

## Constraint on woody cover in relation to nutrient content of soils in western southern Africa

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The influence of soil nutrients on woody plants is poorly understood. Are trees – fire and other disturbance factors being equal – generally promoted by nutrient-rich or by nutrient-poor soils? To determine the edaphic parameters controlling woody cover, we sampled soils and summed the extent of the crowns of trees and tall shrubs on 364 plots at 20 sites in Namibia and adjacent South Africa, ranging from desert lichen-fields to caesalpiniaceous woodland with associated mean annual rainfall of 11 mm to 535 mm. Our analysis included the macro-nutrients N, P, Mg, K and Ca and the trace elements Mn, Fe, Cu and Zn. A boundary line analysis showed that woody cover was densest, with the greatest large-scale heterogeneity, at intermediate nutrient contents, but consistently constrained at extreme nutrient richness as well as poverty. If aridity exerted the ultimate constraint at extreme nutrient richness, no such correlation with climate apparently applies at extreme nutrient poverty, where our graphs show an ‘oligotrophic decline’. Notwithstanding the importance of water, we suggest that extreme nutrient richness and poverty both favour grasses over tree seedlings. This is because catabolic dystrophy – a regime in which the supply of catabolic nutrients shortfalls their demand – is unlikely in environments where nutrient richness allows catabolic rates to match anabolic rates or where nutrient poverty constrains anabolic rates. We also reason that surpluses of photosynthate resulting from dystrophy can be allocated to lignin and that the potential for woody growth thus corresponds to soils of intermediate nutrient content. This explains why woody cover is consistently but not homogeneously densest in nutritionally intermediate plots in our dataset. Hence, the abundance of woody plants in various biomes may be determined partly by soil nutrient content, particularly of Cu, Zn, and other elements indispensable for catabolism.

The cover of woody plants, particularly trees and tall shrubs, in natural biomes varies from dense (e.g. forest or thicket) to sparse (e.g. open savanna). In savannas, woody plants coexist as an upper stratum with grasses. The height of trees and shrubs in this biome varies greatly, as does the density of the woody component, from dense in savanna woodlands to sparse in nearly treeless savannas. Despite an extensive literature (see Bond 2008 for examples), there remains a ‘savanna-grassland problem’ of determining which environmental factors cause this variation and how woody plant forms represent adaptations to these factors (Mills et al. 2006b). Bond (2008) divides the environmental factors into top-down fire and herbivory and bottom-up climate and soils.

Exclusion experiments in African savannas show that tree densities, biomass and species composition are strongly influenced by fire regimes and herbivory (Goheen et al. 2010). However, neither fire nor herbivory appear to be ultimate determinants of the geographic location of grassland, savanna and forest biomes. With respect to fire:

grassland–forest boundaries often occur at soil boundaries with no obstacles to fire spread (Bond 2008); many woody plants such as *Eucalyptus* (Attiwill 1994) and Miombo trees (Trapnell 1959) are resilient to fire; and some woody plants are capable of excluding fire even under semi-arid climates (e.g. *Portulacaria afra*) (Vlok et al. 2003). Indeed the pyrophily of many woody plants suggests that fire is as much the result of adaptation as the cause of adaptation. With respect to herbivory: notwithstanding the effects of megaherbivores such as elephants which promote grasses (Owen-Smith 1987), savannas are often replete with herbivores (Bond 2008), and intense herbivory is often associated with an increase, not a decrease, in woody plants (Goheen et al. 2010). Indeed, the effect of herbivory on woody plants is acknowledged to be complex, with strong interactions with fire (Bond 2008).

The effect of climate on the woody cover of vegetation is also unclear. Delineation of major biomes on temperature–precipitation axes show large areas of uncertainty where woodiness of the biome cannot be predicted

(Whittaker 1975). The long dry season characteristic of savannas was, more than a century ago, thought to be the reason why trees do not increase in density to form forests (Schimper 1903). Yet aridity does not exclude the formation of closed woody vegetation such as arid thickets (Mills et al. 2005, Bond 2008). Another aridity-related hypothesis – the root-niche differentiation hypothesis (Walter 1971) – focuses not on climate per se but rather the extent to which water percolates beyond grass roots to deeper soil layers where trees have exclusive access. Numerous studies have refuted this hypothesis empirically (Higgins et al. 2000), possibly because tree seedlings compete directly with grasses (Bond 2008). Other authors have explained the gross structure of vegetation as being the result of a balance between the major water requirement of trees and the deleterious effect of surface waterlogging (Tinley 1982). Yet the occurrence of both treeless marshes and forested swamps in poorly-drained areas highlights the inconsistency of the effects of waterlogging on trees (Hook 1984). It is consequently not clear that trees are intrinsically more vulnerable to root anoxia than are herbaceous plants.

Soil nutrient content is also frequently cited as influencing woody cover (Lehmann et al. 2011), but it is not clear whether nutrient-rich soils are generally more favourable, or less favourable, than nutrient-poor soils for the general life form category of trees and tall shrubs. In a recent analysis, Bond (2010) found that Ca and K were more important for forest establishment than other nutrients such as P that have been portrayed as pivotal for ecosystem structure (Beadle 1954). Cole (1986) also investigated the importance of nutrients in tree establishment, and suggested that nutrient poverty may in fact lead to the exclusion of trees from grasslands. Yet grasslands in Australia tend to occur on more clayey, nutrient-rich soils than those on which adjacent woodlands occur (Lunt 1997). At the biome scale, it is acknowledged that the most extensive forest (e.g. taiga, tropical rainforests) and thicket (e.g. chaparral, macchia, rhododendron) biomes in the world occur typically on nutrient-poor soils, and that some of the most successful plantation trees (e.g. *Eucalyptus*) originate in nutrient-poor habitats (Orians and Milewski 2007). Indeed, in both African and Australian savannas, sandy soils tend to favour woody over herbaceous plants, regardless of the probable infertility of the sands (Sankaran et al. 2005, Bond 2008). This is highlighted by the observation that nutrient-poor savannas generally support more woody biomass ( $> 15$  tonnes  $\text{ha}^{-1}$ ) than do nutrient-rich ones ( $< 15$  tonnes  $\text{ha}^{-1}$ ) (Scholes 1990). However, other authors have regarded nutrient poverty as an ultimate limitation for trees and tall shrubs in certain African vegetation types, such as fynbos (Cowling et al. 1992) and communities of geoxylic suffrutices (woody plants with no perennial stems above ground) in dambos (grassy and usually treeless drainage lines which are dry in the dry season but marshy in the rainy season) of the tropics (White 1976). The latter example of sparse and stunted trees appears to be in line with presumed effects of the nutrient poverty of siliceous, podzolic or lateritic soils on various other forest, savanna and chaparral vegetation types worldwide (Furley 1999).

Woody cover is also thought to be related in some landscapes to competition from grasses. Indeed, problems of

woody plant encroachment into the grassy rangelands of the world have been partly ascribed to weakening of the grass sward by overgrazing of livestock (Scholes and Archer 1997). This reasoning implies the inherent dominance of herbaceous over woody plants in an intact ecosystem, yet an acknowledgement of this has not been integrated into a consistent theoretical synthesis. Although it is accepted that grasses compete strongly with tree seedlings for belowground resources (Scholes and Archer 1997, Bond 2008), there is an implicit assumption in much of the literature on woody cover that trees are metabolically more powerful than herbaceous plants. Consequently it is predominantly gross damage to trees (e.g. by fire, frost, herbivory and/or tree-cutting) that is assumed to prevent woody cover from reaching the potential set by available water (Sankaran et al. 2005). This assumption has led to a focus on the demographics of tree species and the factors determining whether tree seedlings are able to escape from fire and herbivory by growing to a certain height (Higgins et al. 2000). However, it is now known that, per unit area of land, vegetation dominated by herbaceous plants can match, or exceed, the total metabolic power of vegetation dominated by woody plants (Price et al. 2010). This is because trees, although more massive, more likely to intercept sunlight, and far more demanding of water, have a slower average metabolism per cell than that of smaller plants. Consequently, herbaceous plants are, cell for cell, likely to be more powerful than trees, other factors being equal. This has potentially important ramifications for understanding competitive interactions between these life-forms especially when tree seedlings or saplings are entangled with herbaceous plants.

The effect of different nutrients on the metabolic power of woody versus herbaceous plants has to date not been considered in studies of the ultimate versus the proximate factors influencing the amount of woody cover in a landscape (Mills et al. 2006b). To understand potential effects of nutrients on woodiness of the vegetation, the underlying cause of woodiness needs to be examined. What is the adaptive value of wood? Does wood provide plants with a competitive edge in terms of competition for light, or perhaps competition rather for certain nutrients? The explanation that wood enables plants to grow tall and shade out herbaceous plants fails to explain the great variation in the height of trees and shrubs in open vegetation such as savannas or open woodlands; the question why woody plants grow taller than the meter or two required to shade out the competing herbaceous layer would remain. It is therefore conceivable that woodiness in savannas provides advantages other than capturing light. Increased acquisition of certain nutrients may be one such advantage. A first step in examining the latter proposition is to establish which nutrients are likely to be involved, and how woodiness would promote their acquisition.

Few soils are rich, or poor, in all nutrients, which means that, theoretically, the ratios of availability of certain sets of nutrients to each other may have been overlooked as environmental factors influencing the woodiness of different vegetation types. Could optimal concentrations of certain nutrients (as exemplified by the dark, carbon-rich mollisols, characteristic of prairie, steppe and pampas) possibly restrict the growth of woody plants in an indirect way by promoting the competitive vigour of herbaceous plants? Expressed in

another way: is it conceivable that woody plants, irrespective of successional potential, will remain sparse owing to superior competition by herbaceous plants at the root level, provided that the nutritional demands of the herbaceous plants are met?

Although competition between woody and herbaceous plants begins at the microscale of the rhizosphere, its effects could potentially play out at the macroscale of biomes, thus determining vegetation structure. The physiological basis for such competition may lie in the intrinsically different nutrient demands of woody plants, which sequester energy in the form of durable lignified fibre, and herbaceous plants, which do not. Woody plants may, for example, enjoy competitive advantage over herbaceous plants where there is a potential surplus of photosynthate available relative to the quantity of nutrients available for manufacturing proteins (Orians and Milewski 2007). This idea is further developed within a new theory of 'biological energy intensity' proposed by Milewski and Mills (2010). The theory predicts firstly that the demand and supply of catabolic nutrients (i.e. those

elements essential for catabolism of photosynthates but not correspondingly essential for photosynthesis) are likely to have a strong influence on the competitive outcome between woody and herbaceous plants; secondly that as the ratio of demand to supply increases, so the competitive advantage of woody plants increases because woody plants can increase the supply of catabolic nutrients in ways unavailable to herbaceous plants – e.g. by reducing rates of leaching through transpiration (Raven 2008) and by capturing aerosols through growth to maximum height (Graustein and Armstrong 1983, Mills et al. 2012); and thirdly that although most nutrients are involved in a wide range of physiological processes (both catabolic and anabolic), the distinction between nutrients that are predominantly catabolic (e.g. Cu, Zn) and those that are predominantly anabolic (e.g. Mg, Mn) in function may aid our understanding of the interactions between the uppermost and lowermost strata of vegetation. Following this theory of biological energy intensity, dense woody cover would be expected where discriminate poverty of nutrient elements keeps catabolic nutrient supply short of demand,

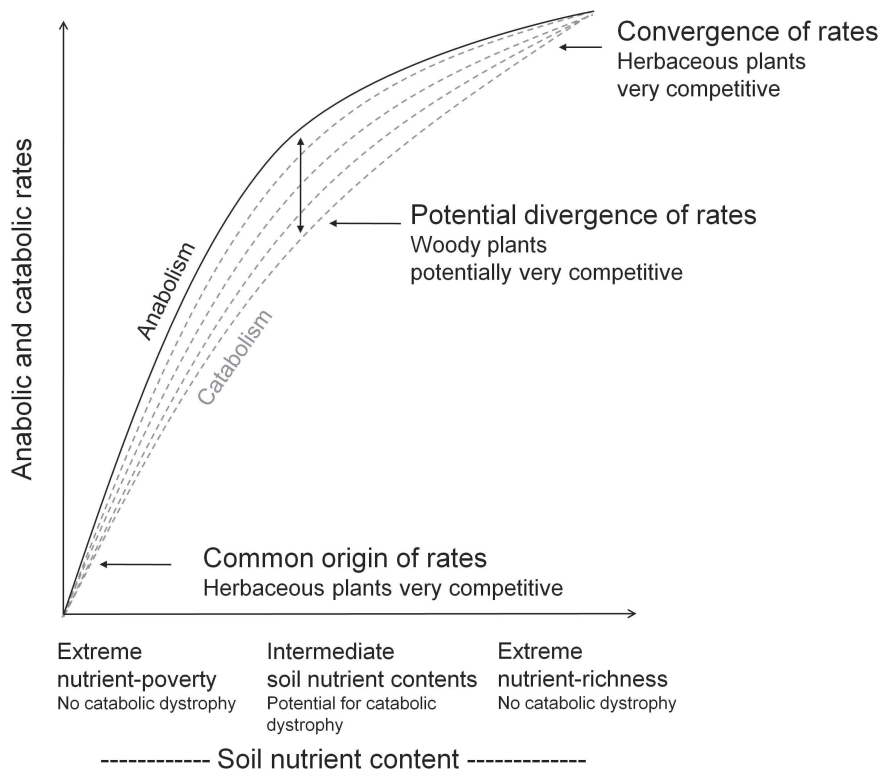


Figure 1. Anabolic (black continuous line) and catabolic (grey broken lines) rates in relation to soil nutrient content. Catabolic rate refers to the sum of within-plant catabolism and catabolism of any part of the plant digested by either herbivores or microbes including fungi; it is thus a parameter of the plant-consumer system and not the plant alone. Common origin: following an approach of biological energy intensity, there will be no metabolism at zero nutrient content; axiomatically, the rates of anabolism and catabolism originate at a single point. Catabolic dystrophy is not predicted where catabolic and anabolic rates are similar and only small amounts of photosynthate are available for synthesis of fibre. Herbaceous plants are predicted to be more competitive than woody plants and to dominate on soils with minimal nutrient content. Convergence at maximal nutrient content of soils: nutrient availability does not constrain anabolic or catabolic rates. Anabolic rates are constrained by other factors such as climate. Catabolic dystrophy is not predicted. Catabolic and anabolic rates resume similarity and only small amounts of photosynthate are available for synthesis of fibre. Herbaceous plants are predicted to be more competitive than woody plants and to dominate on soils with maximal nutrient content. Potential divergence: catabolic and anabolic rates can diverge at intermediate contents of nutrients, depending on the availability of particular elements and the potential rate of photosynthesis as determined by climate. Where the supply of catabolic nutrients falls short for much of the photosynthate produced (resulting in catabolic dystrophy), a large surplus of photosynthate is predicted. Woody plants are predicted to be more competitive than herbaceous plants because they capitalise on surplus photosynthate by building fibrous structures that augment their supply of scarce nutrients (e.g. deep roots and large canopies for aerosol capture).

resulting in what Milewski and Mills (2010) call catabolic dystrophy within the ecosystem. At either extreme of the soil fertility continuum (i.e. extreme nutrient poverty or extreme nutrient richness) catabolic dystrophy would not be expected (Fig. 1). This is because under the most extreme conditions of nutrient poverty, photosynthate production would be curtailed to such an extent – due to anabolic dystrophy – that demand for catabolic nutrients and consequently the ratio of demand to supply would be greatly reduced. In such an environment of anabolic dystrophy, woody cover would be expected to be restricted by competition with herbaceous plants. By contrast, under the most extreme conditions of nutrient richness, the demand for catabolic nutrients – by both producers and consumers – is likely to be met, even with rapid photosynthesis. In summary, based on considerations of biological energy intensity, woody cover would be densest on soils of intermediate nutrient content where catabolic dystrophy manifests, and sparsest on extremely nutrient-poor soils where anabolic dystrophy manifests, as well as on nutrient-rich soils exempt from nutrient dystrophy. To explore whether woody cover shows constraint at extreme nutrient poverty and richness, we sampled soils and measured woody cover on 364 plots at 20 sites in western southern Africa, covering several biomes, and used a boundary line approach to analyse the data collected.

## Methods

Our dependent variable was woody cover, which we defined as the summed percentage of ground surface covered – when crowns are projected vertically – by each species of tree and tall shrub (> 0.5 m high), and which we recorded as a composite index. This definition differs from authors such as Sankaran et al. (2005) who did not sum the overlapping parts of the crowns of different species but instead estimated a collective value for the multi-species canopy as a whole. Identifying the potential influence on woody cover of numerous edaphic parameters, such as content of individual elements, within the milieu of other potentially interacting factors (i.e. herbivory, fire and soil water availability) would be daunting were it not for recent advances using boundary line analysis (Milne et al. 2006). By identifying boundary lines around the scatter of data in plots of x and y variables from a large dataset (n preferably > 100), constrained and relatively unconstrained zones can be graphically depicted (Fig. 2). The constrained zones delineate areas in the graph where the independent variable x conceivably exerts constraint on the dependent variable y. The qualifier ‘conceivably’ is important because the constraint could be from another variable that is correlated with the independent variable. Consequently, causality cannot be established but only surmised. Identification of constraint may nevertheless help to reveal which environmental properties ultimately affect trees and tall shrubs. In contrast to the constrained zone, the relatively unconstrained zone delineates an area in the graph where the independent variable exerts minimal constraint on the dependent variable. It is important to note, however, that within this relatively unconstrained zone the dependent variable will in most instances be constrained by other variables, and consequently only a small proportion of the data points have minimal constraint and occur near the boundary line.

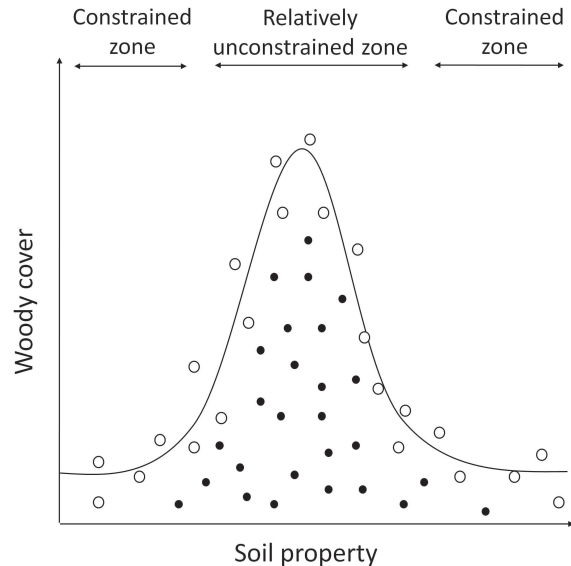


Figure 2. A hypothetical relationship between woody cover and any given soil property depicting constrained and relatively unconstrained zones. White circles – boundary points; black circles – all other data points; continuous line – boundary line.

## Study sites and vegetation parameters

The long-term biodiversity observatory sites (each 1 km<sup>2</sup>) of BIOTA Southern Africa from northern Namibia to adjacent western South Africa (Jürgens et al. 2012) were used for this study (Fig. 3). The study area spanned a gradient in vegetation structure from woodland (16–18 m high, Privette et al. 2004) with a grassy understorey, through savanna of intermediate height, to low scrub (Karoo), in which succulent dicyledonous plants replace grasses, to desert lichen-fields. The woodland understorey burns on average every second year, the savanna grasses burn infrequently (after seasons of heavy rain) and the Karoo is fire-free due to the succulence and sparsity of plant cover. Within the savannas of northern Namibia there is a shift in composition according to substrate, from Mimosaceae to Caesalpiniaceae. The very small, short-lived leaflets (attractive to folivorous mammals) and large stipular spines of *Acacia* spp. on loams contrast with the relatively large, long-lived leaflets (unattractive to folivorous mammals) and lack of spines in e.g. *Burkea*, *Bauhinia* and *Guibourtia* on Kalahari sands (Owen-Smith and Cooper 1987). Rainfall data for different observatories was obtained from WorldClim (Hijmans et al. 2005). Mean annual rainfall across this vegetation gradient ranges from 535 mm in woodland to 11 mm in lichen-fields.

Plant species data were obtained from the BIOTA database (2005–2006; 20060306), hosted by BIOTA Data Facility at Biocentre Klein Flottbek, Univ. of Hamburg (< www.biota-africa.org >). The number of botanical plots (20 × 50 m, the standard Whittaker plot size, much used in ecological studies in southern Africa) per site varied from 5 to 20. Mean values from botanical data collected from 2001 to 2005 (release date 19-12-2006), included the vertically projected crown area of each species classified by plant form as phanerophytes (woody plants higher than 0.5 m) as well as chamaephytes (dwarf shrubs), hemicryptophytes

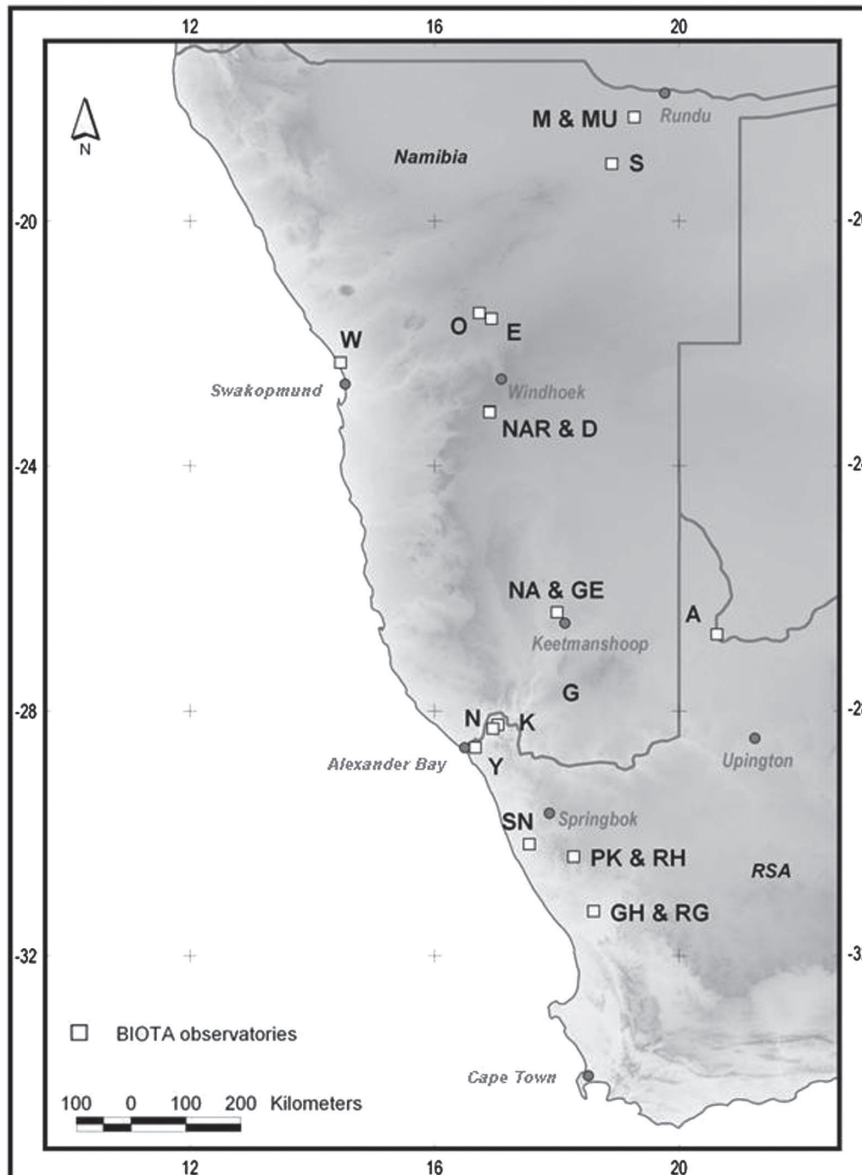


Figure 3. Study sites in western southern Africa. Open squares and abbreviations correspond to the observatories established by BIOTA Southern Africa. The grey shading shows increasing elevation from light to dark grey.

(predominantly grasses), therophytes (predominantly annual herbs), and geophytic cryptophytes (predominantly bulbs and rhizomes) (according to Raunkiaer 1934). It should be noted that we excluded shrubs lower than 0.5 m from our definition of woody cover, despite the dominance of such shrubs in the treeless vegetation typical of the Karoo of southern Namibia and the undisputed woodiness of their stems. These dwarf shrubs were allocated to Raunkiaer's chamaephyte category rather than to his phanerophyte category. We measured woody cover as a composite index of the extent of the crowns of trees and tall shrubs within the areas sampled as follows. The percentage of each plot covered by the crowns of each species of phanerophyte was estimated. Our woody cover index was then calculated by adding the percentage cover of each species together and dividing by 100. Whereas projected woody cover of other studies (Sankaran et al. 2005) cannot exceed a score of 100%, our index could exceed a score of 1 because of horizontal and

vertical crown overlap among species, particularly in the woodlands with high abundances of woody plants. Phanerophytes were further classified into four different height-classes, namely 0.5–2 m, 2–5 m, 5–20 m and 20–50 m. The proportion of woody cover contributed by each height-class varied with woody cover (data not shown). The first height-class predominated where total woody cover was  $< 0.2$  (woody cover index), and the first, second and third height-classes made up approximately equal proportions (with the fourth height-class comprising a negligible proportion) where woody cover was  $> 0.2$ . Woody cover is consequently positively correlated with the height of the woody plants in this dataset.

#### Edaphic parameters

Topsoil samples were taken at 0–15 cm, 4 m to the south of each plot (from the centre of the 50 m boundary) during visits in 2000–2006. Analyses performed routinely by BIOTA

Southern Africa (Haarmeyer et al. 2010) allowed investigation of the influence of a wide range of topsoil properties on woody cover. The soils were air-dried and sieved to < 2 mm. Analyses included: pH in  $\text{CaCl}_2$ , electrical conductivity (EC) in distilled water (1:2.5 soil:water ratios) (Van Reeuwijk 2002), total concentration of the elements Na, Mg, K, Ca, Mn, Fe, Cu, Zn, Al, Si and P by X-ray fluorescence spectroscopy using the method described by Kikkert (1983), ammonium acetate extractable cations ( $\text{Na}_{\text{Ac}}$ ,  $\text{Mg}_{\text{Ac}}$ ,  $\text{K}_{\text{Ac}}$  and  $\text{Ca}_{\text{Ac}}$ ) using the centrifuge method described by Helmke and Sparks (1996), total N via complete combustion using an CN elemental analyzer, and particle size (seven fractions) analysis using the pipette method detailed in Van Reeuwijk (2002). A subset of soil samples was selected for the ammonium acetate extract and particle size analyses.

## Data analysis

Analysis of boundary lines suits our approach because it allows scrutiny of the potential constraint exerted by each independent variable such as content of a single nutrient element on the dependent variable (i.e. woody cover) without disregarding the additional effects of various other environmental properties. In previous studies using the boundary line approach (Mills et al. 2006a), quantile regression was employed for delineating boundary lines. Quantile regression fails, however, firstly to identify actual boundary points (i.e. data points marginal to the scatter plot) and secondly tightness of fit of the boundary points with the boundary line (e.g.  $\text{Na}_{\text{Ac}}$ ; Fig. 4). Tightness of fit (i.e.  $R^2$  value) is important for distinguishing scatter plots with clearly demarcated boundary lines (i.e. few outlier data points) versus those with poorly demarcated boundary lines (i.e. a large number of outlier data points). Milne et al. (2006) highlighted that the problem of existing methods of boundary line analysis is that they rely on arbitrary decisions (e.g. the bin size). We consequently developed a new objective method for delineating

boundary lines with  $R^2$  values as follows. For each predictor variable, we extracted the boundary points using a new algorithm developed by the authors and generated a boundary line based on these boundary points using specialised software. The details of this method are described below.

The algorithm (R code details in Supplementary material Appendix A1) identifies boundary points by selecting the smallest and greatest predictor variable values on the scatterplot in a sequential manner moving from a y value of zero to a y value of 1.4. (illustration of the algorithm in Supplementary material Appendix A1 Fig. A1). We applied the algorithm twice; first on the whole set of data in the scatterplot and secondly on the set of data remaining after the boundary points from the first algorithm run had been removed. The final set of boundary points was the combination of boundary points extracted from the first and second run of the algorithm.

We then used Table Curve 2D software ver. 5.01 to generate a boundary line based on these boundary points. The most appropriate boundary line was determined after analysing tightness of fit of more than 3665 non-linear equations. Boundary line equations were ordered according to their  $F$ -statistic, and the ten tightest-fitting equations were 'short-listed'. The final selection of a boundary line from the short-list was based on a visual assessment of outliers, always giving priority to the simplest equation (Supplementary material Appendix A2 Table A2). In most cases the selected equation was also that with the largest  $F$ -value. However, the principle of parsimony (that one should make the minimum number of assumptions) was applied to visually similar boundary lines when comparing a simple equation to a more mathematically complex equation with a slightly larger  $F$ -value. It is important to note that although  $F$ -values and  $R^2$ -values were used to select equations and to differentiate the likely magnitude of influence of different variables on woody cover, deriving accurate equations for boundary lines of the different datasets was not the main objective

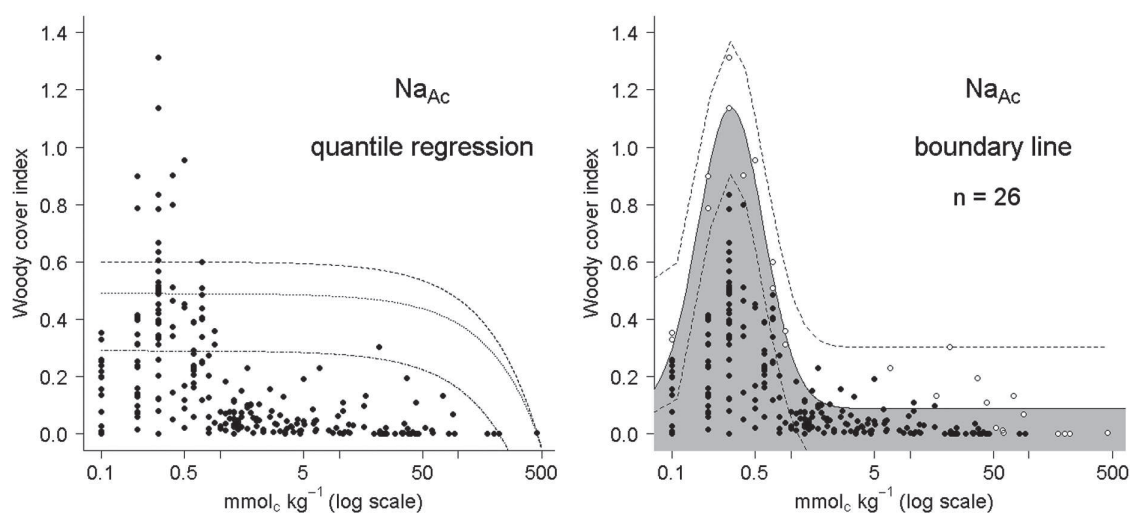


Figure 4. Comparison of the quantile regression method and the boundary line method to study the relationship between woody cover and Mg across 364 plots in western southern Africa. For the quantile regression method, dashed lines correspond to 0.95, 0.9 and 0.75 quantiles. For the boundary line method, white circles correspond to boundary points identified using an algorithm described in the methods section; black circles are all other data points; the continuous line represents the boundary line and dotted lines correspond to the 95% confidence interval; 'n' refers to the number of boundary points.

in this particular study. We rather used the boundary lines to highlight in a qualitative manner the broad patterns of constrained and relatively unconstrained zones in the various datasets (with the strength of constraint being related to the maximum woody cover value in the dataset), to develop an understanding of factors operating at the landscape and/or biome scale. A focus on deriving equations of considerable accuracy (with narrow confidence intervals) for applied purposes at a plot scale (e.g. designing protocols for ecosystem restoration) would require a different study design in which gaps in the scatter of data are filled in by additional, targeted sampling. A log scale was used for the elements Na, Mg, K, Ca, Mn, Fe, Cu, Zn, Al and P, and the cations  $\text{Na}_{\text{Ac}}$ ,  $\text{Mg}_{\text{Ac}}$ ,  $\text{K}_{\text{Ac}}$  and  $\text{Ca}_{\text{Ac}}$  as well as EC and total N to reduce the asymmetry inherent within the data and to highlight the change in constraint on woody cover over small ranges of the independent variable near the origin. It should be noted that a smooth increase near the origin in the log scale corresponds to a steep increase near the origin in a linear scale (e.g. Mn; Fig. 5).

## Results

Well-defined boundary lines showed that woody cover in the study area is constrained under extreme values of each of the following abiotic variables: pH, EC, nutrient content (i.e. K, Mg, Ca, Fe, Cu, Zn, P and N), other elemental content (Na, Al and Si), silt content, sand content and rainfall (Fig. 6). These variables yielded boundary line equations with  $F$ -values larger than 6.2 (range: 6.2–164), and  $R^2$ -values larger than 0.52 (range: 0.52–0.94). Several variables were associated with relatively large  $F$ - and  $R^2$ -values, suggesting that woody cover is more likely to be constrained by several variables concomitantly rather than a single variable in particular. Moreover, certain variables (notably pH, EC, Ca, Cu,  $\text{Na}_{\text{Ac}}$ ,  $\text{Mg}_{\text{Ac}}$ ,  $\text{Ca}_{\text{Ac}}$ , silt content and sand content) showed

sharply declining boundary lines to the right of their graphic apex, leading into an asymptote at approximately 0.1 woody cover. Sparse ( $< 0.2$ ) woody cover at the highest contents of nutrients coincided with the greatest salinity ( $> 20 \text{ g kg}^{-1}$  total Na;  $> 1 \text{ dS m}^{-1}$ , 1:5 soil:water) and aridity ( $< 150 \text{ mm}$  rainfall). Apart from  $\text{Mg}_{\text{Ac}}$ ,  $\text{Ca}_{\text{Ac}}$  and Si, all elements had convex boundary lines which, when initially plotted on a linear scale, skewed towards the origin of the graph (the Si boundary line skewed away from the origin).

The boundary lines for several elements dipped markedly over a narrow range towards the origin as elemental content approached zero. These narrow ranges, which may relate to a nutrient deficiency threshold, were as follows: K (0.01–1.2  $\text{g kg}^{-1}$ );  $\text{K}_{\text{Ac}}$  (0.3–3.6  $\text{mmol}_c \text{ kg}^{-1}$ ); Mg (0.05–0.72  $\text{g kg}^{-1}$ ); Ca (0.32–1.04  $\text{g kg}^{-1}$ ); Mn (0.02–0.11  $\text{g kg}^{-1}$ ); Fe (0.26–3.68  $\text{g kg}^{-1}$ ); Cu (1–5  $\text{mg kg}^{-1}$ ); Zn (2–11  $\text{mg kg}^{-1}$ ); and P (0.15–0.25  $\text{g kg}^{-1}$ ). The decrease in woody cover along the boundary line of the above ranges corresponds to a switch from *Acacia* spp. (Mimosaceae) to Caesalpinieae such as *Burkea africana*. We emphasise that, although the densest caesalpinieaceous savannas are generally denser than mimosaceous savannas in Africa, our finding concerns the maximum values for the range of woody cover in our plots, in which savanna characterized by *Burkea* nowhere matched the woody cover of the thicket-like stands of e.g. *Acacia mellifera*.

The  $R^2$ -values and the patterns of constraint provide an indication of which variables are likely to play a strong role in determining woody cover. Variables with  $R^2$ -values greater than 0.8 and with boundary lines that show a levelling out below or near a woody cover index of 0.1 include pH, EC,  $\text{Mg}_{\text{Ac}}$ , Ca,  $\text{Ca}_{\text{Ac}}$ , Cu,  $\text{Na}_{\text{Ac}}$  and silt content. The tightness of fit of these variables and their accentuated asymptotes suggest respectively that they (or correlated unmeasured variables) are strongly related to woody cover, and exceed other soil properties in terms of their constraint on woody cover.

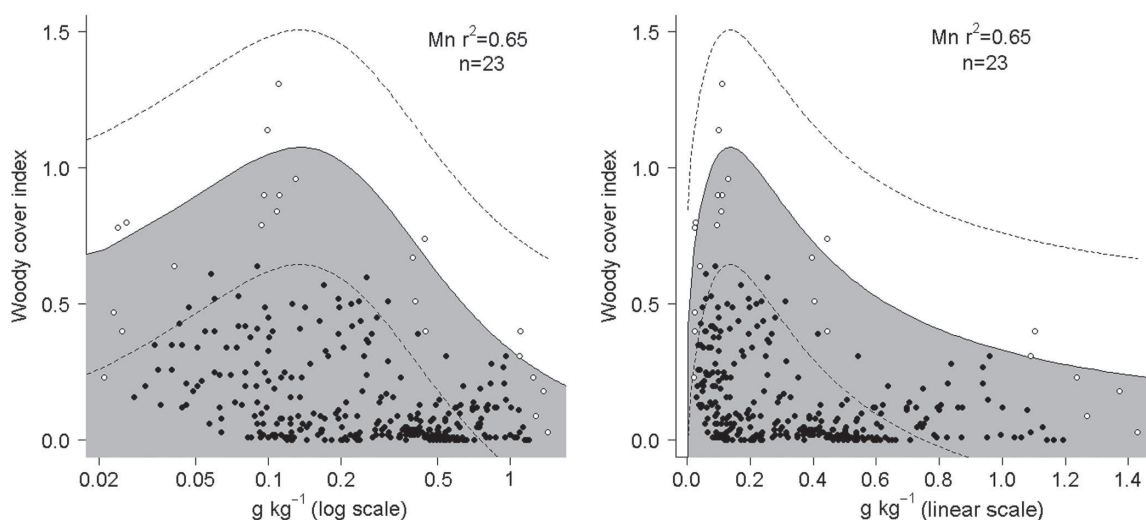
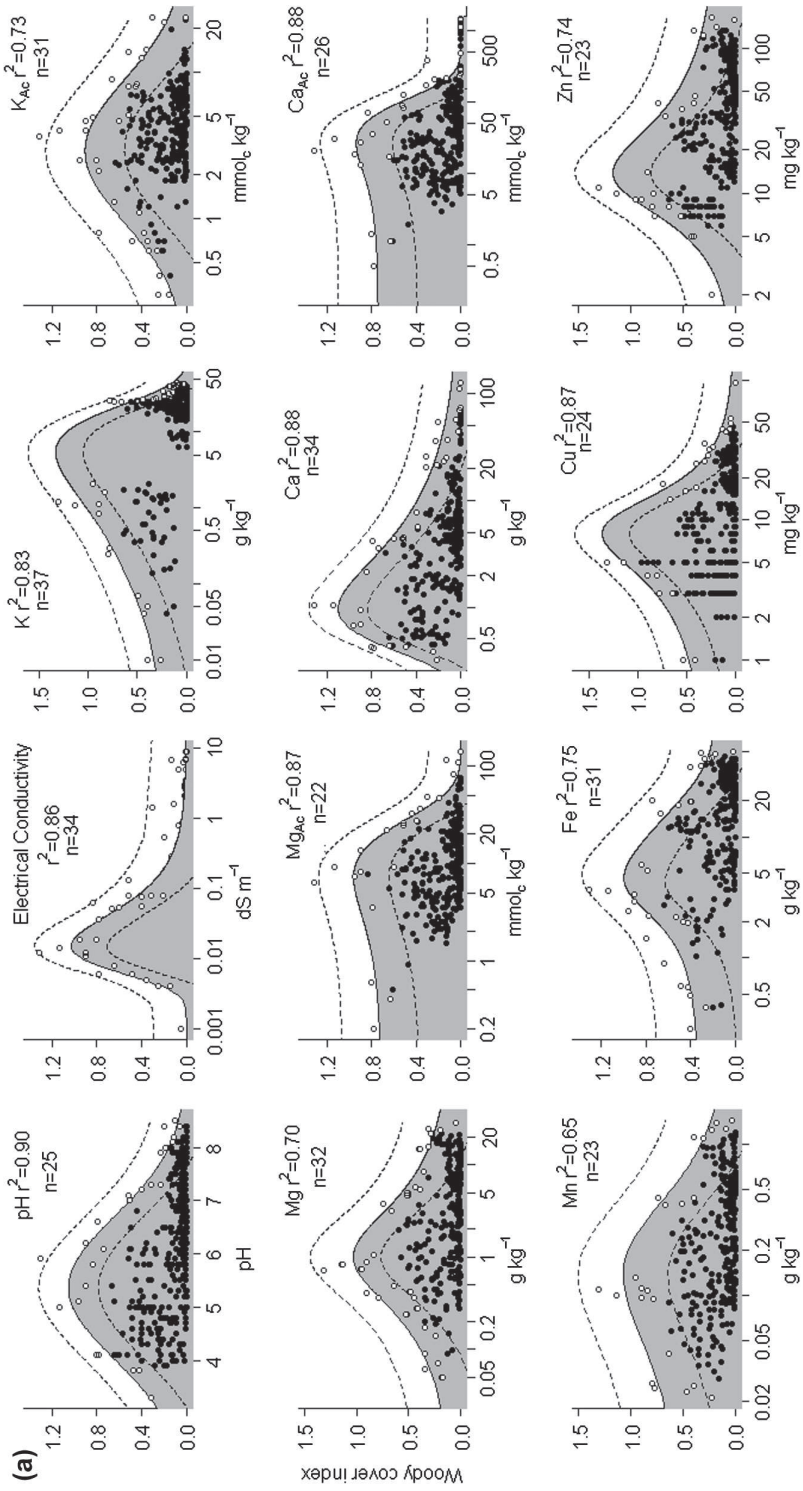


Figure 5. Comparison of the relationship between woody cover and Mn across 364 plots in western southern Africa between a log scale and a linear scale representation. The equation for the boundary line is presented in Table A2 (Supplementary material Appendix A2). White circles – boundary points identified using an algorithm described in the methods section; black circles – all other data points; the continuous line represents the boundary line and dotted lines correspond to the 95% confidence interval; 'n' values refer to the number of boundary points.





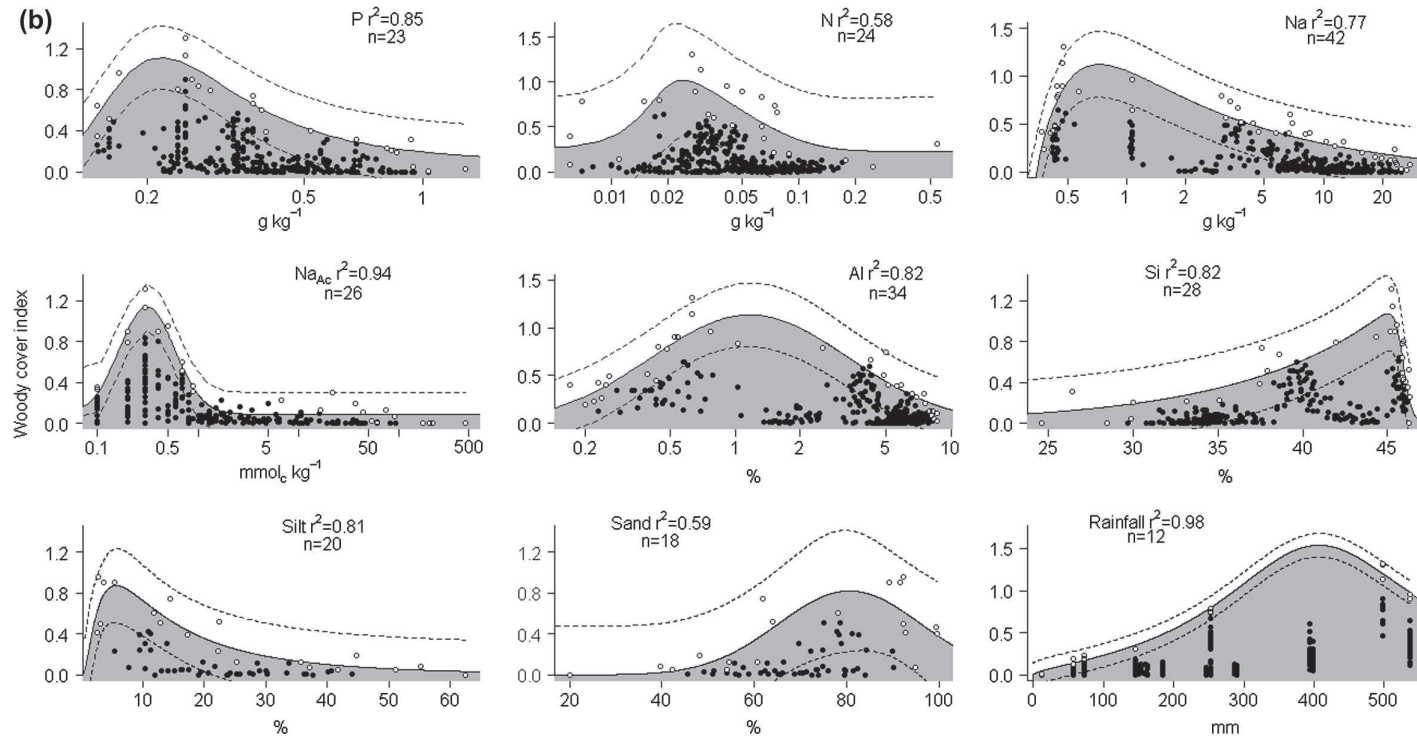


Figure 6a–b. Relationships between woody cover and the soil properties across 364 plots in western southern Africa. Equations for boundary lines are presented in Table A2 (Supplementary material Appendix A2). White circles – boundary points identified using an algorithm described in the methods section; black circles – all other data points; continuous lines represent the boundary lines and dotted lines correspond to the 95% confidence intervals; 'n' values refer to the number of boundary points.

## Discussion

As predicted from the theory of biological energy intensity (Fig. 1) woody cover across western southern Africa showed apparent constraint at sites with extreme nutrient poverty as well as richness (Fig. 6), and was sparse through to dense at sites with intermediate soil nutrient content. The theory holds that this pattern results from catabolic dystrophy – which favours woody plants over herbaceous plants – and only occurs in certain sites with intermediate soil nutrient content (Fig. 1). Quantifying the status of a site in terms of catabolic or anabolic dystrophy will require soil chemical analyses that focus on the proportion of a particular nutrient available to plants. This would be an appropriate next step in this investigation of how soil nutrient content may affect woody cover. Given the patterns of constraint in our dataset, it is noteworthy that, at the biome level, extensive treeless grasslands tend to be either nutrient-poor on sandy soils as in Australian hummock grasslands and Western Zambezian grasslands (Werger and Coetzee 1978, Griffin 1990) or nutrient-rich on black earth soils as in the Argentinian pampas, North American prairies, Serengeti grasslands and central Eurasian steppes (Krupenikov et al. 2011). It is also noteworthy that the patterns of constraint – especially with extreme nutrient poverty – evident in our entire dataset for western southern Africa (Fig. 6) were unclear in data subsets for vegetation types within the study area (see Fig. 7 which shows the relationship of woody cover with total Na). This highlights the value of examining patterns across a range of scales and suggests that studying spatial trends in several factors is likely to improve our understanding of the mechanisms controlling woody cover. It also suggests that only part of the pattern relating soil properties to woody cover

can be elucidated within each vegetation type, and that data spanning biomes are required to elucidate such patterns (Medinski et al. 2010).

The question emerging from our observation (i.e. woody cover shows constraint at extremes of nutrient content) is whether nutrient content directly influences woody plants as an ultimate factor, or whether it is merely a proximate factor. Woody cover is known to be strongly linked to water availability and mean annual rainfall (Sankaran et al. 2005), so relationships between woody cover and soil nutrient content in our dataset may ultimately reflect availability of water. Indeed, the availabilities of nutrients and water across a region of similar soil parent materials are often inversely correlated because amount of rainfall and rate of leaching are linked (Donkin and Fey 1993). Aridity is consequently a plausible explanation for the decrease in woody cover as nutrient content increases, congruent with the decrease in mean annual rainfall. It should, however, be noted that nutrient content could directly affect the interaction between herbaceous and woody plants, potentially favouring the herbaceous layer (Kraaij and Ward 2006). Indeed there is evidence that nutrient richness promotes competition by grasses either directly for nutrients and water (Riginos 2009), or indirectly through competition for light (Scholes and Archer 1997).

According to the theory of biological energy intensity, aridity would be a proximate rather than an ultimate factor influencing woody cover. This is because aridity is likely to reduce the potential for catabolic dystrophy, firstly because a scarcity of water will reduce the anabolic rate and accordingly reduce the demand for catabolic nutrients, and secondly because minimisation of leaching will increase the availability of catabolic nutrients. Consequently, catabolic dystrophy

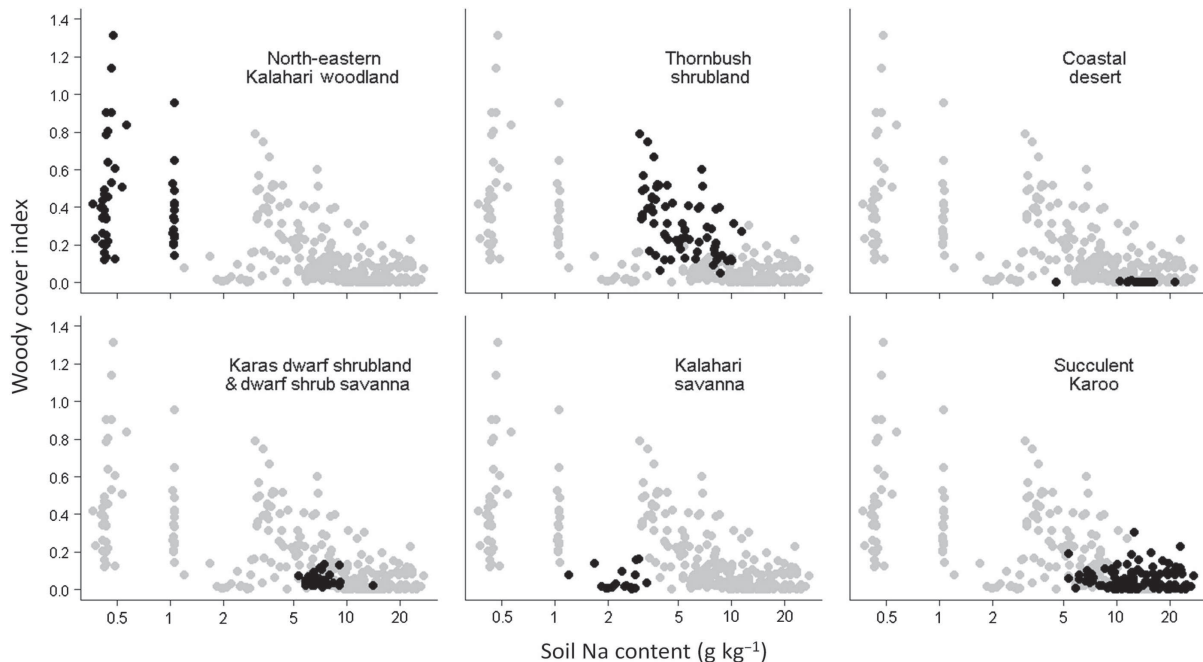


Figure 7. The relationship between woody cover and total soil Na in vegetation types of the study area. Black circles – all sites within a specific region; grey circles – sites in all other regions. Sites shown in Fig. 2 were grouped as follows: northeastern Kalahari woodland – M, MU and S; thornbush savanna – O and E; Karas dwarf shrubland and dwarf shrub savanna – NAR, D, NA, GE and G; coastal desert – W; Kalahari savanna – A; and succulent Karoo – N, K, Y, SN, PK, RH, GH and RG.

and an associated abundance of woody plants are unlikely in an arid environment. It should, however, be noted that aridity does not necessarily exclude woody plants; it only predicts that woody cover will not be dense in most arid environments, and that in certain arid environments where catabolic dystrophy does manifest – due to poverty of a particular nutrient (as a result of parent material elemental content) or the availability of groundwater (which boosts the anabolic rate) – woody cover will be dense. It is noteworthy in this context that there are several arid environments where trees and tall shrubs are abundant (e.g. the Great Western Woodlands of Western Australia; Hobbs and O'Connor 1999; spekboom thicket in the Eastern Cape, South Africa; Vlok et al. 2003; and *Acacia* woodlands in the Horn of Africa; Hemming 1966). Consideration of anabolic versus catabolic rates in these environments may inform our understanding of how woody plants can thrive in environments that textbooks – according to climatic data – would label deserts.

The decrease in woody cover as nutrient content decreases towards the origin of the graphs in Fig. 6 (hereafter referred to as the oligotrophic decline) could also be attributed to aridity but the rationale would be more complicated. The data delineating the oligotrophic declines in Fig. 6 refer predominantly to two adjacent observatories in the northern Namibian woodlands (M-Mile 46 and MU-Mutombo) which receive similar amounts of rain. It is, however, conceivable that within these climatically similar observatories there could be considerable variation in terms of soil water availability. The most nutrient-poor sites could for example be where leaching is greatest and water holding capacity is least due to minimal clay content in topsoils (Chadwick and Graham 2000). Equally plausible, however, is that the sites with the greatest leaching and hence greatest nutrient-poverty are those to which water gravitates as a result of surface or subsurface flow, where groundwater accumulates and where water is consequently most available (Chadwick and Graham 2000). Consequently, resolution of the influence of aridity on the oligotrophic decline requires further data.

Several other factors are more easily discounted as plausible explanations for the oligotrophic decline. These include 1) periodic waterlogging – because waterlogging in Kalahari sand environments is associated with treeless dambos, which are nutrient-richer than the surrounding soils (Scholes 1990); 2) intense fires – because the nutrient-poorest sites would be expected to have the least intense fires due to constrained accumulation of fuel in the grass sward (Belsky 1992); and 3) intense herbivory – because the nutrient-poorest sites would be expected to have the least intense herbivory due to constraints on the value of grazing and browsing (Mills and Fey 2005).

A factor which is not as easily discounted as an explanation for the oligotrophic decline, and indeed would be favoured according to the principle of parsimony (Ockham's razor), is nutrient poverty. The plausibility of this explanation is corroborated by investigations in a wide range of vegetation types across the world where nutrient poverty has been invoked as the main cause of scarcity and/or stunting of woody plants. These vegetation types include: kwongan in Western Australia, short, gnarled forms of cerrado on the southern plateau of Brazil, pygmy forests in California,

keranga heath forests in Borneo, and campina in the Rio Negro catchment of Brazil (Furley 1999). The physiological mechanisms by which nutrient poverty influences woody cover have not been investigated in detail. It is, however, implicit in the literature that stunting and scarcity of trees in the aforementioned vegetation types are thought to result directly from the poverty of specific nutrients. Yet, we note that nutrient poverty could also affect woody cover by influencing the competitive interactions between the herbaceous layer and tree seedlings (Scholes and Archer 1997). It is accepted that herbaceous plants can compete successfully with woody plants for nutrients in topsoils (Bond 2008), suggesting that herbaceous plants might have the competitive advantage over woody plants in regimes of extreme nutrient poverty. Because trees in the northern Namibian woodlands are not overtly stunted or gnarled, we suggest that the oligotrophic decline reflects the effects of nutrient poverty on herbaceous–woody plant competition (and rates of anabolism vs catabolism as depicted in Fig. 1) rather than the effects of nutrient poverty on tree growth per se. Since we have shown a wide range of nutrients, including K, Mg, Ca, Mn, Fe, Cu, Zn, P and N, to participate in the oligotrophic decline, the results do not provide evidence of which nutrient or suite of nutrients is likely to be most powerful for this hypothesized effect.

Our dataset showed trends in variables apart from nutrients that could be interpreted as consistent with the oligotrophic decline. For example, woody cover showed a very sharp decrease as Si content approached 47%. This may represent a threshold of Si content beyond which soils are so leached and sandy that extreme nutrient poverty is inevitable. Woody cover also showed a trend of decreasing at the sites with greatest rainfall. This is possibly because greater rainfall results in greater leaching (and ultimately extreme nutrient poverty) at these sites. Confirmation of this trend would, however, require considerably more data because the boundary points for rainfall in particular are not evenly distributed across the x-axis.

Apart from the nutrient elements, there are other factors such as pH, sodicity and soil texture that could influence woody cover. We suggest, however, that these factors, which tend to correlate with both aridity and nutrient content, are unlikely to have major direct effects on woody cover. This is because trees as a life form show a wide tolerance of pH, sodicity and soil texture (Kozłowski 1997).

Notwithstanding the scope and complexity of potentially interacting factors leading to the patterns of constraint in our analysis, we suggest that further theorizing and data collection on the influence of nutrient content on woody cover is warranted. It would be instructive, for example, to test whether the surprising: 1) prevalence of trees on xeric plains (e.g. Western Australia and the Horn of Africa); 2) prevalence of trees on plains subject to intense and frequent fires (e.g. well-drained northern Australian savannas); and 3) absence of trees on nutrient-rich plains experiencing copious rainfall (e.g. the mesic Argentinean pampas) are part of a global pattern of woody cover being constrained at extremes of nutrient content, and favoured in environments with both intermediate nutrient contents and a measure of catabolic dystrophy. It would also be instructive to extend the range of our western southern African dataset to

determine whether the western Zambebian grasslands – which occur on the same Kalahari sand substrate as the northern Namibian woodlands but under greater rainfall and corresponding leaching – would conform to the oligotrophic decline predicted by our analysis. On a smaller scale, there is a need for precision with respect to the requirements of various nutrients by woody versus herbaceous plants, and the effects of each nutrient element on competition between these life forms, particularly to test the concept of catabolic dystrophy.

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