# Fire and grazing in subalpine heathlands and forests of Bale Mountains, Ethiopia

## Fire ecology and traditional use of fire

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# Fire and grazing in subalpine heathlands and forests of Bale Mountains, Ethiopia. Fire ecology and traditional use of fire

## Abstract

Pastoralists frequently depend on fire to produce forage for their livestock, but traditional burning is often banned, despite being essential for livelihoods and ecosystem maintenance. In the subalpine heathlands of Bale Mountains traditional fire management is still practiced. This offered a rare opportunity to analyze fire ecology and traditional fire knowledge in a fire-managed shrub system. My aim was to disentangle the interactions between livestock, fuels and vegetation in the heathlands and the forests below, through a combination of experimental and observational studies. My results show that the subalpine forests had a low fire potential due to lack of good surface fuels. In contrast, the *Erica*-dominated heathlands produced highly flammable fuel complexes. Here anthropogenic burning resulted in a regime of high-intensity fires with an average fire return interval of ~10 years. However, the grazed heathlands were non-flammable the first ~4 years post fire, due to lack of fine dead fuels and a discontinuous fuel bed. This helps create a patchy landscape in which young vegetation patches act as fire breaks, limiting the extent of subsequent fires.

Interviews with pastoralists revealed three objectives for burning: to improve pasture, to remove an insect pest and to reduce livestock loss to predators. The informants were well aware of the critical relations between fuel structure, weather and fire behaviour, showing intimate knowledge of fire as a management tool.

Cattle exclusion had relatively little impact on the vegetation and fuel development in both heathland and forest. Cattle browsing, however, dramatically altered the competitive balance between the two co-dominant shrubs *E. arborea* and *E. trimera*, favouring *E. arborea*. In the heathland the return to a flammable state was somewhat faster when cattle were excluded, but in the forest a denser field layer developed which did not increase flammability.

Vegetative regeneration dominated after both fire and mechanical disturbance, despite a large seed bank in the top 10 cm of soil in both heathland and forest sites. In heathland sown *Hagenia* tree seedlings grew extremely poorly, probably due to unsuitable soil conditions. Neither did *Hagenia* seedlings survive in the forest zone, except in exclosures in large canopy gaps, showing that cattle exclusion alone is not sufficient for tree regeneration. Thus, the present division between heathland and forest is stabilized by the lack of fire potential in the forest and lack of potential for tree expansion into heathland.

My results suggest that fire exclusion is not a viable option for the heathlands. It would destroy the pasture quality and is also unlikely to succeed, since huge tracts of highly flammable vegetation would soon develop. To successfully protect these ecosystems and pastoralist livelihoods, I recommend that a joint management plan is created that allows burning, but with defined prescriptions with regard to both fire intervals and fire weather.

*Keywords: Erica arborea*, *Erica trimera*, *Hagenia abyssinica*, Afro-alpine, Ericaceous vegetation, browser selectivity, fire ecology, fuel succession, heathland pasture, subalpine forest, traditional fire management

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# Dedication

to the Bale Mountain pastoralists

*”For them, fire is not a single entity. It is not an undifferentiated force that is constant in its effects. Instead it is recognized as a multidimensional tool of great value that is inherently neither good nor evil, only potentially so in how it is used and, also, not used.”*

Henry T Lewis 1989

# Contents

# List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Johansson, M. U., M. Fetene, A. Malmer, and A. Granström (2012). Tending for cattle: traditional fire management in Ethiopian montane heathlands. *Ecology and Society* **1 7**(3): 19. http://dx.doi.org/10.5751/ES-04881-170319

II Johansson M. U. and A. Granström. Effects of cattle on fuel succession and fire behaviour in fire-managed ericaceous shrubland in Bale Mountains, Ethiopia. *Manuscript*

III Johansson M. U., T. Rooke, M. Fetene, and A. Granström (2010). Browser selectivity alters post-fire competition between *Erica arborea* and *E. trimera* in the subalpine heathlands of Ethiopia. *Plant Ecology* 207(1), 149-160. http://www.springerlink.com/content/d5327x1474j25m6h/?MUD=MP

IV Johansson, M. U., A. Malmer, M. Fetene, and A. Granström. Grazing and fire as controlling factors for tropical montane vegetation at the tree line. Effects of five years of grazing exclusion in Bale Mountains, Ethiopia. *Manuscript*

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# 1 Introduction & Objectives

Both fire and herbivores consume vegetation. Therefore herbivores and fire interact with each other and the vegetation. This thesis analyses the effects of fire and grazing in subalpine forests and fire-managed heathlands in Bale Mountains in the southern highlands of Ethiopia.

## 1.1 Fire

Fire is a natural ecosystem process in biomes covering more than half of the global land area (Krawchuk *et al.*, 2009). In such flammable systems, fire influences vegetation composition, and the vegetation reciprocally influences fire behaviour. Fire has been acting as an evolutionary force ever since the first terrestrial plants appeared, and ecosystems and plants have co-evolved with their own distinct fire regimes (Pausas & Keeley, 2009). Fire is a complex phenomenon depending on many different variables interacting, mainly fuels, climate and ignition. A fire regime includes the typical patterns, sizes, frequencies, season and intensities of fires and differs between biomes (Gill, 1975). Fire shapes ecosystems by determining properties such as species composition, nutrient cycling and ecosystem productivity (DeBano *et al.*, 1998; Neary *et al.*, 1999; Bowman *et al.*, 2009; Keeley, 2012). Historically humans have altered natural fire regimes to suit their needs and ecosystems have through centuries of burning adapted to anthropogenic fire (Bird *et al.*, 2008; Bowman *et al.*, 2011).

A controlled burn is intended and managed by people, whereas a wildfire is an uncontrolled fire lit accidentally or intentionally by people or by lightning (Pyne, 1993). Due to rapid land use changes, fire regimes are currently changing, and abrupt change may be devastating, since ecosystems and species are not adapted to fire per se, but to their own particular type of fire regime (Pausas & Keeley, 2009; Keeley *et al.*, 2011).

### 1.1.1 Prerequisites for fire

For fire to occur, fuel, oxygen and a source of ignition is necessary. Wildland fuel is composed of live and dead plant biomass. In order to carry fire, the fuels need to be of enough quantity and continuously distributed across the surface (Bradstock & Gill, 1993). Also the vertical arrangement of fuels is important, particularly in forests. If the tree canopy is too widely separated from the surface fuels on the ground, normally fire cannot climb up in the canopy (Albini, 1985) and the fire regime will be dominated by surface fires rather than crown fires. A continuous cover of surface fuels (i.e. field-, moss- or litter layers) is necessary for forest fires to occur; crown fire cannot be sustained without support from surface fire below, unless under extreme wind conditions or steep slopes (Raymond & Peterson, 2005). Fuel arrangement at a finer scale includes the bulk density, or compactness, of plant structures which influences oxygen supply and radiant heat transfer between particles (Andrews, 2009). Certain plant species have an ideal particle arrangement in their canopy or in their litter beds which makes them more flammable. Also, the particle size of the individual fuel components determines the amount of heat necessary to remove moisture and raise the temperature to the ignition point (Rothermel, 1972), therefore it is much easier to ignite thin twigs than thick branches. Thick branches and logs (if not piled up) will not be completely consumed due to the short residence time of a constantly moving wildfire (Andrews, 1996).

The moisture content of dead fuels is very important for fire behaviour and determines when combustion is at all possible. Live fuels regulate their moisture content internally and their quality as fuels is determined by their inherent, species specific, moisture content and chemical composition. Evergreen sclerophyllous plants (e.g. Ericaceous plants) typically have low moisture content and high concentrations of oils, waxes and terpenes which are easily volatized and contribute to the energy release of the fire (Rothermel & Philpot, 1973). Deciduous mesophytic plants have higher moisture contents and retard fire when green and need to wilt and cure to become good fuel (Van Wilgen *et al.*, 1990; Cheney *et al.*, 1993).

The climatic preconditions for fire include, firstly, enough precipitation to produce a continuous vegetation cover, plus secondly, a distinct period of drought conditions when the fuel bed becomes dry enough to burn. Drought includes a period without rain, but also with low relative air humidity (RH) which will increase the drying rate of fine dead fuels (Britton *et al.*, 1973). Fine dead fuels can only burn when moisture contents are below the moisture of extinction threshold, ca 15– 40 % moisture content per dry weight (MC/DW) depending on the type of fine fuel (Scott & Burgan, 2005b). During longer droughts live herbaceous vegetation cures and adds to the fine dead fuels.

Droughts occur at very different intervals in different systems, from annual, to decadal, or even at timescales of thousands of years (Wård *et al.*, 2007). Often there is a diurnal variation with increasing RH at night caused by lower night temperatures (Van Wagner, 1977).

Wind is a very important factor for the rate of spread (ROS) of head fires (fires travelling with the wind) because it pushes the flames closer to the fuel bed (slope has the same effect), increasing fuel preheating efficiency and flame contact (Beer, 1995; Finney *et al.*, 2010). An exponential increase in rate of spread with increasing wind speed is an often used approximation for head fires (Scott & Burgan, 2005a). For backing fires wind has little effect on rate of spread. In order to understand the fire ecology of an ecosystem it is necessary to consider natural ignition sources, mainly lightning ignitions, which are very common in Africa, especially in the highlands where they typically occur at the start of the rainy season (Archibald *et al.*, 2012).

Taken together, fuel properties and weather factors determine fire behaviour, and in particular fire intensity. Byram (1959) defined fire-line intensity as the energy output rate per unit length of the flaming front (expressed as kW $m^{-1}$), and it is calculated as the product of the energy content in the fuel (kJ $kg^{-1}$), the mass of the fuel load consumed (kg $m^{-2}$), and the rate of spread (m $s^{-1}$). Of these factors the rate of spread is the most variable and the most important for local variation in fire behaviour during the same fire event.

The fire-line intensity is correlated to flame length, and varies greatly between different ecosystems.

Rothermel (1972) constructed a mathematical fire spread model that includes fuel quantity, structure and moisture contents as input variables, and estimate rate of spread, flame length and fire-line intensity. They form the basis of the Behave fire behaviour prediction system (Alexander, 1982; Andrews *et al.*, 2008) which was used in paper II.

Fire intensity should not be confused with “fire severity” (sensu Rowe, 1983), which is a problematic term, since it has been defined and used in many different ways (Keeley, 2009). Also, a fire that is “severe” to one species may be beneficial for another (Johnson & Miyanishi, 2007). “Fire severity” is usually understood as the impact of the fire on the ecosystem, e.g. tree mortality and biomass consumption. It may sometimes be correlated with fire intensity but also with depth of burn in the organic soil layer, which is often more or less independent from fire intensity (Schimmel & Granström, 1996).

### 1.1.2 Fire effects on soils and nutrient cycling

Fire affects soil and belowground processes both directly by heat from the fire, and indirectly through an altered post-fire environment, e.g. reduction in canopy cover and altered species composition.

The direct effects on soils depend both on residence time and the temperature of the flaming front (normally ca 700–1100 °C (Wotton *et al.*, 2012)) and on the soil moisture content at the time of fire (Neary *et al.*, 1999). Heat conduction in mineral soil is generally very poor (Beadle, 1940; Bradstock & Auld, 1995; Giovannini & Lucchesi, 1997). In areas with slow decomposition rates, due to harsh climate and/or poor litter quality, such as in boreal or subalpine forests and in heathland ecosystems, there is often a well developed organic humus layer on top of the mineral soil. Here soil impact depends mainly on the moisture content of the humus, controlling how deep down smoldering combustion (ground fire) can occur (Miyanishi, 2001). Smoldering combustion can, if the humus is dry enough, continue long after the flaming front has passed, and has, despite lower temperatures (ca 250-450 °C (Miyanishi, 2001)), greater impact on the soil due to a longer residence time. Also, the temperature gradient downwards is usually very steep, with non-lethal temperatures (below ca 60 °C) only a few cm below the combustion zone (Hobbs & Gimingham, 1984; Schimmel & Granström, 1996).

Plant nutrients can be lost either directly during the combustion phases, or later due to post-fire erosion. There are large differences between volatilization temperatures of different elements. Nitrogen volatilization starts at relatively low temperature, from ca 200 °C (Raison, 1979), whilst phosphorous volatilization occurs above ca 770 °C (Raison *et al.*, 1985). Therefore a larger proportion of nitrogen than phosphorous is lost to the atmosphere (Christensen & Muller, 1975; Raison *et al.*, 1985). Gaseous and particulate losses occur mainly from the combusted material (Debano & Conrad, 1978; Raison, 1979). Studies of the effects of fire on total soil nitrogen are contradictory; some are showing a decrease (Debano & Conrad, 1978; Dunn *et al.*, 1979) and some find no substantial effect (Christensen & Muller, 1975; Giovannini & Lucchesi, 1997; Williams *et al.*, 2012). Even if total ecosystem nitrogen decreases after fire, plant available nitrogen can temporarily increase through a number of different mechanisms; unavailable organic forms may have been chemically oxidised to more readily available forms (Choromanska & DeLuca, 2002). The higher post-fire pH (due to the alkaline ash) favours nitrification, causing an increase of the nitrate to ammonium ratio (Schafer & Mack, 2010). The higher soil pH also increases phosphorous availability (Schafer & Mack, 2010). Heat-killed soil organisms decompose and cause a temporal boost of all plant nutrients (Christensen & Muller, 1975; Dunn *et al.*, 1979). The reduction in soil organic matter affects soil structure, water holding capacity and microbial activity (Williams *et al.*, 2012). Another indirect long-term effect is caused by the addition of charcoal. It has been suggested to contribute to increased rates of nutrient cycling by adsorbing phenolic compounds from the humus (Wardle *et al.*, 2008).

Often mentioned post-fire effects on soil are increased solar radiation due to a reduced canopy, and the blackened soil surface which both significantly increase daytime soil temperatures (Auld & Bradstock, 1996). This may affect seed germination and seedling survival as well as below-ground processes. The reduced canopy alters ecosystem water balance by reduced transpiration, (Malmer, 1992), but also reduced interception which may increase leaching and erosion (Malmer *et al.*, 2005). Altered post-fire vegetation may cause changes in litter quantity and quality which may have long-term effects on soil processes (Malmer *et al.*, 2005). Generally, many long-term effects on the soil stem from the altered above- and below-ground community composition, mainly depending on canopy mortality, depth of burn and different abilities of species to re-colonize (Dunn *et al.*, 1979; Bradstock & Auld, 1995; Schimmel & Granström, 1996; DeLuca & Sala, 2006; Risberg & Granström, 2012).

### 1.1.3 Interactions between herbivores and fire

Bond and Keeley (2005) compare fire to herbivory by large mammals, since both consume vegetation and therefore can be competing for the same biomass. Fire may temporarily exclude herbivores by removing herbaceous forage (Augustine & McNaughton, 1998; Fuhlendorf *et al.*, 2009) and intense grazing can exclude fire by removing surface fuels (Norton-Griffiths, 1979; Savage & Swetnam, 1990; Archibald *et al.*, 2005; Waldram *et al.*, 2008; Fuhlendorf *et al.*, 2009). The main difference is that mammal herbivores are selective and preferably graze young herbaceous components early in the vegetation period, whilst the fire indiscriminately takes the dead and unpalatable vegetation components, often later in the dry season or later in succession (McNaughton, 1985; Hobbs & Gimingham, 1987; Augustine & McNaughton, 1998).

Both mammalian herbivores and fire exercise top-down control of the vegetation, limiting interspecific competition and therefore allowing species to co-exist, instead of reaching competitive exclusion of weaker competitors (Bond & Keeley, 2005). The impact of mammalian herbivores on vegetation mainly depends on animal size and feeding guilds (grazers vs. browsers), population densities and the mixture of different animal species (Augustine & McNaughton, 1998). Domestic livestock often have a larger impact on vegetation since they are less mobile and are kept at higher densities (Skarpe, 1991). Cattle are considered to be mainly grazers and they lack upper front teeth and have to rip off the grass by wrapping their tongue around it. Therefore they have problems grazing very short grass. Also, cattle lack the tannin-binding saliva proteins typical of browsers (Robbins *et al.*, 1987). But African Zebu cattle can be productive also with a high proportion of browse in their diet (Sanon *et al.*, 2007). Because herbivores consume potential fuel, a relaxed grazing pressure after a population crash (e.g. caused by epizootic disease) should cause a build-up of fuels and an altered fire regime (Norton-Griffiths, 1979; Trollope *et al.*, 1996) but there are few documented examples of this in the literature.

Plants defend themselves against herbivores by, among other things, producing different types of secondary metabolites (Herms & Mattson, 1992). Phenolics and terpenes are considered to have evolved as defence against herbivores (Coley *et al.*, 1985) and the waxes and oils typical for sclerophyllous leaves may function both for water conservation and defence (Rundel, 1981). Some of these secondary metabolites also increase vegetation flammability by increasing the energy content of the live plant parts and produce volatiles when heated, and therefore make the vegetation more flammable (Rundel, 1981; Snyder, 1984; Bond & Midgley, 1995). They are also unpalatable to the soil microbes and will slow down decomposition rates (Bardgett & Wardle, 2003) allowing formation of a humus layer which will influence fire behaviour and effects, as described earlier.

Heavy investment in chemical defence should be less advantageous when aboveground biomass is repeatedly removed non-selectively by fire (Rundel, 1981). But for long-lived plants simultaneously responding to several different selection pressures, such as fire, herbivory and competition, there must be a trade-off in investment in regenerative capacity, defence and growth (Herms & Mattson, 1992).

### 1.1.4 Fire in different biomes

Due to differences in climate and vegetation, fire regimes differ between biomes (Bowman *et al.*, 2009). On high tropical mountains this becomes even more evident since the different montane biomes often occur as compressed ecological zones across the altitudinal gradient due to steep gradients in temperature and precipitation (Hedberg, 1951; Körner, 2012). This allows for large variation in fuels, climate and fire potential in different biomes situated only a few kilometres apart.

The field studies underlying this thesis were done in tropical subalpine ericaceous shrublands and forests. These have very contrasting physiognomies and presumably different fuel conditions. The heathlands are situated at a higher elevation with lower temperatures and higher precipitation. Despite this, fire frequency is higher in the heathlands than in the forests. The plain below the forest, the open gaps in the forest and young heathland post-fire stages are dominated by grass vegetation.

### *Grasslands*

Grasses comprise excellent fuels when they have cured. The upright stature and thin leaves and stems in an airy arrangement makes cured grass fast-drying and easily ignited. Grass species have their meristems located at the soil surface and are well adapted to recurrent loss of their above-ground parts.

Grasslands dominate where precipitation is high enough for grass growth, but too low for closed forests, or where frequent fires limit tree growth (Bond *et al.*, 2005). For fires to occur there must also be a dry period long enough for the grasses to cure. The typical grassland fire regime is one of low intensity surface fires, with short fire-return-intervals. After each fire the vegetation normally quickly returns to the pre-fire state, in terms of species composition and fuel structure, due to the quick regrowth of the grasses.

The relationships between trees, shrubs and grasses in i.e. savannahs depend both on the amount of precipitation and the fire- and grazing regimes (Sankaran *et al.*, 2005; Hoffmann *et al.*, 2012). Lightning-ignited natural fires have, ever since the first grasses evolved, extended the grassland biome into areas where the precipitation is high enough to support forests, and this fire-caused savannization has been further exaggerated, especially in Africa, by thousands of years of anthropogenic burning (Bond *et al.*, 2005).

### *Shrublands*

Shrublands exist where some abiotic factor or combination of factors, such as climate, soil, or fire limits tree growth, but still allows for woody perennial plant growth (Breckle & Walter, 2002). Fire-maintained evergreen sclerophyllous shrublands are typically found in Mediterranean climates, with hot dry summers, mild winters and enough precipitation to support large biomass production (Keeley, 2012). Flammable sclerophyllous shrublands are also found above the tree line on tall mountains (Hedberg, 1951; Ellenberg, 1979; Smith, 1980; Corlett, 1984; Young, 1993; Miehe & Miehe, 1994b; Bradstock *et al.*, 2002 ; Körner & Paulsen, 2004; Wesche *et al.*, 2008).

Sclerophyllous shrublands are often characterized by high fuel loads consisting of a large proportion of fine fuels with a high energetic content (Mooney & Dunn, 1970). Therefore shrubland fire regimes are typically dominated by high-intensity, stand-replacing crown fires occurring with a wide range of different fire-return-intervals, from around five years to many decades, depending on plant species, climate, topography and ignition frequency (Hanes, 1971; Trabaud & Lepart, 1980; Keeley, 1986; Cowling *et al.*, 1996; van Wilgen *et al.*, 2010). Multi-stemmed shrubs are often better adapted to recurrent high-intensity fires than most trees, since their strategy is to invest in resprouting capacity, rather than thick bark and tall canopies above scorch height.

Since all aboveground plant parts typically die in shrubland fires, and a large share of the biomass is consumed, there should be a time-dependent increase in fuel quantity and quality after each fire, for example by accumulation of fine dead material in the canopy (Rothermel & Philpot, 1973). This succession of fuels may put a lower limit on the minimum fire-return-interval, if the young successional stages are dominated by non-flammable vegetation (Baeza *et al.*, 2006; Pearce *et al.*, 2010; Potts *et al.*, 2010), or if the resprouting shrubs are situated too far apart, creating a discontinuous fuel bed (Bradstock & Gill, 1993). Despite the recent increased interest in fuel reduction by prescribed fire or herbivores in shrub-dominated ecosystems there are few studies of successional changes in fuels over time and its potential effect on fire behaviour (Pearce *et al.*, 2010) and how this can be influenced by grazing or browsing herbivores.

All shrubland species have some kind of strategy to cope with recurrent fire, such as the ability to resprout from underground structures (such as roots, rhizomes, bulbs, corms and lignotubers), seed banking (Holmes & Newton, 2004), or wind-dispersed seeds. Some shrub species, especially the obligate seeders, may be sensitive to changes in fire-return intervals and fire season (Bond, 1980; Seydack *et al.*, 2007), whilst others, especially the resprouters are quite resilient to a wider range of fire regimes (Keeley, 1986; Trabaud, 1991).

Invasive exotic grasses can cause alterations of shrubland fire-regimes into more frequent fires, causing shrub ecosystems to switch into grasslands (Keeley *et al.*, 2005).

Many resprouters have lignotubers. These are genetically determined, specialised woody underground structures containing dormant buds and stored nutrients and carbohydrates (Canadell & Lopez-Soria, 1998). Resprouting typically occurs from adventitious buds that are protected under heat-insulating soil (James, 1984). Lignotubers increase the individual’s ability to quickly compete after fire and to persist over countless fire cycles (Canadell & Zedler, 1994; Bond & Midgley, 2001; Lamont *et al.*, 2011). In shrublands dominated by resprouters there should be little room for new colonization from seed since the persistent old individuals may live for many hundreds of years (Garland & Marion, 1960; Head & Lacey, 1988; Tyson *et al.*, 1998). Also, seedlings lack underground storage and should be more sensitive to grazing.

*Forests*

Forests are found in areas with higher precipitation and shorter drought periods than are shrublands and grasslands (Bond *et al.*, 2005). Besides this, in closed-canopy forests, the trees themselves regulate the interior climate under the canopy. During hot sunny days the temperatures and wind speeds are lower and the relative air humidity is higher under trees compared to outside (Hoffmann *et al.*, 2012). This reduces evaporation rates from the surface fine fuels (Van Wilgen *et al.*, 1990; Agee *et al.*, 2000). Also, because of the shading of the tree canopy, there is often little biomass in the field layer and decomposition of litter may be fast due to the moister interior climate (Vitousek *et al.*, 1994; Eriksson *et al.*, 2003). Therefore closed-canopy forests are less fire-prone than grasslands and shrublands (Van Wilgen *et al.*, 1990; Bond *et al.*, 2005; Mermoz *et al.*, 2005; Cochrane, 2009). Forest fire regimes can either be dominated by low intensity surface fires, or high-intensity stand-replacing crown fires (Bond & Van Wilgen, 1996). Stand-replacing fires typically occur at very long intervals, from hundreds up to several thousands of years (Wård *et al.*, 2007).

Furthermore, it has been observed that many of the dominant tree species in tropical subalpine forests have typical pioneer species traits (Lange *et al.*, 1997; Fernández-Palacios & Arévalo, 1998; Fetene & Feleke, 2001; Demel, 2005; Cierjacks *et al.*, 2008; Teshome & Glatzel, 2011), and should be adapted to regenerate after large-scale disturbance such as fire, but there are no studies analysing tropical subalpine forests surface fuel dynamics and its potential effects on forest flammability.

## 1.2 Traditional use of fire

For traditional societies fire is often a necessary tool to open up forests and create a more open habitat (Bowman *et al.*, 2011). Closed-canopy forests often provide little food resources for humans due to the fact that trees invest a large share of their primary production in wood. Open landscapes have a higher proportion of grasses, large-seeded annuals, corms and tubers which are directly edible for humans or serve as forage for wild game or domestic livestock (Grimm, 1984; Pyne, 1993; Bowman, 1998; Kull, 2000; Bond & Keeley, 2005). Today it is generally agreed that fire has been used by man to manage landscapes for thousands of years (Bird & Cali, 1998; Marlon *et al.*, 2008; Bowman & Murphy, 2011; Trollope, 2011; Archibald *et al.*, 2012) especially in Africa and Australia.

In ecosystems where young vegetation is non-flammable, increased vegetation heterogeneity would create fuel breaks in the landscape. This could reduce the risk of large-scale landscape-covering wildfires (Lewis, 1973; Bowman *et al.*, 2004; Mermoz *et al.*, 2005; Bird *et al.*, 2008).

Pastoralists often use fire to improve pasture for their livestock. African pastoralism has a long history and pre-dated agriculture in the East African Savannahs (Marshall & Hildebrand, 2002). The North African wild ox (*Bos primigenius africanus*) was probably domesticated more than 7000 years ago, and the Zebu cattle arrived ~4000 years ago (Hanotte *et al.*, 2002). Cattle and other livestock allow people to explore land marginal for agriculture. The pastoralist life-style is an adaptation to survive in harsh or unpredictable climates and it was traditionally characterized by seasonal migration and communal land ownership. (Marshall & Hildebrand, 2002). Due to population growth and increased land scarcity, African pastoralists are currently in a process of sedentarization, which has large ecological and societal consequences (Scoones *et al.*, 2012).

Pastoralist burning typically has multiple purposes, i.e. to remove litter and rejuvenate grasses, to control encroaching shrubs, to eliminate parasites and to limit hiding places for large predators (Solomon *et al.*, 2007; Angassa & Oba, 2008; Butz, 2009; Trollope, 2011). Savannah management fires are often set early in the dry season when the grass is not completely cured, in order to keep intensity low to protect trees (Laris, 2002). In West Africa pastoralists use early-season burning to create a “seasonal mosaic” of fire breaks in the landscape to prevent large high-intensity late-season wild fires (Hough, 1993; Mbow *et al.*, 2000; Laris, 2002).

Pastoralists have traditional ecological knowledge regarding plant species and ecological processes, and manage their ecosystems accordingly (Bollig & Schulte, 1999; Berkes *et al.*, 2000; Fernandez-Gimenez, 2000; Mapinduzi *et al.*, 2003). The few studies of traditional ecological knowledge concerning fire have found that traditional fire management has already undergone considerable change due to population growth, increased grazing pressure, sedentarization and burn bans imposed by authorities (Mbow *et al.*, 2000; Oba & Kotile, 2001; Laris, 2002; Solomon *et al.*, 2007; Butz, 2009). This implies that pastoralist fire regimes are dynamic and can change over time, but there is a lack of ecological studies quantifying living traditional fire knowledge in relation to fire variables, such as fuel and weather.

Authorities often perceive traditional fire management as solely destructive to ecosystems and try to control it through legislation (Fairhead & Leach, 1996; Pyne, 2001; Kull & Laris, 2009). In some ecosystems, such as rainforests, increased traditional burning may be detrimental if forest structures are changed, causing unnatural fuel build-up and increased drying of surface fuels, creating vicious cycles of increased fire frequencies (Uhl *et al.*, 1988;

Goldammer, 1990). But in ecosystems with a long history of anthropogenic fire, instead the exclusion of traditional burning causes abnormal fuel build-up and increased risk of devastating wildfire (Yibarbuk *et al.*, 2001; Bowman *et al.*, 2004; Métailié, 2006; Pausas & Keeley, 2009).

Anthropogenic fire can be regulated to maintain ecosystems and increase carbon storage. In a unique project in the West Arnhem Land savannah in Australia, the traditional anthropogenic fire-regime is re-introduced in order to abate the higher carbon release from wildfires (Fitzsimons *et al.*, 2012).

It may seem as a paradox that at the same time as controlled burning is re-introduced to control fuels in industrialized parts of the world (Pyne, 2001), fire use is still questioned in poor countries (Oba *et al.*, 2000; Laris & Wardell, 2006; Eriksen, 2007; Butz, 2009; Kull & Laris, 2009; Tacheba *et al.*, 2009) with prevailing traditional fire management. Despite fire often being a prerequisite both for pastoralist livelihoods and for ecosystem maintenance.

## 1.3 Objectives

The Bale Mountain subalpine heathlands and forests are complex and dynamic systems governed by multiple interactions between climate, fire and livestock. Current landuse intensification, in combination with increased forest conservation efforts, requires an increased understanding of the role of fire and grazing in these ecosystems. The main objective of this study is to quantify fire potential and effects of fire and grazing in different vegetation zones in order to form a base for informed land management decisions. A further aim is to document this, for shrubland ecosystems unique, still living fire-culture, and its effects on the ecosystem. This might also advance the understanding of shrub ecosystems elsewhere, which may have been under similar management in the past.

The work underlying this thesis focused on analysing vegetation dynamics in subalpine heathlands and forests in order to quantify effects of fire and grazing on the vegetation and the impact of livestock on vegetation, fuel succession and fire potential.

More specifically, I pose the following questions:

1. How does grazing and browsing influence fuel dynamics of the subalpine heathlands (paper II) and forests (paper IV)? and how does heathland fuel dynamics influence fire behaviour (paper II)?

2. What are the effects of fire on the pasture resource (paper III and I)? and how does grazing influence post-fire competition between *Erica* species (paper III)?

3. What are the effects of fire, soil disturbance and grazing on soils and regeneration in the subalpine heathlands and forests (paper IV)?

4. How is the current fire regime related to fire weather? and how does this affect heathland vegetation structure at a landscape level (paper I)?

5. What are the management strategies of the local population? what is the state of their traditional ecological knowledge regarding fire (paper I)?

# 2 Study System

## 2.1 Study area

The studies underlying this thesis were undertaken in the districts of Adaba, Dodola, Ashena Robe and Serofta in Bale Mountains in the southern highlands of Ethiopia. The study area is located on the northern slopes of the east–westerly oriented mountain chain, in an area (~50 x 25km) centred at 6°50′ N, 39°18′ E ranging in elevation from ca 2950 to 3700 m (Fig. 1).

### 2.1.1 Soils and climate

Bale Mountains make up the highest section of the southern Ethiopian highlands which were formed by relatively young lava flows poured out in association with Tertiary Rift Valley formation (Mohr, 1971). The tallest peak is at ca 4400 m.a.s.l. and located ca 60 km east of the study area. A large plain is situated to the north at ca 2400 m. The peaks in the study area reach ~3650–3750 m. The bedrock consists of volcanic alkaline basalts and rhyolites which weather to fertile dark-coloured silty loams (Weinert & Mazurek, 1984). The slopes are mostly quite gentle and a mineral soil layer is covering the bedrock almost everywhere, except in eroded cattle tracks and horse trails (Plate 1a). The top soils are increasingly rich in organic matter with increasing altitude, and have a distinct humus layer at high altitudes (Yimer *et al.*, 2006).

The climate is Afro-alpine and characterized by little seasonal but large diurnal variation in temperature (Hedberg, 1951). At ca 3400 m.a.s.l. the average seasonal max and min temperatures (recorded during two years at two sites in the study area) were ca 15 °C and 5 °C during the rainy season, and ca 22 °C and 2 °C during the dry season (Fig. 3). In the dry season night-time frost is common during clear nights (Miehe & Miehe, 1994a).

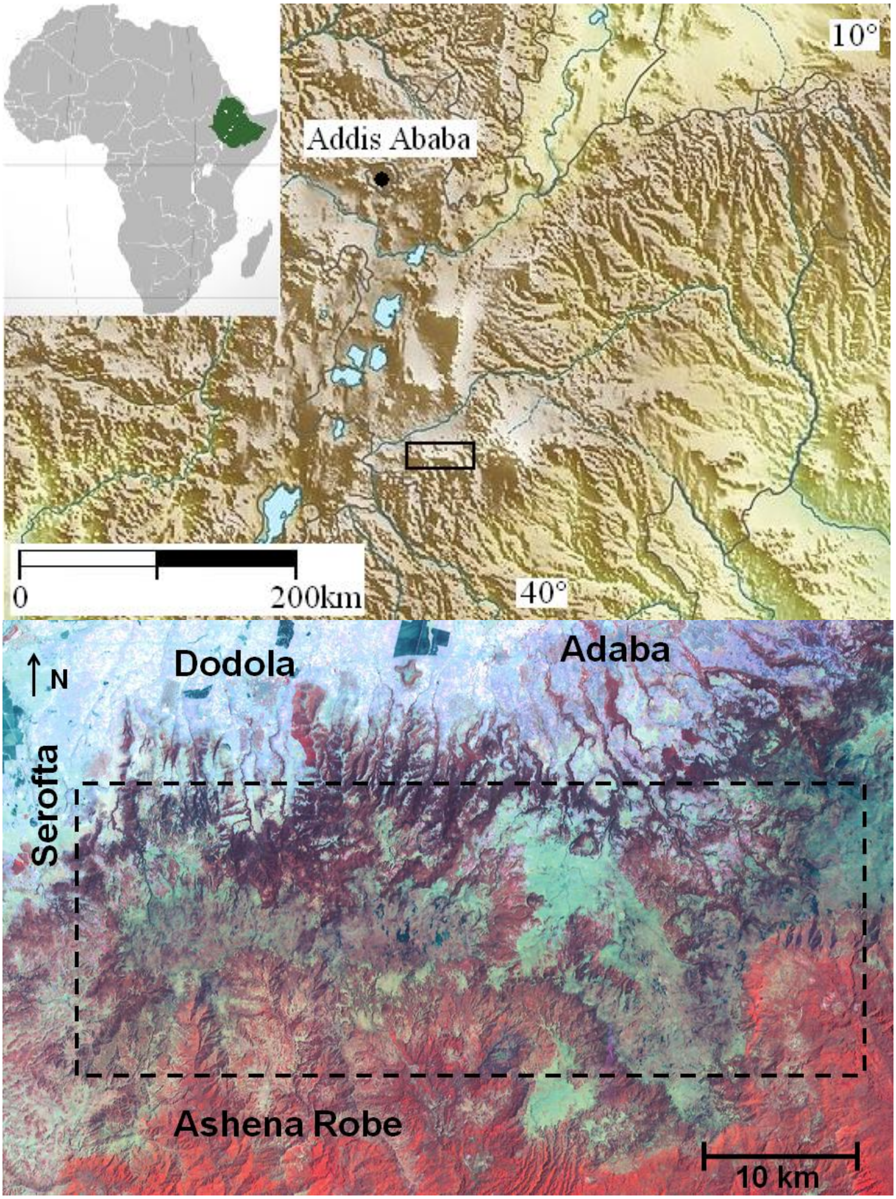


*Figure 1.* Location of the study area in Bale Mountains south-east of the Ethiopian Rift Valley. The lower panel is a Landsat image of the study area from Feb. 5th 2000. The light-blue at the top is the plain at ~2400 m (today cultivated). The dark-red is the montane forests on the northern slopes at ~2600–3500 m. The red-green in the centre is Ericaceous shrubland at ~3500–3700 m. The bright-red at the bottom is the evergreen montane forest on the southern slopes.

The climate is wet during most of the year, except during the brief dry season which normally lasts from December to January (Fig. 2) or, in drought years continues into March or April (Fig. 3). In Ethiopia, severe droughts typically return at ~10-year intervals (Seleshi & Demaree, 1995). Region-wide droughts which affected the study area (Abera & Kinahan, 2011) occurred in 2000 and 2008 (Kurnik *et al.*, 2011). The northern aspect of the mountain is drier than the southern, especially at lower altitudes (Miehe & Miehe, 1994a). Precipitation generally increases with increasing altitude (Miehe & Miehe, 1994a). Mean annual precipitation at ~3450 m was ~1740 mm, and often included small amounts of rain or mist also in the dry season (Fig.3). Dry season orographic winds are generally quite mild, 1–4 m/s with only occasional wind gusts up to ca 10 m/s. The wind direction is up-slope in the morning and down-slope in the afternoon. The strongest dry season winds are just after sunset and just before sunrise. Lightning storms are common during the rainy season.

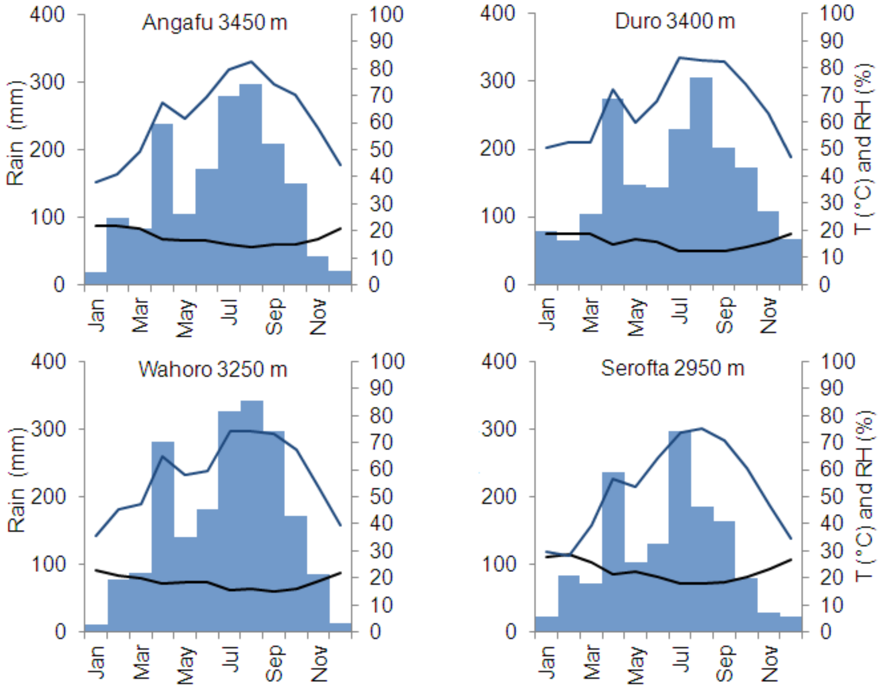


*Figure 2.* Climatic diagrams for the study sites showing monthly average rainfall 2006-2008 (blue bars), average noon (=max) temperature (black line) and noon (=min) RH (blue line). The climate data is collected by us near our permanent study sites.

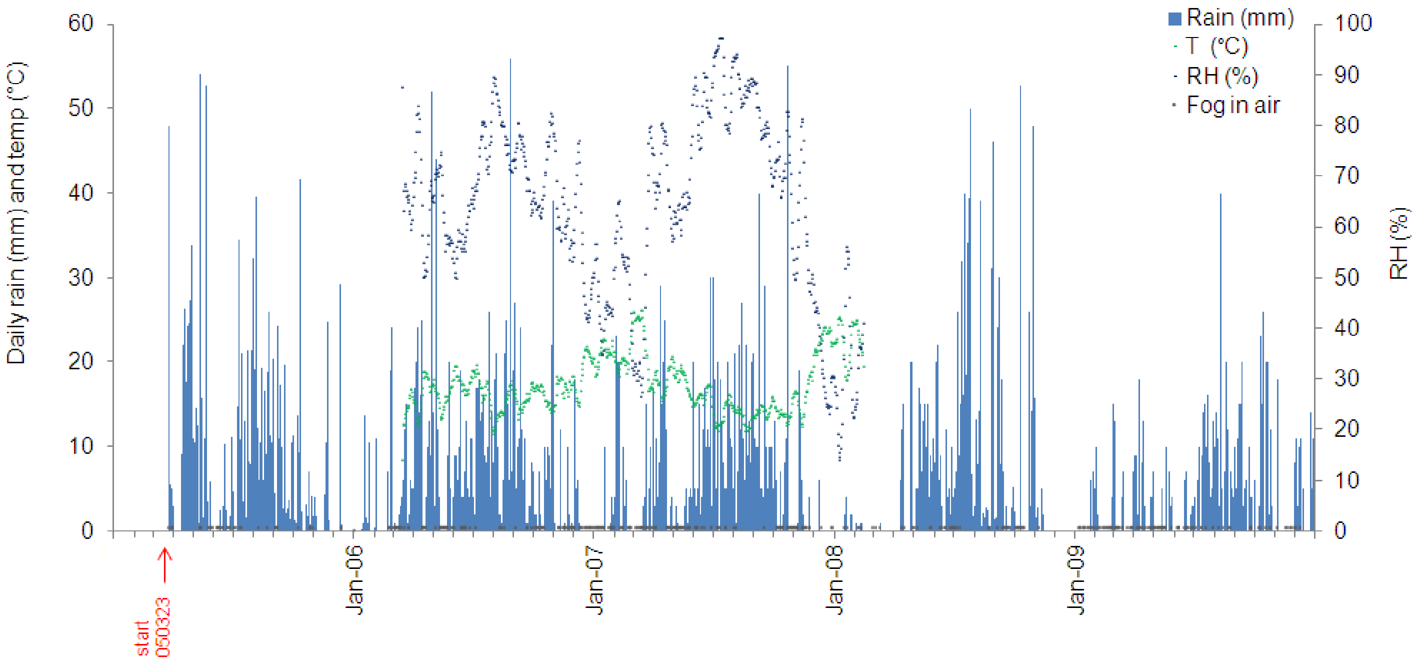


*Figure 3.* Example of daily rainfall patterns at ~3450 m elevation. Rain data compiled from Duro 2005 and Angafu 2006–2009 (compiled, because Duro lacked data from 2009 and Angafu lacked data from 2005 and the rainfall was rather similar at the two sites, see Fig 2.). Rain (blue bars), fog in the air (grey dots), noon temperature (green dots) and noon RH (blue dots). Days with 0 mm in the rain gauge, but with mist or rain in the air are displayed as 0.5 mm grey dots. Temperature and RH were recorded by climate loggers in Angafu March 2006–February 2008 and displayed values are ten-day running averages.

### 2.1.2 Vegetation

The vegetation of Bale Mountains shows a distinct altitudinal zonation (Friis, 1986; Miehe & Miehe, 1994a) (Fig. 1). Typically, alpine grasslands dominate above ~4000 m, and subalpine Ericaceous shrubland, or heathland, is found between ~4000–3500 m, which is dominated by multi-stemmed *Erica arborea* and *Erica trimera* (formerly *Philippia trimera*) shrubs kept short by repeated burning by pastoralists (Plate 1b). Below the heathlands a narrow belt of subalpine Ericaceous forest is situated between ~3500–3350 m, which is dominated by tree-formed *E. trimera* with a few emergent *Hagenia abyssinica* and *Myrsine melanophloeos* (formerly *Rapanea melanophloeos*). The vegetation zones are similar on the northern and southern aspects at the highest altitudes, but show increasing differences at lower altitudes. On the north side from ca 3350 m, there is a subalpine mixed broadleaved forest dominated by *Hypericum revolutum*, *H. abyssinica* and *M. melanophloeos* with an increasing component of *Juniperus procera* (absent on the southern aspect). Between ~3200–2600 m *J. procera* becomes the dominating tree species in the northern montane forests which include also *H. abyssinica*, *H. revolutum, M. melanophloeos*, *E. arborea*, and *Podocarpus falcatus*. At ~2600–2500 m a savannah plain commence, today dominated by agriculture (Miehe & Miehe, 1994a).

The vegetation zones are dynamic over time (Mohammed & Bonnefille, 1998). The peak and the highest plateau have been repeatedly covered by ice-cap glaciers. The last ice-cap probably reached down to ~4000 m on the northern slopes (Osmaston *et al.*, 2005). According to pollen analyses the last deglaciation ended ~11000 years BP during a period of dry climate (Mohammed & Bonnefille, 1998; Umer *et al.*, 2007). Due to long-term warming since the Last Glacial Maximum forest zones would be expected to migrate upwards and the habitat for Afro-alpine species to shrink (Thompson *et al.*, 2002).

Ericaceous vegetation is typically found in cold and wet climates on acid soils, but on the tall East African Mountains it forms the uppermost woody vegetation belt despite the alkaline bedrock. Hedberg (1951) defined the Afromontane Ericaceous belt as including both the shrubby heathlands and the tree heather forests below. These two, more or less distinct, vegetation zones often consist of the same *Erica* species (Hedberg, 1964). The Ericaceous belt typically span 1000 m in altitude (~3000–4000 m) (Hedberg, 1951). Fire has been suggested to be an important factor for its vegetation dynamics, especially on the drier aspects of Kilimanjaro (Hedberg, 1964; Hemp & Beck, 2001), Mount Elgon (Wesche, 2002) and Rwenzori (Wesche *et al.*, 2000). In the Bale

Mountains the transition line between forest and heathland is unusually distinct at ca 3500 m with a few scattered groups of stunted, but tree-formed, tree heathers in rocky places high above the treeline. Therefore it has been suggested by Hedberg (1975; 1978), Miehe & Miehe (1994b), Wesche (2008) and Fetene et al. (2006) that anthropogenic fire keep the shrubs in the heathlands short and multi-stemmed (Plate 1b and 4b). The presence of large lignotubers (Plate 1c) also suggests a long history of recurrent fire.

In Bale Mountains the heathlands are co-dominated by multi-stemmed lignotuberous *E. arborea* and *E. trimera* but the forest below is dominated by tree-shaped *E. trimera* and here *E. arborea* is absent (Assefa *et al.*, 2011).

Shrub-formed *E. trimera* and *E. arborea* are morphologically similar and have often been collectively referred to as *E. arborea* since they are difficult to distinguish from each other, especially when co-occurring completely intermixed in the heathlands. *E. trimera* is endemic for East Africa whilst *E. arborea* is common on all tall African mountains and all around the Mediterranean basin, both as a tree and a shrub.

Besides having some species in common, the Afro-montane heathlands are very similar to Mediterranean-type shrublands also in terms of plant adaptations, and with respect to the fire regimes, despite very different climatic conditions. The largest difference being the tropical alpine climate with “winter-every-night and summer-every-day” (Hedberg, 1951) which is much colder and wetter than the Mediterranean climate. This allows for the formation of a distinct humus layer (Read & Perez-Moreno, 2003) which should influence the effects of fire on both nutrient cycling and regeneration (paper IV). In this aspect Afro-montane heathlands are more similar to temperate heathlands with the main difference that the equatorial subalpine shrub species, such as *E. arborea* and *E. trimera* grow much larger, potentially into tall trees.

In order to improve pasture the Bale Mountain heathlands are regularly burnt by the local pastoralists (Front cover, Plate 2a). Therefore the vegetation consists of patches of *Erica* shrubs in different stages of regeneration depending on time passed since the last fire (Johansson *et al.*, 2012). All aboveground vegetation is killed by the fire and the only remains are the dead, charred stems from the pre-burn stand and the blackened soil surface. Both *Erica arborea* and *E. trimera* are facultative seeders, i.e. they can regenerate both by resprouting and from seed (Fetene *et al.*, 2006) (paper IV) but in the heathlands they mainly regenerate by re-sprouting, which occurs within a few months after fire (paper IV). In young post-fire stages the gaps between the lignotubers are filled with a short lawn of grasses and herbs (Johansson *et al.*, 2009). The cattle consume both the *Erica* shoots and the grass/herb lawn in young stands (paper I) (Gustafsson, 2009). Old stands have an almost continuous shrub cover with a dense moss layer below (paper IV), and these stands are less preferred by the cattle (Arvidsson, 2009).

### 2.1.3 Land use, livelihoods and forest conservation

The Bale region has been inhabited by pastoralists for many centuries (Huntingford, 1955; Haberland, 1963). Early landuse is largely unknown but it is likely that population density was low and that cattle were herded between seasonal pastures in a transhumance system (Flintan *et al.*, 2008). The alpine pastures have probably been improved and expanded by fire ever since pastoralism arrived. The first European explorers described a fire-maintained “moorland” landscape above the treeline (Bourg des Bozas, 1906; Smeds, 1959; Mooney, 1963; Brown, 1969).

Throughout history, the intensity of landuse should have varied due to conflicts, famines, population growth, migration and resettlement programmes (Flintan *et al.*, 2008). A disastrous famine at the end of the 19th century was caused by the Rinderpest, which killed the majority of the cattle (Pankhurst, 1966) and this severely affected the pastoralists who were entirely dependent on cattle husbandry for their subsistence (Tiki & Oba, 2009). Since Bale Mountains have been remote, road-less and relatively sparsely populated, the transhumant life-style has survived in the heathlands and forests until recent times (Watson, 2007; Flintan *et al.*, 2008). Uniquely for heathlands and shrub ecosystems globally, the traditional fire management system here has persisted until present day, despite the fact that burning of vegetation has been regarded as illegal in Ethiopia since the 1970’s (Melaku Bekele, pers. comm.).

The study area is currently under increasing pressure from population growth, sedentarization and landuse intensification (Stephens *et al.*, 2001; Flintan *et al.*, 2008; Vial *et al.*, 2011b). The adjacent Bale Mountains National Park (BMNP) was established in 1971 (Hillman, 1988) to preserve the Afromontane habitats with their unique biodiversity (Fetene *et al.*, 2006). The Adaba-Dodola forests and heathlands were designated a national forest priority area in 1988 to serve as a buffer zone to the national park. A joint forest management project was introduced in 1995 to reduce deforestation (Amente, 2005; Yemiru *et al.*, 2010). This project has recently been integrated into the Bale Ecoregion project (the national park together with surrounding forest priority areas) to secure conservation funds via the REDD+ system. The aim of the project is to increase carbon storage in the forests and heathlands, to reduce deforestation rates and number of heathland fires, and to reduce grazing in the forest (Oromia Forest and Wildlife Enterprise, 2011).

The montane pastoralists have recently settled more or less permanently and many have started to cultivate barley in small clearings in the forest. According to the local people barley cultivation is limited by night-time frost above altitudes of ca 3200 m. For montane households, especially the highest situated, a large share of the income is still derived from livestock (Bekele *et al.*, 2007; Yemiru *et al.*, 2010): butter, meat, and riding horses. The grass is grazed very short in the whole area. In contrast to other burnt and grazed shrubland systems, no exotic plant species are known from the heathlands, and only one from the forests, (Miehe & Miehe, 1994a), but on the agricultural plain below 2600 m.a.s.l. there are a number of invasive exotic herbs. In order to protect crops livestock is normally herded. Herding also serves to protect small livestock from large predators, mainly spotted hyenas (*Crocuta crocuta*), leopard (*Panthera pardus*) and common jackals (*Canis aureus*), (Atickem *et al.*, 2010). In the heathlands there is no cultivation and here adult cattle range freely during daytime. Occasionally sheep and goats were observed in the heathland, herded by children. There are also wild mammalian herbivores in the heathlands: the Mountain Nyala (*Tragelaphus buxtoni*) which is mainly a browser (Brown, 1969) and the Bohor reedbuck (*Redunca redunca*), a grazer, (Afework *et al.*, 2010) and large populations of small grass-eating rodents (SilleroZubiri *et al.*, 1995).

In the forest zones there is a small-scale extraction of marketable timber and poles, charcoal and fuel wood leading to the canopy becoming increasingly opened up (Amente, 2005; Kidane *et al.*, 2012), which at the same time improves forest pasture. Cutting of large *E. trimera* and *H. revolutum* trees at the treeline has recently increased for the construction of fences around homesteads (personal observation). There seems to be very little regeneration of tree species in all forest zones and the only common tree seedlings found are of the unpalatable species *M. melanophloeos* and *Discopodium penninervum* (Tesfaye *et al.*, 2002; Assefa *et al.*, 2011). Many of the important timber species, such as *H. abyssinica* and *J. procera* display typical pioneer traits (Lange *et al.*, 1997; Teketay & Granstrom, 1997; Fetene & Feleke, 2001) but their regeneration ecology is not fully understood, probably due to multiple interactions between seedling survival, herbivory and fire.

# 3 Materials & Methods

In order to investigate the effects of fire and grazing on the vegetation a combination of experimental and observational studies were used. Permanent grazing exclosures were erected to compare vegetation dynamics with and without livestock in *Erica* heathland, *Helichrysum citrispinum* shrub, *E. trimera* forest and *H. abyssinica* forest (Table 1).

Table 1. *Description of the grazing exclosure sites.*

| Vegetation | Site | Alt.[1] (m.a.s.l.) | Coordinates (lat./long.) | Aspect, slope (%) | Fenced (year[1]) | Exclosure sizes (m) |
|---|---|---|---|---|---|---|
| *Hagenia* forest | Serofta | 2950 | N 06°50’37’’/ E 039°02’41’’ | NE, 1.5% | 2006 | 30x30 |
| | Wahoro | 3210 | N 06°51’13’’/ E 039°11’07’’ | N, 3% | " | 30x30[2] |
| | Moda | 3350 | N 06°51’32’’/ E 039°12’21’’ | N, 2.5% | " | 30x30[2] |
| *Erica* forest | Angafu | 3400 | N 06°51’36’’/ E 039°13’50’’ | SW, 15% | 2007 | 6x6 |
| | Angafu | 3440 | N 06°51’21’’/ E 039°14’26’’ | S, 10% | " | 6x6 |
| *Helichrysum* | Angafu | 3450 | N 06°50’49’’/ E 039°14’26’’ | N, 10% | 2006 | 5x5 |
| | Angafu | 3490 | N 06°50’41’’/ E 039°14’29’’ | SW, 28% | " | 5x5 |
| | Angafu | 3530 | N 06°51’53’’/ E 039°14’09’’ | W, 32% | " | 5x5 |
| Heathland | Duro | 3510 | N 06°51’38’’/ E 039°39’28’’ | N, 27% | 2005 | 10x10[3] |
| | Angafu | 3530 | N 06°50’30’’/ E 039°14’07’’ | SW, 34% | 2006 | 10x10[3] |
| | Gama | 3630 | N 06°50’38’’/ E 039°14’30’’ | N, 17% | " | 10x10[3] |

[1] All fences were erected at the beginning of the year, in January–February. [2] At two *Hagenia* sites an additional 5x5 m fence was built in a forest gap not more than 300 m away. [3] At the heathland sites fences were built in pairs, one in a recent burn and one in adjacent mature *Erica* vegetation.

The different studies were mainly conducted in the vicinity of the exclosures. Inside and outside the exclosures we monitored vegetation development, collected biomass samples, conducted sowing and planting experiments, light measurements, seedbank analyses, soil analyses, etc. Climate data was collected at four sites near the permanent plots. Heathland fire observations and data on heathland biomass and patch structure at the landscape scale were collected across the whole study area. Interviews with the pastoralists were done in communities across the whole study area.

Approximately 400 days of field work was undertaken during four consecutive dry seasons: February–April 2005, December 2005–April 2006, November 2006–February 2007 and December 2007–February 2008. Additional vegetation data was collected by a trained field assistant in Dec. 2008 and Jan. 2011. More details are given in the individual manuscripts. There are no roads in the study area so field work and transport of fencing materials and samples was limited by the fact that all material had to be carried on horse-back.

## 3.1 Climate data collection & fire observations

Rain data was collected by local staff at four sites from March 2005 until December 2009. Temperature and RH was logged by climate loggers at the same sites during 2 years (Fig. 3). This weather data was used to calculate daily fire weather index (FWI) values used in paper I. During field work additional portable climate loggers were used for short-term recordings of local temperature and RH at sowing plots, in recently burnt vs. “mature” (>180 cm tall) heatland vegetation and inside/outside closed canopy forest (paper IV).

During the, in total, 249 days spent in the heathlands, all observed fires were recorded and notes were taken on timing, vegetation, terrain and fire behaviour (paper I). Test burns were performed in *Erica* heathland (paper II) and *Hagenia* surface fuels (paper IV) to collect data on rates of spread, flame lengths, and surface temperatures.

## 3.2 Grazing exclosures

In order to quantify the effect of livestock grazing (the correct term would be browsing when cattle consume woody *Erica* spp., but since their feeding behaviour in the heathlands is more similar to bulk feeding of both grasses, herbs and *Erica* spp., I will hereafter refer to cattle foraging as grazing) on vegetation species composition, fuel accumulation, germination and seedling survival, etc., we successively built 16 grazing exclosures in the three studied vegetation zones (Table 1), described below for each zone separately, since study design differed slightly. All fences were guarded and maintained regularly by local staff during the study period. The size of the fenced plots differed between studies (Table 1), but the construction was similar; a ~160 cm tall fence with 6 strands of barbed wire ~20 cm apart (at the base); when necessary to exclude also small livestock reinforced by vertical wood splints interwoven with the wire every ~10 cm from the ground up to ~70 cm. The fences also excluded the large native antelope Mountain Nyala (*Tragelaphus buxtoni)* which is present in small numbers, but maybe not the native Bohor reedbuck (*Redunca redunca*) which can jump high, nor monkeys (in the forest) or small grass-eating rodents (common in the heathlands). Grazed plots were placed on all sides of the exclosures and at enough distance to avoid sampling the possibly more grazed and trampled area just next to the fence.

### *Exclosures in the heathlands (paper I, II, III and IV)*

At three heathland sites a pair of 10x10 m grazing exclosures were established: One exclosure in a recently burnt *Erica* stand (burnt by the local herders, so pre-burn measurements were not possible) and one in the adjacent stand of “mature” shrub assumed to be of the same height as the pre-burn stand. The Duro pair of fences was built in February 2005 and the other two pairs in February 2006. The fences were erected less than a month after fire, before new *Erica* shoots had yet emerged from the lignotubers. Inside and outside exclosures vegetation height and cover was measured yearly in the four different treatments: Burnt x Fenced, Burnt x Grazed, Mature x Fenced and Mature x Grazed. The closest two heathland exclosure sites were ~1 km apart, and the farthest was ~26 km away. The fenced mature plot in Gama was accidentally burnt in December 2007, almost two years after fencing, the same thing happened to the mature plot in Angafu in February 2008.

### *Exclosures in Helichrysum citrispinum shrub*

There are sometimes treeless patches in the uppermost *Erica* forest zone which are dominated by *Helichrysum citrispinum* shrubs. This is an alpine, silver-coloured, thorny cushion-formed everlasting plant which is avoided by the cattle. In this type of vegetation in Angafu (~3500 m.a.s.l.) we built three 5 x 5 m fences were in February 2006. We selected sites which were dominated by large (~1.0–1.2 m tall and 1.0–2.5m wide). Inside several of these shrubs were *Erica* (of both species), evidently protected by the thorny canopy but unable to expand beyond it. By erecting the exclosures we wanted to test if release from grazing would allow *Erica* to outcompete *Helichrysum*. The closest two *Helichrysum* fences were ~300 m apart, and the furthest was ~2 km away.

*Exclosures in the Erica trimera forests (paper IV)*

In order to quantify vegetation development and potential surface fuel dynamics with and without grazing, two 6 x 6 m exclosures were built in *E. trimera* forests at ~3400 m. a. s. l., ~600 m apart, in Angafu in February 2007. The *E. trimera* trees were ca 11 m tall, had 2–6 main stems and the lower part of the canopy was separated ~8 m from the ground. The sites were chosen to have as little slope as possible and a closed canopy. The basal area was 30 and 38 $m^2$ $ha^{-1}$ (including a few *H. abyssinica* and *H. revolutum* at some distance from the exclosures). The canopy was fully closed over the fenced plots and the surrounding grazed plots. The field layer was an herb carpet cropped short by livestock.

*Exclosures in the Hagenia forests (paper IV)*

In order to quantify surface fuel dynamics with and without grazing in the *Hagenia* forests, and with the intention to later perform burning experiments, we searched the study area for large patches of closed-canopy *Hagenia* forest in more or less level terrain. At three suitable sites, we built 30 x 30 m grazing exclosures in January–February 2006. The canopy was dominated by *H. abyssinica*, with some *H. revolutum* and *M. melanophloeos* trees. Basal area ranged 27–75 $m^2$ $ha^{-1}$ and canopy cover was estimated to 80–90 %. The field layer was a short herb carpet. Each of the three exclosure sites had an at least equally large unfenced area of similar conditions surrounding the fences. Grazed plots were established on all sides of the fence and more than 5 m away from the fence to avoid the fence effect. At two of the *Hagenia* sites we also built a 5 x 5 m exclosure in a close-by canopy gap (less than 300 m away) chosen to represent similar altitude, slope and soil conditions but having full sunlight for germination and seedling survival tests. During all visits to the *Hagenia* sites, the field- and litter layer in the forest never cured (not even during the extreme drought in March–April 2008) so the planned burning experiment was replaced by a soil scarification experiment (see below).

## 3.3 Vegetation, germination and seedling survival

*Vegetation development*

In the heathlands we used 10 m long line-intercept transects (Bauer, 1943) to quantify area cover and heights of the resprouting stems of the two different *Erica* species and the herb/grass-, or moss-carpet in-between shrubs. In permanent plots inside and outside fences marked individuals in line-transects were repeatedly measured during a 6- (in Duro) or 5-year period. Lignotuber diameter, number of stems, proportion of shrub surface with fresh browsing stumps (Fig. 3, paper IV) and presence/profusion of inflorescence was also documented.

In order to quantify herbaceous recolonization with and without grazing, we established small permanent field-layer vegetation plots (30 x 30 cm) inside and outside the heathland exclosures in burnt and mature vegetation, adding a soil scarification treatment (Fig. 1, paper IV). In these plots we recorded area cover of charred humus, bare soil and all plant species until February 2008 (paper IV).

At the forested sites we recorded herb species composition and field- and litter layer depths inside and outside grazing exclosures during 5 years (*Hagenia* forest) and 4 years (*Erica* forest). The last line-transect measurements were made in Jan 2011 (paper IV).

### *Sowing & planting experiments*

At the heathland sites the above described small vegetation plots were also used for a sowing experiment with *Hagenia*, *Hypericum* and *E. arborea* seeds. Germination and seedling survival/growth was monitored during 2 or 3 years. Light measurements were taken for each sowing plot (paper IV).

Inside the *Hagenia* forest exclosures a similar sowing experiment was done, with the same seed batches, with three different treatments: leaf litter burning, mechanical scarification and control. In the gap fences only soil scarification was applied (Plate 3g). Additional germination tests with the same seed batches were made in the laboratory in Sweden.

Since there was no germination/survival in the closed-canopy *Hagenia* plots, additional planting of *Hagenia* seedlings was done by the field assistants in June 2006 inside and outside the three *Hagenia* forest exclosures and in each of the two adjacent gap exclosures. Light measurements were taken for each planted spot during two consecutive years. Seedling survival and height was monitored for 5 years.

### *Seedbank analyses*

In order to analyze the potential for seedling establishment from buried seeds, the soil seedbank was quantified using the seedling emergence method described by Demel & Granström (1995) (paper IV). Soil samples were collected from just outside the grazing exclosures at each of the three *Erica* heathland paired treatments burnt & mature, and two *Hagenia* and two *Erica trimera* forest sites. Seven soil samples were collected per site/treatment and divided into different depth horizons. Seedlings of unidentifiable species were transplanted and cultivated to flowering (when possible), pressed and identified by the National Herbarium in Addis Ababa. *Erica* seedlings were identified to species by their indumentums; *E. trimera* has glandular hairs and *E. arborea* has branched hairs.

## 3.4 Forage quality & cattle selectivity

In order to quantify forage quality of the two *Erica* species in stands differing in time since fire a chemical assay of *Erica* shoot forage quality was performed (paper III). Top-shoot samples (the top 10 cm, corresponding to what the cattle normally browse) including leaves and stem were collected from both species in three different age classes. The samples were analyzed for water content, tannin- and phenolics-, acid detergent fibre- and crude protein contents (paper III). Also samples from inside exclosures were analysed in order to detect weather induced defence existed. A clipping experiment was performed inside exclosures to quantify possible differences in browsing tolerance between the two species.

Two MSc students quantified cattle selectivity between the two *Erica* species and the herb/grass component (Gustafsson, 2009) and cattle preference of patches of heathland vegetation of different time since last fire (Arvidsson, 2009) by using time-analyses of foraging behaviour and vegetation analyses.

## 3.5 Fuels & landscape patch structure

### *Heathland fuel succession and potential fire behaviour*

In order to estimate fuel quantity in heathland vegetation in relation to height and age a chronosequence of *Erica* heathland stands of differing time since last fire was used (paper II). Stand age was determined by counts of annual rings. Biomass was harvested from a representative plot within each shrub canopy and separated into different fuel fractions, weighed in the field, transported to a local lab and dried to constant weight. Biomass per hectare was calculated by compensating for different canopy cover for different heights. All fuel data was fed into the BehavePlus 5.0 fire behaviour model (Andrews, 2009) to model potential fire behaviour for each age-class at different weather conditions and slopes, which was compared with observed fire behaviour (paper II).

### *Erica heathland landscape patch structure*

In order to analyze the effect of current fire and pasture management at the landscape scale, we sampled long transects across the heathland landscape, marking borders between patches of different time since fire by GPS (paper I). Stem age of current and previous generation stems (when present) was determined by counts of annual rings. The relative area of patches of different time since last fire was calculated and an age-class structure at the landscape scale was calculated. Two of the transects were re-sampled a second year in order to estimate the proportion of stands of known age burnt during one fire season to be able to estimate average fire-return intervals (paper I).

*Forest surface fuel dynamics*

In both *Hagenia* and *Erica* dominated forests, different fractions of surface fuel biomass were harvested inside and outside exclosures, in the dry season one and two years after fencing (paper IV). *Hagenia* leaf litter is plentiful and the leaves have curly edges and form airy layers and hence has potential of becoming important surface fuel. Therefore we estimated quantity and seasonality of litter fall using four 1 x 1 m litter traps placed under closed *Hagenia* canopy in fenced areas (to prevent livestock eating the leaves) (paper IV). Small-scale burning experiments of *Hagenia* leaf litter were performed in January 2006 and January 2008 (paper IV).

## 3.6 Soil characteristics and plant available nutrients

Soil samples were collected and analysed for pH, soil organic matter (SOM) and bulk density (BD) (paper IV). In order to estimate in-field plant available nutrients, resin capsules were placed in the root horizon in each of the four different heathland treatments (burnt/mature and fenced/grazed) (paper IV).

Since no large burning experiment was possible in the *Hagenia* forest, in order to simulate disturbance, a soil scarification experiment was established in which resin capsules were used to compare possible plant available nutrients in four different treatments: scarified/control and fenced/grazed (paper IV).

In order to detect possible limitations in water availability in the heathland and in the *Hagenia* forest, across the rainy- and dry seasons, gypsum blocks were placed under undisturbed soil, with the base at 10 cm depth (where SOM was ~35–45 % in the heathland and ~20% in the *Hagenia* forest) in all four heathland treatments and inside the *Hagenia* exclosures. The gypsum blocks were read monthly with a Delmhorst Soil Moisture Tester (KS-D1, Delmhorst Instrument Co, NJ, USA) by local field assistants from February 2006 until February 2008.

To compare the different soils at the permanent sites and to determine *Hagenia* seedlings soil and nutrient requirements, a soil bioassay and fertilization experiment was conducted by a student at Wondo Genet College of Forestry (at 1800 m.a.s.l.).

## 3.7 Interviews

In order to document the traditional ecological knowledge regarding fire and pasture, to elucidate local management strategies, and to understand the system, interviews were done with 18 pastoralists living close to the heathlands (paper I). They were all utilising the heathlands for pasture for their cattle and were involved in fire management. I used qualitative semi-structured interviews, partly by using photos of vegetation and asking about heathland vegetation age, pasture quality, ignitability, quality of burns etc. Additionally two in-field interviews were made looking closely at vegetation, insects and soil, discussing fire potential and fire effects. Further, in order to document local fire technology and at the same time quantify fire behaviour close-up, a small experimental test-burn (for which legal permit had been obtained) was performed together with one of the informants. Here flame-lengths and temperatures (in order to calculate flame residence time) were recorded (paper II).

# 4 Results & Discussion

## 4.1 Current fire potential

During four dry seasons of fieldwork, I observed 192 fires in the heathlands (paper I) but none in the forests (paper IV). This suggests widely different fire potential in respective system.

### *Heathland fire potential in relation to post-fire age*

The *Erica* shrubs in the heathlands increased in height and accumulated enough biomass to burn in about 5–6 years, according to observations and simulations (paper II). The fuel mainly consisted of the *Erica* shrubs themselves and the moss and litter beneath since all accessible grass was cropped short by cattle (paper II & IV).

The average fire return interval was around 10 years according to the landscape transect study (paper I). There were no observations of burns in vegetation younger than 5 years, or shorter than ~60 cm, (Fig. 7, paper II). This suggests that young patches normally cannot burn (paper II). This allows recently burnt patches to act as fire breaks in the landscape and limit the extent of subsequent fires. Fires were frequently observed to stop when reaching young stands (Fig. 2 paper I). About 40% of the heathland was covered by 0–4 year old vegetation (Fig 8, paper I) which means that there were abundant fire-breaks in the landscape and hence each subsequent burn will be relatively limited in size.

The lower age limit for stand flammability stems partially from the fact that the regenerating shrubs are spatially separated (Fig. 2, paper II). Discontinuous fuel beds are typically less flammable due to a poor ability of flames to bridge gaps (Bradstock & Gill, 1993). Another reason for non-flammability could be the higher moisture content of young shoots (Fig. 6, paper III). But most important is probably the fact that young stands lack fine dead fuels (Fig. A1, paper II). In this shrubland system there is evidently a fuel limitation to the minimum fire-return interval, resulting in that anthropogenic burning creates a patchy landscape with abundant, relatively long-lasting fire breaks. This prevents landscape-covering wildfires since the landscape is virtually free from natural fire breaks.

Fine dead fuels start accumulating from around year 4 (Fig. A1, paper II) and increase from ~5–6 years, then consisting of self-thinned branches, litter and moss, which increase due to canopy closure. After passing this flammability threshold, heathland fuel quantity and quality increased rapidly (Fig. A1, paper II) resulting in a steep increase in modelled fire intensity in ~8–20 year old vegetation (Fig. 6, paper II) (Plate 2a). The test-burn in ~160 cm tall, ten-year old vegetation at a FWI of 35, produced maximum flame lengths of ~2.8 m (Fig. 8a, paper II) and a rate of spread of ~7.5 m $min^{-1}$. This agreed reasonably well with modelled fire behaviour (Fig.6, paper II). The dominant moss under the *Erica* shrubs, *Breutelia borbonica*, is a large and airy ground-living moss mainly growing under shrub canopy (Plate 1e) where it is protected from trampling, to which mosses are sensitive (Olofsson, 2006). The moss is probably a vital component of the fuel complex since the Bale heathlands mainly burn at very high FWI (fire weather index) (Fig 6, paper I), when moss moisture contents are low. Smoldering fire in the humus typically stopped within one hour after the flames had passed according to observations. Probably because the humus layer was normally too moist for deep smoldering to occur (see *Heathland soils* below).

When shrubs reach ~3–4 m height (at ~25–30 years) the *Erica* shrub canopy starts to become separated from the surface fuels, and flammability decreases, according to interview results and observations (paper I). And at ~50 year’s age the stand has developed into a low-statured (~6 m) forest, where cattle have access to graze under the canopy (Fig. 1d, paper II) further decreasing flammability. This observation supports the hypothesis that vertical fuel discontinuity is one important factor for the lower flammability of forests compared to shrublands (*cf.* Van Wilgen *et al.*, 1990).

### *Heathland fire potential in relation to fire weather*

Most fires burnt at the height of the day when temperatures were highest, and RH lowest (Fig. 7, paper I). Most fires were observed in January and February (Fig. 4) and the number of observed fires per day was highly correlated with daily FWI (Fig. 6 paper I). Number of observed heathland fires and the total area burnt varied between years (Fig. 4). This might partly be explained by the length and quality of the dry season. But also the amount of available vegetation tall enough to burn could influence the total area burnt each year

(Fig. 8, paper I). The 2006/2007 dry season was short and moist with fog almost every day (Fig. 3) and few burns were observed (Fig. 4). In contrast the 2007/2008 dry season was dry and lasted for 4 months; from December to April resulting in extremely high FWI and 136 fires were observed between December 2007 and February 2008 (Fig. 4). The fires continued after the fieldwork period ended according to local assistants.

In October 2008 a supervisor and two MSc students observed many new burns (compared to stand photo maps from Feb 2008) which according to the local herders had continued until rains returned in mid April. In some cases deep smoldering had occurred in humus and lignotubers (paper I) (Plate 1d). 2008 was a year of region-wide extreme drought (Kurnik *et al.*, 2011) and large heathland areas burnt also in the adjacent national park (Abera & Kinahan, 2011).

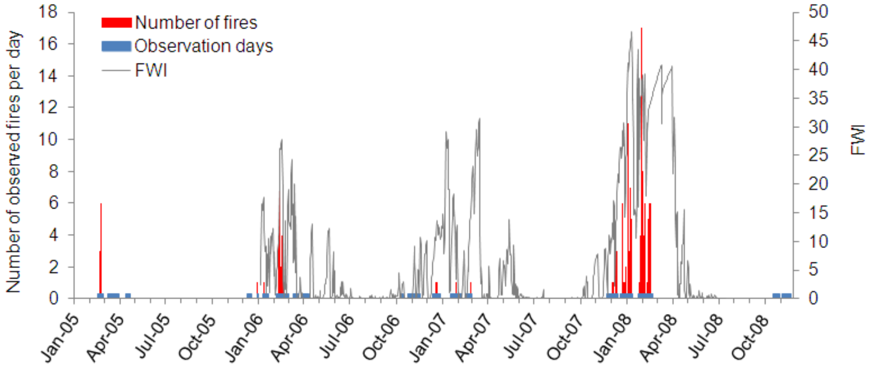


*Figure 4.* Number of observed fires per day (red bars) during the 249 observation days (observation days are indicated by short blue bars at the bottom) and calculated FWI (black dashed line). In total 192 fires were observed: 16 in the 2004/2005 dry season, 36 in the 2005/2006 dry season, 4 in the 2006/2007 dry season and 136 fires in the 2007/2008 dry season. Field work terminated at the end of February 2008 but fires continued until rains returned in mid April according to interviews and observations in October 2008.

### *Fire potential in Helichrysum vegetation*

According to interview results and observations, *Helichrysum citrispinum* shrubs are less flammable than *Erica* shrubs (paper I). This might be caused by differences in foliar chemistry (*cf.* Van Wilgen *et al.*, 1990). The pastoralists wished to get rid of this thorny grazing-weed, which is not browsed by cattle. However they considered *Helichrysum* being too laboursome to burn because each cushion had to be ignited individually since fire does not transfer between them (paper I). This was corroborated by our observations of many individually ignited *Helichrysum* shrubs where the fire had stopped after burning only one, or a few individuals (Plate 2b & c). Only once a large burnt patch of *Helichrysum* was observed, and this had burnt during the prolonged drought in March–April 2008. Frequently seedling establishment of *Helichrysum* was observed in patches of burnt *Helichrysum*.

### *Fire potential in the forests*

In the forest zones surface fuels were poor, both under closed canopy and in the open gaps (paper IV). Grasses and herbs were grazed to an extremely short (~1 cm tall) lawn (Plate 3e and 4c) both in the *Hagenia* and *E. trimera* forests (paper IV). The only common apparently un-grazed field-layer species were *Kniphofia foliosa* and *Kalanchoë petitiana* which are both semi-succulent and highly non-flammable. The dry *Hagenia* leaf litter which could potentially constitute surface fuel was also consumed by the livestock (paper IV). The *E. trimera* forest canopy consists of highly flammable biomass, but crown fire normally cannot occur without support from a surface fire below (Van Wilgen *et al.*, 1990; Raymond & Peterson, 2005). Also, the forests had a cooler and moister dry-season microclimate than the gaps (Fig 5a).

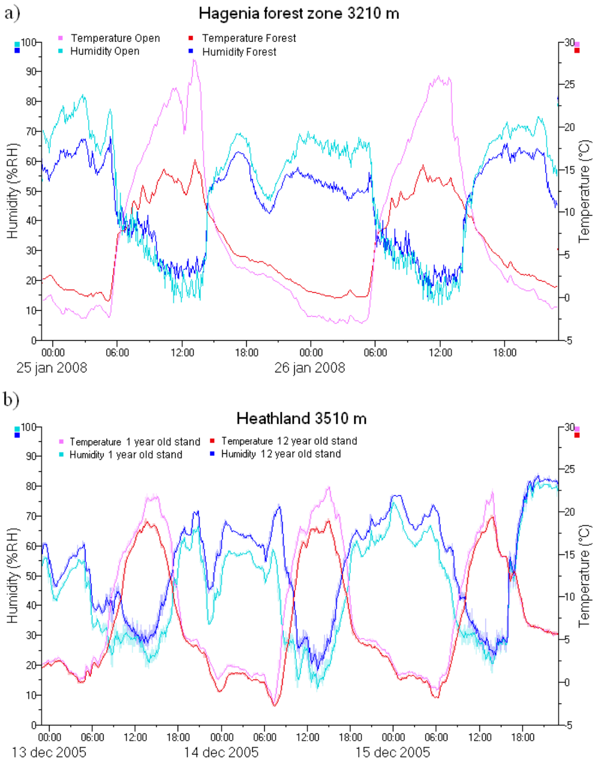


*Figure 5. a)* Example of diurnal variation in dry season temperature (red) and air humidity (blue) in closed-canopy *Hagenia* forest (dark colour) compared to adjacent open gap (light colour). *b)* The same for recently burnt (~1 year old) heathland stand (light colour) and the adjacent ~180 cm tall, 12 year old stand (dark colour). Recorded 50 cm above ground.

This moister climate could make the surface fuels less prone to cure or dry out enough under closed canopies (Agee *et al.*, 2000), but this also depends on root competition for water between field layer and trees (Gerhardt, 1996). The field layer did never cure during the study period, not even during the extreme drought in early 2008. No traces of recent fires were observed in the forest zones, despite searching large areas. The most recent forest burn found was a small patch in steep-terrained *Juniperus* forest at lower altitude which had burnt during the previous extreme drought in early 2000.

## 4.2 Effects of livestock exclusion

In all studied vegetation zones the exclusion of livestock caused an increased accumulation of biomass compared to grazed vegetation (Fig. 5, paper II & Fig. 5, paper IV) (Plate 3). Despite this the change in vegetation composition and fire potential were rather small.

### *Heathland*

Excluding cattle from burnt heathland resulted in a 2–4 times greater increase in *Erica* canopy height compared to grazed vegetation (Fig. 4a, paper II). Canopy closure was reached after ~3–4 years inside exclosures, compared to ~6–7 years in grazed vegetation (Fig 4b, paper II). This implies that grazing may cause a ~2–3 year delay in reaching the biomass threshold at which this vegetation becomes flammable.

One important factor for the non-flammability of the young patches could be the fact that the herb/grass component is cropped extremely short by the cattle. Livestock consumption of grass biomass in-between shrubs increases fuel heterogeneity (*cf.* Blackmore & Vitousek, 2000) which could decrease vegetation flammability since flames have difficulties in bridging fuel bed gaps (Bradstock & Gill, 1993).

Grass/herb biomass was larger inside heathland exclosures than outside (paper II). Grass consumption by rodents, not excluded by the fences, might also have had a moderating effect on differences between inside and outside exclosures. Grass-eating rats and mice are common in the heathlands (Yalden, 1988; SilleroZubiri *et al.*, 1995) and were frequently observed in the study area. Rodent droppings and entrance holes were common (personal observation). The short-cropped grass/herb lawn between shrubs cannot carry fire but relaxed grazing could potentially provide an important grass fuel component, creating a more homogenous fuel bed that allows for shorter fire return intervals. However, the quantity of grass and herb vegetation in the first years after fire inside the exclosures was relatively small. Also, it would have to cure enough during the dry season to support fire and we never observed complete grass curing. Extreme drought years could possibly be important in this respect (Wesche, 2003).

The cattle selectively preferred to browse *E. trimera* (paper III). The two species look almost identical in the heathlands, but in browsed vegetation *E. trimera* was always shorter than adjacent *E. arborea* (Fig. 1, paper III)). However, inside exclosures it was equally tall or taller than *E arborea* (Fig. 4a paper II). Both species recovered equally well after an artificial clipping experiment inside the exclosures suggesting that the height difference should be the result of cattle selectivity for *E. trimera* rather than differences in browsing tolerance (paper III). Direct observation of cattle preference was not possible due to their shyness, but cattle preference for *E. trimera* was indicated by larger bite diameters of its browsed shoots compared to *E. arborea* (Gustafsson, 2009).

### *Helichrysum*

Excluding cattle from *Helichrysum* shrub resulted in that the *Erica* shrubs that were present inside the thorny cushions increased in height, from ~0.5 to ~2 m within 4.5 years (Plate 3d). Outside exclosures *Erica* remained the same height as the *Helichrysum* cushions. This succession could initially increase fire potential, due to the higher biomass accumulation and better fuel quality of the *Erica* species but would in the long run reduce it, if the *Erica* would eventually grow into a forest.

### *Forests*

In both the *Hagenia* and *Erica* forests the herb-dominated field layer was taller inside than outside exclosures and had a higher biomass (Fig 5, paper IV). After two years of cattle exclusion the field layer was however still dominated by the same shade-tolerant mesophytic herb species as in grazed vegetation, typically *Alchemilla abyssinica*, *Geranium arabicum* and *Parochetus communis*, with a slight increase in area cover of *P. communis* (paper IV). These mesophytic herb field-layer species had a high moisture content (~300–350 % water per dry weight (paper IV) and would be poor fuels unless completely cured (Cowling & Campbell, 1983). The forest field layer never cured during the study period, not even during extreme drought situation in early 2008 (paper IV). There was little grass and no moss up to five years after fencing. However, this period might have been insufficient to reach a new equilibrium in field-layer composition. Grasses and mosses are better surface fuels than mesophytic herbs and if they increased this would increase the flammability of closed-canopy forests. For example the grass *Poa* *schimperiana* was abundant in the seedbank (Table A3, paper IV) but not in the vegetation. In the microphyllous *E. trimera* forest, a ground-living moss (which was present, but in small quantities) might increase after a longer period of grazing exclusion due to protection from trampling.

According to the litter trap study, *Hagenia* leaf litter is falling throughout the year and there was no large difference in light levels under the canopy between October and January suggesting that the *Hagenia* canopy is continuously renewed throughout the year (paper IV). The annual leaf litter fall under closed-canopy *Hagenia* (~430g m$^{-2}$) seems sufficient to allow surface fire, judging from our ignition tests, where the limit for successful fire propagation was around 320 g m$^{-2}$ (paper IV). However, the cattle consume also *Hagenia* leaf litter, first the fresh fallen leaves, but at the end of the dry season even the dry leaf litter (personal observation). Surprisingly, there was not more leaf litter inside exclosures than outside (Fig 5, paper IV). This might be explained by an increased rate of decomposition when the leaf litter becomes incorporated into the moist green herb layer. When collecting leaf litter entangled in the herb layer the deeper lying leaves were partly decomposed and only the basal thick part of the rachis remained.

Despite the apparent lack of fire potential forests in the study area bear some evidence of past fires. For example fire-scars in large *Juniperus* trees at lower elevations (personal observation). Also, charcoal pieces mixed into the mineral soil were found in the majority of the collected soil samples (personal observation). The tree-less *Helichrysum*-dominated patches between forest and heathland were evidently forested earlier. Remnant living trees with fire-scars and charred dead tree trunks (Plate 4d) were found which reveal that at least some *Erica* forests have burnt occasionally. Also, during the extreme drought in early 2008 fires occurred in the uppermost *E. trimera* forests on the southern side of the mountain (Yoseph Assefa, personal communication).

For certain, there have been large fluctuations in cattle densities historically, and this should have influenced the fire potential in the forest zones. According to interview results, more than 100 years ago a cattle plague killed the majority of the cattle in the area. After this, we were told: “ *– grasses grew tall and a fire came from Arsi and crossed the wide grass plain to Bale and burnt large areas in the forests*” (paper I). This cattle plague was probably the 1890’s Rinderpest epizootic which killed 95% of the cattle in East Africa and large numbers of wild ungulates (Holdo *et al.*, 2009; Tiki & Oba, 2009).

When grazing pressure is suddenly reduced, surface fuels can build-up quickly (Davison, 1996; Blackmore & Vitousek, 2000), especially if the canopy has been opened up, allowing light to the ground (Uhl *et al.*, 1988; Goldammer, 1990). According to my results, 5 years of cattle exclusion did not increase fire potential in the closed-canopy *Hagenia* and *Erica* forests. This suggests that the fire potential of these forests is low also after cattle exclusion, and that fires are rare events, probably requiring extreme conditions of drought, wind and slope, as well as surface fuels. Also, they must be lit from below for the slope effect to act. According to interview results, authorities banned heathland fire partly out of fear that they could ignite the forests below, but his is unlikely to happen due to fires lower spread rate downhill and the lack of surface fuels.

## 4.3 Effects of fire on the pasture resource and biodiversity

Young stands provide good pasture because of the young *Erica*-resprouts and the high proportion of the grass/herb lawn component (paper I). Cattle spend most foraging time in young stands (Arvidsson, 2009). Grasses and herbs, especially the nitrogen–fixing *Trifolium* spp. (covering up to ~15% of the lawn vegetation) (Fig. 4, paper IV) are more nutritious than tannin-rich *Erica* spp. and the grass/herb lawn is selectively chosen by the cattle (Gustafsson, 2009).

The native perennial *Trifolium* species are highly productive, especially the procumbent *T. cryptopodium (Kahurananga, 1986)*. Cattle also selectively choose the one-year old re-sprouts of the *Erica* (Gustafsson, 2009) which agrees well with the forage quality results; First-year top shoots contained on average ca 25% more protein than corresponding top shoots of mature shrubs, whilst the 2–3 year old shrubs only had on average ~6 % higher protein contents than top shoots from old *Erica* shrubs (Fig. 6, paper III). This is consistent with other findings of temporal post-fire peaks in foliar nitrogen (Rundel & Parsons, 1980; Cook *et al.*, 1994; Erwin *et al.*, 2001; Schafer & Mack, 2010). The reasons could be post-fire increase in plant available soil nitrogen (Fig. 10 paper IV) or, possibly, a higher post-fire allocation to shoot growth for increased competitiveness in early succession. A higher leaf: stem ratio in the first-year shoots might also explain the higher protein contents. There was no significant effect of post-fire age on top-shoot contents of phenolics and tannins, but both species had slightly lower concentrations in fenced individuals (paper III) indicating a partly induced defence.

There were some chemical differences between the two species. Contrary to expectation, the preferred species *E. trimera* had higher tannin activity, higher fibre- and lower protein contents than *E. arborea* (Fig. 6, paper III). This would be expected to reduce palatability, so this first screening of leaf chemistry could not explain the cattle preference for *E. trimera*. Both species have almost identical morphology and occur completely intermixed, often in equal proportions, so cattle preference should be based on a difference in taste.

There is a wide range of plant secondary metabolites deterring herbivores, such as e.g. monoterpenes, which at sunny weather are emitted in large quantities by *E. arborea* (Llusia & Penuelas, 2000), but nothing is known about *E. trimera* in this respect.

The selective browsing altered the post-fire competitive balance between *E. trimera* and *E. arborea* but the resulting height difference is erased by each new fire since all aboveground biomass is killed. But there are carry-over effects into the next regeneration cycle; *E. arborea* probably manages to store more carbohydrates in its lignotuber due to its lower loss to herbivory (Paula & Ojeda, 2006; Paula & Ojeda, 2011), if the cost of defence does not outweigh the gains in growth and storage (Herms & Mattson, 1992). Maybe a more important legacy of pre-burn shrub size is the size of the remnant dead stumps, which are larger for *E. arborea* (paper II). The stumps limit cattle access to the re-sprouting shoots (Plate 1f) which should give *E. arborea* further advantage in heavily browsed vegetation (paper III). The height of the remaining stumps mainly depends on pre-fire shrub size. Shorter fire-return intervals results in smaller stumps which offer less browsing protection to the young *Erica* shoots. Where settlements are located close to the heathlands we observed that burnt stumps were occasionally collected as fuelwood which also increase cattle access to new shoots.

Cattle, who are considered to be mainly grazers, typically browse only the soft top ~10 cm of the *Erica* shoots leaving ~1 mm thick browse stumps (Fig. 3, paper IV, which later prevent browsing further down in the shrub. This allows the shrubs to increase in height every year despite heavy grazing pressure (paper II). In contrast goats are true browsers and adapted to more tannin-rich diets (Owensmith *et al.*, 1993) and can browse shrubs harder (Jauregui *et al.*, 2009). Due to the predator risk small livestock are normally kept close to the settlements in the forest zones (paper I), and only at one study site a few sheep and goats were occasionally observed in the heathlands.

The efficient lignotuber regeneration allows for quick re-vegetation and a succession from hard-grazed young grass/herb-dominated stands, with high rates of nutrient cycling and nutrient export (dairy products and meat) into older non-grazed “fallow” stands. These probably have slower nutrient cycling due to the accumulation of tannin-rich *Erica* litter (Read & Perez-Moreno, 2003) and reduced cattle trampling. The nitrogen that is lost from the system in each fire and in the exported produce is probably mainly replaced by nitrogen fixation in the abundant *Trifolium* species. But there should also be some nitrogen fixation taking place in old stands due to their rather high biomass of mosses and foliose lichen, such as *Peltigera* spp. A brief lab-test of collected samples of the dominant moss species *Breutelia borbonica* found acetylene reduction indicating presence of nitrogen fixation also in the moss.

The traditional fire and grazing regime introduces disturbance to the otherwise homogenous heathlands. Disturbance at an intermediate level increases biodiversity by increasing vegetation heterogeneity which allows for co-existence of more species with different types of life-histories (Grime, 1973; McNaughton, 1983; Collins, 1987). Burning allows for many grassland species to exist in temporal open patches in the Ericaceous shrub vegetation. Many herb species were only found in the grass/herb-dominated young stands, such as *Senecio fresenii* and *Myosotis abyssinica*. Also, the shrubs offer herbs a grazing refuge under high grazing pressure. Flowering herbs were frequently observed inside *Erica* and *Helichrysum citrispinum* shrubs (unpublished data). This should allow herbs to flower and produce some seeds despite heavy grazing (*cf.* Pihlgren & Lennartsson, 2008). Young grass-dominated patches also benefit the two endangered species; the Mountain Nyala and the Simien wolf (*Canis simensis*). Both were frequently seen in young heathland stands in the study area and the Mountain Nyala has been reported to browse on young post-fire *Erica* shoots (Brown, 1969). Open grass-dominated patches have relatively high densities of grass-eating rodents which is the prey of the Simien wolf, therefore the heathlands are a secondary habitat for the wolf, having its prime habitat in the Afro-alpine grasslands (SilleroZubiri *et al.*, 1995). The wolf is currently negatively affected by overgrazing of the alpine grasslands reducing available grass for its prey (Vial *et al.*, 2011a). But since its prey needs grass, the wolf is favoured by heathland burning, and it is often seen hunting near cattle herds scaring up rodents and providing cover (Sillerozubiri & Gottelli, 1995). Its Oromo name is “jedalla farda” meaning the jackal who follows horses.

## 4.4 Vegetation dynamics

### *Heathland post-fire succession*

Because of the high intensity of the heathland fires, all aboveground plant parts were heat-killed. Post-fire *Erica* re-sprouting occurred from the buried portions of the lignotuber which had been protected under the moist humus (paper IV). The lignotubers provided quick regeneration of both *Erica arborea* and *Erica trimera* (Fig. 4, paper III and Fig. 2, paper IV). The large sizes of the lignotubers, especially those of *Erica trimera* which were up to 1.5 m in diameter, suggest that they may be hundreds of years old since radial growth probably is slow, about 0.5 cm per year has been reported for *E. arborea* from Algeria (Garland & Marion, 1960).

The re-sprouts emerged as soon as the rains returned and after one year the shoots were on average ~15 cm tall for *E. arborea*, and ~10 cm for *E. trimera* in grazed vegetation (Fig. 3, paper III). Both heights (Fig 4, paper III) and area cover of both *Erica* species (Fig 2 paper IV) increased faster inside exclosures than in grazed controls.

The heathland seedbank analyses showed that there was a large seedbank; between 8800–25000 seeds m$^{-2}$, consisting of between 18–33 species at the different sites (Table A3, paper IV). The dominating species was *E. arborea* and the most common herbs were *Wahlenbergia pusilla* and *Alchemilla abyssinica*. The majority of seeds were found in the 0–10 cm soil layer (Fig. 6, paper IV). The large seedbank of *E. arborea* conforms with observations by Miehe & Miehe (1994a) who suggested that *E. arborea* should be favoured by disturbance, since it was dominating in heavily disturbed areas.

The near absence of *E. trimera* seeds in the heathland seedbank was surprising, since *E. trimera* also produces a seedbank (in the forest), and since it was often the dominating shrub in the heathland vegetation (paper I). This could be explained by their differences in timing of reproduction; *E. arborea* flowers profusely already from ~4 years post-fire, whist *E. trimera* starts flowering first at around ~11 years (paper IV). Therefore the fact that *E. arborea* accounted for ~99% of the woody species in the seedbank indicates that the heathland vegetation has been kept in a young state for a long time, prohibiting *E. trimera* to reach reproductive age.

Humus consumption was minor (see soil section below) and therefore the post-fire soil surface was covered with a thick charred, rather spongy, humus layer near the lignotubers (paper IV). In trampled lawn areas the post-fire soil was more compact. Despite the large seed bank, the dominant mode of post-fire recolonization in the herb and grass species was by vegetative propagation from roots or rhizomes that had survived in the moist humus layer, in for example: *Haplocarpha rueppellii, Alchemilla haumannii, Alchemilla abyssinica, Thymus schimperi, T. acaule, Trifolium cryptopodium, T. burchellianum* (paper, IV). In scarified plots vegetative colonization was slower (Fig 4a and b, paper IV) indicating that the majority of the roots and rhizomes were located within the top 1–2 cm of the soil. The area cover of the forage-valuable *Trifolium* species was up to ~15% and grasses up to ~10% in two year old vegetation (Fig. 4a and b, paper IV). Extremely few seedlings were observed in the plots, and then mainly in scarified plots. But this can be due to the fact that all inventories were done in the dry season. Probably seedlings germinate at the beginning of the rainy season. But generally, also in March and April, when the rains had started, seedlings with cotyledons were very rarely observed. In the small plots annual species such as *Wahlenbergia* *pusilla and Hydrocotyle manii* were mainly found in the scarified treatments (paper IV). Poor seed recruitment could be due to the spongy humus layer which should be a bad substrate for germination. Also the extreme diurnal temperature fluctuations at the soil surface (from +45°C– -5 °C measured in the dry season) due to the black soil surface and the lack of canopy protection creates a very harsh environment for seed germination and seedling survival.

In the heathland sowing experiments with *Erica arborea*, *Hagenia* and *Hypericum,* seedlings emerged of all species but in highly variable numbers (Fig. 8, paper IV). *Hagenia* seedlings were most numerous, with maximum establishment around 15–20% of germinable seeds. Germinants of all species developed very slowly. *Hagenia* seedlings were only 2–4 cm tall after 2 years and discoloured (reddish), probably due to the acid soil (see discussion on bio-assay below). *Erica* seedlings were maximum 7.5 cm tall 3 years post-fire. This could be explained by the harsh climate and inherently slow growth rates in *Erica* species, or maybe by herbivory by small herbivores. Earlier studies have reported that *Erica* seedlings are very rare in the vegetation (Miehe & Miehe, 1994a; Wesche *et al.*, 2008; Teshome & Glatzel, 2011). This could be due the fact that they are small and consumed by cattle in the short-cropped lawn. The *E. arborea* population consists of individuals in all size classes, but the *E. trimera* population consists mainly of individuals with very large lignotubers; up to 1.5 m in diameter (unpublished data). Resprouting shoots grow much faster than seedlings due to stored reserves (Paula & Ojeda, 2011) so when the canopy consisting of the old individuals closes, those seedlings that managed to escape grazing would perish in the shade.

### *Fire effects on heatland soils*

The direct effects of fire on the soil were rather small. Flame residence time (temperatures >500 °C) is short in the *Erica* vegetation. In the instrumented experimental fire residence time was ~2 minutes (paper II). This indicates that the heat impact on the soil should be small. Also, humus smoldering was normally minor and mainly in moss-covered areas under *Erica* shrubs. It normally stopped within one hour according to many observations. This suggests that the humus layer is often too moist for smouldering fire to occur. According to the gypsum block readings, the humus moisture content (at 10 cm depth) stayed almost constantly at the highest value during rainy season as well as the dry season in 2007. Only at the beginning of the severe drought in January–February 2008 slightly lower values were recorded (personal observation).

In the heathlands and *Erica trimera* forests the phenolics-rich *Erica* and moss litters form recalcitrant humic substances, which in combination with the cool humid climate allows for the formation of a moor layer (Read & Perez-Moreno, 2003). The moor layer has an almost unaltered organic litter at the surface and a gradually more decomposed material at 10–20 cm depth. The heathland soils had a soil organic matter of ~60–80 % in the top 2 cm, gradually decreasing downwards in the profile. Soil mixing seemed minor, according to the high SOM (35–40%) at 10 cm depth. But there are mole-rats and soil-digging rodents present in high quantities (Yalden, 1988). In larger gaps covered by grass/herb lawn the moor layer was thinner or absent, probably due to the absence of moss and *Erica* litter and the heavy trampling.

The heathland soils were slightly acidic and had a pH between ~5.0–5.5 at the surface. pH increased in the top 2 cm of the humus after fire.

According to the resin capsule analyses, plant available nutrients (especially nitrate) in the heathlands were higher in burnt stands 5 and 10 months post-fire, but after 17 months there was no difference compared to mature stands (Fig. 10 paper IV). This was also in agreement with the peak in *Erica* shoot protein content in first-year re-sprouts (Fig 6, paper III).

The repeated burning consumes humic substances and adds ash which increases soil pH, but the overall effect of fire on the heatland soils appears to be relatively small due to the minor humus consumption and the rapid re-growth of the *Erica* canopy.

### *Hagenia Forest soils and Hagenia soil requirements*

Soil pH was higher in the *Hagenia* forest than in the heathlands, ~6.0–6.5 in the top soil and there was a higher degree of mixing of humus into the mineral soil. Soil organic matter nevertheless was as high as ~20–30% in the top 20 cm soil. According to the resin capsule data soil scarification in the *Hagenia* forest (simulating disturbance) caused a strong increase in nitrate but not in ammonium or phosphorous (Fig. 11, paper IV). The low ammonium:nitrate ratio might be explained by the higher pH which increases nitrification rates (Giesler *et al.*, 2005). The lack of increase in plant-available phosphorous could also be explained by the higher pH which increase phosphorous complexation with Al and Fe (Giesler *et al.*, 2005). Also Yimer (2006) found that available phosphorous was lower in the *Hagenia* forest than in the heathlands.

The nursery bioassay indicated that *Hagenia* seedling growth rates were higher in *Hagenia* soils than in *Erica* soils (Abebe, 2008). This suggests that *Erica* soil was unsuitable for *Hagenia* which normally grows in less acidic soils. (Miehe & Miehe, 1994a). Sowed *Hagenia* seedlings grew extremely poorly in the heathlands compared to the rapid growth at lower altitude (paper IV). Greenhouse trials with *Erica* and *Hagenia* seedlings indicated that the

*Erica* species preferred acid soils (pH <4.5) and that *Hagenia* seedlings preferred higher pH (>5.0) (unpublished data). The fertilization test of the bioassay soils indicated that *Hagenia* seedlings were nutrient limited in the *Hagenia* soils and more strongly limited by nitrogen than phosphorous (Abebe, 2008). *Hagenia* colonisation upwards on the mountain is limited by fire and grazing, but also the acid heathland soils could limit *Hagenia* establishment. Individual *Hagenia* trees have been observed in Bale Mountains at even at higher elevations than our study sites, but mainly in fire-protected habitats with atypical soils such as road banks or rock outcrops (personal observation).

### *Forest vegetation dynamics*

The forest seedbanks consisted of 33–35 species and the dominating woody species were *E. trimera* and *H. Revolutum* (Table A3, paper IV). Number of seeds per $m^2$ was 23000–35000 and the majority of the seeds were situated in the top 10 cm of the soil (Fig. 7, paper IV). The *Hagenia* forests contained a relatively small seedbank of woody species compared to the *E. trimera* forest, mainly consisting of *Hypericum*, and some *E. trimera*, despite the absence of *E. trimera* in those stands.

In the sowing experiments in the *Hagenia* forest there was no germination or seedling survival neither in grazed control plots nor inside exclosures. But in the open gap exclosures a few seeds germinated, and few survived until year five. Since the seeding experiment was not followed continuously, it is unknown whether seeds in the forest failed to germinate, or if they germinated, but that the young seedlings were quickly outcompeted by the lush herb carpet which had completely recovered in burnt and scarified plots in less than a year (paper IV). The planted *Hagenia* seedlings were after 6 months of the same height, or shorter than the ~12 cm tall herb carpet (Plate 4e). Many etiolated, yellow dying seedlings were found under the herb carpet. After two years only 6% of the seedlings were alive and after 4.5 years none. The only successful tree regeneration inside forest exclosures was by root suckers of *Hypericum revolutum* which are absent in grazed forest due to heavy browsing, but inside forest exclosures there were ~30 stems ~1.5 m tall after 3 years (Plate 4f).

The results show that forest regeneration can be very difficult and that it is determined by multiple interactions between light, soil, germination, competition (*cf.* Gerhardt, 1996) plus the effect of selectively browsing herbivores (*cf.* Kuijper *et al.*, 2010). But when all conditions are right, seedling growth can be fast. Survival of the planted *Hagenia* seedlings in the open gap exclosures was 50% after 4.5 years and in one of the exclosures the five surviving individuals were in average ~4.2 m tall with a DBH of max 11 cm (Plate 3g).

It is clear that *Hagenia abyssinica* is heavily browsed by cattle, and therefore does not regenerate at current grazing pressure. But even when livestock were excluded and seeds sown and seedlings planted, *Hagenia* regeneration under closed canopy still was unsuccessful. Also wild herbivores, some of which were not excluded by the fences (i.e. reedbuck, monkeys and rodents), might consume *Hagenia* seedlings, but the surviving seedlings inside the forest exclosures had no signs of browsing. Rather the light-demanding *Hagenia* seedlings (Fetene & Feleke, 2001) were probably outcompeted in the earliest phase by the shade-tolerant herbaceous field layer.

For successful *Hagenia* regeneration there is a need for both livestock exclusion and openings in the canopy, but this could also increase competition from grasses and herbs and maybe increase wildfire risk. Field layer competition with seedlings in open gaps is often a serious problem for forest regeneration in the tropics (Chapman & Chapman, 1999; Reed & Clokie, 2000). Also other biotic interactions may limit tree seedling survival in forest gaps. In the other gap exclosure there was extensive soil digging by mole-rats which might have limited growth of both the sowed and the planted seedlings (personal observation).

So, what conditions might have allowed for the establishment of the present old-growth *Hagenia* and *E. trimera* forests? Regeneration of palatable tree species can be nearly impossible during periods with high herbivore densities (*cf.* Raffaele *et al.*, 2011). Regeneration windows might appear only after events of herbivore population crashes (Dublin *et al.*, 1990). In addition wildfires might create aggregations of fallen logs creating browsing refugia for palatable tree seedlings (de Chantal & Granström, 2007). In the study area, the Rinderpest killed the majority of the livestock 100 years ago (paper I) and this might have increased fire-potential, at least in grass-dominated areas. According to interview results there were large forest fires after this event, but it was not detailed in which forest zones they occurred (paper I). *Hagenia* does not produce annual rings, but the *Erica* species do. We counted rings in *E. trimera* trees that were ~20 cm GBH (a typical diameter in the ~11 m tall *E. trimera* forests) and they were around 90 years old. This suggests that many of the *Erica* forests could have established in the period following the Rinderpest epizootic.

## 4.5 Traditional fire knowledge and management

The interviews revealed three important reasons for burning the heathlands, 1) to improve pasture, 2) to discourage large predators, and 3) to get rid of an insect pest (paper I). Tall heathland provides poor pasture since the cattle cannot reach the shoots of tall shrubs and because the grass/herb component is reduced. The first three years post-fire were said to provide the best pasture and most valued was the grass/herb component, especially the *Trifolium* spp., *Thymus schimperi* and grasses. But according to some respondents the *Erica* species are increasingly important during the dry season when the grass stops growing. According to the respondents there is an increased risk of cattle loss to hyenas and leopards in tall shrub vegetation. Losses to large predators is still a severe threat to the pastoralists livelihoods (Atickem *et al.*, 2010) and the informants explained that in burnt heathland the cattle can spot the hyenas and leopards from far and avoid them. The objective get rid of a stinging moth caterpillar (Plate 4a) has not been reported from Ethiopia earlier. This would not have been discovered without using interviews. This moth caterpillar has microscopic urticating setae for defence (Andrea Battisti, pers. comm.) which cause respiratory illness and skin problems in humans and livestock (Battisti *et al.*, 2011). This agrees with the symptoms described by the informants. They further claimed that the caterpillar is found only on tall flowering *Erica* and we only saw it a few times, always in vegetation taller than 2m.

There is a large base of traditional fire knowledge within the montane population and people were not afraid to discuss pasture burning, despite it being considered illegal. All informants had a detailed understanding of fire behaviour and fire effects and could estimate vegetation age and flammability, and had specific names for flammable and non-flammable vegetation. They were aware of the interrelation between grazing and surface fuels and the importance of fine fuel moisture contents and vertical and horizontal fuel continuity for fire behaviour. They agreed that young stands are used as fire breaks to control the sizes of burns and some emphasized the need of small-scale patchiness in order to always have young stands within the daily cattle range. All respondents claimed that if everyone followed the law there would be no pasture in less than ten years. And they agreed when asked, that in such event also the risk of large-scale wildfire would increase, even though they had not experienced this.

All informants said that burning is illegal but they also stated that they did not know since when, or the reason why. Some informants suggested that maybe it is illegal because the agricultural bureau is afraid that the fire would spread downhill to the forests below, which they also claimed would be impossible due to lack of surface fuels in the forests. Since a few men had recently been imprisoned for burning, some informants said that adult men have become more afraid to burn and instead children ignite the fires. The informants did not mention fire in the forests, except as a historic fact.

The traditional fire management system of the heathlands has evolved out of the need to obtain good quality pasture for cattle (paper I). It is highly rational from the perspective of the montane pastoralists who produce and export meat and butter from the heathlands (Watson, 2007). But they claim that population growth and increased grazing pressure has reduced pasture productivity and that milk production per cow has declined severely (paper I). A new phenomenon in the study area, starting from around 2006, is to fence off areas near the treeline as pasture for calves. One field assistant estimated several hundred of meters of new fences, built of piled large *E. trimera* and *Hypericum* logs, only in the Angafu valley in 2008. This could be an indication that the grass sward in the communal grazing land is too short for the calves. The Bale Mountains heathland pasture is probably fairly productive, due to the short dry season, the efficient regeneration of the *Erica* species, the large proportion *Trifolium* spp. and the relatively limited problems of cattle parasites and grazing weeds.

# 5 Conclusions & Management implications

The results of my studies have implications for future management options for these ecosystems. Especially so in the light of increased population pressure, increased conservation efforts and current proposals to increase carbon sequestration here.

According to my results, the upper zones of the sub-alpine forests cannot burn due to lack of good surface fuels, even after five years of cattle exclusion. But if livestock numbers could be reduced, fuel management might eventually become important in the forest zones, especially in open gaps.

In the heathlands the traditional fire management has shaped the ecosystem for a long time, and it maintains biodiversity as well as fuel breaks. According to my results, if burning ceased, in less than 10 years the fire breaks would be lost. This would increase the risk of landscape-wide wildfire, since the mountain is almost devoid of natural fire-breaks. Without burning, the *Erica* in the heathlands could theoretically grow into a less flammable dwarf forest after maybe 50 years. But given the highly flammable nature of the vegetation and the interests of the pastoralist population, a long enough period without any ignition over a large area is highly unlikely to occur.

My results suggest that the heathland vegetation is quite resilient to changes in fire regimes and grazing intensities due to the high re-sprouting capability of the *Erica* lignotubers. The large lignotubers are likely more than hundred years old and have obviously survived large variations in cattle densities, and probably also fire frequencies.

This ecosystem with its fire-regime has evolved under a combination of fire and cattle grazing and therefore controlled cattle grazing is suggested to be part of the future land management system. Cattle browse only soft *Erica* shoots and probably cannot kill the *Erica* shrubs. But browsing by goats and sheep might be more detrimental and should be avoided in the heathland.

Since fuel limitation puts a lower limit on fire-return intervals, the *Erica* lignotubers probably cannot be killed by too high fire frequencies either. But with shorter fire intervals, the post-fire remaining stumps become smaller, allowing cattle access to the youngest shoots. Therefore fire-return intervals need to be controlled, with an average fire-return interval not less than ~10 years. Also, fuel-wood collection of the fire-killed *Erica* stumps should be avoided, to protect early resprouts from grazing.

Lignotubers probably can be killed by deep smoldering in the humus. Therefore burning should not be done when the humus layer is dry after long periods of drought.

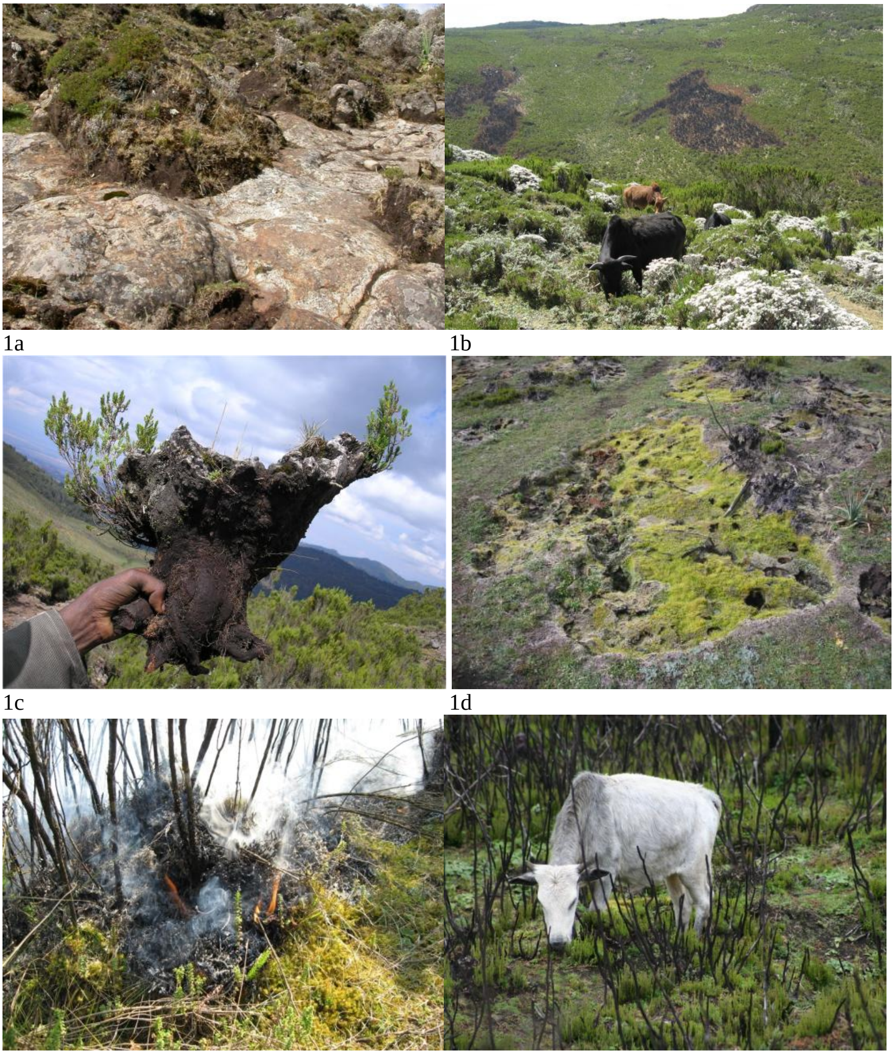
Since the heathlands and sub-alpine forests have so far been spared from invasive exotic species, any future attempts of pasture improvement should not include introduction of exotic grass species, because of their potential to change fire-regimes (Keeley *et al.*, 2005).

Given the highly flammable nature of the heathland vegetation, the unsuitable climate for agriculture, and the need for efficient land use and biodiversity conservation, I believe that the optimal landuse for the heathland zone is pasture but with specific management regulations.

In order to be successful, a management plan for the heathlands and forests should be developed in cooperation with the pastoralists, accounting for their needs, and making use of their traditional ecological knowledge, especially their expertise regarding fire management. I suggest that the following points should be included in a joint fire management plan:

1. Controlled burning of the heathlands, with an average fire return interval of not less than ~10 years, in order to maintain pasture quality, limit fuel build-up and maintain fire-breaks.
2. Burning should be avoided during severe drought when the humus layer is dry.
3. Controlled grazing in the heathlands, allowing only cattle.
4. Fuel-wood collection of the fire-killed *Erica* stumps should be avoided in order to protect emerging shoots from cattle browsing.
5. If *Hagenia* regeneration is desired in the forest zones, temporary complete exclusion of livestock in selected areas is necessary, and this will work only in open areas.

# 6 Colour Plates



1a 1b

1c 1d

1e 1f

*Plate 1 a*) Cattle track in heathland cut down to the bedrock, showing a ca 20 cm deep soil layer. *b*) Heathland scenery at ca 3500 m with cattle, *Erica*, *Helichrysum* and black burns in the background. *c*) Lignotuber of *E. trimera*, ca 40 cm in diameter (photo Anders Granström). *d*) Lignotubers killed by deep humus smoldering during the prolonged drought in early 2008 (photo Anders Granström). *e*) The final kindling flames in ~10 cm deep moss in the experimentally burnt ten year old stand. *f*) Cow in one year old re-sprouting heathland. The *Erica* sprouts are ~10 cm tall and the fire-killed *Erica* stems limit cattle access to the fresh shoots (photo Jenny Gustafsson).

2a

2b 2c

*Plate 2 a*) Heathland fire on the 4th of February 2008 at 12:40. The burning shrubs (~2 m tall) are standing in a narrow stand (~30 m wide) surrounded by shorter vegetation. The ~1 m tall shrubs in the front are mainly flat-topped *Erica trimera*. The fire is most intensive in the tall shrub (~8 m long flames), but also the 1 m tall shrub is burning, visible as small (~ 2 m long) flames to the left. The grass-dominated patch to the front left is a two year old stand which did not burn. *b*) Fire in a cushion of *Helichrysum citrispinum* and *E. trimera* in February 2008. *c*) After the same fire extinguished when reaching the ca 50 cm wide grass/herb lawn to the left.

*Plate 3:* Exclosures before (right) and after (left): *a*) heathland (3510m) in February 2005 and *b*) December 2008, *c*) *Helichrysum* shrub (3450 m) in December 2006 and *d*) January 2011, e) *Hagenia* forest (3350 m) February 2006 and *f*) December 2008, *g*) *Hagenia* gap (3350 m) February 2006 and h) January 2011.


4a


4b


4c


4d


4e


4f

*Plate 4 a*) The urticating moth caterpillar causing cattle illness. *b*) Five year old heathland vegetation with mixed *E. arborea* and *E. trimera*. *b) E. trimera* forest at ca 3400 m. The ~11 m tall trees are ~90 year old and the field-layer is a hard-grazed herb/grass lawn. *b*) Fire-killed *E. trimera* tree trunks with *Helichrysum* shrubs at 3400 m. ***e)*** **~**10 cm tall *Hagenia* seedling (at the centre with serrated leaves) 5 months after planting, in a ~12 cm tall herbaceous field layer. *f*) ~1.5 m tall root suckers of *H. revolutum* in one of the *Hagenia* exclosures three years after fencing.

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