correspond to the first and third quartiles (the 25th and 75th percentiles), lines within the box depict the median, whiskers show 1.5 × the inter-quartile range and data beyond the end of the whiskers are outlier points. The elements presented are all extractable concentrations as per the methods described in the main text.

*P*, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; S, sulfur; Mn, manganese; Cu, copper; Zn, zinc; B, boron; Na, sodium; C, carbon.

\* , \( p = 0.01–0.05 \); \** , \( p = 0.001–0.009 \); \*** , \( p < 0.001 \).

**FIGURE 2:** The soil chemistry of composite pedoderm samples from grassland (n = 20) and adjacent treed savanna (n = 20) at the study site in the northern Kruger National Park, South Africa.
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