

Facilitative Effects of *Aloe* Shrubs on Grass Establishment, Growth, and Reproduction in Degraded Kenyan Rangelands: Implications for Restoration

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Abstract

Under the harsh environmental conditions present in severely overgrazed, semiarid rangelands, facilitator plants offer a promising tool for ecological restoration. This study investigated facilitative effects of *Aloe secundiflora*—a native drought-tolerant, unpalatable, thorny shrub—on grass establishment in degraded rangelands in Kenya. We planted native perennial grass seeds adjacent to three neighbor treatments: transplanted mature aloe shrubs, piles of thorn branches that provided similar physical protection to aloes, and control treatments with no facilitator. We monitored grass performance for three growing seasons. During the first growing season, association with aloe shrubs significantly improved seedling survival and plant size of individual grasses, whereas grass survival in thorn treatments was intermediate between aloe and control

treatments. At the population level, aloe neighbor treatments were associated with the greatest grass abundance and cover in all three seasons and reproductive output in the second season. Control treatments were associated with the poorest grass performance for all three variables. The findings indicate that planting aloes can improve the effectiveness of grass reseeding for rangeland restoration, exceeding the benefits gained from the more common strategy of using thorn branch piles. The utility of aloes in particular is further enhanced by the economic value of these plants; medicinal sap can be sustainably harvested from aloes planted for restoration.

Key words: *Aloe secundiflora*, *Cenchrus ciliaris*, desertification, facilitation, Kenya, nurse-shrubs, overgrazing, positive interactions, rangeland restoration.

Introduction

Facilitation, the phenomenon by which one plant's presence positively affects the survival, growth, or success of other plants, has long been recognized as an important interaction in dryland vegetation (Muller 1953; Niering et al. 1963; Crawford & Gosz 1982; Flores & Jurado 2003). Facilitation is also emerging as a particularly relevant concept in rangeland restoration ecology. In stressful environments such as dry, overgrazed rangelands, augmenting populations of facilitator plants can locally ameliorate degraded abiotic and biotic conditions to accelerate the recovery of healthy ecosystem dynamics. This approach has been advocated by rangeland restorationists (Whisenant et al. 1995; Ludwig & Tongway 1996; Aronson et al. 2002; King & Hobbs 2006), and a growing number of empirical studies have successfully utilized facilitators in dryland restoration (Maestre et al. 2001; Tongway & Ludwig 2002; Maestre et al. 2003a; Singh et al. 2003; Anderson et al. 2004; Castro et al. 2004).

The existence of facilitative effects, however, does not necessarily lead to utility in restoration (Maestre et al. 2002, 2003b; Barchuk et al. 2005). Interactions between organisms are a complex web of both positive and negative effects (Callaway & Walker 1997; Bruno et al. 2003; Lortie et al. 2004). Thus, a facilitator's potential utility in restoration will depend on the various dynamics underlying facilitation (Padilla & Pugnaire 2006), such as the beneficiary's life history stages that are impacted (Foster 2002; Miriti 2006; Schiffers & Tielborger 2006), the performance traits that are improved (Sans et al. 2002; Castro et al. 2004; Maestre et al. 2005), the net effect of facilitation on a recovering beneficiary population (McPeck & Peckarsky 1998; Maestre et al. 2003a; Armas & Pugnaire 2005), and shifts in environmental conditions that affect the strength of facilitation (Tielborger & Kadmon 2000; Barchuk et al. 2005; Liancourt et al. 2005; Wipf et al. 2006).

A previous study in a heavily overgrazed Kenyan grassland found that naturally occurring *Aloe secundiflora* (Asphodelaceae) shrubs were associated with higher surrounding vegetation cover, plant species diversity, soil seed banks, and soil retention (King 2003). The present study sought to assess the utility of using facilitation by *A. secundiflora* shrubs in the restoration of a potential beneficiary grass species, *Cenchrus ciliaris*. We measured

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facilitative effects on several individual grass performance traits over three growing seasons and also examined aggregate population-level responses of grasses to facilitator treatments, all under typical environmental conditions in which actual restoration efforts would be undertaken.

This research was conducted in an applied context of particular significance because of the ecological severity and socioeconomic consequences of rangeland degradation in Kenyan drylands and because the putative facilitator itself is of social and economic importance. Over 75% of Kenya is arid and semiarid land, most of which supports traditional livestock husbandry (UNEP 1992). Kenya's population has quadrupled since independence in 1963 (Lahmeyer 2003); the concomitant increase in livestock has led to widespread rangeland degradation, compromising the livelihoods of hundreds of thousands of pastoralists (Swift 1988; Doyo 2003). Thus, there is a pressing need for environmental conservation and economic diversification (Hesse & Trench 2002). *Aloe secundiflora* offers great potential for dryland income generation because its medicinal sap and gel are economically valuable. A national program is underway to promote *A. secundiflora* production in Kenyan drylands. If *A. secundiflora* can facilitate grass recovery, rangeland rehabilitation can be simultaneously combined with sustainable sap production for a win-win combination of ecological and economic benefits.

Methods

Study Site

The study was performed at Koija Group Ranch, a 7,500-ha tract in north central Kenya (lat 00°33.6'N, long 36°54.0'E, 1,600 m elevation), which receives about 400 mm annual rainfall, concentrated in two rainy seasons. Since 1976, the human population has risen from 148 to 1052 Group Ranch members (Njenga 2001). Present livestock densities are estimated at 0.3 cattle and 2.4 goats and sheep per hectare (J. Mosiany 2004, Laikipia Wildlife Forum, personal communication). The intensified land use has led to greatly reduced herbaceous ground cover, large areas of bare ground, and substantial soil erosion. Trees, predominantly *Acacia tortilis* and *Ac. mellifera* (Mimosaceae), provided less than 10% canopy cover, and shrubs and large succulents provided about 10% cover. Herbaceous vegetation provided less than 10% cover and was distributed in clumped patterns, usually around a tree or shrub. Notably absent were several palatable perennial grass species that are common in nearby, less impacted areas, thus presumably extirpated locally due to overgrazing.

The experiment was established inside a fenced 4 ha compound, which had an average of 0.8 goats and sheep per hectare throughout the study (personal observations). At the onset of the experiment, the 25 × 5-m experimental site was a large bare patch within the compound, with less than 1% perennial vegetation cover, a cement-like

soil surface, a moderate slope (2.5% grade), and extensive sheet erosion.

Study Species

Aloe secundiflora is a long-lived perennial shrub, which has a protection-providing architecture of a single-domed rosette (0.2–1.2 m diameter) of sharply toothed leaves (King 2003). The shrubs are succulent, evergreen, extremely drought tolerant, and highly unpalatable to livestock. *Cenchrus ciliaris* is a perennial C₄ grass native in East African drylands. It forms dense, leafy tufts and spreads by rhizomes. *Cenchrus ciliaris* establishes easily, stabilizes soil, is drought and grazing tolerant, has high nutritional quality (Edwards & Bogdan 1951; van Oudtshoorn & van Wyk 2002), and has been used successfully for rangeland rehabilitation in Kenya (RAE Trust 2000). It is naturally occurring at Koija Group Ranch but had been extirpated within a 2 km vicinity of the experimental site, apparently due to overgrazing (personal observation).

Experimental Design

The experiment was installed on 23 April 2002, before the onset of seasonal rains. We delineated nine parallel rows, each 1.2 m long and 2.5 m apart, perpendicular to the general slope of the terrain. Along each row, we dug 21 holes, 14 cm diameter, 25 cm deep, spaced 20 cm apart. Each set of seven adjacent holes was randomly assigned a neighbor treatment: seven transplanted mature aloes, seven thorny *Acacia* branch piles anchored into holes, or seven refilled holes (referred to as "aloe," "thorn," and "control" treatments herein). Aloe treatments created a continuous strip of vegetation cover; thorn piles were constructed to be the same size and shape as aloe treatments. The thorn piles were included because they are commonly used for protective shelter in restoration (Ludwig & Tongway 1996; Whisenant 1999; Tongway & Ludwig 2002) and they offer a structural surrogate for a facilitator shrub without direct biotic interactions (Holzapfel & Mahall 1999; Gomez-Aparicio et al. 2005). To plant *C. ciliaris* seeds adjacent to the treatments, we dug 5-cm-deep furrows parallel to the rows, 10 cm uphill and 10 cm downhill from the treatment holes. Wire markers between adjacent treatments delineated "furrow segments." We spread preweighed 0.2000 g packets of approximately 900 *C. ciliaris* seeds (five packets counted: \bar{X} = 898, SD = 38) into each furrow segment and then covered the furrows with soil (Fig. 1). Seeds were acquired from a local rangeland rehabilitation organization.

Monitoring began with the onset of rains on 29 April 2002 (7 days after planting) and continued until 6 November 2003 (558 days after planting) through three complete growing seasons. The second and third growing seasons began 222 and 362 days after planting, respectively. The rainfall totals were 171, 196, and 331 mm during seasons 1, 2, and 3, respectively. During the first growing season, three measures of grass performance were taken for each furrow segment at evenly spaced census times: seedling

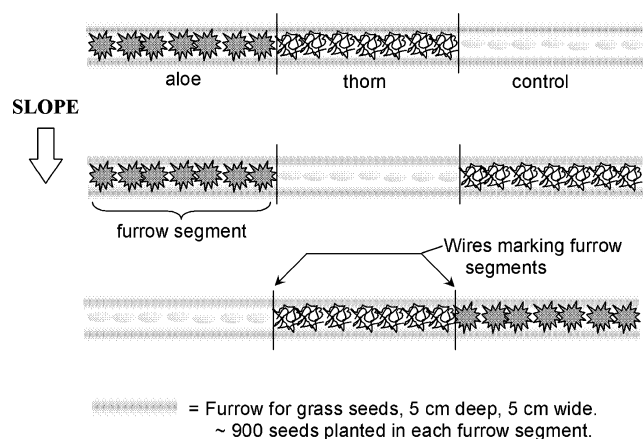


Figure 1. Schematic diagram of experiment, showing three of the nine total rows.

emergence (maximum number of seedlings counted during any census, divided by 900), longest stem length (base to leaf tip, measured on three marked seedlings), and seedling survival (relative to maximum seedling count). During the second and third growing seasons, no new *C. ciliaris* seedlings emerged. At regular intervals, four measurements of individual grass performance were taken for every *C. ciliaris* grass that survived from the first season: survival during that growing season, longest stem length, plant basal area (calculated from two perpendicular axes using the formula for an ellipse), and number of inflorescences. The total cover of *C. ciliaris* associated with each furrow segment was estimated at the beginning of the second and third seasons, using a 50 × 50-cm frame, divided into twenty-five 10 × 10-cm squares, placed over each furrow segment, with one side aligned with the neighbor treatments. *Cenchrus ciliaris* cover was visually estimated to the nearest 5% in each square and then averaged for all 25 squares.

Analysis

Treatment was the factor of primary interest. Uphill or downhill orientation of furrow segments was also included as a factor in the analyses. Rows were treated as random effect blocks. The resulting experimental design was a strip-plot (or split-block) design (Steel et al. 1997), with furrow segments as the experimental units for analyses. Row, row × treatment, and row × orientation terms were specified as random effects to generate the appropriate error terms for the strip-plot design, but effect tests were not produced (Littell et al. 1996). Because we were interested in identifying season-specific treatment effects, as well as within-season temporal patterns, we analyzed each growing season separately using repeated measures from within that season. For each growing season, longest stem length, basal area, and number of inflorescences were analyzed as univariate repeated-measures (RM) analyses of variance (ANOVAs) using the MIXED procedure of SAS

(SAS 2001). We used a three-stage protocol to analyze each response variable in each season (Littell et al. 1996; King 2004; Zhao et al. 2005). First, we performed sequential sum of squares (type I SS) RM ANOVAs with three different time-related terms: linear effect of time, quadratic effect of time, and time × treatment interaction. Temporal terms that were nonsignificant and decreased overall model goodness-of-fit were excluded. Second, we selected the best fitting model for covariance structure among repeated measures by performing orthogonal sum of squares (type III SS) ANOVAs, with each of five different plausible covariance structures, then comparing their goodness-of-fit (Akaike's Information Criterion) scores. The antedependence structure yielded the best depiction of actual covariance patterns for all the response variables, so was used in all RM ANOVAs. Third, we performed the final type III RM ANOVAs using the relevant time-related terms (from stage 1) and the best fitting covariance structure (from stage 2). King (2004) and Littell et al. (1996) provide complete procedures and statistical rationale for the procedures.

Seedling emergence in the first growing season was analyzed similarly, but no repeated measurements were involved. In the second and third seasons, longest stem length and basal area were log transformed and inflorescence number was square root transformed prior to analysis to meet assumptions of normality and homogeneity of variance. Rows with missing furrow segments weakened the reliability of statistical analyses, so in the second and third seasons, analyses used only rows with grasses in at least five of the six furrow segments (rows 2, 7, 8, and 9).

Seedling survival within each season was analyzed with logistic regression using the GENMOD procedure of SAS (SAS 2001). Instead of cumulative mortality through the entire experiment, this approach separately tested for effects on survival within each particular growing season. If cumulative survival had been analyzed, any differences in individual mortality during second and third seasons would have been confounded or obfuscated by treatment effects that occurred during the first season.

In the first growing season, we tested for effects of treatment and orientation at five census times. In the second and third growing seasons, logistic regressions were based on the number of plants surviving at the end of the growing season versus the number of plants present at the beginning of the growing season and did not involve repeated measures. Due to very low mortality in the second season, the GENMOD procedure could only parameterize a simplified model, containing just the treatment effect.

Throughout the analyses, if significant differences were found among treatments, we used pairwise comparisons to determine which treatments differed from one another. The *p* values were adjusted using the Tukey's method to maintain an experiment-wise error rate of $\alpha = 0.05$ (Sokal & Rohlf 1995; SAS Institute, Inc. 1996). No analyses showed significant main effects of orientation, but we

examined significant treatment \times orientation interactions using post hoc pairwise contrasts among treatment combinations with Tukey's experiment-wise error corrections.

To assess the population-level effects of treatments, we analyzed three aggregate responses of grasses in furrow segments: total number of *C. ciliaris* individuals per furrow segment, *C. ciliaris* cover around each furrow segment, and total number of *C. ciliaris* inflorescences per furrow segment. Unlike the individual-based measurements, these aggregate properties were calculated for every furrow segment, even those without surviving grasses. The data contained many zeros, so we used Mack–Skillings nonparametric tests to look for treatment effects. This rank-based test is similar to the more familiar Kruskal–Wallis test but is designed for randomized block designs with replication within treatment–block combinations. We calculated the test statistic MS using a spreadsheet following the procedure given by Hollander and Wolfe (1999). MS is approximately chi-square distributed with $(k \text{ treatments} - 1) = 2$ degrees of freedom (Hollander & Wolfe 1999).

Where relationships between different performance traits were of potential interest, we performed linear regressions on the transformed variables using PROC GLM of SAS (SAS 2001). Regressions utilized data from the peak census interval in each growing season: day 268 in season 2 and day 418 in season 3.

Results

Seedling Emergence

Cenchrus ciliaris seedling emergence was low, averaging 2.6% across treatments. Seedling emergence did not vary significantly among treatments (Table 1). No new seedlings were observed to emerge after the first growing season.

Survival

Over the course of the first growing season, *C. ciliaris* seedling survival varied significantly among treatments. At every census period, survivorship was greatest in the aloe treatment, lowest in the control treatment, and intermediate in the thorn treatment (Fig. 2a). When pairwise contrasts were performed, only aloe and control treatments differed significantly (adjusted $p < 0.001$). At the end of the first season, 16% of seedlings in the aloe treatment, 9% in the thorn treatments, and 6% in the control treatments had survived. Thereafter, within-season (as opposed to cumulative) survivals of *C. ciliaris* grasses during the second and third seasons were 98 and 90%, respectively, and did not differ among treatments (Fig. 2b & 2c, Table 1).

Plant Size

Treatment significantly affected seedling size in the first growing season; grasses adjacent to aloe treatments had

the longest mean stem lengths at each census during the first season (Fig. 3a). In pairwise comparisons, only the difference between aloe and control treatments was significant ($p = 0.026$). In the second season, *C. ciliaris* longest stem length tended to be greatest adjacent to aloes, smallest in control treatments, and intermediate in thorn treatments (Fig. 3b). As the effect of treatment on stem length was only marginally statistically significant ($p = 0.067$), we can neither safely accept nor reject the null hypothesis of no treatment effect. In the third season, there was no effect of treatment on stem lengths (Table 1). Stem length in the second season exhibited a significant treatment \times orientation interaction. But because treatment and orientation both had weak main effects on stem length, the meaningfulness of this interaction term is limited. Indeed, post hoc contrasts did not detect significant treatment combination differences.

The basal area of individual grasses did not vary significantly among treatments in the second season (Fig. 3d). In the third season, basal area tended to be smallest in the aloe treatments, but the statistical test was inconclusive ($p = 0.08$), and we could neither reject nor accept the null hypothesis (Fig. 3e). There was a treatment \times orientation interaction in the third season but without significant main effects. Post hoc contrasts were unable to identify meaningful trends that gave rise to the interaction.

To explore whether individual grasses exhibited trade-offs between leaf length and basal area, we regressed individual basal area against longest stem length (both variables natural log transformed) for the peak census in the second and third seasons, and a significant positive relationship was found in both seasons ($r^2 = 0.10$, $p = 0.005$ and $r^2 = 0.21$, $p < 0.0001$ in seasons 2 and 3, respectively). Regression slopes and intercepts did not differ among treatments in either season. Instead of a trade-off between growth variables, plants with larger basal areas also had longer stems, a trend that was not affected by treatments.

Reproduction

There was no significant difference in the number of inflorescences among treatments in the second or third growing season. Large plant-to-plant variance in inflorescence production within treatments resulted in particularly low statistical power in these analyses (Fig. 4). No significant post hoc contrasts were found to help explain the third season treatment \times orientation interaction (Table 1).

Temporal Trends Within Seasons

Most variables that were repeatedly measured within a season showed significant changes with time (Table 1)—usually an early-season increase followed by a late-season decrease. The exceptions were third season stem length and inflorescence number. The third season was marked by an atypical period of rainfall during the latter part of

Table 1. Statistical analyses of individual performance traits.

Effect	Emergence						Survival															
	First Season			Second Season			Second Season			Third Season												
	df	F	p	df	F	p	df	F	p	df	F	p										
				χ ²																		
Treatment	2,16	1.7	0.22	2	10.9	0.004	2	1.03	0.60	2	3.32	0.19										
Orientation	1,8	0.01	0.94	1	1.33	0.25				1	0.03	0.85										
Treatment × orientation	2,16	0.01	0.91																			
	<i>ln (Stem Length)</i>						<i>ln (Basal Area)</i>						<i>Sqrt (Inflorescences)</i>									
	First Season			Second Season			Third Season			Second Season			Third Season									
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p							
Treatment	2,16	4.24	0.033	2,6	4.37	0.07	2,6	2.66	0.15	2,6	3.75	0.09	2,6	0.97	0.43	2,6	2.43	0.17				
Orientation	1,8	1.09	0.33	1,3	6.07	0.09	1,3	1.65	0.29	1,3	2.66	0.22	1,3	1.04	0.38	1,3	2.87	0.19				
Treatment × orientation	2,16	1.14	0.35	2,6	5.17	0.050	2,6	1.44	0.31	2,6	17.5	0.003	2,6	1.94	0.44	2,6	6.22	0.034				
Time	1,254	457.6	< 0.001	1,134	0.24	0.63	1,87	3.71	0.06	1,112	3.50	0.06	1,86	13.2	0.001	1,90	28.82	< 0.001	1,82	0.83	0.36	
Time ²	1,254	49.49	< 0.001	1,134	146.9	< 0.001	1,112	34.05	< 0.001	1,112	34.05	< 0.001	1,86	5.04	0.027	1,90	74.72	< 0.001	1,82	1.98	0.17	
Time × treatment																				2,82	7.12	0.001

Seedling emergence was analyzed using mixed model ANOVA, and survival using logistic regression. All others used repeated-measures mixed model ANOVA, in which three time-related terms—linear effect, quadratic effect, time × treatment interaction—were first assessed using type I SS ANOVA. Nonsignificant terms that decreased model goodness-of-fit were excluded from the type III SS analyses reported here (see Methods). p Values in boldface denote statistically significant effects.

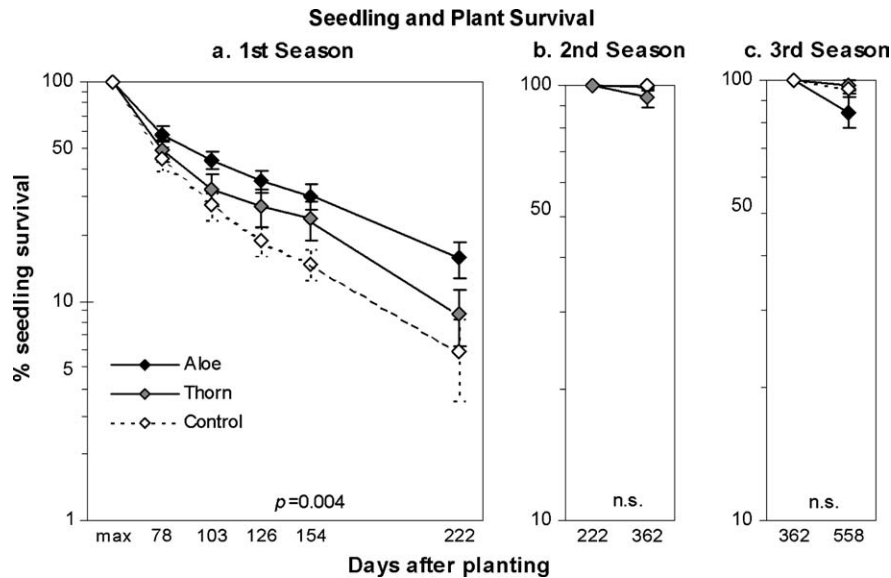


Figure 2. Percent survival of *Cenchrus ciliaris* seedlings planted adjacent to aloe, thorn, and control treatments. (a) First season, (b) second season, and (c) third season. Logistic regressions indicated significant variation in survivorship among treatments over the course of the first growing season but not during the second or third season. Graphs show mean percent survival \pm 1 SE, relative to the beginning of each growing season ($n = 18$ per treatment in season 1; $n = 8, 7,$ and 7 for aloe, thorn, and control treatments, respectively, in seasons 2 and 3).

the season, which could have disrupted the typical seasonal patterns of performance. Stem length showed two growth peaks in the third season. Inflorescence number in the third season showed erratic census-to-census shifts and high within-census variability, leaving no clear temporal trend.

In cases where treatment significantly affected a performance variable, the time \times treatment interaction indicated whether treatments differed in their pattern of seasonal change. With the exception of third season inflorescence number, time \times treatment interactions were never found to be significant. In the third season, inflorescence number varied erratically with time, and there was no significant main effect of treatments.

Aggregate Responses to Facilitator Treatments

To complement the individual-level assessments of grass establishment, growth, and reproduction described above, we assessed the effect of treatments on population-level variables calculated for whole furrow segments, including total number of grasses, grass cover, and total number of inflorescences per furrow segment. At the end of each growing season, there were significantly more grasses in furrow segments associated with aloe treatments than with thorn or control treatments (Fig. 5a). At the beginning of the second and third seasons, cover of *C. ciliaris* around aloe-associated furrow segments was greater than that around thorn and control treatments (Fig. 5b). The total number of inflorescences in furrow segments was greatest around aloe treatments and least around control treatments in both the second and the third seasons (Fig. 5c).

The variation among treatments was highly significant in the second season but not in the third season (Table 2).

We looked for evidence of intraspecific competition among grasses by regressing individual performance traits (leaf length, basal area, and number of inflorescences) against the number of grasses per furrow segment during the peak censuses in the second and third season. There were no correlations between any of the individual-based performance traits and grass density in either season ($r^2 < 0.10$ and $p > 0.15$ in all cases).

Discussion

In a previous study, *Aloe secundiflora* shrubs were observed to occur as foci of vegetation islands in degraded rangelands (King 2003), a pattern which could have arisen in one or both of the following ways: the shrubs may have protected small remnant patches of vegetation during decades of gradual vegetation degradation (Tongway & Ludwig 1994; O'Connor 1995; Bisigato & Bertiller 1997; Van de Koppel et al. 1997; Milchunas & Noy-Meir 2002; Gomez 2005) or they may actively catalyze the formation of vegetation islands by enhancing the recruitment and establishment of other plants in their immediate vicinity (Garner & Steinberger 1989; Ludwig & Tongway 1996; El-Bana et al. 2003; Visser et al. 2004). The ability of shrubs to facilitate the formation of new vegetation patches is an important criterion for their use in restoration.

We approached facilitation effects by studying multiple performance traits at different life history stages because numerous studies have found that positive effects on one performance trait can be counterbalanced by negative

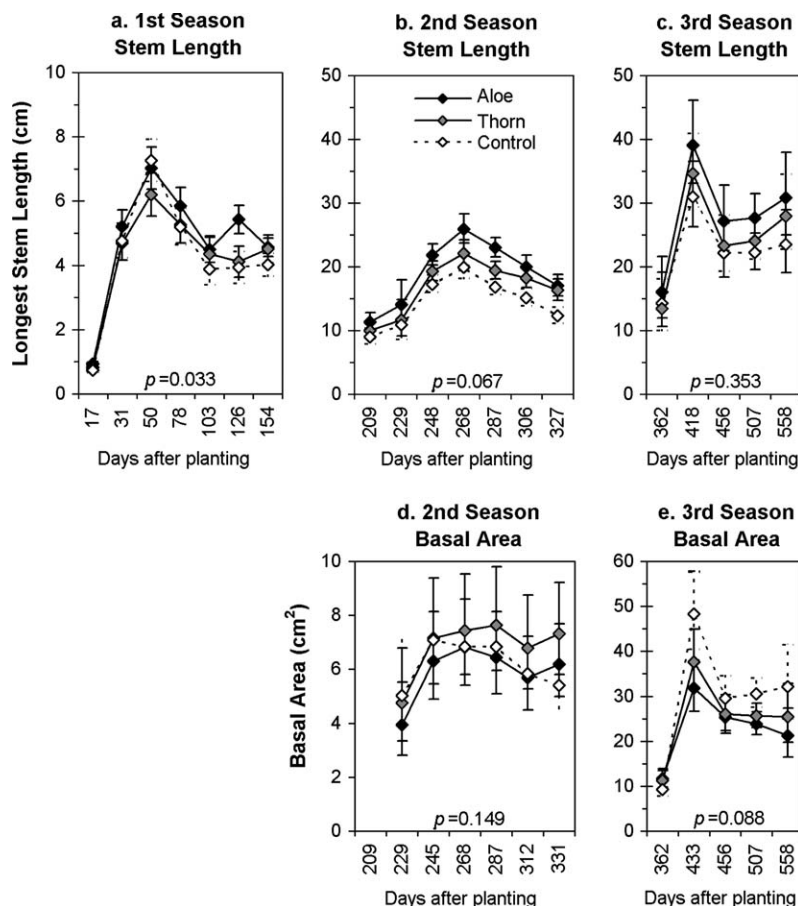


Figure 3. The longest stem length and basal area of *Cenchrus ciliaris* grasses adjacent to aloe, thorn, and control treatments. (a) First season, (b) second season, and (c) third season longest stem length. (d) Second and (e) third season basal area. Analyses for both variables in the second and third seasons were performed on natural log-transformed data. Graphs show least squares means \pm 1 SE, which were back transformed to the original measurement units for seasons 2 and 3. Aloe, thorn, and control treatments: $n = 18, 18,$ and $17,$ respectively, for first season; $n = 8, 7,$ and $7,$ respectively, in the second and third seasons.

effects on another. Alternatively, facilitation at one life history stage can switch to competition at another stage (Padilla & Pugnaire 2006). Indeed, the most salient finding in this study was trait and life history specific: seedling survival was the performance trait most strongly influenced by aloe treatments and only in the first season.

In contrast to other systems in which enhanced early survival is later counterbalanced by competition with the facilitator plant (Rousset & Lepart 2000; Gasque & Garcia-Fayos 2004; Miriti 2006), the effect of aloe treatments on all the performance traits measured was either positive or neutral during this three-season study. As a result, the enhanced first season survival around aloe treatments translated into greater grass abundance, cover, and reproductive output in subsequent seasons. In the context of restoration, the absence of neighbor treatment effects in the second and third seasons is encouraging. Once established, *Cenchrus ciliaris* grasses are able to survive, grow, and reproduce, regardless of facilitator presence. If *A. secundiflora* planting is to be used simultaneously for rangeland restoration and aloe sap production, we specu-

late that cutting aloe leaves will not compromise grass performance once the grasses have established.

Environmental conditions are a critical factor in the balance between facilitative and competitive interactions. Because Bertness and Callaway (1994) presented the hypothesis that facilitation should become more prevalent along gradients of environmental harshness, a vast body of research has emerged to explore how interactions vary with environmental conditions. Although the generality of the stress gradient hypothesis is still debated (e.g., Maestre et al. 2005, 2006; Lortie & Callaway 2006), there can be no doubt that shifts in environmental conditions can strongly impact the balance between facilitation and competition, within growing seasons (Holzapfel & Mahall 1999; Hastwell & Facelli 2003; Kikvidze et al. 2006), among years (Callaway 1998; Rousset & Lepart 2000; Gasque & Garcia-Fayos 2004; Miriti 2006), or both (Schiffers & Tielborger 2006). We observed distinct patterns of within-season and among-season rainfall, which could have affected the balance between facilitation and competition, but we were unable to detect effects in this study.

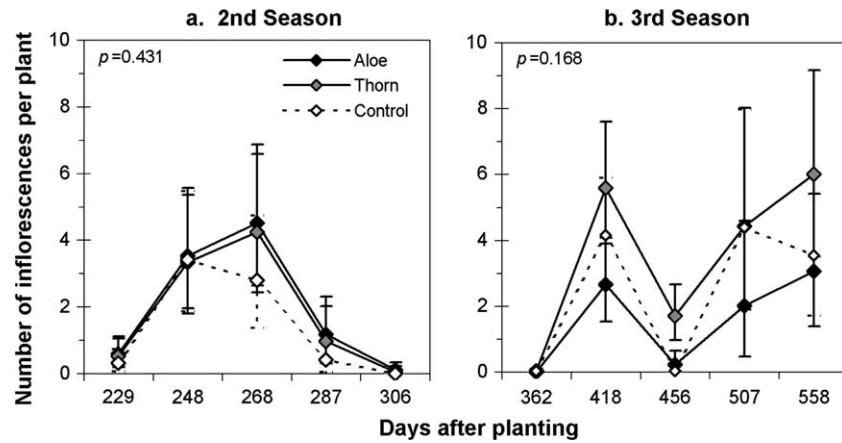


Figure 4. Number of inflorescences per plant on *Cenchrus ciliaris* grasses in aloe, thorn, and control treatments. (a) Second season and (b) third season. Analyses were performed on square root-transformed data. Graphs show back-transformed least squares means \pm 1 SE. At each time interval, $n = 8, 7,$ and 7 for aloe, thorn, and control treatments, respectively.

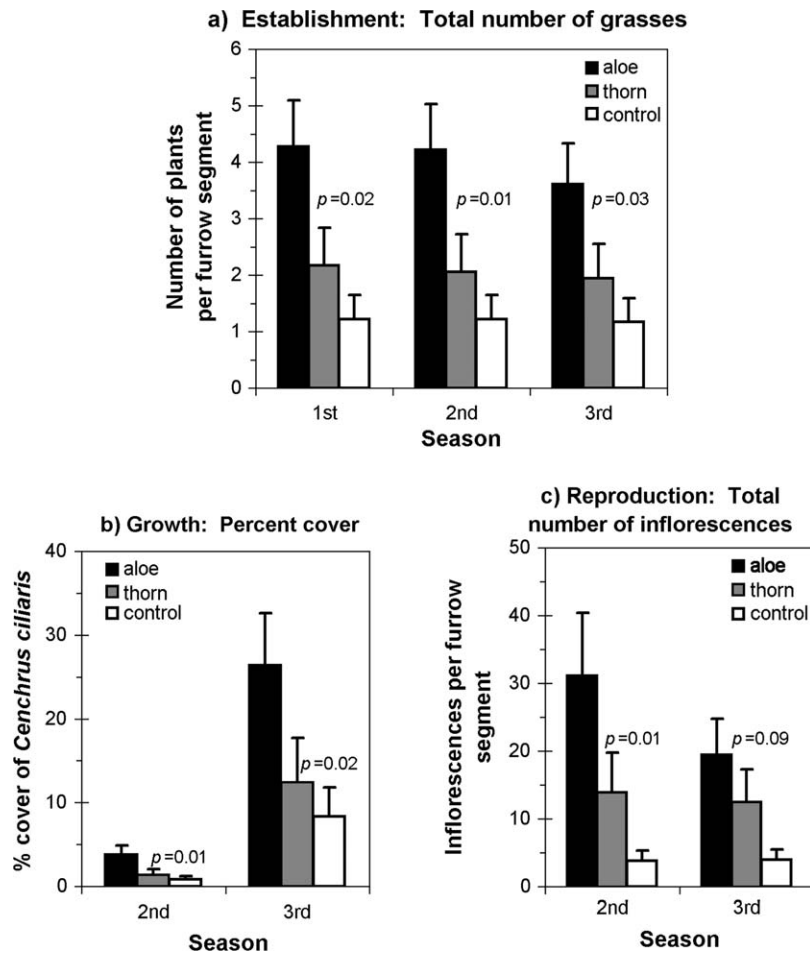


Figure 5. Aggregate measures of *Cenchrus ciliaris* performance, assessed per furrow segment: (a) establishment, (b) growth, and (c) reproduction. In contrast to the individual-based measures of grass performance, these measures represent the population-level response of grasses to facilitator treatments. Treatment means \pm 1 SE are plotted; $n = 18$ for each treatment. In each graph, p values are given for tests of treatment effect within each season.

Table 2. Effect of neighbor treatment on aggregate performance variables.

Effect: Treatment	Season 1		Season 2		Season 3	
	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
Aggregate response variable						
Number of grasses	8.27	0.018	9.63	0.009	7.20	0.027
Percent cover of <i>Cenchrus ciliaris</i>			9.39	0.009	8.27	0.018
Total inflorescences			9.77	0.008	4.82	0.090

Aggregate measures of *C. ciliaris* performance were assessed at the level of furrow segment and tested using the nonparametric, rank-based Mack-Skillings test for randomized block designs (see Methods). *p* Values in boldface denote statistically significant effects.

The inclusion of the thorn branch facilitator treatment did permit us to make some mechanistic inferences. Thorn branch piles offered a similar degree of physical protection from herbivores as the aloe treatments but provided substantially less shading and soil surface obstruction. During the first season, survivorship and plant size in thorn treatments were intermediate between the aloe and the control treatments. Thus, we hypothesize that the intermediate performance of grasses next to thorn treatments was due primarily to their provision of physical protection, whereas greater facilitation around aloe treatments could have arisen from a wide array of mechanisms in addition to physical protection.

King and Hobbs (2006) argued that using nurse-plants to stimulate vegetation patch formation can yield stronger and more diverse positive effects in rangeland restoration than abiotic or nonliving treatments. By improving soil structure, increasing water infiltration (Dunkerley 2000; Bhark & Small 2003), providing hydraulic lift (Ehrenfeld et al. 2005; Zou et al. 2005), increasing mycorrhizal abundance (Carrillo-Garcia et al. 1999), contributing to soil organic matter and nutrient cycling (Hysell & Grier 1996; Pugnaire et al. 1996; Ehrenfeld et al. 2005), and providing habitat for seed dispersers (Garner & Steinberger 1989; Vieira et al. 1994), shrubs can initiate a suite of biotic and abiotic feedback dynamics that can regulate resource dynamics in a restored vegetation patch, leading to "autogenic recovery" (Whisenant et al. 1995; Whisenant 1999; King & Hobbs 2006). We observed that even our small-scale experiment made a broader, self-perpetuating impact. Four seasons after establishing the experiment, we found 12 young *C. ciliaris* plants growing and flowering underneath shrubs around the experimental plots, some up to 50 m away. This indicates that the reproductive output from the experimental grasses may have provided enough propagules to initiate recovery of the locally extirpated *C. ciliaris* population in the surrounding heavily degraded area.

Using Aloes for Restoration

This study demonstrates the ability of transplanted aloes to enhance the success of a target beneficiary species for

rangeland rehabilitation. The use of aloes is motivated not only by their ecological merit but also because of their practicality. Identifying a native species that can facilitate the recovery of desired vegetation is ecologically ideal, but the practical considerations of propagation and transplanting can restrict the list of candidates. For instance, nitrogen-fixing, fodder-yielding leguminous shrubs and trees have well-documented facilitative effects (Ahmed 1986; Belsky et al. 1989; Kiyiapi 1994) but require watering and substantial protection from wild and domestic herbivores, especially when other vegetation is scarce. Aloes, on the other hand, are extremely hardy when transplanted, require no watering at all, and livestock are strongly deterred by their bitter sap.

The use of aloes in restoration is practical and economically beneficial, which can be as important as ecological effectiveness in determining whether a strategy is adopted and supported. The prospect of sustainable harvesting and sale of medicinally valuable aloe sap has generated local enthusiasm for new aloe enterprises and has spawned a national-level effort in Kenya to promote aloe propagation for sap and land rehabilitation (P. Kameri-Mbote, unpublished report). Environmental and economic pressures threaten the sustainability of rangelands and pastoralist societies not only in Kenya but also internationally. Use of *A. secundiflora* in restoration is a regionally targeted strategy, but we hope this study will encourage others to seek restoration solutions that can offer both ecological and economic benefits.

Implications for Practice

- Facilitators and nurse-plants are often important in dryland vegetation dynamics and are potentially useful tools for dryland restoration.
- Assessing multiple performance traits of beneficiary plants at both the individual and the population level can provide a deeper understanding of the interaction, as well as the potential consequences if used in restoration.
- By affecting early survivorship and plant size, *Aloe* shrubs encouraged higher abundance, density, and reproductive output in the target grasses around them.
- Identifying facilitators that are hardy and/or unpalatable adds practical feasibility to their use in restoration and using culturally or economically important species can stimulate further incentive for restoration.

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