ADDIS ABABA UNIVERSITY
SCHOOL OF GRADUATE STUDIES

FINE ROOT BIOMASS OF *ERICA TRIMERA* (ENGL.) ALONG AN ALTITUDINAL GRADIENT ON BALE MOUNTAINS, ETHIOPIA

A THESIS SUMITTED TO THE SCHOOL OF GRAGUATE STUDIES IN PARTIAL FULFILMENT OF THE REQUIRMENTS FOR THE DEGREE OF MASTER OF SCIENCE IN BIOLOGY

BY

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List of abbreviations

C/N	Carbon to nitrogen ratio
DBH	Diameter at breast height
TFBM	Total fine root biomass (live + dead)
DFBM	Dead fine root biomass
LFBM	Live fine root biomass
pp.	Precipitations

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Abstracts

The responses of fine roots to a changing environment are suggested to affect the growth and form of an individual plant or the structure and function of forest ecosystems.

The depth-wise distribution and seasonal variation of fine roots of *Erica trimera* was investigated at three altitudinal levels, i.e., 3000, 3300 and 3500 masl up to 40 cm depth separated into three depth classes (0 - 10, 10 - 20 and 20 - 40 cm) using sequential soil coring. Soil chemical characteristics and moisture were analyzed for all the three altitudinal levels and depth classes.

Total fine root mass and biomass increased significantly with altitude. Total nitrogen, available phosphorus, organic carbon, moisture content and pH of the soils increased significantly with altitude. In the two lower altitudinal levels, 3000 and 3300 masl, fine root mass and biomass decreased as depth increased, but at the higher altitude (3500 masl) fine roots tended to be more concentrated at the deeper depths. In all of the three sites the availability of soil nutrients and soil acidity showed a tendency to decrease as depth increased. The highest fine root mass and biomass was recorded at the major rainy season followed by the transition period, the small rainy season and dry period, in that order.

The higher belowground biomass and lower aboveground biomass in contrast to higher soil nutrients at higher altitudes suggested that sink limitation may occur at the *Erica trimera*'s upper altitudinal limit due to the lower temperature. The night frost at higher elevation that is sever above 10 cm in the soil may also be responsible for the limited abundance of fine roots at the depth of 0 - 10 cm than at the two deeper depth classes (10 - 20 and 20 - 40 cm). The highest fine root mass during the major rainy season and lowest

fine root mass in the dry season indicated that soil moisture was critical in governing the pattern of root growth in these ecosystems. Fine root production increased markedly from 35.75 kg ha^{-1} yr^{-1} at 3000 malsl and 65.37 kg ha^{-1} yr^{-1} at 3300 masl to 158.64 kg ha^{-1} yr^{-1} at 3500 masl. The figures indicate that fine root production and turnover by this species plays an important role in global carbon sequestration.

1. Introduction

Forest growths are limited at high latitudes and at high elevations in lower latitudes, and the limits of tree growth in these environments are marked by tree-line, transition from vertical, erect tree stems to prostrate, stunted shrub forms. The tree-lines represent one of the most striking examples of vegetation discontinuity in nature and, therefore, have been studied intensively in the extratropical as well as tropical mountains of the world (e.g., Wardle, 1971; Tranquillini, 1979; Stevens and Fox, 1991). The extended mountains of the Americas, the high volcanoes of East and Central Africa and the mountains of Papua New Guinea, Indonesia and Malaysia represent the mountain regions where most of the tropical timber-line and alpine vegetation are studied (Leuschner, 1996). Tree-lines are defined as the transition zones (‘ecocline’) between the upper limit of the closed montane forest and the beginning of the treeless alpine zone (Korner, 1999). In general, above the closed montane forest, stem height decreases with increasing altitude (Hedberg, 1964).

Hedberg (1951) identified three distinctive belts of high altitude vegetation along the altitudinal gradients of tropical East African Mountains namely; montane forest belt, ericaceous belt, and the alpine belt. The lower and the upper limit of montane forest belt varies from 1700 to 2300 masl and from 3000 to 3300 masl, respectively depending on the mountain on which it occurs. The lower limit of the ericaceous belt ranged between 2600 and 3400 masl, while its upper limit varies from 3550 to 4100 masl. The alpine vegetation occurs above the ericaceous belt.

Several attempts have been made to investigate the physiognomic and floristic composition of the ericaceous belt in east African mountains (Hedberg, 1975; Lovett, 1993; Miehe and Miehe, 1994). The ericaceous belt is usually dominated by *Erica* *arborea* and *Erica trimera*. Floristically, different areas of this belt are rather similar, but the physiognomic appearance varies from a forest to open scrub due to climate, edaphic factors and fire (Hedberg, 1951).

The mountains of East Africa were created following the uplift and volcanism movement during the Miocene and Oligocene geologic periods (Mohr, 1963). Among these mountains Bale Mountains, which lie in the southern part of the Ethiopian highlands consist of the largest alpine ecosystem in the continent. The physiognomic and floristic patterns of the vegetation in Bale Mountains have been studied by a number of botanists and ecologists (e.g., Hedberg, 1964; Friis, 1986; Zerihun *et al*., 1989; Miehe and Miehe, 1994; Masresha Fetene and Minassie Gashaw, 1996; Yoseph Assefa, 2004; Masresha *et al*., 2006).

The ericaceous belt in the southern slope of Bale Mountains is dominated by *Erica trimera*. The species was found in wide altitudinal range (3000 - 4200 masl). The height and diameter at breast height (DBH) of *Erica trimera* decrease significantly as altitude increases (Yoseph Assefa, 2004; Masresha Fetene *et al*., 2006). In these ecosystems the *Erica trimera* is a species with a potential to grow to a tree height of 8 - 12 m when the condition is favorable but at higher altitudes it exhibits shruby life-form even lower than 2 m height (Meihe and Meihe, 1994). Masresha Fetene *et al*. (2006) suggested that the decrease of temperature with increasing altitude could be the possible reason for the inverse relation between altitude and height of *Erica trimera* in Bale Mountains. Occasional droughts and the consequent fires are also suggested to influence the afroalpine ecology in east African Mountains (Wesche, 2003; Miehe and Miehe, 1994).

According to Cavelier (1996) soil and air temperatures, light quality and quantity, water supply, and decomposition of organic matter and nutrient availability are the most important environmental factors that change along the elevation gradients of mountains governing the physiognomic pattern of forests in tropical mountains. Among those environmental factors, the decrease in temperature with altitude is the most evidenced factor that is proposed to explain the decrease in height of tree-line trees and the gradual replacement of trees by non-trees as altitude increases (Smith, 1980; Korner, 1998, 1999; 2003; Smith *et al*., 2003; Piper *et al*., 2006). However, there is a continuous debate on how the low temperature affects the habit and life form of trees and shrubs.

Currently, there are at least four contrasting arguments to explain this change of structure and function of vegetation along an elevation gradient in accordance with temperature. The most popular idea is the one which considers the lower temperature at high elevation as a severe stress that limits the growth and development of trees due to frost injury (Lüttge, 1997; Masresha Fetene *et al*., 1998; Piper *et al*., 2006). According to these authors the replacement of trees by non-trees as altitude increased in the tree-line ecotone is because tree species lack either the avoidance or tolerance adaptation to the low temperature at high altitudes. The giant rosette plant (*Lobelia rhynchopetalum)* that builds tree like life-form in Bale Mountains shows adaptation mechanisms to coldness, such as having an arborescent habit, the formation of a night bud, or controlled extra cellular freezing to escape the pronounced diurnal fluctuations of temperature (Masresha Fetene et al., 1997; 1998).

Others suggest the retarded photosynthetic rate by the low temperature as a possible reason for the limited tree growth at high altitudes. The low temperature could have direct or indirect impact on the rate of photosynthesis. The rates of photosynthesis of high elevation trees are found to be 30 - 50 % lower than low elevation trees (Grace, 1989). Moreover, low temperatures decrease the quantum yield of photosystem II because turnover of the protein electron acceptor Qb is restricted in cold environments, which results in photoinhibition (Grace, 1989). Or indirectly, low soil temperature can limit enzymically driven root processes such as root growth, nutrient uptake and respiration, decreasing the demand for carbon that results in accumulation of non structural carbohydrate in the leaves which ultimately limit the rate of photosynthesis (Pregitzer et al., 2000; Davis *et al*., 2003).

There are also reports that relate the phenomenon to the response of fine roots of plants to different environmental factors. According to these authors the reduced temperature at higher elevations affects the soil condition negatively, reduces nutrient availability that force the plants to partition more biomass to their below ground part by hindering the above ground growth in order to maximize belowground resource capture (e.g., Tilman, 1988 in Tateno *et al.*, 2004; Rongling *et al*., 2004). Tateno *et al*. (2004) suggested that difference in carbon allocation pattern of plants between structural (coarse roots, stems and branches) and litter components (fine roots and leaves) may be the driving force to create variation in forest structure along the elevation gradient.

Recent evidences give strong support for a theory based on sink limitation, i.e., new tissue development is restricted not by carbon availability but by cold tree-line temperatures which limit cell division (Korner, 1998; 1999; Smith *et al*., 2003; Richardson and Friedland, 2007). According to this hypothesis tree-line species are unable to use the carbon gained from day time photosynthesis in growth because of low temperature at higher altitudes.

The influences of different environmental factors including temperature on the above ground part of tree-line vegetation are well documented (e.g., Nobel, 1980 in Cavelier, 1996 Smith *et al*., 1980; Korner, 1998; Piper *et al*., 2006). However, little is known about their effect on the belowground part of these vegetations despite the fact that belowground parts of the plants have considerable impact on the plant life functioning as they are important for anchorage, storage, support, absorption of resources, and sensing the environment (Jackson *et al*., 2000).

Belowground parts of plants consist of the coarse roots and small roots (2 - 5 mm diameter) that are relatively persistent throughout the life history of plants, and the fine roots (<2 mm diameter) are deciduous. Even though fine roots consist of small fraction (<5 %) of the total biomass of standing crop, fine root production represents a large proportion (30 % - 65 %) of annual net primary production (Gill and Jackson, 2000). Moreover, they constitute 60 % - 90 % of total below ground net primary production (Tateno *et al*., 2004) and their production and turn over may be a sensitive indicator of changing soil condition (Bloomfield 1996 in Hertel and Leuschner, 2001). Therefore, investigation on the relationship between tree fine root dynamics and environmental gradients along elevational transects could provide insight into the response of tree root system and also the change in allocation pattern that entails.

The present study aims to investigate the fine root biomass of *Erica trimera* along an elevation gradient in Bale Mountains. The study also aims to investigate the correlation between the soil nutrients and fine root biomass of *Erica trimera* along the elevation gradient.

In addition, since monitoring the amount and timing of the fine root production reflect tree and ecosystem health (Bloomfield *et al*., 1996 in Hertel and Leuschner, 2002), the present study also aimed to provide the baseline data of fine root biomass for the continuing assessment of fine root biomass to evaluate and monitor the conservation status of the ericaceous belt of the Bale Mountains.

The annual fine root production of different forest biomes of the world was documented in relation to carbon sequestrations (Jackson *et al.*, 1997). However the afro-alpine ecosystems were not represented, therefore the present study also aimed to provide an estimate of the annual fine root production of *Erica trimera* in the ericaceous belt of the southern slope of Bale Mountains.

2. Objectives

2.1. General objective

To investigate altitudinal, depth wise and seasonal variation of fine root biomass of *Erica trimera* in the southern slope of Bale Mountains.

2.2. Specific objectives

1. To investigate the fine root biomass of *Erica trimera* along an altitudinal gradient.
2. To examine the vertical distribution of fine roots biomass of *Erica trimera* and its variation (if any) along altitudinal gradient.
3. To investigate the seasonal variation in fine root biomass of *Erica trimera* along altitudinal gradient.
4. To estimate the fine root production of *Erica trimera* in the southern slope of Bale Mountains

3. Literature review

3.1. Tree fine root system

On the basis of morphological (diameter-based) classification, a tree root system consists of buttress roots, coarse roots, small roots, and fine roots. Buttressed and coarse roots function mainly as support or anchorage organs and are responsible for long distance transport whereas the fine roots function as an organ for nutrient and water uptake. There are no standard criteria of classifying the different components of the plant root system. Commonly the plant root system is classified based on arbitrary diameter classes. However, within this school of root classification different authors use different diameter classes to differentiate between fine roots and other root systems. Some authors identify ‘fine’ roots as those with diameters ranging 0 - 1 mm (Burton *et al*., 2000; Nambiar, 1987) while, the majorities are in favor of the widely accepted diameter class 0 - 2 mm (i.e. ≤ 2 mm) (e.g. Nadelhoffer *et al*., 1985; Hendrick and Pregtizer, 1993a; Yang *et al*., 2004; Green *et al*., 2005). Still others defined fine roots as < 0.5 mm diameter (e.g., Hendricks *et al*., 2006).

On the other hand some authors suggest root classification should be based on function and internal structure. Therefore, fine roots should be defined to include root tips and small diameter roots without secondary growth (McClaugherty, 2003). Pregtizer *et al* (2002) defined fine roots as part of root systems that are deciduous with a distinct lateral branch scar having life span that varies from a week to a year depending on the species and soil condition. According to Zobel (2003) a plant root system is best described as an integration of multiple genetically and anatomically determined functional root classes that are not determined by simple diameter classes. However, considering roots < 2 mm diameter as fine rots is the most popular idea in the literature. The rationale behind the classification of fine roots (≤ 2 mm) as one class is based on the notion that all roots in this diameter class are structurally and physiologically identical (Kosola *et al*., 1995).

3.2. The need to study fine roots

Although fine roots constitute a small fraction (< 5 %) of total standing biomass (Gill and Jackson, 2000), fine root production represent a large proportion of total annual net primary production in most forest ecosystems (Fogel, 1983; Joslin and Henderson, 1987; Nadelhoffer and Raich, 1992). Nonetheless, estimates vary from study to study possibly owing to differences in tree species, sampling method, and study site. For example, based on fine root biomass in 253 field studies in a wide range of ecosystems, Jackson *et al*. (1997) estimated that approximately 33 % of global net primary production is used for fine root production. Other studies on belowground production in forest ecosystems have indicated that fine root litter production is equivalent to (McClaughterty, 1982), or up to five times larger than (Joslin and Henderson, 1987) foliar litter production. According to Santantonio and Grace (1987), 67 % of annual net primary productions have been estimated to be allocated to fine roots in some forest ecosystems.

Fine roots constitute the most dynamic portion of the belowground component and are believed to have high turnover rate. Fogel (1983) estimated that annual loss of fine roots in forest ecosystems ranges from 40 - 72 % of the standing crop. Accordingly, the flux of carbon through the production and mortality of fine roots in forest ecosystems is considered as a major component of terrestrial carbon and nutrient cycles (Cox *et al*., 1978; Grier *et al*., 1981; Ruess *et al*., 1996; Eissenstat *et al*., 2000). Several authors estimated that the amount of carbon and nitrogen cycled via fine root-decomposition may be as high as or more than that returned to the soil from above ground litter fall (Joslin and Henderson, 1987; Vogt *et al.*, 1986a; Arthur and Fahey, 1992). Hence, the production and mortality of fine roots can have a substantial influence on ecosystem carbon and mineral nutrient cycling. For example, 100 kg/ha/yr of N were cycled through fine roots in a mature *Abies amabillis* stand in Washington (Vogt *et al.*, 1986b). Gill and Jackson (2000) estimated that 20 kg N/ha could be released annually from fine roots in undisturbed, mature Douglas fir forests. In addition the production and turnover of fine roots are suggested to be sensitive indicators of changing soil environment (Bloomfield 1996 in Hertel and Leuschner, 2001). Hence, investigation on the relationship between tree fine root dynamics and different environmental gradients could provide insight into the response of tree root system and also the change in allocation pattern that entails.

3.3. Factors affecting fine root dynamics

Fine root dynamics of forest ecosystem or individual plant are influenced by biotic and abiotic factors. Biotic factors include mycorrhizal fungi, herbivores and pathogens. Abiotic factors include soil moisture, soil temperature, and soil nutrient (Jackson *et al*., 2000).

3.3.1. Soil moisture

Fine root dynamics of a plant or a forest is dependent on the amount of moisture in the soil. Higher fine root biomass after the preceding rain fall and lower fine root biomass after the preceding dry season in the tropical rain forest of eastern Malaysia reported by Green *et al*. (2005) indicates the positive relationship between fine root growth and the amount of moisture in the soil. Investigation of the relationship between soil moisture gradients and fine root life span across three Douglas fir dominated stands in western Oregon showed that fine root longevity increased with increased water availability (Santantonio and Hermann, 1985). Increased fine root longevity with increased soil moisture availability was suggested to be the possible result of increased litter decomposition rates and nutrient (particularly nitrogen) release from decomposing litter and also the accompanied increased nutrient mobility in wet soil (Eissenstat and Yania, 2001). On the contrary, Joslin *et al*. (2000) reported higher fine root production and turnover (shorter life span) in wet treatments than in dry treatments after a long-term (5 year) study on the effect of altered soil water regime on fine root biomass production and turnover of upland oaks.

3.3.2. Soil nutrient

Even though the results are not consistent the dynamic and static parameters of fine roots are responsive to soil fertility. Root dynamics in relation to nutrient availability can be examined in two ways: along a natural fertility gradient and in response to fertilization. Along natural fertility gradients, plants growing on nutrient-poor sites have greater root-to-shoot biomass ratios (Tilman, 1988 in Tateno *et al*., 2004; Rongling *et al*., 2004). In addition, Keyes and Grier (1981) reported increased fine root biomass and root turnover rates in nutrient limited soils. On the contrary, Aber *et al*. (1985) reported a positive relationship of fine-root biomass and turnover rates to the nitrogen availability of a site in 13 temperate hardwood and pine forest sites.

There are two contradicting reports about the effect of fertilization on fine root biomass. Fertilization of a tropical montane forest in Hawii was reported to decrease fine root biomass significantly (Gower and Vitousek, 1989). In contrast, increased nutrient availability was found to increase net fine root production in Loblolly pine plantation in Scotland (King *et al*., 2002). Similarly, root turnover rates have been reported to be both faster and slower after fertilization. Increased nutrient availability reported to be associated with faster fine root turnover rate in: hardwood and coniferous forest stands of USA (Aber *et al*., 1985; Nadelhoffer *et al*., 1985), Loblolly pine plantation in Scotland (king *et al*., 2002), tropical wet forest of Costa Rica (Gower, 1987), and Juniper, Eucalypt and Cupressus plantation in Ethiopia (Michelsen *et al*., 1993). On the other hand, fertilization induced slower fine root turnover rate in Tierra firme forest of Venezuela (Jordan and Escalante, 1980) and coniferous forest of Washington in USA (Keyes and Grier, 1981).

According to Nadelhofer (2000) collective results of studies that use sequential sampling of fine root biomass to estimate production suggest that fine root turnover and production either; do not vary systematically, or that they decrease as nitrogen availability increases. By contrast, studies using ecosystem C or N budgets suggest that both the fine root turnover and production increase with nitrogen availability.

While all nutrients are not equally important for plant functioning, some authors argued that nitrogen might have played an important role in fine root dynamics (Wilson, 1988; Burton *et al*., 2000; Tilman, 1988 in Tateno *et al*., 2004). On the other hand, Ostertag (2001) argued that phosphorus rather than nitrogen may be responsible for the increase in fine root turnover rate and reduced abundance. Similarly according to Gower (1987) fine root dynamics is influenced by phosphorus and calcium rather than nitrogen.

3.3.3. Soil temperature

Interpretations of the responses of roots to soil temperature are complicated because changes in soil temperature interact with changes in other essential resources (Pregitzer *et al*., 2000). For example both water and nutrient availability often co-varies with changes in soil temperature. Higher soil temperatures result in increased nitrogen mineralization. However, drought conditions may occur when soil temperatures are relatively high (Piatek and Allen, 1999 in Pregtizer, *et al*., 2000). Currently there are contradicting reports about the effect of temperature on fine root production and turnover. King *et al*. (1999) conducted a study on *Populus tremuloides* in temperature controlled-containers in the field and found that cooling the soil temperature from 20 ^{0}C to 13 ^{0}C decreased cumulative root production and mortality. In the same line, Fitter *et al*. 1998 in Pregtizer *et al*. (2000) reported fine root mortality and production decreased up the slopes of the mountains of United Kingdom where the mean soil temperature decreased from 9.1 ^{0}C to 4.5 ^{0}C. Moreover, Pregtizer *et al*. (2000) stressed that soil temperature could influence fine root production and mortality through its effect on increased respiration. On the contrary Johnson *et al*. (2005) claimed that elevated CO_2 and elevated temperature may not enhance fine root production and mortality but it is the nitrogen supply that governs the response of plants. In addition, soil freezing was found to increase fine root mortality and production in northern hard wood forests of USA (Tierney, 2001).

4. Materials and methods

4.1. Study area description

4.1.1. Location, geology and soil

The study was conducted in the Bale Mountains National Park (BMNP) at the ericaceous vegetation of the Harrena escarpment. The BMNP occupies an area of 2400 km^2 and is located in the south-eastern Ethiopia, 400 km by road from Addis Ababa. The Bale Mountains form the south-eastern limit of the eastern Ethiopian highlands, along the eastern edge of the Rift Valley. The BMNP is located between 6°29'and 7°10' N and 39°28'and 39°57'E (Masresha Fetene and Menassie Gashaw, 1996). The study area includes the ericaceous belts of three mountains in the park, i.e., Gara Dema, Degebato and the one which is known locally as 'Berbercha' in the altitudinal range of 3000 to 3500 masl.

The study area consists of tertiary (Oligocene) trapean lavas which cover the Mesozoic marine sediments and underlying pre-Cambrian rocks after the Eocene uplifting of the Ethiopian highlands (Mohr, 1971 in Meihe and Meihe, 1994). The shield volcanoes of the area consist of basalt and trachyte. The soils are mainly derived from the basaltic and trachytic parent rock and are young, fairly fertile, silty loams of reddish-brown to black colored alfisols (Weinert and Mazurek, 1984 in Meihe and Meihe, 1994).

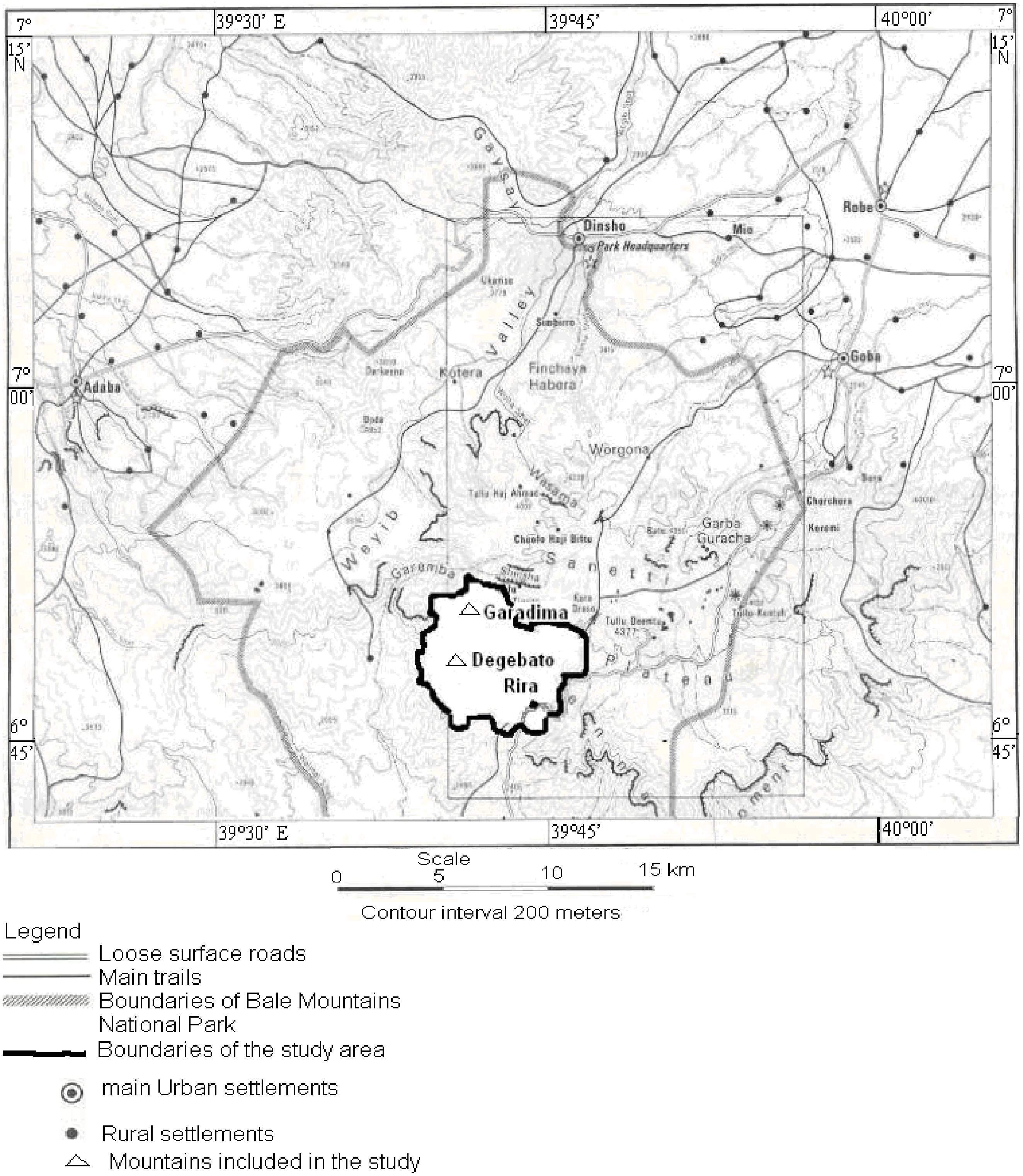

Fig. 1 Location of the study area.

4.1.2. Climate

The precipitation in Bale Mountains is highly influenced by southeasterly winds from the Indian Ocean during most of the year. The Inter Tropical Convergent Zone (ITCZ) and local altitudinal and topographic influences affect the distribution of the precipitations in the Bale Mountains. The immediate vicinity of the Harrena escarpment moderates the seasonal contrasts in Rira by a pronounced local water circulation with the daily formation of convective clouds that mist and showers (Meihe and Meihe, 1994). The mean annual rainfall based on the data between 1997 and 2004 from the Rira station is 633.11 mm. Mean maximum monthly precipitation is 181 mm in April and mean minimum monthly precipitation is 13 mm in May.

Since, there is no temperature data from the Rira Station; temperature records of the Dinsho Climate Station were used in the present study. Hence, the mean annual minimum and maximum temperatures based on the data between 1997 and 2006 are 3.85 and 17.17 °C, respectively. The mean monthly maximum temperature, 19 °C, was recorded in March, and the mean minimum temperature, 2.25 °C, was recorded in January. The diurnal amplitude of the temperature is widest during the dry season and smallest during major rainy season. The maximum difference between mean minimum and maximum temperatures (15.58 °C) was recorded in February, while only 11.33 °C difference was recorded in October at the end of major rainy season.

The ecologists who worked in the Bale Mountains reported night frosts in the area. Hilman (1986) has recorded a minimum temperature of -15 °C in Weyib valley (3850 masl), while Miehe and Miehe (1994) has reported a nocturnal minimum temperature of -3 °C in the sparsely vegetated area of ericaceous belt. Frosts are also reported to occur at

Dinsho and Rira (Miehe and Miehe, 1994). Mooney, 1992 in Miehe and Miehe (1994) recorded a monthly minimum temperature of 2.2 °C in January at Dinsho. Similarly, based on the recent 10 year (1997-2006) climatic data from Dinsho a 2.25 °C minimum temperature was recorded in January.

Although, different topographic situations of the stations and different recording methods and periods increase the difficulties to calculate a regression of lapse rate of annual mean temperatures in dependence of the altitude, Miehe and Miehe (1994) calculated 0.63 °C/100 m lapse rate in Bale Mountains. The average lapse rate for dry seasons was 0.75 °C/100 m altitudes whereas; it was 0.5 °C/100 m altitudes for rainy seasons (Miehe and Miehe, 1994). Based on this lapse rate Miehe and Miehe (1994) estimated 100 potential needle ice nights per year in the ericaceous belt at 4000 m. However, frosts never penetrate deeply into the soil for example Miehe and Miehe (1994) recorded minimum temperatures of -12 °C , -7 °C, and 0 °C at the soil surface, at 1 cm soil depth and at 5 cm soil depths, respectively at Wasama (3880 masl) west of Dinsho.

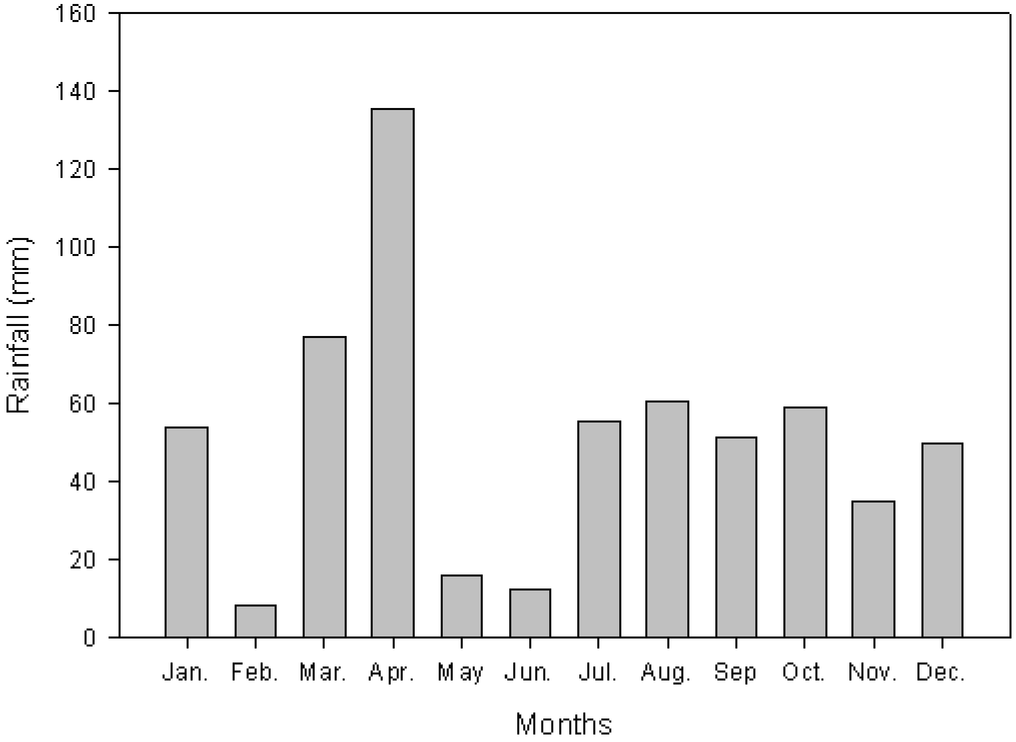

Fig. 2 Monthly total precipitation from Rira based on the data between 1997 and 2004.

Source: National Meteorological Service Agency of Ethiopia

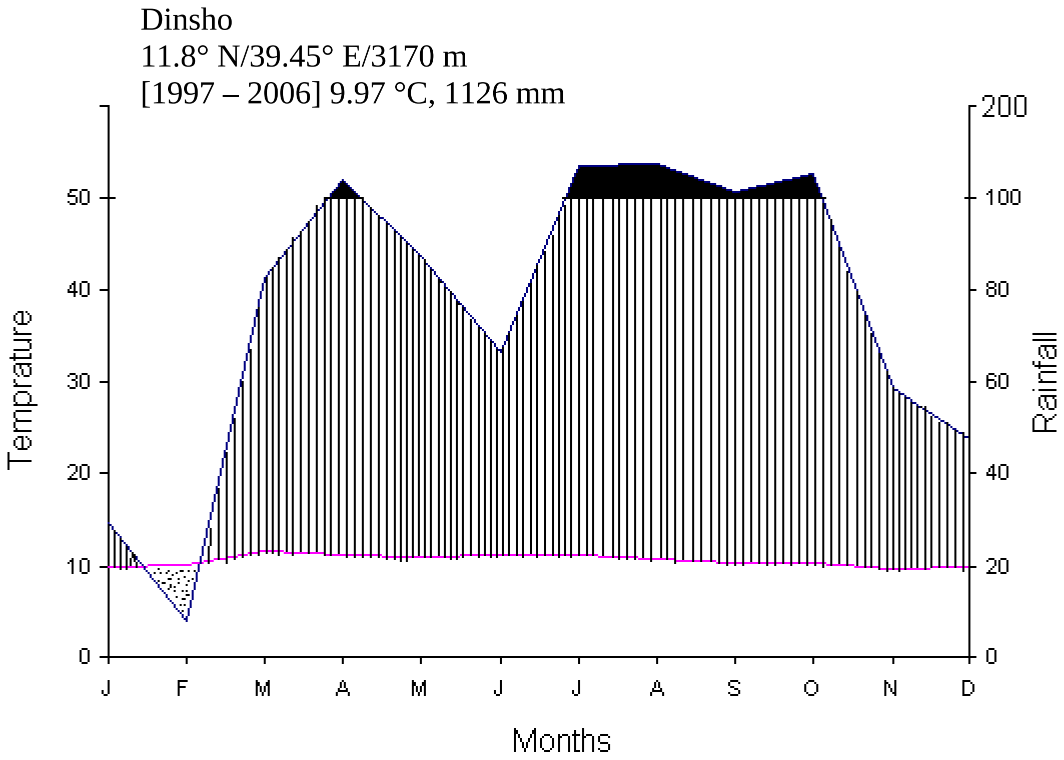

Fig. 3 Climate diagram of the study area from Dinsho Meteorological Station based on the data recorded from 1997 to 2006. Dry periods are dotted and wet periods are hatched or blacked (for pp. above 100 mm). Source the national meteorological service agency of Ethiopia.

4.2. Sampling method

4.2.1 Plot establishment

Three sites were selected along an altitudinal gradient (3000-3500 masl) on the Harrena escarpment of Bale Mountains. One permanent plot of size 30 m X 30 m or 20 m X 20 m was established at each of the three sites at the beginning of the study period. Plots were laid based on the homogeneity of the vegetation (Muller Domboois and Ellenberg, 1974). Hereafter, we refer the plots as Site 1 (3000 masl), Site 2 (3300 masl), and Site 3(3500 masl).

4.2.2. Vegetation description of the permanent plots

The vegetation of the area (southern slope of Bale Mountains) was intensively described in Masresha *et al*., (2006). In the two lower sites (3000 and 3300 masl) *Hagenia abyssinica*, *Shefleria volkensi*, and *Hypericum revolutum*, share the upper canopy layer, while *Erica trimera* dominate the lower canopy layer. On the other hand, the vegetation in the higher site (3500 masl) was dominated by *Erica trimera* with very few *Erica arborea* and *Rapanea melanophloeos* with no clear stratification. The Number of trees other than *Erica trimera* decrease as altitude increased. We found 23, 19 and 14 trees other than Erica *trimera* in Site 1, 2 and 3, respectively. As the area is known for its luxuriant vegetation (Miehe and Miehe, 1994), we found fern species such as *polystichum sp*., *Discopodium penninervium* and *Cynoglossum amplifolium.* The herbaceous layer includes *Alchemilla haumanii, Alchemilla abyssinica, Salvia merjamie*, *Cerastium afromontanum*, *Agrocharis melallntha*, *Cynoglosum lanceolatum*, *Geranium arabicum*, *Ranunculus oreophytus*, etc.

4.2.3. Sampling schedule

In the Bale Mountains in general and in the study area in particular there are three main seasons. A dry season that extends between November and February, a small rain season between March and April and a major rainy season from August to October. The months from May to July represent a transition period between the small rainy season and the major rainy season. Accordingly, fine root samples were collected at the end of each season. Hence, core samples were collected in first week of May 2006 (small rainy season), end of July 2006 (transition period), November 2006 (major rainy season) and in February 2007 (dry season).

4.2.4. Fine root sampling

Five individual *Erica trimera* trees were selected from each of the three sites for the fine root excavation. The height and DBH of the selected individuals were made to represent the mean height and DBH of *Erica trimera* at each of the three sites. Four points were randomly identified at 1 m radiuses around the bole of selected trees on the ground. Using a modified auger of 5 cm diameter and 80 cm long, core samples were extracted to a depth of 40cm. Three depth classes were considered: d1= (0-10 cm), d2= (10-20 cm), and d3= (20-40 cm). Core samples of similar depths from different points around an individual plant were mixed. A total of 15 core samples from each plot and 45 core samples from the three plots were collected and transported to the lab at each sampling occasions. As much as possible, the samples were processed immediately after collection. When it is not the case the samples were stored in refrigerator at 4 °C until processing to slow down weight loss through root respiration and root decay (Olveira et al., 2000).

4.2.5. Fine root processing

Core samples were soaked in a bowl of water over night. The soaked samples were then sieved and washed on series of mesh sieves of decreasing diameter (2.8 mm, 2.0 mm, and 1.0 mm). The fine roots (< 2 mm diameter) of *Erica trimera* were separated from fine roots of other tree species on the basis of color and texture. Roots of *Erica trimera* are dark black in color and rough surface.

Washed fine roots of *Erica trimera* were sorted into live and dead fine root fractions on the basis of visual, mechanical, and/or microscopic techniques (Hertel and Leuschner, 2002; Vogt and Persson, 1991). Live roots were much more elastic than dead ones and did not break down easily when bent. Dead roots have poor cohesion between their cortex and periderm while live roots have good cohesion between their periderm and cortex. Dry weight was determined after drying the samples at 70 ^{o}C to a constant weight.

4.3. Calculation of fine root production and turnover

Estimates of fine root production from sequential soil cores often differ depending on the method of calculation used (Vogt and Persson, 1991; Vogt *et al*., 1998; Hertel and Leucshner, 2002). In the present study, fine root production was estimated by the simple and widely used, Min-Max method, which is subtracting the minimum from maximum fine root standing crop within the sampling period (Hendrick and Pregtizer, 1993). Mathematically the Min-Max method is: $P = Max_{TFBM} – Min_{TFBM}$, Where P is annual fine root production in kg ha^{-1} yr^{-1}, Max_{TFBM} and Min_{TFBM} are the maximum and minimum total fine root biomass in the sampling period, respectively.

4.4. Soil chemical analysis

Soil samples were collected at the same time of root sampling for the dry season from each of the three sites by using a modified auger as in root sampling. Soil samples were collected for each of the depth classes that were considered for the fine root samples. Soil nitrogen, available phosphorus, organic carbon, and pH were analyzed at the National Soil Laboratory, Ethiopian Agricultural Research Organization. Soil moisture content was determined gravimetrically at the ecophysiology laboratory, Department of Biology AAU.

4.5. Data analysis

All the data collected were subjected to analysis of variance (ANOVA) test (SPSS/Pc$_{+}$, statistical package and version 11). Multiple comparisons of means were carried out using Tukey’s Honestly Significant Difference (HSD). Mean differences were considered significant at $p \leq 0.05$.

5. Results

5.1. Aboveground parameters

At the time of plot establishment the above ground parameters height, DBH, and number of stems were measured at the three sites. The height and DBH of *Erica trimera* decrease significantly ($P < 0.05$), as altitude increase. On the other hand, the number of stems per unit area increase as altitude increases (Table 1). According to the aboveground biomass estimation model described in Chave *et al*. (2005) the estimated aboveground biomass decrease as altitude increase.

Table 1. Aboveground parameters of *Erica trimera* at the three sites

Site	Altitude (masl)	DBH (cm) Mean±SE	Height (m) Mean±SE	Number of stems	Plot size (m^2)	Stem density (number of stem/ha)
1	3000	44.65±10.7	9.9±1.0	21	900	233
2	3300	25.81±2.44	8.1±0.45	81	900	900
3	3500	16.8±2.72	2.95±0.27	40	400	1000

5.2. Fine root dynamics

5.2.1. Total, live and dead fine root biomass across sites

In all of the sampling times total fine root biomass (TFBM) which is the sum of live and dead fine root biomass increased significantly ($P < 0.05$) as altitude increased. On average TFBM at Site 3 was greater than at Site 1 and 2 by 305.6 % and 74.4 %, respectively (Fig. 4). The average TFBMs of Sites 1, 2 and 3 were 1089.85, 3215.04 and 5349.81 g/m^3, respectively. Live fine root biomass (LFBM) also increased significantly as altitude increased. On average live fine root (< 2 mm diameter) biomass from Site 3 was greater than Site 1 and 2 by 400 % and 71.6 %, respectively ($p < 0.05$) (Fig. 5). The average LFBMs of Sites 1, 2 and 3 were 980.41, 2712.76 and 4738.67 g/m^3, respectively. Dead fine root biomass (DFBM) increased significantly as altitude increased during May /2006 and July /2006 but it didn't show altitudinal pattern during November /2006 and February /2007 (Fig. 6).

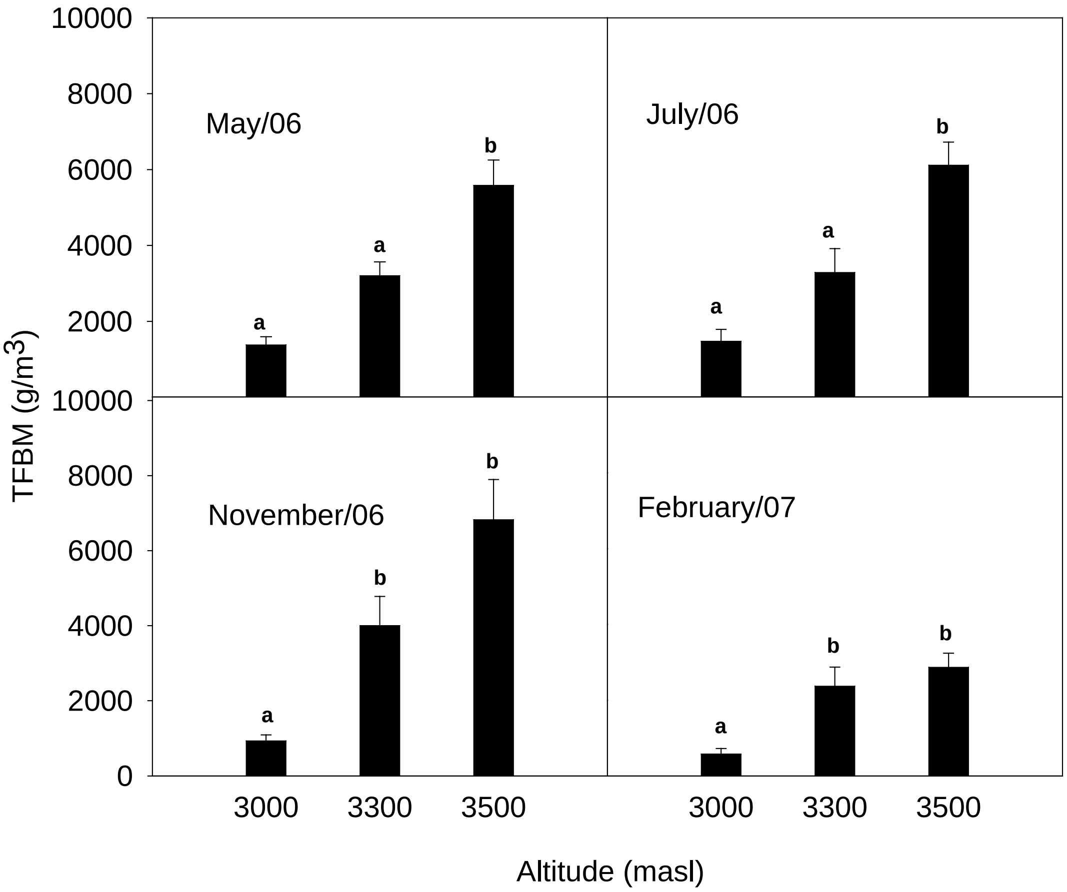

Fig. 4 Total fine root biomass (LFBM + DFBM) of *Erica trimera* along an elevation gradient sampled on May, July, November of 2006 and February of 2007. Within a block (sampling time) different letters at the top of a bar indicate significant mean differences ($P < 0.05$).

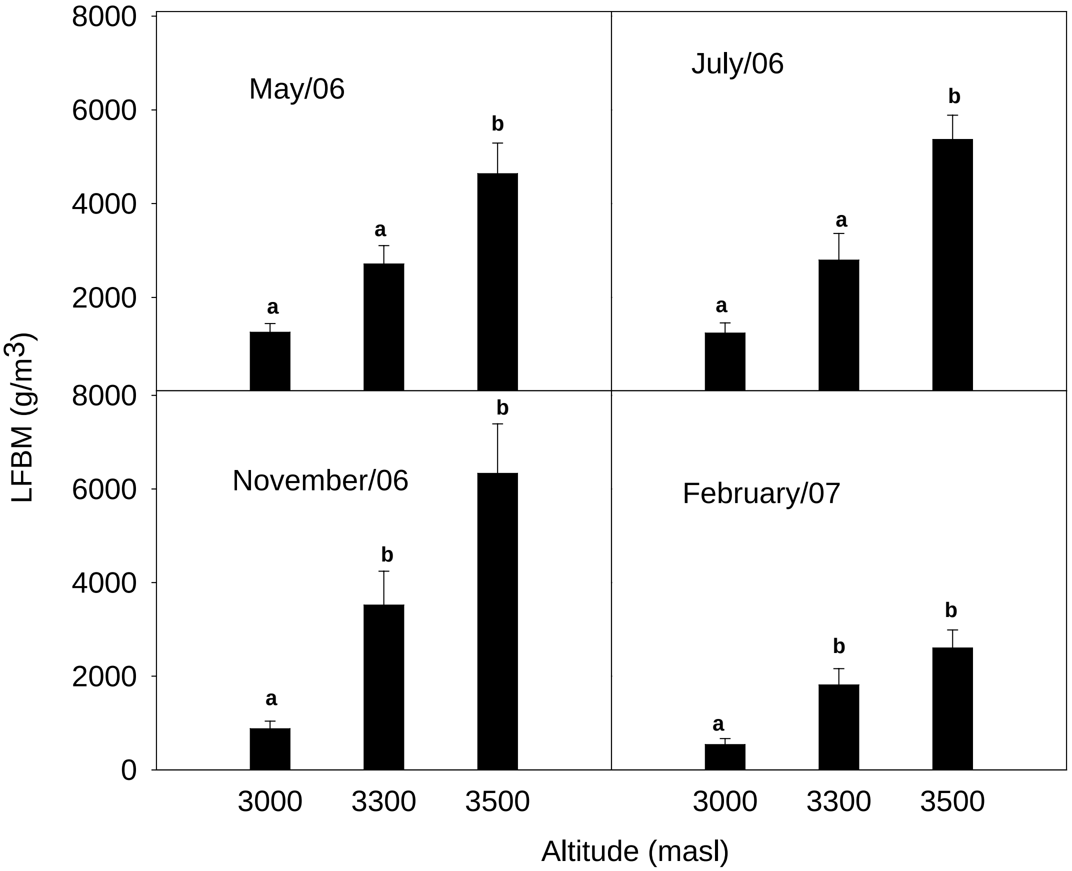

Fig. 5 Live fine root (< 2 mm diameter) biomass along an elevation gradient sampled on May, July, November of 2006 and February of 2007. Within a block (sampling time) different letters indicate significant mean differences ($P < 0.05$).

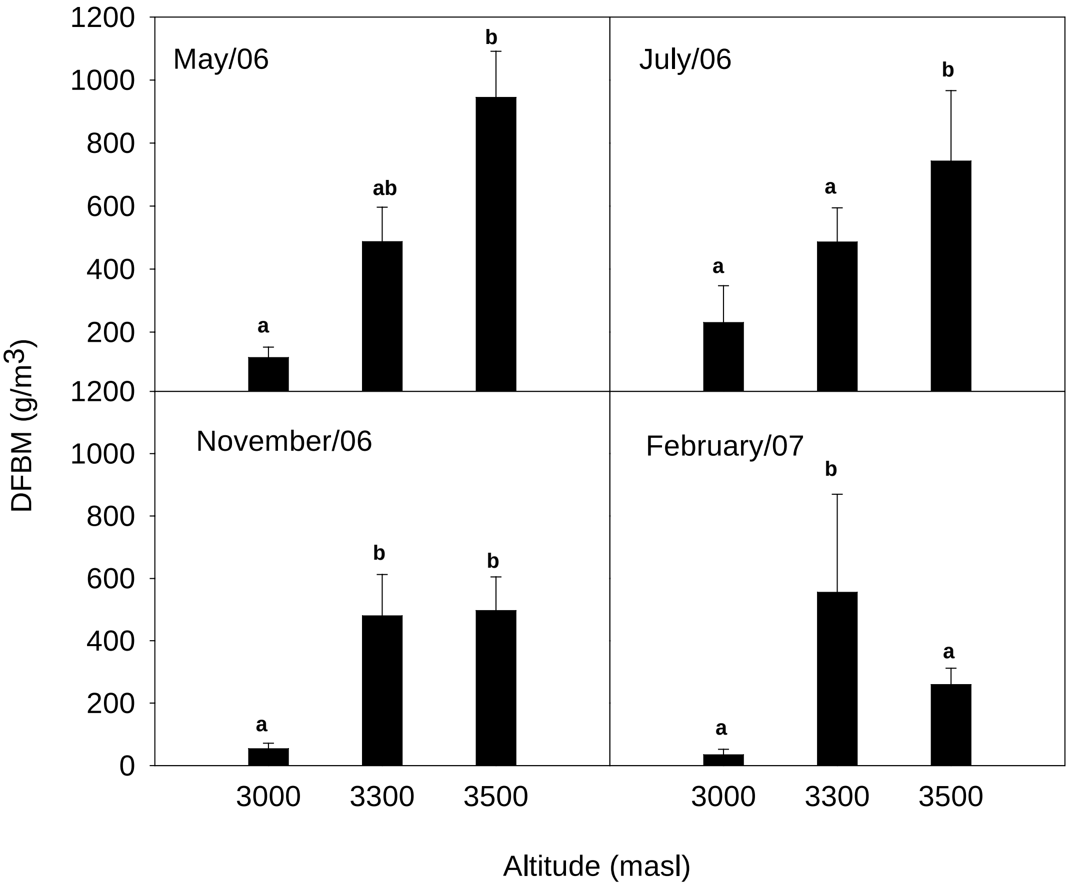

Fig. 6 Dead fine root biomass along an elevation gradient sampled on May, July, November of 2006 and February of 2007. Within a block (sampling time) different letters indicate significant mean differences ($P < 0.05$).

5.2.2. Live fine root biomass of different diameter fractions

Live fine root (0 - 2 mm diameter) biomass increased significantly ($p < 0.05$) as altitude increased. In general LFBM of Site 3 was greater than Site 1 and 2 by 400 % and 71.6 %, respectively (Fig. 5). In all of the three sites and during all of the sampling times fine roots of less than 1 mm diameter comprised larger portion of LFBM (Fig. 7). On average 64.74 % of fine root (< 2 mm diameter) biomass was comprised of fine roots of less than 1 mm diameter. The difference in LFBM between sites was also largely covered by the LFBM of roots less than 1 mm diameter. Numerically; 49 %, 55 %, 55 % and 74 % of difference in LFRBM between Site 3 and Site 1 was contributed by the roots of less than 1 mm diameter at the small rain, transition, major rain, and dry seasons, respectively. Similarly, 79 %, 51 % and 44 % of the difference between the maximum and minimum peaks of LFRBM at Site 1 (3000 masl), Site 2 (3300 masl) and Site 3 (3500 masl), respectively were contributed by the roots of less than 1 mm diameter (Table 5).

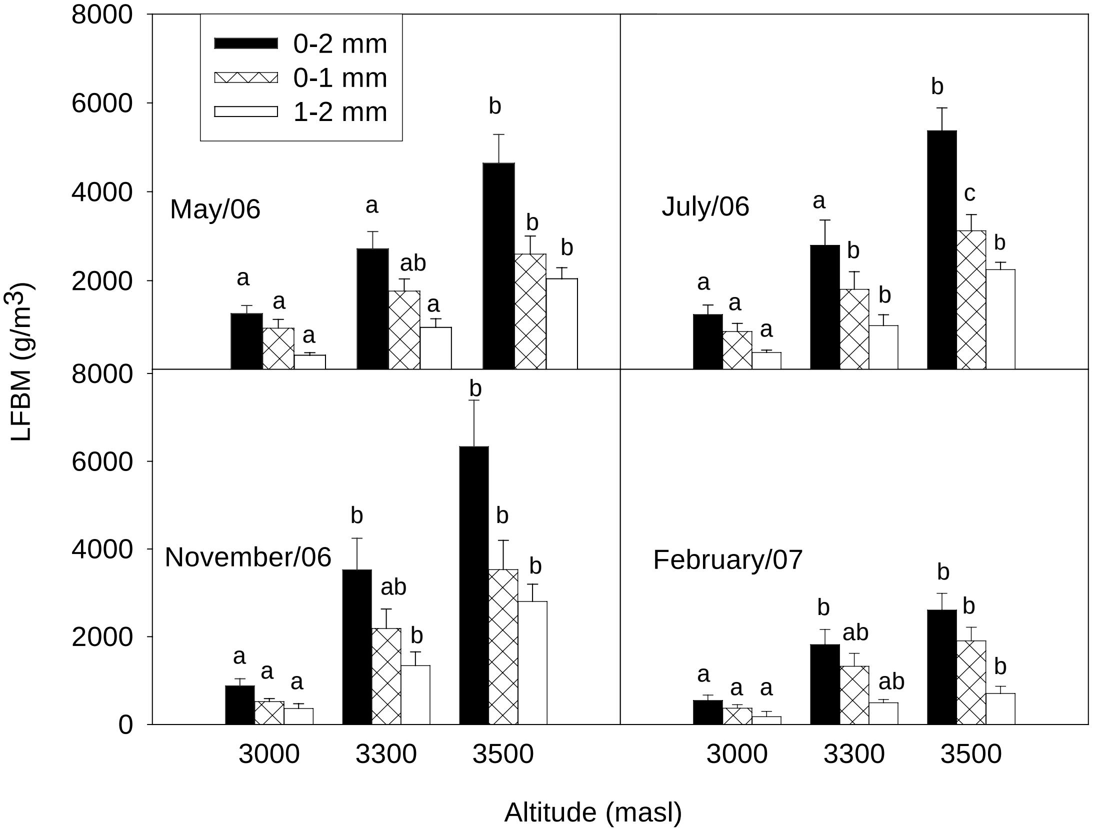

Fig. 7 Live fine root biomass for different diameter fractions (0-1 mm, 1-2 mm and 0-2mm dm) along an elevation gradient. Within a block (sampling time) different letters indicate significant mean difference across sites ($P < 0.05$).

5.2.3. Depth wise variation of total and live fine root biomass

The vertical variation of TFBM and LFBM were more or less similar during all of the sampling periods. In the two lower altitudes TFBM decreased as depth increased but in the higher altitude higher TFBM was recorded in the deeper depths than at the surface. On average more than 75 and 71 % of TFBM in Site 1 and Site 2, respectively were found at the depth of 0 - 20 cm while, around 74 % of TFBM at Site 3 were from the depth of 10 - 40 cm (Table 3). Depth wise variation of LFBM showed similar pattern as the TFBM. LFBM also found to decrease as depth increased in the two lower altitudes and higher LFBM was recorded at the deeper depths in the higher altitude. More than 78.3 and 74 % of LFBM in Site 1 and Site 2, respectively were found at the soil depth of 0 - 20 cm. In contrast, 60 - 74 % of LFBM was found from the depth of 10 - 40 cm at Site 3 (Table 4).

Table 2. Depth wise variation of total fine root biomass in g/m^3 in the three sites at the four seasons of sampling. Within a row different superscript letters indicate significant mean differences (P < 0.05). Values are mean ± SE, n = 5.

Season	Site	Altitude (masl)	Depths (cm)		
			0-10	10-20	20-40
Small rain	1	3000	750.95±217.05^a	358.07±63.46^b	268.32±21.89^c

	2	3300	1483.16±215.95^{a}	896.94±238.06^{b}	741.55±346.64^{b}
	3	3500	1478.03±243.39^{a}	2378.70±516.26^{b}	1623.51±134.61^{c}
Transition	1	3000	358.10±64.53^{a}	335.55±71.80^{a}	241.3917±47.58^{b}
	2	3300	1210.56±309.48^{a}	1128.62±308.21^{ab}	943.49±257.75^{b}
	3	3500	1673.86±290.48^{a}	2478.67±312.03^{b}	1963.45±158.90^{b}
Major rain	1	3000	648.43±112.19^{a}	510.29±124.41^{a}	311.65±125.62^{a}
	2	3300	1443.17±238.04^{a}	1342.44±183.96^{b}	1218.66±444.04^{b}
	3	3500	1667.143±359.82^{a}	2092.88±495.04^{ab}	3071.13±640.10^{b}
Dry	1	3000	265.42±62.13^{a}	190.64±51.25^{ab}	120.56±24.85^{b}
	2	3300	1361.75±123.43^{a}	742.78±74.80^{b}	265.43±135.57^{c}
	3	3500	682.84±70.02^{a}	1089.03±214.00^{b}	1093.31±233.08^{b}

Table 3. Depth wise variation of live fine root (< 2mm diameter) biomass at the three sites in all of the sampling times. Within a row different superscript letters indicate significant mean differences ($P < 0.05$). Values are mean ± SE, n = 5.

Season	Site	Altitude (masl)	Depths (cm)		
			0-10	10-20	20-40
Small rain	1	3000	557.92±55.30^{a}	415.01±69.51^{a}	267.23±135.47^{b}

	2	3300	1307.79±222.39^{a}	778.56±236.33^{b}	547.86±260.00^{b}
	3	3500	1207.79±277.65^{a}	2008.37±480.28^{b}	1318.88±106.38^{a}
Transition	1	3000	352.56±65.38^{a}	309.64±67.76^{a}	218.85±54.72^{a}
	2	3300	1036.78±300.00^{a}	955.55±264.52^{a}	804.27±221.46^{a}
	3	3500	1552.46±27.16^{a}	2207.83±270.49^{b}	1612.45±134.58^{a}
Major rain	1	3000	717.90±207.73^{a}	319.44±62.96^{b}	220.64±21.61^{c}
	2	3300	1303.10±220.25^{a}	1186.00±195.04^{a}	1035.01±392.57^{a}
	3	3500	1540.76±372.71^{a}	1885.44±483.12^{a}	2908.12±601.73^{b}
Dry	1	3000	158.99±49.27^{a}	120.56±24.85^{a}	262.88±136.06^{a}
	2	3300	683.82±82.69^{a}	599.04±181.06^{a}	531.68±100.48^{a}
	3	3500	617.67±59.43^{a}	1058.53±206.52^{b}	929.73±258.26^{ab}

5.2.4. Seasonal dynamics of total and live fine root biomass

Samplings took place on the seasonal bases to include all the seasons of a year round in the study area. In all of the three plots TFBM of *Erica trimera* showed seasonal variation with the highest peak at November/ 2006, the end of major rainy season and lowest in February/ 2007, the end of dry season (Fig. 8). In Site 1 and 3 TFBM at major rainy season (November/2006) was significantly ($P< 0.05$) greater than at the dry season (February/ 2007) and the transition period (July/06). The greatest raise in TFBM from

July/2006 to November/20006 recorded in Site 1 was 32.11 %. The increments in Site 2 and 3 were 20.0 % and 18.21 %, respectively. However, the greatest fall in TFBM from November/2006 to February/2007 was in Site 3 i.e., 58 %. The falls in TFBM between the same sampling times in Site 1 and 2 were 38.33 % and 40.81 %, respectively.

The maximum and minimum TFBMs of Site 1 were 1470.37 g/m^3 and 576.62 g/m^3 on November/2006 and February/2007, respectively. The minimum and maximum TFBMs of Site 2 were 2369.96 g/m^3 and 4004.26 g/m^3 on February/2007 and November/2006, respectively. Similarly, the maximum 6831.16 g/m3 and minimum 2865.18 g/m3 TFBMs were recorded during November/2006 and February/2007 in Site 3. The seasonal pattern of LFBM was similar to that of TFBM (Table 5).

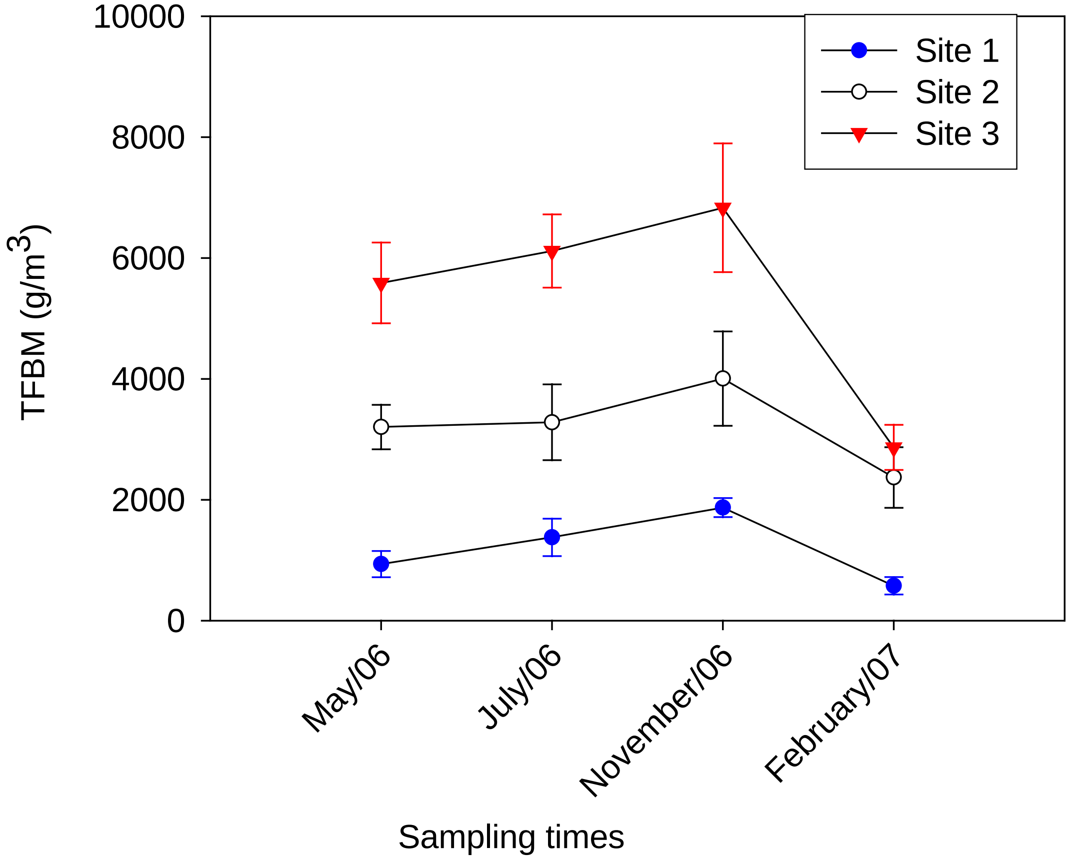

Fig. 8 Seasonal dynamics of total fine root biomass in the three sites

Table 4. Seasonal dynamics of live fine root biomass of different diameter fractions (0 - 1, 1 - 2, and 0 - 2 mm dm) in all of the three sites. Within a row different superscript letters indicate significant mean differences ($P < 0.05$). Values are mean ± S.E, n = 5.

Site	Altitude (masl)	Diameter classes (mm)	Season			
			Small rain	Transition	Major rain	Dry
1	3000	0 - 1	854.0 ± 186.0^{a}	520.8 ± 67.6^{b}	881.1 ± 162.0^{a}	366.3 ± 83.8^{c}
		1 - 2	360.3 ± 112.7^{a}	325.8 ± 55.4^{a}	386.2 ± 54.6^{a}	176.1 ± 121.0^{a}
		0 - 2	1214.2 ± 214.0^{a}	875.6 ± 197.7^{b}	1267.3 ± 184.4^{a}	542.4 ± 127.2^{c}
2	3300	0 - 1	1764.7 ± 275.2^{a}	1807.2 ± 394.7^{a}	2185.5 ± 444.9^{a}	1322.0 ± 298.2^{b}
		1 - 2	951.1 ± 190.8^{a}	989.4 ± 243.1^{a}	1338.6 ± 316.8^{a}	492.6 ± 72.1^{b}
		0 - 2	2715.8 ± 389.9^{a}	2796.6 ± 566.7^{a}	3524.1 ± 719.3^{a}	1814.5 ± 346.8^{b}
3	3500	0 - 1	2595.9 ± 408.4^{a}	3125.0 ± 359.3^{ab}	3531.5 ± 666.7^{b}	1902.9 ± 312.7^{c}
		1 - 2	2045.8 ± 247.5^{a}	2247.8 ± 168.7^{a}	2802.8 ± 392.1^{b}	703.1 ± 167.4^{c}
		0 - 2	4641.7 ± 649.6^{a}	5372.8 ± 515.2^{a}	6334.3 ± 1056.6^{ab}	2605.9 ± 383.4^{b}

5.2.5. Fine root production

The annual fine root production of *Erica trimera* in the 40 cm soil profile was estimated based on the Min-Max method in the three sites. Fine root production increased markedly from 35.75 kg ha $^{-1}$yr^{-1} at 3000 masl and 65.37 kg ha^{-1} yr^{-1} at 3300 masl to 158.64 kg ha^{-1} yr^{-1} at 3500 masl. Fine root production at Site 3 (3500 masl) was greater than at Site 2 (3300) and Site 1 (3000 masl) by 142.7 % and 343.7 %, respectively.

5.3. Soil chemical characteristics and moisture along an altitudinal gradient

In general soil fertility was found to increase as altitude increase. Total nitrogen, available phosphorus and organic carbon increased significantly ($P < 0.05$) as altitude increased. Carbon to nitrogen ratio (C/N) of the soils also increased significantly ($P < 0.05$) as altitude increased. Soils of all the three study sites were found to be acidic and soil acidity decreased as altitude increased. The soil pH of Site 1 was significantly ($P < 0.05$) lower than Site 2 and 3, and even though the difference was not significant the soil pH of Site 2 was less than that of Site 3. Soil moisture content increased significantly ($P < 0.05$) as altitude increased (Table 6).

Table 5. The average soil chemical characteristics and moisture to the depth of 40 cm, along an altitudinal gradient. Within a column different letters indicate significant mean differences ($P < 0.05$). Values are mean ± SE, n = 4.

Altitude (masl)	pH (H_2O 1: 2.5)	Soil nutrient				Soil moisture (%)
		Total nitrogen (%)	Available phosphorus (ppm)	Organic carbon (%)	C/N ratio	
3000	5.00 ± 0.02^a	0.71 ± 0.02^a	8.68 ± 0.32^a	8.30 ± 0.11^a	11.75 ± 0.14^a	11.91 ± 0.57^a
3300	5.08 ± 0.05^b	1.09 ± 0.06^b	11.60 ± 0.69^b	13.85 ± 1.0^b	12.67 ± 0.33^b	21.15 ± 1.09^b
3500	5.22 ± 0.13^b	1.31 ± 0.08^c	14.94 ± 2.01^c	20.52 ± 1.6^c	15.58 ± 0.46^c	32.06 ± 1.34^c

5.4. Depth wise variation of soil chemical characteristics and moisture.

In all of the three sites soil fertility decrease as the soil depth increased. Available phosphorus, total nitrogen and organic carbon showed a significant decrease as the soil depth increased in all of the three sites ($P < 0.05$). On the other hand, there is no significant difference in soil moisture between the three depths in the two higher sites. Soil acidity decrease significantly as the soil depth increased in all of the three sites (Table 7).

Table 6. Depth wise variation of soil chemical charachteristics and moisture in the three sites. Within a row different superscript letters indicate significant mean differences ($P < 0.05$). Values are mean ± SE, n = 4.

Site	Altitude (masl)	Chemical characteristics and moisture	Depth (cm)		
			0-10	10-20	20-40
1	3000	pH (H_2O 1: 2.5)	4.99 ± 0.03^{a}	5.00 ± 0.00^{a}	5.05 ± 0.03^{b}
		Total nitrogen (%)	0.75 ± 0.01^{a}	0.69 ± 0.02^{b}	0.68 ± 0.01^{b}
		Available phosphorus (ppm)	9.25 ± 0.29^{a}	8.66 ± 0.10^{b}	8.13 ± 0.17^{c}
		Organic carbon (%)	8.53 ± 0.29^{a}	8.23 ± 0.09^{b}	8.15 ± 0.20^{b}
		C/N ratio	11.5 ± 0.65^{a}	12.00 ± 0.00^{a}	11.75 ± 0.25^{b}
		Soil moisture (%)	11.87 ± 0.74^{a}	11.29 ± 1.50^{a}	12.57 ± 0.55^{b}
2	3300	pH (H_2O 1: 2.5)	5.00 ± 0.00^{a}	5.05 ± 0.03^{b}	5.16 ± 0.03^{c}
		Total nitrogen (%)	1.20 ± 0.01^{a}	1.07 ± 0.01^{b}	1.02 ± 0.01^{c}
		Available phosphorus (ppm)	12.97 ± 0.27^{a}	11.02 ± 0.27^{b}	10.80 ± 0.48^{b}
		Organic carbon (%)	15.71 ± 0.18^{a}	13.72 ± 0.11^{b}	12.1 ± 0.37^{c}
		C/N ratio	13.00 ± 0.00^{a}	13.00 ± 0.00^{b}	12.00 ± 0.40^{c}
		Soil moisture (%)	23.31 ± 1.61^{a}	20.67 ± 1.69^{a}	19.47 ± 1.04^{a}

3	3500	pH (H$_2$O 1: 2.5)	4.99±0.03^{a}	5.25±0.09^{b}	5.43±0.05^{c}
		Total nitrogen (%)	1.44±0.00^{a}	1.35±0.02^{b}	1.16±0.01^{c}
		Available phosphorus (ppm)	17.27±2.80^{a}	16.61±2.01^{a}	10.94±2.59^{b}
		Organic carbon (%)	23.50±0.33^{a}	20.05±0.38^{b}	18.00±0.22^{c}
		C/N ratio	16.50±0.29^{a}	15.00±0.41^{b}	15.25±0.25^{b}
		Soil moisture (%)	34.39±1.67^{a}	31.86±2.12^{a}	29.93±4.07^{a}

6. Discussion

6.1. Total and live fine biomass along an elevation gradient

Both total fine root biomass (TFBM) and live fine root biomass (LFBM) increase significantly ($P < 0.05$) as altitude increased in all of the seasons (Fig. 4 and Fig. 5). A similar pattern was reported by Soethe *et al*. (2007) from the Ecuadorian Andes forest. However, the result of the present study could not be explained as in Soethe, *et al*. (2007) or in earlier literatures based on a functional equilibrium of carbon partitioning between the root and the shoot (Farrar and Jones, 2000) where plants in nutrient limited sites allocate more biomass to their belowground part so as to maximize nutrient uptake. In this study the most important soil nutrients such as nitrogen and phosphorus were found to increase as altitude increased (Table 5). Moreover, the soil pH range 5.00 - 5.22 found in the study area was in the optimum range for the ericaceous plants (Witte, 1978). Hence, the hypothesis that state plants at higher elevation allocate more carbon to their belowground part in response to low nutrient availability due to reduced mineralization rate was not supported by the result of the present study.

The increased TFBM and LFBM along an elevation gradient as the natural fertility increased disagrees with the fact that plants in nutrient rich site have lower root-shoot ratio but it agrees with the report of Aber *et al*. (1985) which revealed the abundance and turnover rate of fine roots of 13 temperate hard wood and pine forests of a site were positively related to nutrient availability. The results are also in agreement with the report of increased fine root production as soil nutrient increased by King *et al*. (2002).

The results contradict with the general rule that states plants in nutrient rich soils have increased aboveground biomass than belowground biomass, as Site 3 (3500 masl) had highest fine root biomass (Fig. 4 and Fig. 5) was richest in soil nutrients (Table 5) but it had the least above ground biomass (Masresha Fetene *et al*., 2006; Table 1). This relation in biomass partitioning between the roots and shoots of *Erica trimera* in Site 3 might be due to the lower temperature than at the other sites.

The relatively low temperature at Site 3 (which is closest to the upper ericaceous subzone sensu Masresha Fetene *et al*., 2006) could limit the production of new cells and the development and differentiation of functional tissue of higher plants (Korner, 1998; 1999). According to the shared hypothesis (Farrar and Jones, 2000) between the shoot and the root, carbon partitioning is governed by the activities that take place in both the shoot and the root. As far as growth in the shoot of tree species at higher elevation is limited due to the low temperature, excess photosynthate is translocated to the root. Moreover, Korner (1998), reported higher abundance of non-structural carbohydrates, lipids, and leaf nitrogen in tree-line trees and dwarf shrubs at higher elevation. He suggested that the greater abundance of these ingredients in the plants at high altitude is because of a lack of dilution by growth. Recently Piper *et al*. (2006) studied the photosynthetic activity and leaf nonstructural carbohydrate content of a tree-line species *(Kageneckia angustifolia)* in central Chile along altitudinal gradient and found no change in photosynthesis, while, nonstructural carbohydrates expressed on leaf area bases increased as altitude increased. Hence they concluded that carbon sink limitation may occur at tree-line trees at upper altitudinal limit. According to Korner (1998) at higher elevation, tree life-form is disadvantageous because the shoot apical meristems of trees cannot benefit from radiant canopy warming during the day or stored warmth in the topsoil during the night, whereas subsoil leaf meristems of many alpine graminoids and rosette forbs or dwarf shrubs do but experience convective cooling through tight atmospheric coupling. Therefore, tissue expansion may become blocked periodically, and trees lose a substantial fraction of the season and most nights for structural growth. Hence, the reduction of tree height and DBH as altitude increase is neither due to carbon shortage, nor due to allocation pattern change in response to resource limitation but is created by sink (growth) inhibition as a result of low temperature.

In fact it is worth mentioning that at high altitudes, reduced capture of belowground resources, which forces higher belowground biomass partitioning according to the functional equilibrium theory (Farrar and Jones, 2000), may not only be due to less soil nutrient availability but also due to low nutrient uptake ability of roots due to low oxygen availability in soil (Bruijnzeel and Veneklaas 1998). Hence, the nutrient content of the fine roots of *Erica trimera* should be studied along an elevation gradient to understand to which extent do trees at higher elevation are using the relatively high soil nutrients.

6.2. Depth-wise variation of total and live fine root biomass

While, the decrease in TFBM and LFBM with increase in depth at Site 1 (3000 masl) and 2 (3300 masl) is in agreement with previous reports (Harris *et al.*, 1977; Joslin and Henderson, 1987) the greater TFBM and LFBM on the deeper depths in Site 3 (3500 masl) is a deviation (Table 2 and Table 3). For example 63 % of fine root biomass was in the upper 15 cm of a *Liriodendron tulpifera* (L.) forest soil sampled to 60 cm, while 71 % of biomass in a 70 cm profile was concentrated in the upper 20 cm of a soil under *Pinus taeda* (L.) (Harris *et al.*, 1977). In addition one half of the biomass of all fine roots was in the upper 22 cm of soil excavated to a depth of 100 cm in a *Quercus alba* (L.) forest (Joslin and Henderson, 1987).

The greater TFBM and LFBM at the depth of 0 - 20 cm and the high abundance of important nutrients at the same depth in Site 1 and 2 indicate higher turnover rate occurred in this layer at those sites. Whereas in Site 3, higher TFBM and LFBM at lower layer than the upper did not agree with nutrient availability. This may be due to the frequent freezing and thawing in the upper 0 - 5 cm soil depth that occur at higher altitudes of Bale Mountains (Miehe and Miehe, 1994). According to Miehe and Miehe (1994) the night frosts in Bale Mountains never penetrate into the ground hence the surface temperature fluctuation may be inhospitable for root growth.

6.3. Seasonal variation of total and live fine root biomass

In all of the three plots TFBM and LFBM of *Erica trimera* showed seasonal pattern with the highest peak in the major rainy season and lowest in the dry season (Fig. 8 and Table 4). Highest fine root biomass following the rainy season agrees with much of the reports from tropical, subtropical, and temperate forests. For example Green *et al*. (2005) reported higher standing fine root biomass in the rainy season, and low fine root biomass in the dry season in a tropical rainforest of eastern Malaysia. Similarly, Usman *et al*. (1999) also reported highest fine root biomass in the rainy season in Indian evergreen forest. Furthermore, in temperate forest ecosystems a burst of fine root production take place in spring and significant mortality in the fall (Pregtizer *et al*., 2000).

According to Pregtizer *et al*. (2000) highest fine root biomass in spring corresponds to the canopy development and significant mortality of fine roots in fall is correlated to canopy senescence in the temperate ecosystems. However, highest fine root biomass in the rainy season in tropics is mainly correlated to the improvement of soil moisture (Cavelier *et al*., 1999 cited in Green *et al*., 2005). In addition, soil nutrient availability has been shown to be influenced by periodicity of precipitation (Nomura and Kikuzawa, 2003).

6.4. Fine root production and turnover

Root production and turnover have important consequences for carbon and nutrient cycling, water and nutrient acquisition, competition between plants and the survival and reproduction of species under changing environmental conditions (Eissenstat and Yanai, 1997). Root turnover has often been used synonymously with annual root production or annual root mortality (Eissenstat and Yanai, 2002). In this respect the present study revealed increased fine root production and turnover as altitude increased. This could be associated with the increase of soil nutrient availability as altitude increased in two ways. First the increased soil fertility as altitude increased may cause higher fine root production and faster fine root turnover (Aber *et al*., 1985; Michelsen *et al*., 1993; King *et al*., 2001). On the other hand, the increased fine root turnover and production as altitude increased may contribute to the increased soil fertility as altitude increased (Cox *et al*., 1978; Grier *et al*., 1981; Ruess *et al*., 1996; Eissenstat *et al*., 2000). Considering Site 3 which had the lowest temperature of the study sites, the result also agrees with the report of Tierney (2001) in which case soil freezing increased production and mortality of fine roots of Northern hard wood forests in USA. However, the result contradicts with the conclusion made by Pregitzer, *et al*. (2000) i.e., when temperature increased fine root turnover rate and production also increased if soil nutrient and moisture availability are adequate.

6.5. Fine root dynamics of different diameter classes

The greater share of fine root dynamics by the roots of 0 - 1 mm diameter in the present study indicates that the fine roots of *Erica trimera* are most likely to be confined to < 1 mm diameter (Fig. 7). Besides root tissue composition and various environmental factors, root diameter is a key factor that governs the nutrient return to soil via root turnover (McClaughtery *et al*., 1982; Nambiar 1987; Ostertag and Hobbie 1999; Baddley and Watson, 2005; Janisch *et al*., 2005). Pregitzer *et al*. (2002) reported that specific root length, nitrogen concentration, and mortality decreased with increasing root order (root diameter) in nine North American trees. Nambiar (1987) reported that root turnover of *Pinus radiata* is largely confined to roots < 1 mm in diameter. We propose the diameter class 0 - 1 mm for future study in fine roots dynamics of *Erica trimera*.

6.6. The results in relation to climate change

The decrease of fine root production and turnover rate down the slope of Bale Mountains imply that climate change may reduce the amount of carbon, nitrogen, and phosphorus flux to the soil through the decomposition of tree roots in the system. Global warming may reduce the low temperature induced sink limitation on *Erica trimera* at its upper altitudinal limit so that the ericaceous belt could have a chance to expand into the alpine vegetation provided that fire and grazing are controlled in the area. Since the soils of the higher altitude (Site 3) are not limited with nitrogen and phosphorus *Erica trimera* could grow to a greater height in the future as a result of global warming. The speculation made earlier, that the flux of carbon from leaves to the roots and into soil should increase with warming (Pregitzer, *et al*., 2000) is challenged by the results of the present study as fine root production and turnover, the main source of carbon flux to the soil, decreased down the slope (increasing temperature).

Considerable amount of terrestrial CO_2 are sequestered in forest ecosystems (Vogt *et al*., 1996), approximately 20 % of atmospheric CO_2 is being sequestered by forest ecosystems of the world (Clark, 2002). In 1994, around 37 % of the total CO_2 sequestered worldwide in forest ecosystems was sequestered by tropical forests (Malhi *et al*., 1999). The amounts of carbon and nutrients returned to soil from fine-root turnover may equal or exceed that from leaf litter (Joslin and Henderson 1987, Raich and Nadelhoffer 1989; Chen *et al*., 2001). Moreover tree fine roots are believed to have high turnover rate (Fogel, 1983), therefore; fine root production and turnover of different forest ecosystems are being documented in terms of carbon sequestration. For example based on the minimum-maximum method annual fine root production estimate of different forest types ranges from 160 to 689 kg ha^{-1} yr^{-1} (Keyes and Grier, 1981; Singh and Singh, 1988; Hertel and Leuschner, 2002). The annual fine root production 35 to 158 kg ha^{-1} yr^{-1} of a single tree species (*Erica trimera*) indicates that these ecosystems could have a significant role in global carbon sequestration.

7. Conclusion and recommendation

This study has shown that the increased biomass allocation to fine roots as altitude increase is not due to resource limitation at higher altitudes because soil nitrogen, phosphorus, organic carbon and soil moisture increased as altitude increased. Higher fine root production and turnover at higher altitude can not be a strategy to tolerate resource limitation stress rather it could be due to the excess carbohydrate following limited growth by the relatively low temperature at higher altitudes. Therefore, the decrease in height and DBH of *Erica trimera* as altitude increases might be caused by the inhibition of growth (cell division and expansion) by the lower temperature at higher altitudes rather than due to resource limitations. However, to understand the extent to which the plants of the higher elevation use the available soil nutrients, the nutrient content of the fine roots should be studied in the future.

The concentration of more fine roots at the depth of 0 - 20 cm in the two lower sites could be related to the presence of higher organic carbon and other nutrients at the surface. The night frost that can't go deeper in the study area might inhibit the development of roots at the surface in the upper site (3500 masl) which makes the concentration of fine roots at the deeper depths in contrast to nutrient availability. The seasonal pattern of fine root mass was clearly related to the annual rainfall distribution of the study area. Highest fine root mass was recorded in the rainy season while the lowest was in the dry season. This indicated that soil moisture was important in determining patterns of root growth.

Fine root dynamics of *Erica trimera* were found to be more dominated by the roots with 0-1 mm diameter. Therefore, it will be worthy to consider roots < 1 mm diameter in the future fine root study of the species.

Since the annual fine root productions of different forest types ranged between 160 to 689 kg ha^{-1} yr^{-1}, the annual fine root production estimates 35.75, 65.37, and 158.67 kg ha^{-1} yr^{-1} in the Sites 1, 2 and 3, respectively from a single species *Erica trimera* imply that these ecosystems could play significant role in global carbon sequestration.

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Appendices

Appendix - 1 Monthly mean precipitation of Rira station based on the data between 1997 and 2004. Source: National Meteorological Service Agency of Ethiopia.

Months	Mean rainfall (mm)
Jan.	50.81
Feb.	12.17
Mar.	68.62
Apr.	91.41
May	39.7
Jun.	22.33
Jul.	55.61
Aug.	71.83
Sep.	60.38
Oct	122.56
Nov.	34.5
Dec.	30

Appendix - 2 Monthly minimum and maximum, temperatures and rainfall data between 1997 and 2006 from Dinsho. Source: National Meteorological Service Agency of Ethiopia

Months	Max. Temperature (^{0}C)	Min. Temperature (^{0}C)	Average Temperature (^{0}C)	Rainfall (mm)
Jan.	16.87	2.79	9.83	29.24
Feb.	17.83	2.25	10.04	7.93
Mar.	19	4.1	11.55	82.31
Apr.	17.17	4.93	11.05	139.83
May	17.36	4.35	10.85	87.40
Jun.	17.62	4.55	11.09	66.36
Jul.	17.13	5.06	11.09	165.96
Aug.	16.72	4.57	10.65	175.87
Sep.	16.8	3.98	10.39	113.46
Oct.	16.00	4.67	10.33	151.18
Nov.	16.18	2.84	9.51	58.54
Dec.	16.68	2.80	9.74	47.51