PUBLISHED ARTICLE

Citation*

Aerts R., Maes W., November E., Behailu M., Poesen J., Deckers J., Hermy M., Muys B. 2006. Surface runoff and seed trapping efficiency of shrubs in a regenerating semiarid woodland in northern Ethiopia. *Catena* **65**, 61-70.

DOI: [10.1016/j.catena.2005.09.004](https://doi.org/10.1016/j.catena.2005.09.004)

Authors: **Raf Aerts^{1,3}, Wouter Maes¹, Eva November^{2,3}, Mintesinot Behailu³, Jean Poesen⁴, Jozef Deckers², Martin Hermy¹ and Bart Muys^{1,*}**

¹ Division Forest, Nature and Landscape, K. U.Leuven, Leuven, Belgium

² Division Soil and Water Management, K. U.Leuven, Leuven, Belgium

³ Land Resources Management and Environmental Protection Department, Mekelle University, Ethiopia

⁴ Physical and Regional Geography Research Group, K.U.Leuven, Leuven, Belgium

* Corresponding author: Prof. Bart Muys, Celestijnenlaan 200E-2411, BE-3001 Leuven (Belgium). Tel. +32-16-32 97 26; Fax: +32-16-32 97 60

E-mail: bart.muys@ees.kuleuven.be

*Elsevier authorized the authors to post this revised personal version of the text of the final journal article on the author's institutional server, incorporating the complete citation and with a link to the Digital Object Identifier (DOI) of the article.

Creative Commons Attribution-Noncommercial-Share Alike 2.0 Belgium License

Permissions beyond the scope of this license may be available at

<http://www.elsevier.com/wps/find/authorsview.authors/copyright#whatrights>

**Surface runoff and seed trapping efficiency of shrubs in a regenerating
semiarid woodland in northern Ethiopia**

**Raf Aerts^{1,3}, Wouter Maes¹, Eva November^{2,3}, Mintesinot Behailu³, Jean Poesen⁴,
Jozef Deckers², Martin Hermy¹, Bart Muys^{1*}**

¹*Division Forest, Nature and Landscape, K.U.Leuven, Celestijnenlaan 200E-2411, BE-3001
Leuven, Belgium;* ²*Division for Soil and Water Management, K.U. Leuven, Celestijnenlaan 200E-
2411, BE-3001 Leuven, Belgium;* ³*Land Resources Management and Environmental Protection
Department, Mekelle University, P.O. Box 231, Mekelle, Ethiopia;* ⁴*Physical and Regional
Geography Research Group, K.U. Leuven, Celestijnenlaan 200E-2409, BE-3001 Leuven,
Belgium*

Abstract

In forest restoration areas in northern Ethiopia, natural regeneration of *Olea europaea* ssp. *cuspidata* only occurs under pioneer shrubs. To assess the impact of erosion on the spatial distribution of *Olea* recruits, secondary dispersal of olive seeds by surface runoff was determined in and near the micro-environment of two important pioneers (*Acacia etbaica* and *Euclea racemosa*). We hypothesized that (1) *Olea* seeds deposited under the protective crowns of shrubs are less likely to be lost by surface wash than seeds in the bare inter-plant areas and (2) that seeds in the latter are more prone to be translocated by runoff to microsites under shrubs than to open areas.

* Corresponding author.

1 Runoff experiments were conducted in August–September 2003 in ten $3 \times 3 \text{ m}^2$ plots laid out
2 around isolated shrubs in two sites. Twenty-eight marked tracer seeds were dropped at the upper
3 end of each plot at 0.10 m intervals. Ten seeds marked in another way were deposited under the
4 crown in each plot simulating seed dispersal by birds. The seeds were collected after the rainy
5 season and their positions recorded. In a third experiment, mulch under shrubs was removed and
6 ten marked seeds were deposited under each crown. Rainfall simulation experiments were
7 conducted with a maximum intensity of $120 \text{ mm} \cdot \text{h}^{-1}$ for a ten minute duration. For all
8 experiments, seed movement was analyzed in relation to slope and shrub variables.
9 Seed movement was limited in one site, where only 21% of the seeds were translocated.
10 Movement was significantly higher in the other site (61%) although it had a lower slope gradient.
11 The number of seeds moved by surface runoff was not significantly related to shrub species,
12 slope gradient or slope roughness. There was a strong linear relationship between the distance
13 parallel to the contour from the shrub center to the seed and the extent of the downhill
14 translocation. No seeds moved to a position under a shrub crown and no shrub lost a seed
15 deposited under its crown. Simulated rainfall after mulch removal resulted in a seed loss of nearly
16 33%.
17 Micro-topographic structures under shrubs, especially under *E. racemosa*, cause some soil and
18 sediment retention, but more importantly divert runoff water and concentrate flows to rills
19 alongside shrubs. From an eco-geomorphological point of view, shrubs show poor seed trapping
20 efficiency contradictory to expectation. Seeds in sediment flows are deposited in the bare inter-
21 plant areas. However, seeds under shrubs are not likely to be lost by surface wash. Surface
22 runoff has little effect on the general pattern of the primary seed rain.
23 Since *Olea* recruits were exclusively found under shrubs and not in the spaces between shrubs in
24 the studied field sites, it appears plausible that seeds deposited in the open field are almost
25 without doubt lost to post-dispersal seed predation, unsuccessful germination or seedling
26 predation and mortality. Recovery of *Olea europaea* in degraded shrubland communities
27 therefore depends upon direct dispersal of seeds under shrubs by frugivorous birds.
28

- 1 **Keywords:** African wild olive, erosion, exclosure, *Olea europaea* ssp. *cuspidata*, seed
- 2 displacement, vegetation cover

1. Introduction

In northern Ethiopia, poverty of the increasing highland population and its search for a subsistence income has led to a wave of deforestation, site degradation and soil erosion since 1700 AD (Feoli et al., 2002; Asefa et al., 2003; Darbyshire et al., 2003). As a result of these, recurrent droughts have a strong negative impact on agricultural production and the environment (Taddese, 2001; Nyssen et al., 2004). Recent revegetation efforts primarily focus on region-wide establishment of protected areas, where free grazing and cutting is no longer permitted and vegetation is allowed to regenerate naturally (Aerts et al., 2004; Mengistu et al., 2005). These protected areas – also known as ‘exclosures’ and ‘enclosures’ – are characterized by a discontinuous cover of shrubs and small regenerating trees in a matrix of herbaceous species and bare soil. They can be defined as semiarid degraded savannas (Vetaas, 1992; De Villiers et al., 2001).

Natural regeneration of forest tree species in exclosures mainly depends on seed dispersal from nearby forest patches (Duncan and Duncan, 2000; Turner and Corlett, 1996) because most Afromontane forest trees lack persistent soil seed reserves (Teketay and Granström, 1997; Tekle & Bekele, 2000). Dispersal, in particular over long distances, may be a key factor in the survival of local populations, especially in fragmented landscapes (Cain et al., 2000, 2003; Ozinga et al., 2004). Wind, water, large mammals and birds can potentially disperse seeds far from the parent plant (Couvreur et al., 2004; Ozinga et al., 2004; Couvreur et al., 2005). In many tropical and subtropical regions seed dispersal by animals has the potential to facilitate recolonisation of native vegetation on degraded sites (Wunderle, 1997; Wenny, 2001). These animals regurgitate, defecate, spit out or otherwise drop seeds away from the parent plants and therefore provide the crucial dynamic link between many fruiting plants and their seedling bank in natural and recovering communities (Jordano, 2000; Rey and Alcántara, 2000; Willson and Traveset, 2000; Stiles, 2000; Wang and Smith, 2002). They determine the

1 spatial distribution of the seeds (seed rain) and the initial seed deposition patterns affect
2 seed survival and seedling establishment in various ways (Howe, 1990; Alcántara et al.,
3 2000; Wang and Smith, 2002). African wild olive (*Olea europaea* subsp. *cuspidata* (Wal.
4 ex G. Don) Cif.) is an important but threatened (Negash, 2003), bird-dispersed
5 (Alcántara et al., 2000) climax tree species in the secondary dry Afromontane forest of
6 northern Ethiopia (Friis, 1992; Teketay and Granström, 1997). During a three-year study
7 by Aerts et al. (2005), *O. europaea* recruitment ($3 - 15$ recruits $\cdot$ ha⁻¹) was exclusively
8 found under shrubs, primarily under the evergreen, fleshy-fruited pioneer *Euclea*
9 *racemosa* subsp. *schimperi* (A. DC.) White, although the thorn shrub *Acacia etbaica*
10 Schweinf. was dominant in both grazed and ungrazed sites. The spatial correlation
11 between tree seedling recruitment and pre-established pioneer shrubs can usually be
12 explained by facilitative effects, where nurse plants cause reduction of dormancy
13 (Franco-Pizaña et al., 1996), increase fertility or soil moisture (e.g. Pugnaire et al., 1996;
14 Moro et al., 1997; Whitford et al., 1997; Verdú & García-Fayos, 2003) or offer protection
15 against high irradiance, temperature or predation (e.g. Valiente-Banuet & Ezcurra, 1991;
16 Vetaas, 1992; García and Obeso, 2003).

17 Some plants on the other hand attract seed dispersers resulting in an accumulation of
18 seeds under their canopies (e.g. Duncan and Chapman, 1999; Alcántara et al., 2000;
19 Rey & Alcántara, 2000; Holl 2002; Verdú & García-Fayos 2003). But in semiarid
20 environments where soils are crusted, vegetation is sparse and rainfall intensities are
21 very high, soils are prone to generate surface runoff (Cerdeira and García-Fayos, 2002),
22 and secondary dispersal by surface wash may alter the primary seed deposition pattern
23 considerably. In this context, shrubs may not only act as preferential perching sites
24 for avian seed dispersers during primary dispersal but also as seed traps during
25 secondary dispersal by surface runoff (Bochet and García-Fayos, 2004; Rey, 2004).

1 The shrubs in the exclosures are generally associated with micro-topographic structures
2 that break the overall slope continuity and give rise to islands of improved topsoil
3 properties, a situation comparable to the Mediterranean matorral studied by Bochet et al.
4 (1999, 2000). From an eco-geomorphological point of view, these shrubs may act as
5 vegetation barriers effective in trapping eroded sediment (Rey, 2004) which may contain
6 forest tree seeds and thus contribute to an accelerated forest regeneration.
7 Nevertheless little information is available about the role of water in the removal,
8 translocation and deposition of seeds and successive plant establishment and
9 distribution (but see García-Fayos and Cerda, 1997; Cerda and García-Fayos, 2002;
10 Hampe, 2004).
11 The aim of the present study is to examine secondary dispersal in exclosures, and more
12 specifically to test the hypotheses that (1) seeds of African wild olive deposited under the
13 protective crowns of shrubs are less likely to be lost by surface wash than seeds in the
14 bare inter-plant areas and (2) that seeds in the latter are more likely to be translocated
15 by runoff to microsites under shrubs than to other open areas.

16

17 **2. Study area**

18 The study area (Fig. 1) is located in the Geba river catchment (13° 37' N, 39° 21' E) in
19 the Dogu'a Tembien district of central Tigray, northern Ethiopia, 20 km NW of the
20 regional capital Mekelle, between 1980 and 2000 m a.s.l. The area is located on the
21 Eastern African rift shoulder to the west of the Wushatay ridge (2532 m) and the Danakil
22 depression. It was selected for this study as it contains several small Afromontane forest
23 remnants, which are typical of the northern Ethiopian highlands and part of a wider
24 project aimed at understanding the natural regeneration dynamics of African wild olive
25 (Aerts et al., 2005). The climate is related to the mountainous facies of the Sudanese
26 zone with a mean annual temperature of 18 °C and a mean annual precipitation between

1 550 and 600 mm, most of which occurs during the summer rainy season (June–
2 September) in the form of highly erosive rains (65–77% of the rains $> 25 \text{ mm} \cdot \text{h}^{-1}$)
3 brought in by the prevailing east-west winds. The winter is hot and dry due to the winds
4 received from the Sahara (Nyssen et al., 2004).
5 The experimental sites were located in the protected areas of Mheni and Sesemat (Fig.
6 1) on SW and NE facing slopes over sub-horizontal calcareous rocks and lacustrine
7 silified Mesozoic Antalo limestone layers, with a modal slope gradient of $0.075 \text{ m} \cdot \text{m}^{-1}$
8 comparable to the $0.1 \text{ m} \cdot \text{m}^{-1}$ gradient measured by Nyssen et al. (2000) around Hagere
9 Selam in the center of the district. The soil (Verti-Skeletal Cambisol) is shallow (45 cm)
10 with moderate rock outcrops and high calcium carbonate and organic carbon content.
11 The average soil loss by sheet and rill erosion on wooded highland slopes in Ethiopia is
12 in the order of $5 \text{ t} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Nyssen et al., 2004).

13

14 (Insert Fig. 1)

15

16 **3. Materials and methods**

17 *3.1. Experimental setup*

18 Runoff experiments were conducted in August–September 2003, thus during the
19 summer rainy season. At five locations in two sites (Mheni and Sesemat) with a varying
20 slope gradient, roughness and herbaceous cover, two $3 \times 3 \text{ m}^2$ plots were laid out next to
21 each other, one around an isolated *E. racemosa* shrub and one around an isolated *A.*
22 *etbaica* shrub (in total four plots in Mheni and six in Sesemat) (Fig. 2; Table 1). The plot
23 boundaries were open, allowing water and sediment transfer from surrounding zones.
24 In a first experiment, 28 marked tracer seeds were dropped from a height of 0.10 m
25 along the contour coinciding with the upper limit of each runoff plot at 0.10 m intervals
26 (*inflow* set). Ten seeds marked in a different way were deposited under the shrub crown

1 of each plot simulating seed dispersal by birds (*outflow* set). This was accomplished by
2 releasing individual seeds from random positions along branches in the upper half of the
3 crown, where frugivorous birds were observed perching most frequently. The seeds of
4 both inflow and outflow sets were collected at the end of the rainy season (end
5 September 2003) and their final locations were recorded. Coordinates of seeds
6 recorded after individual rainfall events and the patterns of small rills, flow lines and
7 displaced silt and organic matter observed in the field were used to link final locations of
8 tracers with original positions. The component of the distance parallel to the contour
9 between the initial tracer position and the shrub axis (= the distance between the seed
10 and the shrub center along the upper limit of the runoff plot) will further be referred to as
11 the 'horizontal distance'. Inflow seeds were considered to have moved if the Euclidean
12 distance between their initial and final position was greater than 0.10 m. Rainfall events
13 were measured with simple, open pluviometers installed at each location and had a
14 maximum intensity of $60 \text{ mm} \cdot \text{h}^{-1}$ for a duration of 30 minutes during the experiment.
15 Only six of these events occurred between the start and the end of the experiment, three
16 in both sites. The rest of the precipitation was delivered by daily drizzles, which could
17 not be quantified, but which did not cause surface runoff either, as observed in the field.
18 To test the effect of mulch on seed retention capacity, the mulch under the shrubs in the
19 Mheni plots was removed in a third experiment and ten marked seeds were deposited
20 under each crown at equal intervals on a circle around the shrub center with a half crown
21 diameter radius. Because of a lack of adequate maximum hourly rain intensity data
22 (Nyssen et al., 2004), rainfall simulation experiments were conducted with an extreme
23 intensity of $90\text{--}120 \text{ mm} \cdot \text{h}^{-1}$ for a ten minute duration by pouring 60 l water over every
24 shrub through a 5 mm mesh wire frame.

25 All *Olea* seeds used in the experiments were viable (determined by means of a floating
26 test), regurgitated or defecated seeds collected from nearby forest relics. Mean

1 ellipsoid-ovoid dimensions of the seeds (based on a random sample $n = 300$ regurgitated
2 seeds) were: width $W_s = 6$ mm, height $H_s = 6$ mm and length $L_s = 8$ mm with a volume V_s
3 $= 151 \text{ mm}^3$ (0.15 cc) and mass $M_s = 225$ mg. The mean flatness index $[Fl_s = (L_s + W_s) \cdot$
4 $(2H_s)^{-1}]$ and eccentricity index $[El_s = L_s \cdot W_s^{-1}]$ (Poesen, 1987; Cerda and García-Fayos,
5 2002) were 1.17 and 1.33 respectively, both indicating an almost spherical shape.

6

7 (Insert Fig. 2)

8

9 (Insert Table 1)

10

11 Average slope gradient Δ ($^\circ$) was calculated from four Suunto inclinometer
12 measurements perpendicular to the contour in each plot. Slope roughness CR was
13 calculated from five parallel measurements per plot using Saleh's chain roughness
14 method (1993) according to the formula:

15

$$16 \quad CR = (L - G) \cdot L^{-1}$$

17

18 where L is the full length of the chain (3 m with a link length of 0.04 m) and G the
19 horizontal distance in m between chain ends when placed on the soil perpendicular to
20 the slope contour. Maximum height H (m), mean crown diameter ϕ_{crown} (m) and mean
21 diameter at the coppice stool or stem base ϕ_{base} (m) of the shrub in each plot were
22 measured. Because of the multi-stemmed nature of most shrubs and the occurrence of
23 secondary, smaller species within the coppice stool, the total number of stems N_{stems} was
24 also counted. Crown density ρ_{crown} was estimated on an ordinal scale ranging between
25 one (open) and five (very dense). In a similar way, the micro-topographic structure

1 under the shrub was estimated, each shrub receiving a score between zero (no mound)
2 and two (large mound, approximately 0.2 m high) (see Aerts et al., 2005).

3

4 3.2. Data analysis

5 A small amount of inflow tracer seeds was not recovered at the end of the experiments
6 (Table 2). Although they could have been eaten by rodents in theory, they were
7 considered to be displaced since post-dispersal seed predation is restricted to narrow
8 strips along stone bunds in the protected areas, independent of shrubs (R. Aerts,
9 unpublished data) and all runoff plots were located > 2 m from these structures.

10 The average number of displaced tracer seeds (including those not recovered) was
11 compared between sites and shrub species using the *t*-test for independent samples
12 after Levene's test for homoscedasticity (equal variances are not assumed when $p_{Levene} <$
13 0.01 and in such cases unequal variance *t*-values were used). The relationship between
14 the displacement rate R_{si} (%) and slope and shrub variables was assessed using the
15 Pearson product moment correlation coefficient *r* for quantitative variables and
16 Spearman's rank correlation coefficient r_s for ordinal variables (see Table 3). Logistic
17 regression was used to predict the probability of inflow tracer seed translocation in Mheni
18 ('moved' versus 'not moved') based on their initial position in relation to the shrub axis.

19 The relationship between downslope tracer seed displacement s_i (m) in Mheni (only for
20 recovered tracers) and three measures of horizontal distance between the initial tracer
21 position and the shrub axis (absolute distance $|dx|$ in m and relative distances $|dx| (\phi_{base})|$

22 and $|dx| (\phi_{crown})|$ expressed in coppice stool base width ϕ_{base} and shrub crown diameter

23 ϕ_{crown} respectively) was analysed using linear regression. Levels of significance for these

24 regressions were obtained by *F*-tests derived from analysis of variance. s_i was square-

25 root transformed to $s_i^{0.5}$ before analysis to ensure homogeneity of variances. All

1 statistical analyses were carried out with SPSS 11.0 for Windows (SPSS Inc., Chicago,
2 IL.)

4. Results

4.1. Inflow

6 During the observed rainy season, 37% of the seeds deposited in the bare inter-plant
7 areas were translocated by surface runoff or concentrated flows, and none of these
8 seeds were deposited under shrub crowns (Fig. 3; Table 2). The tracer displacement R_{Si}
9 was fairly limited in the Sesemat site, where only 21% of the inflow seeds were found at
10 an euclidean distance greater than 0.10 m from the upper limit of the runoff plots. Seed
11 movement was significantly higher in Mheni (61%) ($p_{Levene} = 0.148$; $t_{3.8} = 3.028$; $p =$
12 0.042) although the site had a lower average slope gradient with a comparable slope
13 roughness (Table 2). Average displacement rate did not differ significantly between
14 *Euclea* (41%) and *Acacia* (34%) plots ($p_{Levene} = 0.316$; $t_{6.5} = 0.414$; $p = 0.692$). The
15 displacement rate showed low correlations with shrub and slope variables (Table 3).
16 Over both sites, only the shrub crown diameter ϕ_{crown} showed a weak significant negative
17 correlation with the tracer displacement ($r = -0.57$, $p = 0.089$). Shrubs with a high
18 number of stems had a high base diameter ($r = 0.730$; $p = 0.016$), typically separating *E.*
19 *racemosa* from *A. etbaica* shrubs (Table 1). Taller shrubs had a wider crown ($r = 0.667$;
20 $p = 0.035$). Both relations can be explained by the many mutual interactions between
21 various size variables of shrubs (size relationships).

23 (Insert Tables 2 and 3)

24 (Insert Fig. 3)

1 Further analyses were only carried out for the Mheni plots where slightly more
 2 precipitation was detected in the pluviometers and seed displacement was more
 3 pronounced. Logistic regression showed that the probability of individual seeds to be
 4 translocated by runoff depends on the horizontal distance $|dx|$ between the initial position
 5 of the seed and the shrub axis (model $\chi^2_{1.0} = 4.449$, $p = 0.035$, regression coefficient
 6 $B(dx) = 4.94$) and, as shown before, not on the overall plot characteristics in terms of
 7 shrub or slope variables. Regression analysis furthermore demonstrated strong linear
 8 relationships between the actual extent of the downhill translocation s_i and the horizontal
 9 distance of the seeds from the shrub centers (Table 4), although most of the regression
 10 R^2 values were rather low (Fig. 4.). The absolute horizontal distance from the shrub axis
 11 expressed in shrub crown diameters ($|dx| (\phi_{crown})$) provided the best fit for both the full
 12 and the reduced (displaced seeds only) dataset. Thus, seeds far away from a shrub
 13 were more likely to be transported by surface runoff, and if translocated, usually over a
 14 larger distance than seeds nearer to the center of a shrub (Fig. 5).

15

16 (Insert Table 4)

17 (Insert Fig. 4 & Fig. 5)

18

19 4.2. Outflow and simulated rainfall

20 In the outflow experiment, there was no shrub that lost any of the seeds deposited under
 21 its crown in any replication (Table 2). In the second experiment, simulated rainfall after
 22 mulch removal resulted in an average seed loss Q_r of nearly 33%, but this average was
 23 strongly influenced by a seed loss of 70% in only one plot (1.1), compared to a moderate
 24 20% in the other three plots (Table 2).

25

5. Discussion

A high probability for seed displacement is reported by Bochet and García-Fayos (2004) on slopes with a gradient above 45° in semiarid Mediterranean Europe. In the Mheni and Sesemat plots, all with a substantially lower slope gradient ranging between 8° and 18° (Table 1), the overall displacement rate of tracer seeds deposited in the spaces between shrubs amounted to nearly 40% (Table 2). Although the quantity of seed displacement may seem to be exceptionally high for slopes with such a comparatively low gradient, Cerda and García-Fayos (2002) recorded a high susceptibility for removal by water erosion in seeds with a mass above 50 mg on slopes with an angle of 11° under laboratory conditions. In that study, seeds greater than the threshold of 50 mg of weight tended to be spherical in form, which favours rolling down the slope. Not the relative high seed mass of *O. europaea* (mean = 225 mg) but its ovoid shape may therefore explain the high displacement.

Seed displacement rates were higher in the Mheni site, which had a lower slope gradient than Sesemat (Table 2). This observation is in agreement with the results obtained earlier by Cerda and García-Fayos (1997) and Nyssen et al. (2000), where seed losses and stone tracer displacements were negatively correlated to the slope gradient. In this case, some upslope catchment variables, such as a higher grazing pressure and less vegetation cover, and not the slope angle as such, may be responsible for generating more runoff in Mheni and are thus more likely to explain the contrast.

Species identity of the examined shrubs had no significant effect on seed deposition or loss by runoff, and neither did shrub or slope variables at plot level (Table 3). On the other hand, sharp contrasts were found between tracer seeds initially positioned in the bare inter-plant areas and those deposited under the microenvironments of shrubs (Fig. 3). Despite the relatively high displacement rates of seeds in the inter-shrub areas, not a single seed moved out of its protective shrub cover during the first runoff experiment.

1 Even extreme rainfall simulated over shrubs after removal of their sub-canopy mulch
2 layer failed to translocate more than one third of the seeds from positions under shrub
3 crowns to areas outside the shrub perimeters (Table 2). Under shrub canopies,
4 mulch/mound characteristics control surface wash and crown characteristics limit seed
5 displacement by splash erosion. Both factors are therefore responsible for the retention
6 of seeds under shrubs. This observation corroborates with numerous studies that state
7 that both below- and aboveground characteristics of vegetation are of particular
8 importance with respect to soil erosion, runoff and as a result, seed loss control (e.g.
9 Gysels and Poesen, 2003; Rodríguez et al., 2005).

10 Although it may seem contra-intuitive that shrubs exert influence over runoff and seed
11 movement upslope, previous studies already showed that mounds under shrubs tend to
12 divert runoff water rather than allowing the surface flow through the shrub bases (Bochet
13 et al., 2000). Shrubs and associated micro-topographic structures therefore divert seeds
14 away from their crowns, mounds or mulch layers. Seeds are consequently embedded in
15 the bare inter-plant sediment and not in the mulch under the shrubs, an effect observed
16 noticeably in the left half of plot 1.1 (Fig. 3a). Shrubs do cause some sediment retention
17 (especially *E. racemosa*), but in the context of secondary dispersal, they are diverting
18 seeds to unsuitable germination and seedling survival sites, given that no *Olea*
19 recruitment occurs between the shrubs (Aerts et al., 2005). Since micro-topographic
20 structures under shrubs have been shown to facilitate water and nutrient storage by
21 plants on slopes (Bochet et al., 1999, 2000) and in dry savannas (Vetaas, 1992),
22 diversion of seeds by these very structures may prove to be a successional
23 disadvantage for *O. europaea* regeneration.

24

25 **6. Conclusions**

1 In contradiction to expectation, seed trapping efficiency of multi-stemmed shrubs with
2 mulch-rich mounds such as *E. racemosa* is not superior to the efficiency of few-stemmed
3 shrubs like *A. etbaica*. Micro-topographic structures under either species cause runoff
4 water to be diverted to rills next to shrubs. Seeds in these flows are embedded in the
5 sediment deposited in the bare inter-plant areas, and not in the mulch under the
6 protective crowns of the shrubs. However, seeds deposited under shrubs are not likely
7 to be lost by surface wash, even under extreme rainfall conditions.

8 Since *O. europaea* recruits were exclusively found under shrubs and not in the spaces
9 between shrubs in the studied field sites (Aerts et al., 2005), it appears plausible that
10 seeds deposited in the open field are resource losses: propagules almost without doubt
11 lost to post-dispersal seed predation, unsuccessful germination or seedling predation
12 and mortality. Recovery of African wild olive in degraded shrubland communities in
13 northern Ethiopia therefore most likely depends upon directed dispersal of seeds under
14 shrubs by frugivorous birds, a process which according to Wenny (2001) may be seen
15 in particular among animal-dispersed plants and in arid ecosystems or successional
16 areas. Structural traits of shrubs and their suitability as a bird perch or the presence of a
17 fruit reward may influence the movement patterns of avian seed dispersers between
18 forest relics and forest restoration areas and for that reason determine the spatial pattern
19 of African wild olive regeneration.

20

21 **Acknowledgements**

22 This research was funded by a Ph.D. grant of the Flemish Interuniversity Council (VLIR)
23 and by the VLIR-OI project 'Forest Rehabilitation through Natural Regeneration in Tigray,
24 northern Ethiopia' of the Katholieke Universiteit Leuven (Belgium) and Mekelle University

- 1 (Ethiopia). Constructive comments on an earlier draft of this paper by Robert O'Carroll
- 2 and two anonymous reviewers are gratefully acknowledged.

1

2 **References**

- 3 Aerts, R., Van der Borght, I., November, E., Behailu, M., Hermy, M., Muys, B., 2005. The
4 importance of early successional shrubs for recruitment of African wild olive (*Olea*
5 *europaea* subsp. *cuspidata*) in central Tigray, Ethiopia. In: Ghazanfar, S.A., Beentje,
6 A.J., (Editors), African Plants. Biodiversity, Ecology, Phytogeography and Taxonomy.
7 Royal Botanic Gardens, Kew, (in press).
- 8 Aerts, R., Wagendorp, T., November, E., Behailu, M., Deckers, J., Muys, B., 2004.
9 Ecosystem thermal buffer capacity as an indicator of the restoration status of protected
10 areas in the Northern Ethiopian highlands. Restoration Ecology 12(4), 586-596.
- 11 Alcántara, J.M., Rey, P.J., Valera, F., Sánchez-Lafuente, A.M., 2000 . Factors shaping
12 the seedfall pattern of a bird-dispersed plant. Ecology 81(7), 1937-1950.
- 13 Asefa, D.T., Oba, G., Weladji, R.B., Colman, J.E., 2003. An assessment of restoration of
14 biodiversity in degraded high mountain grazing lands in Northern Ethiopia. Land
15 Degradation & Development 14(1), 25-38.
- 16 Bochet, E., García-Fayos, P., 2004. Factors controlling vegetation establishment and
17 water erosion on motorway slopes in Valencia, Spain. Restoration Ecology 12(2), 166-
18 174.
- 19 Bochet, E., Poesen, J., Rubio, J.L., 2000. Mound development as an interaction of
20 individual plants with soil, water erosion and sedimentation processes on slopes. Earth
21 Surface Processes and Landforms 25(8), 847-867.
- 22 Bochet, E., Rubio, J.L., Poesen, J., 1999. Modified topsoil islands within patchy
23 Mediterranean vegetation in SE Spain. Catena 38(1), 23-44.
- 24 Cain, M.L., Milligan, B.G., Strand, A.E., 2000 . Long-distance seed dispersal in plant
25 populations. American Journal of Botany 87(9), 1217-1227.
- 26 Cerda, A., García-Fayos, P., 2002. The influence of seed size and shape on their

1 removal by water erosion. *Catena* 48(4), 293-301.

2 Cerda, A., García-Fayos, P., 1997. The influence of slope angle on sediment, water and
3 seed losses on badland landscapes. *Geomorphology* 28(2), 77-90.

4 Couvreur, M., Christiaen, B., Verheyen, K., Hermy, M., 2004. Large herbivores as mobile
5 links between isolated nature reserves through adhesive seed dispersal. *Applied*
6 *Vegetation Science* 7(2), 229-236.

7 Couvreur, M., Cosyns, E., Hermy, M., Hoffmann, M., 2005. Complementarity of epi- and
8 endozoochory of plant seeds by free ranging donkeys. *Ecography* 28(1), 37-48.

9 Darbyshire, I., Lamb, H., Umer, M., 2003. Forest clearance and regrowth in Northern
10 Ethiopia during the last 3000 years. *The Holocene* 13(4), 537-546.

11 De Villiers, A.J., Van Rooyen, M.W., Theron, G.K., 2001. The role of facilitation in
12 seedling recruitment and survival patterns, in the Strandveld Succulent Karoo, South
13 Africa. *Journal of Arid Environments* 49(4), 809-821.

14 Duncan, R.S., Chapman, C.A., 1999. Seed dispersal and potential forest succession in
15 abandoned agriculture in tropical Africa. *Ecological Applications* 9(3), 998-1008.

16 Duncan, R.S., Duncan, V.E., 2000. Forest succession and distance from forest edge in
17 an Afro-tropical grassland. *Biotropica* 32(1), 33-41.

18 Feoli, E., Vuerich, L.G., Zerihun, W., 2002. Evaluation of environmental degradation in
19 Northern Ethiopia using GIS to integrate vegetation, geomorphological, erosion and
20 socio-economic factors. *Agriculture Ecosystems & Environment* 91(1-3), 313-325.

21 Franco-Pizaña, J.G., Fulbright, T.E., Gardiner, D.T., Tipton, A.R., 1996. Shrub
22 emergence and seedling growth in microenvironments created by *Prosopis glandulosa*.
23 *Journal of Vegetation Science* 7(2), 257-264.

24 Friis, I., 1992. Forests and forest trees of Northeast Tropical Africa. Royal Botanic
25 Gardens, London.

26 García, D., Obeso, J.R., 2003. Facilitation by herbivore-mediated nurse plants in a

1 threatened tree, *Taxus baccata*: local effects and landscape level consistency.
2 Ecography 26(6), 739-750.

3 García-Fayos, P., Cerda, A., 1997. Seed losses by surface wash in degraded
4 Mediterranean environments. Catena 29(1), 73-83.

5 Gysels, G., Poesen, J., 2003. The importance of plant root characteristics in controlling
6 concentrated flow erosion rates. Earth Surface Processes and Landforms 28(4), 371-
7 384.

8 Hampe, A., 2004. Extensive hydrochory uncouples spatiotemporal patterns of seedfall
9 and seedling recruitment in a 'bird-dispersed' riparian tree. Journal of Ecology 92(5), 797-
10 807.

11 Holl, K.D., 2002. Effect of shrubs on tree seedling establishment in an abandoned
12 tropical pasture. Journal of Ecology 90(1), 179-187.

13 Howe, H.F., 1990. Seed dispersal by birds and mammals: implications for seedling
14 demography. In: Bawa, K.S., Hadley, M., (Editors), Reproductive ecology of tropical
15 forest plants. Unesco, Paris, pp. 191-218.

16 Jordano, P., 2000. Fruits and frugivory. In: Fenner, M., (Editor), Seeds. The ecology of
17 regeneration in plant communities. CAB International, Oxon, pp. 125-162.

18 Mengistu, T., Teketay, D., Hulten, H., Yemshaw, Y., 2005. The role of enclosures in the
19 recovery of woody vegetation in degraded dryland hillsides of Central and Northern
20 Ethiopia. Journal of Arid Environments 60(2), 259-281.

21 Moro, M.J., Pugnaire, F.I., Haase, P., Puigdefabregas, J., 1997. Mechanisms of
22 interaction between a leguminous shrub and its understorey in a semi-arid environment.
23 Ecography 20(2), 175-184.

24 Negash, L., 2003. Vegetative propagation of the threatened African wild olive [*Olea*
25 *europaea* L. subsp. *cuspidata* (Wall. ex DC.) Cififieri]. New Forests 26(2), 137-146.

26 Nyssen, J., Poesen, J., Moeyersons, J., Deckers, J., Haile, M., Lang, A., 2004. Human

1 impact on the environment in the Ethiopian and Eritrean highlands - a state of the art.
2 Earth-Science Reviews 64(3-4), 273-320.

3 Nyssen, J., Poesen, J., Haile, M., Moeyersons, J., Deckers, J., 2000. Tillage erosion on
4 slopes with soil conservation structures in the Ethiopian highlands. Soil and Tillage
5 Research 57(3), 115-127.

6 Ozinga, W.A., Bekker, R.M., Schaminee, J.H., Van Groenendael, J.M., 2004. Dispersal
7 potential in plant communities depends on environmental conditions. Journal of Ecology
8 92(5), 767-777.

9 Poesen, J., 1987. Transport of rock fragments by rill flow - a field-study. Catena, 35-54.

10 Pugnaire, F.I., Haase, P., Puigdefábregas, J., 1996. Facilitation between higher plant
11 species in a semiarid environment. Ecology 77(5), 1420-1426.

12 Rey, F., 2004. Effectiveness of vegetation barriers for marly sediment trapping. Earth
13 Surface Processes and Landforms 29(9), 1161-1169.

14 Rey, P.J., Alcántara, J.M., 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea*
15 *europaea*): connecting patterns of seed dispersal to seedling establishment. Journal of
16 Ecology 88(4), 622-633.

17 Rodriguez, A.R., Mora, J.L., Arbelo, C., Bordon, J., 2005. Plant succession and soil
18 degradation in desertified areas (Fuerteventura, Canary Islands, Spain). Catena 59(2),
19 117-131.

20 Saleh, A., 1993. Soil roughness measurement: chain method. Journal of Soil and Water
21 Conservation 48, 527-529.

22 Stiles, E.W., 2000. Animals as seed dispersers. In: Fenner, M., (Editor), Seeds. The
23 ecology of regeneration in plant communities. CAB International, Wallingford, UK, pp.
24 111-124.

25 Taddese, G., 2001. Land degradation: a challenge to Ethiopia. Environmental
26 Management 27(6), 815-824.

- 1 Teketay, D., Granström, A., 1997. Seed viability of Afromontane tree species in forest
2 soils. *Journal of Tropical Ecology* 13, 81-95.
- 3 Tekle, K., Bekele, T., 2000. The role of soil seed banks in the rehabilitation of degraded
4 hillslopes in Southern Wello, Ethiopia. *Biotropica* 32(1), 23-32.
- 5 Turner, I.M., Corlett, R.T., 1996. The conservation value of small, isolated fragments of
6 lowland tropical rain forest. *Trends in Ecology & Evolution* 11(8), 330-333.
- 7 Valiente-Banuet, A., Ezcurra, E., 1991. Shade as a cause of the association between the
8 cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacan
9 Valley, Mexico. *Journal of Ecology* 79(4), 961-971.
- 10 Verdú, M., García-Fayos, P., 2003. Frugivorous birds mediate sex-biased facilitation in a
11 dioecious nurse plant. *Journal of Vegetation Science* 14(1), 35-42.
- 12 Vetaas, O.R., 1992. Micro-site effects of trees and shrubs in dry savannas. *Journal of*
13 *Vegetation Science* 3(3), 337-344.
- 14 Wang, B.C., Smith, T.B., 2002. Closing the seed dispersal loop. *Trends in Ecology &*
15 *Evolution* 17(8), 379-385.
- 16 Wenny, D.G., 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal.
17 *Evolutionary Ecology Research* 3(1), 51-74.
- 18 Willson, M.F., Traveset, A., 2000. The ecology of seed dispersal. In: Fenner, M., (Editor),
19 *Seeds. The ecology of regeneration in plant communities*. CAB International,
20 Wallingford, UK., pp. 85-110.
- 21 Wunderle, J.M., 1997. The role of animal seed dispersal in accelerating native forest
22 regeneration on degraded tropical lands. *Forest Ecology and Management* 99(1-2), 223-
23 235.

Fig. 1. Location of the study area. A and B indicate the selected sites where the experiments were conducted. The FAO-SOTER slope classification is based on the CORE EthioGIS DTM with 200 m resolution (CDE, Bern).

Fig. 2. Open runoff plots 1.1 and 1.2 in Mheni, Ethiopia, around an isolated *Euclea racemosa* (*Er*) and *Acacia etbaica* (*Ae*) shrub respectively. The arrow shows the overall direction of the runoff. Plot sizes are $3 \times 3 \text{ m}^2$ and soil surface slope is 8° .

Fig. 3. Displacement s (m) of *Olea europaea* tracer seeds by surface runoff for (a) plot 1.1 (*Euclea racemosa*) and (b) plot 1.2 (*Acacia etbaica*) in Mheni, Ethiopia. The central circle is the vertical projection of the shrub crown. The curve shows the quadratic regression between the displacement and the horizontal distance to the shrub center. Displacement arrows are indicative. Inflow tracer seeds: ● displaced; ○ not displaced; all outflow tracer seeds (◇) were retained under the shrub crowns.

Fig. 4. Displacement s of *Olea europaea* tracer seeds by runoff in Mheni, Ethiopia, near shrubs that act as natural sediment traps (● *Euclea racemosa*; Δ *Acacia etbaica*) in relation to the horizontal distance from the shrub axis dx expressed (a) in absolute distance (m), (b) relative to shrub base diameter ϕ_{base} and (c) relative to the shrub crown diameter ϕ_{crown} . Trend lines are linear regressions (— *E. racemosa*; --- *A. etbaica*). Only displaced seeds are shown ($n = 58$); eight outliers that moved more than 2 m (2.4–4.6 m) were removed from the figures.

1 Fig. 5. Probability p and magnitude s (m) of *Olea europaea* tracer seed displacement by
2 surface runoff near shrubs in Mheni, Ethiopia, in relation to the horizontal distance dx from
3 the shrub axis expressed in shrub crown diameter ϕ_{crown} after pooling displaced seeds in
4 $1/10^{\text{th}}$ crown diameter distance classes. Eight outliers that moved more than 2 m (2.4–4.6 m)
5 were removed from the figure.

1 **Figures**

2 Fig. 1

3

1 Fig. 2

2

1 Fig. 3 (a, b)

2

1 Fig. 4 (a, b, c)

2

1 Fig. 5

2

3