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Effects of pioneer shrub species on the recruitment of a fleshy-fruited tree in a degraded Afromontane savanna

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Abstract

Question: Is seedling recruitment of a fleshy-fruited tree in degraded Afromontane savanna dependent on the shelter provided by pioneer shrubs, and is shelter ability related to shrub traits?

Location: Degraded montane savanna in northern Ethiopia (13° 36' N, 39° 21' E).

Method: Nurse plants of *Olea europaea* ssp. *cuspidata* seedlings were recorded using T-square plotless sampling and clustered according to shrub traits, using Ward's method after Principal Components Analysis. Facilitation was further examined through experimental planting and Kaplan-Meier survival analysis.

Results: Both in grazed and protected areas, *O. europaea* recruits were found exclusively under shrubs, primarily under *Euclea racemosa* although *Acacia etbaica* was more abundant. *Olea* recruitment is distributed randomly at landscape scale, but depends on shelter at patch scale. Shelter ability is related to shrub shape and species identity. Dense multi-stemmed shrubs with a wide base and crown on a mulch-rich mound are key recruitment foci. *Euclea* shrubs have these favoured traits and probably act as preferential perching sites for avian seed dispersers. Soil and organic matter accumulation under *Euclea* shrubs may also create favourable conditions for *Olea* germination and survival. Experimentally planted seedlings had a better chance for survival under *Euclea*.

Conclusions: *Olea* regeneration is probably subject to both passive (disperser-mediated) and active facilitation. Small changes of shrub traits can alter the suitability of a patch for *Olea* recruitment. Protection of shrubs can increase facilitation for seedlings, while pruning may reduce competition for saplings and thus enhance forest succession. Planting of raised *Olea* seedlings under *Euclea* shrubs in years with a good rainy season may further assist forest restoration.

Keywords: Ethiopia; *Euclea racemosa* ssp. *schimperi*; exclosure; facilitation; nurse plants; *Olea europaea* ssp. *cuspidata*; secondary succession; structural traits

Abbreviations: PCA = Principal Components Analysis; TSB = Byth robust T-square estimator

Nomenclature: Hedberg & Edwards (1989); Hedberg et al. (2003); Klopper et al. (2005)

Introduction

Early-successional species may alter the environment or the availability of resources in a habitat so that they favour the establishment of certain plant species (Holl 2002). This process, known as facilitation (Connell & Slatyer 1977), has been documented extensively in various ecological systems (Callaway 1995) and is a widespread phenomenon in arid and semiarid ecosystems (Franco-Pizaña et al. 1996; De Villiers et al. 2001).

The most commonly reported mechanisms of facilitation include passive facilitation, where some plants attract seed dispersers resulting in an accumulation of seeds under the plant (e.g. Duncan & Chapman 1999; Rey & Alcántara 2000; Holl 2002; Verdú & García-Fayos 2003) and active facilitation where nurse plants (Franco & Nobel 1989) cause reduction of dormancy (Franco-Pizaña et al. 1996), increase fertility or soil moisture (e.g. Pugnaire et al. 1996; Moro et al. 1997; Whitford et al. 1997; Verdú & García-Fayos 2003) or offer protection against high irradiance, temperature or predation (e.g. Valiente-Banuet & Ezcurra 1991; Vetaas 1992; García & Obeso 2003).

Shrub species often rapidly invade disturbed lands and abandoned pastures or cropland. The establishment of impenetrable thickets by invasive woody plants, or bush encroachment, for example, is a well-described rangeland degradation process (for Africa see e.g. Van Vegten 1984; Benshahar 1991; Skarpe 1991; Holmes & Cowling 1997). But in terms of forest succession, little is known about whether pioneer shrubs facilitate, tolerate or inhibit subsequent tree recruitment and growth (Holl 2002; Duncan & Chapman 2003). Under high abiotic stress, resource limitation may induce a shift from facilitation to competition (Maestre & Cortina 2004; Maestre et al. 2005), but in the restoration process of mountainous areas and degraded semiarid ecosystems, facilitation has been documented to play a fundamental role (Maestre et al. 2001; Callaway et al. 2002; Maestre et al. 2003; Castro et al. 2004).

In northern Ethiopia, impoverishment of the steadily expanding human population and their search for subsistence income has led to massive deforestation, site degradation and soil erosion since 1700 CE (Darbyshire et al. 2003). As a result, recurrent droughts severely impacted the agricultural production and the environment (Nyssen et al. 2004). Recent revegetation efforts are primarily focused on region-wide establishment of protected areas (Plate 1), where free grazing and cutting are no longer permitted and vegetation is allowed to regenerate naturally (Mengistu et al. 2005). In this context, the identification of facilitation mechanisms has proved to be useful for local management of threatened and ecologically as well as economically important plants, since their population viability is often determined by the ability of nurse plants to provide suitable microhabitats for their recruitment and establishment (García & Obeso 2003).

The objective of this study was to test the hypothesis that seedling recruitment and survival of the threatened *Olea europaea* ssp. *cuspidata* (African wild olive) is dependent on the shelter provided by pioneer shrub species (nurse-plant hypothesis). Given that *O. europaea* is a bird-dispersed tree (Rey & Alcántara 2000) and that protected areas are in principle less subject to herbivory and degradation, we hypothesized that the number of *O. europaea* seedlings should be greater (1) in protected areas than in grazing land; (2) beneath pioneer shrubs than in interspaces between shrubs, in particular beneath fleshy-fruited shrubs due to disperser-mediated facilitation; and (3) beneath dense or spiny shrubs in grazed areas due to herbivore-mediated recruitment limitation under less dense or unarmed shrubs.

[Insert Plate 1 (photograph); may be included as a digital appendix only]

Methods

Study site

The study was conducted near the villages of Mheni (13° 36’ N, 39° 21’ E) and Sesemat (13° 37’ N, 39° 19’ E), located 20 km NW of Mekelle (Central Tigray, Ethiopia) at 1860-1940 m a.s.l. The climate of the study area is determined by its mountainous nature and falls within the Sudanese zone with a mean annual temperature of 18 °C and mean annual precipitation of 625 mm (Meze-Hausken 2004), most of which occurs during the summer rainy season (July-September). The winter is hot and dry due to the winds received from the Sahara (Nyssen et al. 2004).

The study sites were located in grazing land and exclosures protected since 1996 (Plate 1) on SW and NE facing slopes over Mesozoic limestone. The soil (Verti-Skeletic Cambisol) is shallow (45 cm) with moderate rock outcrop and high calcium carbonate content. The forest relics around the churches of Mheni and Sesemat are tiny fragments of secondary dry Afromontane forest, respectively *Acacia*-*Olea* (21 ha) and *Combretum*-*Olea* (12 ha) communities, and serve as seed sources for the area under study. Both grazing land and protected area are characterized by a discontinuous cover of shrubs and small regenerating trees in a matrix of herbaceous species and bare soil. The vegetation can thus be defined as semiarid degraded savanna (Vetaas 1992; De Villiers et al. 2001).

Species description

Olea europaea ssp. *cuspidata* (Oleaceae) is a sclerophyllous tree with a heavy branched and rounded crown. It grows to 5-15-(25) m tall and is widely distributed as relic tree and in Afromontane forests, particularly in drier highland forests in association with *Juniperus procera*, forest margins, riverine forests and evergreen montane scrub from 1250 to 3000 m a.s.l. in Sudan, Somalia and south through East tropical Africa to South Africa. The 5-7 mm long ovoid-ellipsoid fleshy drupes are green and dark purple-black when ripe (Green 2003) and are dispersed in the main rainy season (Teketay & Granström 1997), primarily by frugivorous birds. In undisturbed forest, germination results in populations of shade-tolerant and slowly growing seedlings (Teketay & Granström 1997), but regeneration has not yet been documented in protected areas or grazing land. Once established, the tree is hardy and drought resistant, but because of its multiple uses (e.g. durable timber, traditional ox-ploughs, firewood, charcoal and toothbrushes) both young and mature trees have been over-harvested dramatically in Ethiopia (Negash 2003).

Data collection and analysis

Recruitment of *O. europaea* was assessed along transects in August-November 2002 at the end of the summer rainy season. The main dataset was collected in Mheni. Two transects were laid out in areas with relatively low grazing pressure: one transect in a protected area (P), where grazing and cutting has been banned since 1996, and one transect in a semi-protected area (SP), where grazing is only permitted during the dry season. Both P and SP were characterized by a high grass and herb cover during the rainy season. Three transects were laid out in a patchy landscape of bushy and degraded grazing land (GL), where free grazing and browsing by cattle and goats is allowed. These two groups represent extremes on a grazing intensity gradient: overgrazed areas (GL) versus set-aside areas and sustainable grazing land (P-SP).

The woody species composition of the study area was assessed in 11 10×10 m^2 plots laid out around randomly chosen transect points in P-SP (n = 4) and GL (n = 7). The Mann-Whitney test was used to test for differences on shrub species abundance between land uses and the Wilcoxon signed ranks test for pairwise comparison of relative species abundances.

At equal intervals along the transects (50 m), T-square plotless sampling (T^2; see Engeman et al. 1994) was applied to sample *O. europaea* recruits and their nurse plants (Fig. 1). Plotless sampling was used as the primary measurement because *O. europaea* recruits were assumed to be distributed so sparsely that conventional quadrat sampling was inappropriate. 43 transect points were used (n = 10 [P]; 10 [SP]; 23 [GL]). Grazing land was sampled more intensively because of an expected higher number of missing nearest-neighbour seedlings in severely degraded areas (NN, Fig. 1), but in contradiction to expectations, more NN seedlings were missing in the (semi-)protected areas. Altogether, 13 transect points in P-SP and 21 in GL could be used for T^2 density estimation. Byth Robust T^2 plotless density estimates (TSB, Eq. 1) of *O. europaea* recruits and T^2 t values (Eq. 2) were calculated from random subsets of T^2 sample points, using 100 Monte-Carlo permutations per land use and per sample size, ranging from 5 up to 10 points. The Mann-Whitney test was used to test for differences in seedling densities between the two land uses. The TSB t-test (Sutherland 1996) was used to detect the spatial pattern of recruits in the landscape (± 25 km²), whereas all other analyses were carried out at patch scale (< 10 m²).

$$D_{TSB} = \frac{n^2}{\left[2\sqrt{2}\sum_{i=1}^{n} R_{(1)i} \sum_{i=1}^{n} T_i\right]} \qquad \text{(Eq. 1)}$$

$$t = \left(\sum_{i=1}^{n}\left(\frac{R_{(1)i}^2}{\left(R_{(1)i}^2 + \frac{T_i^2}{2}\right)}\right) - \frac{n}{2}\right) \cdot \sqrt{\frac{12}{n}} \qquad \text{(Eq. 2)}$$

where [ ] denotes the greatest integer function (for symbols see Fig. 1)

(Insert Fig. 1, 1 col.)

At each transect point, the shrub located the nearest to that point was added to the dataset to provide data of random shrubs, independent of *O. europaea* recruitment (point-to-individual plotless sampling). For all sampled shrubs (nurse plants and random shrubs), 17 shrub traits and eight environmental variables were measured (Appendix 1). Browsing damage, position in relation to the shrub centre and height of recruits were recorded.

The Fisher exact probability test was used to determine whether the land use groups GL and P-SP had different nurse plant proportions. Non-parametric binomial tests were carried out to test the randomness of recruit allocation among nurse plants, using mean observed shrub proportions as the test proportions. Randomness is assumed when nurse plant proportions are not significantly different from observed shrub proportions. Departure from random allocation of recruits among nurse plants would indicate species preference. Further binomial tests using decreasing test proportions were applied to estimate the most likely proportions in the nurse plant pool.

Trait differences between shrubs were evaluated by means of Principal Component Analysis (PCA) and Spearman's rank correlation. Ward's cluster analysis method was applied on standardized PCA I and PCA II scores to identify shrub types based on the essential variance in the dataset. The association between shrub traits and seedling height was analyzed by means of Spearman's rank correlation. The relationships between land use and nurse plant species and the proportions of grazed and ungrazed seedlings were analyzed using the Fisher exact probability test.

T^2 sampling was used to record *Olea* seedlings and nurse plants along three validation transects in Sesemat: one in a protected area (three transect points) and two in grazing land (six transect points).

Seedlings of *Olea europaea* were planted during spring and summer rains in 2003 in three microhabitats: under *Acacia etbaica* shrubs, under *Euclea racemosa* shrubs and in open patches. Seedling survival was monitored until the end of the main winter drought (February 2004). Experimental planting was carried out in the protected areas of Mheni and Sesemat, and in one additional protected area, Bubu Hills (13°30' N, 39°29'E), which was selected for its vicinity to Mekelle and easy access for follow-up. Planting points were distributed randomly in two areas (plots) of circa 400 m^2 per site. In each plot, five seedlings were planted per treatment (microhabitat) in 15–20 cm deep and 20–25 cm wide planting holes. Spring rain planting was carried out in Mheni and Bubu Hills (60 seedlings: 2 sites × 2 plots × 3 treatments × 5 seedlings; 17 April–19 May 2003); summer rain planting was carried out in Sesemat, Mheni and Bubu Hills (90 seedlings: 3 sites × 2 plots × 3 treatments × 5 seedlings; 9 July–19 August 2003). The effect of patch type on *O. europaea* survival was examined using Kaplan-Meier survival analysis and the Breslow test statistic for significance of survival functions (Altman & Bland 1998; Bland & Altman 1998).

Analyses were performed using SPSS 11.0 and 12.0 for Windows (SPSS Inc., Chicago, IL).

Results

Shrub composition across land uses

Rank-abundance curves of all plots (Fig. 2) followed geometric series (sensu Gray 1987) indicating strong dominance of one or few species (Hubbell 2001). Pairwise comparison of relative shrub abundance between species confirmed that *Acacia etbaica* was proportionally more numerous in all samples (Wilcoxon z = -2.934, p = 0.003). Overall relative density of *A. etbaica* amounted to 47.8 % compared to only 15.5 % for *Aloe macrocarpa* and 10.2 % for *Euclea racemosa* ssp. *schimperi*. *Acacia etbaica* and *Aloe macrocarpa* were significantly more abundant in grazing land, which may be attributed to overgrazing (Table 1).

(Insert Table 1)

(Insert Fig. 2 page wide)

Olea europaea recruitment

Recruit densities were low, ranging between five and 17 recruits·ha^{-1} (Fig. 3). There were significantly less seedlings in the (semi-)protected areas than in grazing land (p < 0.001; Table

2). Recruits were neither regularly spaced, nor clustered: they had a random spatial pattern in the landscape in both land use groups (Table 2).

(Insert Table 2)

(Insert Fig. 3)

Conversely, *O. europaea* recruits were not distributed randomly at the patch scale. Not a single seedling was found in the open field. The majority of recruits was found under *E. racemosa* and the rest under the dominant shrub *A. etbaica*, apart from three exceptions under *Aloe macrocarpa* in the grazing land. There was no significant association between nurse plant proportions and land use (Fisher p = 0.558). Within the pool of sampled *Euclea* and *Acacia* nurse plants (n = 67), the proportions of *A. etbaica* were significantly lower than the test proportions (Table 3), indicating non-randomness of recruit allocation and thus, a preference for *E. racemosa*. Although *A. etbaica* was more abundant in the studied field sites (Table 1), *Olea* nurse plants were more likely to be *E. racemosa* shrubs. In a random sample of *Olea* recruits, between 68 and 85% are expected to be found under *E. racemosa*, with a maximum probability for 77% (p = 0.55). There was only a slight bias towards female plants in the *Euclea* pool (p > 0.05 for the proportions between 46 and 70%). These results were corroborated by the 16 seedlings sampled in the three validation transects in Sesemat: 13 seedlings (81%) were located under *E. racemosa*, and only three under other nurse shrubs (*A. etbaica*, *Dodonaea viscosa* var. *angustifolia* and *Dichrostachys cinerea*).

Shrub traits

There was a high degree of intercorrelation among the shrub traits, which can be explained by the many mutual interactions between the various size variables of the shrubs (size relationships). Fig. 4 gives the ordination of the sampled shrubs along the first two principal axes of the PCA; the first two principal components explained 42 % of the initial variance in the dataset.

(Insert Fig. 4; page wide)

The axis I of the PCA represented a set of intercorrelated traits that distinguished shrubs based on their number of stems, diameter at ground level, crown density, thorns and mulch characteristics under the shrub. *Euclea racemosa* shrubs (positive side) were separated from *A. etbaica* (negative side) (30.8 % of the total variance). The axis II of the PCA could be interpreted as the shrub height component. Shrubs lower than the surrounding vegetation were found on the negative side of the axis. Larger shrubs were found in the mid-range and tree forms (high shrubs with crowns starting relatively high above ground level) at the upper positive side of the axis.

Seven shrub types (Fig. 5) were identified by means of Ward's cluster analysis method (Fig. 4). The structural variety in the nurse plant pool was high for *E. racemosa* shrubs (four types), but low for *A. etbaica* (only one type). Shrub traits related to PCA II clearly restrict the shelter ability of *A. etbaica* compared to *E. racemosa*.

(Insert Fig. 5; page wide)

The majority of all sampled recruits (70 %) was found nearer to the shrub centre than to the nurse plant crown perimeter (Fig. 5). Shrubs did not offer adequate protection against ungulates, since 71 % of the recruits showed visible damage by grazing or browsing. The Fisher exact probability test determined that grazed and (semi-) protected areas did not differ significantly in the proportion of grazed and ungrazed seedlings sampled in them (p = 0.183), and over both land uses, neither did *Acacia* and *Euclea* shrubs (p = 0.121). Seedling height was significantly correlated to the lower crown density (r_s = 0.357, p = 0.003), but against expectation, not to the relative thorniness of the nurse plant (r_s = -0.010, p = 0.934).

Experimental planting

Six months after planting, the overall mortality rate was 89.3 % for the seedlings planted during the spring rains. The highest mortality rates occurred during the first three months (Fig. 6a), which contained substantial dry periods prior to the onset of the summer rains. For the seedlings planted during the main summer rains, the overall mortality rate was 54.9% six months after planting, excluding 19 seedlings that were lost due to human disturbance. In contrast to spring rain planting, almost no mortality occurred during the first three months (Fig. 6b). Four months after planting, mortality under shrub cover was <10%, while already 30% of all seedlings in the bare interspaces had died. Since seedlings dried out without any visible damage, drought was considered the main cause of mortality in both planting seasons.

The microhabitat had a significant effect on seedling survival in both planting seasons (Table 4). The contrast between *Euclea* and open patches was significant in either season, while the contrast between *Acacia* and open interspaces was only significant in the summer planting season. Within-plot data analysis showed that the differences of mean survival times between microhabitats and the levels of significance for these differences were highly variable and plot-dependent, but the patterns of variation among microhabitats were similar for most plots in both seasons, with the longest survival times under *Euclea*, generally followed by *Acacia*. Mortality was higher and occurred sooner in the open interspaces (Fig. 6a,b).

[Insert Table 4]

[Insert Fig. 6a,b]

Discussion

Although natural regeneration of *O. europaea* was rather sparse, presence of recruits in both grazing land and (semi-)protected areas demonstrates a potential for forest rehabilitation using natural regeneration. Unexpectedly, recruit densities were lower in the less disturbed land use types, protected area and reserve grazing land. In recently protected areas, grasses and weedy annuals dominate the vegetation during the rainy season, when *O. europaea* seeds are dispersed (Teketay & Granström 1997). Grass tussocks have been documented to facilitate shrub establishment in semiarid degraded steppes (Maestre et al. 2001), but high grass cover has also been described as a selective barrier on colonizing woody species, inhibiting the establishment of forest (Aide et al. 1995; Posada et al. 2000).

Our results agreed with the prediction that more seedlings of *O. europaea* occur beneath canopies of pioneer shrubs than in open patches. In addition, we found evidence that nurse plant shape was coupled strongly with shrub species identity. Dense multi-stemmed shrubs with a wide base and crown on a mulch-rich mound offer the key recruitment foci. Interestingly, this shape results from frequent cutting of shrubs, an observation similar to the one of García & Obeso (2003) in NW Spain, where cone-shaped nurse plants with branches at their bases resulted from heavy browsing. *Euclea racemosa*, a dioecious, sclerophyllous-evergreen, fleshy-fruited shrub, corresponds best to these characteristics, and is more suitable over a wider range of certain shrub traits (shrub height, crown height and relative shrub height) than *A. etbaica* (Fig. 5). Since *O. europaea* recruitment was only marginally greater under female *E. racemosa* shrubs, shrub configuration and suitability as a bird perch appear to matter more than the presence of a fruit reward. Female-biased spatial associations with the nurse plants have been described in the Mediterranean mountains (e.g. Verdú & García-Fayos 2003) and rejected in coastal vegetation in Brazil (e.g. Liebig et al. 2001). In this case, seed dispersers may have become familiar with *E. racemosa* while feeding and as a result use males or females during periods when they are not fruiting too, a behaviour pattern of seed vectors observed on *Ficus* and *Cecropia* in Costa Rica (Slocum & Horvitz 2000).

A high grazing and browsing pressure in the non-protected areas could explain the absence of recruits in the interspaces between shrubs, but interestingly, in the protected areas where ungulate herbivory is principally absent, *O. europaea* recruits were also restricted to microhabitats under shrubs. Herbivory by domestic livestock is therefore not likely to be the prime factor that controls the spatial pattern of recruits. The relative importance of mulch and crown density –and not thorniness– suggests that active facilitation in the germination and seedling stage is more important: harsh conditions in the interspaces between shrubs or under less protective crowns may prevent seed germination or limit seedling survival due to excessive irradiation and evaporation (Verdú & García-Fayos 2003), especially for shade-tolerant species such as *O. europaea*. This may also explain the higher survival probabilities of seedlings planted under shrubs compared to those planted in the open field (see also Castro et al. 2004; Gómez-Aparicio et al. 2004).

Directed dispersal of seeds by birds often gives rise to clumped regeneration patterns or nucleation (Verdú & García-Fayos 1996; Stiles 2000; Willson & Traveset 2000). In very few samples more than one recruit was found under the same nurse plant. Complementary research indicated low post-dispersal seed predation rates (R. Aerts, unpubl. data) and marginal effects of secondary dispersal by runoff on artificial seed rain (Aerts et al. 2006). The current absence of nucleation in our study, therefore, suggests seed limitation (seed production at population level is insufficient to saturate available safe sites), quantitatively or distance-restricted seed dispersal (insufficient disperser activity), establishment limitation (biotic and abiotic factors limit establishment of new individuals) or a combination of these factors (Jordano & Godoy 2002).

Dependence on animals for seed transport means that the plants are susceptible to dispersal failure when their seed vectors become rare or extinct (Willson & Traveset 2000). Small-fruited, vertebrate dispersed species such as *O. europaea* tend to have many dispersal agents, and the loss of one vector species may have minor consequences for plant population biology (Willson & Traveset 2000). However, if the already rare forest fragments continue to be reduced, not only the seed source but also many dispersers will be lost and there will be potentially severe consequences for tree species regeneration and ultimately survival. Natural regeneration strategies should provide adequate protective measures for both source (remaining forest fragments) and target areas (protected areas) as well as for the seed disperser population (in the case of *Olea*, frugivorous birds).

Small changes of shrub traits can alter the suitability of the patch for *O. europaea* recruitment (Fig. 5). Protection and creation of suitable patches may therefore significantly increase facilitation for *O. europaea* seedlings and enhance forest succession. Although several *O. europaea* saplings originating from rootstock shoots managed to break through the crowns of their nurse plants in the study area (R. Aerts, pers. obs.), further research on successional mechanisms operating during later stages of establishment is needed. Shrub manipulations to reduce competition for saplings need special attention in the future, especially since other species of the *Euclea* genus (*E. divinorum*, *E. natalensis*, *E. undulata*) have been classified as invasive weeds responsible for bush encroachment in the past (Benshahar 1991). Nevertheless, planting of rooted cuttings (Negash 2003) or nursery-raised *O. europaea* seedlings under *Euclea* shrubs should be encouraged in years with a good summer rainy season to assist forest restoration.

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Table 1. Shrub composition and abundance (mean ± SE; ha^{-1}) in (semi-)protected areas (P-SP) and degraded grazing land (GL) in Mheni, Ethiopia.

Species	P-SP [1] n = 4	GL n = 7	U [2]	p
Acacia etbaica	925 ± 239	2157 ± 297	1.50	0.018
Aloe macrocarpa	175 ± 85	771 ± 163	1.00	0.013
Capparis tomentosa	75 ± 48	-	-	-
Carissa edulis	100 ± 71	-	-	-
Euclea racemosa	300 ± 71	400 ± 138	12.50	0.771
Jasminum abyssinicum	50 ± 29	-	-	-
Leucas abyssinica	325 ± 189	314 ± 94	13.0	0.847
Maytenus senegalensis	-	43 ± 20	-	-
Rhus natalensis	50 ± 29	29 ± 18	11.0	0.498
Senna singueana	150 ± 65	43 ± 43	6.50	0.100

[1] In the protected area, *Acacia saligna* and *Dodonaea viscosa* were planted at 300 and 500 stems·ha^{-1}. *Olea europaea*, *Combretum collinum*, *Clerodendron myricoides* and *Psiadia punctulata* were each recorded in only one plot in the (semi-)protected area. [2] Mann-Whitney U for differences between groups.

Table 2. Plotless density estimation of *Olea europaea* recruitment (ha^{-1}) in Mheni, Ethiopia.

Land use	D_{TSB} [1]	t	Spatial pattern [2]
Grazing land (GL)	16.04 ± 0.64	0.83 ± 0.09	Random pattern
(Semi-)protected area (P-SP)	4.76 ± 0.14	-0.31 ± 0.11	Random pattern

Contrast	Mann-Whitney U	p
GL – P-SP	28.0	< 0.001

[1] Robust Byth T² estimator (see Engeman et al. 1994). Values are means ± SE (ha^{-1}) of 100 densities calculated from random subsets of 5 T² sample points from a total of 13 points in P-SP and 21 points in GL. [2] TSB t-test for randomness of distribution: $t < -1.96$: clustered pattern; $-1.96 \le t \le 1.96$: random pattern; $t > 1.96$: regular pattern (Sutherland 1996).

Table 3. Observed proportions of *Acacia* and *Euclea* in the pool of sampled *Olea* nurse plants (n = 67) in Mheni, Ethiopia, and non-parametric binomial tests to determine departure from random allocation of recruits.

			Proportion		
Land use	Nurse shrub	n	Observed	Test	p [1]
Grazing land (GL)	*Acacia*	10	0.26	0.84	<0.001
	Euclea	29	0.74		
	Total	39	1.00		
(Semi-)protected area (P-SP)	*Acacia*	5	0.18	0.76	<0.001
	Euclea	23	0.82		
	Total	28	1.00		
Overall (GL and P-SP)	*Acacia*	15	0.22	0.82	<0.001
	Euclea	52	0.78		
	Total	67	1.00		

[1] The test proportions are the mean observed proportions *Acacia*/(*Acacia*+*Euclea*) recorded in random sample plots (Table 1). A significance $p < 0.05$ supports the alternative hypothesis H_1 that the proportion of *Acacia* shrubs is lower than the test proportion and thus that there is an asymmetry towards *Euclea* shrubs among nurse plants.

Table 4. Differences in survival for *Olea europaea* seedlings planted in three microhabitats during spring and summer rains in protected areas in northern Ethiopia, obtained from Kaplan-Meier survival analysis.

	Spring rains (n = 60)		Summer rains (n = 90)	
	BS [1]	p	BS [1]	p
Full model (PLOT × TREATMENT)	7.73	0.02	9.98	0.01
Contrasts in survival time between microhabitats (TREATMENTS adjusted for PLOT)				
Euclea cover <> *Acacia* cover	2.53	0.11	0.70	0.40
Euclea cover > Open patch	6.31	0.01	7.75	0.01
Acacia cover > Open patch	2.53	0.11	4.80	0.03

[1] BS = Breslow statistic for differences between groups in Kaplan-Meier survival analysis.

Appendix 1. Shrub traits and environmental variables measured for random shrubs and nurse plants of *O. europaea* in Mheni, Ethiopia.

Structural variables	Method	Unit/Range
Main species	identification	–
Shrub height	measurement	m
Number of stems	count	–
Lower crown height	measurement (from base to start of crown)	m
Broadest crown height	measurement (from base to broadest point)	m
Diameter at ground level	average of 2 perpendicular measurements	m
Crown diameter	average of 2 perpendicular measurements	m
Lower shrub density	visual estimation of shrub density in lowest 1/3 of the shrub	1 (open) – 2 – 3 (medium) – 4 – 5 (very dense)
Middle shrub density	visual estimation of shrub density in central 1/3 of the shrub	1 (open) – 2 – 3 (medium) – 4 – 5 (very dense)
Upper shrub density	visual estimation of shrub density in upper 1/3 of the shrub	1 (open) – 2 – 3 (medium) – 4 – 5 (very dense)
Degree of thorniness	visual estimation of the proportion of branches with thorns or spikes (in 20% classes)	0 (0%) – 1 – 2 – 3 – 4 – 5 (100%)
Presence of raptor perch	presence of a high branch offering wide view for birds of prey	0 (none) – 1
Human disturbance	visual evidence of cutting	0 (none) – 1
Disturbance by livestock	visual evidence of grazing/browsing	0 (none) – 1
Relative shrub height	height of shrub is lower, the same or higher than surrounding shrubs	1 (lower) – 2 – 3 (higher)

Presence of mulch	visual estimation of mulch layer density	0 (no mulch) – 1 – 2 (rich)
Presence of mound	visual estimation of soil accumulation under shrub	0 (none) – 1 – 2 (well developed)
Environmental variables	Method	Unit/Range
Aspect	measurement of bearing (compass)	degrees
Slope	measurement (inclinometer)	degrees
Average soil depth	average of 5 soil depth measurements (steel probe)	m
Surface rockiness	visual estimation of surface rockiness	0 (no rocks) 1 (loose rocks) 2 (loose rocks + bedrock) 3 (bedrock)
Number of thorny shrubs	number of thorny shrubs in a 100 m² circular plot surrounding the shrub	–
Number of spherical shrubs	number of spherical shrubs in a 100 m² plot surrounding the shrub	–
Number of *Aloe* shrubs	number of *Aloe* shrubs in a 100 m² plot surrounding the shrub	–
Number of open shrubs	number of open low shrubs in a 100 m² plot surrounding the shrub	–

Plate. 1. Protected area of Mheni, Ethiopia, where *Olea europaea* recruitment was measured in 2002. Dense spherical shrubs are *Euclea racemosa*. The stonebunds along the contour lines are soil conservation measures. The slope at the other side of the valley is degraded grazing land.

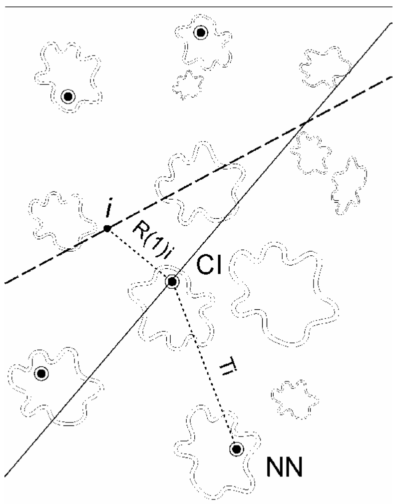


Fig. 1. T-square plotless sampling method. *Olea europaea* seedlings are represented by dots under shrub outlines. - - - = transect; CI = closest individual for transect point *i*; NN = nearest neighbour of CI on the far side of the line (—) perpendicular to the line *i* – CI; $R_{(1)i}$ = the distance from transect point *i* to CI; T_i = the distance from CI to NN (symbols after Engeman et al. 1994). See Eq. 1 and 2 for formulae.

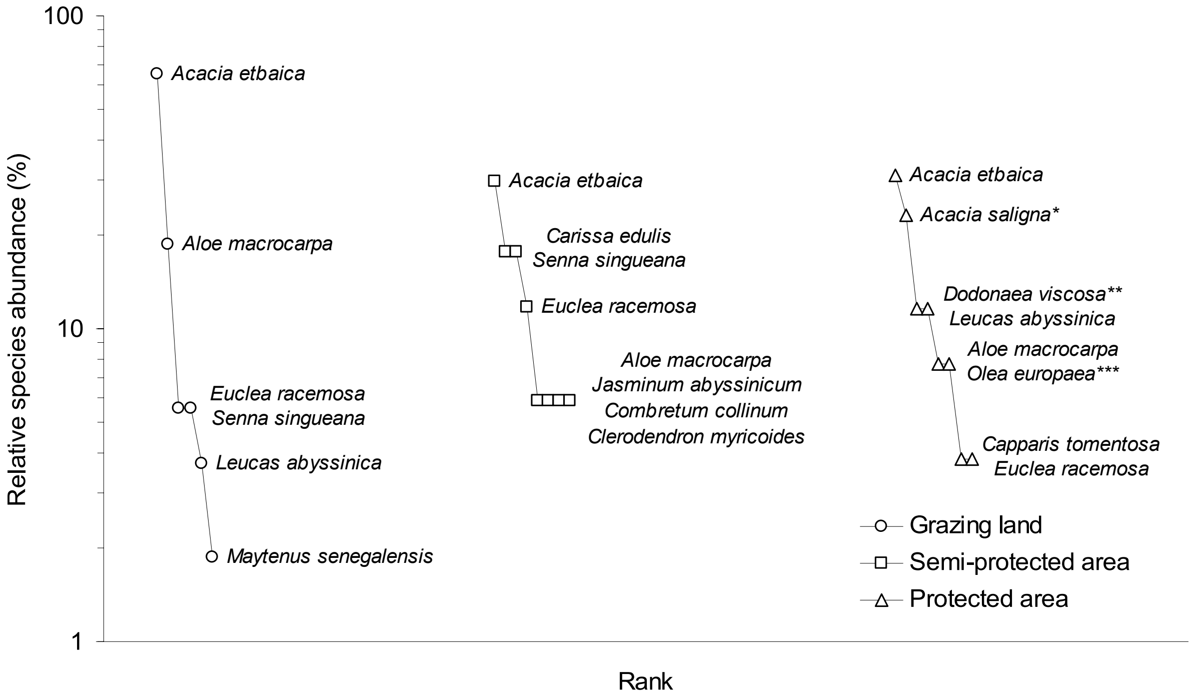


Fig. 2. Rank-abundance curves for one representative plot in each sampled land use in Mheni, Ethiopia: grazing land (○), semi-protected area (□) and protected area (∆). * and ** are an exotic and a native shrub planted in a reforestation program. *** are nanophanerophytic/chamaephytic life forms of *Olea europaea* that developed under high browsing pressure. Note logarithmic vertical scale.

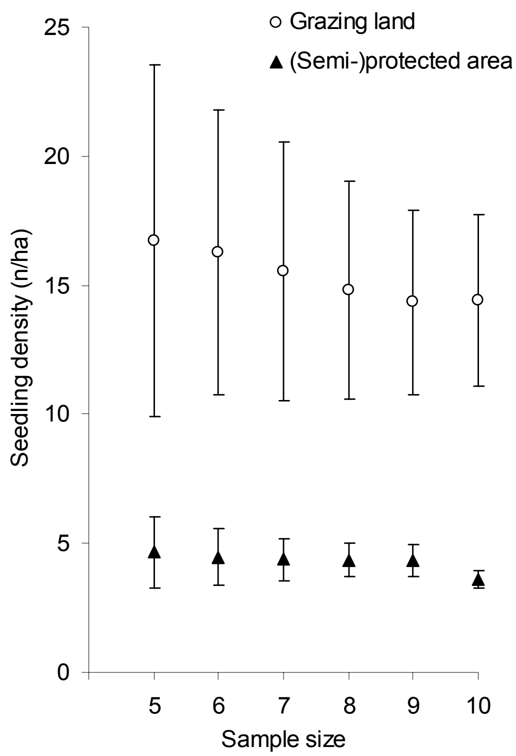


Fig. 3. *Olea europaea* seedling density in grazing land and (semi-)protected areas in Mheni, Ethiopia. Each value is the mean ± SD (ha^{-1}) of 100 densities calculated from T^2 data subsets of the given sample size, based on Monte-Carlo permutations.

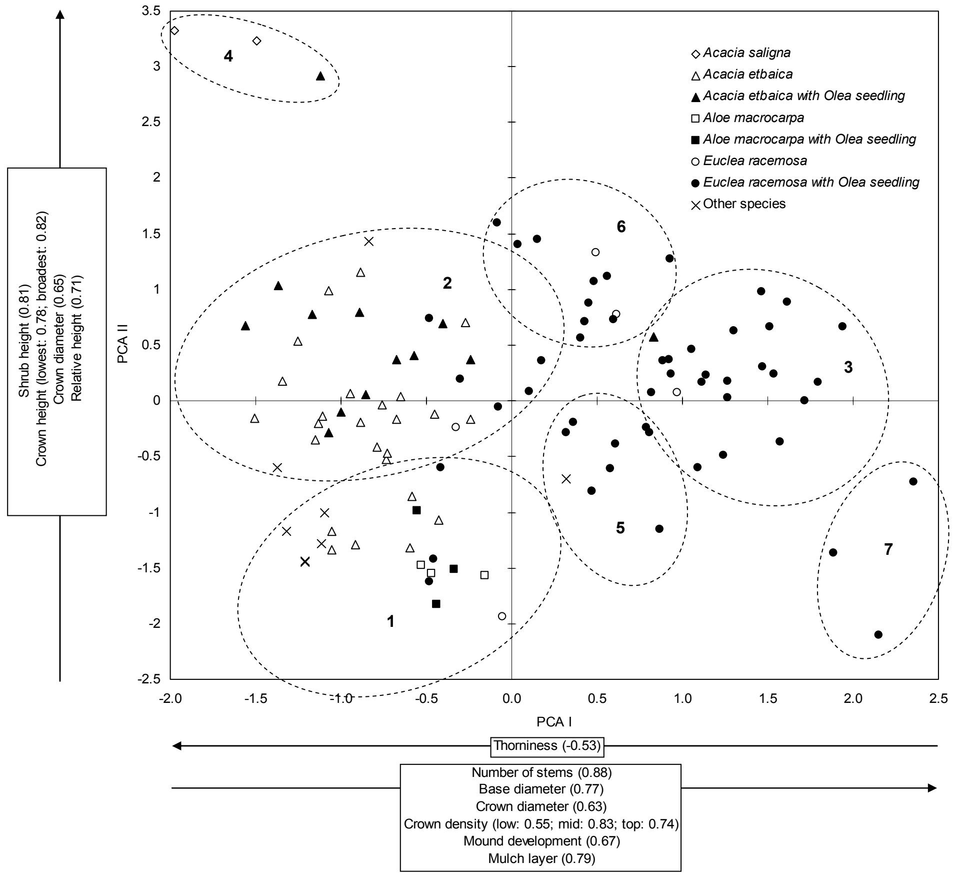


Fig. 4. PCA ordination and Ward's cluster analysis of structural characterisation of all sampled shrubs in Mheni (Ethiopia). Nurse plants of *O. europaea* recruits are represented by full symbols. The variables explaining the principal axes are significantly correlated to PCA I and/or PCA II (all given $|r_s| > 0.5$; $p < 0.001$).

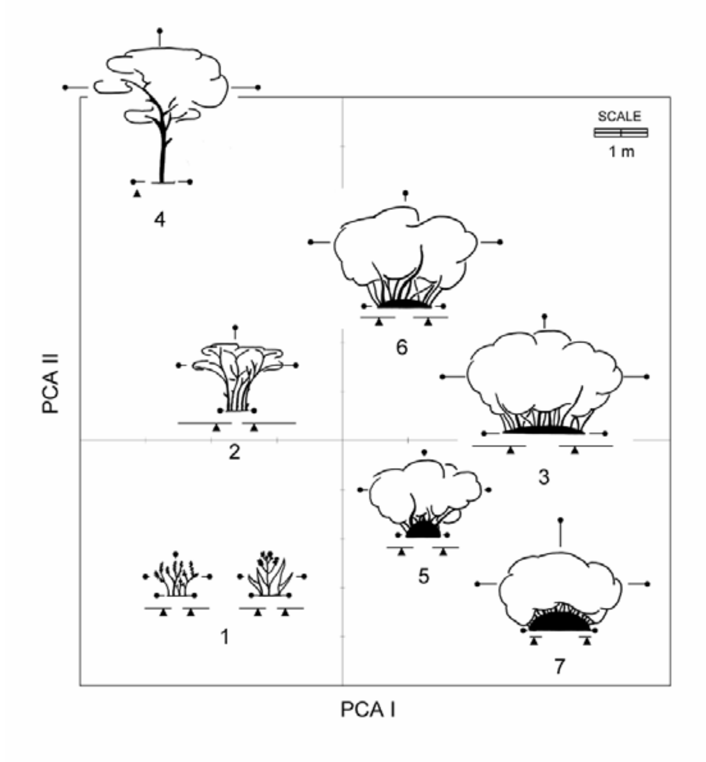
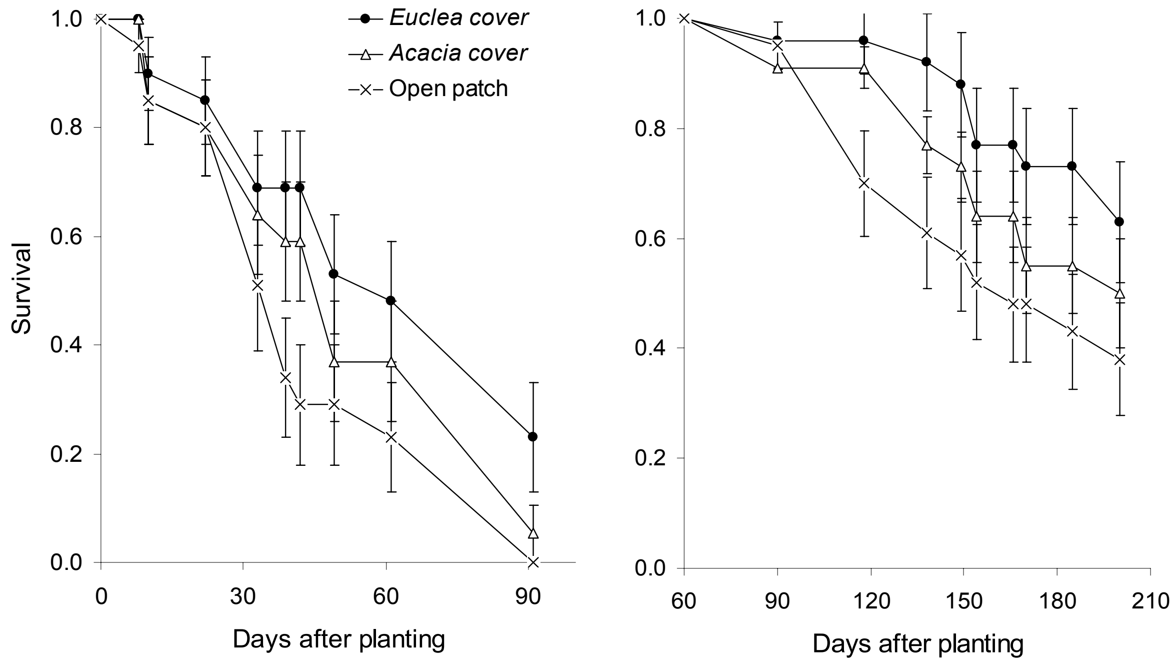


Fig. 5. *Olea europaea* nurse plants identified in Mheni, Ethiopia. Shrub dimensions are means per Ward's cluster + 1 SD shown as horizontal & vertical bars. Horizontal bars and arrows under shrubs are range and average position of *O. europaea* recruits. The majority of recruits was found under shrub types 3, 5 and 6.



a

b

Fig. 6. Cumulative survival curves of *Olea europaea* seedlings planted under *Euclea* cover, under *Acacia* cover and in open patches in protected areas in northern Ethiopia: a. spring rain experimental planting (n = 60; significance of difference between treatments: p = 0.02); b. summer rain experimental planting (n = 90; significance of difference between treatments: p = 0.01). Values are mean cumulative survival in days ± SE.