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What are the effects of substrate and grass removal on recruitment of *Acacia mellifera* seedlings in a semi-arid environment?

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Abstract *Acacia mellifera* is one of the most important encroaching woody plants in southern African savannas. Previous studies found that this species encroaches far more readily on rocky areas than on sandy substrates, although it grows larger on sandy substrates. Rocky substrates are known to retain more water than sandy substrates, which may be of vital importance during recruitment in semi-arid and arid environments. A number of studies have also indicated that competition with grasses may reduce the recruitment and biomass of tree seedlings. We created an experiment in a semi-arid environment (mean annual rainfall = 388 mm) that tested for the effects of rockiness on *A. mellifera* recruitment. We also tested the hypothesis that grasses effectively compete with *A. mellifera* in this environment by simulating the effect of grazing by clipping grasses from half the plots in both the rocky and sandy treatments. Significantly more *A. mellifera* seedlings established in plots where grasses were clipped than in control plots. *A. mellifera* seedlings had greater biomass on sandy substrates than on rocky substrates. No significant interaction effects were found between substrate and grass clipping treatment for either seedling number or biomass. We conclude that *A. mellifera* seedlings are more likely to encroach in habitats with low grass density, although they may achieve greater biomass on sandy soils. Thus, it may be the lower grass density rather than rockiness, which increases the encroachment observed in naturally rocky habitats. These results are also consistent with our observations that adult *A. mellifera* trees are larger on sandy soils than on rocky soils.

Keywords Shrub encroachment · Arid · Rocks · Sand · Herbivory · Clipping

Introduction

We have long been interested in the factors that cause recruitment of one of southern Africa's most serious encroaching species, *Acacia mellifera* (Ward 2005; Kraaij and Ward 2006; Wiegand et al. 2006; Britz and Ward 2007; Meyer et al. 2007a). We have observed that encroachment by *A. mellifera* is more common on rocky than on sandy substrates, although the rate of increase in encroachment is greater on sand (Britz and Ward 2007). Retention of soil moisture, as well as infiltration of rainfall, can be increased by the presence of rocks at the soil surface (Noy-Meir 1973; Agassi and Levy 1991; Nobel et al. 1992). Surface rock fragments can improve soil conditions for plant growth by protecting soil for

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crust development, by slowing down surface run-off of water, and by decreasing the loss of water by evaporation (Poesen and Lavee 1994; Cerdà 2001). Furthermore, rock fragments may increase the infiltration of water into soil (Poesen and Lavee 1994). Noy-Meir (1973) has indicated that trapped water under rocks may be an important source of water in arid and semi-arid environments. In rocky soil, moisture is very unevenly distributed in the profile, being concentrated in soil pockets and fissures, at soil–rock interfaces, and under stones (Drew 1979; Kadmon et al. 1989).

In addition to decreasing the evaporation of water, rocks on the soil surface can result in water vapour migration to their cooler lower surfaces, where condensation can increase the water availability for roots of desert plants (Stark 1970; Jury and Bellantuoni 1976). For example, Nobel et al. (1992) found that, for *Agave deserti* in the Sonoran desert (mean annual rainfall = 150 mm), the frequency of lateral roots per unit length of main root was about 11 times greater under rocks compared with exposed soil regions with no rocks. Similarly, Nobel et al. (1992) found that, for *Echinocereus engelmannii*, the total length of main roots, primary lateral roots, and secondary lateral roots was fourfold higher surrounding a boulder than in the nearby area. Similar results were obtained for two other species (*Ferocactus acanthodes* and *Opuntia acanthocarpa*) that these authors studied.

Nobel et al. (1992) have shown that soil under rocks had an average water potential of about −0.15 MPa, while the soil just 5 cm away had a water potential of about −0.4 MPa. Although some studies have indicated that rocks can reduce fluctuations in ambient temperature (see e.g. Poesen and Lavee 1994); Nobel et al. (1992) found that 5-cm-thick buried rocks decreased the diel variation in soil temperatures on their undersurface very little (about 0.4°C) when compared to exposed soil. Thus, Nobel et al. (1992) concluded that the primary influence of rocks was caused by influences on soil water content.

Rocky habitats can also influence patterns of recruitment in vegetation. Mori et al. (2006) found that recruitment by the tree *Salix arctica* was greater on the upper slopes of glacial moraines on Ellesmere Island in Canada, where small rocks were present. Similarly, Jumpponen et al. (1999) found that pioneer species were more likely to establish on rocky substrates in recently deglaciated terrain, perhaps because of protection from desiccation and a greater degree of seed trapping. In a long-term study, Keith (2002) found that the endangered heathland shrub *Epacris stuarti* recruited better on rocks than on the neighbouring substrates because of reduced mortality.

Another factor that may affect the recruitment of tree seedlings in arid savannas is the presence of grasses. Grasses tend to compete with trees for water and nutrients. Walter's (1939) two-layer hypothesis of savanna structure is based on this concept and predicts that grasses use shallow water, while trees outcompete grasses for deeper water sources. Cramer et al. (2007) have shown that access to nutrients may also be important for savanna trees. Their data indicated that *Acacia* trees fix nitrogen when they compete with grasses, and do not when grasses are absent.

Acacia mellifera is a multi-stemmed shrub up to 3 m high but it can become a tree reaching up to 7 m (Smit 1999). It is considered well suited to arid conditions with a shallow, widely spreading root system (Smit 1999). Kraaij and Ward (2006), Meyer et al. (2007a) and Joubert et al. (2008) have shown that rainfall is a key factor in controlling the recruitment of *A. mellifera*. We predicted that more recruitment of seedlings would occur on rocky substrates because of the greater availability of water and that plants would grow bigger there. Furthermore, we tested the hypothesis that removal of aboveground grass biomass (by simulated grazing) would also increase the recruitment and growth of *A. mellifera* tree seedlings. One of the growth parameters that we measured was plant height. We also wished to assess whether there was a relationship between fitness and the size of adult trees by relating seed production to plant height in adult plants because this would indicate that larger plants have a direct reproductive benefit.

Methods

Acacia mellifera is native to semi-arid and arid environments in the Northern Cape province of South Africa, Namibia and in Botswana. It also occurs further north in arid regions of East Africa.

This experiment was conducted on Pniel Estates (28°36′ S, 24°28′ E; 1125 m asl) near Barkly West, Northern Cape province, South Africa. Two main substrates occur on Pniel Estates. Adjacent to the Vaal river, there is andesite (a rocky substrate, with an acidic pH), while away from the river, aeolian sands occur. Mean annual rainfall is 388 mm at Barkly West. The main tree species are *A. mellifera*, *A. tortilis*, *A. erioloba* and *Tarchonanthus camphoratus* in a matrix of grassland (dominated by *Schmidtia pappophoroides*).

We used a balanced experimental design with substrate and grass clipping as the factors. There were 28 plots, each 2 × 2 m^2 in area, which were dug to a depth of 1.5 m. Half of the plots were entirely re-filled with sand (sandy substrate, $n = 14$) and the remaining half were filled with a mixture of rocks and sand (rocky substrate, $n = 14$). The rocks were taken from the surrounding area and were approximately 40 × 40 × 20 cm^3 in size. All the plots were placed 2 m apart. We planted 400 *A. mellifera* seeds in each of the 28 plots. No prior treatment was applied to these seeds. Grasses were also re-planted in the plots (*S. pappophoroides* being mostly the dominant species) with the same densities in each plot. The grass on one half of the sandy substrate plots and the other half of the rocky substrate plots were clipped each year in spring to simulate grazing (carefully avoiding *A. mellifera* seedlings) to test whether there was any effect of grass cover on early germination and growth. In 2007, the grass cover on the clipped plots was (mean ± 1 SE) 18.6 ± 2.59% and on the unclipped plots was 41.1 ± 4.74%.

We ran these experiments for 4 years (2004–2007). In addition to counting the seedlings, we weighed the aboveground biomass of all *A. mellifera* seedlings after the 2007 census. We found that belowground biomass could not be accurately assessed because these trees had very long, fine roots that were easily broken.

We also measured the relationship between the seed production and adult *A. mellifera* height on 15 trees. All the trees were stripped of seeds by shaking the seeds onto plastic sheets.

All analyses were conducted with SPSS using generalised linear models. All data on *A. mellifera* seedling number, height and mass are presented as mean ± 1 SE.

Results

There was a significant effect of year on the number of *A. mellifera* seedlings in the experimental plots, with the fewest in 2004, the most in 2005, and a significant decline in number in 2007 (Scheffe post hoc test, Fig. 1). In November 2004, less than a year after the onset of the experiment, very few tree seedlings were found in the experimental plots (12 plots contained seedlings; Fig. 1). At this time, there was no significant effect of substrate ($F = 1.283$, $P = 0.269$, error df = 24) or clipping ($F = 0.011$, $P = 0.919$) and no significant interaction between these two factors ($F = 0.519$, $P = 0.478$).

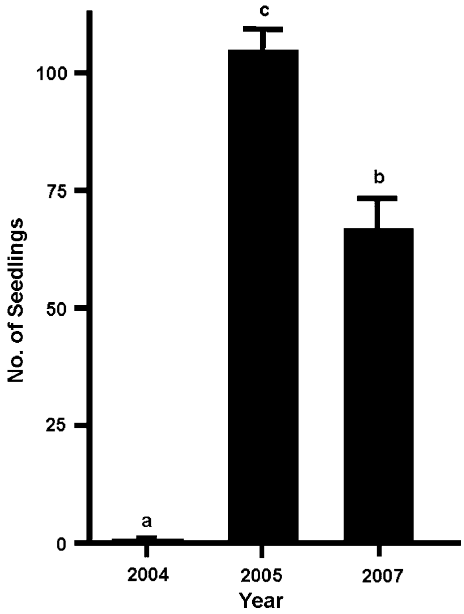

Fig. 1 Changes in the number of seedlings in all plots over 4 years. Note the decline in the number of seedlings in 2007. All differences were significant (Scheffe post hoc test)

In April 2005, all the 28 plots contained seedlings (Fig. 1). There was no significant effect of substrate ($F = 0.298$, $P = 0.590$, error df = 24) or clipping ($F = 1.037$, $P = 0.319$) and no significant interaction between these factors ($F = 0.017$, $P = 0.898$).

In March 2007, there was a significant effect of clipping ($F = 6.651$, $P = 0.016$) but no significant effect of substrate and no interaction between these factors ($P > 0.05$). More *A. mellifera* seedlings grew on the clipped plots (80.3 ± 8.40) than on the unclipped plots (51.1 ± 8.00; Fig. 2A). There were no significant differences in the heights of these plants. The tree seedlings (saplings) growing on the rocky substrates in our experiment in 2007 were 134.1 ± 6.95 cm tall, while plants growing on the sandy substrates were 151.3 ± 8.43 cm tall (Fig. 2B).

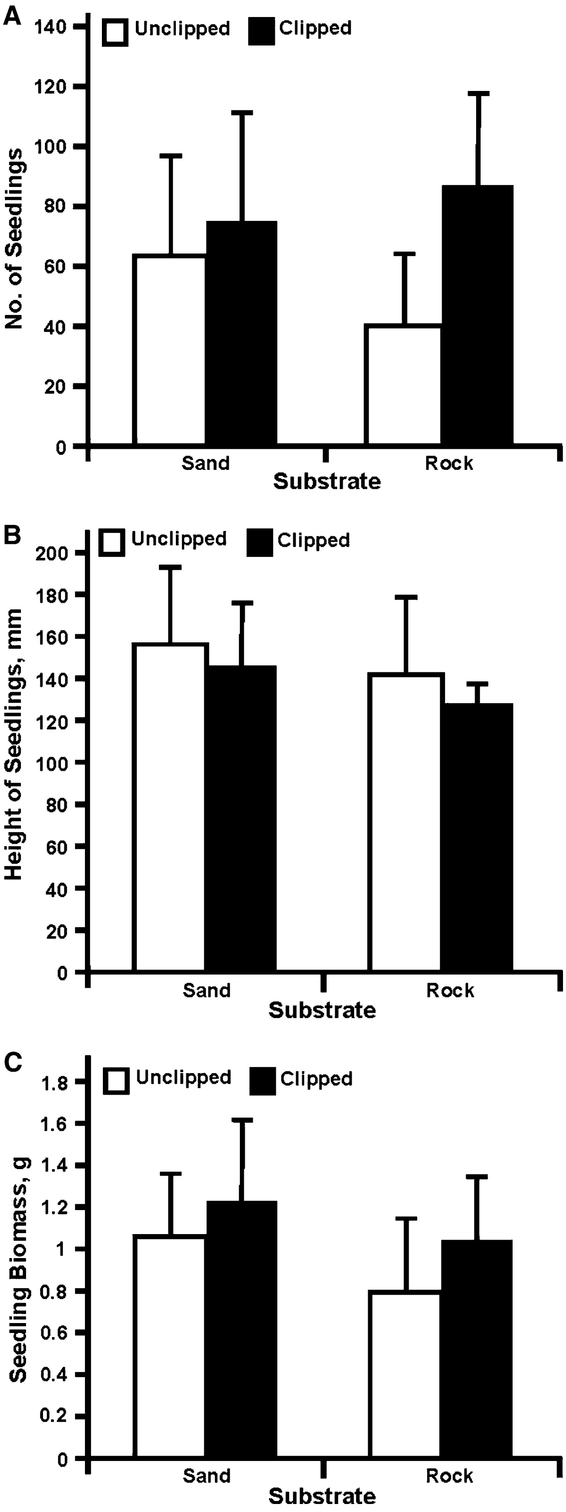

Fig. 2 **A** Number of seedlings in all plots where grasses were clipped ($n = 14$ plots) and unclipped ($n = 14$ plots) on rocky and sandy substrates in 2007. **B** Seedling heights in plots where grasses were clipped ($n = 14$ plots) and unclipped ($n = 14$ plots) on rocky and sandy substrates in 2007. **C** Seedling biomass in plots where grasses were clipped ($n = 14$ plots) and unclipped ($n = 14$ plots) on rocky and sandy substrates in 2007

On clipped plots, plants were 136.5 ± 5.69 cm tall while plants on control (unclipped) plots were 148.9 ± 9.62 cm tall. In the case of aboveground biomass, there was a significant effect of substrate ($F = 5.293$, $P = 0.03$) but no significant effect of clipping nor a significant interaction between substrate and clipping ($P > 0.05$). Plants that grew on sandy soils were heavier (1.2 ± 0.10 g) than those growing on rocky soils (0.9 ± 0.09 g; Fig. 2C). There was no effect of the covariates (% cover of live or dead grass or total grass cover) on any of the analyses. The self-thinning rule did not affect the relationship between the log biomass and log density (data not shown).

There was a significant positive relationship between seed production and adult *A. mellifera* height ($r^2 = 0.76$, $P < 0.001$, $n = 15$) (Fig. 3). Thus, taller trees produce more seeds. Shrubs shorter than 104 cm did not produce seeds (see also Meyer et al. 2007b). The tallest trees were all in sandy habitats, with one individual reaching 7 m.

Discussion

There was an initial increase in the number of recruiting *A. mellifera* followed by a decline, perhaps due to herbivory, desiccation, a competitive effect between trees and grasses related to water or nutrient access or some or all of the above. Overall, there were more seedlings on clipped plots than on unclipped plots. In addition, the aboveground biomass of seedlings on the rocky substrate was significantly lower than on the sandy substrate.

Interestingly, the higher biomass of *A. mellifera* on sandy soils is maintained in adult trees (Meyer et al. 2007a). Adult *A. mellifera* trees growing in rocky substrates are shorter than trees growing in sandy substrates (Ward et al. unpubl. data). We found that there was a significant positive correlation between fitness (measured as seed production) and plant size. In contrast, Young and Augustine (2007) found that *A. mellifera* did not exhibit a significant relationship between plant height and fruit production in a study that tested for the effects of protecting these plants

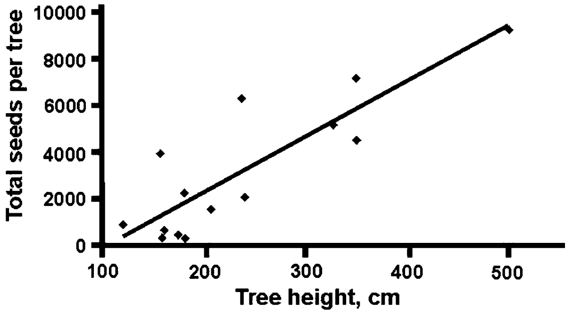

Fig. 3 Regression relationship between *A. mellifera* seed production and tree height

from mammalian herbivory ($P > 0.40$). Thus, there is likely to be a fitness benefit to the higher biomass of tree seedlings on sandy substrates because they grow tall, and thus, produce more seeds.

Why are there more trees recruiting in rocky areas yet they are smaller there? In our experimental plots, seeds were planted in sandy and rocky soils at the same time, so there are no differences in age. Similarly, it is unlikely that the rocky sites received more rainfall than the sandy sites because these are adjacent on Pniel Estates. Rocky sites are predicted to have more nutrients than sandy soils because of the greater cation exchange capacity in an 'ideal' soil (Albrecht 1957). However, 'ideal soils' are typically basic in pH; plant growth is limited in acidic soil conditions (reviewed by Kopittke and Menzies 2007). Nodulation of legumes, such as our study species *A. mellifera*, is particularly sensitive to acidic conditions (Alva et al. 1987). The rocks that we used in our study are andesite which is acidic (Ramezanpour and Akef 2008). Thus, the acidity of these rocks may have caused the reduction in seedling biomass, and the subsequent decreased adult size. Further studies will be needed to elucidate this issue.

Meyer et al. (2007b) used a spatially explicit model to predict changes in the cover and number of *A. mellifera* in our study site. In their model, they found that three of the four most important sensitivity parameters for density of plants were related to soil moisture, namely interception of moisture by shrubs, field moisture capacity of the soil and cumulative amount of moisture available to seeds. Only browsing mortality of shrubs factored more highly. However, the results obtained here are inconsistent with the observations that water is more available on rocky than on sandy areas (e.g. Nobel et al. 1992; Poesen and Lavee 1994; Cerdà 2001), or that bush encroachment is more common on rocky than on sandy areas on Pniel Estates (Kraaij and Ward 2006; Britz and Ward 2007).

We found that seedlings were more numerous when the grass was clipped than in the control, indicating that there was either a gap effect (Coffin and Lauenroth 1990) making it easier for tree seedlings to establish or that grasses were unable to compete for resources when the trees are small. This latter explanation is consistent with the results of Cramer et al. (2007), who showed in the mesic Hluhluwe game reserve (ca. 900 mm annual rainfall) in South Africa, that competition with grasses had a significant negative impact on seedling germination of *A. karroo, A. tortilis, A. nilotica* and *A. nigrescens*. Similar results regarding competition with grasses have been obtained in a field study with *A. drepanolobium* in Kenya (Riginos 2009) and in a pot experiment with *A. mellifera* (Kambatuku et al. in prep.). Cramer et al. (2007) ascribe the differences to a change in nitrogen fixation; that is, when competing with grasses, these *Acacia* species fix nitrogen (there was a decrease in δ^{15}N in plants grown with grass). Similar conclusions were made by Kambatuku et al. (in prep.) for *A. mellifera*.

The experimental results are inconsistent with Walter's (1939) two-layer hypothesis, at least in terms of encroachment. Following this equilibrium hypothesis, grasses access water in the upper soil layer while trees use deeper water. When the grasses are removed by grazing, trees have an opportunity to encroach en masse. We found that there was a significant negative effect due to the presence of grasses on tree seedling recruitment. This is likely because tree seedlings need to grow through the grass root layer to reach the deeper soil layers. Walter's (1939) hypothesis is an equilibrium hypothesis only after the trees become larger and avoid direct competition with grasses (see also Knoop and Walker 1985).

Mbatha and Ward (2010) found that there was about 65–70% lower biomass of grasses in rocky habitats at Pniel Estates (i.e. the same study site as our study) than that of the sandy soils in open savannas. We suggest that it is the lower densities of grasses competing against the *A. mellifera* seedlings on rocky soils, which causes the increased number of *A. mellifera* in these soils, and not the increased water availability from the rocky substrate.

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