

Restoring dry Afromontane forest using bird and nurse plant effects: Direct sowing of *Olea europaea* ssp. *cuspidata* seeds

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Abstract

To identify the perspectives of seed sowing for reforestation of degraded dry Afromontane savanna in exclosures in northern Ethiopia, seeds of a fleshy-fruited, secondary climax tree, *Olea europaea* ssp. *cuspidata*, were placed under two pioneer shrub species (*Euclea racemosa* and *Acacia etbaica*) and in open microhabitats. Seed removal and germination rates were examined. The effects of bird ingestion, manual pulp removal and mechanical endocarp treatments on germination rates were also studied.

Pulp removal promoted seed germination, in particular in seeds without endocarp manipulation. Seed removal, presumably by rodents, was concentrated in narrow strips along linear soil conservation structures, and not different between shrubs and open microhabitats. In the absence of water stress, humus types did not have a significant effect on germination rates. Under field conditions however, germination was higher under *Euclea* canopies. The observed facilitative effect of *Euclea* shrubs on germination may be attributed to moisture retention effects, related to the deep humus layer and canopy architecture, preventing desiccation and promoting imbibition of seeds. When readily available *Olea* seeds are not used for seedling production, direct sowing of seeds in the humus under dense *Euclea* shrubs could offer a cheap complement to planting of nursery-raised seedlings for forest restoration projects in recovering Afromontane savanna.

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1. Introduction

Changing land use and land cover, population growth, unsustainable use of resources and climate change are some of the most widely recognized proximate causes and driving forces of land degradation and desertification in many parts of the world (Geist and Lambin, 2004). This particularly holds for the arid and semiarid regions of Sub-Saharan Africa (Darkoh, 1998; Zeleke and Hurni, 2001). The consequences of desertification, especially in the least-developed countries, are poverty and food insecurity but also large-scale loss of biodiversity. Biological conservation and restoration policies therefore need to take account of the diverse relationships

between conservation needs and the demands of poverty reduction (Adams et al., 2004).

Despite their low productivity, dry tropical forests are often of vital importance to rural communities in Sub-Saharan Africa, in particular in the Horn and eastern Africa (Lamprecht, 1989). Conversion to agriculture (e.g. Lemenih et al., 2005), accidental and intentional fires, wood and gum collection, grazing by livestock and selective logging of valuable species continue to transform dry tropical forests to such significant extent that they are considered by some to be the most endangered ecosystem in the tropics (Gillespie, 1999; Kalacska et al., 2004).

In northern Ethiopia, the regional government and local NGOs have implemented a forest rehabilitation strategy built on the needs of local communities by formally declaring community-managed protected areas where removal of remnant vegetation and free grazing are currently suspended (Tekle, 2001; Asefa et al., 2003; Mengistu et al., 2005). Land

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rehabilitation efforts in these set-aside areas or exclosures aim at restoring the natural Afromontane forest vegetation (Aerts et al., 2004; Nyssen et al., 2004). Natural regeneration of tree species in exclosures depends on seed dispersal from nearby forest patches (Turner and Corlett, 1996; Duncan and Duncan, 2000) or vegetative resprouting of pioneers because most Afromontane forest trees lack persistent soil seed reserves (Teketay and Granström, 1997; Tekle and Bekele, 2000; Wassie and Teketay, 2006). But as most of the Afromontane tree species exhibit limited long-distance seed dispersal as well (Teketay and Granström, 1995), exclosures face serious limits to natural forest regeneration, especially in a landscape where forest relics are small, fragmented and highly isolated (Aerts et al., 2006b). In such cases, planting of nursery-raised seedlings may accelerate regeneration (e.g. Aide et al., 2000; Martínez-Garza and Howe, 2003; Yirdaw and Luukkanen, 2003). An alternative, easier and cheaper technique which is slowly being adopted in restoration ecology of degraded tropical lands, is direct sowing of seeds (see, e.g. Sun et al., 1995; Hardwick et al., 1997; Guariguata and Pinard, 1998; Chapman and Chapman, 1999; Engel and Parrotta, 2001; Camargo et al., 2002). Particularly when combined with facilitative effects of pioneer shrubs, which may help overcome seed predation and desiccation (Woods and Elliott, 2004), the use of direct sowing may be an efficient and easy to implement forest restoration technique. Assisting regeneration may expedite the productivity of the exclosures, hereby serving both conservation and poverty-alleviation.

In our study area, naturally established seedlings of *Olea europaea* ssp. *cuspidata* (Wall. ex G. Don) Cif. (Oleaceae, African wild olive), an important shade-tolerant, fleshy-fruited component of dry Afromontane forest (Friis, 1992), are restricted to microhabitats under shrubs, primarily under the fruit-bearing pioneer *Euclea racemosa* ssp. *schimperi* (A. DC.) White (Ebenaceae), and to a lesser extent under the dominant thorn shrub *Acacia etbaica* Schweinf. (Fabaceae) (Aerts et al., 2006a). The seeds are dispersed in the summer rainy season (Teketay and Granström, 1997), primarily by frugivorous birds (see Alcántara et al. (2000b) for *O. europaea* ssp. *sylvestris*). Seeds may be dropped during flight and may thus land anywhere, including on bare soil. Nevertheless, it is more likely that seeds are dropped when the bird is perched (Mcclanahan and Wolfe, 1993; Stiles, 2000; Schupp et al., 2002), resulting in a primary seed rain concentrated under shrubs and trees (e.g. Alcántara et al., 2000a,b; Stiles, 2000; Holl, 2002). As secondary dispersal by run-off does not alter this pattern (Aerts et al., 2006), the absence of seedlings in the patches between shrubs may be explained by lower recruitment, i.e. higher seed removal or predation, less seed germination and seedling emergence, higher seedling mortality, or a combination of these factors (see, e.g. Herrera et al., 1994; Rey and Alcántara, 2000; Holl, 2002).

In this study, we analyzed the post-dispersal fate of *O. europaea* seeds to evaluate the possibilities and constraints of direct sowing for reforestation of dry Afromontane savanna. We test whether different microhabitats in exclosures have an effect on seed removal patterns and germination rates. We also test the

effects of bird ingestion, pulp removal and mechanical endocarp treatment on seed germination. We hypothesize that avian gut treatment will provide highest germination and that germination in microhabitats under pioneer shrubs will be higher compared to bare soil patches due to humus and moisture effects, despite the expected higher seed predation by rodents under shrub cover (Alcántara et al., 2000a; Mohr et al., 2003).

2. Materials and methods

2.1. Study species

O. europaea ssp. *cuspidata* (African wild olive) is a sclerophyllous evergreen tree with a heavy branched and rounded crown. It grows to 5–15 m (maximum 25 m) tall and is widely distributed in Afromontane forests, particularly in drier highland forests in association with *Juniperus procera* Hochst. ex Endl. (Cupressaceae, East African pencil cedar), forest margins, riverine forests and evergreen montane scrub from 1250 to 3000 m above sea level in Sudan, Somalia and southward through east tropical Africa into South Africa (Green, 2003). The ovoid-ellipsoid drupes have a fleshy mesocarp (pulp) and are green and dark purple-black when ripe (Green, 2003). The seeds are dispersed in the main rainy season (Teketay and Granström, 1997), primarily by frugivorous birds. The seeds have a width $W_s = 6$ mm, height $H_s = 6$ mm and length $L_s = 8$ mm with a volume $V_s = 151$ mm³ and mass $M_s = 225$ mg (Aerts et al., 2006). In undisturbed forest, germination results in populations of shade-tolerant and slowly growing seedlings (Teketay and Granström, 1997), and both in set-aside areas and grazing land, natural regeneration has been documented under early-successional shrubs (Aerts et al., 2006a). Once established, the tree is drought resistant, but because of its multiple uses (e.g. durable timber, traditional ox-ploughs, firewood and charcoal) both young and mature trees have been over-harvested dramatically in Ethiopia. As a result this valuable tree is now under threat of local extinction (Negash, 2003).

2.2. Site description

The experiments were set-up during the 2002 and 2003 summer rainy seasons in the Enderta and Doga Tembien districts of Tigray, northern Ethiopia (Table 1). Two study sites, Sesemat and Mheni, were located 1800–1900 m above sea level in the Geba river catchment of central Tigray, northern Ethiopia, on slopes over calcareous rocks and lacustrine silified Mesozoic Antalo limestone layers 20 km NW of the regional capital Mekelle, and are set-aside areas since 1996. A third site, Bubu Hills, was located at the foot of a dolerite cliff at the edge of Mekelle town next to a peri-urban eucalypt plantation. The vegetation in the three field sites was characterized by a discontinuous cover of shrubs and small regenerating trees in a matrix of herbs and bare soil (see Aerts et al., 2006a for details). It can thus be defined as semiarid degraded savanna (Vetaas, 1992; De Villiers et al., 2001). In the three sites, soil

Table 1
Study sites and seed removal and germination experiments carried out in northern Ethiopia

Site	Location	Elevation (m a.s.l.)	Rainfall (mm year ⁻¹)	Land use type	Experiments ^a			
					SR	DS	HG	BG
Endayesus	13°28'N, 39°30'E	2200	625 ± 155 ^b	Experimental tree nursery	–	–	×	×
Bubu Hills	13°30'N, 39°29'E	2150	≈Endayesus ^c	Peri-urban enclosure	–	×	–	–
Mheni	13°36'N, 39°21'E	1860	<Endayesus ^c	Rural community enclosure	×	×	–	–
Sesemat	13°37'N, 39°19'E	1940	<Endayesus ^c	Rural community enclosure	×	–	–	–

^a SR: seed removal experiments; DS: direct sowing experiments; HG: controlled germination experiments in reconstructed humus; BG: controlled germination experiments after pulp and endocarp treatments.

^b Meze-Hausken (2004).

^c R. Aerts, personal observation (2001–2004).

erosion rates are partially controlled by stone bunds. These are stone walls back-filled with soil along the slope contours and are widely used in the Ethiopian highlands as a soil and water conservation measure. Sediment accumulates behind these structures, which results in the development of progressive terraces (Herweg and Ludi, 1999; Hengsdijk et al., 2005; Vancampenhout et al., in press).

The climate is related to the mountainous facies of the Sudanese zone with hot and dry winters (October–January) and two rainy seasons: a short and moderate, highly variable spring rain (*belg*, coefficient of variation 31–55%) in (February)–March–April–(May–June) and a long, heavy and more reliable summer rain (*kremt*, coefficient of variation 19–31%) in (June)–July–August–September (Meze-Hausken, 2004). Mean annual precipitation is 625 ± 155 mm (spring rain 125 ± 11 mm; summer rain 466 ± 22 mm; means ± S.E. for the years 1960–2003; Meze-Hausken, 2004) and mean annual temperature 18 °C. Total spring and summer rains for 2003 were 149.3 and 357.3 mm (Mekelle Quiha station, National Meteorological Services Agency). In our study area, dry Afromontane forest relics and Afromontane savanna woodland are communities dominated by *O. europaea*, *A. etbaica* and *Combretum collinum* Fresen (Combretaceae) (Aerts et al., 2006b).

2.3. Post-dispersal seed removal experiments

To measure seed removal, seeds were placed in 8 cm × 8 cm mesh wire seed containers (depots), with 10 seeds and 3 stones as dummies per depot. The depots had a 2-cm high side that prevented seeds from washing away (abiotic secondary seed dispersal; see Aerts et al., 2006), but allowed for entry of seed predators (see Holl, 2002 for a similar protocol). All seeds were collected under mature mother trees in a forest relic and were similar to naturally dispersed seeds (no fleshy mesocarp). Only viable seeds were used, determined by a floating test (Schatral and Fox, 1994), since rodents have the ability to detect and avoid sterile seeds (Kollmann and Pirl, 1995). Depots were placed in three microhabitats: (1) open, in areas of bare soil between shrubs; (2) *Euclea*, under the canopy of individuals of *E. racemosa*; and (3) *Acacia*, under the canopy of individuals of *A. etbaica*. On 12 August 2003, 60 depots were placed in the Mheni enclosure in 2 areas of approximately 100 m × 100 m (20 per

treatment, 1 shrub or bare patch per depot). Remaining, intact seeds were counted after 1, 3, 6, 9 and 12 days. Preliminary analyses showed that seed removal only occurred in depots near stone bunds. A second experiment was therefore carried out in the enclosure of Mheni to test the effect of these stone bunds on seed removal. On 2 September 2003, 52 depots were placed under seven treatments. Twenty-four depots were placed under *Acacia* and *Euclea* shrubs (2 × 8 depots) and in open areas (8 depots). The remaining depots were placed directly next to the base and on top of stone bunds (2 × 14 depots). Remaining, intact seeds were counted after 1, 3, 6, 9, 13, 15, 18, 21, 24 and 30 days. On 24 September 2003, a duplicate of this experiment was initiated in the Sesemat enclosure.

2.4. Direct sowing experiment

To measure in situ germination, *Olea* seeds were sown in open areas, under *Euclea* and under *Acacia* shrubs in the enclosures of Mheni and Bubu Hills on 23–24 July 2003. In both sites, ten seeds were sown 1–2 cm deep in each of 30 randomly assigned patches (10 per treatment). Seed positions were marked with wooden tooth-picks to facilitate follow-up. Germination was monitored once a week for 14 weeks (well beyond the end of the rainy season, at 11 September 2003), and regularly followed up during the next spring and summer rains. Viable seeds without fleshy mesocarp, collected under mature trees in a nearby forest relic, were used.

2.5. Controlled germination experiments

The ectorganic layer under *Euclea* shrubs is deep with a very low bulk density and is generally characterized by a thick litter layer of slowly-decomposing leathery leaves (oligomull). The ectorganic horizon under *Acacia* shrubs is thin, with few remains of leaves and a litter layer of small twig fragments and thorns (eumull) (K. Descheemaeker, unpublished data). There is little or no humus in open patches, only a cover of loose stones with very little organic objects. To measure the effects of these two humus types or the absence of humus on germination, independently from water stress, humus from under *Euclea* and *Acacia* shrubs (10–15 cm deep) and stony surface covers of open areas (5 cm deep) were collected from the enclosure of Mheni and carefully reconstructed in 15

1 m × 0.5 m plots in seedling beds of the *Endayesus* tree nursery (see Franco-Pizaña et al., 1996 for a similar protocol). On 24 July 2003, 20 *Olea* seeds were sown 1–2 cm deep in each treatment replication. Germination was monitored for 30 weeks. Viable seeds without fleshy mesocarp collected under mature trees in a nearby forest relic were used, and were soaked in water for 24 h prior to sowing to promote imbibition and germination.

The effect of avian pulp removal (for instance, through gut passage) was tested using a second controlled germination experiment. The factors ‘pulp removal’ (removal of the fleshy mesocarp by birds, manual pulp removal and no pulp removal; see Samuels and Levey, 2005) and ‘mechanical treatment’ (scarification of the endocarp, splitting of the endocarp and no mechanical treatment) were combined to seven treatments (omitting the meaningless combinations no pulp removal × mechanical endocarp treatments). In each of 21 1 m × 0.5 m plots in seed beds of the *Endayesus* tree nursery (three per treatment), 50 seeds were sown 1–2 cm deep on 11 August 2002. Seeds of the ‘pulp removal by birds’ treatment were viable, regurgitated or defecated seeds. Seeds for the manual pulp removal and control treatments were obtained from fresh, ripe drupes collected in a nearby forest relic. All treatments (including control) were soaked in water for 24 h prior to sowing.

In both controlled germination experiments, germinants were recorded and then removed from the seed beds to avoid double counts. Grass mats 1 m above the beds provided shade; beds were watered twice daily.

2.6. Data analysis

For the first seed removal experiment, non-parametrical Kruskal–Wallis one-way ANOVA (KW) was used to compare seed removal in the three microhabitats. In the second seed removal experiment, seed survival was analyzed using a time-to-event approach, which measures the time to an event for each case (depot) (Altman and Bland, 1998). In this study the critical event is seed removal. Because seed removal is inherently linked to escape from removal or predation, this data is conventionally called survival data. Since rodents and other seed consumers often hoard food from a dense concentration of resources and frequently revisit such resources (Vander Wall, 1990), data of seed removal in a single depot on subsequent days does not reflect independent events. A depot was therefore treated as completely removed as soon as at least one seed had disappeared. The characteristic feature of survival data is that at the end of the follow up period, the critical event will probably not have occurred for all depots. For these depots, the survival time is said to be censored (Altman and Bland, 1998). Because of the censoring, we used Kaplan–Meier survival analysis, a model for censored survival data based on estimating conditional probabilities for each time interval in which an event occurs (Bland and Altman, 1998). Equality of survival distributions for the seven different microhabitats was tested using the Breslow statistic (BS). After reclassification of the data in depots near stone bunds (<1 m) and those further away

(>1 m), a second survival analysis was used to test for differences in seed removal between these two distance classes.

The first germination experiment (humus type) was analyzed using Kruskal–Wallis one-way ANOVA. The second germination experiment (pulp removal and mechanical treatment) was analyzed using two-way ANOVA on untransformed proportion data (Levene’s test for homoscedacity indicated homogeneity of variance).

In the controlled germination experiment to test the effect of pulp removal by birds, one plot of the treatment pulp removal by birds × endocarp scarification was disturbed by nocturnal animals and omitted from analysis. The seed removal experiment in Sesemat was seriously disturbed between days 4 and 6: 25 depots were destroyed. Analyses were performed using SPSS 11.0 and 12.0 for Windows (SPSS Inc., Chicago, IL).

3. Results

3.1. Seed removal

In the first experiment designed to capture seed removal differences between the three major microhabitats, seed removal was limited and highly localized in one site. Only 39 seeds were removed from the depots (6.5%): 19 (3.2%) from three open depots and 20 (3.3%) from two depots under *Acacia*. There was no significant effect of microhabitat on the

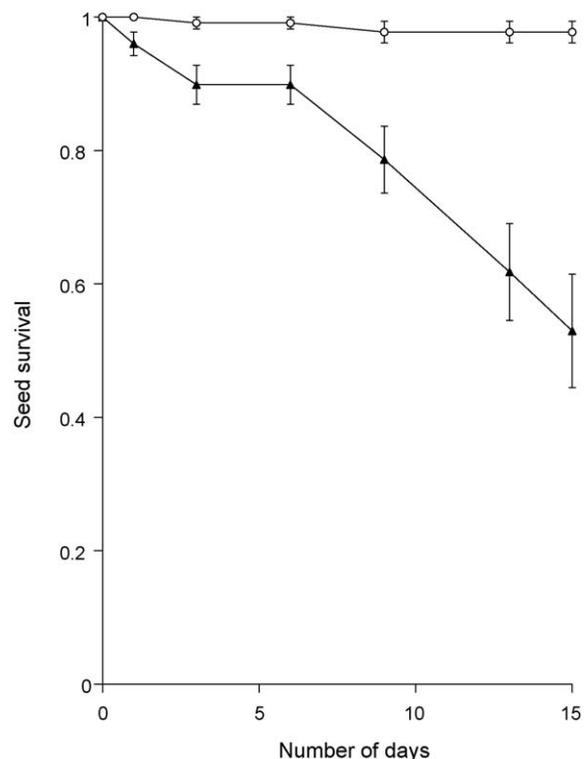


Fig. 1. Seed survival probability calculated as mean probability ± S.E. for depots with 10 *Olea* seeds to remain undetected: (▲) near stone bunds (<1 m; $N = 31$) and (○) further away from stone bunds (>1 m; $N = 20$) in the Mheni enclosure, September 2003. Day 0 is 2 September 2003. After 20 September, no further seed removal was detected.

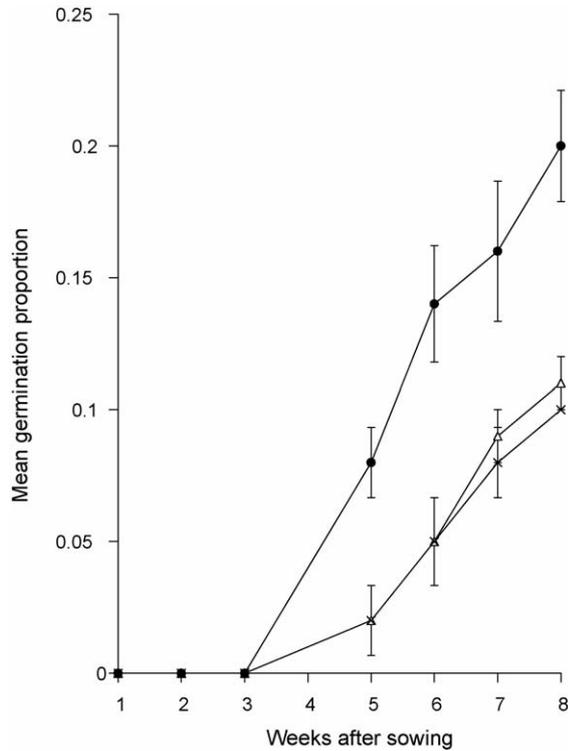


Fig. 2. Germination probability of *Olea* seeds (mean \pm S.E.; 10 seeds per replication) in three microhabitats of the Bubu Hills enclosure, 24 July–17 September 2003: (●) under *Euclaea* cover ($N = 10$), (△) under *Acacia* cover ($N = 10$) and (×) in open patches between shrubs ($N = 10$).

number of remaining seeds (KW, $\chi^2 = 3.06$, $P = 0.216$), but interestingly, the five depots where seed removal occurred, were all positioned in the immediate vicinity of stone bunds.

For the second experiment, with depots explicitly placed near stone bunds, survival analysis showed that microhabitat had a significant effect on seed survival time (BS = 15.6, $P = 0.004$), but between treatments, only contrasts with depots near stone bunds were significant. Seed removal in depots near stone bunds (<1 m) was significantly higher than in depots placed further away (>1 m) (BS = 22.1, $P < 0.001$; Fig. 1). At the end of the experiment, $52 \pm 7\%$ of all seeds deposited near stone bunds were removed, while this was only $3 \pm 2\%$ for those deposited further away (Fig. 1). No seed removal was detected in Sesemat, possibly due to disturbance, but more probably because of factors related to movement of predators (see Section 4).

3.2. Germination after direct sowing

In situ germination was limited and site-dependent. In the Mheni enclosure, none of the seeds germinated. In the Bubu Hills enclosure, germination was significantly higher under *Euclaea* cover ($20 \pm 2\%$) compared to *Acacia* cover and open microhabitats (11 ± 1 and $10 \pm 0\%$) (KW, $\chi^2_{\text{week 8}} = 15.54$, $P < 0.001$; Fig. 2). Eight weeks after sowing, the summer rainy season stopped and no further germination occurred. No further

germination could be detected during the following spring and summer rains.

3.3. Controlled germination

Humus type did not have a significant effect on controlled germination (KW, $\chi^2_{\text{week 30}} = 0.005$, $P = 0.997$; Fig. 3). After 30 weeks, $34 \pm 4\%$ of all seeds pooled over treatments had germinated.

Germination in the pulp removal and endocarp treatment experiment was characterized by two distinct phases, in which both the pulp removal and the endocarp treatments had significant effects without interaction (Table 2; Fig. 4). Endocarp splitting resulted in rapid and uniform germination until the seventh week, while germination in the other treatments continued slowly and gradually. After 23 weeks, $32 \pm 4\%$ of the seeds with split endocarps had germinated compared to 14 ± 4 and $13 \pm 4\%$ for the scarified seeds and the controls (Table 2). At this stage, pulp removal was a crucial factor for germination since only marginal germination was observed in the overall control. In week 24, which coincided with the onset of the spring rains (27 January 2003), a second wave of germination occurred in the endocarp control treatments (Fig. 4). After 46 weeks, the highest germination was recorded in seeds with intact endocarp: first of all by those with pulp removed by birds ($63 \pm 10\%$), followed by those with

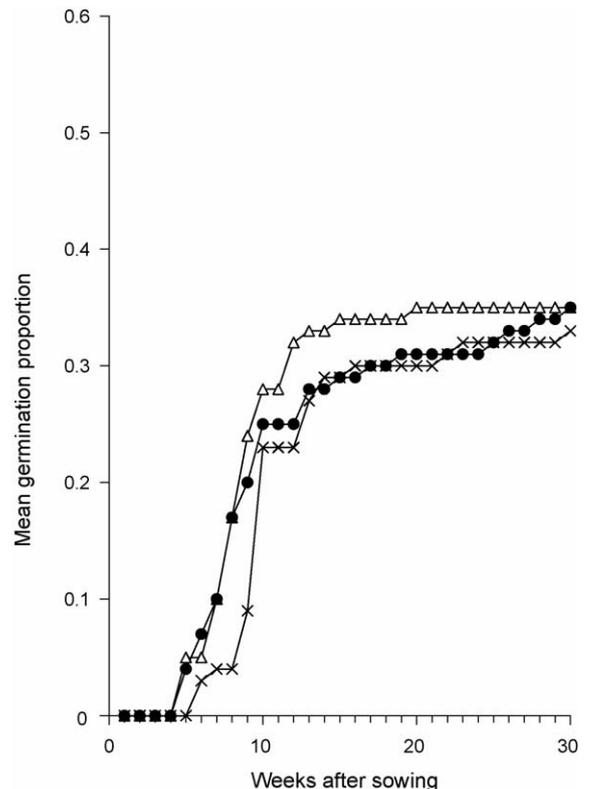


Fig. 3. Germination probability of *Olea* seeds (mean; 20 seeds per replication) in reconstructed humus of three microhabitats, 24 July 2003–20 February 2004: (●) *Euclaea* humus ($N = 5$), (△) *Acacia* humus ($N = 5$) and (×) stone cover of open patches between shrubs ($N = 5$). Standard errors of means were omitted for clarity.

Table 2

Two-way ANOVA significance and mean percent seed germination \pm S.E. of pulp removal and mechanical endocarp treatments in a controlled germination experiment of *Olea europaea* seeds

Pulp removal	Treatment means \pm S.E. ^a			Factor significance ^b	
	Control	Manual	Bird	$F_{2,13}$	P
23 weeks after sowing	3 \pm 1a	17 \pm 4ab	27 \pm 4b	4.838	0.027*
46 weeks after sowing	37 \pm 7a	35 \pm 6a	44 \pm 7a	3.933	0.046*
Endocarp treatment	Treatment means \pm S.E. ^a			Factor significance ^b	
	Control	Scarification	Splitting	$F_{2,13}$	P
23 weeks after sowing	13 \pm 4a	14 \pm 4a	32 \pm 4b	5.510	0.018*
46 weeks after sowing	52 \pm 5a	24 \pm 5b	32 \pm 4b	12.789	0.001***

^a Letters indicate significant differences between groups ($P < 0.05$; Tukey's HSD).

^b Interaction between pulp removal and endocarp treatment not significant: week 23, $P = 0.665$; week 46, $P = 0.920$.

* $P < 0.05$.

*** $P < 0.001$.

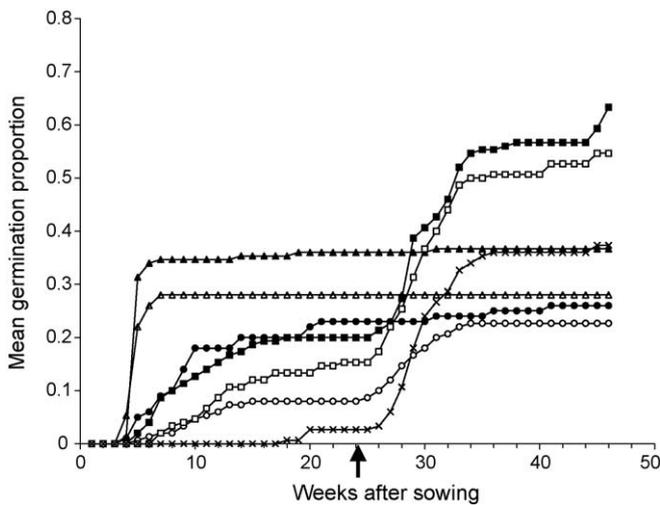


Fig. 4. Germination probability of *Olea* seeds (mean; 50 seeds per replication) after pulp removal and endocarp scarification treatments: pulp removed by birds, no endocarp treatment ($N = 3$; ■), pulp manually removed, no endocarp treatment ($N = 3$; □), pulp removed by birds, endocarp split ($N = 3$; ▲), pulp manually removed, endocarp split ($N = 3$; △), pulp removed by birds, endocarp scarification ($N = 2$; ●), pulp manually removed, endocarp scarification ($N = 3$; ○) and intact drupe (overall control) ($N = 3$; ×). Standard errors of means were omitted for clarity. Seeds were sown in the seed beds on 11 August 2002. The arrow indicates the onset of the 2003 spring rains (27 January 2003).

manually removed pulp ($55 \pm 3\%$) and then the overall control ($37 \pm 7\%$). Endocarp splitting, combined with pulp removal, facilitated germination immediately after sowing, but ultimately, germination was more successful in seeds with intact endocarp.

4. Discussion

We examined removal and germination rates of seeds of an animal-dispersed secondary climax tree placed in three different microhabitats. We also studied the effects of bird ingestion, pulp removal by hand and mechanical endocarp treatments on germination rates. Our analysis confirms that full or partial passage through the digestive tract of frugivorous birds influences germination of *O. europaea* seeds (Fig. 4). In

general, ingested seeds germinated in greater numbers and took less time to germinate than uningested seeds (cf. Traveset and Verdú, 2002). Additional germination trials using seeds of three other fleshy-fruited Afrotropical tree species, *Cordia africana* Lam. (Boraginaceae), *Juniperus procera* and *Afrocarpus falcatus* (Thunb.) C.N. Page (Podocarpaceae), also showed improved germination in seeds with naturally removed pulp, especially in those seeds not subjected to supplementary endocarp treatments (A. Negussie and R. Aerts, unpublished data). This observation is in line with evidence provided by Murray et al. (1994) showing that germination success decreases as gut retention time, and thus mechanical and chemical endocarp scarification, increases (Stiles, 2000). In any case, removal of the lipid-rich pulp, which repels water and thus prevents imbibition of the embryo, is necessary for germination (García-Fayos and Verdú, 1998). Effective pulp removal may be achieved by birds or by hand (Wenny, 2000), but also by natural decay in the soil, all yielding different germination rates, but similar final germination proportions (Fig. 4). Many tropical species whose seeds disperse during the main rainy season, exhibit a strong innate dormancy, lasting 3–6 months, regardless of the watering regime during this period (Garwood, 1989). But the germination in two distinct phases (Fig. 4) suggests that seed passage through the gut of birds breaks this physiological dormancy in a fraction of the seeds. Seeds germinating immediately after dispersal have a lower predation and removal probability than seeds germinating after the winter drought; but seedlings, on the other hand, have a higher survival probability when emerging after the winter drought, since only those seedlings can take advantage of a full rainy season before being exposed to subsequent drought stress (see also Kitajima and Fenner, 2000). The dual germination observed in *O. europaea* may thus be seen as a mechanism to enhance offspring survival, by providing both dormant seeds and overwintering seedlings.

Olea seeds may exceed the maximum size that can be removed and predated by ants and other litter-dwelling invertebrates, but are in contrast very attractive to vertebrate seed predators, such as rodents (Rey et al., 2002; Fornara and Dalling, 2005). Although we did not find direct evidence for

vertebrate seed predation, and cannot conclude that all seed removal resulted in seed predation since secondary dispersal via scatter-hoarding is possible (Vander Wall et al., 2005), trails and droppings found along stone bunds indicated considerable rodent activity, probably by species from the genera *Mastomys* and *Arvicanthis*, the major rodent pests in the highlands of Ethiopia (Bekele and Leirs, 1997; Gebresilassie et al., 2004). The presence of refuges for seed predators may explain high seed predation rates (Verdú and García-Fayos, 1996). In our study area, nesting and burrowing activities of rodents are often concentrated in stone bunds (R. Aerts, personal observation), hereby increasing the probability of foraging animals to encounter seeds in the vicinity of these structures (Fig. 1). But further away from stone bunds, post-dispersal seed removal was fairly low and not higher under shrubs compared to open patches. These results support the theory that predator population densities and within-site differences can strongly influence patterns of seed removal and predation in space and time (Holl and Lulow, 1997; Alcántara et al., 2000a; Garcia, 2001; Holl, 2002; Rey et al., 2002; Jones et al., 2003). Cessation of seed removal in the exclosures approximately mid-September (17 September), the absence of removal in the Sesemat site, and the overall low seed removal rates may be related to the preference of rodents for ripened crops in fields near the exclosures, as revealed by stomach content analysis of trapped animals in an irrigation field near our study area (Gebresilassie et al., 2004). Thus, in our study and at least one other (Alcántara et al., 2000a), the seed dispersal pattern of *O. europaea* is not reshaped by biotic post-dispersal seed removal, because the initial seed rain is not altered significantly.

In Mheni seeds failed to germinate, probably due to the very poor summer rains in that area during the study; in semiarid areas seeds may need long and abundant rain events to germinate (García-Fayos and Verdú, 1998). In Bubu Hills, which generally receives more rainfall (Table 1), seeds placed under shrubs and in bare soil initially showed germination rates similar to those in controlled germination experiments (Fig. 2), but germination stopped after the summer rains and did not resume during the spring rains. In the absence of water stress, microhabitat humus types did not have a significant effect on germination rates (Fig. 3). Under field conditions, however, higher germination rates were observed under *Euclea* canopies (Fig. 2). Since *Olea* removal rates were not significantly different between *Acacia*, *Euclea* and bare soil treatments, the observed facilitative effect of *Euclea* shrubs on germination may probably be attributed to moisture retention effects. This may be related to the humus structure, but also to canopy architecture. The sclerophyllous-evergreen *Euclea* shrubs provide more shade than the leguminous-deciduous *Acacia* shrubs (Aerts et al., 2006a), reducing solar radiation, soil temperature and soil evaporation and thus preventing desiccation of seeds more effectively.

5. Conclusions

Overall, our results agree with previous studies that have shown that seed pre-treatment shortens seed dormancy and thus

decreases the time available for seed removal or predation to occur. Duncan and Chapman (2002), commenting on previous seed sowing studies in degraded sites, found limited or no success in most cases. Nevertheless, the low germination and seedling survival typically found in direct sowing techniques (Engel and Parrotta, 2001) may be overcome by sowing more seeds, selecting larger, more vigorous seeds (Kidson and Westoby, 2000; Moles and Westoby, 2004; Rey et al., 2004) or imbibing seeds prior to sowing (Camargo et al., 2002). Seeds with naturally removed pulp, thus suitable for sowing, can usually be found in large quantities under fruiting *Olea* trees in forest relics, and under solitary trees in the vicinity of these relics (R. Aerts, personal observation). When these seeds are not used for seedling production (which is often the case), direct sowing of *Olea* seeds pre-treated by birds in the humus under dense *Euclea* shrubs could offer an effective, cheap complement to planting of nursery-raised seedlings for forest restoration projects in recovering Afromontane savanna. Sowing seeds 1–2 cm deep is preferable to broadcasting, since it may help to protect the seeds from removal and predation and to prevent seed desiccation (Woods and Elliott, 2004). In ecological terms, this technique would increase the seed density under safe sites in degraded areas using seeds that would otherwise have been lost due to dispersal limitation.

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