Journal of Arid Environments 73 (2009) 542–549

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

The effects of exclosures in restoring degraded semi-arid vegetation in communal grazing lands in northern Ethiopia

T. Yayneshet [a,*], L.O. Eik [b], S.R. Moe [c]

[a] Department of Animal, Rangeland, and Wildlife Sciences, Mekelle University, P.O. Box 231, Mekelle, Ethiopia
[b] Department of Animal and Aquacultural Sciences, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432, Aas, Norway
[c] Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432, Aas, Norway

ARTICLE INFO

Article history:
Received 28 January 2008
Received in revised form
21 November 2008
Accepted 4 December 2008
Available online 30 January 2009

Keywords:
Biomass
Diversity
Herbaceous
Rangeland
Tigray
Woody

ABSTRACT

Rangeland degradation is a widespread problem throughout sub Saharan Africa and its restoration is a challenge for the management of many semi-arid areas. This study assessed the effectiveness of exclosures that have been protected from livestock from 5 to 15 years in restoring vegetation in northern Ethiopia. The species composition and diversity of herbaceous and woody plants were higher in the exclosures than in the grazed areas. Species richness responded positively to an increase in herbaceous productivity. The mean aboveground biomass measured inside the exclosures was more than twice that of the adjacent grazed areas and more biomass was produced from the young than the old exclosures. Stem height, canopy height, canopy cover, and browsing capacity of woody species were higher in the exclosures than in the grazed areas. Our study shows that degraded semi-arid vegetation is able to recover in a relatively short time when protected. Extended protection, beyond 8–15 years, reduces herbaceous species diversity and in one of the sites also the herbaceous biomass. Therefore, we suggest a slight shift in management where exclosures protected for longer periods may be moderately used by livestock.

1. Introduction

Rangeland degradation is a widespread problem throughout sub Saharan Africa and its restoration is a challenge for the management of many semi-arid areas. There are two contrasting paradigms explaining the role of herbivores in land degradation in the arid and semi-arid grazing systems. The first paradigm is based on the traditional succession theory that promotes a constant carrying capacity-derived stocking rate as a way to avoid long-term degradation (e.g. Belsky et al., 1993; Sullivan and Rohde, 2002). It gives more emphasis to herbivory while largely ignoring the spatial and temporal variability of ecosystems typical of semi-arid grazing systems (Ellis and Swift, 1988; Westoby et al., 1989). The second paradigm, commonly referred to as the non-equilibrium paradigm, recognizes this variability and ascertains that differences in the impact of herbivores are driven by variability in abiotic factors (Ellis and Swift, 1988; Westoby et al., 1989).

Land degradation in Ethiopia is triggered by population expansion and over-exploitation of the natural resources and degradation is a major threat to sustainable land uses (Hurni et al., 2005). Although not explicitly stated, the problem of land degradation in the semi-arid Tigray region in northern Ethiopia is addressed based on the succession model, in that in some communal areas livestock is completely excluded for an extended number of years (REST, 1998). The restoration success of such efforts is an issue of considerable importance to regional planners, researchers, and producers (Betru et al., 2005; REST, 1998). Despite the fact that such exclosures have been operated in the region for about two decades, empirical data on the effectiveness of these protected areas in restoring vegetation are lacking. Particularly, a clear understanding of the relationship between fallow length and productivity and plant species richness is needed for an effective management.

Depending on the specific ecosystem, previous studies have found complex relationships between species richness and productivity, ranging from the classical 'hump-back shaped' (Waide et al., 1999) to positive, negative or inconsistent relationships (Grace et al., 2007) have been reported. The relationship between species richness and productivity is generally not known for semi-arid areas.

Therefore, this study was carried out with the following objectives: (1) To determine species composition, biomass production, and structure of herbaceous and woody vegetation of different

* Corresponding author. Tel.: +251 4764966064; fax: +251 4764965101.
E-mail addresses: yayneshet.tesfay@umb.no, yayneshet_tesfay@yahoo.com (T. Yayneshet).

0140-1963/$ – see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2008.12.002

fallow age exclosures and adjacent communal grazing areas; and (2) To assess the species diversity of exclosures and identify the pattern of relationship between species richness and productivity of herbaceous vegetation in exclosures.

2. Materials and methods

2.1. Study site location

The study sites were located in Tembien (13°41–13°43 N and 38°57–39°00 E), and Wukro (13°39–13°47 N and 39°30–39°34 E) in Tigray region, northern Ethiopia. Both sites are characterized by semi-arid climate. Average annual rainfall and temperature in Tembien for 1973–1979 and 1995–2005 were 519 mm and 21.6 °C, respectively. However, the average annual rainfall for the period since the exclosures were created was 585 mm. The corresponding values for 1992–2005 (covers the period when the exclosures were established) in Wukro were 500 mm and 19.4 °C, respectively. At both sites, more than 90% of the rainfall occurs during the long summer rainy season from late June to early September. The dry season usually extends from October to February, although when the short rains fail the dry season can extend to May or June. The short rain season in March and April is not observed as frequently as the long rain and is generally characterized by a coefficient of variation as high as 55% among years (Meze-Hauske, 2004). Altitude in Tembien and Wukro ranges between 1780–1980 and 2050–2250 m above sea level, respectively.

The dominant soil types include Cambisols, Leptosols, and Regosols (FAO, 1998). The vegetation is typical of the East African montane area that is part of the Sudano–Sahelian transition subzone and common plant formations include mesophyllic deciduous woodland, mixed evergreen and deciduous open woodland (Le Houérou, 1989).

2.2. Exclosure description and sampling

An exclosure refers to a specific land unit that is protected from the activities of a particular class of animals using appropriate barriers such as fencing to control the influence of animals (Young, 1958). The exclosures, also known by some authors (e.g. Mengistu et al., 2005) as enclosures, in the study areas were effectively protected from tree cutting and grazing by domestic animals in the early and late 1990s (Betru et al., 2005). These protected communal areas range in size from 20 to 700 ha (District Agricultural Office, Unpublished). Prior to protection, the exclosures were severely degraded supporting sparse unpalatable vegetation with little grazing value (Betru et al., 2005). The priority areas were identified by the local agricultural experts and user groups who agreed to strictly protect them from any form of grazing, manual harvesting of grass, and tree cutting. As the exclosures are not fenced, guards are hired by the local administration on a food-for-work basis. Some predators (mostly hyena and foxes), rabbits, and birds are present in the exclosures, although large wild ungulates are generally absent due to the severe land degradation and long civil war history of this region.

The two sites (Tembien and Wukro) were selected because both sites have an extensive exclosure system. A list of exclosures established during the 1990s was obtained from the respective local Agricultural Offices and grouped into two broad categories based on their fallow ages (years since effective protection initiated) from less than 8 years (henceforth termed 'young exclosures') to more than 12 years (henceforth termed 'old exclosures'). At the time of this study, the youngest exclosures were only 5 years old while the oldest exclosures were 15 years old and the 8-year cut-off between the young and old exclosures was arbitrarily determined. From each site and each age category, three exclosures of 50–120 ha in size and 3–10 km apart (aerial distance, measured using Garmin GPS 72 (Garmin International Inc., USA)) were then randomly selected for sampling of herbaceous and woody vegetation.

Three parallel line transects of 1200 m long and 200–500 m apart were designated in each exclosure and immediately outside it. Nine 10 × 10 m plots, used to sample woody species canopy cover, composition, diversity, and structure, were located along each transect at an interval of 100 m. Previous studies have shown that plot sizes $\leq$100 m^2 are effectively used for sampling shrub dominated vegetation in the present study area (Asefa et al., 2003; Abebe et al., 2006; Aerts et al., 2006). The areas outside the exclosures are subjected to year round grazing by livestock.

To assess herbaceous species composition, biomass, and diversity inside and outside the exclosures, six 0.5 × 0.5 m small quadrats were randomly nested within the larger 100 m^2 plots used for woody species. During each sampling period, two of these small 0.25 m^2 quadrats were randomly chosen for sampling. Two sampling events (one for woody and one for herbaceous vegetation) were carried out for each season. Three sampling seasons were conducted during the long rainy season (mid September), dry season (end of January), and short rainy season (mid April). The first sampling was conducted during vegetative growth stage of both browse and grass species, the second during pod dehiscence of browse species and seedshedding and senescence of grass species, and the third when the majority of browse species initiated new regrowth but when grass species were still at senescence stage. Sampling started in September 2004 and ended in May 2006.

Herbaceous aboveground biomass production was estimated using the destructive method (t'Mannetje and Jones, 2000). Grass and forb materials rooted within the 0.25 m^2 frame were harvested to ground level using sickle and their fresh biomass immediately weighed using a 0.1 g scale. About 20–30% of this biomass was retained for oven drying (105 °C for 24 h) and used to estimate dry matter. The amount of forage utilized by grazing livestock was estimated following the procedures outlined by Cook and Stubbendieck (1986). An estimate of aboveground productivity of herbaceous species was obtained as the difference in aboveground biomass measured from the 0.25 m^2 quadrats during the dry and main rainy seasons (McNaughton, 1985). The species composition of woody species was assessed using the quadrat count method (t'Mannetje and Jones, 2000) while woody vegetation structure was analyzed by measuring canopy diameter, canopy height, and stem height of the woody species using a 5-m long graduated metal pole. Canopy cover refers to the proportion of the ground area covered by the vertical projection of the canopy. Stem height was measured as the total height of the plant from the ground level to the tip of the canopy and measurements were classified into nine classes of 0.5 m intervals. These data were used to compute browsing unit (BU), browsing capacity (BC), and tree equivalent (TE). One BU is a tree or shrub that is consumed by goats and is either 1.5 m tall or has browse within 1.5 m of ground level (Teague et al., 1981). BC refers to the productivity of a homogenous vegetation unit that is grazed or browsed and it is expressed as the area of land required to maintain a single animal unit over time without causing deterioration to the vegetation and soils (Booysen, 1967). TE is a term used in relation to a tree or shrub that is 1.5 m tall (Teague et al., 1981). BU, BC, and TE were computed according to Beckerling et al. (1995). The BC value was expressed in terms of Small Stock Unit (SSU), referring to smaller livestock such as sheep and goats approximately 1/6 of the size of a large ruminant (Beckerling et al., 1995).

The species composition of exclosures and grazed areas, and the young and old exclosures was compared using the Sørensen's Similarity Index and species diversities in the exclosures and grazed areas were computed using the Shannon–Weiner Index (Krebs, 1999). The Shannon–Weiner Index (H) was converted to effective number of species diversity using the following formula (Jost, 2006): $N_1 = \text{Exp}\ (H')$. Where: N_1 = Effective number of species; H' = Shannon–Weiner function. Whittaker's β-diversity, computed using the multiplicative approach, was used to compare the species diversity of exclosures and grazed areas, different sites and fallow ages. Species richness was considered as the total number of species per plot (Polley et al., 2005).

For each plant species duplicate specimens that included leaves, flowers, fruits, and seed heads were collected during the main rainy season for further identification at the National Plant Herbarium of the Addis Ababa University in Ethiopia.

2.3. Experimental design and data analysis

We used a model that included year, season, protection, fallow age, site, and their interactions for herbaceous aboveground biomass analysis. For BU, BC, and TE data, only year, protection, fallow age, site, and their interactions were included in the model, as browsing capacity of different land units is commonly expressed on a yearly basis. Exclosures were used as random blocking factors without interaction. Woody species stem height, canopy height, and canopy cover (arc-sine square root transformed) data were analyzed with a separate repeated measure analysis of variance with year, fallow age, protection, and site as independent variables and season as the repeated measure was applied. A repeated design was used because the same individual plants were repeatedly measured during each of the sampling seasons. The Huynh–Feldt epsilon was used to check violation of the sphericity assumptions. Data were analyzed using SAS (SAS Institute, 2001) and Tukey's HSD tests were used for post-hoc multiple comparisons.

Species composition and diversity data were analyzed using the nonparametric Kruskal–Wallis test. Both linear and nonlinear regressions were used to determine the relationship between species richness and productivity of the herbaceous layer. Significant differences were declared at $P < 0.05$ and tendency to significance accepted at $0.05 < P < 0.1$.

3. Results

3.1. Herbaceous and woody species composition

A total of 61 different herbaceous and 34 woody species were recorded in the two sites (Annex 1a and b). The dominant herbaceous species identified from the exclosures belonged to the genera *Aristida*, *Eragrostis*, *Cenchrus*, *Hyparrhenia* and *Sporobolus* while *Cynodon*, *Eragrostis* and *Tetrapogon* dominated the grazed areas. *Acacia etbaica* and *Dichrostachys cinerea* were the dominant species in the exclosures while *A. etbaica* and *Euclea racemosa* dominated the grazed areas.

Sørensen's Similarity Index between the exclosures and the grazed areas were 0.45 and 0.46 for herbaceous and woody species, respectively (Table 1). Herbaceous and woody species composition

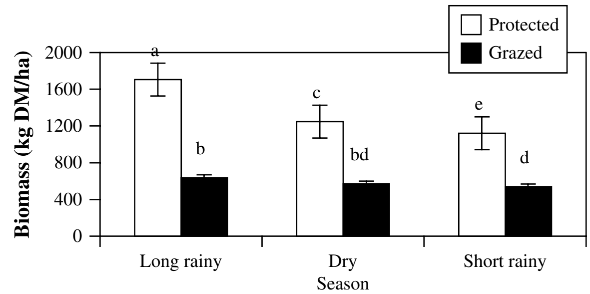

Fig. 1. Effects of protection and season on mean (±SE) herbaceous biomass production (kg DM/ha) of exclosures in the semi-arid Tigray region, northern Ethiopia. Bars with different letters significantly ($P < 0.05$) differ from each other.

differed between the exclosures and the grazed areas (herbaceous: $\chi^2 = 6.36$, DF = 1, $P = 0.01$; woody: $\chi^2 = 8.90$, DF = 1, $P < 0.003$). The Similarity Index for herbaceous and woody species composition for the young and old exclosures was 0.54 and 0.62, respectively. Site affected woody species composition ($\chi^2 = 3.86$, DF = 1, $P = 0.05$) while this effect on herbaceous species composition showed tendency to significance ($\chi^2 = 3.14$, DF = 1, $P = 0.08$).

3.2. Herbaceous aboveground biomass and utilization by livestock

Biomass was affected by season ($F_{2,24} = 79.2$, $P < 0.001$), site ($F_{1,24} = 81.8$, $P < 0.001$), year × site ($F_{1,24} = 4.3$, $P = 0.05$), site × age ($F_{1,24} = 5.9$, $P = 0.02$), protection ($F_{1,24} = 921.6$, $P < 0.001$), season × protection ($F_{2,24} = 38.1$, $P < 0.001$), and site × protection ($F_{1,24} = 5.5$, $P = 0.03$).

The mean biomass measured in the exclosures was more than twice of the adjacent grazed areas during all sampling periods (Fig. 1). The proportion of biomass consumed by grazing animals ranged from 51 to 69% and livestock removed a higher proportion of the standing aboveground biomass during the long rainy season than during subsequent lean periods. The old exclosures in Tembien, yielded lower biomass than the young exclosures while in Wukro fallow age did not influence biomass production of exclosures (Fig. 2).

3.3. Species diversity and richness–productivity relationship

Herbaceous species diversity was higher in the exclosures than in the adjacent grazed areas ($\chi^2 = 11.8$; DF = 1; $P < 0.0001$) (Table 2). For herbaceous species, the young exclosures were more diverse than the old exclosures ($\chi^2 = 5.34$; DF = 1; $P = 0.0208$). Woody species diversity differed between the exclosure and the grazed areas ($\chi^2 = 38.3$; DF = 1; $P < 0.0001$). However, woody species diversity did not differ between the young and old exclosures ($\chi^2 = 2.3$; DF = 1; $P = 0.13$). Only herbaceous species diversity was influenced by season ($P < 0.05$) and more diverse species were recorded during the long rainy than during the dry and short rainy seasons (Table 3).

Table 1
Effects of exclosure (protected versus grazed), fallow age (young versus old) and site (Tembien versus Wukro) on herbaceous and woody species Similarity Index[a] in the semi-arid Tigray region, northern Ethiopia (Mean ± SE).

Vegetation	Protection		Fallow age		Site	
	Protected versus grazed	P	Young versus old	P	Tembien versus Wukro	P
Herbaceous	0.45 ± 0.03	0.012	0.54 ± 0.05	0.485	0.40 ± 0.08	0.077
Woody	0.46 ± 0.07	0.003	0.62 ± 0.10	0.658	0.44 ± 0.03	0.050

SE = standard error of the means. Mean values calculated from $n = 6$. P, probability.
[a] Sørensen's Similarity Index.

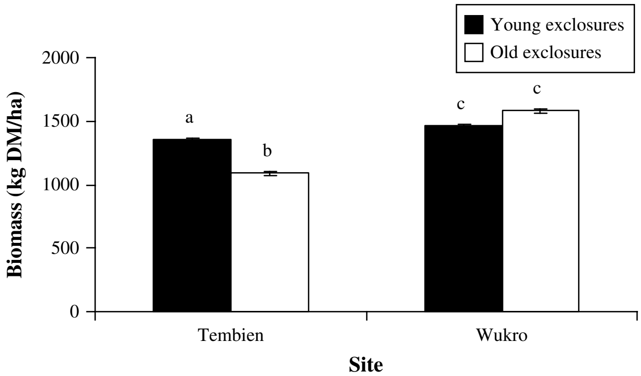

Fig. 2. Effect of fallow age on mean herbaceous biomass production (kg DM/ha) of exclosures in the semi-arid Tigray region, northern Ethiopia. Bars with different letters significantly ($P < 0.05$) differ from each other.

Species richness responded positively to increased productivity of the exclosures at both sites, explaining 94% of the variance in species richness in Tembien and 69% in Wukro (Fig. 3).

3.4. Woody vegetation structure and browsing capacity

Protection influenced stem height ($F_{1,6} = 229.4$, $P < 0.0001$), canopy height ($F_{1,6} = 1023.4$, $P < 0.0001$) and canopy cover ($F_{1,6} = 7.9$, $P < 0.0001$) of woody species (Table 4). Site influenced stem height ($F_{1,6} = 7.65$, $P = 0.03$) and canopy height ($F_{1,6} = 13.03$, $P = 0.04$) while fallow age only affected stem height ($F_{1,6} = 10.99$, $P = 0.001$). Season (data not shown) influenced the three measured variables (stem height: $F_{5,30} = 107.95$, $P < 0.0001$; canopy height: $F_{5,30} = 175.07$, $P < 0.0001$; canopy cover: $F_{5,30} = 9.68$, $P = 0.02$). Season and protection interacted in influencing stem height ($F_{5,30} = 122.29$, $P < 0.0001$) and canopy height ($F_{5,30} = 162.73$, $P < 0.0001$).

Trees taller than 1 m were present only in small numbers in the grazed areas (Fig. 4). Average stem height was higher ($P < 0.001$) in the exclosures than in the adjacent grazed areas (1.3 versus 0.9 m).

The available browse (BU) was higher in the exclosures than in the adjacent grazed areas in Tembien ($F_{1,4} = 770.50$; $P < 0.0001$) while in Wukro protection did not lead to increased BC ($F_{1,4} = 3.88$; $P = 0.1204$) (Table 5). Protection improved the BC of the exclosures in Tembien ($F_{1,4} = 756.32$; $P < 0.0001$) and Wukro ($F_{1,4} = 8.74$; $P = 0.04$). Exclosures located in Tembien supported higher ($F_{1,4} = 608.50$; $P < 0.0001$) numbers of TE than the adjacent grazed areas while a similar comparison in Wukro did not significantly affect the TE values ($F_{1,4} = 2.65$; $P = 0.1787$). Fallow age of influenced BU and BC values in Tembien ($F_{1,4} = 14.97$; $P = 0.0180$ for BU, and $F_{1,4} = 111.94$; $P = 0.0005$ for BC) but not in Wukro (data not shown).

4. Discussion

4.1. Herbaceous and woody species composition

Tall erect grass genera such as *Aristida* and *Sporobolus* dominated the exclosures while prostrate and creeping species such as *Cynodon dactylon* and *Tragus racemosus* invariably dominated in the adjacent grazed areas. Shifts in species composition between grazed and ungrazed areas have also been found in other semi-arid vegetation types (Hein, 2006; Noy-Meir et al., 1989) and reflect, among other things, a long evolutionary adaptation to grazing (Milchunas and Lauenroth, 1993). When the data were analyzed separately for each site, however, it was only in Tembien that protection led to an increase of some woody species such as *Albizia schimperiana*, *Cadaba farinosa*, *D. cinerea*, *Grewia* sp. and *Maerua angolensis* and these species were either present in small proportions or totally absent in the grazed areas. Such difference in the response of protection to composition in Tembien and Wukro calls for clearly understanding the responsible factors that operate at different spatial scales and may affect the number and relative abundances of species differently (Polley et al., 2005).

4.2. Herbaceous aboveground biomass and utilization

Herbaceous aboveground biomass varied considerably between the two sites and across the three seasons. Such spatial and temporal variation in aboveground biomass is typical for non-equilibrium systems (Ellis and Swift, 1988). Grazing throughout the year has consistently reduced the herbaceous aboveground biomass production capability of the grazed areas at both sites. The 60% utilization attributed to grazing by domestic animals is within the 30–90% off-take range reported for East African savanna areas (McNaughton, 1985) and such level of utilization is regarded as being severe, compared to the sustainable 25–35% recommendation (Holechek et al., 2003). The severe utilization of aboveground biomass is also illustrated by the ratio of biomass in the grazed areas and exclosures, which averaged 0.55, a threshold well above what is needed to shift to a shrub dominated state (Christensen et al., 2003). If the current level of herbaceous aboveground biomass removal is sustained for a longer period of time, it may eventually reduce the productivity of the grazing resource (Keya, 1998). However, fallow ages beyond 8 years had a negative influence on herbaceous aboveground biomass production of exclosures in Tembien while in Wukro this was not the case, largely attributed to the low woody species density at the latter site.

Table 3
Effects of season on diversity of herbaceous species and woody species in the semi-arid Tigray region, northern Ethiopia (Mean ± SE).

Season	Herbaceous	Woody
	Diversity	Diversity
Long rainy	5.41 ± 0.34^a	2.58 ± 0.27
Dry	3.24 ± 0.35^b	2.62 ± 0.28
Short rainy	3.25 ± 0.35^b	2.60 ± 0.28
Significance (P)	0.001	0.677

Values bearing different letter superscripts significantly ($P < 0.05$) differ. SE = standard error of the means. Mean values calculated from $n = 6$. P, probability.

Table 2
Effects of exclosure (protected versus grazed areas), fallow age (young versus old) and site (Tembien versus Wukro) on diversity of herbaceous species and woody species in the semi-arid Tigray region, northern Ethiopia (Mean ± SE).

Vegetation	Protection			Fallow age			Site		
	Protected	Grazed	P	Young	Old	P	Tembien	Wukro	P
Herbaceous	4.00 ± 0.30	2.70 ± 0.10	<0.0001	4.50 ± 0.30	3.40 ± 0.40	0.021	3.00 ± 0.25	5.00 ± 0.31	<0.0001
Woody	5.47 ± 0.29	2.97 ± 0.14	<0.0001	4.98 ± 0.23	5.97 ± 0.51	0.568	6.32 ± 0.46	4.63 ± 0.23	0.002

SE = standard error of the means. Mean values for protection and site calculated from $n = 6$ and values for fallow age calculated from $n = 3$ each. P, probability.

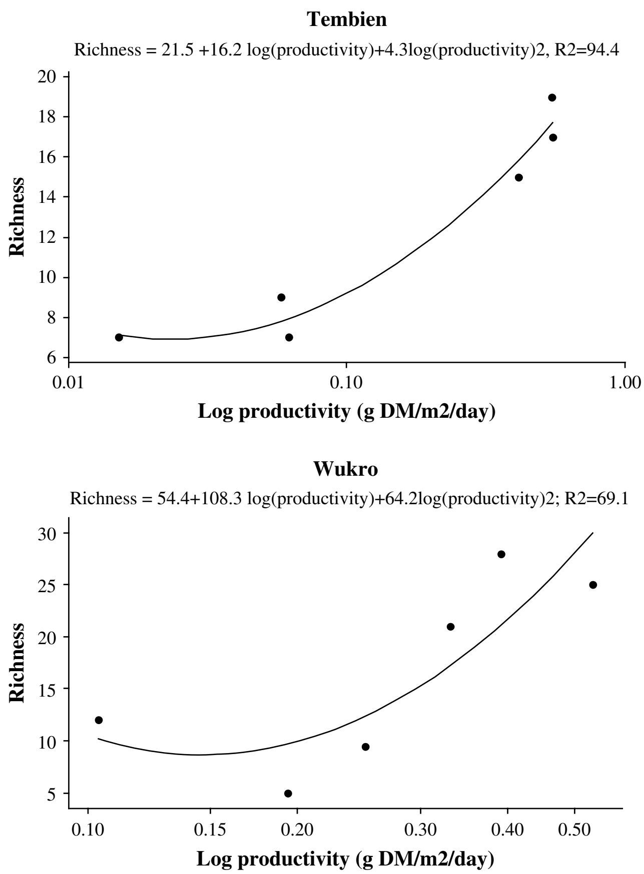

Fig. 3. The relationship between herbaceous species richness and productivity (g DM/m^2/day) of exclosures in the semi-arid Tigray region, northern Ethiopia.

4.3. Species diversity and richness–productivity relationship

A total of 61 herbaceous species and 34 woody species were recorded. The exclosures had higher herbaceous and woody species diversity compared to adjacent grazed areas and a similar pattern of species diversity was reported for northern Ethiopia (Aerts et al., 2006) and Kenya (Oba et al., 2001). The high diversity measured in the exclosures might be explained by the increased litter accumulation (Descheemaeker et al., 2006), improved soil organic matter and other nutrients (Mekuria et al., 2007) inside the exclosures. However, our results contrast to other studies that reported increased species diversity under moderate grazing compared to no or heavy grazing (e.g. Dorrough et al., 2007; Girma et al., 2002; Mwendera et al., 1997). Although we do not have data from intermediate grazing areas, our study shows that areas protected from grazing do develop higher diversity than areas subjected to a high grazing pressure. Although grazing pressure is an important determinant of plant diversity, other factors like precipitation, site, edaphic and other environmental variables may interact with grazing and play a key role in determining the number of species (Milchunas and Lauenroth, 1993; Olff and Ritchie, 1998). Seasonal species diversity oscillations were more evident in herbaceous than in woody species with peak diversity values recorded during the long rainy season.

Herbaceous species diversity responded positively to shorter fallow ages and this is largely consistent with other studies (Asefa et al., 2003; Abebe et al., 2006; Hiernaux, 1998; Oba et al., 2001). The diverse herbaceous species recorded in the young exclosures might be attributed to the presence of a low density of woody species since high density of woody species suppress growth of the understory vegetation (Scholes and Archer, 1997). Thus, it is essential to avoid long fallow periods that may result in suppression of the herbaceous vegetation.

Previous studies have shown that the relationship between productivity and species richness is not consistent and is scale dependent (e.g. Anderson and Hoffman, 2007; Grace, 2001; Gillman and Wright, 2006; Waide et al., 1999; Whittaker et al., 2001). In this study, species richness of both sites increased with increased productivity without necessarily showing changes in the species composition of the herbs, a typical response reported for ecosystems characterized by lower productivity (e.g. Grace et al., 2007; Jiang et al., 2007; Lambers et al., 2004; Osem et al., 2002; Tilman et al., 2001). Our results indicate that, within the exclosures, there is a positive curvilinear relationship with a steep increase in species richness at higher productivity levels. While we found a strong relationship between species richness and productivity in our semi-arid study area, Oba et al. (2001) found no such relationship within exclosures in arid Kenya and Cox et al. (2006) concluded that productivity is a weak predictor of species richness in arid areas.

Given the degraded matrix feature of the fragmented patches of the present exclosures that limit the dispersal capability of most species (Aerts et al., 2006), increased herbaceous richness is conceived to be from local species pools maintained in the form of persistent soil seed banks in the sub-soil (Abebe et al., 2006). However, a more elaborated mechanism for such pattern might be explained by the fact that these exclosures are regularly subject to intermediate disturbance in the form of grass mowing once a year at the end of the rainy season in October and this might have triggered an increased species richness (Maron and Jefferies, 2001), or maintained richness (Collins et al., 1998) in accordance with the disturbance dynamic equilibrium hypothesis (Huston, 1979).

4.4. Woody vegetation structure and browsing capacity

Protection led to increased woody plant height and cover. The data presented in Fig. 4 were pooled by site due to the fact that both sites exhibited similar pattern of plant height in relation grazing and protection. At both sites the presence of continuous grazing and browsing led to herbivore-mediated reduction in plant height. Where the browsing pressure is high, a similar pattern of shorter height woody structure was reported for southern Ethiopia (Tefera et al., 2007). The presence of heavy browsing leads to reduced recruitment and skewed age structure, small seedlings being dominant in the grazed areas (Butler and Kielland, 2008).

Table 4
Effects of protection, fallow age, and site on browse height, canopy height and canopy cover in the semi-arid Tigray region, northern Ethiopia (Mean ± SE).

Attribute	Protection			Age (years)			Site		
	Protected	Grazed	*P*	Young	Old	*P*	Tembien	Wukro	*P*
Height (m)	1.27 ± 0.02	0.89 ± 0.02	<0.0001	1.11 ± 0.04	1.05 ± 0.04	0.001	1.10 ± 0.04	1.06 ± 0.03	0.003
Canopy height (m)	0.86 ± 0.01	0.56 ± 0.01	<0.0001	0.70 ± 0.03	0.73 ± 0.03	0.264	0.73 ± 0.03	0.69 ± 0.03	0.041
Canopy cover (%)	28.01 ± 1.81	10.45 ± 1.28	<0.0001	16.45 ± 1.92	22.01 ± 2.28	0.095	22.73 ± 2.36	15.73 ± 1.74	0.009

SE = standard error of the means. Mean values calculated from $n = 27$ plots of 10 × 10 m. *P*, probability.

Table 5
Effects of protection on mean browsing unit (BU), browsing capacity (BC) and tree equivalent (TE) in the semi-arid Tigray region, northern Ethiopia (Mean ± SE).

Site	BU (browse/ha)			BC (ha/SSU[a])			TE (tree/ha)		
	Protected	Grazed	*P*	Protected	Grazed	*P*	Protected	Grazed	*P*
Tembien	619.03 ± 15.82	197.68 ± 21.52	<0.0001	3.17 ± 0.22	11.01 ± 1.42	<0.0001	796.22 ± 21.62	252.86 ± 24.32	<0.0001
Wukro	290.48 ± 24.87	90.43 ± 11.86	0.1204	8.63 ± 1.52	24.03 ± 2.79	0.0417	349.41 ± 24.33	125.58 ± 27.51	0.1787

SE = standard error of the means. Mean values calculated from $n = 27$ plots of 10 × 10 m. *P*, probability.
[a] Small Stock Unit (SSU) refers to a small stock such as sheep and goats approximately 1/6 of the size of a large ruminant (Beckerling et al., 1995).

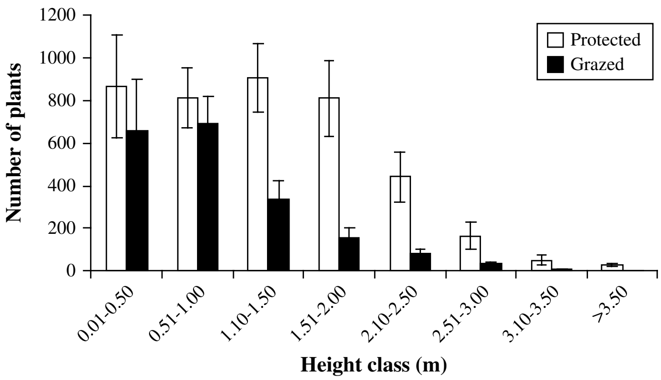

Fig. 4. Height class distribution of woody species in exclosures and grazed areas in the semi-arid Tigray region, northern Ethiopia (Mean ± SE).

Compared to the grazed areas, woody species cover also increased in the exclosures and this is largely consistent with results reported by others (Augustine and McNaughton, 2004; Manier and Hobbs, 2007). Exclosures left intact for extended period of time (more than 12 years) did not linearly increase in woody vegetation height and shorter fallow periods gave on average taller woody species, suggesting the existence of aboveground resource competition in the denser old exclosures.

The density of woody species measured inside the exclosures was more than twice that of adjacent browsed areas reflecting the lack of recruitment of woody species in the heavily browsed and trampled areas. A recent experimental study from Botswana has shown that medium-sized browsers can severely limit woody species recruitment through seedling predation (Moe et al., 2009). Similarly, Augustine and McNaughton (2004) reported that the rate of shrub recruitment was significantly reduced by ungulate browsing in the East African rangelands. A higher density of woody species (TE/ha) has resulted in increased browsing capacity of the exclosures without adversely affecting the grass layer. The negative influence of bushes on grass density is generally low when the density of bushes is less than 1000 TE/ha, while bush densities above 2500 TE/ha may limit grass production (Richter et al., 2001). In the southern Ethiopian rangelands, a TE of 1100/ha is taken as a threshold for bush encroachment (Bille and Assefa, 1984). By this criterion, all exclosures investigated in this study were far from being threatened by bush encroachment. This is in contrast to most East African rangelands where bush encroachment is a common feature in areas subjected to high grazing and browsing pressure (Augustine and McNaughton, 2004; Oba et al., 2000; Tefera et al., 2007).

5. Conclusions

Exclosures established in Tigray region of northern Ethiopia have been effective in restoring plant species composition, diversity, biomass, cover, and structure of both herbaceous and woody vegetation, factors that normally lead to improved ecosystem function. Extended protection reduces herbaceous species diversity while herbaceous biomass is either reduced or unchanged when areas are protected beyond 8 years. Thus, there is a need to consider alternative management that allows selectively and carefully timed utilization of exclosures protected for longer period of time.

Acknowledgements

We are grateful to the Norwegian Agency for Development Cooperation (NORAD) for financially supporting the fieldwork part through the Phase II Institutional Support Programme. The first author is also grateful to the Norwegian State Educational Loan Fund (Lånekassen) for providing financial assistance and the Department of Animal, Rangeland, and Wildlife Sciences of Mekelle University in Ethiopia for granting a study leave.

Annex 1a: List of herbaceous species identified from exclosures constructed in Tigray region, northern Ethiopia

Species
Amaranthus spinosus
Andropogon abyssinicus
Anthephora pubescens
Argemone mexicana
Aristida adscensionis
Aristida congesta
Aristida kenyensis
Arthraxon prionodes
Asystasia gangetica
Bidens macroptera
Bidens pilosa
Bothriochloa insculpta
Brachiaria eruciformis
Brachiaria lachnantha
Cenchrus ciliaris
Chloris amethystea
Chloris pycnothrix
Chloris virgata
Corrigiola capensis
Cynodon aethiopicus
Cynodon dactylon
Cynodon nlemfuensis
Dactyloctenium aegyptium
Digitaria abyssinica
Digitaria milanjiana
Digitaria ternata
Digitaria velutina
Echinops giganteus
Enneapogon cenchroides
Enneapogon persicus
Enteropogon machrostachys
Eragrostis cilianensis
Eragrostis cylindriflora
Eragrostis papposa

(*continued on next page*)

(*continued*)

Species
Eragrostis pilosa
Eustachys paspaloides
Harpachne schimperi
Heteropogon contortus
Hyparrhenia anthistiroides
Hyparrhenia hirta
Leucas microphylla
Ocimum forskolei
Panicum atrosanguineum
Pennisetum villosum
Rapistrum rugosum
Scorpiurus muricatus
Sehima nervosum
Setaria incrassata
Setaria pallide-fusca
Setaria pumila
Setaria verticillata
Sporobolus panicoides
Sporobolus pellucidus
Tetrapogon villosus
Themeda triandra
Tragus racemosus
Trifolium schimperi
Urochloa trichopus

Annex 1b: List of woody species identified from exclosures constructed in Tigray region, northern Ethiopia

Species
Acacia etbaica
Acacia saligna
Acacia seyal
Acocantheria osyris
Albizia schimperiana
Aloe harlana
Balanites aegyptica
Boscia salcifolia
Cadaba farinosa
Calpurina aurea
Capparis tomentosa
Carissa edulis
Clerodendron myricoides
Combretum molle
Commiphora schimperi
Dichrostachys cinerea
Dodonea anguistifolia
Euclea racemosa
Grewia bicolor
Grewia flavensis
Grewia tembensis
Grewia villosa
Leucas abyssinica
Maerua angolensis
Maytenus arbutifolia
Maytenus senegalensis
Merendra bengalensis
Osyris quadripartita
Ormocarpum pubescense
Otostegia fruticosa
Rhus natalensis
Sageretia thea
Sennea sanguinea
Ziziphus mucronata

References

Abebe, M.H., Oba, G., Angassa, A., Weladji, R.B., 2006. The role of area enclosures and fallow age in the restoration of plant diversity in northern Ethiopia. Afr. J. Ecol. 44, 507–514.
Aerts, R., Van Overtveld, K., Haile, M., Hermy, M., Deckers, J., Muys, B., 2006. Species composition and diversity of small Afromontane forest fragments in northern Ethiopia. Plant Ecol. 187, 127–142.
Anderson, P.M.L., Hoffman, M.T., 2007. The impacts of sustained heavy grazing on plant diversity and composition in lowland and upland habitats across the Kamiesberg mountain range in the Succulent Karoo, South Africa. J. Arid Environ. 70, 686–700.
Asefa, D.T., Oba, G., Weladji, R.B., Colman, J.E., 2003. An assessment of restoration of biodiversity in degraded high mountain grazing lands in northern Ethiopia. Land Degrad. Dev. 14, 25–38.
Augustine, D.J., McNaughton, S.J., 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. J. Appl. Ecol. 41, 45–58.
Beckerling, A.C., Trollope, W.S.W., Mbelu, M.M., Scogings, P.F., 1995. Simplified Techniques for Assessing Veld Condition for Livestock Production in the Ciskei Region. Agricultural and Rural Development Research Institute and University of Fort Hare, Alice, Ciskei, South Africa.
Belsky, A.J., Carson, W.P., Jense, C.L., Fox, G.A., 1993. Overcompensation by plants: herbivore optimization or red herring? Evol. Ecol. 7, 109–121.
Betru, N., Ali, J., Nyborg, I., 2005. Exploring Ecological and Socio-Economic Issues for the Improvement of Area Enclosure Management: A Case Study from Ethiopia. DCG (Drylands Coordination Group), Oslo, Norway.
Bille, J.C., Assefa, E., 1984. The Marginal Land of Western Sidamo. ILCA (International Livestock Centre for Africa), Addis Ababa, Ethiopia.
Booysen, P.deV., 1967. Grazing and grazing management terminology in southern Africa. Proc. Grassld. Soc. Sth. Afr. 2, 45–57.
Butler, L.G., Kielland, K., 2008. Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems. J. Ecol. 96, 136–144.
Christensen, L., Coughenour, M.B., Ellis, J.E., Chen, Z., 2003. Sustainability of inner Mongolian grasslands: application of the savanna model. J. Range Manage. 56, 319–327.
Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M., Steinauer, E.M., 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280, 745–747.
Cook, C.W., Stubbendieck, J., 1986. Range Research: Basic Problems and Techniques. Society for Range Management, Denver, Co.
Cox, S.B., Bloch, C.P., Stevens, R.D., Huenneke, L.F., 2006. Productivity and species richness in an arid ecosystem: a long-term perspective. Plant Ecol. 186, 1–12.
Descheemaeker, K., Muys, B., Nyssen, J., Poesen, J., Raes, D., Haile, M., Deckers, J., 2006. Litter production and organic matter accumulation in exclosures of the Tigray highlands, Ethiopia. For. Ecol. Manage. 233, 21–35.
Dorrough, J., Ash, J., Bruce, S., McIntyre, S., 2007. From plant neighborhood to landscape scales: how grazing modifies native and exotic plant species richness in grassland. Plant Ecol. 191, 185–198.
Ellis, J.E., Swift, D.M., 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. J. Range Manage. 41, 450–459.
FAO (Food and Agriculture Organization of the United Nations), 1998. The Soil and Terrain Database for Northeastern Africa; Crop Production System Zones of the IGAD Sub Region. FAO, Rome, Italy.
Gillman, L.N., Wright, S.D., 2006. The influence of productivity on the species richness of plants: a critical assessment. Ecology 87, 1234–1243.
Girma, T., Mohamed Saleem, M.A., Abiye, A., Wagnew, A., 2002. Impact of grazing on plant species richness, plant biomass, plant attribute, and soil physical and hydrological properties of vertisol in East African Highlands. Environ. Manage. 29, 279–289.
Grace, J.B., 2001. The roles of community biomass and species pools in the regulation of plant diversity. Oikos 92, 193–207.
Grace, J.B., Michael Anderson, T., Smith, M.D., Seabloom, E., Andelman, S.J., Meche, G., Weiher, E., Allain, L.K., Jutila, H., Sankaran, M., Knops, J., Ritchie, M., Willig, M.R., 2007. Does species diversity limit productivity in natural grassland communities? Ecol. Lett. 10, 680–689.
Hein, L., 2006. The impacts of grazing and rainfall variability on the dynamics of a Sahelian rangeland. J. Arid Environ. 64, 488–504.
Hiernaux, P., 1998. Effects of grazing on plant species composition and spatial distribution in rangelands of the Sahel. Plant Ecol. 138, 191–202.
Holechek, J., Galt, D., Joseph, J., Navarro, J., Kumalo, G., Molinar, F., Thomas, M., 2003. Moderate and light cattle grazing effects on Chihuahuan Desert rangelands. J. Range Manage. 56, 133–139.
Hurni, H., Kebede, T., Gete, Z., 2005. The implications of changes in population, land use, and land management for surface runoff in the Upper Nile Basin area of Ethiopia. Mt. Res. Dev. 25, 147–154.
Huston, M., 1979. A general hypothesis of species diversity. Am. Nat. 113, 81–101.
Jiang, X., Zhang, W., Wang, G., 2007. Biodiversity effects on biomass production and invasion resistance in annual versus perennial plant communities. Biodivers. Conserv. 16, 1983–1994.
Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375.
Keya, G.A., 1998. Herbaceous layer production and utilization by herbivores under different ecological conditions in an arid savanna of Kenya. Agric. Ecosyst. Environ. 69, 55–67.
Krebs, C.J., 1999. Ecological Methodology. Addison Wesley Longman Inc., California.
Lambers, J.H.R., Harpole, W.S., Tilman, D., Knops, J., Reich, P.B., 2004. Mechanisms responsible for the positive diversity–productivity relationship in Minnesota grasslands. Ecol. Lett. 7, 661–668.
Le Houérou, H.N., 1989. The Grazing Land Ecosystems of the African Sahel. Springer-Verlag, Berlin.
Manier, D., Hobbs, N., 2007. Large herbivores in sagebrush steppe ecosystems: livestock and wild ungulates influence structure and function. Oecologia 152, 739–750.

Maron, J., Jefferies, R.L., 2001. Restoring enriched grasslands: effects of mowing on species richness, productivity, and nitrogen retention. Ecol. Appl. 11, 1088–1100.

McNaughton, S.J., 1985. Ecology of a grazing ecosystem: the Serengeti. Ecol. Monogr. 55, 259–294.

Mekuria, W., Veldkamp, E., Haile, M., Nyssen, J., Muys, B., Gebrehiwot, K., 2007. Effectiveness of exclosures to restore degraded soils as a result of overgrazing in Tigray, Ethiopia. J. Arid Environ. 69, 270–284.

Mengistu, T., Teketay, D., Hulten, H., Yemshaw, Y., 2005. The role of enclosures in the recovery of woody vegetation in degraded dryland hillsides of central and northern Ethiopia. J. Arid Environ. 60, 259–281.

Meze-Hauske, E., 2004. Contrasting climate variability and meteorological drought with perceived drought and climate change in northern Ethiopia. Clim. Res. 27, 19–31.

Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soil over a global range of environments. Ecol. Monogr. 63, 327–366.

Moe, S.R., Rutina, L.P., Hytteborn, H., Du Toit, J.T., 2009. What controls woodland regeneration after elephants have killed the big trees. J. Appl. Ecol 46, 223–230.

Mwendera, E.J., Saleem, M.A.M., Woldu, Z., 1997. Vegetation response to cattle grazing in the Ethiopian highlands. Agric. Ecosyst. Environ. 64, 43–51.

Noy-Meir, I., Gutman, M., Kaplan, Y., 1989. Responses of Mediterranean grassland plants to grazing and protection. J. Ecol. 77, 290–310.

Oba, G., Post, E., Syvertsen, P.O., Stenseth, N.C., 2000. Bush cover and range condition assessments in relation to landscape and grazing in southern Ethiopia. Landscape Ecol. 15, 535–546.

Oba, G., Vetaas, O.R., Stenseth, N.C., 2001. Relationships between biomass and plant species richness in arid-zone grazing lands. J. Appl. Ecol. 38, 836–845.

Olff, H., Ritchie, M.E., 1998. Effects of herbivores on grassland plant diversity. Trends Ecol. Evol. 13, 261–265.

Osem, Y., Perevolotsky, A., Kigel, J., 2002. Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. J. Ecol. 90, 936–946.

Polley, H.W., Derner, J.D., Wilsey, B.J., 2005. Patterns of plant species diversity in remnant and restored tall grass prairies. Restor. Ecol. 13, 480–487.

REST (Relief Society of Tigray), 1998. Soil and Water Conservation Programme. REST, Mekelle, Ethiopia.

Richter, C.G.F., Snyman, H.A., Smit, G.N., 2001. The influence of tree density on the grass layer of three semi-arid savanna types of southern Africa. Afr. J. Range Forage Sci. 18, 103–109.

SAS Institute, 2001. Statistical Analysis Software. SAS Institute Inc., Cary, NC, USA.

Scholes, R.J., Archer, S.R., 1997. Tree–grass interactions in savannas. Annu. Rev. Ecol. Syst. 28, 517–544.

Sullivan, S., Rohde, R., 2002. On non-equilibrium in arid and semi-arid grazing systems. J. Biogeogr. 29, 1595–1618.

t'Mannetje, L., Jones, R.M., 2000. Field and Laboratory Methods for Grassland and Animal Production Research. CABI.

Teague, W.R., Trollope, W.S.W., Aucamp, A.J., 1981. Veld management in the semi-arid bush–grass communities of the Eastern Cape. Proc. Grassld. Soc. Sth. Afr. 16, 23–28.

Tefera, S., Snyman, H.A., Smit, G.N., 2007. Rangeland dynamics of southern Ethiopia: (2). Assessment of woody vegetation structure in relation to land use and distance from water in semi-arid Borana rangelands. J. Environ. Manage. 85, 443–452.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and productivity in a long-term grassland experiment. Science 294, 843–845.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P., Parmenter, R., 1999. The relationship between productivity and species richness. Annu. Rev. Ecol. Syst. 30, 257–300.

Westoby, M., Walker, B.H., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. J. Range Manage. 42, 266–274.

Whittaker, R.J., Willis, K.J., Field, R., 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. J. Biogeogr. 28, 453–470.

Young, S., 1958. Exclosures in big game management in Utah. J. Range Manage. 11, 187–190.