
Cyanobacterial soil crusts and woody shrub canopies in Kalahari rangelands

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Abstract

Intensive grazing of Kalahari rangelands has led to woody plant encroachment, notably of *Acacia mellifera* and *Grewia flava*. The mechanisms causing this process, and the ecological stability of woody plant encroached ecosystems, remain uncertain. Past studies suggest that canopy–soil relations may enhance woody plant competitive dominance. This study aims to investigate one element of this ecological change by examining the spatial distribution of cyanobacterial soil crusts in two vegetation sub-habitats at sites of different disturbance. Crust burial by litter was also assessed to analyse the dynamics of canopy–crust relations. Our results show there is enhanced cyanobacterial crust cover under *A. mellifera* canopies and that unlike *G. flava* canopies, the crust cover remains under *A. mellifera* even at highly disturbed sites. This canopy–crust association suggests *A. mellifera* encroachment exhibits intrinsic resilience because of the crusts ability to stabilize the soil surface and increase nutrient retention. Crust burial by litter that accumulates under larger woody plants restricts crust development under canopies. Disturbance restricts crust development in plant interspaces and under *G. flava*. These two mechanisms combine to restrict crust development to an observed 40% threshold, with nonlinear models required to explain spatial patterns of crust dynamics.

Key words: *Acacia mellifera*, cyanobacterial soil crusts, *Grewia flava*, Kalahari, woody shrub encroachment

Résumé

Le surpâturage des pâturages du Kalahari a mené à l'empiètement de plantes boisées, notamment *Acacia mellifera* et *Grewia flava*. Il est incertain quels mécanismes

déclenchent ce processus, ou si les écosystèmes empiétés par les plantes boisées sont écologiquement stables. Les études du passé suggèrent que la relation feuillage-sol peut augmenter la dominance compétitive des plantes boisées. Cette étude examine un élément de ce changement écologique à travers des analyses de la distribution spatiale des croûtes du sol cyanobactérien dans deux sous-habitats végétaux de chambardement différent. L'enterrement des croûtes par litière fut aussi évalué afin d'analyser les dynamiques des relations feuillage-sol. Les résultats montrent que la couche de croûte cyanobactérienne sous le feuillage de *A. mellifera* est augmentée, et que contrairement aux feuillages de *G. flava*, la croûte reste intacte sous *A. mellifera* même aux sites bien chambardés. Ce lien entre le feuillage et la croûte suggère que l'empiètement de *A. mellifera* déploie une endurance intrinsèque grâce à la capacité de la croûte de stabiliser la superficie du sol et augmenter la rétention des nutriments. L'enterrement des croûtes par litière qui s'accumule sous les plantes boisées plus grandes limite le développement de la croûte sous le feuillage. Le chambardement limite le développement de la croûte dans les espacements entre les plantes et sous *G. flava*. Ensemble, ces deux mécanismes limitent le développement de la croûte à un seuil observé de 40%, avec les modèles non-linéaires nécessaires pour expliquer les configurations spatiales des dynamiques de la croûte.

Introduction

Livestock farming in the Kalahari is dependent on boreholes that provide groundwater to cattle. Intensive grazing pressure around these waterpoints has led to concerns over rangeland degradation (e.g. Moleele & Perkins, 1998; Dougill, Thomas & Heathwaite, 1999; Moleele *et al.*, 2002), notably over the increased dominance of woody plant species over grasses. This process, referred to as bush

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encroachment, has been linked to the spatial heterogeneity of soil resources and the reorganization of nutrients into 'islands of fertility' (Titus, Nowak & Smith, 2002) that can contribute to the competitive advantage of encroaching woody species (Schlesinger *et al.*, 1990; Dougill & Thomas, 2004). This paper aims to improve understanding of the relationship between the encroaching woody shrub cover and sub canopy soil biochemical characteristics that may influence ecological changes in Kalahari rangelands.

One component of the Kalahari ecosystem that has been largely overlooked in past research are biological soil crusts; comprising cyanobacteria, algae, lichens, mosses, microfungi and other bacteria (Belnap, Büdel & Lange, 2003). Biological soil crusts are present in all arid and semi-arid regions (Belnap & Lange, 2003). The ecological roles of these crusts include; increasing soil surface stability by binding erodible soil particles into aggregates thus decreasing erosion by wind and water (Eldridge & Leys, 2003); fixing atmospheric nitrogen (Aranibar *et al.*, 2003), and sequestering CO₂ into organic carbon (Zaady *et al.*, 2000). Dougill & Thomas (2004) have documented a cyanobacterial soil crust cover of between 19 and 40% at a range of disturbed sites on Kalahari Sand soils. They identified three morphologically distinct crusts: a weakly consolidated crust with no surface discolouration (type 1); a more consolidated crust with a black or brown speckled surface (type 2); and a crust with a bumpy surface with an intensely coloured black/brown surface (type 3).

Fundamental to understanding the ecological significance of cyanobacterial soil crusts in the Kalahari is a comprehension of their spatial distribution. Several factors are recognized as influencing crust distribution and development, especially substrate, vegetation type and cover, and disturbance levels (Belnap *et al.*, 2003). It has been demonstrated that plants growing in crusted soils may exhibit enhanced nutrient levels compared with those growing on noncrusted surfaces (Belnap, 2002). Conversely, it is also reported that vegetation and biological crust cover are inversely proportional because of the effects of competition for light (Malam Issa *et al.*, 1999) and nutrients (Harper & Belnap, 2001). It is generally accepted that trampling, as a result of grazing, damages biologically crusted surfaces (e.g. Eldridge, 1998), thus in areas of intense grazing such as around boreholes, the spatial distribution of crusts will be limited. The hypothesis that crust cover increases with distance from borehole (i.e. with decreasing disturbance) is yet to be examined and may be

complicated by increases in woody shrub cover away from waterpoints (Ward *et al.*, 2000). Zaady & Bouskila (2002) describe disturbance as the key factor in determining biological crust development in areas where physical conditions are relatively constant. Given the spatial homogeneity of the Kalahari, in terms of altitude, relief and surface water (Thomas & Shaw, 1993), it is reasonable to impart a significant role to grazing disturbances in affecting the distribution of cyanobacterial soil crusts. In this context the canopies of woody plants may represent quasi-discrete environments, in which the response of crusts to local disturbance regimes is altered. This phenomenon is yet to be tested but could be important in controlling the response of the Kalahari ecosystem to grazing-related disturbance and ultimately the relative abundance of grasses and woody plants. The concentration of leaf litter below these canopies complicates the situation. Litter may smother crusts and prevent photosynthesis, or alternatively may only shade crust and provide a moister habitat conducive to crust development.

That cyanobacterial soil crusts may develop differentially within subcanopy habitats has important implications in terms of the spatial heterogeneity of resources, ecosystem resilience and long-term ecological stability of rangelands. It is probable that the roles of vegetation and disturbance on cyanobacterial crust distribution are not mutually independent of one another. The aim of this study is to examine how the distribution of cyanobacterial soil crusts at grazed Kalahari sites is affected by vegetation and disturbance. We test the hypothesis that suggests there are species-specific, subcanopy effects on cyanobacterial soil crusts and determine the impact of plant litter on their distribution.

Materials and methods

Site selection

Research was undertaken during July 2003 on communal grazing lands near Tsabong, southern Kgalagadi District, Botswana (Fig. 1). Four sites, at different settings around a communal borehole, were selected for data collection. Disturbance was quantified at each site using a disturbance index rather than the proxy of distance from borehole. The closest and furthest sites, with respect to the borehole, correspond to the 'sacrificial zone' (site 1) and 'un-encroached zone' (site 4) of the piosphere model described by Molelele *et al.* (2002), with the intermediate sites

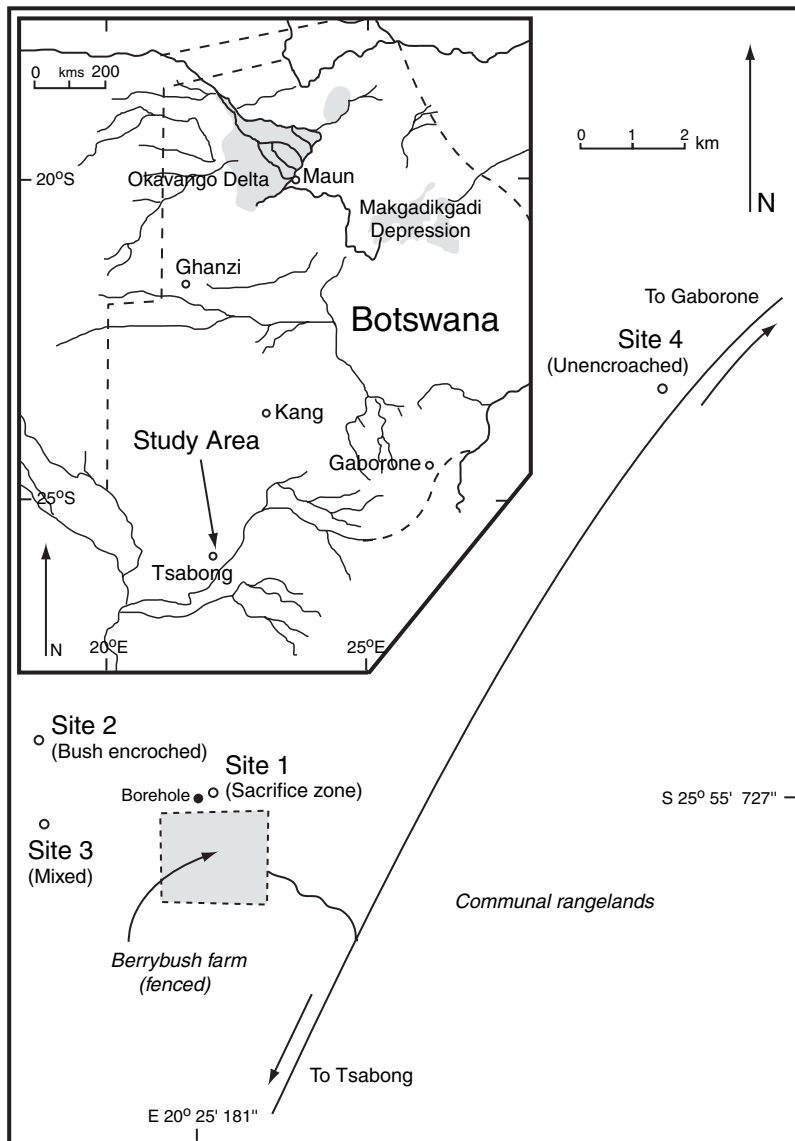


Fig 1 Study site

representing the 'bush encroached' (site 2) and 'mixed bush and grass' (site 3) zones respectively (Fig. 1).

Quantification of disturbance

At each site, disturbance levels were quantified using cattle track frequency and dung density (as per Dougill & Thomas, 2004). At each site, a 50×50 m grid was established. The grid was crossed at 10 m intervals in two perpendicular directions. Cattle tracks and dung were counted along each of these gridlines, cattle tracks being defined as well established 'routes', and a dung 'count' being a single or

collection of pats (as opposed to total fragments) laying within an arbitrary 0.5 m either side of the gridline.

Assessment of cyanobacterial crust cover in interspaces

Crust cover data were estimated within a 0.5×0.5 m quadrat at intervals of 10 m inside the 50×50 m grid. Percentage cover was estimated for each cyanobacterial soil crust type (according to the morphological classification system of Dougill & Thomas, 2004), unconsolidated soil, litter and grass within twenty five 0.5×0.5 m quadrats at each site.

Assessment of crust cover beneath woody shrub canopies

The two most common encroaching species in the southern Kalahari were selected for sampling, the thorny *Acacia mellifera* (Vahl) Benth and the nonthorny *Grewia flava* DC (Reed & Dougill, 2002). The canopy dimensions of every woody shrub within the 50 × 50 m quadrat were measured. Crust cover estimates under every canopy were taken in 0.5 × 0.5 m quadrats, adjacent to one another along a line extending from the bowl to the canopy edge in a northerly and southerly direction to account for any orientation-controlled differences in cover. Within each quadrat, crust cover was quantified, as well as unconsolidated substrate and litter.

Results

Woody shrub canopies and cyanobacterial crust cover

Table 1 summarizes the results from all sites and sub-habitats. In order to test the hypothesis that *A. mellifera* subcanopies exhibit enhanced crust cover, analyses were required between sites and between sub-habitats (Fig. 2). One-way ANOVA showed that there is a significant difference in interspace crust cover between sites characterized by different levels of disturbance ($F_{3,140} = 42.7$, $P < 0.01$). A Bonferroni adjustment demonstrated that at the woody shrub encroached and least disturbed site 2, crust cover is significantly greater than at the mixed grass and woody shrub site 3 ($P < 0.01$). Crust cover at site 3 is also significantly greater than at both the sacrifice zone (site 1) and the un-encroached site 4 ($P < 0.01$). Similarly, crust cover beneath the canopy of *G. flava* differed significantly between sites ($F_{3,252} = 27.8$, $P < 0.01$). Beneath *A. mellifera*, however, there was no statistically significant difference in crust cover between sites ($F_{3,504} = 1.9$, $P = 0.14$).

This pattern is also apparent in the crust cover under shrub canopies and in the neighbouring interspaces. At the most disturbed sacrifice zone (site 1), interspace and *G. flava* subcanopy crust cover were not statistically significantly different, although crust underneath *A. mellifera* is significantly higher than under *G. flava* and in interspaces ($P < 0.01$; Fig. 2). At the least disturbed shrub encroached site, there were no differences in sub-habitat crust cover ($F_{2,225} = 0.45$, $P = 0.64$). At the mixed shrub and grass site, *G. flava* subcanopies had significantly higher crust cover ($F_{2,204} = 3.94$, $P < 0.05$). Finally, at the

Table 1 Summary of site data (means with standard errors

	n	Cyanobacterial crust cover (%)				Total	% cover				Disturbance	
		Type 1	Type 2	Type 3	Type 3		Unconsolidated	Buried crust	Litter	Grass	Dung count	Track density
Site 1												
<i>Acacia mellifera</i>	151	9.1 (1.3)	22.6 (2.2)	9.8 (2.0)	41.5 (2.6)	58.5 (2.6)	9.1 (0.8)	32.6 (2.4)	–	7.3 (0.7)	11 (1.3)	
<i>Grewia flava</i>	82	13.5 (2.1)	2.1 (0.9)	–	15.6 (2.2)	84.4 (2.2)	2.4 (0.8)	15.1 (1.8)	–	–	–	
Interspace	36	9.4 (1.9)	2.7 (0.9)	–	12.1 (2.2)	87.9 (2.2)	0.6 (0.4)	2.2 (0.3)	–	–	–	
Site 2												
<i>Acacia mellifera</i>	127	15.7 (1.8)	23.4 (2.6)	3.1 (0.7)	42.2 (2.5)	57.8 (2.5)	7.8 (0.9)	35.8 (2.6)	–	2.1 (0.4)	0.3 (0.2)	
<i>Grewia flava</i>	65	29.7 (3.2)	12.1 (2.4)	1.4 (0.6)	43.3 (3.1)	56.7 (3.1)	7.8 (1.3)	26.3 (2.6)	–	–	–	
Interspace	36	32.8 (3.4)	14.0 (2.9)	0.2 (0.2)	47.0 (4.1)	53.0 (4.1)	10.4 (1.8)	7.0 (1.2)	–	–	–	
Site 3												
<i>Acacia mellifera</i>	119	13.8 (1.7)	22.4 (2.5)	3.9 (0.8)	40.1 (2.4)	59.9 (2.4)	9.3 (1.0)	37.1 (2.6)	–	5.1 (0.4)	1.3 (0.3)	
<i>Grewia flava</i>	52	31.4 (3.6)	14.0 (2.8)	2.3 (0.8)	47.6 (3.0)	52.4 (3.0)	8.8 (1.3)	25.9 (2.4)	–	–	–	
Interspace	36	26.1 (2.0)	6.5 (2.4)	0.6 (0.4)	33.2 (2.7)	66.8 (2.7)	27.0 (2.5)	9.9 (1.4)	–	–	–	
Site 4												
<i>Acacia mellifera</i>	111	9.4 (2.1)	16.4 (2.6)	7.8 (2.0)	33.6 (3.5)	66.4 (3.5)	20.0 (2.5)	59.8 (3.3)	–	4.4 (0.4)	–	
<i>Grewia flava</i>	57	18.5 (3.6)	3.5 (1.8)	2.1 (1.4)	24.1 (3.8)	75.9 (3.8)	10.6 (1.7)	49.1 (3.3)	–	–	–	
Interspace	36	3.7 (1.6)	2.3 (1.6)	–	6.0 (2.2)	94.0 (2.2)	5.5 (1.3)	8.8 (1.1)	13.1 (2.2)	–	–	

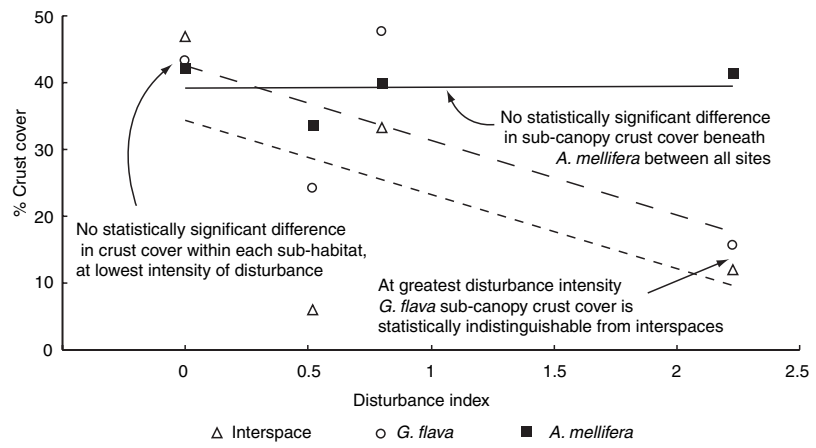


Fig 2 Site and sub-habitat differences in crust cover with respect to disturbance

un-encroached site *A. mellifera* subcanopies had significantly greater crust cover than under *G. flava* ($P < 0.05$) and in the interspaces ($P < 0.01$).

Litter and cyanobacterial crust cover

By comparing subcanopy mean values for crust cover and litter cover, a statistically significant negative relationship is present for the subcanopy environment of *A. mellifera* ($F_{1,63} = 16.21$, $P < 0.01$, $R^2 = 20.5\%$; Fig. 3a). Specifically, those shrubs with a higher subcanopy litter cover have significantly lower cyanobacterial crust cover. Furthermore, the variability in litter density beneath *A. mellifera* is related to canopy size. As *A. mellifera* grow larger, the proportion of ground covered by litter increases ($F_{1,63} = 7.42$, $P < 0.01$, $R^2 = 10.5\%$; Fig. 3b). In contrast, no significant statistical relationship exists between litter and cyanobacterial crust, or between litter and canopy size, beneath *G. flava* canopies. If litter has a detrimental effect on crust development, and the amount of litter is a function of canopy size, it follows that larger shrub canopies should host less crust cover. This is demonstrated for *A. mellifera* (Fig. 3c) where subcanopy crust cover is shown as a function of canopy size, with relative subcanopy crust area decreasing with increasing canopy size ($F_{1,63} = 61.46$, $P < 0.001$, $R^2 = 49.4\%$). No such relationship exists for *G. flava*.

Additional support for the deterministic role of litter on crust development beneath the canopy of *A. mellifera* is revealed when comparing the north and south axes of the sub canopy environment. North facing sides of *A. mellifera* have significantly less litter than the south facing sides

(paired t test; $t = 7.0$, d.f. = 64, $P < 0.01$), but significantly more cyanobacterial crust cover ($t = 3.55$, d.f. = 64, $P < 0.01$). Whilst *G. flava* also has a statistically greater litter load beneath its southern facing portion ($t = 3.28$, d.f. = 62, $P < 0.01$), crust characteristics in the two directions were statistically indistinguishable ($t = 0.21$, d.f. = 62, $P = 0.42$). Figure 3d shows the nature of the relationship between crust and litter. Litter cover increases from the canopy edge towards the base, eventually gaining a density great enough to produce a decline in crust cover. Maximum cyanobacterial crust development occurs between the disturbance-affected canopy edge and the litter-dense plant interior (Fig. 3d).

Discussion

The physiology of livestock and smallstock constrains them to graze within several kilometres of drinking water. This has the effect of concentrating them into stocking densities greater than those associated with nomadic pastoralism or wildlife alone (Legget, Fennessey & Schneider, 2003). Because of the intense localized grazing pressure, a zone of decreasing intensity of disturbance (or *piosphere*) radiates from waterpoints (Moleele & Perkins, 1998). This adds a new environmental gradient to the ecology of a region subject to otherwise relatively homogenous environmental conditions. This has led to the encroachment of woody shrub species, notably *A. mellifera* and *G. flava* (Moleele & Perkins, 1998; Reed & Dougill, 2002). The mechanism appears species-specific, owing much to the selectivity of browsing livestock, but also to the relationship between shrub canopies and the underlying soil properties. It has

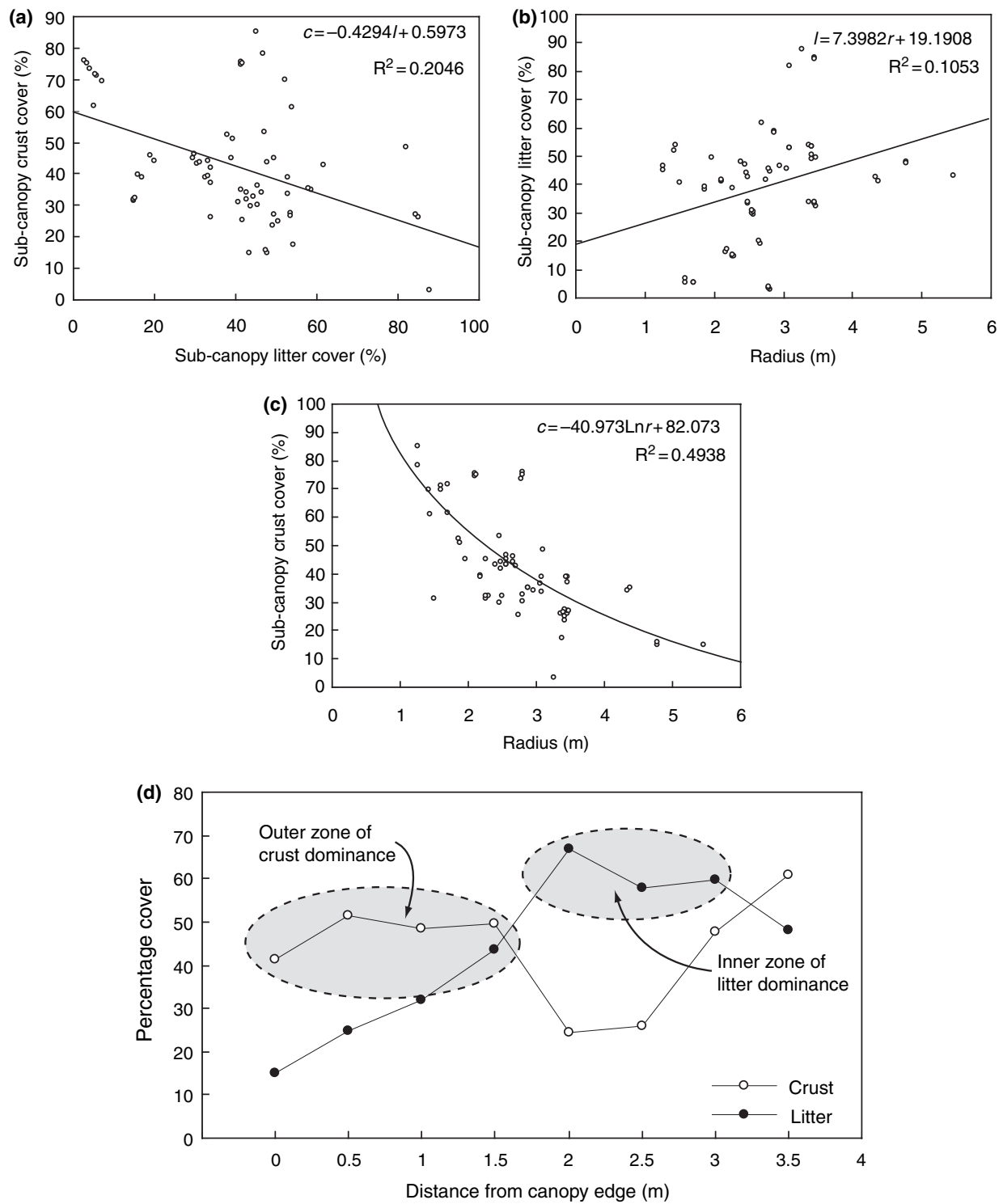


Fig 3 The relationship between crust cover and subcanopy characteristics of *Acacia Mellifera*

been suggested that once established the encroachers may monopolize soil moisture and nutrients (Moleele *et al.*, 2002), preventing the original vegetation from re-establishing.

Results presented in this paper describe the distribution of enhanced cyanobacterial crust cover found beneath the canopies of woody shrubs. Furthermore, this study has shown that, whilst crust cover in the interspaces and beneath the canopy of *G. flava* varies significantly across a disturbance gradient, cyanobacterial crust cover beneath *A. mellifera* remains at the same elevated level even in disturbed locations. This demonstrates that there is a species-specific association between canopy and crust development that is facilitated best by the dense and thorny *A. mellifera* canopy. In contrast, at the least disturbed site the subcanopies of *A. mellifera* and *G. flava* and the interspace had similar levels of crust cover. This shows that when disturbance is limited, each environment provides an equally suitable habitat for crust development

and that without disturbance localized differences in crust cover disappear.

Subcanopy litter cover per unit area increases with *A. mellifera* size (Fig. 3b) and has a detrimental effect upon cyanobacterial crust development (Fig. 3a), with crust area reducing with canopy dimensions (Fig. 3c). Figure 3d shows that the distribution of crust and litter beneath the canopy of *A. mellifera* is not uniform or random, but sorted into an interior dominated by litter and an outer concentric zone of cyanobacterial crust. It follows that the increase in litter cover with canopy size and corresponding decrease in area-relative crust cover is mediated through a migrating outward of the litter-dominated interior as total woody plant volume becomes gradually larger. Figure 4 demonstrates this schematically and is based on the logarithmic model used in Fig. 3c and the data in Fig. 3a,b. At relatively small canopy sizes most of the subcanopy floor is dominated by cyanobacterial crust, with only a small area of litter. As the area underneath the canopy

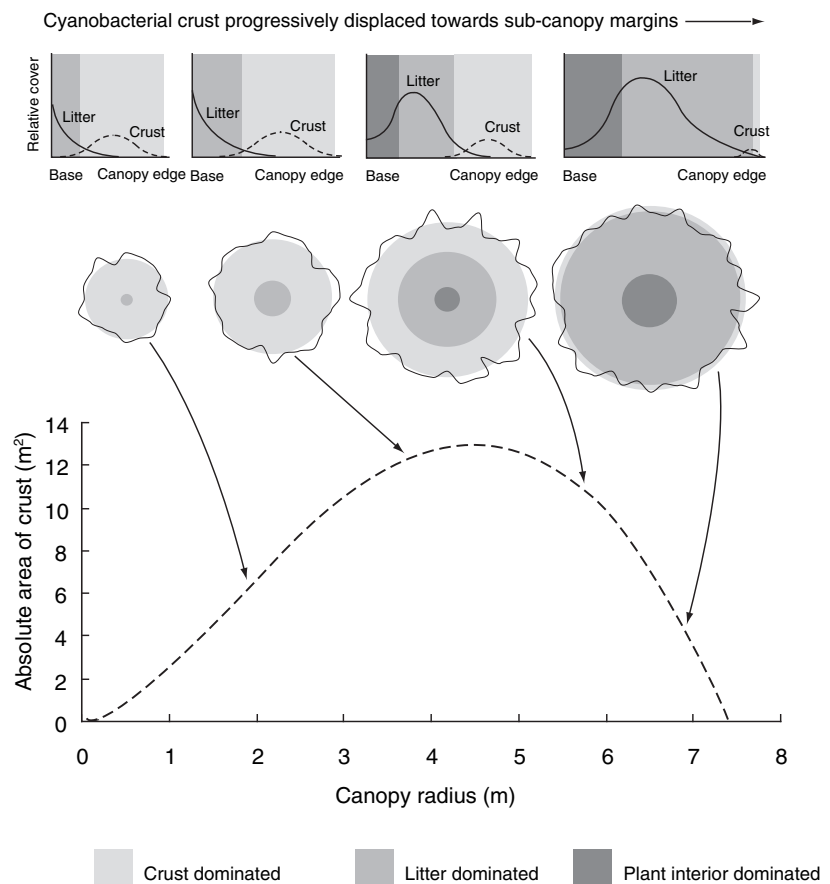


Fig 4 Proposed model of crust/litter dynamics beneath the canopy of *Acacia mellifera*

increases the zone of litter dominance increases in proportion with plant volume and thus spreads outwards, pushing the zone conducive to crust growth further out. At this stage, the absolute area covered by crust may still be increasing with canopy growth. Eventually the litter load increases more rapidly than canopy edge advances, resulting in the zone of litter dominance expanding at the expense of the crust dominant zone. According to the model presented here, the cyanobacterial crust is progressively pushed towards the canopy exterior until at a radius of *c.* 7.4 m the shrub produces enough litter to cover the entire subcanopy zone with sufficient a density to prevent photosynthesis and cyanobacterial crust development. Field observations suggest that *A. mellifera* rarely reach such sizes and thus a relationship between *A. mellifera* and cyanobacterial crust communities may be sustained throughout the life cycle of the plant.

Aranibar *et al.* (2003) found that all cyanobacterial soil crusts sampled along the International Geosphere-Biosphere Programme's (IGBP) Kalahari transect fixed small but significant amounts of nitrogen. Furthermore, $\delta^{15}\text{N}$ data in Aranibar *et al.* (2004) suggest that *A. mellifera* do not fix atmospheric nitrogen but the high foliar content suggests another mechanism of N acquisition. If it can be demonstrated that *A. mellifera* are the recipients of crust-associated nutrients (as demonstrated elsewhere for other species, e.g. Evans & Belnap, 1999; Harper & Belnap, 2001) then an important relationship may be revealed. Such a relationship would suggest that the alternative stability domain established with woody plant encroachment may exhibit intrinsic resilience because of the association between woody plant canopies and subcanopy cyanobacterial soil crust development.

Conclusion

This study has presented data on the association between cyanobacterial soil crusts and the subcanopies of two common shrubs (*A. mellifera* and *G. flava*) in the southern Kalahari. In frequently disturbed areas close to water-points, crust cover under *A. mellifera* is significantly higher than under *G. flava* and in shrub interspaces, as the dense thorny canopy deters disturbance. Crust cover under *G. flava* varies significantly with the level of disturbance as the shrub has no thorns and thus offers little protection. Crust development under *A. mellifera* is restricted by the accumulation of litter and the resultant lack of light reaching the crust surface.

It has been reported in the literature that biological soil crusts can provide additional nutrients to those plants growing in crusted soils. Aranibar *et al.* (2004) suggest that *A. mellifera* do not fix atmospheric nitrogen but obtain N from other mechanisms in addition to mineralization of soil organic matter. Future work needs to establish whether crusts are the source of this additional N and if the shrub is afforded a competitive advantage that could lead to the stability of the woody plant encroached ecosystem that is now prevalent across much of the Kalahari.

Acknowledgements

The authors are grateful for the financial support provided by Manchester Metropolitan University and the University of Leeds. Research in Botswana was conducted with the Republic of Botswana Research Permit No. OP46/1XCVI(87).

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(Manuscript accepted 9 February 2005)