

Facilitative effects of *Aloe secundiflora* shrubs in degraded semi-arid rangelands in Kenya

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Abstract

Livestock overgrazing can threaten the ecological integrity of rangelands, and can also threaten the sustainability of pastoralist societies who depend on rangelands for their livelihood. Using facilitator plants in the restoration of degraded semi-arid rangelands offers a promising strategy because in such environments, facilitators can ameliorate harsh conditions that often limit the establishment and success of surrounding vegetation. In a degraded rangeland in Kenya, I compared local biotic and abiotic environmental conditions around naturally occurring *Aloe secundiflora* shrubs to conditions around *Maerua decumbens* shrubs and points without shrub cover. The presence of *A. secundiflora* shrubs was positively associated with increased vegetation cover, species richness, litter cover, soil seed banks, and soil retention within a 2 m radius of shrubs, as compared with conditions surrounding *M. decumbens* and areas lacking shrub cover. The pattern is consistent with the hypothesis that *A. secundiflora* acts as a facilitator in this plant community. These findings are the basis for additional studies to determine whether transplanted *A. secundiflora* shrubs can also elicit the formation of patches with ameliorated environmental conditions. If so, augmenting populations of native *A. secundiflora* shrubs may be a feasible strategy in the ecological restoration of degraded rangelands.

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1. Introduction

Facilitation, whereby the presence of one plant species enhances the survival or performance of other plants, is most often documented in stressful environments, such as arid, saline, alpine, and arctic ecosystems (Callaway, 1995). In such environments, the presence of stress-tolerant plants can ameliorate the harsh environmental conditions in their immediate vicinity, and thereby provide favorable sites where less tolerant species can then succeed. Through such positive interactions, facilitators can strongly influence plant community composition, dynamics, and diversity (Bertness and Callaway, 1994; Goldberg and Novoplansky, 1997).

In arid and semi-arid ecosystems, the presence of shrubs can increase water infiltration, reduce soil moisture evaporation, trap litter and propagules, and create sites protected from herbivores. These processes tend to

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concentrate resource cycling around shrubs, with limited movement of water, nutrients, and propagules outward into the inter-shrub areas. Other plants respond positively to the concentrated resources around shrubs, leading to the formation and maintenance of vegetation patches around shrubs, or ‘islands of fertility’ (Garner and Steinberger, 1989; Schlesinger, 1997). Based on the ‘islands of fertility’ model, augmenting populations of facilitator shrubs emerges as a promising strategy for enhancing resource dynamics and restoring degraded vegetation in arid and semiarid rangelands (Aronson et al., 2002; King and Hobbs, 2006; Ludwig and Tongway, 1996; Tongway and Ludwig, 1996; Whisenant, 1999). Indeed, a growing number of studies are reporting successful utilization of facilitators in dryland restoration (Anderson et al., 2004; Castro et al., 2004; Maestre et al., 2003; Padilla and Pugnaire, 2006; Singh et al., 2003).

In Kenya, over 75% of the land is classified as arid or semi-arid, a great proportion of which has become heavily degraded as a consequence of increased human populations and livestock pressure in the last several decades. Stressed by intense livestock densities and frequent droughts, the semi-arid bushed grasslands of Baringo District show some of the most severe degradation in the country, with extreme soil erosion and lack of herbaceous cover between shrub patches (Bryan, 1994; Thom and Martin, 1983). *Aloe secundiflora* Engl. (Asphodelaceae) shrubs are fairly common in the degraded and patchily distributed vegetation of Baringo District, where they often appear to be foci of vegetation patches. This suggests that *A. secundiflora* shrubs may facilitate the formation of vegetation islands, or facilitate the persistence of surrounding vegetation under intense grazing conditions, or both. If so, propagating and out-planting *A. secundiflora* shrubs could become a feasible restoration tool to support the re-establishment of other plant species.

The ‘islands of fertility’ model predicts that improved physical and biotic conditions are associated with shrubs that trap and retain resources. *A. secundiflora* shrubs provide perennial shade, direct leaf cover on the ground, and armed domed architecture, which can promote soil moisture retention, erosion prevention, litter accumulation, and physical protection for other plants. As a first step in assessing the potential suitability of *A. secundiflora* as a restoration tool in degraded Kenyan rangelands, we tested the hypothesis that physical and biotic conditions were better near *A. secundiflora* than near the deciduous, unarmed common shrub *Maerua decumbens*, or on ground that lacked shrubs.

2. Methods

2.1. Study site

The study was conducted January 1999, approximately 1.5 months after the last rainfall, at a site 2 km northeast of Lake Kamnarok, in the alluvial plains on the Kerio Valley floor, Baringo District, Kenya (N0°38.65' E35°37.75'; 1100 m elevation; Fig. 1). The area is semi-arid *Acacia mellifera*–*Salvadora persica* bushed grassland, receives about 400 mm annual rainfall concentrated in two rainy seasons, and is populated by pastoralist Tugen people who tend cattle, goats and sheep. Based on interviews with local residents and surveys conducted by Adams and Watson (2003), high livestock densities and fuelwood cutting have reduced vegetation cover dramatically over the last 30–40 years. Soil erosion, in the form of rills, washes, and gullies, is ubiquitous and severe.

An area of approximately 2 ha was subjectively selected as the study site because *A. secundiflora* density, as well as tree and shrub densities, were relatively homogenous across the site. Using a stratified random sampling strategy, I visually estimated the total percent vegetation cover and the presence/absence of individual plant species in 144 1 m² quadrats throughout the study site. There was not adequate plant material to identify individual grass species, so all grasses were lumped together in the vegetation characterizations and measurements described below.

2.2. Vegetation and soil measurements around foci

Within the study site, I randomly selected 23 *A. secundiflora* shrubs and 22 *M. decumbens* (Brongn.) De Wolf (Capparaceae) shrubs as foci around which to measure vegetation and soil characteristics. Both shrubs reach up to 1 m tall and 1 m in diameter; the selected shrubs were all mature and averaged 55 cm tall and 70 cm in diameter. These two species are hereafter referred to as *Aloe* and *Maerua*. I also located 10 random points within

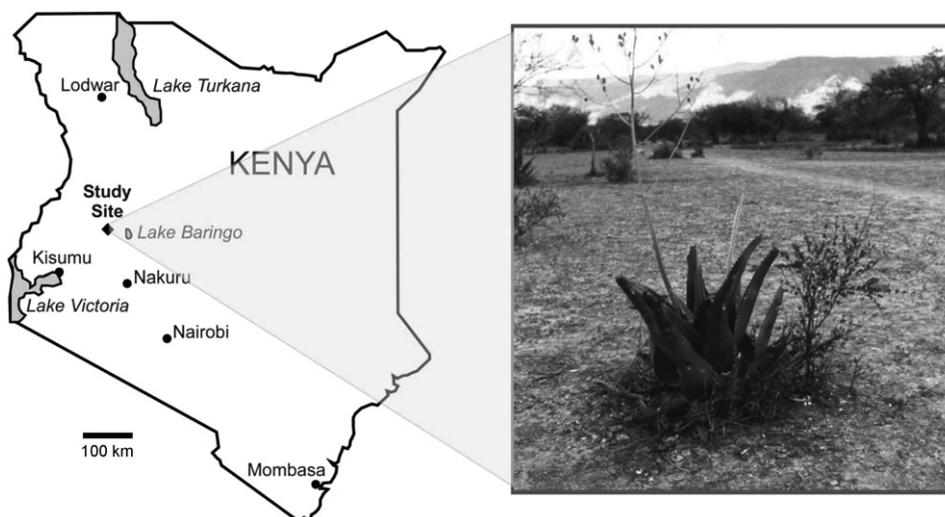


Fig. 1. Map of Kenya and photograph of study site, which shows the characteristically patchy distribution of vegetation, with very little vegetation cover between patches. The succulent shrub in the foreground is *Aloe secundiflora*; the leafy shrub adjacent to it is *Maerua decumbens*.

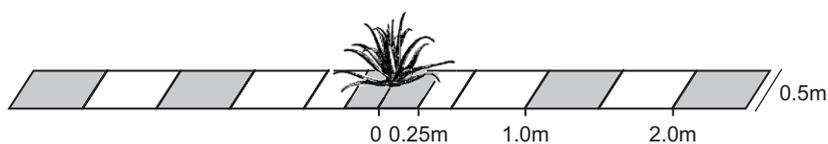


Fig. 2. Schematic diagram of transects for measurements around foci. Focus types were *Aloe* shrubs ($n = 23$), *Maerua* shrubs ($n = 22$), or randomly selected points, all of which lacked shrub cover ($n = 10$). Measurements were taken in the shaded 0.5×0.5 m quadrats located 0, 1, and 2 m from foci.

the study area to serve as reference foci, irrespective of vegetation cover. All lacked shrub cover, but some had herbaceous cover, and are subsequently referred to as “shrubless foci.” Centered on each focus, I placed a ladder-like transect of 50×50 cm quadrats in a randomly selected compass orientation, as shown in Fig. 2.

Vegetation cover of each species, litter cover, and number of plant species were visually estimated independently by two observers to the nearest 5%, with additional categories of 3% and 1%, in five 50×50 cm quadrats. These were located 0, 1, 2 m from foci. Measurements taken in the equidistant pairs of quadrats at 1 and 2 m were averaged for each focus. Total vegetation cover in each 50×50 cm quadrat was calculated as the sum of cover values of all individual species present (excluding the focal plant), and thus could exceed 100%. The total number of species encountered in all five quadrats around each focus was calculated, providing a measure of the neighborhood species richness, or the number of species per 1.25 m^2 in a 2 m radius around foci. For *Aloe* and *Maerua* foci, I measured focal plant height, diameter, and focal plant canopy cover and direct ground cover at 0 m.

Microtopography was measured by extending a level horizontal line from the focal plant or shrubless focal point along the transects, then measuring the vertical distance to soil surface at distances of 0, 0.25, 1, and 2 m from the focus. Soil level at 2 m was considered zero for each transect, thus positive values indicate soil levels higher than that at the 2 m reference point. Bias due to the overall slope at the site (less than 0.5%) was nullified by randomly selecting the each transect's orientation and by averaging the two opposite transects for each focus.

For nine of the *Aloe* foci, the soil seed bank was evaluated by collecting 8 cm diameter \times 10 cm deep soil samples at 0.2 and 2 m from the focus, in one randomly selected direction only. The volume of each soil sample was about 500 cc. Seeds were removed from soil samples by gently crumbling soil with fingers and passing through a 0.6 mm mesh sieve. All seeds >0.6 mm were removed by hand. Very few entire seeds smaller than

0.6 mm were recognizable. The total number of seeds and number of distinguishable species represented in each soil sample were recorded.

2.3. Analyses

I tested the effects of focus type and distance separately for each of the following response variables: vegetation cover, species richness, litter cover, microtopography, seed bank size, and seed bank species richness. The distributions of all response variables were either grossly non-normal, or showed considerable heterogeneity of variance among focus types, or both. Since the data could not be transformed to satisfactorily meet ANOVA assumptions, I used analogous non-parametric statistical tests.

The following three-step procedure was used to analyze most of the response variables. For some variables, the procedure was modified slightly, as described below: (1) For each variable, the main effect of focus type was evaluated separately for each distance using the Kruskal–Wallis test for multiple levels of one factor (Sokal and Rohlf, 1995). (2) If focus type was significant, I performed multiple pairwise comparisons to determine which particular focus types differed from one another, using the Dwass, Steel, Critchlow–Fligner (DSCF) procedure for distribution-free, two-sided, all-treatments multiple comparisons based on pairwise rankings. The DSCF test incorporates corrections for multiple comparisons, so additional Bonferroni type corrections were not needed (Hollander and Wolfe, 1999). (3) For each focus type, I tested for differences between adjacent distance intervals using Wilcoxon signed-rank tests for paired observations, which is the non-parametric analog of the paired *t*-test. All *p* values were corrected to maintain an experiment-wise type I error of $\alpha = 0.05$.

The above three-step procedure was slightly modified for the remaining variables. For number of species, steps 1 and 2 were used to analyze the effect of focus type only. The analysis of microtopography used different distances from foci: 0, 0.25, and 1 m. Soil seed bank variables were assessed at only two distances per focus, and only around *Aloe* foci, using Step 3.

The potential effect of focal shrub size on response variables was investigated by regressing *Aloe* and *Maerua* shrub diameters against response variables at 0 m. No significant relationships were found, so focal plant size was not incorporated into analyses. To explore possible mechanisms for microtopography effects around *Aloe* and *Maerua* foci, I used non-parametric Spearman's rank order correlations (Hollander and Wolfe, 1999) to look for relationships between soil level and vegetation cover, species richness, and litter cover at 0 m. I also tested correlations between soil level and three focal plant attributes: plant diameter, percent cover at 0 m, and percent direct ground cover at 0 m. These analyses were performed separately for *Aloe* and *Maerua* foci to avoid confounding the relationships with focal type effects.

3. Results

3.1. Study site vegetation characterization

The average vegetation cover at the study site was 5.5%, and strongly patchily distributed. Of the 144 1 m² quadrats used to assess vegetation characteristics for the site, 77% had 1% or less vegetation cover, 15% had 3–25% vegetation cover, and 8% had greater than 25% cover. Tree canopy cover was approximately 3%, and dominated by four species (frequency of occurrence in quadrats given in brackets): *A. mellifera* (Vahl) Benth. [11.8%], *Balanites aegyptiaca* (L.) Del. [3.4%], *S. persica* L. [2.7%], and *Rhus natalensis* Krauss [1.4%]. The shrub layer was dominated by succulent shrubs and vines, with the following species occurring most frequently: *Cissus rotundifolia* (Forsk.) Vahl [8.3%], *Sansevieria robusta* N.E.Br. [4.9%], and *A. secundiflora* [4.2%]. By far the most abundant species at the study site were two sprawling weedy herbs common in disturbed areas, *Portulaca oleracea* L. [71.5%] and *Alternanthera pungens* Kunth [58.3%]. Grasses, usually evidenced only by leafless culm bases, occurred in 21.5% of quadrats.

3.2. Vegetation cover around foci

At each distance from foci, percent vegetation cover was highest around *Aloe* foci and lowest around shrubless foci (Fig. 3, Table 1). The variation among focus types was highly significant at 0 and 1 m, but not at

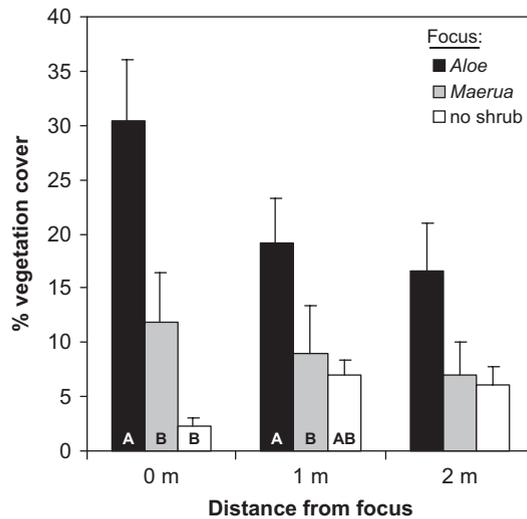


Fig. 3. Mean percent vegetation cover (+1 SE) in 0.5×0.5 m quadrats located 0, 1, and 2 m from *Aloe*, *Maerua*, and shrubless foci. Cover values exclude cover due to focal plant, if any. At each distance, $n = 23$, 22, and 10 for *Aloe*, *Maerua*, and shrubless foci, respectively. Focus types that differed significantly within each distance are indicated by different capital letters.

2 m ($p = 0.06$). Pairwise comparisons indicated that at 0 m, the percent vegetation cover associated with *Aloe* foci (30%) was significantly greater than cover around *Maerua* (12%) and shrubless foci (2%) (DSCF tests $p = 0.003$ and 0.001, respectively). At 1 m from foci, *Aloe* shrubs had 19% associated vegetation cover, which was significantly greater than the 9% cover observed 1 m from *Maerua* foci (DSCF test $p = 0.005$). The difference between *Aloe* and shrubless foci at 1 m was not significant in the pairwise comparison, probably due to the smaller sample size of 10 transects for shrubless foci, as opposed to 22 transects *Maerua* foci.

The pattern of vegetation cover change over distance also varied among focus types (Fig. 3, Table 1). Vegetation around *Aloe* foci decreased sharply and significantly from 0 to 1 m, from 30.4% to 19.1%, but there was no significant decrease from 1 to 2 m. Vegetation cover associated with *Maerua* shrubs showed a modest overall decrease with distance from foci, from 11.8% at 0 m to 7.0% at 2 m, but the changes over each distance interval were not significant. There was no significant vegetation cover change with distance from shrubless foci. The average vegetation cover for all distances along shrubless focus transects was 5.2%. This figure agrees well with the estimate of 5.5% vegetation cover in the study area derived from the 144 1 m^2 quadrats used for study site vegetation characterization. Thus, the transects around shrubless foci appeared to adequately represent background vegetation levels at the study site.

3.3. Species richness around foci

At 0 and 1 m, species richness varied significantly among focus types (Fig. 4, Table 1). At 0 m, *Aloe* foci had the highest number of species per 0.25 m^2 quadrat ($\bar{x} = 3.3$), shrubless foci had the lowest species richness ($\bar{x} = 1.7$), and species richness around *Maerua* foci was intermediate ($\bar{x} = 2.6$). At 1 m distance from foci, *Aloe* foci still had the greatest number of associated plant species ($\bar{x} = 1.6$), while shrubless foci had intermediate species richness ($\bar{x} = 1.4$) and *Maerua* foci had the lowest number of species ($\bar{x} = 1.1$). At 2 m from foci, species richness did not vary significantly among focus types.

Aloe and *Maerua* foci showed similar patterns of change in species richness over distance (Fig. 4, Table 1). The number of species around *Aloe* foci dropped significantly over the 0 m-to-1 m interval, from 3.3 to 1.7 species per 0.25 m^2 , but showed no significant decrease over the 1 m-to-2 m interval. Likewise, the number of associated species around *Maerua* foci decreased significantly over the 0 m-to-1 m interval, from 2.6 to 1.1 species/ 0.25 m^2 . Number of species associated with shrubless foci showed no significant changes with distance.

Table 1
Effects of focus type and distance from focus on vegetation cover, species richness, litter cover, and microtopography

Response variable	Distance	<i>Aloe</i>			<i>Maerua</i>			Shrubless			Kruskal–Wallis	
		<i>x</i>	s.e.	<i>n</i>	<i>x</i>	s.e.	<i>n</i>	<i>x</i>	s.e.	<i>n</i>	χ^2	<i>p</i>
Vegetation cover	0 m	30.4 ^a	5.8	23	11.8 ^a	4.7	22	2.3 ^a	0.8	10	18.3	<0.001
	1 m	19.2 ^b	4.1	23	9.0 ^a	4.6	22	7.0 ^b	1.5	10	9.4	0.009
	2 m	16.6 ^b	4.4	23	7.0 ^a	3.2	22	6.1 ^b	1.7	10	5.5	0.06
Species richness	Pooled	5.4	0.4	23	3.3	0.5	22	3.4	0.6	10	10.7	0.005
	0 m	3.3 ^a	0.4	23	2.6 ^a	0.4	22	1.7 ^a	0.5	10	4.7	0.04
	1 m	19.2 ^b	4.1	23	9.0 ^b	4.6	22	7.0 ^a	1.5	10	5.9	0.05
	2 m	16.6 ^b	4.4	23	7.0 ^b	3.2	22	6.1 ^a	1.7	10	3.0	0.22
Litter cover	0 m	47.0 ^a	5.3	23	13.2 ^a	3.0	22	3.3 ^a	1.0	10	30.6	<0.001
	1 m	19.6 ^b	3.4	23	4.1 ^b	1.6	22	3.9 ^a	0.8	10	21.0	<0.001
	2 m	13.8 ^c	3.3	23	3.0 ^b	1.1	22	4.1 ^a	1.0	10	16.9	0.002
Microtopography	0 m	5.2 ^a	1.7	23	3.7 ^a	0.7	22	-2.3 ^a	1.6	10	16.7	0.002
	0.25 m	-1.8 ^b	1.6	23	0.7 ^b	0.5	22	-2.2 ^a	1.5	10	4.4	0.22
	1 m	-1.2 ^b	0.9	23	0.3 ^b	0.2	22	-1.2 ^a	1.0	10	2.8	0.25
	2 m	0.0 ^b	0.0	23	0.0 ^c	0.0	22	0.0 ^a	0.0	10	-	-

Kruskal–Wallis tests indicate the significance of focus type effect at each distance; with significant values in boldface. Significant pairwise contrasts among focus types are reported in the text. Within each focus type and response variable (i.e., within each block in the table), means with different superscripted letters were significantly different (Wilcoxon paired test $p \leq 0.05$). See Methods for full explanation of statistical analysis.

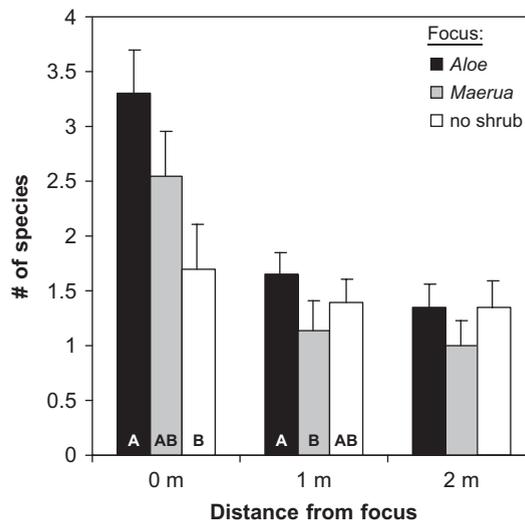


Fig. 4. Mean number of plant species (+1 SE) encountered in 0.5×0.5 m quadrats located 0, 1, and 2 m from *Aloe*, *Maerua*, and shrubless foci. Focal plant, if any, is excluded from species count. At each distance, $n = 23$, 22, and 10 for *Aloe*, *Maerua*, and shrubless foci, respectively. Focus types that differed significantly within each distance are indicated by different capital letters.

Neighborhood species richness, calculated by pooling all five quadrats around foci and counting the total number of species present, also varied significantly among focus types (Table 1). The mean number of species present in all the quadrats around *Aloe* foci was 5.4 species/1.25 m², significantly greater than the 3.3 species/1.25 m² found around *Maerua* foci (DSCF test $p = 0.01$) and the 3.4 species/1.25 m² found around shrubless foci (DSCF test $p = 0.04$).

3.4. Percent litter cover

The percentage of ground surface covered by litter varied among focus types at each distance from foci, with *Aloe* foci having consistently more associated litter than *Maerua* or shrubless foci (Fig. 5, Table 1). At 0 m, 47% of the ground around *Aloe* foci was covered with litter, while there was 13% litter cover around *Maerua* foci and 3% litter cover around shrubless foci (DSCF tests $p = 0.0001$, 0.0001 , and 0.01 for *Aloe-Maerua*, *Aloe-shrubless*, and *Maerua-shrubless* contrasts, respectively). At 1 m from foci, the 20% average litter cover associated with *Aloe* foci was significantly greater than the 4% litter associated with both *Maerua* and shrubless foci (DSCF tests $p = 0.0001$ and 0.005 for *Aloe-Maerua* and *Aloe-shrubless* contrasts, respectively). At 2 m, the 14% litter cover associated with *Aloe* foci was significantly greater than the 3% litter cover around *Maerua* foci (DSCF test $p = 0.003$). Even though the 4% litter around shrubless foci was one third of the litter around *Aloe* foci, the difference was not statistically significant, again probably due to small sample size for shrubless foci.

Each focus type showed a different pattern of change in associated litter with distance (Fig. 5, Table 1). Litter around *Aloe* foci decreased significantly with each distance interval, from 47.0% to 19.6% to 13.8%, at 0, 1, and 2 m, respectively. Litter cover associated with *Maerua* shrubs decreased significantly from 0 to 1 m, but did not change from 1 to 2 m. Litter cover associated with shrubless foci was low at all distances from foci (3–4%), and showed no significant change with distance.

3.5. Microtopography

When microtopography was measured relative to soil level 2 m from foci, *Aloe* and *Maerua* shrubs were associated with greater soil retention, but only at a very local scale (Fig. 6, Table 1). At 0 m, the average soil levels for both *Aloe* and *Maerua* foci (5.2 and 3.7 cm, respectively) were significantly higher than the average soil level at shrubless foci (DSCF tests $p = 0.003$ and 0.001 for *Aloe-shrubless* and *Maerua-shrubless* contrasts, respectively). At greater distances from foci, 0.25 and 1 m, soil levels did not differ between any of the focus types.

The pattern of change in soil level with distance was more dramatic around *Aloe* foci than *Maerua* foci (Fig. 6). Soil level around *Aloe* foci dropped significantly, by an average of 7.0 cm, within the first 25 cm of horizontal distance from the base of *Aloe* shrubs, and did not change significantly over subsequent distance intervals. *Maerua* foci showed a smaller drop of 3.0 cm within the 0–0.25 m interval, and no significant change in soil level thereafter. For shrubless foci, soil level did not change significantly with distance.

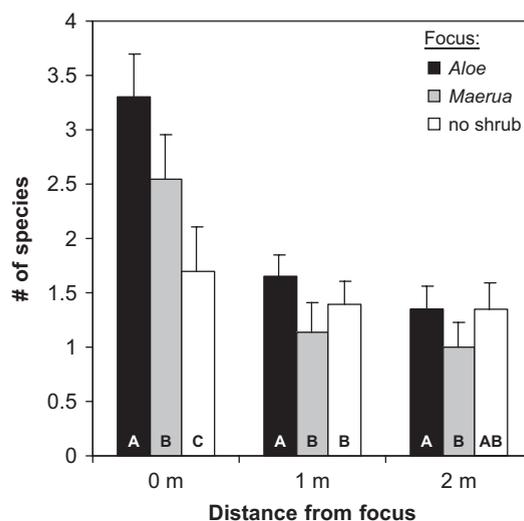


Fig. 5. Mean percent litter cover (+1 SE) in 0.5×0.5 m quadrats located 0, 1, and 2 m from *Aloe*, *Maerua*, and shrubless foci. At each distance, $n = 23$, 22 , and 10 for *Aloe*, *Maerua* and shrubless foci, respectively. Focus types that differed significantly within each distance are indicated by different capital letters.

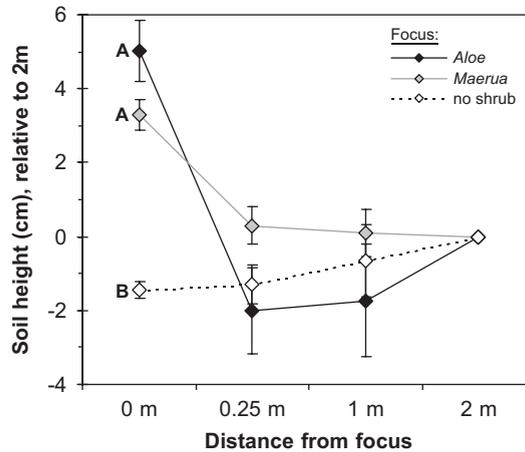


Fig. 6. Mean soil height (± 1 SE) located 0, 0.25, 1, and 2 m from *Aloe*, *Maerua*, and shrubless foci. Soil height measurements were calculated relative to soil height at 2 m. At each distance, $n = 23$, 22, and 10 for *Aloe*, *Maerua*, and shrubless foci, respectively. Focus types that differed significantly at 0 m distance are indicated by different capital letters.

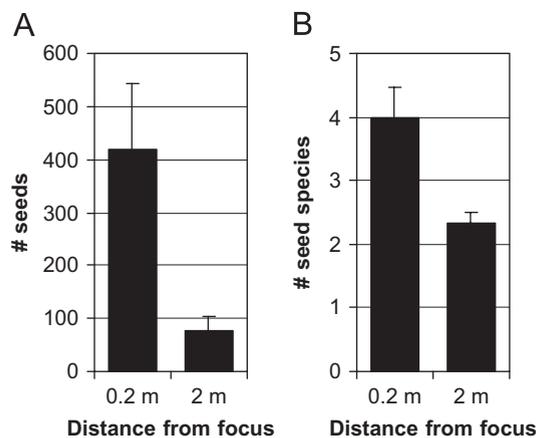


Fig. 7. Seed bank characteristics measured underneath *Aloe* shrubs and 2 m away. (A) Mean number of seeds, and (B) mean number of species represented ($+1$ SE), were significantly greater in soil samples taken 0.2 m from *Aloe* shrubs than in soil samples taken 2 m from *Aloe* shrubs ($p = 0.004$ and 0.020 , respectively, $n = 9$ for each distance).

For *Aloe* foci, soil level at 0 m was positively correlated with the amount of ground cover provided by focal *A. secundiflora* plant leaves (Spearman's $\rho = 0.40$, $p = 0.04$), but was not correlated with surrounding vegetation cover, species richness, or litter cover measured within 0.25 m. For *Maerua* foci, soil level at 0 m was not correlated with any environmental or focal plant variables measured.

3.6. Soil seed bank: number of seeds and species represented

The soil seed bank quantity and diversity was markedly richer beneath *Aloe* foci than 2 m away. Soil samples collected 0.2 m from *Aloe* foci contained an average of 420 seeds, while soil samples taken 2 m away had an average of 78 seeds (Wilcoxon test $p = 0.004$, $n = 9$; Fig. 7A). Soil samples collected 0.2 m from *Aloe* foci contained seeds from an average of 4.0 plant species, whereas an average of 2.3 species were represented in soil samples collected 2 m from foci (Wilcoxon test $p = 0.020$, $n = 9$; Fig. 7B).

4. Discussion

The objective of this study was to test the hypothesis that in a heavily overgrazed Kenyan grassland, naturally occurring *A. secundiflora* shrubs are associated with improved biotic and abiotic conditions, as one would expect if they were acting as facilitators in ‘islands of fertility’ dynamics. The results indicated that *A. secundiflora* shrubs were indeed spatially associated with significantly greater vegetation cover, litter cover, species richness, and soil retention, as compared to conditions around *M. decumbens* shrubs and shrubless points within the study area. Also, soil seed bank quantity and richness were greater beneath *A. secundiflora* canopies than at points 2 m away.

While the results are entirely consistent with the hypothesis that *A. secundiflora* shrubs act as facilitators, an alternative explanation is that the observed spatial associations could be the result of many plant species responding similarly to some underlying environmental or substrate heterogeneity. However, the argument for substrate heterogeneity alone is less probable when one considers the recent drastic changes in environmental conditions in the area relative to the longevity of *A. secundiflora* shrubs.

Forty or 50 years ago, the study area had more uniform herbaceous cover and modest human and livestock densities (Little, 1992; Thom and Martin, 1983). Most of the mature *A. secundiflora* shrubs probably established during that time, or even decades earlier (based on accounts of *A. secundiflora* age and growth rates; L. Newton, G. Powys, pers. comm.). Today, there is drastically reduced vegetation cover and severe erosion, so younger and shorter lived species are now establishing in a very different environment. As part of our general understanding of semi-arid landscapes, we expect the presence of a shrub or tree in a sparsely vegetated landscape to create over time a drastically different microenvironment (Noy-Meir, 1985; Schlesinger and Pilmanis, 1998; Tongway and Ludwig, 1994). Thus, the observed patterns of improved environmental conditions associated with *A. secundiflora* shrubs are most likely due to long-term ameliorating effects on local edaphic conditions, as well as current, short-term facilitation mechanisms.

4.1. Potential mechanisms of facilitation

Physical protection from herbivores and/or shading could contribute to the increased associated vegetation around *Aloe* foci at the smaller spatial scales (< 1 m). But beyond the shrub canopy, other mechanisms may play a role, such as soil improvements, patterns of livestock passage and trampling, propagule dispersal, or clonal growth of plants into inter-shrub spaces. In drylands of Australia, Spain, and North America, researchers have linked similar vegetation patterns to enhanced nutrient and resource cycling within shrub islands, with a spill-over effect extending centimeters to a few meters beyond shrub canopies (Connin et al., 1997; Schlesinger and Pilmanis, 1998; Tongway and Ludwig, 1994).

Maerua foci were associated with increased vegetation in their immediate vicinity, but to a lesser extent than *Aloe* foci, and the effect did not extend beyond 0.5 m from focus plants, suggesting that the magnitude and/or diversity of facilitative effects were less than for *Aloe* foci. In contrast to *A. secundiflora*, *M. decumbens* shrubs are deciduous and unarmed. Providing less shade and less shelter from herbivores could contribute to the smaller amount of associated vegetation within their canopy zone. The lesser degree of facilitation was apparently inadequate to create a spill-over effect beyond the canopy.

The differences in pooled species richness over 0–2 m around foci indicated that *A. secundiflora* shrubs were associated with greater neighborhood diversity, whereas *M. decumbens* shrubs had similar neighborhood diversity to shrubless areas. However, comparisons of diversity at each distance indicated that the positive effects of *Aloe* foci on species richness were mostly restricted to their immediate vicinity (0–0.5 m from the plant). Even though total cover was enhanced up to 2 m from *Aloe* foci, it appears that only a few species were able to respond to the fewer or less intense forms of amelioration occurring at greater distances from focal plants.

Two pantropical ruderal forbs, *Portulaca oleracea* and *Alternanthera pungens*, were the most common plant species occurring 1 and 2 m away from *Aloe* foci, and were also the most common species around *Maerua* and shrubless foci. In the context of restoration, facilitation of opportunistic or weedy species can be problematic if those plants persistently out-compete more desirable species (Kulmatiski, 2006; Maron and Connors, 1996; Walker and Vitousek, 1991). However, Callaway et al. (2000, 2005) found that undesirable rangeland weeds

can facilitate pasture diversity. Furthermore, [Rodriguez \(2006\)](#) recently reviewed numerous studies in which non-native or early successional weedy species facilitated native and desirable vegetation. While that review focused on forests, the principles also seem plausible for revegetation in degraded drylands, where ruderal species can provide soil stabilization, re-establish nutrient cycling, and then later be out-competed once environmental conditions improve and favor other species. Thus, even though weedy or non-native species are ultimately undesirable, they may nevertheless serve as effective intermediate facilitators. Indeed, another study of vegetation associated with *A. secundiflora* did find that several ruderal species, including *P. oleracea*, decreased and were replaced by more desirable rangeland species when grazing pressure and drought stress were reduced ([King, 2004](#)).

While tree seedlings constituted a very small fraction of species observations, their ecological importance is disproportionately large in terms of maintaining community structure ([Kiyapi, 1994](#); [Reid and Ellis, 1995](#)), and facilitative interactions can be critical to tree establishment ([Gomez-Aparicio et al., 2004](#); [Vieira et al., 1994](#)). It is therefore noteworthy that the only four tree seedlings encountered in all of the transects in this study were found growing within the canopy of *A. secundiflora* shrubs. The sample sizes were too small to test the significance of this association, but this suggests that tree seedling establishment in this plant community may depend on shrub facilitation.

There was markedly higher litter accumulation around *Aloe* foci than *Maerua* or shrubless foci, at all distances. *Aloe* shrub architecture may aid in the trapping of litter because lower leaves rest directly upon the soil surface, while *Maerua* shrubs provided very little direct ground cover. But *A. secundiflora* architecture cannot explain the significantly increased litter accumulation seen at 1–2 m. This may instead be related to surrounding vegetation cover, which can deposit litter, as well trap litter that is windblown and washed by surface water flow. Nutrient cycling through litter can be a powerful determinant of vegetation structure in dryland ecosystems ([Ehrenfeld et al., 2005](#); [Hysell and Grier, 1996](#)). If a facilitator shrub used in restoration can regulate and conserve nutrient cycling through litter, this is expected to strengthen the positive feedbacks that drive ‘island of fertility’ formation and maintenance ([King and Hobbs, 2006](#); [Ludwig and Tongway, 1996](#)).

A. secundiflora individuals were generally associated with a small increase in soil elevation within 25 cm of their base, and individuals with greater ground cover tended to be perched on higher pedestals of soil. These findings suggest that ground cover prevented erosion, probably by reducing surface water flow velocities and wind speed ([Ludwig et al., 2005](#); [Tongway and Ludwig, 1994](#)). *Maerua* shrubs also retained soil in their immediate vicinity, but pedestals were only about 3 cm high, and soil retention was not related to any above-ground plant measurements. It is therefore plausible that soil retention was affected by below-ground dynamics; root structure and active soil biota associated with roots can retard erosion by enhancing soil stability and by increasing water infiltration rates ([Whisenant et al., 1995](#); [Wilcox and Newman, 2005](#)).

Comparisons of the soil seed bank underneath and 2 m from *Aloe* foci showed a notable, but again localized, effect of *A. secundiflora* shrubs on resource retention. Of the thousands of seeds counted, there were only four *A. secundiflora* seeds, so the effect was not due to seed rain from the focal plant. The majority of seeds were *A. pungens*, indicating another possible mode of facilitation for this ruderal species. The true spatial extent of the enhanced soil seed bank associated with *Aloe* foci is still unclear, because soil samples were not collected around *Maerua* or shrubless foci for comparison. Nevertheless, the results indicate that seeds are accumulating under *A. secundiflora* shrubs, in microsites with ameliorated abiotic conditions, protection from herbivores, and reduced erosion, thereby creating an opportunity for seed bank effects to interact synergistically with other modes of facilitation, all of which can contribute to increased plant establishment in the vicinity of facilitators ([Franks, 2003](#)).

4.2. Using *A. secundiflora* in restoration

This study documented that *A. secundiflora* shrubs are associated with six different indicators of microenvironmental amelioration, some of which occur only within the canopy of *A. secundiflora*, whereas others occur up to 2 m away from the focal shrubs. These findings support the hypothesis that *A. secundiflora* shrubs are acting as facilitators, potentially through several or all of the mechanisms proposed under the ‘islands of fertility’ model. Because of the positive and crucial effects that facilitator shrubs can exert on

resource dynamics, they present an excellent potential tool for restoration of degraded semi-arid areas like those in Kenya.

A critically important question remains: is the facilitation effect serving to maintain small pockets of favorable conditions in the face of decades of intense grazing, or are the observed ‘islands of fertility’ dynamics actively improving environmental conditions and facilitating the establishment and success of new vegetation? While *A. secundiflora* shrubs may be doing both, the effectiveness of planting them as a restoration tool will depend on their ability to catalyze the formation of new ‘islands of fertility’ when planted into a degraded landscape. To answer that question, two experiments were conducted to study the effects of mature *A. secundiflora* shrubs transplanted into degraded areas. One study showed that over four growing seasons, *A. secundiflora* shrubs generated a successional response similar to that seen when grazing intensity was reduced (King, 2004). In the other experiment, *A. secundiflora* shrubs were planted adjacent to furrows sown with native grass seeds, and they facilitated grass seedling establishment and growth (King and Stanton, in press). Based on the findings of this study and the others cited above, there is now a strong body of research indicating that *A. secundiflora* is an appropriate candidate for use as a restoration tool.

These findings, which suggest links between plant characteristics and patterns of facilitation, provide useful guidelines for identifying potential facilitators in other dryland ecosystems. Plants that (1) are resistant to salient environmental stresses in an ecosystem, (2) have physical or ecological traits that ameliorate particular forms of stress or disturbance, and (3) are associated with increased vegetation in their vicinity, are likely candidates for use in restoration. However, further studies would still be necessary to determine whether they can catalyze new fertile island formation and whether their propagation and transplanting is logistically feasible.

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