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The impact of browsing-induced degradation on the reproduction of subtropical thicket canopy shrubs and trees

A.M. Sigwela [a], G.I.H. Kerley [a], A.J. Mills [b], R.M. Cowling [c,*]

[a] *Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela Metropolitan University, P.O. Box 7700, Port Elizabeth 6031, South Africa*
[b] *Restoration Research Group, Department of Soil Science, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa*
[c] *Restoration Research Group, Department of Botany, Nelson Mandela Metropolitan University, P.O. Box 7700, Port Elizabeth 6031, South Africa*

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Abstract

The regeneration dynamics of South African subtropical thicket are poorly understood. This lack of knowledge hampers the development of appropriate restoration protocols in degraded landscapes. To address this we compared the magnitude of seed production and the frequency seedlings of canopy species in intact and browsing-degraded forms of *Portulacaria afra*-dominated thicket. Severe browsing had a negative impact on sexual reproduction of canopy species. Seed production for all species was lower in the degraded than the intact states of both vegetation types. In the case of seedlings, almost all individuals were associated with beneath-canopy microsites, irrespective of degradation status. Exceptions were *P. afra*, *Putterlickia pyracantha* and *Grewia robusta*. Of the 511 seedlings that we observed, 480 (94%) were found in the beneath-canopy microsite and 31 (6%) in the open. In both intact and degraded sites, there were significantly fewer seedlings (all species combined) in open microsites than would be expected on the basis of the aerial extent of this microsite. The results show firstly that preservation of remnant clumps of closed-canopy thicket in degraded landscapes is of paramount importance for restoration, and that for recruitment of a wide range of canopy species to occur outside of these remnant clumps, it is essential to restore closed-canopy conditions as speedily as possible.

Keywords: Carbon credits; *Portulacaria afra*; Restoration; Seed production; Seedling establishment; Soil organic matter

1. Introduction

South African subtropical thicket, which is centered on coastal forelands of the Eastern Cape Province, is part of a global biome of semi-arid, rainforest-like vegetation whose origin dates to the mid Cenozoic (Cowling and Vlok, 2005). Component woody canopy (2–5 m) plants, e.g. *Azima tetracantha*, *Euclea undulata*, *Gymnosporia* spp., *Pappea capensis*, *Putterlickia pyracantha*, *Rhus* spp., *Schotia afra*, are long-lived and reproduce mainly via ramets, or occasionally via seedlings that originate mostly from short-lived propagules, the majority of which are dispersed by vertebrates (Midgley and Cowling, 1993; Cowling et al., 1997; Sigwela, 2005).

While relatively resilient to browsing by indigenous herbivores (Stuart-Hill, 1992), subtropical thicket is highly vulnerable to browsing by domestic goats. Sustained, heavy goat browsing can transform the dense closed-canopy shrubland into an open community comprising scattered and degraded thicket clumps and isolated trees in a matrix of ephemeral herbs (Hoffman and Cowling, 1990; Stuart-Hill, 1992; Moolman and Cowling, 1994; Kerley et al., 1995; Lechmere-Oertel et al., 2005a,b). Particularly vulnerable are drier forms of thicket (Arid and Valley forms) (Vlok et al., 2003) dominated by the tree-like leaf succulent, *Portulacaria afra* (spekboom) (Stuart-Hill, 1992; Lechmere-Oertel et al., 2005a,b). Of the 16,942 km^2 of solid (unbroken canopy) thicket with a substantial *P. afra* component, 46% has been heavily degraded and 36% moderately degraded by domestic herbivores (Lloyd et al., 2002).

Excessive goat browsing of *P. afra*-dominated thicket transforms this dense vegetation to a “pseudosavanna” where isolated trees of *P. capensis* and *S. afra* persist precariously in a field-layer matrix of ephemeral herbs such as *Atriplex lindleyi* subsp. *inflata* and the grass *Cynodon dactylon* (Lechmere-Oertel et al., 2005a). In degraded sites, spekboom – which comprises the bulk of thicket plant cover – is entirely eliminated, rate of leaf litter

* Corresponding author. Tel.: +27 42 2980259.
E-mail address: rmc@kingsley.co.ca (R.M. Cowling).

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deposition is reduced by ~30% (4126 vs 2881 kg dry matter/ha/yr), biomass carbon by ~75% (52 vs 8 t C/ha), soil carbon by ~40% (0–10 cm, 71 vs 40 t C/ha), soil nitrogen by ~30% (0.33 vs 0.24%), and rate of infiltration by ~60% (51 vs 19 mm/h, laboratory test) (Mills and Fey, 2004; Mills et al., 2005b; Lechmere-Oertel et al., 2008). Degradation reduces natural capital by reducing species diversity (especially of rare plants) and plant productivity (and hence livestock and game stocking capacity) (Hoffman and Cowling, 1990; Stuart-Hill, 1992; Stuart-Hill and Aucamp, 1993; Moolman and Cowling, 1994; Lechmere-Oertel et al., 2005a). Differences in plant productivity between degraded and intact thicket are especially apparent during drought years (Stuart-Hill and Aucamp, 1993). Degradation also reduces the availability of wood, fruit and medicines for local communities, with a potential financial loss of approximately $150 per annum per household (Cocks and Wiersum, 2003).

Spontaneous recovery of populations of canopy species does not appear to occur in browsing-degraded Arid and Valley forms of subtropical thicket (Stuart-Hill and Danckwerts, 1988; Sigwela, 2005; Lechmere-Oertel et al., 2005a). Browsing by goats initially destroys the canopy skirt on the edge of thicket clumps (Stuart-Hill, 1992), thereby altering the beneath-canopy microclimate and destroying the rich layer of organic mulch that accumulates there (Lechmere-Oertel et al., 2008). Deprived of an organically enriched soil medium, and subject to browsing higher up on the canopy, the remnant shrubs and trees eventually die, and the thicket clumps steadily dwindle (Lechmere-Oertel et al., 2005a).

Very little, however, is known about impacts of degradation on the reproduction of canopy shrubs and trees. Information on this has important implications for restoration of thicket, which is typically kick-started by planting truncheons (cuttings) of *P. afra* in an attempt to restore soil carbon, and hence conditions for seedling establishment (Swart et al., 1994; Mills and Cowling, 2006; Mills et al., 2007). But do thicket seedlings establish in degraded thicket? Anecdotal and indirect (Holmes and Cowling, 1993; Todkill et al., 2006) evidence suggests otherwise, but we simply do not know. Hence, the need for this study, in which we compared the magnitude of seed production and the frequency seedlings of canopy species in intact and browsing-degraded forms of *P. afra*-dominated thicket. We also assessed the abundance of seedlings in relation to microsites, namely open sites and beneath-canopy sites in both intact and degraded thicket.

2. Methods

2.1. Location and description of study sites

We located six sites of approximately 20 ha, three in each of two subtropical thicket vegetation types, in the Sundays River Basin near Uitenhage in the Eastern Cape Province of South Africa. The two vegetation types are Sundays Spekboom Thicket and Sundays Spekboomveld, both dominated by *P. afra* (spekboom) (Vlok et al., 2003). Spekboom Thicket (ST hereafter) is a form of Valley Thicket, which, in the Sundays River Basin, is found in areas of higher rainfall (320–400 mm/yr) than Spekboomveld (SV) (220–280 mm/yr), which is a form of Arid Thicket (*sensu* Vlok et al., 2003). In addition to spekboom, both vegetation types have a high cover of the trees/tall shrubs *P. capensis*, *Rhus longispina* and *E. undulata*; however, their compositions differ in many other respects; for example, *Crassula ovata* in SV and *Euphorbia ledienii* in ST (Vlok et al., 2003).

The three SV sites were located on moderately steep (15–25°), north-facing foothills of the Groot Winterhoek Mountains where soils are clay-rich. The underlying geology of these sites (Bokkeveld Group shale and mudstone from the Cape Folded Belt) yield shallow stony soils with a high fine texture fraction. The three ST sites were located on relatively level areas overlying Uitenhage Group sediments that give rise to fine-textured soils, often overlying a calcrete layer. Mean annual rainfall at the SV sites is about 260 mm and at the ST sites 400 mm. While rain may fall in any month of the year, spring and autumn are the wettest seasons on average and the hot summer months – when mean maxima are up to 40 °C – are the most stressful for plants (Hoffman, 1989). Prolonged droughts, which may span the usually wetter months, are not uncommon. Frost is rare. Mills and Fey (2004) and Lechmere-Oertel et al. (2005a,b) provide more details on the vegetation, topography, soils and climate of the study sites.

Each site comprised two environmentally matched sub-sites located on either side of fence line, reflecting contrasting management histories. Intact sub-sites are those where sustainable livestock browsing (mainly goats) has maintained a dense cover (ca 70%) of thicket clumps (2–50 m in width and 2–5 m in height), interspersed with narrow tracts of bare ground, which may have low plant cover in wetter years. Degraded sub-sites are those where livestock browsing has reduced thicket clump cover to 10–15% of the area.

2.2. Experimental design and statistical analysis

We conceptualised our study system as a natural "snapshot" experiment (Diamond, 1986), where management regime – leading to intact and degraded states – was the treatment. We stratified the sites according to vegetation type (ST and SV) and within these types, treated each site as a replicate (thus, $n=3$ for each vegetation type), comprising intact and degraded states that were closely matched for environmental factors such as slope, aspect and soil form. Within each site, we located a number of sub-sites in order to sample the variation of the site. These we treated as pseudoreplicates and used the data to compute mean values for statistical analysis. Since all data sets were not normally distributed, we used the non-parametric Wilcoxon's Matched Pairs test (two-tailed) (Zar, 1999) to test the null hypothesis that there was no difference in species' seed production and seedling abundance in intact versus degraded sites. Given that matched-site and two-tail tests have stringent requirements for critical values of the test statistic Z (Zar, 1999), and the low number of replicates, we regarded any value of $\alpha \leq 0.1$ as statistically significant.

2.3. Seed production

We measured seed production using seed traps comprising a mesh bag (50 cm × 50 cm × 10 cm) suspended on steel pegs