

Grass, rainfall and herbivores as determinants of *Acacia erioloba* (Meyer) recruitment in an African savanna

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Abstract *Acacia* species in arid environments are thought to only establish in years of above-average rainfall, so should exhibit cohorted or pulsed recruitment. I studied population demography of *Acacia erioloba* Meyer in semi-arid savanna in the Kimberley area (mean annual precipitation = 425 ± 132 mm), South Africa, to establish whether they recruit episodically. This species was found to have a sapling bank at the sites, indicating that even though cohorted recruitment probably occurs, it is not the primary factor limiting recruitment to larger size classes. *A. erioloba* saplings given supplementary water and protection from herbivory showed significantly less height growth than saplings given water but not protected from herbivores, and grass within exclusion plots was taller and denser than outside of exclusion plots. The generalized linear model, although finding a significant difference between watered and protected and watered and unprotected saplings, explained only 16% of variation in growth,

demonstrating the importance of factors other than competition from grass when rainfall is above-average. Average height increase across all treatments for a growing season was small (43.1 ± 30.81 mm), suggesting most investment is belowground. *A. erioloba* sapling below surface stem diameter correlated positively with aboveground growth, indicating larger, and presumably older, individuals grow faster. When grass was removed around saplings, growth rates were not significantly greater than for saplings surrounded by grass, over a growing season. Thus, in these study sites, pulsed events allow seedlings to establish, and then saplings slowly accumulate over many growing seasons within the grass sward, owing to slow aboveground growth combined with competition from grass in absence of grazers. Release events, e.g., heavy grazing combined with good rainfall, may allow mass release, giving the impression of cohorted or pulsed recruitment.

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Introduction

In arid savannas, the tree component may appear to be constituted by even aged cohorts (Ernst et al. 1990; Wiegand et al. 2005), which is widely

interpreted as evidence of the importance of abiotic factors (particularly quantity and temporal pattern of rainfall) to intermittent bouts of successful recruitment (Ernst et al. 1990; Reid and Ellis 1995; Barnes et al. 1997; Midgley and Bond 2001). Alternatively, what appear to be cohorts amongst adult trees may not be even-aged individuals at all. An event allowing release from herbivory or fire could allow different aged saplings to recruit into larger height classes simultaneously, giving the appearance of equal aged individuals (Midgley and Bond 2001 and references therein).

Although much research has implicated large herbivores, e.g., African Elephants *Loxodonta africana* (Laws 1970; Wackernagel 1993; Barnes 1999; Western and Maitumo 2004) and fire (Bond and van Wilgen 1996; Scholes and Archer 1997; Barnes 2001a; Roques et al. 2001) in suppressing the woody component of savannas, the influence of smaller herbivores such as duiker (*Sylvicapra grimmia*) and steenbok (*Raphicerus campestris*) has received less attention. Smaller herbivores appear to be at least as important as fire, however, in restricting saplings to heights of <1 m where they remain susceptible to fire and further herbivory (Belsky 1984; Martin and Moss 1997; Weltzin et al. 1997; Barnes 1999). The effects of small browser herbivory can be significant: Augustine and McNaughton (2004) found impacts of small browsers to be equivalent to a 6-fold reduction in shrub recruitment into the 0.5–1.5 m height class, so browsing may be particularly important in keeping the height of tree saplings in check.

Woody plants in savanna systems invest in belowground growth in response to fire (Bond and van Wilgen 1996) and could conceivably respond to herbivory in a similar fashion. Saplings may not necessarily be young, and may have extensive belowground root systems. Responses of saplings to herbivory and competition from grass may be influenced by the size of their belowground root systems, with saplings with larger root systems better able to survive and resprout. In addition to herbivory, saplings in arid environments may be water-limited and therefore slow growing.

On Kalahari sands in areas where rainfall is below 400 mm·year⁻¹, *Acacia erioloba* is the only tree to reach any great size (Acocks 1953). Large trees have been demonstrated to be important for maintenance

of certain biodiversity patterns and processes in the southern Kalahari (Milton and Dean 1995; Dean et al. 1999; Seymour 2006; Veldtman et al. 2007), an area extending over 500,000 km² in three southern African countries. Large *A. erioloba* are also important in rangeland agriculture, providing fodder and shade. Although this species is listed as protected, trees have also been harvested on a large scale for sale as firewood for barbeques in South Africa's major cities (Anderson and Anderson 2001), so it is important to understand the processes facilitating or hindering establishment of the large tree component (i.e., *A. erioloba*) in the southern Kalahari, to help assess the sustainability of harvesting.

A survey of the literature suggests that on Kalahari sands in regions with mean annual precipitation (MAP) below 550 mm, rainfall is indeed a limiting factor in *A. erioloba* seedling establishment (e.g., Theron et al. 1985; Skarpe 1991; Barnes 1999; Barnes 2001b). Therefore, I expect rainfall driven cohorts in the drier extents of the southern Kalahari, represented in this study by a set of sites located at Kimberley, in the Northern Cape Province of South Africa, where rainfall is about 425 ± 132 mm·year⁻¹. The question arises as to whether, in addition to supposed rainfall-limited establishment, there are other factors limiting recruitment to larger height classes.

This study set out to investigate the following: (i) Does the size class distribution (height and belowground stem diameter) of *Acacia erioloba* at two sites near Kimberley, South Africa, suggest cohorted, or continuous recruitment? (ii) Does provision of supplementary water increase growth rates of *A. erioloba* saplings? (iii) Does protection from herbivores increase relative growth rates of *A. erioloba* saplings?, and (iv) Does competition from surrounding grasses impair *A. erioloba* sapling growth?

Methods

Study sites

This study was conducted at Benfontein Cattle and Game Farm (28°52'S; 24°51'E), and the neighbouring Susanna Cattle and Game Farm (28°46'S; 24°56'E) in the southern Kalahari. The Kalahari is a semi-arid, summer-rainfall savanna characterised by dystrophic

reddish-brown sands. Vegetation at the study sites is described as Kimberley Thornveld (Mucina and Rutherford 2006), which is typically open savanna with grasses (*Aristida* spp., *Eragrostis* spp. and *Stipagrostis* spp.) and scattered trees (*A. erioloba*, *Acacia tortilis*, *Acacia mellifera*, *Rhus lancea* and *Boscia albitrunca*) and shrubs (e.g., *Grewia flava*, *Ziziphus mucronata*, *Tarchonanthus camphoratus*, *Acacia hebeclada*, *Lycium* spp. (Mucina and Rutherford 2006). Benfontein is grazed all year round, with stocking rates varying between 7.8 ha/LSU (LSU = large stock unit) and 10 ha/LSU. Susanna is subdivided into small camps averaging 200 ha in size, which are intensively grazed for 3 days in summer, and 4–5 days in winter, at 0.23–0.26 ha/LSU. Camps are rested for 132 days between grazing intervals. Fire has been actively and successfully excluded on Benfontein for at least 11 years, whereas the relative greater distance and bad roads on Susanna makes fire control on that farm problematic, and some moderate fires have occurred there in the last 3–5 years. As Benfontein and Susanna farms border each other, and there are no significant orographic features to influence rainfall or temperatures between the two, their climates would expectedly be similar if not identical.

Acacia demography

I used a random number generator to select grid squares on a map in which to survey *A. erioloba* demography within the Kimberley Thornveld of Benfontein (35 plots) and Susanna (18 plots), in November 2003. Plots were 25 m × 25 m, and randomly located within the study sites. Each plot was thoroughly searched for *A. erioloba* individuals. For each individual found, height, maximum canopy width (d_1) and canopy width at 90° to d_1 (d_2), number of stems, diameter of thickest stem 10 mm aboveground (d_a), and for small (<1.5 m) individuals, stem diameter 30 mm below surface (d_b) were measured. These measures were used to ascertain if these variables were good predictors of subsurface stem size.

Exclusion plots

In November 2003, I also set up five plots of 300 m × 300 m on both Benfontein and Susanna.

Within each plot, 12 saplings (all less than 1.10 m in height) were allocated to three replicates of each of the four following treatments: (A) herbivores excluded; (B) herbivores excluded and supplemental water given; (C) herbivores not excluded and supplemental water given; and (D) no supplemental water or exclusion of herbivores (i.e., controls). I ensured equal representation of different below-ground stem size classes within each treatment, because larger (assumed older) individuals may grow faster than smaller individuals. In total, there were 30 saplings in each treatment distributed across 10 sites at the two farms. Exclusion plots were built around individual saplings, and were made of wire mesh (25 mm holes), supported by iron rods (12 mm diameter, 1.4 m height), which effectively excluded any browsing herbivores larger than a small rodent. Exclusion plots were constructed so that the sapling was in the centre of the exclusion plot and there was at least 25 cm between the edge of saplings' branches and the fencing. The same amount of supplemental water (5 l over an area of 0.25 m²) was given to water treatments, fortnightly for the austral summer growing season (i.e., the 5 months from November 2003 to March 2004), the time over which the experiment was run. Water was dispensed using a watering can and the main stem of the sapling chosen as the central point of the watered area. This amounted to an equivalent of 200 mm additional precipitation during the wet season, over which time 247 mm of rain was recorded (South African Weather Service 2007). Therefore, saplings given supplemental water received a total of 447 mm water, comparable to above-average rainfall years (e.g., 1975/76, 1987/88) (South African Weather Service 2007) over the study area.

At the end of the experiment (i.e., March 2004), I measured height of the tallest growing stem from the ground, the extent of the canopy (d_1 , the longest axis, and d_2 , at right angles to it), number of stems, and diameter of the thickest live stem. Because the focus is on what is preventing escape to greater height size classes, height was the primary variable of interest.

A generalized linear model (all effects, Poisson distribution, log link function) was used to test whether farm, plot, supplementary water and/or enclosure could best explain differences in height between the four treatments. Replicates within plots were grouped, with plots nested within farm.

Goodness of fit was assessed and corrected for overdispersion, and the model residuals checked to assess model adequacy. The generalized linear model was run in Statistica v. 7 (StatSoft Inc. 2004).

Grass-removal experiment

In September 2004, using the same individuals from the Benfontein exclusion experimental plots, exclusion structures were removed and entire grasses including roots were dug out from a 1 m² area around half of the saplings, with the sapling main stem in the centre of the cleared area. To minimise effects from the previous season's experiment, individuals from treatments A, B, C, and D were equally represented between individuals from which surrounding grass was and was not removed. Six and a half months after removal of surrounding grass, and a summer season of below average (257 mm) rainfall, which was nevertheless evenly distributed across the season, I measured the length of all new growth on the saplings. New growth twigs are a shiny reddish-brown, whereas older growth twigs are grey (Coates Palgrave 1983). To ascertain growth, the length of all new twigs was summed for each individual sapling. A linear regression, run in Statistica (StatSoft Inc. 2004), was used to test for effects of stem diameter on growth, and a Mann–Whitney *U* test to compare residuals enabled comparison of effects of grass removal on growth.

Results

Within the 35 Benfontein plots, 108 *A. erioloba* were recorded in total. The number of *A. erioloba* found per plot varied from 0 to 31 individuals (Median (Q_2) = 3; Q_1 = 2; Q_3 = 12). Within the 18 Susanna plots, 61 individuals were found, with between 3 and 18 found per plot (Median (Q_2) = 10; Q_1 = 8; Q_3 = 10).

Size-class distributions

The majority of *A. erioloba* were shorter than the grass sward (average grass height = 410.7, \pm 142.9 mm): 93 and 73% were less than or equal to 400 mm

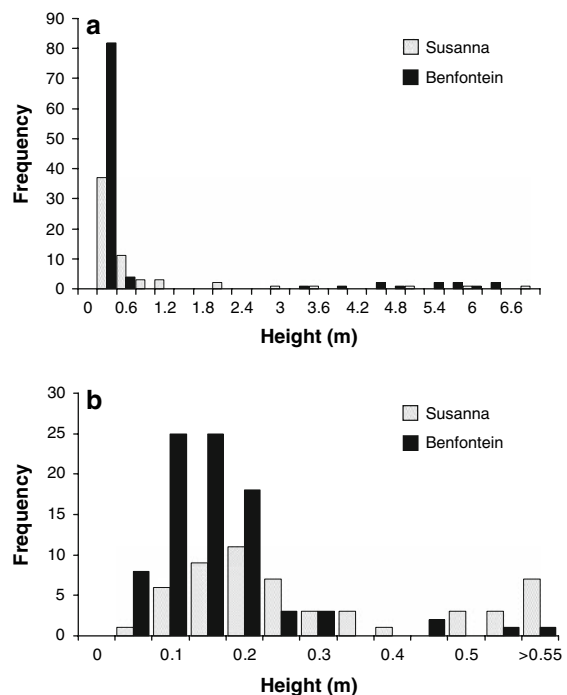


Fig. 1 (a) Frequency of *A. erioloba* within all height size classes at Benfontein and Susanna and (b) Height size class distribution of *A. erioloba* individuals less than 1 m in height at Susanna and Benfontein

in height on Benfontein and Susanna, respectively (Fig. 1).

Within the entire data set, 80% of individuals were below 500 mm and 86% were below 1 m in height. As many as 94 and 63% had subsurface stem diameters less than or equal to 20 mm on Benfontein and Susanna, respectively (Fig. 2). The size distribution of below surface stem size suggests that there is an array of ages amongst these smaller individuals, however (Figs. 1 and 2).

Individuals found at Susanna had significantly larger subsurface stem sizes than those at Benfontein (Mann–Whitney *U* test, $U = 521$, $z = -7.40$; $n_1 = 85$, $n_2 = 51$; $p < 0.001$). Although the distribution of height size classes (Fig. 1) suggested only one major successful recruitment event on Benfontein and two on Susanna, below surface stem size distributions suggested that there had been two successful seedling establishment events on Benfontein and three on Susanna, and that two of the events on Susanna had occurred before those on Benfontein (Fig. 2). Height vs. subsurface stem diameter found a positive correlation for both sites ($r = 0.629$ and 0.661 at Susanna

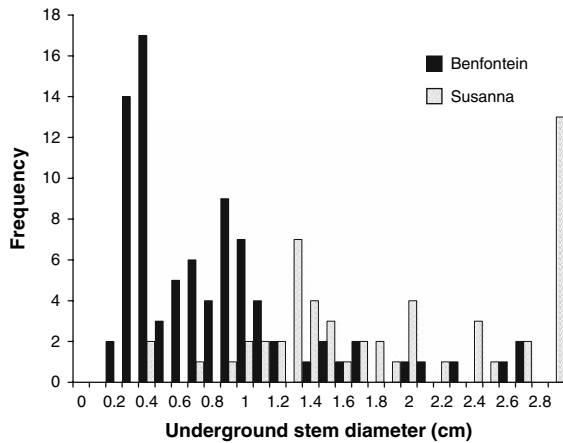


Fig. 2 Subsurface stem diameters of individuals below 1 m in height on Benfontein and Susanna

and Benfontein respectively) and a comparison of slopes and intercepts showed no significant difference in this relationship between the two sites, suggesting that differences in management between the two sites has not influenced the relationship between below surface stem diameter and growth in height. Although subsurface stem diameter explained 39.6% of variance in sapling height at Susanna and 43.7% at Benfontein, multiple linear regression showed that including number of stems, and stem diameter aboveground increased the variance explained to 92%.

Exclusion plots

Across all treatments, average increase in height over the growing season was 43.1 mm (standard deviation (SD) = 30.81 mm), and the maximum increase in height for any individual was 150 mm, the minimum was a decrease in height of 10 mm.

Although saplings can experience dieback of branches in hot dry periods, and thus effectively decrease in height, this was not the case in this experiment, as saplings were measured and monitored every 3 weeks, and there was no notable dieback of branches during the course of the experiment. Height was the primary variable of interest, but is susceptible to measurement error, owing to factors like soil level shifts relative to the top of the plant. Some plants that had been protected from herbivory still exhibited a decrease in height, and this was therefore assumed a measurement error.

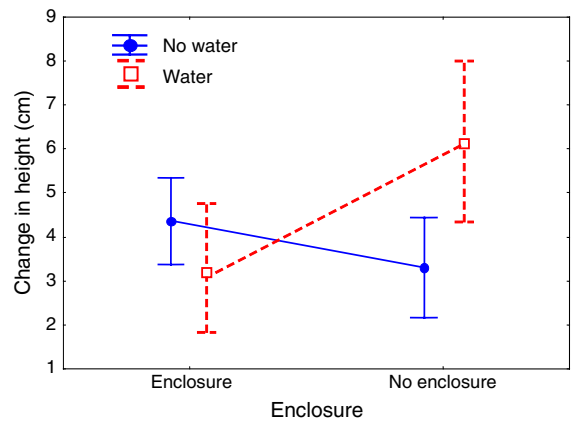


Fig. 3 Whisker plot for weighted marginal means of change in *A. erioloba* sapling height under enclosure and water treatments

I therefore excluded outliers outside the range of ± 2 standard deviations around each group mean. Consequently, 7 out of the total 120 points (6%) were removed: two data points from group A, two from group B, one from group C and two from group D.

Farm, plot and water or enclosure alone did not explain any differences in variation in height between treatments. There was, however, a significant interaction between water and enclosures: saplings given supplemental water and unprotected from herbivory showed a significantly greater increase in height over the growing season than watered, protected saplings ($\chi^2 = 7.87$; log likelihood = -456.7 ; $p = 0.005$, maximum likelihood model: d.f. = 100, scaled deviance = 1.130, deviance explained = 15.8%) (Fig. 3).

Average growth amongst plants in the fastest growing treatment (treatment C) was 61.3 mm (SD = 50.6 mm).

Competition with grass

Growth was significantly linearly related to subsurface stem size, for both plots where grass had and had not been removed (Grass removed: $y = 17.566x + 17.35$; $R^2 = 0.239$; $p < 0.05$; Control: $y = 10.898x + 27.068$; $R^2 = 0.1756$; $p < 0.05$). Comparison of residuals showed that differences between growth rates amongst the two groups were not statistically significant (Mann–Whitney U test; $U = 347$; $z = 1.13$; $p > 0.1$, $n = 58$).

Discussion

A small percentage of *A. erioloba* saplings encountered in random grids in the study area have attained heights reaching above the grass sward. Although successful establishment may only occur in rare years of above-average rainfall in semi-arid savannas (where rainfall is $<500 \text{ mm}\cdot\text{year}^{-1}$ or less), subsequent escape to heights above the grassy layer presents an additional hurdle for *A. erioloba* at these study sites.

Previous studies have found successful establishment of *A. erioloba* seedlings to be restricted to years where rainfall is evenly distributed over a season (Briers 1988; Barnes 1999, 2001b), and this should ordinarily give rise to cohorted recruitment. Peaks within the frequency distribution of below surface stem size classes support cohorted recruitment but also indicate that very few true seedlings survive. Although 73 and 93% of individuals at Susanna and Benfontein respectively were below 400 mm in height, amongst individuals shorter than 400 mm, belowground stem size varied from 1.7 to 48.3 mm, pointing to the presence of different-aged plants within a given height class and that saplings “trickle” into the system as recruits. The predominance of short plants here implies that once established, many plants have yet to escape to higher size classes, so escape or even reversals can present a major obstacle to reaching heights above the grassy layer. Midgley and Bond (2001) point out that few field studies have focused on actual seedlings, and that short individuals are often considered to be seedlings. This study shows, however, that short plants are not always seedlings.

The question arises as to what is preventing escape. Results of the exclusion plot experiments and removal of grass suggested that neither water availability nor competition from grasses exclusively govern growth rates, although these factors produced significant differences in concert. Although the differences produced by supplementary water with protection from grazing were significant, they explained only 16% of variation in growth, suggesting that other factors may be more important determinants of sapling growth.

There was no significant advantage to being within an exclusion plot. Many studies point to detrimental effects of herbivory on woody plant growth and survival rates (Belsky 1984; Weltzin et al. 1997; Barnes 1999; Augustine and McNaughton 2004).

Browsing was noted on two-thirds of the unprotected plants, but was usually limited to two or three stems per plant, possibly because of the relatively low density of browsers at these study sites. Although not measured, grass height and density in watered exclusion plots was observed to be greater than that of grass in un-watered exclusion plots. In addition, grass height in both types of exclusion plots was greater than that in unprotected plots and the surrounding matrix. Exclusion of browsers no doubt also excluded grazers, and it appears as if grass within watered exclusion plots benefited from the watering regime. The literature contains conflicting reports on the influence of grasses on tree recruitment, with both positive (Brown and Archer 1989; Davis et al. 1998) and negative (Walker et al. 1981; Harrington 1991) effects being recorded. It appears as if here, the adverse effects of competition with grass could have obscured potentially positive effects of protection from browsing. Elsewhere, the combination of watering and grass defoliation has also been found to be necessary to trigger mass tree recruitment (Kraaij and Ward 2006).

Removal of grass alone was insufficient to elicit a significant difference in growth rates. This could be because grass was only removed from an area of 1 m^2 around saplings, yet sapling roots likely extend further than 1 m into the surrounding matrix, so removal of grass close to the sapling stem only may have been inadequate to reduce competition from surrounding grass. Nevertheless, this result combined with that of the exclusion plot experiment, and the high variance within that experiment suggests competition from surrounding grass alone is not the only determinant of *A. erioloba* sapling growth.

Browsing and competition with grasses may help keep saplings within the grass sward, and so vulnerable to fire and herbivory (Midgley and Bond 2001) in the study area. The study sites are representative of the land use types in the region, so the findings of this study likely apply to other farms in the area as well. The major constraint seems to be slow growth rate, however: the group that fared best in the exclusion plot experiment only achieved mean height increases of 61 mm during one growing season, and the average across all treatments was 43.1 mm. Barnes (1999) found similar growth rates, where average increase in sapling height was only 48 mm per growing season, although browsing seems to have

been more intense at her sites. At a drier site, (but with shallower groundwater) in the Kgalagadi Transfrontier Park (mean annual rainfall = 233 mm year⁻¹), van Rooyen et al. (1994) found average growth rates of 65 mm a year between 1978 and 1994.

These apparently slow growth rates may be because most early growth in *A. erioloba* is concentrated belowground: a sapling only 250 mm high can have roots longer than 3.2 m (Leistner 1967), and even a tiny seedling (50 mm high and estimated to be two months old) can have a tap root of nearly 110 mm (Seymour and Huyser unpublished data). Larger individuals have been recorded to have roots to depths of 60 m (Canadell et al. 1996). Brown and Archer (1989) attributed slow growth rates of *Prosopis glandulosa* seedlings in Texan savannas to investment in belowground structures, and it is likely that *A. erioloba* seedlings do likewise. On study sites here, groundwater is quite deep—at between 50 and 60 m and so it is likely that only some of the larger saplings will have roots that reach near the water table.

Although supplementary watering appears to have had little immediate benefit for the woody component, it appears to have been advantageous to the surrounding grasses, which grew more vigorously, to the detriment of the tree saplings. Grime (1979) contended that faster growing species would exhibit greater phenotypic plasticity. Grasses, being faster growing, should therefore be able to respond rapidly to increased water availability relative to the slow growing woody component, thus shading saplings, altering ambient air conditions around saplings, and ultimately outcompeting them for nutrients and water.

Despite being neighbouring farms, individuals on Susanna were larger than those on Benfontein (mean underground stem diameter: 20.6 vs. 7.6 mm) for all measurements, a pattern that also held for *A. tortilis* (Seymour unpublished data), the other common *Acacia* at both sites. These size differences are unlikely owing to soil differences, as plots sampled on the two farms were sometimes closer to each other than plots sampled within the same farm. The relationship between height and subsurface stem size was not significantly different between the two sites, suggesting that proportionate investment aboveground and in the subsurface stem is the same at both sites. Differences are therefore likely because the two sites differ in fire and/or grazing history: fires have been actively excluded on Benfontein, the last

fire having occurred 11 years prior to this study. Fire may have created a window of opportunity for seedling establishment in the past, while grass competition for moisture, nutrients and radiation combined with herbivory may have arrested their growth and escape into larger size classes, but this idea requires further testing.

Warner and Chesson (1985) coined the term “storage effect” to describe the phenomenon whereby a species’ continued existence relies on continued survival of its adult population, because recruitment to adult size classes is episodic. Recruitment events are effectively stored in the reproductive adult population until favourable recruitment conditions arise. *Acacia erioloba* is exceptionally long lived for an acacia, living to at least 240 years (Steenkamp 2000), and this life history trait is one that may have been selected for in light of rare recruitment events. More important, however, is that the adult population is critical to continued existence of the species, and unchecked harvesting of adults is of conservation concern, for both the species and the biota and ecosystem processes so reliant upon it. Because, saplings do not effectively contribute to the reproductive pool, the population depends on proportionally few long-lived individuals for the majority of reproductive effort.

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