

This is an author produced version of a paper published in *Plant Ecology*.
This paper has been peer-reviewed and is proof-corrected, but does not
include the journal pagination.

Citation for the published paper:

Maria Johansson, Tuulikki Rooke, Masresha Fetene & Anders Granström.
(2009) Browser selectivity alters post-fire competition between *Erica arborea*
and *E. trimera* in the sub-alpine heathlands of Ethiopia. *Plant Ecology*. Volume:
207 Number: 1, pp 149-160.

<http://dx.doi.org/10.1007/s11258-009-9661-9>

Access to the published version may require journal subscription.
Published with permission from: Springer



Epsilon Open Archive <http://epsilon.slu.se>

Browser selectivity alters post-fire competition between *Erica arborea* and *E. trimera* in the sub-alpine heathlands of Ethiopia

Published in: Plant Ecology, Volume 207, Number 1, 149-160, DOI: 10.1007/s11258-009-9661-9

Authors: Maria Johansson¹ Tuulikki Rooke² Masresha Fetene³ and Anders Granström¹

1: Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden

2: Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden

3: Department of Biology, Faculty of Science, Addis Ababa University, P.O. Box 30193, Addis Ababa, Ethiopia

Corresponding author: email: Maria.Johansson@svek.slu.se, tel: 0046-90-786 8396 fax: 0046-90-786 6163

Keywords: *Erica arborea*; *Erica trimera*; Afro-alpine heathland; fire management; browser selectivity; tannin

Abstract

Mammalian herbivores have the potential to alter the competitive relations of woody species, if consumption is unevenly distributed between species. At elevations above 3500 m in the southern Ethiopian highlands, vegetation is dominated by *Erica arborea* and *Erica trimera*. Both species can potentially grow into short trees, but are burnt on a rotation of 6 to 10 years, and regenerate by re-sprouting from belowground lignotubers. The regenerating scrub is heavily browsed by cattle. We set up browsing exclosures at three burnt sites to quantify the impact of browsing over a three-year period. When protected from browsing, *E. trimera* had similar or better height growth than *Erica arborea*, but in browsed vegetation, *Erica arborea* instead grew taller. Browsing was more intense on *E. trimera* in the first years after fire, indicating a difference in palatability between the species. We checked if browse quality differed, by analysing shoot contents of acid detergent fibre, protein, phenolics and tannins. Contrary to expectations the preferred *E. trimera* contained more acid detergent fibre, less protein and had a higher tannin activity than *E. arborea*. Although the vegetative growth of *E. arborea* is favoured relative to *E. trimera* under high browsing pressure, rapid change in abundance would not be expected, since short-interval fire will repeatedly eradicate any gains in vegetative growth. However, within the typical fire return interval of less than 10 years, *E. trimera* barely reach a reproductive state, whereas *E. arborea* flower profusely. Under the current regime of fire and browsing this may in the long run be more important than differences in height growth, leading to a gradual increase in the proportion of *E. arborea*.

Introduction

Browsers are powerful selective agents with the potential to shape ecosystem structure and function by altering the interspecific competition between woody plants (Augustine and McNaughton 1998; Hobbs 1996). The net effect of browsing on plant competition depends on plant growth rate, tolerance to herbivory, and herbivore selectivity (Dwire et al. 2006; Horsley et al. 2003; Mills 1986; Skarpe and Hester 2008). The latter is often regulated by the type and amount of secondary defence compounds within the plants (Harbourne 1991). However, effective defence comes with a cost. Heavily defended plant species are typically more slow-growing, which becomes a disadvantage when the intensity of herbivory is relaxed (Herms and Mattson 1992; Koricheva 2002). There are also more indirect effects of plant defences, for example impairment of litter decomposition (Grime et al. 1996; Wardle et al. 2002), and increased flammability (Ormeno et al. 2009; Owens et al. 1998; Snyder 1984).

At elevations above c 3200 m asl in the East African Mountains, *Erica* (tree heather) species dominate the vegetation and form a relatively well defined zone, termed the Ericaceous Belt by Hedberg (1951). At the lower part of this belt the *Erica* grow into short trees, but at higher altitudes the same species are kept in a shrubby state due to recurrent fires (Fetene 2008; Hedberg 1971), resulting in a relatively well defined tree line. In Bale Mountains, in the Southern Highlands of Ethiopia, people intentionally burn the ericaceous vegetation above 3500 m elevation (Wesche et al. 2000), in order to produce better pasture for their cattle. The burnt shrubs regenerate by shoots from underground lignotubers, and seedling regeneration is rarely observed (Teshome 1999; Wesche et al. 2008). The dominant mammalian herbivores are domestic, free-roaming cattle (*Bos taurus indicus*), and to a lesser degree the native Mountain Nyala (*Tragelaphus buxtoni*).

The *Erica* scrub is a mosaic of patches of different age since fire, with *Erica* bushes reaching a height of approximately 1.5 to 3 metres before burning. At this stage, the *Erica*-dominated fuel bed is highly flammable, due to the small leaf size and fine branching pattern (Pereira et al. 1995). Fire return interval is normally between 6 and 10 years, and the sizes of the burnt patches typically range between 0.5 and 5.0 ha (M. Johansson, unpublished data). The regenerating individual *Erica* bushes are relatively evenly spaced (ca. 0.5–2.5 m), and separated by a sward of grasses, sedges and herbs such as *Trifolium spp.* and *Haplocarpha spp.* that regenerate from the seed bank and underground structures. For the first years after fire, there is about equal cover of *Erica* and the grass/herb sward. As the bushes grow taller and wider the canopy closes at an age around 5–7 years,

shading out the grass/herb sward. This results in a continuous *Erica* heath with the ground covered by mosses and *Erica* litter (M. Johansson, unpublished data). In the Bale Mountains, the *Erica* scrub consists of two different species; *Erica arborea* (L.) and *E. trimera* (Engl.) Beentje, which are difficult to distinguish from each other. Therefore they have often been wrongly identified, since they grow completely intermixed with each other, and have only slightly different habitus (Hedberg 1971; Miehe and Miehe 1994). The relative proportion of the two species varies but *E. trimera* is usually the most common (Miehe and Miehe 1994).

Plants in the Ericaceous family are generally rich in phenolic compounds (Harborne and Williams 1973), and *Erica arborea* is well-known from the Mediterranean region to have high concentrations of tannins (del Pino et al. 2005; Frutos et al. 2002; Gasmi-Boubaker et al. 2006; Selje et al. 2007), and to be unpalatable to livestock (Bartolome et al. 1998; González Hernandez 2004) and wild browsers (Focardi and Tinelli 2005; Gonzalez Hernandez and Silva-Pando 1996). Despite the reputed unpalatability of *Erica* species, the *Erica* scrub in Bale Mountains is heavily browsed by cattle. In these frequently burned heathlands we observed that *E. arborea* seems to outgrow *E. trimera* in the first years after fire (Fig. 1), and hypothesized that this was an effect of differential browsing pressure on the two species.



Fig. 1 Browsed *Erica* heath two years after fire. The arrow points to one taller individual *E. arborea* surrounded by shorter *E. trimera*

To test if browser selectivity affects the relative performance of these closely related *Erica* species, we set up a browsing exclusion experiment which we followed over three years after fire. We also sampled a sequence of burns that differed in time since fire, for data on the relative performance of the two species in browsed vegetation. To check for differences in browse quality between the species we sampled shoots of the two *Erica* species in burns differing in time since fire and analyzed

them for tannin activity, phenolic content, acid detergent fibre (ADF) and protein content. In this study we ask the following main questions: (1) Are differences in height increment between these two closely related species caused by inherent differences in growth rate or in browsing tolerance, or is it an effect of differential browsing pressure on the two species? (2) Are there differences in browse quality that may account for animal selection?

Materials and Methods

Study area

The study was conducted in the ericaceous zone of the Bale Mountains, in the Southern Highlands of Ethiopia (Fig. 2).

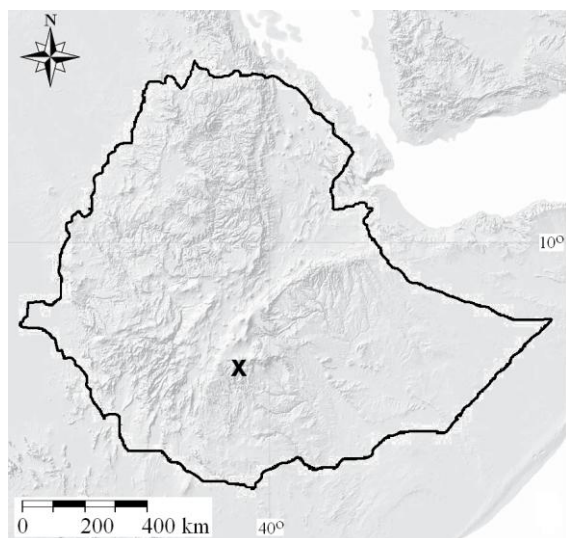


Fig 2. Elevation map of Ethiopia. The study area in Bale Mountains is marked with x.

The bedrock originates from Tertiary lava deposits, and consists of trachytes with basalts and rhyolites which weather to red brown or brown black silty loams (Weinert and Mazurek 1984). The soils of the ericaceous zone are Humic to Leptic Umbrisols (FAO 1998) and typically have a highly organic top soil with a pH around 5.5 (Yimer et al. 2006). Mean annual precipitation measured over

three years in the study area was ca. 1800 mm (M. Johansson, unpublished data). There is a dry period which is highly variable in length, but typically most pronounced in December-January. Mean daily max and min temperatures were ca. 15 °C and 5 °C, measured at 50 cm above the soil surface at two sites at 3500 m altitude (TinyTag plus 2, Gemini data loggers). The dry season is characterised by more extreme daily temperature fluctuation and common night frosts (Wesche et al. 2008).

Field experiment and sampling

In March 2005 one browsing enclosure was erected in a newly burnt area in Duro. In order to replicate the study at sites with very similar vegetation, soil and climate, but browsed by different herds of cattle, two additional enclosures were erected in February 2006 at two recently burnt sites in Angafu and Gama (Table 1). The enclosures were in all cases set up less than a month after fire, before the emergence of resprouting shoots. The enclosure fences were 10 x 10 m, 180 cm high, and had 6 strands of barbed wire; the lower 70 cm was supplemented with interwoven vertical bamboo splints, 10 cm apart. Next to each fence (in the same burn patch) a non-fenced plot of 10 x 10 m was established.

At each site one additional 10 x 10 m plot was established in “old” *Erica* vegetation that had reached a height of ca. 1.5 m. At Duro one plot was also established in a “medium”-aged *Erica* stand with a height around 0.5 m, to obtain three different age-classes. Four permanent 10 m line transects were established in each plot 2.5 m apart. To determine the time since fire at the different plots, basal stem sections of both species were sampled and brought to the laboratory to determine their age. Cross sections were cut with a scalpel, treated with zinc paste, and rings were counted under a magnifier. At these localities, annual rings are regularly produced in the *Erica*, due to the arrested growth during the dry period (M. Johansson, unpublished data.)

Table 1 Study site characteristics

	Duro	Angafu	Gama
Altitude (m asl)	3510	3530	3630
Coordinates (Lat)	N 06° 51' 21"	N 06° 50' 20"	N 06° 50' 12"
(Long)	E 039° 28' 52"	E 039° 14' 41"	E 039° 14' 18"
Fence plot burned in (month, year)	February 2005	January 2006	January 2006
Exclosure erected (year)	2005	2006	2006
Pre-burn veg. height (cm)	170	150	140
Slope (degrees)	15	20	7
Slope aspect	N	SV	N
Age of burns sampled for chemical analyses (years)	1 (Juvenile) 2 (Young) 12 (Old)	1 (Juvenile) 2 (Young) 7 (Old)	1 (Juvenile) 3 (Young) 7 (Old)

All major stems originate from the first shoots emerging after fire.

For the line transects all individual *Erica* bushes touching the line were marked permanently using paint on the base of the two tallest shoots. Their maximum and average heights were measured yearly in the dry season for 3 (Duro) or 2 (Angafu and Gama) years. There were 6–15 individuals of each species in each transect, giving 25–41 individuals of each species per plot. For the 2007 measurement, the proportion of the surface area of each individual bush that had been recently browsed (i.e. had visible browsed shoot tips) was estimated. For each individual, presence of flowering shoots was also recorded to check the reproductive potential of the two species under the current grazing and fire regime. *Erica arborea* starts flowering a little bit earlier in the dry season, but for both species the capsules remain visible on the shoots for several months after flowering. In order to quantify the resprouting ability after browsing in the two species, we clipped the top 10 cm of 5 individuals inside the fences (to simulate the bite from a cow), in February 2007. One year later the length of the resulting axillary shoots were measured. To compare the maximum heights of the two species we located the largest tree-formed individuals of *Erica arborea* and *E. trimera* (at Angafu, slightly below the tree line) and measured their height, using a hypsometer. To compare seedling growth of the two *Erica* species, seeds were collected from both species and sown in peat (pH 4.2–5) and grown in glasshouse at 20 °C (day) and 10 °C (night) with minimum 8 hrs daylight. The height of 25 seedlings per species was measured after 15 months.

To assess forage quality of the two different species, and of different age-classes, we sampled shoots from both *Erica* species at all three sites, from burns differing in time since fire. Since burns with identical age were not represented at all sites, the burns were grouped into three different age-classes: “juvenile” (1 year), “young” (2–3 years) and “old” (7–12 years) (Table 1). Time since fire was determined by counting rings on basal stem sections (see above).

Since there is a marked dry period affecting growth, the sampling was done both in November 2006 (end of the growing season) and in February 2007 (end of the dry season), to test for possible seasonal variation in chemistry. At both occasions the same burns were sampled but not the same individuals. For each treatment combination (site, age-class and species) samples were collected from 5 randomly chosen individuals. The top 10 cm of unbrowsed shoots (stem and leaves) was harvested, corresponding to a stem diameter of approximately 1 mm, which is the average diameter down to which the cattle browse the plants. Five shoots from each individual were collected in a paper bag and dried at room temperature. In order to determine dry matter content, three additional

samples per treatment were collected in plastic bags and immediately weighed to the nearest 0.1 g and reweighed after drying in the lab.

Further, in order to be able to analyse whether shoot chemistry was affected by browsing, 5 additional samples per species and site were collected from inside the enclosures in February 2007. For all sampled individuals, maximum and average height was recorded.

Laboratory assays

The shoot samples taken for assessing forage quality were oven-dried for 24 h at 40 °C and ground in a ball mill at 20 Hz for 2 min, after which a 0.2 g subsample was extracted in 2 ml 50% v/v methanol. Total phenolics were assayed by the Folin-Ciocalteu method according to Waterman and Mole (1994), with tannic acid as standard. The blank consisted of deionised water. The absorbance of all solutions was measured at 760 and 550 nm. The values are expressed as g tannic acid equivalents per kg dry mass of leaf sample.

Potential biological tannin activity was quantified by protein precipitation according to the Hagerman radial diffusion method (Hagerman 1987). We added bovine serum albumin (BSA, Fraction V powder, essentially fatty acid free, Sigma A6003-5G) to agarose solution (Type I, Sigma A6013-25G) and made gels in 145 mm diameter Petri dishes, in which 28 wells, each with a diameter of 6 mm, were punched 2 cm apart. As standard, a dilution series of Quebracho tannin in 50% v/v methanol was added to eight wells dispersed across the gel. Sample extracts (20 µl in 50% methanol) were added to 20 wells per gel in a randomised order. The gels were incubated at 30 °C for at least 96 h. Each extract was analysed on three different gels. Two perpendicular diameters of the protein-precipitated circle were measured under low-magnification microscope, and the mean was used to calculate circle area, from which the well area was subtracted. The net precipitated area was used to quantify tannin activity from the standard curves obtained from the Quebracho tannin standards. The values are expressed as g Quebracho equivalents (QE) per kg dry mass of leaf sample. The nitrogen concentration was analysed by LECO FP-528 Combustion analyzer (anonymous 2000) using EDTA standards. The results were multiplied by the 6.25 conversion factor (Jones 1941) to obtain crude protein content. Acid Detergent Fibre (ADF) was analysed using the ANKOM A200 Filter Bag Technique (anonymous 2005) Samples were individually weighed into filter bags and digested for 75 minutes as a group of 24 in 2 L of ADF solution.

Statistical analyses

For all analyses the unit of replication is the individual plant. Kolmogorov-Smirnov tests showed that the data was normally distributed. Differences between species in maximum heights,

proportion browsed, and resprouting shoot lengths were tested by GLM ANOVAs with species and age-class as fixed factors, and site as random factor. Height differences between fenced and browsed individuals were tested by GLM ANOVA with treatment and species as fixed factors and site as random factor. Seedling height difference was tested with a t-test. Species chemical differences in tannin activity and concentrations of phenolics, ADF and protein, were tested by a GLM ANOVA with species, sampling date, and age-class as fixed factors, and site as random factor. Chemical differences between fenced and browsed individuals were tested by a GLM ANOVA with treatment and species as fixed factors and site as random factor. All statistical analyses were performed using Minitab 15.

Results

Field measurements

In browsed vegetation *E. arborea* was significantly taller than *E. trimera*, for all age-classes above one year ($F = 21.41$; $df = 1,527$; $P = 0.002$). At Duro, the site where a sequence of three different-aged burns was followed during three years, there was a steady height increase in both species (Fig. 3), but with *E. trimera* lagging behind.

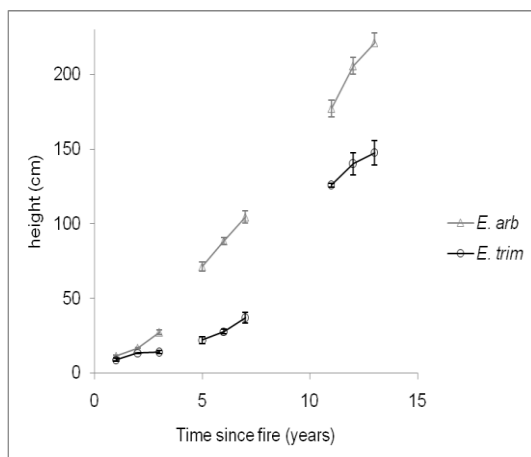


Fig. 3 Average heights of *Erica arborea* (grey line) and *E. trimera* (black line) in three different plots of browsed vegetation followed during three years at Duro. Error bars = S.E. ($n = 21-41$)

At the age of 13 years, *E. arborea* was around 2.2 m tall and *E. trimera* approximately 70 cm shorter. In contrast, inside the exclosures *E. trimera* grew faster than *E. arborea* at Duro ($F = 8.85$; $df = 1,266$; $P = 0.003$), whereas both species grew equally well at Angafu ($F = 3.38$; $df = 1,215$; $P = 0.067$) (Fig. 4). At Gama there were too few *E. arborea* individuals inside the browsing exclosure for quantitative comparison. For two year old *Erica trimera* there was a significant height difference between browsed and fenced individuals, ($F = 215.64$; $df = 1,139$; $P = 0.004$) but not for *E. arborea* ($F = 4.46$; $df = 1,122$ $P = 0.282$) (Fig. 4).

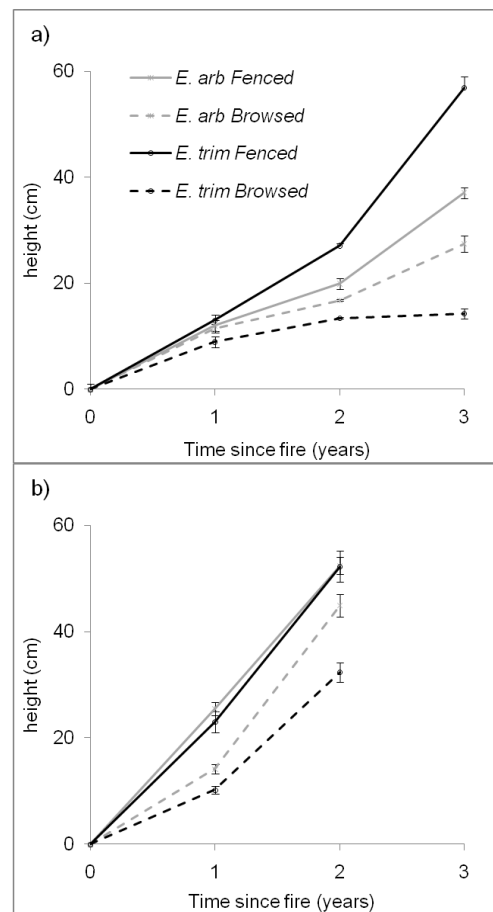


Fig. 4 Height of *Erica arborea* (grey line) and *E. trimera* (black line) inside (solid line) and outside (dotted line) exclosures set up after fire at a) Duro and b) Angafu. Error bars = S.E. ($n = 21-41$)

There were no signs of any browsing on *Erica* inside the exclosures. In the browsed transects, the average percentage of the bush surface that had been recently browsed was significantly higher in *E. trimera* ($F = 701.72$; $df = 1,114$; $P = 0.024$) (Fig. 5).

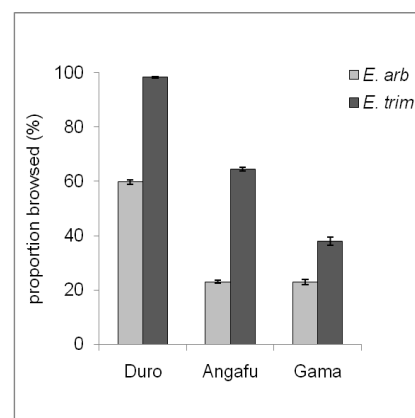


Fig. 5 Average proportion (+/- S.E.) of *Erica arborea* and *E. trimera* with recently browsed shoot tips. Measured on 2 (Angafu and Gama) and 3 year (Duro) old individuals in the browsed line-transects in February 2008 ($n = 21-41$)

In 2 year old vegetation 3% of the individuals of *Erica arborea* had flowering shoots. From the age of 6 years, all *E. arborea* individuals flowered. There were no flowering shoots on *E. trimera* before the age of 11 years, and then only on 2 % of the individuals.

There was no difference in the ability of the two species to resprout after the tops of the shoots had been clipped to simulate browsing. The average annual axillary shoot regrowth over 1 year was 12.6 cm for *E. arborea* and 11.8 cm for *E. trimera*. The maximum height of tree-formed *Erica* below the tree line was 7.1 m for *E. arborea* and 11.2 m for *E. trimera*. In the greenhouse, seedlings of *E. trimera* grew faster than *E. arborea*. After 15 months their average heights were 35.8 cm and 16.1 cm respectively ($F = 98.11$; $df = 1,50$; $P < 0.001$).

Chemical analyses

Shoot dry matter content was significantly higher in *E. trimera* and increased with age for both species (Fig. 6, Table 2).

Dry matter content was higher in February (at the end of the dry season) than in November. The ADF content was higher in *E. trimera* and increased slightly with age for both species, but there was no seasonal difference in ADF contents. The protein concentration was higher in *E. arborea* and decreased with age for both species. There was no significant difference in protein between seasons. Total phenolics content did not differ with species, age or season. Tannin activity was markedly higher in *E. trimera* but did not differ with age or season (Fig. 6, Table 2).

At Duro, where the fence had been in place for two growth seasons at the time of chemical sampling, the non-fenced individuals of both species had a higher tannin activity ($F = 9.73$; $df = 1,9$; $P = 0.014$) and higher concentrations of phenolics ($F = 12.00$; $df = 1,9$; $P = 0.009$) and protein ($F = 7.65$; $df = 1,9$; $P = 0.024$) than the fenced individuals (Fig. 7). The trend was similar for Angafu and Gama (for *E. trimera*) but the effect was not statistically significant. There was no significant difference in ADF concentrations between fenced and non-fenced individuals.

Table 2 GLM ANOVA results for shoot chemistry (Fig. 6)

	DF	DMC		ADF		Protein		Phenolics		Tannin	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Date	1	181.37	0.005	0.07	0.815	4.25	0.175	5.06	0.153	1.06	0.412
Site	2	0.61	0.600	0.08	0.926	0.17	0.852	8.73	0.705	-	-
Age-class	2	14.7	0.014	16.99	0.011	19.70	0.008	5.62	0.069	2.64	0.186
Species	1	149.05	0.007	4739.23	0.000	28.17	0.034	0.01	0.934	484.65	0.002
Date*Site	2	0.20	0.817	33.87	0.063	10.12	0.150	0.91	0.623	0.36	0.758
Date*Age-class	2	1.30	0.279	9.46	0.030	1.87	0.267	0.82	0.502	0.41	0.688
Date*Species	1	0.38	0.541	12.28	0.073	10.31	0.085	0.04	0.856	3.41	0.206
Site*Age-class	4	6.70	0.000	2.21	0.294	2.58	0.210	0.89	0.690	0.22	0.908
Site*Species	2	1.05	0.355	0.06	0.947	5.98	0.369	1.62	0.769	0.16	0.863
Age-class*Species	2	2.34	0.103	3.17	0.150	0.38	0.704	4.66	0.090	2.24	0.223
total	179										

(- Denominator of F-test is zero) Significant results in bold text. There were no significant 3-way interactions.

DF = degrees of freedom, DMC = dry matter content, ADF = acid detergent fibre

Discussion

Our results show that the browsers select *Erica trimera* over *E. arborea*, and that this leads to a more rapid net height increment in *E. arborea* in the first years after fire, despite equal or better inherent height growth in *E. trimera*. Several observations support this conclusion. *Erica arborea* was significantly taller than *E. trimera* in browsed vegetation (Fig. 3), whilst *E. trimera* was taller inside the fences (Fig. 4). Also, *E. trimera* seedlings grew faster in the controlled greenhouse environment. Further, the higher proportion of the bush surface that had been recently browsed for *E. trimera* (Fig. 5) indicates browser preference for this species. Browsing should mainly be due to cattle, given the low numbers of Mountain Nyala in the area (Stephens et al. 2001).

Since there was only one fence at each site, pseudoreplication may pose a risk. But given our constraints, the need to replicate the study at different sites, with different cattle herds, outweighed the need to replicate the number of fences at each site. Since the vegetation is very uniform, and the results were coherent for all three sites, we believe that our results reflect real patterns in this vegetation.

The reason for the observed preference for *Erica trimera* is not evident from the chemical screening. Surprisingly, the preferred *E. trimera* had slightly more ADF, less protein and higher tannin activity than did *E. arborea*, and these properties would be expected to reduce palatability. However, both species have low protein content and a very high tannin activity, and the differences between them may not be sufficiently large to influence browser selectivity. Their protein

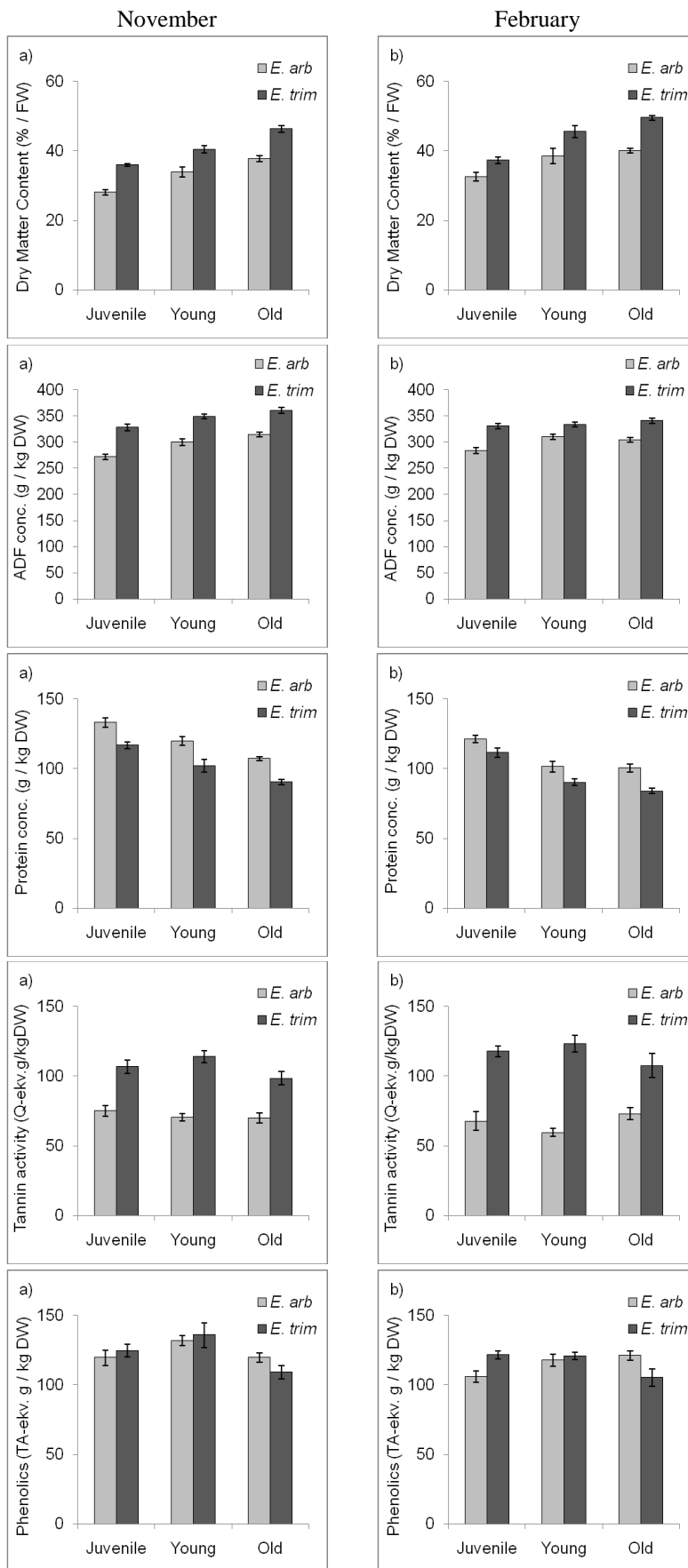


Fig. 6 Average shoot dry matter content, ADF, protein and total phenolics concentrations, and tannin activity of *Erica arborea* and *E. trimera* in a) November b) February. Error bars = S.E. (n=15)

concentrations of around 10% are relatively low for cattle feed (Jackson et al. 1996; Otsyina et al. 1999; Poppi and McLennan 1995) but the concentration is slightly higher in the younger shoots (Fig. 6), indicating that forage value is temporarily increased by burning (Schindler et al. 2004). According to Gustafsson (2009) the cattle spend the major part of their grazing time in recently burnt vegetation. The ADF concentrations of ca. 30% lie within the range characteristic of temperate and tropical shrubs (Balogun et al. 1998; Blair et al. 1977; Van den Bosch et al. 1997). Meanwhile, tannin activities of 7 and 11 % for *E. arborea* and *E. trimera* respectively (Fig. 6) are high compared to grasses and herbs, but within the range of other shrubs (Balogun et al. 1998; del Pino et al. 2005; Hanley et al. 1992; Jackson et al. 1996).

Tannins are large polyphenols that act primarily as digestion inhibitors (Robbins et al. 1987). High tannin activity in the forage may be a problem for cattle on a low-protein diet, since cattle are primarily grazers and do not have the tannin-binding proteins in their saliva that specialized browsers have (Austin et al. 1989). Nevertheless, tannins have very different effects on herbivores depending on their chemical structure (Clausen et al. 1990), and there are even some tannins that have a positive effect on cattle nutrition, e.g. by reducing the effects of intestinal parasites (Mueller-Harvey 2006). Further, the BSA-assay may not fully reflect the true effect in the animal. In a livestock nutrition study of different plant species known for their dietary-inhibiting properties, *Erica arborea* tannins were the most efficient in precipitating BSA, but still had only a minor effect on dietary protein in an in-vitro rumen fermentation experiment (Selje et al. 2007). The fact that we found slightly higher phenolics contents and tannin activity in the browsed compared to fenced individuals for both species (Fig. 7) indicate that phenolics and tannins are partly induced by browsing, but this still does not explain the browser preference for *E. trimera*.

Although *E. trimera* had higher tannin activity, levels of total phenolics were comparable between the two species. This suggests that *E. arborea* contains a higher amount of small, non-tannin phenolic molecules than does *E. trimera*. Small phenolic compounds can enter through the cell membrane and are therefore potentially more toxic than large-molecule tannins (Ayres et al. 1997). Frequently cited examples are phenolic glycosides, which are efficient mammal herbivore deterrents in *Salix* (Stolter et al. 2005) and *Populus* (Donaldson and Lindroth 2007). Phenolic glycosides have been isolated from Mediterranean *E. arborea* (Nazemiyeh et al. 2008a; Nazemiyeh et al. 2008b) and shoot extracts have been shown to have strong antioxidant and analgesic properties (Mohajjel Nayebi et al. 2008). However, there are many other secondary metabolites functioning as herbivore deterrents, for example terpenes (Lawler et al.

2000; Mueller-Schwarze and Thoss 2008; Vourch et al. 2001). High terpene emissions have been reported from Mediterranean populations of *E. arborea* (Llusia and Penuelas 2000; Peñuelas et al. 2002), but nothing is known of *E. trimera* in this respect. Given the similar shoot architecture and similar nutrition value for the two species, the key to the differing browsing preference is likely to be some chemical deterrence, which prompts further comparative studies of their secondary chemistry.

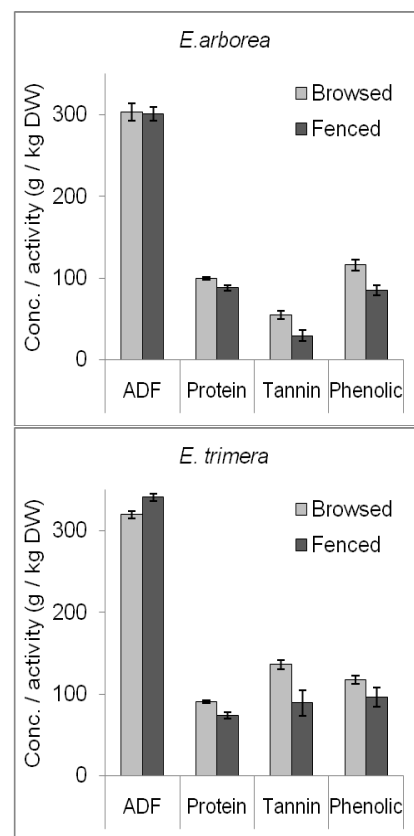


Fig. 7 Average concentrations of ADF, protein and total phenolics and tannin activity of *Erica arborea* and *E. trimera* inside and outside browsing exclosures at Duro. Error bars = S.E. (n=5)

The present disturbance regime of fire and browsing favours *E. arborea*, but both factors need to act in consort. The heavy browsing pressure allows *E. arborea* to outgrow *E. trimera* in early succession after fire. Nevertheless, there is still a yearly height increment of both species, and without short-interval fire *E. trimera* would instead finally out-shade *E. arborea*, since its height at maturity is taller. This form of competitive exclusion is the likely reason for *E. arborea* to be nearly absent from the present *Erica* forest stands of the area (Miehe and Miehe 1994). Judging from ring counts on felled 8 – 11 m tall tree stems (diameter 15 – 30 cm), we believe that such tree stands have not burned for at least 90 years (M. Johansson, personal observation).

It is clear that *E. arborea* achieves a higher net growth rate under heavy browsing pressure, but the question remains as to whether this actually

translates into a long-term competitive advantage, given that the repeated fire kill all above-ground structures. Fire then acts as an alternative consumer of plant biomass (Bond and Keeley 2005), but it is non-selective in contrast to the animal herbivores. Thus, each fire would tend to even out the score of the previous period of competition, although there are also potential carry-over effects: The smaller foliage loss to browsers in *E. arborea* could allow for the accumulation of larger stores of carbohydrates and nutrients in the lignotuber (Canadell and Lopez-Soria 1998; Paula and Ojeda 2006), which could in turn result in better post-fire growth and progressively increase the differences between the species over each cycle of fire and regrowth. Another potential legacy of the pre-burn status is the dead *Erica* stems. When the fire-killed stems are numerous and large, they could provide some protection from browsing in the first couple of years (Davis 1967). The most important mechanism in the long run, however, should be the more effective sexual regeneration in *E. arborea*. Profuse flowering was found only for *E. arborea* within the typical 6–10 year fire cycle, and this is consistent with the occurrence of occasional seedlings of *E. arborea* but not of *E. trimera* at these sites (M. Johansson unpublished). We do not know if the higher browsing pressure on *E. trimera* has an influence on flowering frequency, because the exclosures were not old enough, but it is not unlikely that browsing as well as short-interval fire would enhance any inherent differences in fruiting patterns.

In conclusion, we would suspect that there is a slow, gradual increase in the proportion of *E. arborea* that may have been acting over a very long time. Judging by the huge sizes of the *Erica trimera* lignotubers (frequently more than 1 m in diameter) fire has been prevalent in these heathlands over centuries, although browsing pressure has most likely increased substantially over the last decades due to dramatically increasing human populations (Stephens *et al.* 2001). Nevertheless, certain traits in this system would provide for considerable resistance to change, despite large differences between species in net growth. First, repeated fires will set the system back before serious interspecific competition ensues. Second, the presence of large, resprouting lignotubers should result in low population turnover.

Acknowledgements

We thank Ayano Abraham and Shebru Marefu for field assistance, Helena Königsson for lab assistance, Sören Holm for statistics support and Christina Skarpe and David Wardle for valuable comments on the manuscript. The study was funded by The Swedish International Development Cooperation Agency.

References

- anonymous (2000) Leco Application Note "Nitrogen/Protein in animal feeds". In: Form 203-821-146
http://www.leco.com/resources/application_note_subs/pdf/organic/-146.pdf
- anonymous (2005) Acid Detergent Fiber in feeds filter bag technique ANKOM200 In: http://www.ankom.com/09_procedures/ADF_81606_A200.pdf
- Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. *J Wildlife Manage* 62:1165-1183
- Austin PJ, Suchar LA, Robbins CT, Hagerman AE (1989) Tannin-binding proteins in saliva of deer and their absence in saliva of sheep and cattle. *J Chem Ecol* 15:1335-1347
- Ayres MP, Clausen TP, MacLean SF, Redman AM, Reichardt PB (1997) Diversity of structure and antiherbivore activity in condensed tannins. *Ecology* 78:1696-1712
- Balogun RO, Jones RJ, Holmes JHG (1998) Digestibility of some tropical browse species varying in tannin content. *Anim Feed Sci Tech* 76:77-88
- Bartolome J, Franch J, Plaixats J, Seligman NG (1998) Diet selection by sheep and goats on Mediterranean heath-woodland range. *J Range Manage* 51:383-391
- Blair RM, Short HL, Epps EA, Jr. (1977) Seasonal nutrient yield and digestibility of deer forage from a young pine plantation. *J Wildlife Manage* 41:667-676
- Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol Evol* 20:387-394
- Canadell J, Lopez-Soria L (1998) Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. *Funct Ecol* 12:31-38
- Clausen TP, Provenza FD, Burritt EA, Reichardt PB, Bryant JP (1990) Ecological implications of condensed tannin structure - a case study. *J Chem Ecol* 16:2381-2392
- Davis J (1967) Some effects of deer browsing on chamise sprouts after fire. *Am Midl Nat* 77:234-238
- del Pino MCA, Hervas G, Mantecon AR, Giraldez FJ, Frutos P (2005) Comparison of biological and chemical methods, and internal and external standards, for assaying tannins in Spanish shrub species. *J Sci Food Agr* 85:583-590
- Donaldson JR, Lindroth RL (2007) Genetics, environment, and their interaction determine efficacy of chemical defense in trembling aspen. *Ecology* 88:729-739

- Dwire KA, Ryan SE, Shirley LJ, Lytjen D, Otting N, Dixon MK (2006) Influence of herbivory on regrowth of riparian shrubs following a wildland fire. In: Amer Water Resources Assoc, pp 201-212
- FAO (1998) World reference base for soil resources. In: FAO, Rome
- Fetene M, Assefa, Y., Gashaw, M., Woldu, Z., Beck, E (2008) Diversity of Afroalpine Vegetation and Ecology of Treeline Species in the Bale Mountains, Ethiopia, and the Influence of Fire. In: Spehn E, Liberman M, Korner C (eds) Land Use Change and Mountain Biodiversity
- Focardi S, Tinelli A (2005) Herbivory in a Mediterranean forest: browsing impact and plant compensation. *Acta Oecol* 28:239-247
- Frutos P, Hervas G, Ramos G, Giraldez FJ, Mantecon AR (2002) Condensed tannin content of several shrub species from a mountain area in northern Spain, and its relationship to various indicators of nutritive value. *Anim Feed Sci Tech* 95:215-226
- Gasmi-Boubaker A, Kayouli C, Buldgen A (2006) Feed blocks as a supplement for goat kids grazing natural Tunisian rangeland during the dry season. *Anim Feed Sci Tech* 126:31-41
- González Hernandez MP (2004) Quality of vegetation in silvopastoral systems. In: Mosquera-Losada MR, Rigueiro Rodríguez A, McAdam J (eds) Proceedings of an International Congress on Silvopastoralism and Sustainable Management. CABI Publishing, Lugo, Spain, pp 87-92
- Gonzalez Hernandez MP, Silva-Pando FJ (1996) Grazing effects of ungulates in a Galician oak forest (northwest Spain). *For Ecol Manage*:65-70
- Grime JP, Cornelissen JHC, Thompson K, Hodgson JG (1996) Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. *Oikos* 77:489-494
- Gustafsson J (2009) Habitat and plant selection of livestock in a fire-managed Afro-alpine heathland in Ethiopia. MSc thesis. Department for Forest Ecology and Management, Swedish University of agricultural Sciences
- Hagerman AE (1987) Radial diffusion method for determining tannin in plant extracts. *J Chem Ecol* 13:437-449
- Hanley TA, Robbins CT, Hagerman AE, McArthur C (1992) Predicting digestible protein and digestible dry matter in tannin-containing forages consumed by ruminants. *Ecology* 73:537-541
- Harborne JB, Williams CA (1973) A chemotaxonomic survey of flavonoids and simple phenols in leaves of the Ericaceae. *Bot J Linn Soc* 66:37-54
- Harbourne JG (1991) The chemical basis of plant defence. In: Robbins CT (ed) *Plant Defences Against Mammalian Herbivory*. CRC Press Inc., London, pp 45-59
- Hedberg O (1951) Vegetation belts of the East African mountains. *Sven Bot Tidskr* 45:140-201
- Hedberg O (1971) The high mountain flora of the Galama Mountain in Arussi Province, Ethiopia. *Webbia* 26:101-128
- Herms DA, Mattson WJ (1992) The dilemma of plants - To grow or to defend. *Q Rev Biol* 67:478-478
- Hobbs NT (1996) Modification of ecosystems by ungulates. *J Wildlife Manage* 60:695-713
- Horsley SB, Stout SL, DeCalesta DS (2003) White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol Appl* 13:98-118
- Jackson FS, McNabb WC, Barry TN, Foo YL, Peters JS (1996) The condensed tannin content of a range of subtropical and temperate forages and the reactivity of condensed tannin with ribulose-1,5-bisphosphate carboxylase (Rubisco) protein. *J Sci Food Agr* 72:483-492
- Jones DB (1941) Factors for converting percentages of nitrogen in foods and feeds into percentages of protein. In: Agriculture USDo (ed), vol. Circ. No. 183, Washington DC
- Koricheva J (2002) Meta-analysis of sources of variation in fitness costs of plant antiherbivore defenses. *Ecology* 83:176-190
- Lawler IR, Foley WJ, Eschler BM (2000) Foliar concentration of a single toxin creates habitat patchiness for a marsupial folivore. *Ecology* 81:1327-1338
- Llusia J, Penuelas J (2000) Seasonal patterns of terpene content and emission from seven Mediterranean woody species in field conditions. *Am J Bot* 87:133-140
- Miehe G, Miehe S (1994) Ericaceous forests and heathlands in the Bale Mountains of South Ethiopia : Ecology and man's impact. Stiftung Walderhaltung in Africa, Hamburg
- Mills JN (1986) Herbivores and early postfire succession in southern California Chaparral. *Ecology* 67:1637-1649
- Mohajjel Nayeji A, Nazemiyeh H, Omidbakhsh R, Çobanoğlu S (2008) Analgesic effect of the methanol extract of *Erica arborea* (L.) in mice using formalin test. *Daru* 16:229-232
- Mueller-Harvey I (2006) Unravelling the conundrum of tannins in animal nutrition

- and health. In: John Wiley & Sons Ltd, pp 2010-2037
- Mueller-Schwarze D, Thoss V (2008) Defense on the rocks: Low Monoterpenoid levels in plants on pillars without mammalian herbivores. *J Chem Ecol* 34:1377-1381
- Nazemiyeh H et al. (2008a) Tricetin 4'-O-alpha-L-rhamnopyranoside: A new flavonoid from the aerial parts of *Erica arborea*. *Chem Nat Compd* 44:174-177
- Nazemiyeh H et al. (2008b) Antioxidant phenolic compounds from the leaves of *Erica arborea* (Ericaceae). *Nat Prod Res* 22:1385-1392
- Ormeno E et al. (2009) The relationship between terpenes and flammability of leaf litter. *For Ecol Manage* 257:471-482
- Otsyina RM, B.W. N, M. D (1999) Fodder trees and shrubs in arid and semi-arid livestock production systems. In: In 'XVIII International Grassland Congress, vol. 2, pp 429-438
- Owens MK, Lin CD, Taylor CA, Whisenant SG (1998) Seasonal patterns of plant flammability and monoterpenoid content in *Juniperus ashei*. *J Chem Ecol* 24:2115-2129
- Paula S, Ojeda F (2006) Resistance of three co-occurring resprouter *Erica* species to highly frequent disturbance. *Plant Ecol* 183:329-336
- Peñuelas J, Castells E, Joffre R, Tognetti R (2002) Carbon-based secondary and structural compounds in Mediterranean shrubs growing near a natural CO₂ spring. *Glob Change Biol* 8:281-288
- Pereira JMC, Sequeira NMS, Carreiras JMB (1995) Structural-properties and dimensional relations of some Mediterranean shrub fuels. *Int J Wildland Fire* 5:35-42
- Poppi DP, McLennan SR (1995) Protein and energy-utilization by ruminants at pasture. *J Anim Sci* 73:278-290
- Robbins CT, Mole S, Hagerman AE, Hanley TA (1987) Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* 68:1606-1615
- Schindler JR, Fulbright TE, Forbes TDA (2004) Shrub regrowth, antiherbivore defenses, and nutritional value following fire. *J Range Manage* 57:178-186
- Selje N, Hoffmann EM, Muetzell S, Ningrat R, Wallace RJ, Becker K (2007) Results of a screening programme to identify plants or plant extracts that inhibit ruminal protein degradation. *Br J Nutr* 98:45-53
- Skarpe C, Hester AJ (2008) Plant traits, browsing and grazing herbivores, and vegetation dynamics. In: Gordon IJ, Prins HHT (eds) *The Ecology of Browsing and Grazing. Ecological Studies Vol. 195*, pp 217-261
- Snyder JR (1984) The role of fire - Much ado about nothing. *Oikos* 43:404-405
- Stephens PA, d'Sa CA, Sillero-Zubiri C, Leader-Williams N (2001) Impact of livestock and settlement on the large mammalian wildlife of Bale Mountains National Park, southern Ethiopia. *Biol Conserv* 100:307-322
- Stolter C, Ball JP, Julkunen-Tiitto R, Lieberei R, Ganzhorn JU (2005) Winter browsing of moose on two different willow species: food selection in relation to plant chemistry and plant response. *Can J Zool* 83:807-819
- Teshome T (1999) Effects of grazing and fire on tree regeneration in coniferous montane forest of the Dodola area, Ethiopia. In: Faculty of forestry and ecology, vol. MSc. Georg-August University, Göttingen, p 59
- Van den Bosch S, Guevara JC, Tacchini FM, Estevez OR (1997) Nutrient content of browse species in the arid rangelands of the Mendoza plain, Argentina. *J Arid Environ* 37:285-298
- Wardle DA, Bonner KI, Barker GM (2002) Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Funct Ecol* 16:585-595
- Waterman PG, Mole S (1994) Analysis of phenolic plant metabolites. Blackwell Scientific Publications, Oxford
- Weinert E, Mazurek A (1984) Notes on vegetation and soil in Bale Province of Ethiopia. *Feddes Repertorium* 95:373-380
- Wesche K, Cierjacks A, Assefa Y, Wagner S, Fetene M, Hensen I (2008) Recruitment of trees at tropical alpine treelines: *Erica* in Africa versus *Polylepis* in South America. *Plant Ecol Divers* 1:35 - 46
- Wesche K, Miede G, Kaeppli M (2000) The significance of fire for afroalpine ericaceous vegetation. *Mt Res Dev*:340-347
- Vourc'h G, Martin JL, Duncan P, Escarre J, Clausen TP (2001) Defensive adaptations of *Thuja plicata* to ungulate browsing: a comparative study between mainland and island populations. *Oecologia* 126:84-93
- Yimer F, Ledin S, Abdelkadir A (2006) Soil property variations in relation to topographic aspect and vegetation. community in the south-eastern highlands of Ethiopia. *For Ecol Manage* 232:90-99