DENDROCHRONOLOGY AND BARK ANATOMY OF THE FRANKINCENSE TREE

MOTUMA TOLERA FEYISSA

Thesis committee

Promotor

Prof. Dr F.J.J.M. Bongers
Personal chair in the Forest Ecology and Forest Management Group
Wageningen University

Co-promotors

Dr U.G.W. Sass-Klaassen
Assistant professor, Forest Ecology and Forest Management Group
Wageningen University

Dr F.J. Sterck
Assistant professor, Forest Ecology and Forest Management Group
Wageningen University

Other members

Prof. Dr N.P.R Anten, Wageningen University
Prof. Dr B. Muys, Catholic University of Leuven, Belgium
Dr H. Beeckman, Royal Museum for Central Africa, Tervuren, Belgium
Dr P. Cherubini, WSL Swiss Federal Research Institut, Birmensdorf, Switzerland

This research was conducted under the auspices of the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC)

DENDROCHRONOLOGY AND BARK ANATOMY OF THE FRANKINCENSE TREE

MOTUMA TOLERA FEYISSA

Thesis
submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus
Prof. Dr M.J. Kropff,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Wednesday18 September 2013
at 11 a.m. in the Aula.

Motuma Tolera Feyissa
Dendrochronology and bark anatomy of the frankincense tree

135 pages

PhD thesis, Wageningen University, Wageningen, NL (2013)

With references, with summaries in English and Dutch

ISBN: **978-94-6173-644-4**

The research described in this thesis was financially supported by a PhD sandwich grant from Wageningen University, Swedish International Development Agency (Sida), British Ecological Society (BES grant number 2732/3420) and NWO-WOTRO (Netherlands Organization for Scientific Research-Science for Global Development) through the Integrated Program FRAME (Frankincense, myrrh and gum arabic: sustainable use of dry woodlands resources in Ethiopia), W01.65.220.00.

To my father Tolera Feyissa who was my first teacher and whom with my mother Bizu Dadhi decided to send me to school without hesitating to take all the burdens of farming.

To my wife Tiki Wami and my beloved children Firaol, Nafyad and Meti.

Abstract

Boswellia papyrifera (Burseraceae) trees grow in drylands south of the Sahara. In Ethiopia, it grows in seasonally dry *Combretum-Terminalia* woodlands. It is a source of frankincense, an economically important olio-gum resin used for cultural and religious ceremonies throughout the world and as raw material in several industries. Ethiopia is a major exporter of frankincense. Currently, the populations of this species are threatened by farmland expansion, fire, overgrazing, improper tapping techniques and possibly also by climate change. Focussing on tree ring analyses and resin-production related bark anatomical features, this study had two objectives.

The first objective was to quantify the status of *B. papyrifera* populations with respect to radial stem-growth dynamics and size and age structure. Based on analysis of wood structure and crossdating of tree-rings series, it is shown that *B. papyrifera* forms annual growth rings and that the average age of sampled *B. papyrifera* trees is 76 years. More importantly, it is shown that the *B. papyrifera* populations lack trees that recruited over the last 55 years (1955-2010), and that the remnant trees established continuously between 1903 and 1955. This lack of successful recruitment for such a long period of time is attributed to continuous disturbances, such as fire and grazing accompanying new settlements of people into the area over the past decades. Radial growth patterns over decades suggest effects of heavy disturbances that the trees were experiencing. Remarkably, *B. papyrifera* trees showed a 2-3 year cycle in annual radial growth, and responded significantly to climate. As expected, radial growth increased with rainfall. An increase in ring width with maximum temperature may reflect radiation limits on growth. Radial growth decreased with increasing minimum temperatures, which may reflect temperature impacts on respiration. Overall, the predicted increase in temperature and rainfall for Ethiopia may not pose a direct threat for this species.

The second objective of this study was to describe the resin-secretory structure in the bark of *B. papyrifera*. The aim was to understand the relationship between structure and functioning of the secretory system with special reference to implications for frankincense yield and improvements of current tapping techniques. Resin canals of *B. papyrifera* form a three-dimensional network within the inner bark. In the wood, only few radial resin canals were encountered. The intact resin-producing and transporting network is on average limited to the inner 6.6 mm of the inner bark. Within the inner bark, the density of non-lignified axial resin canals decreases from the vascular cambium towards the outer bark. We also show that whole tree properties, such as total resin-canal area in the bark, stem diameter, tree age, and the number of leaf apices impact frankincense yield.

Finally, this study provides recommendations for improving the existing tapping practice, aiming at maximization of frankincense yield at minimum damage costs to the trees. The new insights can also be used for selection and propagation of trees which are well suited for frankincense production. The information generated in this study is vital for planning sustainable management of the remnant trees and populations of *B. papyrifera* and the widely demanded frankincense.

Contents

Chapter 1

General introduction

Tropical dry forests

Seasonally dry tropical forest covers 40% of all forest areas in the tropics (Miles et al., 2006). This forest type occurs in an environment with seasonal climate characterised by at least three dry months (Menaut et al., 1995; Mayaux et al., 2005; Meir and Pennington, 2011), and with a wide range of annual rainfall from 250 mm to 2000 mm (Murphy and Lugo, 1995). Dry tropical forests host high diversity and endemism (Trejo and Dirzo, 2002; Timberlake et al., 2010). Most tree species of dry forest are deciduous and drop their leaves during the dry season when moisture stress is severe. Latin America hosts about 54% of tropical dry forest (Miles et al., 2006). On the other hand, Mayaux et al. (2005) reported that Africa hosts the largest proportion (i.e. 59%) of global tropical dry forest. Such variations in the extent of dry tropical forest cover worldwide may be attributed to the methods used for the assessment and also variations in the definition of dry forests (Mooney et al., 1995; Sánchez-Azofeifa and Portillo-Quintero, 2011). A global distribution map of tropical dry forest shows that Ethiopia is one of the few African countries with remnants of tropical dry forest (Miles et al., 2006).

Threats to tropical dry forests

Tropical dry forests are highly threatened worldwide (Stern et al., 2002; Miles et al., 2006; Chidumayo and Marunda, 2010). Land-use changes - mainly to agriculture, climate change, fire, overgrazing, over-exploitation and increase of human populations are among the major threats facing tropical dry forests (Miles et al., 2006; Abiyu et al., 2010; Chidumayo and Marunda, 2010; Wright, 2010; Sánchez-Azofeifa and Portillo-Quintero, 2011). 95 % of the tropical dry forests are threatened by one, or a combination of these factors (Miles et al., 2006) and conversion to other land use (mainly agriculture) remains to be the major threat to tropical dry forests (Timberlake et al., 2010). Seasonally dry tropical forest areas are preferred for agriculture because they grow on a relatively fertile soil and the seasonal climate of their environment is suitable for short life-cycle crops (Sánchez-Azofeifa and Portillo-Quintero, 2011). Fire is assumed to be an integral driver of the natural dynamics of tropical dry forests, but its frequency has increased owing to human induced activities (e. g. Cochrane and Laurance, 2002). Frequent fires coupled with overgrazing and trampling can result in recruitment failures (Keith, 1996; Teich et al., 2005; Dufour-Dror, 2007; Auld and Keith, 2009; Haubensak et al., 2009; Tsegaye et al., 2009) and change in the population structure of tree species, particularly for fire intolerant species (Zida et al., 2007). Fire frequency in tropical dry forest areas will probably continue to increase due to climate change with the scenario of increased warming and drying (Timberlake et al., 2010, Meir and Pennington, 2011). In addition, higher deforestation rates in dry tropical forest areas (Mayaux et al., 2005; Chidumayo and Marunda, 2010; Sánchez-Azofeifa and Portillo-Quintero, 2011) provide fuel load that may lead to increased fire risk (Golding and Betts, 2008). Estimates that integrate the effects of land use change, fire and climate change are lacking for dry tropical forests (Meir and Pennington, 2011).

Climate change and tropical dry forests

Climate change may directly affect the growth and population dynamics of trees growing in dry forests (Bogino et al., 2009; Scheiter and Higgins, 2009). Variations in rainfall and temperature are expected to influence tree growth, leaf phenology and survivorship through their impacts on photosynthesis, respiration and nutrient dynamics (Enquist and Leffler, 2001; Timberlake et al., 2010; Wright, 2010; Chidumayo et al., 2011; Meir and Pennington, 2011; Feeley et al., 2012). Some studies show that tree growth will increase due to global warming (Sabate et al., 2002; Lloyd and Farquhar, 2008; Ow et al., 2008; Dong et al., 2012). Others report decreasing growth rates (Battles et al., 2008; Feeley et al., 2007) because the photosynthetic gains are less than the increase in respiration cost with warming (Way and Sage, 2008; Ghannoum and Way, 2011; Wertin et al., 2011). Some studies argue that tropical species risk extinction due to faster rate of change in climate, low genetic diversity in climatic tolerance, land use change and non-climatic environmental factors (e.g. edaphic; Cunningham and Read, 2003; Feeley et al., 2012). Local differences in climate variables, soil texture and nutrient availability determine tree/vegetation response rather than changes in global long-term averages (Jacoby, 1989; Lo et al., 2010; Timberlake et al., 2010). Accordingly, the response of trees to changes in climate variables is both species and site specific (Enquist and Leffler, 2001; Worbes, 2002; Couralet et al., 2010; Corlett, 2011). The potential response of tree species from dry, but also wet tropical ecosystems to the anticipated changes in climate is poorly understood (Wright, 2010; Corlett, 2011; Dong et al., 2012).

In Ethiopia, climate change is predicted to induce variability in rainfall, including increased drought and flood incidences (Tadege, 2007; Funk et al. 2012). Future predictions (until 2080) based on mid-range CO_2 emission scenarios (IPCC, 2007) show a general increase in both average temperature and rainfall in Ethiopia (Tadege, 2007). Current observations show an increase in temperature and a constant but seasonally highly variable annual rainfall over the country. Average minimum annual temperature showed an increase of 0.37 °C every ten years, compared to the 1971-2000 normal, while annual rainfall remained constant when averaged over the whole country (Tadege, 2007). Funk et al. (2012), showed that climate change effects vary within Ethiopia and dryland areas face more challenges of drought and erratic rainfall. These changes may influence growth and population dynamics of trees. To understand the effects of climate change on growth of trees, information on past relationship of climate variables and growth of trees is imperative. Moisture stress during the dry season induces cambial dormancy and changes in wood anatomical features of tree species growing under seasonal climates of the tropics (Worbes, 1995; 2002). The alternation between increased cambial activity and cambial dormancy becomes visible as a growth ring (Roth, 1981). Dendrochronology, the study of tree rings, is an important tool to generate quantitative information on past climate-growth relationships of trees (Fritts, 1976; Worbes et al., 2002; Rozendaal and Zuidema, 2011; Zuidema et al., 2012).

Dendrochronology in the tropics

Previously, the application of dendrochronology in tropical trees was doubted due to the assumption that tropical trees lack annual rings (e. g. Lieberman *et al.,* 1985). However, the formation of growth rings by trees growing across a range of tropical environments that include ever-wet (e. g. Fichtler et al., 2003) and dry areas (e. g. Gourlay, 1995: Gebrekiristos et al., 2008), seasonally flooded plains (e. g. Schöngart et al., 2002) and mangroves (e. g. Verheyden, 2004) have been demonstrated (Jacoby, 1989; Worbes, 2002; Rozendaal and Zuidema, 2011). As a result, different studies used tree rings to understand forest dynamics, determine age structure, construct lifetime growth trajectories, predict timber yield, estimate minimum age for use and understand climate-growth relationships (Worbes et al., 2003; Baker et al., 2005; Brienen and Zuidema, 2006; Therrell et al., 2007; Gebrekiristos et al., 2008; 2009; Sass-Klaassen et al., 2008; Couralet et al., 2010; Rozendaal and Zuidema, 2011; Zuidema et al., 2012).

However, ring boundaries in tree species from tropical but also dry sub-tropical areas are often less distinct than in species from temperate areas (Worbes 2002; Wils et al., 2011; Cherubini et al. 2003; Cherubini et al. 2013). This is because seasonal changes in environmental conditions are often less pronounced in timing and intensity than in temperate areas so that the radial growth dynamics can be more irregular (Rozendaal and Zuidema, 2011; Cherubini et al. 2003; Wils et al. 2011). This is manifested in anomalies like false rings, wedging rings, missing rings, and multiple rings formed per year (Eshete and Ståhl, 1999; Worbes, 2002; Dünisch et al., 2003; Gebrekirstos et al., 2008; Wils et al. 2009; 2011).

Periodicity in growth ring formation needs to be evaluated to prove ring formation to be annual (Worbes, 2002; Rozendaal and Zuidema, 2011). Various techniques have been used to determine periodicity and dynamics in wood formation. These techniques include cambial marking (Worbes, 1995; 1999; Sass et al., 1995; Verheyden et al., 2004; Seo et al., 2007; Lisi et al., 2008; Krepkowski et al., 2011), micro-coring (Couralet, 2010), validating with trees of known age (Worbes, 1995; Verheyden et al., 2004; Couralet et al., 2005), radio-carbon dating (Worbes et al., 1995; Brienen and Zuidema, 2005; Wils et al., 2009) and annual variability of trace element concentration and isotope ratios (Verheyden, 2004; Poussart et al., 2004; Pons and Helle, 2011). Growth of tropical trees is in general positively related to rainfall (Worbes, 2002). However there are variations among trees species in their response to rainfall patterns (Enquist and Leffler, 2001; Brienen and Zuidema, 2005; Couralet et al., 2010).

Combretum-Terminalia woodlands of Ethiopia

The majority of the land mass of Ethiopia is covered by drylands, characterized by strong seasonality in rainfall. According to the Woody Biomass Inventory and Strategic Planning Project (WBISPP, 2004) these dryland areas host woodlands and shrub lands that cover about 50 % of the land mass of the country. It hosts seven of the nine vegetation types identified in Ethiopia (Awas, 2007). One of these vegetation types is the *Combretum–Terminalia* (broad-leaved) deciduous woodland (Friis et al., 2011) that is mostly found in the Northern, North-Western and Western parts of the country (Teketay and Bekele, 2002; Awas, 2007). The *Combretum - Terminalia* woodland is an extension of Sudano-Sahelian vegetation formation and harbours diverse tree species that yield gum and resin (WBISPP, 2004). One of the species that dominates the *Combretum – Terminalia* vegetation type of Ethiopia is *Boswellia papyrifera* (Awas, 2007; Eshete, 2011; Friis et al., 2011), which is the central species of this study.

Boswellia papyrifera and frankincense

B. papyrifera is a tree species which belongs to the Burseraceae family. It is a deciduous tree that grows in a seasonal climate (Figs. 1 and 6). It grows to a height of about 12 m (Ogbazghi et al., 2006; Eshete et al., 2011). *B. papyrifera* trees are encountered in Ethiopia, Eritrea, Nigeria, Cameroon, Central African Republic, Sudan, Chad, and North East Uganda (Vollesen, 1989). These tree populations cover a wide ecological and altitudinal range, as they occur in areas at an elevation range of 220-1800m above sea level, with an annual rainfall of 100–800 mm and a mean annual temperature of 25-40 °C (Lemenih and Kassa, 2011). Trees of this species often grow on degraded sites with very shallow and poor soils, steep rocky slopes and lava flows in Northern Ethiopia, Eritrea and South Sudan (Bekele et al., 1993; Gebrehiwot et al., 2003; Ogbazghi et al., 2006: Abtew et al., 2012). In North-Western (Metema) and Western (Assossa) Ethiopia, the species is growing on relatively flat land and deeper soil (Eshete et al., 2011; Personal observation).

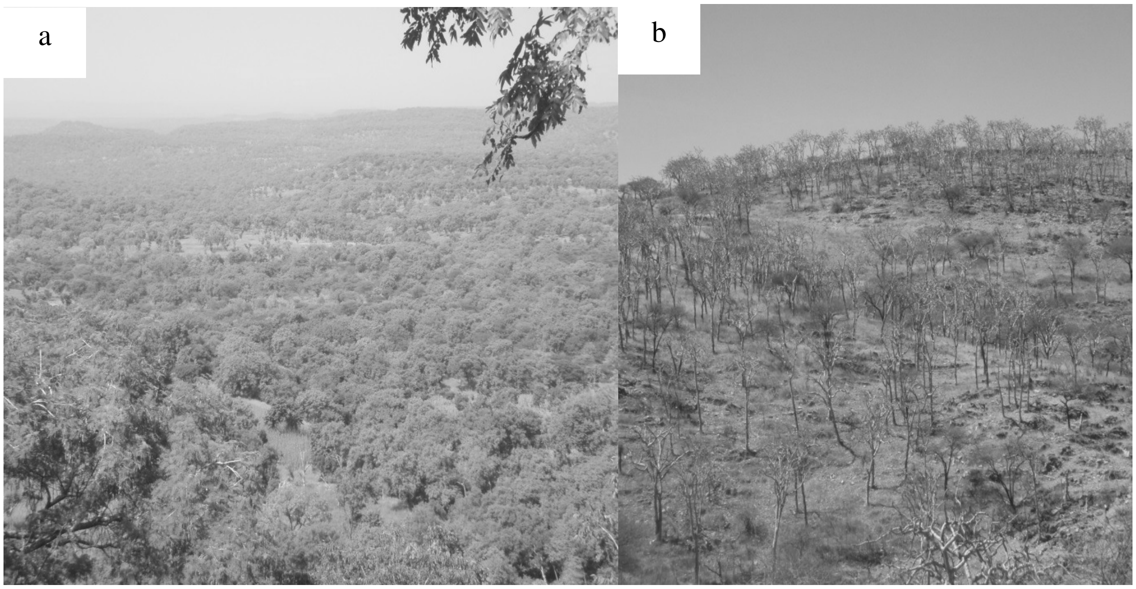

Figure 1. Seasonality in growth of the *B. papyrifera* dominated woodland, North-Western Ethiopia. Wet season (a) and dry season (b).

B. papyrifera is widely known for its production of frankincense, an aromatic oleo-gum-resin consisting of volatile oil, alcohol-soluble resin and water soluble gum (Tucker, 1986; Asseffa et al., 2012a; 2012b). Frankincense is also produced from other *Boswellia* species growing in the dry areas of Northeast Africa and Southern Arabia (Coppen, 2005). These species include *B. sacra* (Yemen, Oman and Somalia), *B. frereana* (Somalia) and *B. serrata* (India).

In Ethiopia, frankincense is produced by wounding the bark of *B. papyrifera* trees and collecting the resin that is subsequently released from the wound. This so-called **tapping** practice is carried out at several spots along the stem depending on the diameter of the tree (Fig. 2; Gebrehiwot et al., 2003; Tilahun et al., 2011; Eshete et al., 2012a). This procedure is repeated 8 to 12 times during the dry season (Gebrehiwot et al., 2003). Recently, more tapping spots per tree and more tapping rounds per season are becoming common (Eshete et al., 2012a) may be due to increasing global and domestic interest for frankincense.

The historical value of frankincense is illustrated by the gifts of the three kings (frankincense, myrrh and gold) to Jesus Christ (Matthew 2:11). Frankincense is globally used as raw material in pharmaceuticals, fragrances, flavours, detergents, soaps, and lotions (Lemenih and Teketay, 2003; Coppen, 2005), but is most famous due to its use for church ceremonies (Lemenih and Kassa, 2011). In Ethiopia, it is additionally used during coffee ceremonies. Currently, the main international trade of frankincense is from *B. papyrifera*, and Ethiopia is the main exporting country (Coppen, 2005). A total of 29,340 tons of natural gum and resins was exported from Ethiopia during the period of the year 1998 to 2008 (Woldeamanuel, 2011). Ninety percent of this product comes from *B. papyrifera* (Lemenih and Kassa, 2011). Consumption of frankincense in Ethiopia has been estimated at 10,000 tons per year (Lemenih and Kassa, 2011). Besides, its use as a source of foreign currency, the employment opportunity and income generated from sales of frankincense contributes to household economy (Tilahun et al., 2011; Woldeamanuel, 2011). In addition, this species has local uses as **source of wood products** like firewood and construction material and it is one of the few tree species that grows in the harshest environments (Abiyu et al., 2010; Ogbazghi et al., 2006).

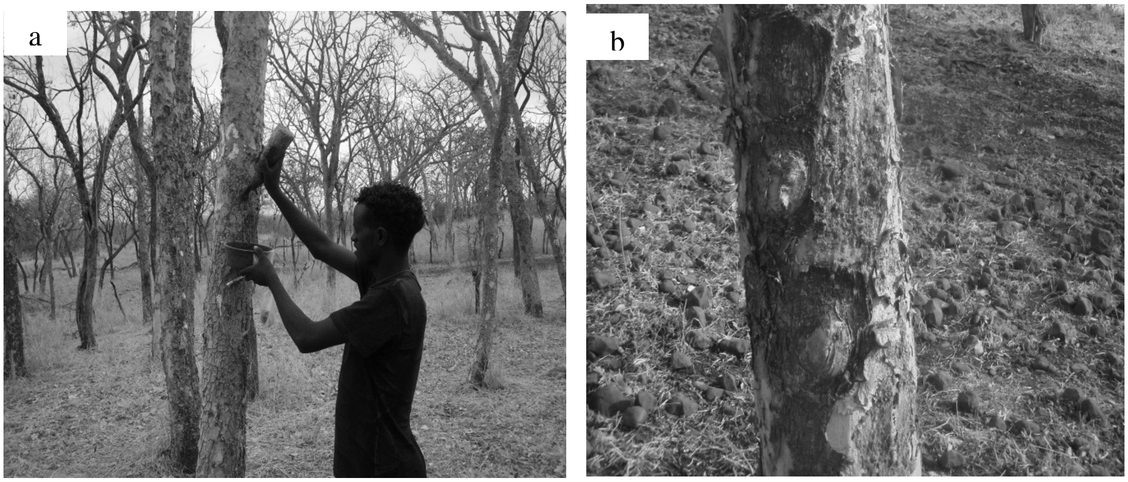

Figure 2. Tapping of *B. papyrifera*, North-Western Ethiopia. (a) Collection of frankincense and widening the wound and (b) wound scars on the stem of *B. papyrifera* from previous tapping.

Challenges facing B. papyrifera

The area of woodlands dominated by *B. papyrifera* is declining both in the North and North-Western Ethiopia. These woodland areas shrank by 35% in 20 years since late 1970s in the North (Gebrehiwot et al., 2003), and by 25% over the last 3 decades in the North-Western

(Lemenih et al., 2012) Ethiopia. Nowadays, many of the remaining populations lack trees in the smaller size classes (DBH <= 10 cm, Groenendijk et al., 2012; Negussie et al., 2008). A recent study on the population dynamics of this species revealed a decline in population size which will result in a reduction of frankincense production by 50% in less than 20 years (Groenendijk et al., 2012). The anticipated decline in the populations of *B. papyrifera* will severely reduce frankincense yield. The reason for such rapid losses are diverse but certainly affected by land-use change, overgrazing, fire, and improper tapping in particular (Fig. 3; Gebrehiwot et al., 2003; Abiyu et al., 2010; Eshete et al., 2012a). While tapping is a species-specific activity, land use change, grazing and fire are among the major threats also affecting other tropical dry forests (Miles et al., 2006; Chidumayo and Marunda, 2010; Sánchez-Azofeifa and Portillo-Quintero, 2011).

Figure 3. Disturbances from crop cultivation (a, b) grazing (b) and fire (d) on the *B. papyrifera* dominated woodland in the North-Western Ethiopia.

Recruitment failures of B. papyrifera

Forest disturbances, like frequent fire and over-grazing, can hinder recruitment success (Dufour-Dror, 2007; Zida et al., 2007; Auld and Keith, 2009; Haubensak et al., 2009; Tsegaye et al., 2009; Timberlake et al., 2010). It has been reported for *B. papyrifera* that seedlings can be observed during the rainy season but these seedlings die-back during the dry season (Birhane et al., 2012; Negussie et al., 2008). This indicates that the transition from seedling to sapling stage is a major bottleneck in the population dynamics of *B. papyrifera* (Groenendijk et al., 2012). It is assumed that seedlings may survive below ground during the dry season, and produce a new aboveground shoot in the next wet season. It has been argued that such successive sprouting and die-back may contribute to root development and storage of carbohydrate, which in turn may lead to rapid and successful development of saplings once the plant starts permanent above-ground growth (Birhane et al., 2012). Such a distinctive strategy has not only been reported for *B. papyrifera*, but also for other species in other tropical dry forests of Africa (Mushove et al., 1995; Stahle et al., 1999; Steenkamp et al., 2008). Seedlings of these species suffer from grazing, trampling and fire during the dry season (Abiyu et al., 2010; Groenendijk et al., 2012) and even be uprooted during grazing (Gebrehiwot et al., 2003). Hence, anthropogenic disturbances are likely to hinder transition from seedling to later stages of development and limit the presence of smaller size trees in the populations of *B. papyrifera* (Eshete et al., 2011). The observed failures of recruitment coupled with higher adult mortality (Groenendijk et al., 2012) may in the long-term lead to local extinction of the species.

Threats from tapping

Frankincense is tapped by wounding the bark of *B. papyrifera* trees. The common practice is to initiate between six and 12 wounds along the stem, with the number of tapping spots depending mainly on the size of the tree (Gebrehiwot et al., 2003; Eshete et al., 2012a). Each wound initially has a surface area of about 2.5 cm^2 and a depth of about 1 mm (Tadesse et al., 2004). These wounds are regularly re-opened and slightly enlarged, during 8 to 12 tapping rounds which occur over the dry season. At each tapping round, the hardened resin is removed and a fresh cut is made. The annual yield of frankincense from one tree can amount to 0.1 – 1.8 kg (Tilahun et al., 2011; Eshete et al., 2012a). Currently, due to the high demand for frankincense, higher number of tapping spots are made per tree in some commercial sites (e.g. Eshete et al., 2012a).

Studies indicated that extraction of resin through tapping likely affects carbohydrate allocation in trees as it enhances the competition for assimilates (Herms and Mattson, 1992; Rijkers et al., 2006; Silpi et al., 2007; Mengistu et al., 2012). Resin extraction also induces mechanical damage to the trees (Abiyu et al., 2006), reduces radial growth (Silpi et al., 2006) and increases adult mortality (Varghese and Ticktin, 2008). For *B. papyrifera,* tapping was found to reduce reproductive effort, indicated by a reduced number of seeds (Rijkers et al., 2006; Mengistu et al., 2012), a lowered germination success (Eshete et al., 2012b) as well as a decreased annual carbon gain and carbon stock (Mengistu et al., 2012). In addition to the human-induced disturbances discussed above, such negative effects of tapping could partly explain the recent lack of successful recruitment observed for *B. papyrifera* populations in Northern and North-Western Ethiopia (Lemenih et al., 2007; Negussie et al., 2008; Abiyu et al., 2010; Groenendijk et al., 2012). Therefore, options that minimize the effect of tapping need to be integrated in any effort for sustainable management of the *B. papyrifera* populations (Eshete, 2011; Mengistu, 2011; Lemenih and Kassa, 2011).

State of the art - the need for sustainable management of B. papyrifera

Recent ecological studies show that current *B. papyrifera* populations will further decline to less than 10% of its density in North and North-Western Ethiopia within the next 50 years (Groenendijk et al., 2012). The reasons for the decline are multifaceted and include land-use change, overgrazing, over-tapping and fire (Abiyu et al., 2010, Lemenih and Kassa 2011; Eshete et al., 2012a, Lemenih et al., 2012). Prevailing policy and livelihood strategies play vital roles as drivers of the decline of populations of *B. papyrifera* in Ethiopia (Woldeamanuel, 2011; Lemenih et al., 2011; 2012; Lemenih et al., in prep.). For instance, human resettlement programs, better financial incentives from crop production and weak regulatory systems are among the drivers for the decline of *B. papyrifera* dominated woodland of the North-Western Ethiopia (Abiyu et al., 2010; Woldeamanuel, 2011; Lemenih et al., 2011; 2012).

Sustainable management of the forests and its resources is crucial to ensure continuity of its socio-economic and ecological services. Previous studies focused mainly on understanding ecophysiology (Mengistu, 2011), productivity and population dynamics (Eshete, 2011), mycorrhizal symbiosis and seedling performance (Birhane, 2011) and livelihoods and governance (Woldeamanuel, 2011) of *B. papyrifera*. Planning of concerted sustainable management of *B. papyrifera* populations requires information also on the current status as well as past dynamics in growth. Essential information on past tree establishment, radial growth level and climate-related growth response can be derived from tree-ring research (Fritts, 1976; Worbes, 2002; Rozendaal and Zuidema, 2011).

Earlier studies on population structure of *B. papyrifera* are mainly based on diameter measurements (e. g. Groenendijk et al., 2012) and lack a longer time perspective to assess dynamics in growth and population structure which is important to identify causes of missing size classes in the populations. Yet, it is unclear during what time period recruitment has been hindered in the past, and whether this lack of recruits is synchronized to a particular external factor. Moreover, it is unknown whether the current population of adult trees originated from a single or multiple cohorts, which successfully established during specific years favouring juvenile tree establishment, growth and survival. Age identification of the remaining tree population can give an indication for how long tree establishment is failing, and whether establishment of the remaining adult trees was linked to distinct periods in the past. Assessment of age, radial growth rates and growth trajectories of single trees as well as the calculation of climate–growth relationships of the tree population is enabled by the rapid development of dendrochronological techniques which allows application to many tropical tree species (Baker, 2003; Rozendaal and Zuidema, 2010; Steenkamp et al., 2008; Trouet et al., 2006; 2010; Worbes, 2002). Dendrochronological studies also demonstrated the potential for tree-ring analyses for different species in various parts of Ethiopia (Briffa and Russell-Smith, 1986; Eshete and Ståhl; 1999; Couralet et al., 2005; Gebrekirstos et al., 2008; 2009; Wils et al., 2009; 2011; Sass-Klaassen et al., 2008; Krepkowski et al., 2011). A comprehensive review of dendrochronological studies undertaken in Ethiopia is given in Wils et al. (2011). The formation of annual tree rings is however species specific (Brienen and Zuidema, 2007; Worbes and Fichtler, 2010) and the distinctness of ring boundaries differs related to the specific environmental conditions under which a species is growing (Wils et al., 2011). So far, no dendrochronological studies have been done on *B. papyrifera.*

Crucial for planning sustainable management of *B. papyrifera* is also exploring options for improving the current tapping techniques. This requires knowledge on the resin-secretory system of the species as it deals with the synthesis, storage and transport of resin (DeAngelis et al., 1986; Blanche et al., 1992; Baier, 2002; Langenheim, 2003). Surprisingly, despite the relevance for tapping and the economic interest in frankincense production, knowledge on the anatomy and distribution of resin secretory structures of *B. papyrifera* is completely lacking. Most features of the resin-secretory system (e. g. density and size of resin canals) are expected to be closely related to tree size (e. g. diameter and bark thickness) and tree ontogeny (e.g. age), (Blanche et al., 1992; Levanic, 1999; Wainhouse et al., 2005 Wimmer and Grabner, 1997; Fabasiak and Czajka, 2011). However, how these factors are correlated, and ultimately drive frankincense yield of a tree is unknown. Knowledge on these aspects is however essential to understand the effect of current tapping techniques on frankincense yield and to generate new, more sustainable tapping techniques.

Research objectives and questions

The major challenges will affect *B. papyrifera* on both, the tree and population level (Fig. 4). This thesis aims to generate vital information that is useful for better understanding of the stress factors and sustainable management of the remaining *B. papyrifera* populations in Ethiopia (Fig. 4). To do so, the study specifically aims to (1) investigate the current status of *B. papyrifera* populations with respect to radial growth dynamics, age structure and climate-growth relationship and (2) characterize resin-secretory structures and evaluate their relation to frankincense yield. Core research questions addressed in this study are: 1) Do *B. papyrifera* trees form annual growth rings? If so, how fast do trees grow and do they show characteristic growth trajectories? How old are the trees in remnant *B. papyrifera* populations? And do trees of the current population originate from a continuous recruitment in the past? Since when is the recruitment of *B. papyrifera* hampered? 2) Is growth of *B. papyrifera* influenced by climate? If so, how will predicted changes in the climate potentially affect its growth in future? 3) How are resin-secretory structures organised and how does the distribution and network of resin secretory structures explain the current patterns in frankincense yield? 4) How is the resin-secretory structure related to tree size and ontogeny and which tree characteristics mainly determine frankincense yield?

Thesis outline

This thesis consists of six chapters. This Chapter 1 provides background information on the ecology of tropical dry forests and observed changes and threats of current *B. papyrifera* populations in North and North-Western Ethiopia. It also motivates the significance of this study and how the chapters of this thesis jointly contribute to generating vital information for the sustainable management of *B. papyrifera* populations.

Chapter 2 deals with dendrochronology and provides information on growth-ring formation, age, growth rate, growth trajectories and population structure of *B. papyrifera*. Two alternative hypotheses are tested in this chapter. The first hypothesis states that while recruits and juveniles lack in most populations, the adults come from multiple years, suggesting that the current lack of recruits results from a recent change in the environment and/or disturbances. Alternatively, the adults come from narrow time windows, indicating that successful recruits and juveniles need favourable recruitment years.

Chapter 3 is dedicated to assessing the climate-growth relationship for *B. papyrifera* by studying the variation in ring-width patterns in relation to contemporary variation in temperature and rainfall. The hypothesis is that growth-ring formation and width in deciduous *B. papyrifera* trees is mainly influenced by the amount of rainfall during the rainy season, i.e. the expected growing period of the trees. This chapter also discusses the potential consequences of predicted changes in climate on the growth of *B. papyrifera*.

In Chapter 4, the anatomy and architecture of the resin-secretory system in the bark and wood of *B. papyrifera* is described and discussed with respect to its role for synthesis, storage and transport of frankincense. It is hypothesized that resin secretory structures of *B. papyrifera* are abundant in the bark, but absent in the xylem. It is also hypothesized that density of axial resin canals show directional changes in the inner bark. The results were discussed in the context of the observed frankincense yield patterns and possibilities for improving tapping practices.

In Chapter 5, the relationship between resin-canal characteristics and tree size and ontogeny is further explored in order to understand which characteristics mainly determine frankincense yield of a tree. It is hypothesized that total resin-canal area increases with stem diameter, tree age, total leaf area and radial growth rate. It is also hypothesized that total area of resin canals, total leaf area, tree age and radial growth rate directly affect frankincense yield, and that stem diameter, age and total leaf area indirectly affect frankincense yield through their effects on total resin-canal area. The results are discussed in the context of sustainable frankincense yield.

Chapter 6 forms a general discussion, where major findings as documented in previous chapters are linked to each other. Discussion is focused on the implications of this study for improving management of remaining *B. papyrifera* populations and sustaining frankincense production for the years to come.

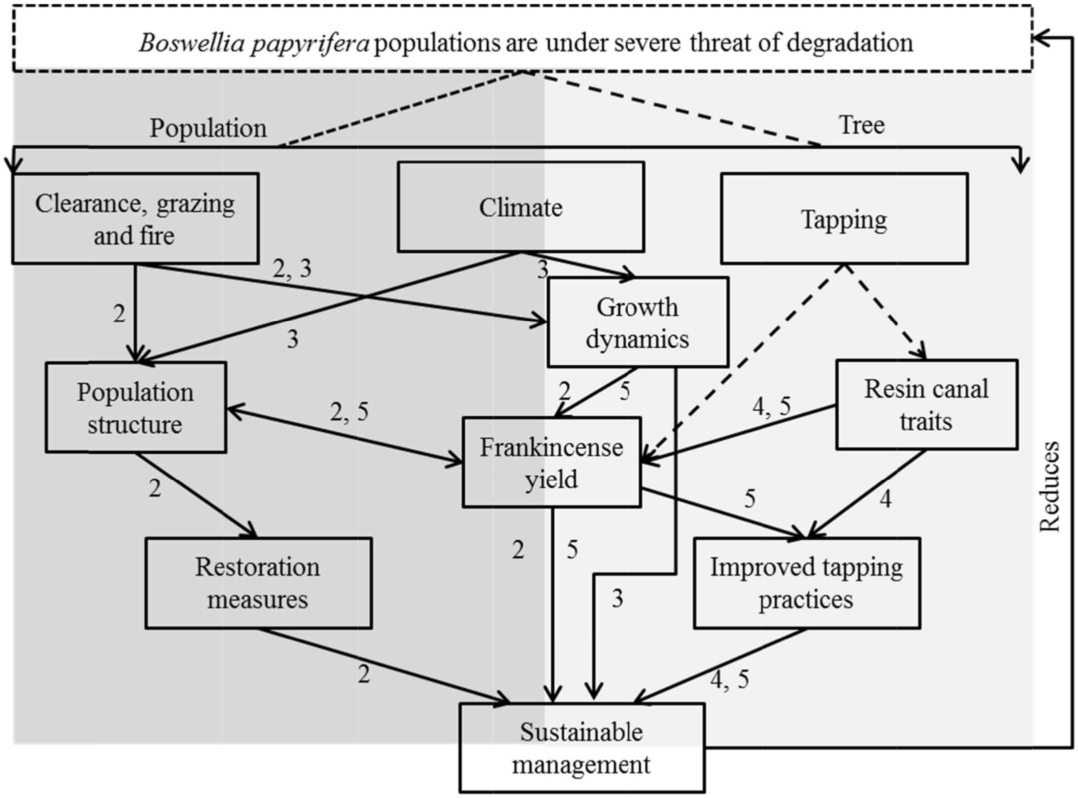

Figure 4. Schematic presentation of major threats to the current populations of *B. papyrifera*. How different chapters deal with the threat-pathways and their implication for the sustainable management of *B. papyrifera* and sustainable production of frankincense is indicated. Solid boxes and arrows indicate central focus of this thesis. The numbers along the arrows indicate the chapters of the thesis which deal with the specific issues.

Description of the study area

The studied populations of *B. papyrifera* are located near the village of Lemlem Terara, Metema district, North-Western Ethiopia (12°39′ to 12°45′N, 36°17′ to 36°23′E; Fig. 5). The study trees were sampled from populations that grow in open woodland around 870 m above sea level. The samples collected for this study include stem discs, increment cores and bark samples. At tree level, information on DBH, number of leaf apices and frankincense yield was collected. Most of this data was collected from tapped populations of *B. papyrifera* from permanent sample plots that were established in 2007 for monitoring recruitment and growth for population dynamics study by Eshete (2011). The bark samples used for the fourth chapter were however collected from untapped population of *B. papyrifera* trees growing close to other study sites. In the study area, *B. papyrifera* has a median height of 9 m, a median stem diameter of 20 cm and grow to a maximum height of 12 m (Eshete et al., 2011).

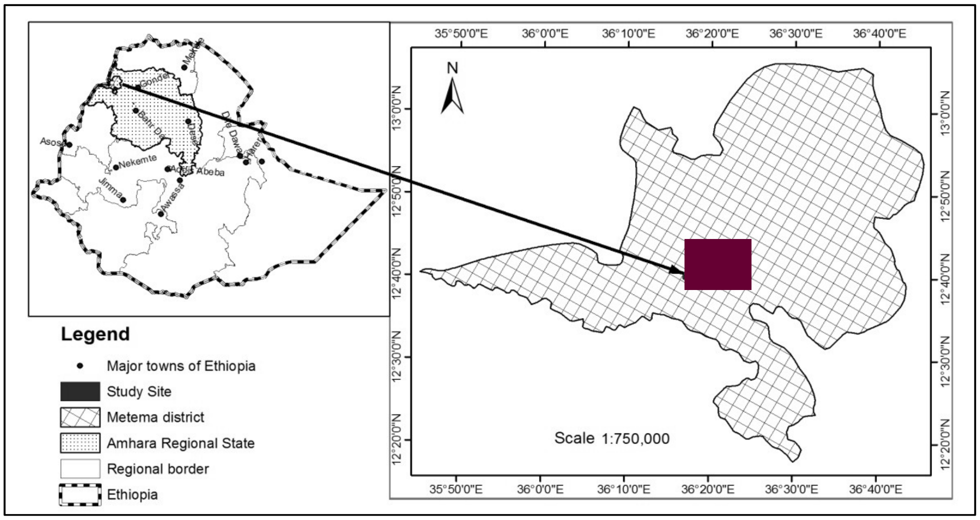

Figure 5. Map of the study area.

Based on data from National Meteorological Agency of Ethiopia, for the period 1971-2008, annual rainfall in Metema ranges from 665 to 1380 mm with a mean annual rainfall of 965 mm (Fig. 6). The major rainy season in the area is from June to September. The mean annual minimum and maximum temperatures are 19 °C and 36 °C, respectively. The study site is dominated by clay soil and its average soil depth is 27.7 cm (Eshete et al., 2011).

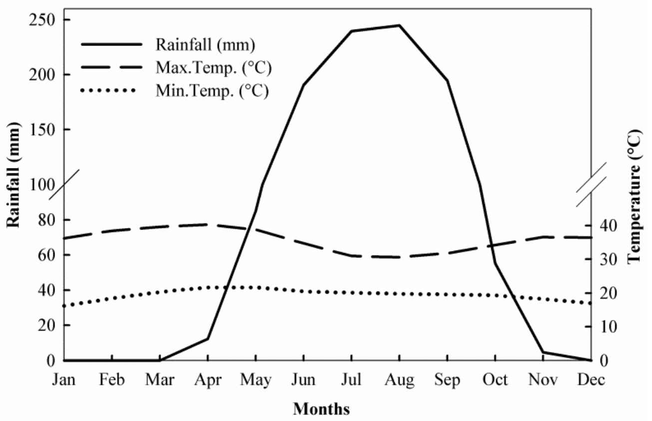

Figure 6. Climate diagram of Metema, North-Western Ethiopia. Monthly averages for the years 1971-1976, 1987-1988, 1995 and 1997-2008 are presented; data for the years 1977-1986, 1989-1994 and 1996 was not available.

Chapter 2

Frankincense tree recruitment failed over the past half century

Motuma Tolera, Ute Sass-Klaassen, Abeje Eshete, Frans Bongers, Frank J. Sterck

(Published in Forest Ecology and Management 304, 65-72 (2013))

Abstract

Boswellia papyrifera (Burseraceae) trees grow in dry woodlands south of the Sahara and produce frankincense, the economically important olio-gum resin used for cultural and religious ceremonies throughout the world and as raw material in several industries. Across its distribution area, this species is threatened by farmland expansion, fire, improper tapping and overgrazing. Most of its populations lack saplings and small-sized trees (e.g. <10 cm). It is unknown whether the older, adult trees represent a single or several cohorts, representing single or plural regeneration and survival waves. To understand such long-term population dynamics, it is imperative to evaluate the age structure of the current populations. We used tree ring analysis to determine the age-diameter relationship. This study, (1) determines radial growth dynamics and age-diameter relationship of *B. papyrifera*, including verification of annual growth-ring formation, and (2) constructs the population age structure and discusses consequences thereof for population maintenance and long-term frankincense production. We could prove that *B. papyrifera* forms annual growth rings. The average radial annual growth rate of *B. papyrifera* is 1.15 mm (s.d. = 0.22) and varies significantly among the sampled trees. Age and diameter of *B. papyrifera* trees are significantly correlated. From the population-age structure, it becomes obvious that the current *B. papyrifera* populations lack successful recruitment since 1955, which we attribute to intensive grazing and fire associated with the escalating increase of human settlement in the area. Lack of recruitment leads to rapidly declining populations resulting in strongly reduced frankincense production. Management aimed at seedling survival and sustainable use of relic trees is urgent.

Keywords: *Boswellia papyrifera*; Age structure; Pinning; Growth rings; Frankincense; Recruitment lack

Introduction

Boswellia papyrifera (Burseraceae) is a co-dominant tree species in many dry deciduous woodland areas south of the Sahara (Vollesen, 1989). It occurs on steep rocky slopes, lava flows or sandy valleys (Bekele et al., 1993). The species produces frankincense, an olio-gum resin which is extracted from the bark (Tolera et al., 2013) and used as raw material in several industries (Lemenih and Teketay, 2003; Lemenih et al., 2007). Modern uses of frankincense include coffee and church ceremonies, perfume and medicine production (Farah, 2008; Gebrehiwot et al., 2003; Lemenih and Teketay, 2003). Ethiopia is the main producer and exporter of frankincense (Coppen, 2005). Annual local use of frankincense in Ethiopia has been estimated to be about 10,000 tons (Lemenih and Kassa, 2011). A total of 29,340 tons of natural gum and resins was exported from the year 1998 to 2008 (Lemenih and Kassa, 2011; Woldeamanuel, 2011). Ninety percent of the exported gum and resin comes from *B. papyrifera* (Lemenih and Kassa, 2011). Moreover, this species has local uses as source of wood products, and it is one of the few tree species that grows in harsh environments (Abiyu et al., 2010; Ogbazghi et al., 2006a).

B. papyrifera is one of the abundant species in the *Combretum-Terminalia* woodlands of Northern and North Western Ethiopia (Eshete et al., 2011). It is currently facing severe degradation from farmland expansion, fire, improper tapping and overgrazing (Abiyu et al., 2010; Groenendijk et al., 2012; Lemenih et al., 2007; Ogbazghi et al., 2006a; Rijkers et al., 2006). Most populations of this species are characterised by high adult mortality and lack of saplings. Interestingly, many seedlings can be observed during the rainy season, however, these seedlings die-back during dry season (Birhane, 2011; Negussie et al., 2008). The assumption is that these seedlings may survive below ground during the dry season, and produce a new aboveground shoot in the next wet season. It has been argued that such die-back over successive dry seasons may contribute to root development and storage of energy, which in turn may lead to rapid and successful development of saplings once the plant starts permanent aboveground growth probably during years with a favourable climate (Birhane, 2011; Boaler, 1966; Stahle et al., 1999). This leads to the idea that populations might consist of cohorts reflecting waves of establishment (Moloney, 1986; Sato and Iwasa, 1993). Currently, saplings are virtually absent in most *B. papyrifera* populations, and the high mortality of the remaining adult size trees might suggest that those larger trees have not been refreshed by younger vital trees for a considerable period. Consequently, these populations are predicted to decline in density by 90-95% over the coming 50 years and will result in a reduction of frankincense production by 50% in the coming 15 years (Groenendijk et al., 2012).

Sustainable management of this resource is crucial to ensure the continuity of its economic, social as well as ecological services. However, planning of concerted management activities requires information on past dynamics in the population and that can only be generated when information on tree age is available. The earlier studies (Abiyu et al., 2010; Groenendijk et al., 2012) lack any time perspective since the analysis of population dynamics were based on diameter distributions. Therefore, it remains unclear during what time period recruitment has been hindered, and whether this lack of recruits is synchronised to one particular external factor. For example, Groenendijk et al. (2012), speculated about increase in fire and grazing intensity as potential primary causes for recruitment failure, but no evidence for this has been shown so far. It is also unknown whether the adult trees represent a single or multiple cohorts, which successfully established during years favouring juvenile tree establishment, growth and survival. Alternatively, a wide spread in ages in the remaining tree population would indicate that the current lack of recruitment is driven by a more recent change in factors that limit tree establishment. Age identification of the remaining tree population can indicate how long tree establishment is failing, and whether establishment of the remaining adult trees was linked to distinct periods in the past.

The population age structure of a given species can vary depending on the site conditions; drought, competition for light, fire and browsing by ungulates (Barnes, 2001; Caro et al., 2005; Steenkamp et al., 2008), elevation (Whipple and Dix, 1979), seed predation (Nakagawa et al., 2005) and insect attacks (Crawley, 1989). For *B. papyrifera*, there is evidence that inverted J-shaped population size structures are rare, and continuous size structure of this species is restricted to areas that are not accessed easily by people (Groenendijk et al., 2012). Here, two alternative hypotheses are tested: first, while most populations lack recruits and juveniles, the adults come from multiple years, suggesting that the current lack of recruits results from a recent change in the environment and/or disturbances. Alternatively, the adults come from a few narrow time windows, indicating that successful recruits and juveniles need favourable years. This information is crucial for planning sustainable management of this species and sustainable production of frankincense.

Assessment of age-diameter relationship is crucial to estimate population-age structure and is enabled by the rapid development of dendrochronology to apply it on tropical tree species (Baker, 2003; Rozendaal and Zuidema, 2010; Steenkamp et al., 2008; Trouet et al., 2006, 2010; Worbes, 2002). Dendrochronological application is species dependent (Brienen and Zuidema, 2005; Worbes and Fichtler, 2010) and it has not been assessed yet for *B. papyrifera.* This study (1) determines radial growth dynamics and age-diameter relationship of *B. papyrifera*, including verification of annual growth-ring formation, and (2) constructs the population age structure and discusses consequences thereof for population maintenance and long-term frankincense production.

Material and Methods

Study area

The study was carried out in Lemlem Terara, Metema district, North-west Ethiopia. *B. papyrifera* is the most abundant species (Eshete et al., 2011) of the *Combretum–Terminalia* woodland (Bekele et al., 1993; Demisew, 1996) that dominates the study area. In this woodland, *B. papyrifera* has a median height of 9 m and median diameter of 20 cm and grows to a maximum height of 12 m (Eshete et al., 2011; Vollesen, 1989). The soil in the study area consists of 39% sand, 24% silt and 37% clay (Eshete et al., 2011). Based on data from National Meteorological Agency of Ethiopia, for the period of 1971-2009, annual rainfall recorded at Metema ranges from 665 to 1380 mm, with a mean annual rainfall of 965 mm (Fig. 1). The site is characterised by uni-modal rainfall with a major rainy season from June to September. Annual mean maximum and minimum temperatures are 36 °C and 19 °C respectively.

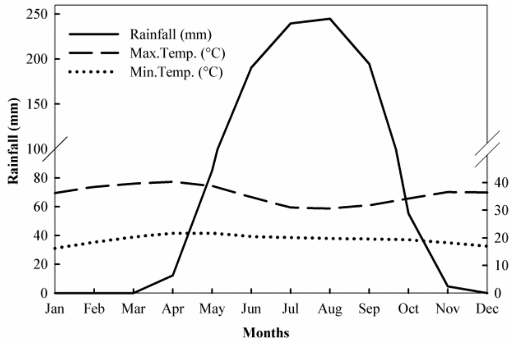

Figure 1. Climate diagram of Metema, North-Western Ethiopia. Monthly averages for the years 1971-1976 and 1997-2008 are presented; data for the years 1977-1996 was not available.

Verification of annual growth-ring formation and estimation of tree age

We collected a total of 12 stem discs from eight trees with stem diameters between 15 and 30 cm in January 2010. We had pin-marked four of these trees at 2 m above the ground in October 2007 and sampled one disc at the marked height (= total of 4 discs) for verification of the periodicity of growth ring formation. From the remaining four trees, discs were collected at soil level and 1 m above the ground (= total of 8 discs). These discs served for wood-anatomical investigation and description of growth-ring features and assessment of differences in number of growth rings between soil level and 1 m stem height as indication for initial height growth. This is important for reliable estimates of tree age based on samples that have been taken at same distance from the stem base. Collection of discs was restricted to eight individuals to limit the damage to the already threatened population of *B. papyrifera*.

Assessment of radial-growth trajectories and diameter-age relationships

Radial growth dynamics and diameter-growth relationships were done based on increment cores taken from a total of 100 trees. The study samples were collected from two sites that are about 5 km apart. The cores were collected from four plots (2 plots in site 1 and 2 plots in site 2) of about 2 ha each. These plots were established in 2007 for monitoring recruitment and growth for population dynamics study by Eshete et al. (2011). During two sampling campaigns, in April and October 2011, we sampled 50 trees from site 1 and site 2 respectively. We randomly selected five trees each from five diameter classes, i.e. 10-15 cm, 16-20 cm, 21-25 cm, 26-30 cm, and >30 cm per plot. Two increment cores were collected per tree from opposite directions at c. 0.4-0.5 m above the ground. In addition, diameter at breast height (DBH) of all sample trees was measured during the sampling.

Sample preparation

The sample discs and increment cores were air-dried at the wood-science laboratory of Wondo Genet College of Forestry and Natural Resources, Ethiopia. After drying, the transverse section of each disc was sanded using progressively finer textures of sand papers (80-1200 grit). The transversal sections of the increment cores were prepared using a core-microtome (Gärtner and Nievergelt, 2010) and when needed sanded with finer (600-1200 grit) sand paper to improve the visibility of growth-ring boundaries.

Wood anatomy and periodicity of growth-ring formation

The wood-anatomical features that define growth-ring boundaries were carefully examined macroscopically on the sanded samples. Wood-anatomical descriptions were made based on micro-thin sections (prepared according to Schweingruber et al. (2006)) and observed under a transmission light microscope. Special attention was given to concentric wood-anatomical features that most likely indicate growth-ring boundaries (Worbes and Fichtler, 2010). To verify annual nature of detected growth rings and assess periodicity of wood formation, the wood anatomy around the pin-marks was studied in detail based on micro-slides prepared from the tissue formed between times of pin-marking (October, 2007) and cutting (January 2010).

Growth-ring measurement, crossdating and radial growth trajectories

Growth rings were identified and marked around the discs and along each increment core. Ring width was measured to the nearest 0.001 mm under a LEICA MS 5 microscope coupled with LINTAB ^{TM}5 digital measuring stage associated to TSAP-dos software (Rinn, 2003). The resulting ring-width series were visually crossdated to trace missing or wedging rings, which can occur in phases of low cambial activity, and to correct for misdetection of ring boundaries due to multiple causes, such as presence of reaction wood. Visual crossdating results were subsequently verified by calculating ‘‘Gleichläufigkeitskoeffizient’’ (GLK, resembles coefficient of parallel run; Schweingruber, 1988), t-values and Pearson correlation coefficients. In cases of significant relationships indicated by significant GLK ($p < 0.001$) and t-values (above 4) mean ring-width series per tree were calculated. The same procedure was used to crossdate all mean ring-width series (e.g. Enquist and Leffler, 2001). Mean annual radial growth was calculated for all sample trees. Life-time growth trajectories per tree were constructed by summing the annual diameter growths (Brienen and Zuidema, 2006, 2007; Xing et al., 2012). ANOVA was used to test if there is difference in average growth rate among the sampled trees. Spearman rank correlation (Brienen et al., 2006) was used to test if there is persistent difference in growth rate among the trees over different age classes.

Age estimation and age-diameter relationship

Age-diameter (DBH) relationships were developed for the study trees using simple linear regression functions. The model (with prediction intervals) was then used to estimate the population age structure of all 2260 *B. papyrifera* trees (646 in site 1 and 1614 in site 2) growing in two sites of the study area. We reconstructed three population structures per site, one based on the average modelled value, one on the lower 95% prediction interval and one on the upper 95% prediction interval. The DBH data used to estimate age structure was measured in 2010.

Results

Annual growth rings

B. papyrifera forms annual growth rings (Fig. 2a, b, c). But distinctiveness of growth-ring boundaries varies with tree age and radial growth level with boundaries being more distinct in juvenile wood and in wider growth rings. Wedging and missing rings occur during periods of low cambial activity and complicated ring detection. Probably due to incidental missing rings or wedging rings, we could only crossdate 84 of the 100 trees, and based our analysis on the 84 crossdated trees. Ring boundaries in *B. papyrifera* are consistently marked by radially flattened fibre cells. Changing density of vessels and tangential rows of vessels are supplementary features indicating ring boundaries in wider growth rings (Fig. 2b) and juvenile wood (Fig. 1c) respectively. Vessel density is lower in earlywood than in latewood.

Pinning of *B. papyrifera* revealed the formation of two distinct growth rings between the time of wounding (October, 2007, dry season) and time of cutting (January, 2010, dry season; Fig. 2d). In all sample trees, the formation of two growth rings after wounding was detected across the entire cross-section. The two growth rings represent the radial growth realised during 2008 and 2009. This indicates that growth-ring formation in *B. papyrifera* is annual.

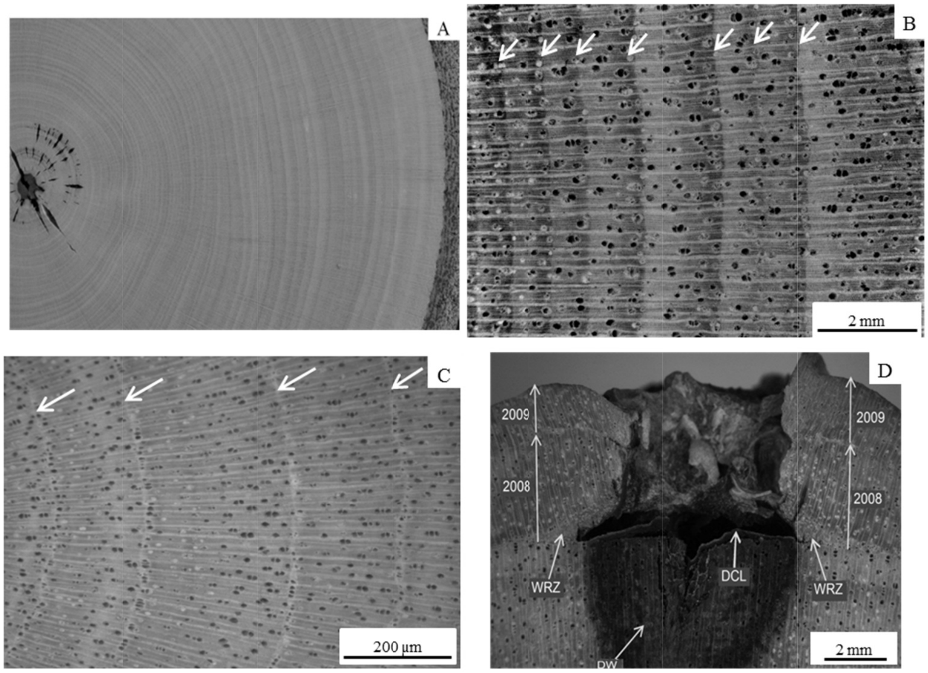

Figure 2. Growth rings in *B. papyrifera*, Ethiopia. (a) Macroscopic view of polished disc with rings indicated by alternating layers of brighter (=earlywood) and darker (=latewood) wood. (b) Wider rings in adult wood with distinct growth ring boundaries and varying density of vessels in earlywood and latewood. (c) Tangential rows of vessels at growth ring boundaries in juvenile wood. (d) Reaction to cambial marking and illustration of periodicity of growth-ring formation after pinning: transverse section of polished stem disc. DCL–dead cambium layer, WRZ–wound reaction zone, DW–discoloured wood. The two growth rings formed after wounding are indicated as 2008 and 2009. Arrows in (b) and (c) indicate growth-ring boundaries.

Age and radial growth

Height-growth rate estimation from discs taken from 4 trees at ground level and at 1 m stem height revealed that it took the trees 3-4 years to reach 1 m height. From this we estimated that the sampling height of 40-50 cm was reached in approximately 2 years. Taking into account this correction to the sampling height, the average age of sampled *B. papyrifera* trees is 76 years (s.d. = 11; n = 84 trees) and ranges between 45 and 101 years. The average radial growth of an individual *B. papyrifera* tree is 1.15 mm per year (s.d. = 0.22; n = 84), and ranges between 0.71 and 1.80 mm. The average growth is significantly different among the sampled trees (ANOVA, $F_{83,\,6142} = 13.57$, $p < 0.001$). Age and stem diameter of *B. papyrifera* were significantly related (linear regression; Predicted age = 1.17 * DBH + 49.62; $r^2 = 0.44$,

$p < 0.001$; Upper prediction interval = 1.18 * DBH + 66.68; Lower prediction interval = 1.16 * DBH + 32.55; $n = 84$), but considerable variation does exist (Fig. 3A). Individual trees show persistent growth difference throughout their lifetime (Table 1; Fig. 3B). Trees growing with faster growth rate grow also faster in the next higher age classes (Table 1) and the stronger correlations extend over 2-4 decades.

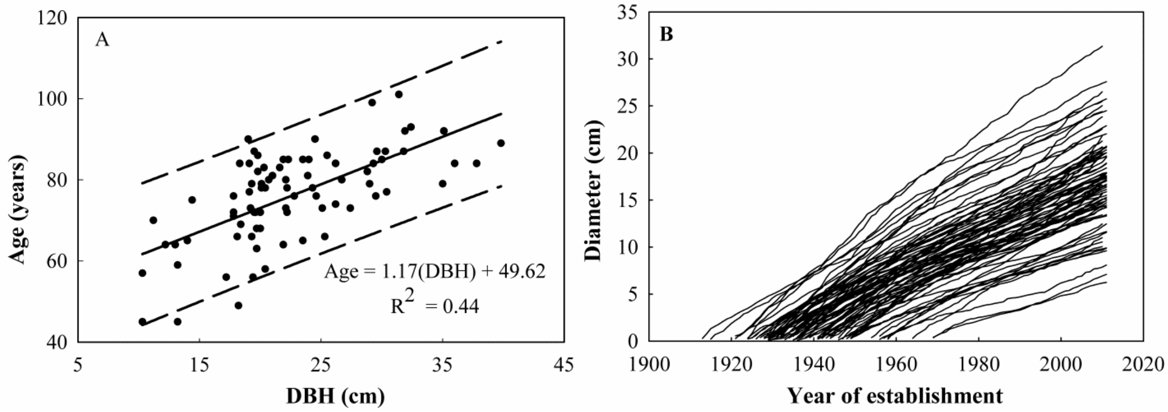

Figure 3. Age-diameter relationship of 84 *B. papyrifera* trees from Ethiopia. (A) Linear regression model with dashed lines showing the upper and lower bound of 95% prediction interval. (B) Life-history growth trajectories with each line representing diameter increment over the life span of a sample tree.

Table 1. Spearman rank correlations of growth rates between subsequent age classes. Significant correlations ($p < 0.05$) are shown in bold. The numbers in the parenthesis in the first row show number of trees in the respective age classes.

Age class (year)	11-20 (84)	21-30 (84)	31-40 (84)	41-50 (84)	51-60 (81)	61-70 (75)	>70 (55)
1-10	**0.638**	**0.325**	0.214	**0.215**	0.040	0.048	0.140
11-20		**0.578**	**0.376**	**0.315**	0.045	0.214	0.035
21-30			**0.692**	**0.542**	**0.341**	**0.285**	0.068
31-40				**0.663**	**0.430**	0.224	0.081
41-50					**0.679**	**0.387**	0.201
51-60						**0.614**	**0.315**
61-70							**0.510**

Population age structure

Based on the modelled age-diameter relationship, the estimated average age of *B. papyrifera* growing in the two sites is 71 (s.d. = 7.48, *n* = 2260 trees) years. The ages of trees in both sites show smooth and normal distributions without peaks that would suggest specific favourable recruitment years (Fig. 4B and D). The size structures of both sites also show similar pattern (Fig. 4A and C). Average tree age for site 1 is 71 (s.d. = 6.73) years and for site 2 is also 71 (s.d. = 7.75) years. Fig. 4B and D shows the age distributions based on the prediction intervals of the modelled diameter-age relationship. Based on the individuals present at the two sites in 2010, no trees were established after 1955 (1951 for site 1 and 1955 for site 2) at the two sampling sites. Even with the fastest growth scenario (lower limit of 95% prediction interval), no tree was established after 1972 in the studied population. The scenario that assumes slowest growth rate (upper limit of 95% prediction interval), indicates no successful recruitment after 1938.

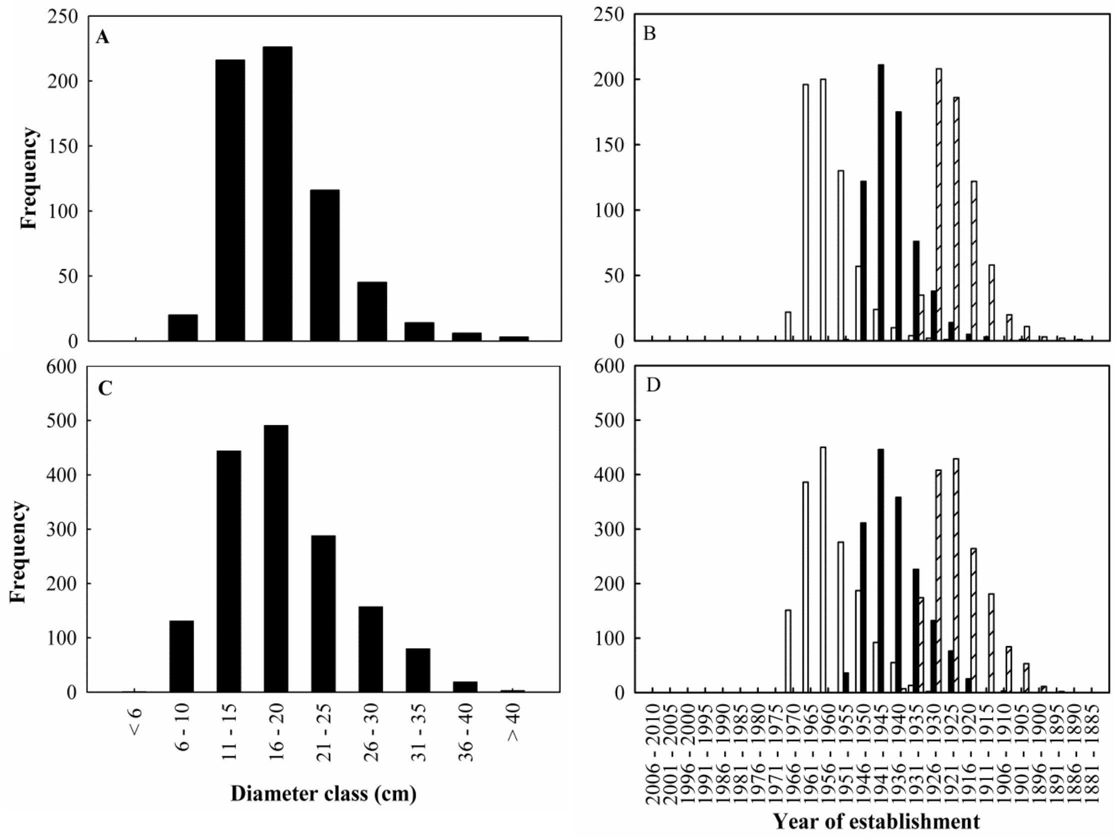

Figure 4. Size (diameter) structure (A and C) and estimated age structure (B and D) of *B. papyrifera* from Ethiopia (*n* = 2260). A and B site 1, C and D site 2. Different colours (B and D) indicate the age structure estimated based on the model of age-diameter relationship

(predicted = black) and the lower (open bars) and upper (stripped bars) bounds of the 95% prediction intervals of the age-diameter relationship (see Fig. 3A).

Discussion

Growth-ring formation

Our analysis confirms the suitability of the pinning method for verifying annual growth-ring formation in *B. papyrifera* (Couralet, 2010; Lisi et al., 2008; Sass et al., 1995; Seo et al., 2007; Verheyden et al., 2004; Worbes, 1999). Worbes (1995) indicated that a dry season with a length of 2-3 months and less than 60 mm precipitation per month can induce cambial dormancy in tropical tree species. Fichtler et al. (2003), showed that even short dry periods of 2-4 weeks can induce the formation of growth rings. The strong seasonality in rainfall characterised by uni-modal pattern with extended dry period is most likely responsible for the annual growth-ring formation in *B. papyrifera,* as has been shown for other dry-forest species of Ethiopia (Eshete and Ståhl, 1999; Gebrekirstos et al., 2008; Sass-Klaassen et al., 2008), African Acacia species (Gourlay and Grime, 1994) and other tropical species from central America and Asia (Borchert, 1999).

Radial growth rate

B. papyrifera is a slow growing tree, with average annual radial growth ranging between 0.71 and 1.80 mm. The mean annual radial growth rate of 1.15 mm is lower than the average annual radial growth rate reported for co-occurring Acacia species (1.93-2.53 mm) growing in the dryland area of central rift valley of Ethiopia (Gebrekirstos et al., 2008). It is also lower than the average annual radial growth of other Acacia species growing in the semi-arid areas (1.8-7 mm) of Africa (Gourlay, 1995; Steenkamp et al., 2008), *Pterocarpus angolensis* (1.5-2 mm) from Miombo woodland of Zimbabwe (Stahle et al., 1999), *P. angolensis* (1.75 mm) from Mozambique (Therrell et al., 2007) and semi-deciduous forest (1.9 mm) of Cameroon (Worbes et al., 2003). Such slow growth rates of *B. papyrifera* compared to Acacia species have also been reported for seedlings (Birhane et al., 2012), suggesting that *B. papyrifera* is much slower in growth over its whole life period compared to other species that co-dominate the same drylands. Within the species, trees with high initial growth rates tend to maintain these higher growth rates over their whole life compared to slower growing trees. Such auto-correlated growth has also been reported for Bolivian timber species (Brienen and Zuidema, 2006, 2007; Brienen et al., 2006) and semi-deciduous forest of Cameroon (Worbes et al., 2003). These persistent growth differences between trees may be attributed to variation in local growing conditions, genetic potential, or a combination of both (Brienen and Zuidema, 2007; Mushove et al., 1995; Stahle et al., 1999).

Age structure and its underlying causes

We found that frankincense trees younger than 55 years are absent from the two studied sites. A lack of smaller trees (<10 cm diameter) was reported earlier (Abiyu et al., 2010; Eshete et al., 2011; Gebrehiwot et al., 2003; Groenendijk et al., 2012; Ogbazghi et al., 2006b). We also estimated that no trees were older than 107 years. Moreover, we found no indication for incidental favourable recruitment peak years or peak periods (e.g. Moloney, 1986; Sato and Iwasa, 1993) implying that the remaining trees established and regenerated continuously over the years between 1903 and 1955. Tree age structures with lack of recruitment in the riverbed and an inverted J-shape for dunes were reported for *Acacia erioloba* from savanna of South Africa (Steenkamp et al., 2008). Since many seedlings establish and temporarily survive (Birhane, 2011; Negussie et al., 2008; Ogbazghi, 2001), our study confirms that the transition from seedling to sapling and maybe also the growth and survival of saplings pose a bottleneck for the populations of *B. papyrifera* (Groenendijk et al., 2012). This is commonly attributed to grazing of the seedlings and continuous disturbance from conversion to agricultural land and frequent fire (Abiyu et al., 2010; Eshete et al., 2005; Lemenih et al., 2007, 2012). Mortality of the remnant trees is also likely to be increased due to damage by these disturbances, ageing, insect attacks or combinations of these (Groenendijk et al., 2012).

The increased disturbance might be related to continuous human settlement in the study area (Eshete et al., 2005; Lemenih et al., 2007, 2012; Woldeamanuel, 2011). Settlement in the area was intensified since the late 1960s (Lemenih et al., 2007). Eshete et al. (2005) also indicated that the human population in our study area increased by more than four times in the 20 years following 1982. The reports from population and housing censuses by Central Statistical Authority (CSA) show that the human population of the study district increased from 12,887 to 110,231 from 1984 to 2007 (CSA, 1994, 2007). However, recruitment of *B. papyrifera* may have already been hampered by the first settlers in the 1960s, who might have used fire to clear land and introduced large numbers of grazing animals. This coincides with our data showing no recruitment since about 1955.

The trend of increased human population is a proxy for increased livestock population and increased fire incidents. Increased frequency and intensity of fire with settlement in the area (Lemenih et al., 2007) opens land for agriculture, stimulates growth of new grass and increases access into the woodland (Eshete et al., 2005). Fire strongly affects both seedlings and saplings. As burning occurs in every dry season, chances for saplings to escape to the next stage are minimal. In addition to the frequent fire in the dry season, our study area receives many people from the highland areas, who stay in the area with their livestock during the rainy season. Tegegne et al. (2009) showed that 60% of the livestock from three nearby districts stays in the district of our study area between May and October, the period when frankincense seedlings are expected to emerge. A high livestock population density during seedling emergence increases the chance of trampling and grazing. Seedlings that escape these effects may then be destroyed by fire during the following dry season (Eshete et al., 2005). Together, frequent fire, grazing and trampling effects may fully block successful regeneration of *Boswellia* trees. Farah (2008) reported similar effects of increased human settlement, effects associated with land conversion, over-tapping and over-grazing on regeneration of *Boswellia sacra* in Oman.

Tapping for frankincense has also been proposed as a possible factor causing the lack of regeneration. Tapping in Metema started in the 1960s (Woldeamanuel, 2011). Tapped trees of *B. papyrifera* produce less flowers, fruits and seeds than non-tapped trees and germination success of seeds from non-tapped trees is much higher than from tapped trees (Rijkers et al., 2006). A study in our specific study site showed that tapping reduces foliage production, annual carbon gain and carbon stocks (Mengistu et al., 2012) and tapped trees of *B. papyrifera* produce less viable seeds (Eshete et al., 2012b). It has been suggested that such negative effects could, at least partly, explain the lack of successful recruitment for *Boswellia* populations in north-western Ethiopia (Abiyu et al., 2010; Lemenih et al., 2007; Negussie et al., 2008). However, untapped populations also showed no successful regeneration (Groenendijk et al., 2012) indicating that impacts of tapping are less severe than grazing and fire disturbance.

Seedlings of *B. papyrifera* die back and stay below-ground during the extended dry period as a means of escaping drought stress, grazing and/or fire (Birhane et al., 2012). This is among the distinctive strategies that different species use to pass stressful growing conditions. For instance, *P. angolensis* growing in Miombo woodland in Zimbabwe shows a prolonged seedling stage with continuous root growth and annual shoot dieback (Boaler, 1966; Stahle et al., 1999). The larger root enables to maximise the utilisation of scarce moisture. In addition to the development of a large root system, these seedlings need other conditions like full light, absence of root competition, supply of adequate nutrients and absence of fire to grow to the sapling stage (Stahle et al., 1999; Steenkamp et al., 2008). Negussie et al. (2008), linked the die-back of *B. papyrifera* seedlings to drought indicating that the situation was similar in open and fenced (free of human and livestock disturbance) stands. The lack of *B. papyrifera* trees in a sapling stage (Eshete et al., 2011) suggests that seedlings may not have sufficient time to accumulate enough assimilates in the root system to be able to overcome the fire, grazing and trampling bottlenecks once they appear permanently aboveground. The lack of new recruitment of *B. papyrifera* for longer period of time coupled with high adult mortality (Groenendijk et al., 2012) may lead to (local) extinction of the species.

Implications for sustainable frankincense yield

The huge gap in the age structure of *B. papyrifera* also has implications for frankincense production. Earlier studies suggested that the minimum DBH to start tapping of frankincense should not be less than 20 cm (Eshete et al., 2012a). This recommendation was based on lower yield of frankincense from smaller trees and higher adverse effect of tapping on these trees. Our results show that *B. papyrifera* is a slow growing tree species. Based on our age-diameter relationship model, it takes about 73 (±17, prediction interval) years for *B. papyrifera* with average growth to reach the suggested 20 cm minimum diameter. This age is additional to the “waiting under the ground” stage (Birhane et al., 2012) of which the time period is still unknown for *B. papyrifera*. An earlier study suggested a possible reduction of frankincense yield by 50% in 15 years and a 90% decline in number of trees in 50 years (Groenendijk et al., 2012). The slow average growth rate of *B. papyrifera* that led to an average of 73 years to reach minimum tapping size strongly indicates that frankincense production may strongly decrease even if seedling to sapling transitions would occur as from today.

Conclusion

The lack of successful recruitment of *B. papyrifera* found in this study is not a local phenomenon. Absence of smaller sized *B. papyrifera* trees has been reported for another 12 populations in our study area (Eshete et al., 2011) as well as for populations from other sites in Northern Ethiopia (Gebrehiwot et al., 2003; Negussie et al., 2008), Eritrea (Ogbazghi et al., 2006b) and Sudan (Abtew et al., 2012). Also other frankincense producing trees of the same genus from Oman (Farah, 2008), Yemen (Attorre et al., 2011) and India (Sunnichan et al., 2005) suffer from absence of recruitment. In all cases, this has been attributed to a complex of disturbance factors, including land conversion, overgrazing, trampling by livestock and frequent fire (Abiyu et al., 2010; Abtew et al., 2012; Gebrehiwot et al., 2003; Groenendijk et al., 2012; Ogbazghi et al., 2006b) which potentially leads to extinction of a species (Auld and Keith, 2009; Dufour-Dror, 2007; Haubensak et al., 2009; Keith, 1996; Teich et al., 2005).

In this study we could show that successful recruitment of *B. papyrifera* across the studied regions and countries is not a recent phenomenon but has been hampered already over at least five decades, coinciding with the period when human impact on the landscape started. The continuous presence of humans in the area and the intensive use of *B. papyrifera* forests likely led to drastic changes in soil properties and vegetation composition in these *Combretum* - *Terminalia* woodlands. Restoration of the woodlands and sustainable management of the remaining populations therefore require measures such as protection against anthropogenic disturbances by fire or grazing to promote successful development from seedling to juvenile and subsequent stages (Dufour-Dror, 2007; Spooner and Briggs, 2008; Tsegaye et al., 2009; Wassie et al., 2009).

Chapter 3

Growth dynamics of the Frankincense tree

Motuma Tolera, Frank J. Sterck, Frans Bongers, Aster Gebrekirstos, Ute Sass-Klaassen

Abstract

Frankincense trees (*Boswellia papyrifera*, Burseraceae) grow in dry woodlands of Ethiopia, where they rapidly decrease in numbers due to land-use change, overgrazing, fire, or improper tapping. Tree populations of this species lack successful new recruits since half a century and the remaining older trees face high mortality. The impact of climate change on the remaining populations is unknown, but might be considerable as for trees of other dry tropical forests. In this study, we sampled stem discs from eight trees and increment cores of 100 trees from North-West Ethiopia and used tree-ring analysis to assess the influence of climate on the radial growth of these trees. Trees synchronized a bi-tri annual cycle in low/high stem growth rates over most of the period covered by site chronology (~1930-2011). The majority of trees shows a synchronous growth depression which lasted for over two decades that coincides with the period when people settled in the area. Radial growth increased with more rainfall and higher maximum temperature, but decreased with increasing minimum temperatures. The positive impact of temperature was attributed to higher irradiation, since higher maximum temperatures coincide with cloudless conditions, and radiation is supposed to be limiting during the wet season. The negative impact of higher minimum temperatures possibly results from high respiration costs. From these results, it remains highly uncertain whether the predicted higher rainfall and higher temperatures will positively or negatively influence the stem growth of these trees in the future.

Key words: *Boswellia papyrifera*, frankincense, disturbance, tree rings, climate-growth relationship, climate change

Introduction

Dryland areas of Ethiopia host a multitude of tree species with high economic and ecological importance (Lemenih and Teketay, 2003; Worku et al., 2011; Abiyu et al., 2010). One of these valuable species is *Boswellia papyrifera* (Burseraceae) which grows in the *Combretum-Terminalia* deciduous woodlands (Friis et al., 2011). This species produces the olio-gum resin, frankincense, which is used in cultural and religious ceremonies and as raw material in several industries worldwide (Lemenih et al., 2003, 2007). Many populations of this species lack recruitment (Groenendijk et al., 2012; Tolera et al., 2013), probably due to overgrazing, fire and improper tapping (Abiyu et al., 2010; Groenendijk et al., 2012; Lemenih et al., 2012; Tolera et al., 2013). It is possible that such disturbances also influence the growth of *B. papyrifera*. Disturbance-related influences can be manifested in radial growth patterns, as synchronous, persistent changes in radial growth (Cook, 1985; Nowacki and Abrams, 1994, 1997; Ruffner and Abrams, 2002, 2003; Baker et al. 2005; Fraver et al. 2005; Rauchfuss and Ziegler, 2011; Rozendaal et al. 2011).

In addition to these human-induced disturbances, climate conditions may directly affect the growth and population dynamics of trees growing in dry forests (Bogino et al., 2009; Scheiter and Higgins, 2009). Variations in rainfall and temperature are expected to influence tree growth, leaf phenology, and survivorship through their impacts on photosynthesis, respiration, and nutrient dynamics (Enquist and Leffler, 2001; Timberlake et al., 2010; Wright, 2010; Chidumayo et al., 2011; Meir and Pennington, 2011; Feeley et al., 2012). However, the level of influence highly depends on local variation in climate in combination with site factors, e.g. soil texture, and nutrient availability. Changes in these site related factors may more strongly determine climate-growth responses than changes in global long-term averages do (Jacoby, 1989; Lo et al., 2010; Timberlake et al., 2010). Accordingly, the response of trees to climate variables is both species and site specific (Enquist and Leffler, 2001; Worbes, 2002; Couralet et al., 2010; Corlett, 2011). Among others, this is the reason why the potential response of tree species from both dry and wet tropical ecosystems to predicted changes in climate is difficult to evaluate (Wright, 2010; Corlett, 2011; Dong et al., 2012).

Effects of different environmental factors, such as climate and disturbances, on radial tree growth can be analysed using dendrochronology (Nowacki and Abrams, 1997; Bräuning et al., 2008; Bogino et al., 2009). Tree-ring research is a tool to generate information on the growth history of a tree population and allows to study climate-growth relationships (Fritts, 1976; Worbes et al., 2002; Lo et al., 2010; Rozendaal and Zuidema, 2011; Zuidema et al., 2012). Earlier, we demonstrated that *B. papyrifera* growing in North-Western part of Ethiopia forms annual growth rings (Tolera et al., 2013). In this study, we first assess if ring-width patterns of different trees can be crossdated to build a reliable chronology, and if so, determine if and how radial growth of *B. papyrifera* in NW Ethiopia is related to past disturbances and climate variables. Second, we discuss how predicted changes in climate variables potentially affect the growth of *B. papyrifera* in the future. Other dendrochronological studies from Ethiopia showed that the growth of three different *Acacia* species and *Balanites aegyptiaca* (Gebrekirstos et al., 2008) and *Juniperus procera* (Sass-Klaassen et al., 2008, Wils et al., 2011) is related to rainfall. Based on coupled seasonality in rainfall patterns and leaf phenology (Mengistu et al., 2012) in the study area, it is hypothesized that the amount of rainfall available during the growing season will mainly determine the annual variation in radial growth of *B. papyrifera* trees, with more rainfall leading to larger growth rings, synchronously in all study trees. It is also expected that higher temperatures during the growing season will negatively affect radial growth owing to higher respiration costs and greater evaporative demands. In addition, we will explore possible long term effects of disturbance on radial growth of *B. papyrifera*.

Material and Methods

Study site

This study is carried out in Lemlem Terara, Metema district, North-Western Ethiopia. *B. papyrifera* is the most abundant species of the *Combretum-Terminalia* woodland that dominates the study area (Eshete et al., 2011). In this open woodland, *B. papyrifera* reaches a median height of 9 m and median diameter of 20 cm; maximum tree height amounts to 12 m (Eshete et al., 2011). The soil in the study area is more fertile, has more clay content (37%) and it is also deeper (~28 cm) as compared to other *B. papyrifera* dominated forest in Northern Ethiopia (Eshete et al., 2011).

Climate data

Climate data covering the period from 1971 to 2008 was acquired from the National Metrological Agency (NMA) of Ethiopia. This data includes average monthly values of rainfall, minimum temperature and maximum temperature. Annual rainfall recorded at Metema ranges from 665 to 1380 mm, with a mean annual rainfall of 965 mm. The study area exhibits a uni-modal rainfall pattern (Fig. 1) with the major rainy season lasting from May/June to September/October. Annual mean minimum and maximum temperatures are 19 °C and 36 °C respectively.

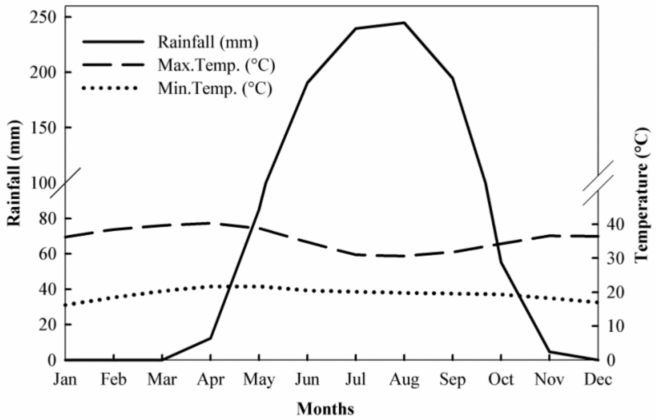

Figure 1. Climate diagram of Metema, North-Western Ethiopia. Monthly averages for the years 1971-1976, 1987-1988, 1995 and 1997-2008 are presented; data for the years 1977-1986, 1989-1994 and 1996 was not available.

The available climate records from Metema are generally short and moreover contain missing values for several months. From the specified period of climate data, only 21 years provide complete data, i.e. 1971 to 1976, 1987 to 1988, 1995 and 1997 to 2008. The option of using an interpolated high-resolution (0.5 degree latitude/longitude) gridded dataset (Mitchell and Jones, 2005; http://climexp.knmi.nl/start.cgi?id=someone@somewhere; http://www.cru.uea.ac.uk/cru/data/hrg) to supplement the fragmentary climate records from Metema was evaluated. However, low correlations between gridded data and the 21 year dataset from Metema prevented us from using the gridded data.

Sample collection

Stem discs were taken from eight trees and increment cores were taken from a total of 100 trees. The stem diameters of sample trees ranged from 10 to 40 cm at breast height (DBH) and covered the diameter range of the whole population in the study area (Eshete et al., 2011). The number of trees selected to collect stem discs was kept to a minimum to limit the damage to the already threatened population of *B. papyrifera.* The study samples were collected from two sites (two plots of 2 ha each from both sites) located at 5 km distance from each other. The sampling was done in three campaigns: first, discs were collected from eight trees at 1 m above the ground from one of the two sites in January, 2010. In April and October, 2011, 100 increment core samples were collected, equally distributed over the four plots. These plots were part of an earlier study on the population dynamics of this species (Eshete, 2011). Trees with straight stem and without symptoms of damages were sampled to minimize the effect of reaction wood and wounds on the ring-width patterns. Two increment cores were collected per tree from opposite directions at c. 0.4 to 0.5 m above the ground.

Sample preparation

The sample discs and increment cores were air-dried at the wood-science laboratory of Wondo Genet College of Forestry and Natural Resources, Ethiopia. The transversal sections of the discs were sanded with progressively finer (600-1200 grit) sand paper to improve the visibility of growth-ring boundaries. Increment cores were prepared using a core-microtome (Gärtner and Nievergelt, 2010) and also sanded with the finer sand papers when needed to enhance the visibility of growth-ring boundaries.

Growth-ring measurement and crossdating

Wood-anatomical features that depict growth-ring boundaries were studied on micro-thin sections (Schweingruber et al., 2006; Worbes and Fichtler, 2010). Growth-ring detection was started on the eight stem discs where single ring boundaries were detected by following concentric features around the stem circumference. When all rings on a disc were detected and ring numbers and characteristics matched along different radii, ring width was measured along four radii of each stem disc. In cases of increment cores, rings were marked, visually compared between the two cores and then measured. Ring width was measured to the nearest 0.001 mm under a LEICA MS 5 microscope coupled with LINTAB $^{\text{TM}}$5 digital measuring stage associated to TSAP-dos software (Rinn, 2003). Growth-ring series were visually crossdated along each radius of the stem discs to check for possible missing and false rings. In case of mismatches, rings in the respective problematic period were again checked. On both, stem discs and increment cores, we used presence of pointer years, e.g. the position of very narrow or very wide rings to link rings detected on different radii or on the two cores. In addition to visual crossdating, all ring-width series were statistically crossdated using TSAP software. Two statistical indicators were taken to evaluate the match between two time series: the ‘‘Gleichläufigkeitskoeffizient’’ (GLK, resembling the percentage of parallel run, Eckstein and Bauch 1969, Schweingruber, 1988) which reflects the percentage of oscillations in the same direction in two time series within a certain period and the “t-value BP” of Baillie-Pilcher (Baillie and Pilcher, 1973). In cases of significant relationships indicated by significant GLK ($p < 0.001$) and t-values (above 4), mean ring-width series per tree were calculated. The same procedure was used to crossdate all mean ring-width series (e. g. Enquist and Leffler, 2001) for building a site chronology. Measured and crossdated ring-width series from discs were used as bench marks to correctly crossdate the core samples. Samples that fail to crossdate through these stages were excluded from the subsequent analysis. COFECHA software (Holmes, 1983) was used to validate the statistical and visual crossdating performed using TSAP. Running correlation was calculated using COFECHA in time-windows of 32 years with overlaps of 16 years in consecutive windows (Grissino-Mayer, 2001). Time-series with lower correlation values than the critical threshold provided by COFECHA were re-examined, taking into account the recommendations on potentially missing or double rings provided by the program. Samples that failed to get fixed through this procedure were also excluded from the dataset before calculation of the site chronology. Statistical attributes of the time series, such as mean ring width, standard deviation, mean sensitivity, autocorrelation as well as correlation of each series with the master chronology are calculated to describe basic patterns and the common variance in the time series considered for this study.

Cluster analyses to group trees according to decadal variation

To identify similar low frequency (decadal) variation in the collective of ring-width series, hierarchical clustering analysis (Ward’s method, IBM SPSS statistics 20) was used to classify the sample trees based on their growth trend. Due to the restrictions in data structure for this analysis, (within the same window of growing period) radial growth of only 52 trees covering the period from 1942 to 2009 were included in this analysis.

Analyses of climate-growth relationship

Before calculating the climate-growth relationship, individual growth-ring series were standardized using ARSTAN software (Cook, 1985) to remove possible ontogenetic trends and low-frequency variation, standardize the variance and maximize the annual variation. To do so, a cubic spline (wavelength of 32 year with 50% cut off, Cook, 1985) was fitted to each raw mean ring-width series. By dividing the original data by the spline curve, a stationary index series (mean=1 and homogenous variance) was calculated.

A general linear model was calculated with the index series of all individual trees as response variable. We added trees as random factor to account for local effects and for individual tree properties, and the different climate variables as explanatory variables. The analysis was done using climate data from 21-years. The climate variables used for the analysis were average monthly values of rainfall, minimum temperature and maximum temperature. The relationships were independently tested for the climate variables in a year (annual), and in the wet season from June to September (JJAS), at the beginning and end of wet season. Only the period that showed the highest relationship was shown in the result. The analysis was done with standardized values of the climate variables. Previous-year growth (year *n-1*) was included in this analysis to account for the visual observation of the occurrence of a bi/tri annual growth cycle. The analysis was done using IBM SPSS statistics 20.

A site chronology, calculated from all crossdated index series (ARSTAN, Cook 1985), was used for visual comparison with time series of climate variables which turned out to have highly significant influences during the analysis. The potential effect of climate change is discussed using predictions made by Tadege (2007) until the year 2080 (spatial resolution of 5° latitude x 5° longitude) based on the mid-range (A1B) CO_2 emission scenario (IPCC, 2007).

Results

Crossdating

Ring-width series of different radii sampled from the same tree synchronized successfully (GLK >85%, $p < 0.001$; t-values >4). Cross-dating of mean ring-width series of different trees was challenging since the trees differed in long-term growth trends (Fig. 3A and B) and varied in distinctness of growth-ring boundaries with increasing size and age. Moreover, other chronologies which could be used for checking the reliability of our chronology were lacking. Missing rings and wedging rings frequently occurred and were more often encountered in trees with longer periods of slow growth (e.g. 1970-1990 in Fig. 3B). Finally, mean ring-width series of 75% of the sample collective correlated significantly with each other (Pearson correlation, $r > 0.41$). Trees from the two sites show no obvious differences in ring-width patterns and we found no indication that trees from the same site show higher correlations than trees from different sites (data not shown). Therefore one site chronology was calculated from all 81 crossdated ring-width series covering a 99-year period from 1913 to 2011 (Fig. 2A). The site chronology is well replicated over a longer period of time (e.g. >40 samples from 1937 to 2010, Fig. 2B). The raw ring-width series showed a high average mean sensitivity, high standard deviation and low average autocorrelation (Table 1), which implies that the growth of the *B. papyrifera* trees is affected by an external environmental factor which induces similar annual variation in the ring-width series of all sample trees.

Table 1. Mean statistical attributes of raw crossdated ring-width series of *B. papyrifera*, Metema, North-Western Ethiopia; t-value BP=t-value Baillie Pilcher, GLK= Gleichläufigkeitskoeffizient (see text)

Variables	Averages (or ranges)
Number of trees	81
Average stem diameter [cm] (range)	23 (10-40)
Average age [years] (range)	73 (43-99)
Time span [years]	1913-2011
Average ring width [mm] (± SD)	1.14 (0.49)
Average correlation with master	0.62
1^{st} order autocorrelation (unfiltered)	0.22
Mean sensitivity	0.41
Standard deviation (filtered)	0.55
Flagged segments [%]	4
t-value BP (± SD)	10 (±2),
GLK (±SD, %)	93 (±3)

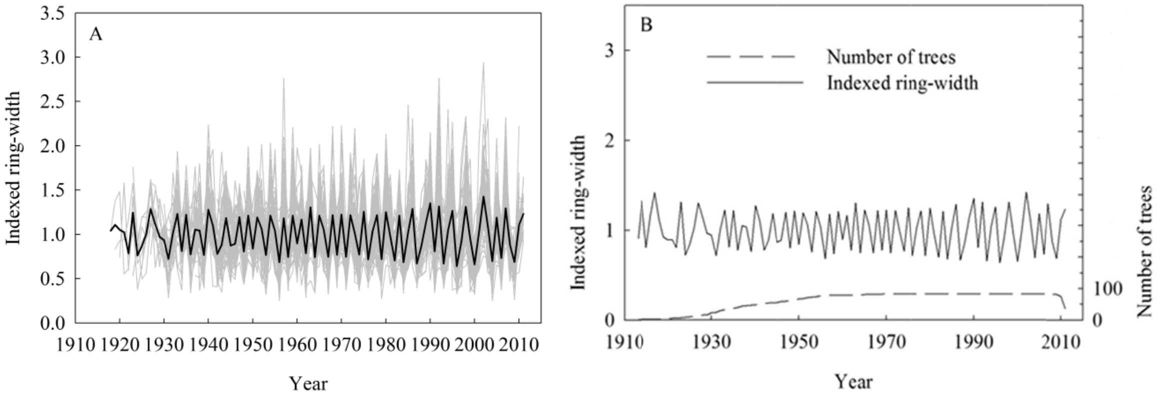

Figure 2. Indexed series of crossdated *B. papyrifera* trees from North-Western Ethiopia. Indexed ring-width series of 81 trees with superimposed site chronology (darker, A) and the site chronology with sampling depth (number of trees) at each year (B).

Decadal variation in radial growth

Trees differed in long-term radial growth variation. Using cluster analysis, three groups of trees were identified (Fig. 3). Most trees of the clusters A and B (Fig. 3) decreased their stem growth over the first 60 years (~1930-1990) and increased stem growth during the recent two decades (1990-2010). The first group of trees (Fig. 3A) shows high annual variability and has the highest average annual growth rate (1.46 mm, s.d. = 0.15, *n* = 12 trees). Trees of the second group (Fig. 3B) showed a similar decreasing and increasing trend with the first group of trees but had a lower average and less variable radial growth (0.99 mm, s.d. = 0.14, *n* = 25 trees). Trees of the third group showed a relatively constant slow growth rate until 1990, but later their growth also increased (Fig. 3C). Their average radial growth was 1.16 mm (s.d. = 0.115, *n* = 15 trees). These synchronized long term radial growth trends were independent of tree age, tree size, and site.

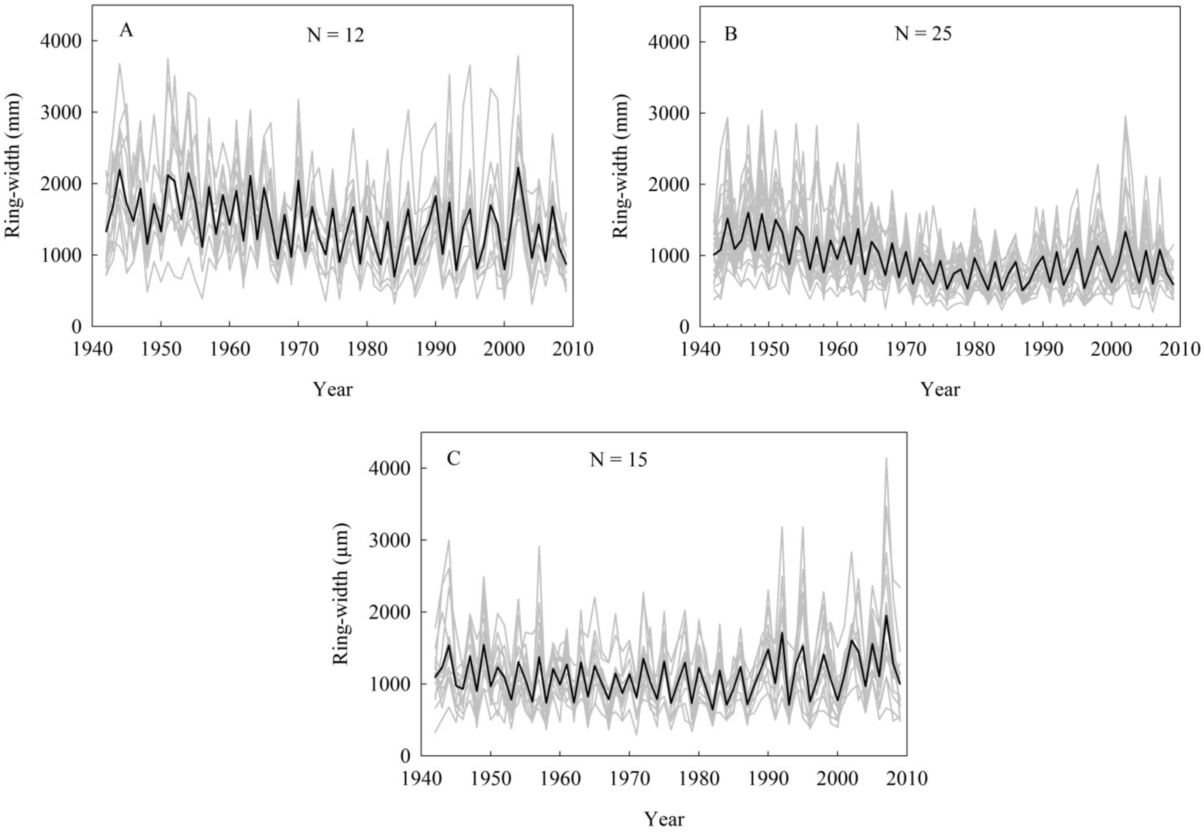

Figure 3. Decadal variation in radial growth of *B. papyrifera* trees from two sites in Metema, North-Western Ethiopia. A, B and C show clusters of trees with similar radial growth pattern. Grey lines represent ring-width series of individual trees, black lines represent associated chronologies. Clustering was restricted to the common period covered by a maximum of series between 1942 and 2009.

Bi/tri annual growth cyclicity in radial growth

A bi/tri year cycle in radial growth was observed for the 81 crossdated index series (Fig. 2), and also for trees of all three clusters (Fig. 3), and was maintained over the whole period of ~80 years (from 1930 to 2011, Fig. 2). About 29 peaks were counted between the year 1930 and 2011 showing that the pattern is dominated by a three year cycle. This remarkable cyclicity of growth gets more pronounced with increasing sample depth (Fig. 2B).

Climate-growth relationship

From all periods of analysis, climate during the wet season showed the highest significant relationship with indexed ring-width. All climate variables of the wet season were significantly related with radial growth ($P < 0.01$, Fig. 4). Radial growth increased with higher maximum temperature (T_{max}) and more rainfall, but decreased with higher minimum temperature (T_{min}) of the wet season. Rainfall during the wet season had the highest positive influence on radial growth (Fig. 4), which also becomes obvious from a visual comparison between this climate variable and average indexed radial growth (Fig. 5). However, it also became obvious that the effect of previous year growth (year *n–1)* on the actual growth is high (Fig. 4).

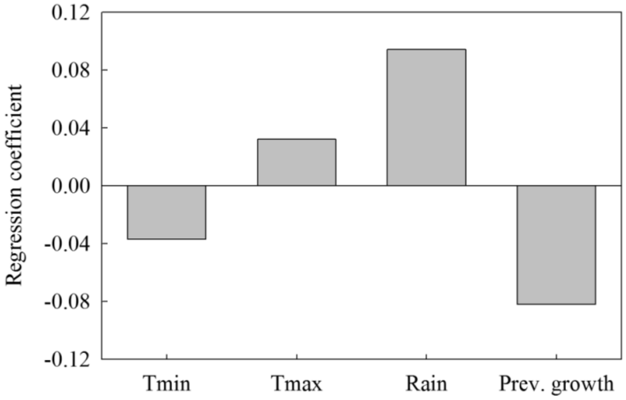

Figure 4. Relationship between index series and respectively, wet season climate variables and previous year growth (year *n-1*) of *B. papyrifera*, North-Western Ethiopia. All variables are significantly ($P < 0.01$) related to indexed ring-width.

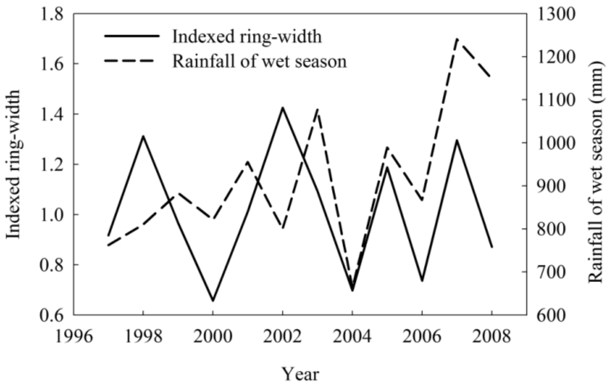

Figure 5. Comparison between site chronology and rainfall during wet season of *B. papyrifera*, North-Western, Ethiopia.

Discussion

In this study, we assessed the radial growth dynamics of *B. papyrifera*, quantified how trees synchronized their growth on an annual and decadal scale, and disentangled influences of different climate factors on radial growth. Trees exhibited a remarkable bi/tri annual cycle of high/slow growth and, moreover, they synchronously had slow growth rates from 1965 to 1990. In addition, rainfall and temperature significantly affected annual stem growth rates, which hints to potential impacts of climate change for this tree species.

Match in annual variation in radial growth patterns

We expected synchronized radial growth patterns, since the climate of the study area is characterized with seasonal changes in rainfall (Fig. 1). Indeed, the results indicate that radial growth patterns of 75% of the sample trees are cross-datable. The ring-width series of the 25% remaining sample trees (27 of 108) did not match with the rest of the collective probably owing to missing rings and wedging rings. Growth-ring detection was challenging for almost all trees due to their slow growth rate and ontogenetic differences in wood-anatomical features that depict growth-ring boundaries (Tolera et al., 2013). Combining different anatomical features (e.g. vessel density, Tolera et al., 2013) to locate growth-ring boundaries was difficult, particularly in very narrow rings. The problems of missing and wedging rings has been reported for other species from Ethiopia (Eshete and Ståhl, 1999; Gebrekirstos et al., 2008; Sass-Klaassen et al., 2008; Wils et al., 2009; Wils et al; 2011) and tropical and subtropical species from elsewhere (Worbes 2002; Cherubini et al. 2003; Verheyden et al., 2004; Brienen and Zuidema, 2005; Couralet et al., 2010; Rozendaal and Zuidema, 2011). Like in this study, missing and wedging rings have commonly been encountered in trees with very slow radial growth rate (e.g. Verheyden et al., 2004), and wedging rings have been attributed to low resource levels (Worbes, 2002). For *B. papyrifera,* some trees showed persistently slow growth throughout their life (Fig. 3B; Tolera et al., 2013) which may be related to locally poor growing conditions, or genetic constraints (Brienen and Zuidema, 2007; Mushove et al., 1995; Stahle et al., 1999). In addition, disturbances by fire, tapping and grazing, may further reduce growth rates in these trees (Abiyu et al., 2006, 2010; Lemenih et al., 2011, 2012; Eshete et al., 2012; Groenendijk et al., 2012). As mentioned by others (Worbes, 2002; Brienen and Zuidema, 2005; Sass-Klaassen et al., 2008; de Ridder et al., 2013), we emphasize that including stem discs allowed for identifying missing and wedging rings and for synchronizing chronologies amongst a large majority of trees.

Radial growth pattern

In this study, we observed two striking radial growth patterns over time; (1) the sample trees showed differences in decadal radial growth (Fig. 3), and (2) the site chronology revealed a bi/tri-annual pattern in radial growth of *B. papyrifera* (Fig. 2). Concerning long-term decadal radial growth, a common trend to all trees is the increased level of growth over the last 20 years. This period of “growth release” was preceded by a long-term growth depression in many trees for more than two decades (1965-1990). We speculate that this long-term growth depression, which is independent of age, size and site, resulted from a high intensity of disturbances, which started around the early 1960ies (Eshete et al., 2005; Lemenih et al., 2011, 2012; Woldeamanuel, 2011).

In an earlier study, Tolera et al. (2013) suggest that grazing and fire caused poor recruitment of *B. papyrifera* since 1955 until present. The growth depression from 1965-1990 started few years after successful recruitment had stopped (Fig. 6), when people with cattle entered the area (between 1949 and 1958, Tegegne et al., 2009), trees were tapped for frankincense in the 1960s (Woldeamanuel, 2011), and fire frequency increased drastically (Lemenih et al., 2012). Fire was used to open-up the woodland for cultivation, to initiate new grasses and to chase wild-animals to reduce the threats to livestock, farmers working in their fields, and also to frankincense tappers (Abiyu et al., 2006, 2010; Lemenih et al., 2012; Lemenih and Kassa, 2011). With increasing settlement, parts of the forest have been cleared (Lemenih et al., 2012), and in the remaining forest trees have been cut continuously for firewood, poles for construction and household furniture. The remaining population also faces higher mortality risks due to disturbances by fire and possibly also by insect attacks (Groenendijk et al., 2012). The continuous loss of adult trees might have improved the availability of resources for the remaining trees, likely explaining the growth release after 1990.

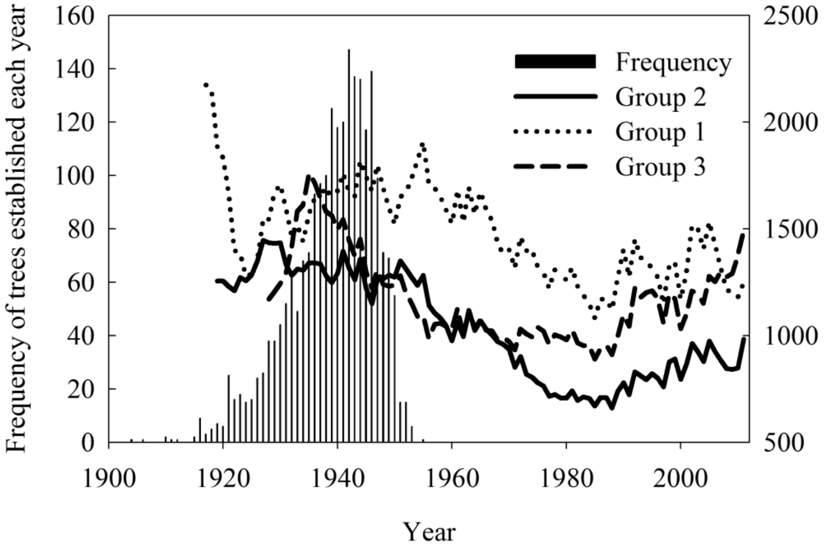

Figure 6. Patterns of radial growth and tree recruitment of *B. papyrifera*, North-West Ethiopia. Tree establishment years were calculated according to Tolera et al. (2013). Radial growth is shown as 5-year moving average of chronologies calculated from clusters as shown in Fig. 3

The second remarkable observation was that the site chronology calculated for *B. papyrifera* shows strong bi/tri annual cycle with alternating years of low and high growth rates. This inherent multiple-year cycle in radial growth plays an important role in determining annual stem-growth variation of the species. The negative correlation between stem growth in current and previous years may be associated with a synchronized allocation to reproduction (Suzuki, 2001; Kelly and Sork, 2002; Miyazaki et al., 2002; Piovesan et al., 2005; Han et al., 2011), which possibly occurred over periods of 2-3 years for *B. papyrifera* (Eshete, personal communication). Investments in reproduction may act as a strong competitive sinks for biomass investments for *B. papyrifera*, and possibly alternate with biomass investments in high stem growth but we lack sufficient observations to support this speculation with data.

Climate impacts on radial growth

As expected, trees increased their stem growth with increasing rain during the wet season. Similar trends have been reported for other species from Ethiopia (e.g. Gebrekiristos et al., 2008; Sass-Klaassen et al., 2008) and other tropical areas (Brienen and Zuidema 2005; Schöngart et al., 2006; Enquist and Leffler, 2001; Worbes, 1999; Couralet et al. 2010; Volland-Voigt et al., 2011). The response in radial growth to increased rainfall was sometimes attributed to more rain at the start or end of the wet season (Brienen and Zuidema, 2005; Couralet et al., 2010), or just more rain during the wet season (Gebrekirstos et al., 2008). The strong positive effect of rainfall during the wet season for the studied *B. papyrifera* trees suggests that rainfall intensity during the wet season is important.

Stem growth decreased with higher minimum temperatures. This result is consistent with some studies of wet tropical forests, where growth rates were also negatively related to, and best explained by, minimum temperatures (e.g. Clark et al., 2003). Since the minimum temperatures are recorded in the night, higher minimum temperatures may best reflect higher respiration costs, which may reduce the carbon that is available for radial growth. Indeed, maintenance respiration costs are considered one of the most carbon demanding sinks in *B. papyrifera* trees (Mengistu et al. 2012). These results imply that increased respiration loads with warming, as expected with on-going climate change, will negatively affect stem growth of these trees.

We expected that higher maximum temperatures will lead to higher evaporative demands and drier soils, which in turn may cause slower radial growth. Contrary to this expectation, stem growth increased with higher maximum temperatures. Rainfall and maximum temperature had additive positive effects on growth even though they are negatively correlated (Pearson correlation, $r = -0.560$, $p < 0.01$), which implies that the maximum temperature effects are not explained by moisture (e.g. Buckley et al., 2007). Since high maximum temperature is associated with less cloudy days, they imply higher irradiation during the wet season, which may release radial growth rate under light limiting growth conditions. Indeed, such light limitations have been proposed for *B. papyrifera* trees during the wet season in this area (Mengistu et al., 2012). Likewise, radiation had positive impacts on stem growth for *Pinus merkusii* from Lao PDR (Buckley et al., 2007), and for various species of wet tropical forests (Clark and Clark, 1994).

Conclusions

The result of this study shows that radial growth of *B. papyrifera* is related to both temperature and rainfall. Based on a mid-range CO_2 emission scenario (A1B, IPCC, 2007), annual rainfall and average annual temperature of the study site are expected to increase by 7.4% (71.4 mm) and 3.4% (1.2 °C) respectively by the year 2080 (Tadege, 2007). It is also indicated that minimum temperature is increasing all over the country by 0.37 °C per decade. This implies that the growth of *B. papyrifera* may benefit from the expected increase in annual rainfall and average temperature, but reduce with increasing minimum temperatures. It is far from clear whether the benefits from extra carbon gains with increasing temperature and rainfall will outweigh the additional respiration costs with increasing minimum temperature (Cunningham and Read, 2003; Lloyd and Farquhar, 2008; Lewis et al., 2009; Feeley et al., 2012). Moreover, for *B. papyrifera*, we showed that radial growth is probably affected by disturbances, such as fire and grazing regime, which may interact with climate change impacts. Management focussing on reducing such disturbances would not only contribute to the radial growth of trees, but also to successful regeneration (Groenendijk et al. 2012; Tolera et al., 2013), and thus seems essential for maintaining *B. papyrifera* for the future.

Chapter 4

Resin secretory structures of **Boswellia papyrifera** *and implications for frankincense yield*

Motuma Tolera, David Menger, Ute Sass-Klaassen, Frank Sterck, Paul Copini, Frans Bongers

(Published in Annals of Botany 111,1-8 (2013))

Abstract

Frankincense, a gum-resin, has been tapped from *Boswellia papyrifera* trees for centuries. Despite the intensive tapping and economic interest of *B. papyrifera*, information on the resin secretory structures, which are responsible for synthesis, storage and transport of frankincense, is virtually absent. This study describes the type, architecture and distribution of resin secretory structures of *B. papyrifera* and its relevance for the ecophysiology and economic use of the tree. The type and architecture of resin secretory structures present in bark and wood was investigated from transversal, tangential and radial sections of bark and wood samples. The diameter and density (number of resin canals mm^{-2}) of axial resin canals were determined from digital images of thin sections across the different zones of inner bark. Resin canals form a three-dimensional network within the inner bark. Yet, the intact resin-conducting and producing network is on average limited to the inner 6.6 mm of the inner bark. Within the inner bark, the density of non-lignified axial resin canals decreases and the density of lignified resin canals increases from the vascular cambium towards the outer bark. In the wood, only radial resin canals were encountered. Frankincense tapping techniques can be improved based on knowledge on bark anatomy and distribution and architecture of resin secretory structures. The suggested new techniques will contribute to a more sustainable frankincense production that enhances the contribution of frankincense to rural livelihoods and the national economy.

Key words: *Boswellia papyrifera, Frankincense, Resin secretory structures, Resin canal, Tapping.*

Introduction

Resin is considered to be the most versatile material in the pre-industrial world (Langenheim, 2003). Resins from *Boswellia* and *Commiphora* species (respectively known as frankincense and myrrh) were traded as incenses from the southern coast of Arabia to the Mediterranean region and Mesopotamia for more than a millennium (Groom, 1981; Gebrehiwot et al., 2003; Langenheim, 2003). Their historical value is illustrated by the gifts of the three kings (frankincense, myrrh and gold) to Jesus Christ (Matthew, 2:11). Currently the main international trade is from *Boswellia papyrifera* and Ethiopia is the main exporting country (Coppen, 2005). The use of frankincense for ritual purpose in Ethiopia dates back to the Aksumite Empire, c. 500 BC (Goldschmidt, 1970). The current commercial harvest of frankincense from this species provides an important export item and is a source of income for rural households in northern Ethiopia (Gebrehiwot et al., 2003; Lemenih and Teketay, 2003; Tadesse et al., 2007; Lemenih et al., 2007). In some areas collection of resin is economically a more attractive land use than crop production and accounts for the majority of income of rural households (Tilahun et al., 2007; Woldeamanuel, 2011; Dejene et al., 2012). Modern uses of frankincense include church ceremonies, perfume and medicine production (Gebrehiwot et al., 2003; Lemenih and Teketay, 2003).

Frankincense is produced by wounding the bark of *B. papyrifera* trees and collecting the resin that is subsequently released from the wound. This tapping practice is carried out at several spots along the stem, using a traditional type of axe. This procedure is repeated in 8 to 12 tapping rounds during the dry season which lasts about 8 months. The wound initially has a surface area of about 2.5 cm^2 and a depth of about 1 mm (Tadesse et al., 2004). At each tapping round, the hardened resin is removed and the tapping wound is re-opened and enlarged. The number of tapping spots on each tree depends on the diameter of the tree. In the past, trees were tapped with 6-12 tapping spots around the stem (Ogbazghi, 2001; Gebrehiwot et al., 2003). Currently, due to the high demand for frankincense, up to 27 tapping spots are made per tree in some commercial sites (Kebede, 2010). Frankincense yield per tree levels off after 9 tapping spots (Eshete et al., 2012a). Frankincense yield per tree per season varies between 41 and 3000 g depending on tree size, site productivity and season, and the yield increases during the earlier tapping rounds after which it levels-off and ultimately decreases towards the end of the dry season (Eshete et al., 2012a; Tilahun et al., 2011).

Extraction of resin through tapping likely affects carbohydrate allocation in trees as it enhances the competition for assimilates (Herms and Mattson, 1992; Rijkers et al., 2006; Silpi et al., 2007; Mengistu, 2011; Mengistu et al., 2012). Resin extraction also induces mechanical damage to the trees (Herms and Mattson, 1992). Silpi et al. (2006), found 80% reduction in radial growth in tapped trees compared with untapped trees in rubber wood (*Hevea brasiliensis*). Higher mortality of tapped adult trees was also reported for black dammar (*Canarium strictum*) by Varghese and Ticktin (2008). For *B. papyrifera,* tapping reduced reproductive effort and seed size (Rijkers et al., 2006): tapped trees produced less flowers, fruits and seeds than non-tapped trees and germination success of the seeds from non-tapped trees was much higher than from tapped trees (Eshete et al., 2012b). Tapping also reduced foliage production, annual carbon gain and carbon stock of *B. papyrifera* trees (Mengistu, 2011; Mengistu et al., 2012). Such negative effects could, at least partly, explain the recent lack of regeneration observed for *B. papyrifera* populations in northern Ethiopia (Lemenih et al., 2007; Nigussie et al., 2008; Abiyu et al., 2010; Groenendijk et al., 2012).

Resin is produced by trees to protect against potential damage from abiotic or biotic stress (Lewinsohn et al., 1990; Langenheim, 1995; Trapp and Croteau, 2001; Baier et al., 2002; Pickard, 2008). Depending on the type of species, resin may be accumulated in resin canals or resin pockets (blisters) (Nagy et al., 2000; Langenheim, 2003) in the wood and/or the bark (Fahn, 1988; Nussinovitch, 2010). In some species tangential rows of traumatic resin canals are induced after wounding (Berryman, 1972; Fahn, 1979; Nagy et al., 2000; Martin et al., 2002). Resin canals (axial or radial) are elongated extracellular structures, which enable long-distance resin transport, while resin pockets are rounded intracellular isolated tissues with limited potential for resin transport (Langenheim, 2003). Resin secretory structures are formed by schizogeny or lysigeny. Lysigeny refers to the process of cell disintegration that occurs when new structures are differentiated with or without cell separation while schizogeny refers to formation of space by pulling apart of cells (Nair and Subrahmanyam, 1998; Pickard, 2008). In both cases, resin is produced by secretory cells known as ‘epithelium’ (Esau, 1965; Fahn, 1979; Wiedenhoeft and Miller, 2002; Kolalite et al., 2003) which surrounds resin canals or resin pockets (Nair and Subrahmanyam, 1998; Wiedenhoeft and Miller, 2002; Langenheim, 2003). In some plants, the epithelial cells may become thick-walled and lignified and becomes non-functional, while in others these cells remain thin-walled, unlignified and functional for longer periods of time (Bannan, 1936; Langenheim, 2003).

Despite the intensive tapping and economic interest in frankincense production, information on the resin secretory structures of *B. papyrifera* is absent. This is the first study that both describes and quantifies the resin secretory structures in the bark of frankincense trees of *B. papyrifera*. After a bark incision a copious amount of white incense was immediately oozing out. Hence, we expect that the resin secretory structures of *B. papyrifera* are abundant in the bark rather than in the xylem. We also hypothesized that density of axial resin canals show directional changes throughout the bark due to dilatation (Junikka, 1994; Kolalite et al., 2003). Tadesse and coworkers (2004) indicated high variations in frankincense yield among trees of the same size classes. Studies indicate that the most important resin canal trait that determines resin yield for Norway spruce and pine trees is the diameter of resin canals (Baier et al., 2002). This leads to the expectation that diameter of resin canals in *B. papyrifera* varies among trees of the same size. This information is crucial to understand resin yield and will help to formulate recommendations for developing a more sustainable tapping regime.

Materials and Methods

Study species

B. papyrifera produces the widely traded white incense and is distributed in Ethiopia, Eritrea, Nigeria, Cameroon, Central African Republic, Sudan, Chad, and North East Uganda (Vollesen, 1989). In Ethiopia, *B. papyrifera* grows in dry *Combretum-Terminalia* woodlands and wooded grasslands in the north (Bekele et al., 1993). It is a deciduous tree that usually dominates on steep and rocky slopes, lava flows or sandy valleys and grows to a height of about 12 m (Vollesen, 1989; Bekele et al., 1993).

Study site

The study area is located near the village of Lemlem Terara, Metema district, northern Ethiopia (12°39´ to 12°45´ N, 36°17´ to 36°23´ E). The samples were collected from trees growing in open woodland located at 870 m a.s.l. Based on data from National Meteorological Agency of Ethiopia, for the period of 1971 to 2009, annual rainfall in Metema ranges from 665 to 1380 mm, with a mean annual rainfall of 960 mm. The major rainy season in the site is from June to September. The mean annual maximum and minimum temperatures are 36 °C and 19 °C respectively. The study site is dominated by clay soil and its average soil depth is 27.7 cm (Eshete et al., 2011).

Study trees, sampling, and sample preparation

The field data collection was done in February 2010, in the middle of the dry season. Twenty healthy looking, adult trees of about 10 m height with a straight stem and diameter at breast height (DBH) between 20 and 25 cm were selected from the same site in Metema. Trees without traces of recent tapping were selected. Non-tapped trees were used since the objective of this study is to describe the basic structure of resin secretory structures of the species. One bark sample per tree was collected from the eastern side at breast height (1.3 m above the ground) using a Trephor (Rossi et al., 2006) of 140 mm in length and 5 mm in diameter.

All samples were stored and transported in plastic tubes filled with a 70% ethanol solution to avoid fungal infestation. At the lab, transversal, radial and tangential micro-thin sections (50 µm) were prepared with a sliding microtome (type G.S.L.1 light weight microtome). The transversal sections were prepared from all 20 samples while radial and tangential thin sections were prepared from a subset of five samples. The thin sections were stained with a mixture of Astra-blue and Safranin for 3-5 minutes to discriminate lignified (red) from unlignified (blue) tissues (Schweingruber et al., 2006). The stained thin sections were rinsed with demineralized water and dehydrated with a graded series of Ethanol (50%, 96% and 100%). Then, for permanent fixation, the sections were rinsed with xylol and embedded in Canada Balsam and dried at 60 °C for 12 hours in the oven.

Bark and resin secretory structures

The micro-thin sections were inspected under a light microscope (Leica DM 2500), with a magnification ranging from 12.5 times to 400 times. Digital images of the secretory structures present in wood and bark of *B. papyrifera* were made from transversal, tangential and radial sections using a Leica camera (DFC 320) attached to the light microscope.

The bark is described using the terminology of Trockenbrodt (1990) and Junikka (1994). For the purpose of this study, we classified the inner bark into three zones (Fig. 1b; Fig. 2a, b, c). The first zone (called intact zone) represents part of the inner bark that is not affected by dilatation and it is found close to the vascular cambium (Fig. 2a). The remaining part of the inner bark which is affected by dilatation is divided into partially dilatated and highly dilatated zones to account for the observed structural variation. The partially dilatated zone (Fig. 2b) is an area adjacent to the intact zone and is less affected by dilatation and has a higher proportion of remnant sclerenchymatic tissues than the highly dilatated zone. The highly dilatated zone (Fig. 2c) is largely dominated by parenchyma.

Data analysis

For the 20 study trees, the diameter of all axial resin canals as well as the density (number of resin canals per mm^2) of axial resin canals was measured and calculated from digital images across the inner bark. Functional and non-functional resin canals were discriminated according to the presence or absence of lignification of the cell wall of epithelial cells, indicated by red (= lignified) or blue (= non-lignified) color. All axial resin canals which did not lose their original shape during the cutting process of thin sections were measured for their internal lumen diameter. All measurements were conducted using the image analysis software ImageJ (http://rsbweb.nih.gov/ij/) version 1.44p.

To test for differences in density of resin canals across the three zones of the inner bark, one way ANOVA accompanied by Tukey post-hoc multiple comparison was used. Differences in density of lignified axial resin canals across the different zones of the inner bark was tested using Kruskal-Wallis accompanied with Scheffe's post-hoc test. To test for differences in average diameter of axial resin canals among the sample trees, one-way ANOVA was used and to understand the relationship between density and average diameter of axial resin canals, correlation analysis was used.

Results

Bark anatomical structure of B. papyrifera

The bark of the studied *B. papyrifera* trees had an average thickness of 17.2 mm (s.d. = 2.3, Table 1), which is about 15% of the stem radius. It consists of two main layers, the inner bark (17.0 ± 2.3 mm), starting directly after the cambium and the much thinner outer bark (0.2 ± 0.1 mm, Fig. 1b). On the transversal section, the outer bark is seen as one to two layers of multiple cells with thin cell walls. These layers peel off in thin flakes. The inner bark is composed of multiple alternating tangential layers of thick-walled sclerenchyma fibers and thin-walled parenchyma layers (Fig. 1b; Fig. 2). Sieve plates with companion cells were observed in the parenchyma layers. Phloem rays cut through sclerenchyma and parenchyma layers. Close to the cambium, these alternating layers are well-ordered and characterised as intact. However, the order gets disrupted with increasing distance from the cambium due to dilatation. Dilatation results in wedge-like structures, piercing into the inner bark. This leads to three distinct zones (Fig. 2) in the inner bark: an intact, partially dilatated and highly dilatated zone. Phloem rays are abundant in the intact zone but decline in density towards the dilatation zones (Fig. 2).

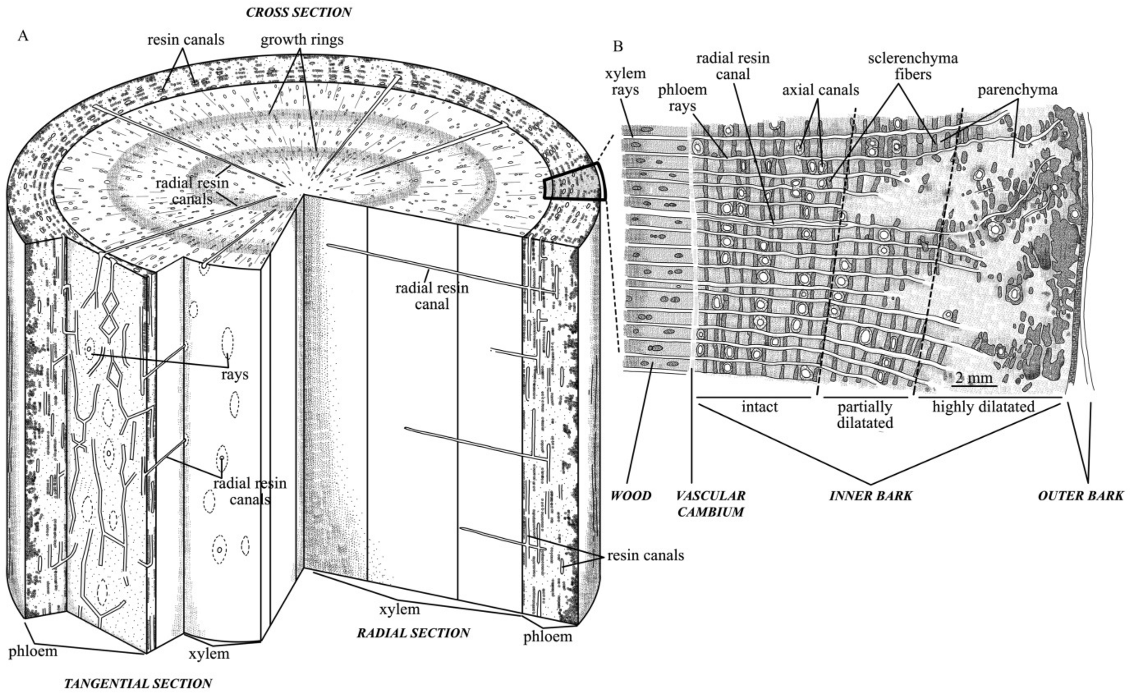

Figure 1. Microscopic view of the bark and resin secretory structures of a *B. papyrifera* tree: (A) three-dimensional view of resin secretory structure in the xylem and bark (re-drawn after Ghosh and Purkayastha, 1960); (B) resin canals and other cell types observed in the bark (note: cell structures of the xylem part are not shown).

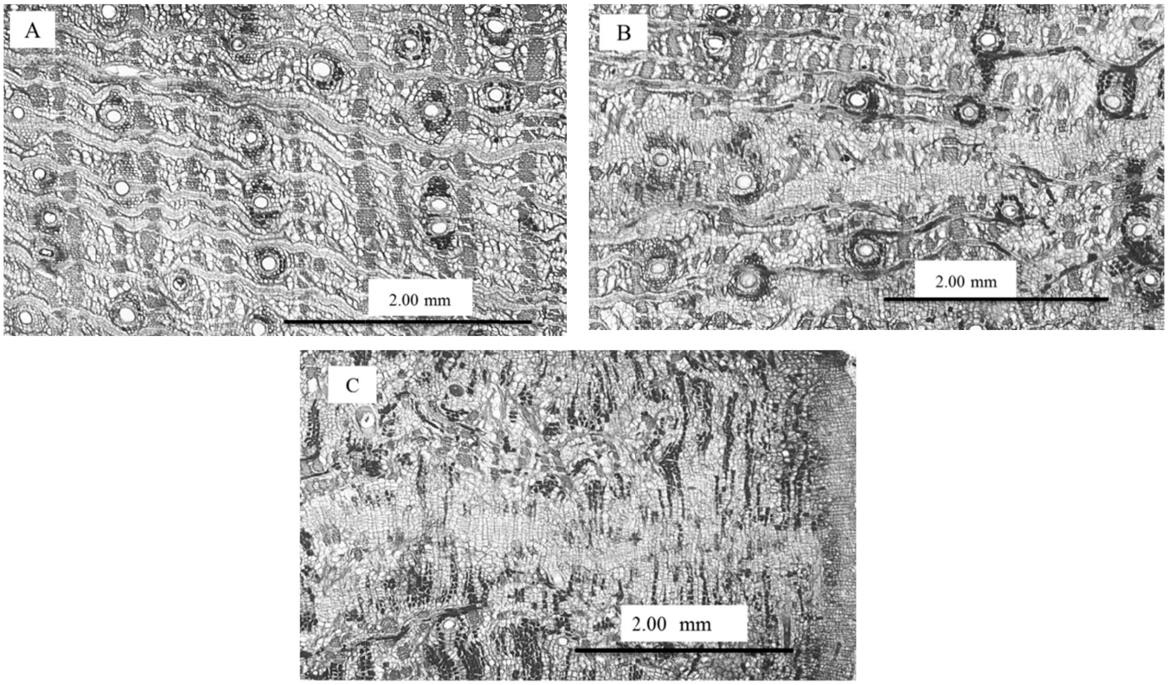

Figure 2. The three zones of inner bark (transversal section) of *B. papyrifera*: (A) the intact zone, (B) the partially dilatated zone and (C) the highly dilatated zone.

Resin secretory structures of B. papyrifera

Resin secretory structures of B. papyrifera occur predominantly in the inner bark as axial and radial resin canals. The wood contains only few radial resin canals, which are embedded in the rays (Fig. 1a, b). These canals continue into the inner bark through phloem rays (Fig. 3a) where they merge into a 3-dimensional network of axial and radial resin canals. No other resin secretory structures such as resin pockets were observed on transversal, radial nor tangential sections of wood and bark samples. On the cross-section, axial resin canals are visible within the multi-layer sheets of axial parenchyma cells arranged in tangential rows (Fig. 2a). Axial canals are much more abundant than radial canals. Both axial and radial resin canals are surrounded with epithelial cells. In the intact zone of the inner bark, epithelial cells around axial resin canals are exclusively non-lignified (Fig. 3c) while epithelial cells around some of the axial resin canals in the dilatated areas are lignified (Fig. 3d).

Tangential sections of the intact zone of the inner bark show that axial resin canals are mutually connected (Fig. 1a). These canals split up and join neighbouring axial resin canals again (anastomosis), thereby forming tangential connections (Fig. 3b). The elongated radial resin canals are connected to multiple axial resin canals (Fig. 1a) completing the three-dimensional network. In the dilatated parts of the inner bark this network gets increasingly disrupted.

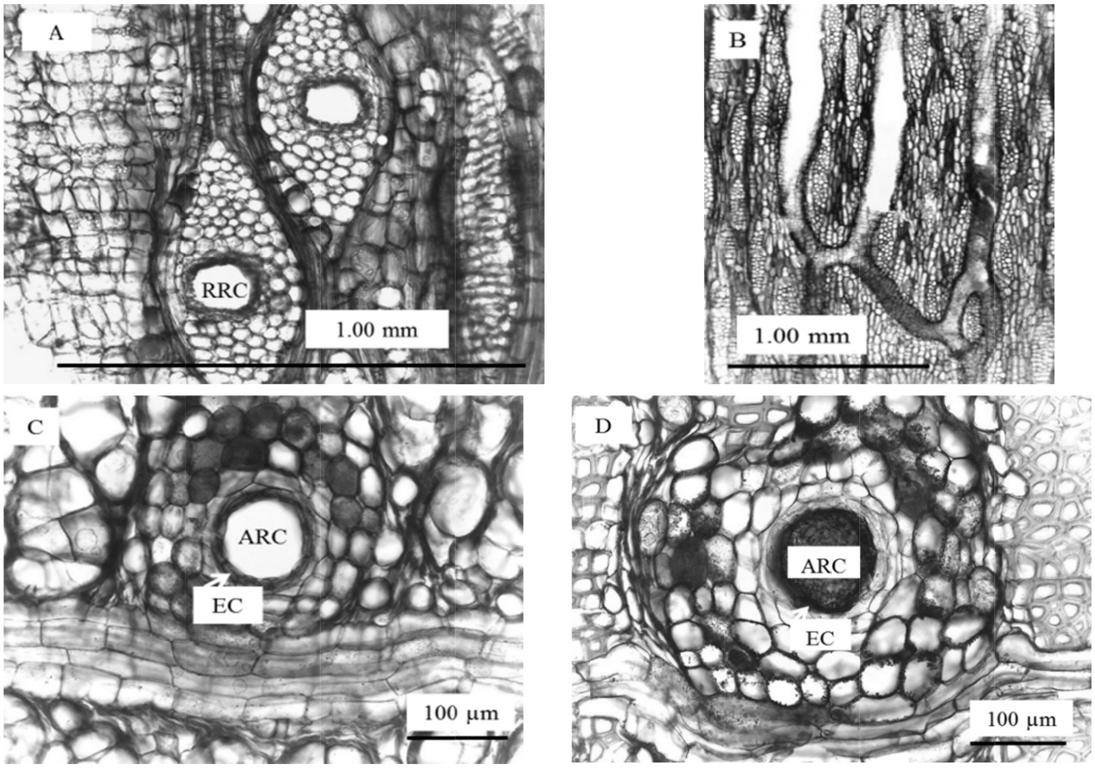

Figure 3. Axial and radial resin canals in the bark of *B. papyrifera*: (A) radial resin canals (RRC) embedded in rays (tangential section); (B) anastomosis of axial resin canals in the inner bark (tangential section); (C) transversal view of axial resin canal (ARC) surrounded by non-lignified epithelial cells (EC, arrow) and other parenchyma cells (indicated by blue stain = living) and (D) axial resin canal (ARC) surrounded by lignified (dead) epithelial cells (EC, arrow) and other parenchyma cells (stained red = dead).

Distribution, density and size of axial resin canals in the inner bark

The intact, the partially dilatated and the highly dilatated zones respectively cover an average of 39%, 28% and 33% of the thickness of the inner bark (Table 1). On average, there are 0.8 axial resin canals per mm^2 (s.d. = 0.2) in the inner bark. However, the density of axial resin canals significantly decreases from the intact towards the highly dilatated zone (Anova, $F_{2, 57} = 14.63$, $P < 0.001$, Fig. 4a, Table 1). Lignified axial resin canals which account for 4% of the average density of axial resin canals exclusively occur in the dilatated zones. The highly dilatated zone contains most lignified resin canals (Kruskal-Wallis, df =2, $\chi^2 = 34.626$, $P < 0.001$, Fig. 4b).

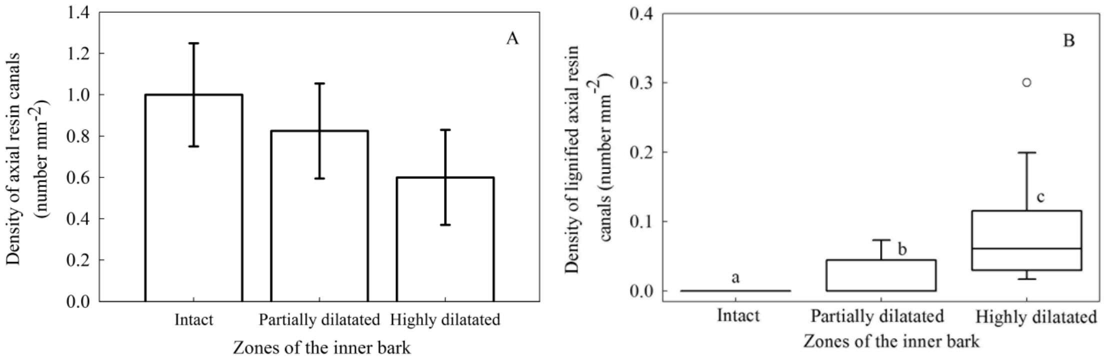

Figure 4. Resin canal density in the three different zones of the inner bark of *B. papyrifera.* (A) Density of all lignified and unlignified axial resin canals (error bars = ± s.d.) and (B) a box plot of density of lignified axial resin canals. The circle above the 'Highly dilatated' box indicates an outlier value. Different letters indicate significant differences, using P <0.05 [Tukey test (A) and Scheffe test (B), n = 20]. Note difference in scales of y-axes.

Table 1. Characteristics of inner bark of *B. papyrifera* trees (N=20) from Metema, Ethiopia. Distinction is made between intact, partially dilatated and highly dilatated parts, encountered in radial direction from vascular cambium to outer bark. All measurements are taken from transversal sections of the bark (SD = standard deviation, Max = Maximum, Min = Minimum).

Zones of the inner bark	Radial thickness (mm)				Density of axial resin canals (number mm^{-2})			
	Mean	s.d.	Min.	Max.	Mean	s.d.	Min.	Max
Intact	6.6	1.8	3.8	10.5	1.0	0.3	0.4	1.5
Partially dilatated	4.7	1.5	2.5	8.3	0.8	0.2	0.4	1.2
Highly dilatated	5.7	2.5	1.2	9.8	0.6	0.2	0.3	1.1
Total inner bark	17.0	2.3	10.8	19.8	0.8	0.2	0.5	1.1

The diameter of all individual axial resin canals measured from 20 trees ranges between 30 and 232 µm with an average of 113 µm (s.d. = 30; n = 1707 axial resin canals). The diameter of resin canals significantly differs between trees (Anova, $F_{19,\ 1687}$= 25.598, P < 0.001). Moreover, the studied trees showed a trade-off between density and average diameter of axial resin canals (Pearson correlation, n = 20, r = -0.625, P < 0.01, Fig. 5).

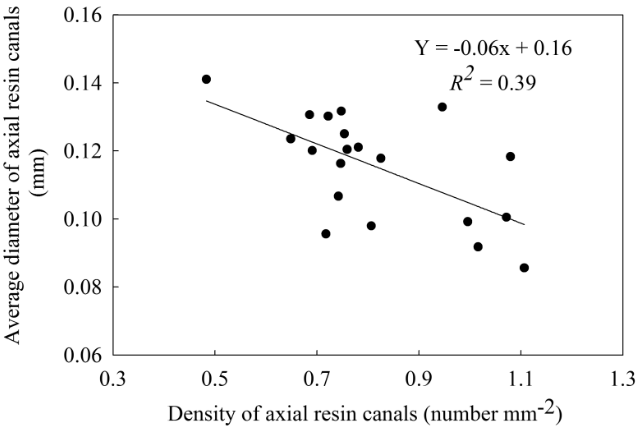

Figure 5. Relationship between resin canal diameter and density in 20 *B. papyrifera* trees. Circles represent individual trees, and the scores represent density (number.mm^{-2}) and average diameter (mm) of axial resin canals for each tree.

Discussion

Resin secretory structures of B. papyrifera

As expected, resin secretory structures of *B. papyrifera* are predominantly found in the bark. Axial and radial resin canals form a three-dimensional network in the intact zone. In this relatively small zone, which accounts for less than half of the thickness of the inner bark, the network of resin canals is most intact and thus most likely functional for short and long-distance resin transport. Radial resin canals connect the canal network of the bark to the wood. This hints to the possibility of radial transport of resin between wood and bark. Previous studies showed similar results for *B. serrata* from India (Ghosh and Purkayastha, 1960) and interconnected canals are also reported for Pinaceae (Bosshard and Hug, 1980; LaPasha and Wheeler, 1990; Lewinsohn et al., 1990) and Araliaceae (Kolalite et al., 2003).

With increasing distance from the cambium, the density of axial resin canals decreases strongly. This decrease is caused by dilatation occurring due to increasing tangential strain as trees grow in circumference (Trockenbrodt, 1990; Kolalite et al., 2003). The dilatation is realized by the production of new parenchyma cells that are formed by phloem parenchyma cells which regain meristematic status (Kolalite et al., 2003; Lev-Yadun, 2011). Resin canals surrounded by lignified epithelium cells occur more frequently within the dilatated zones of the inner bark and can be taken as indicator of non-functionality (Oven and Torell, 1999). Lignification of cells around resin canals is possibly related to the rupture of the secretory system as a consequence of dilatation (Bannan, 1936). However, also without evidence from lignification, it can be assumed that disorder of cells, both in partly and highly dilatated parts of the inner bark will result in disruption of the network of resin secretory structures and disable - at least - long-distant transport of resin in these parts.

Implications for tapping

This study showed that the diameter of resin canals varies among studied trees of the same diameter class. Roosner and Hannup (2004) indicated that resin canal traits are strongly controlled by genetic variations. For spruce and pine the diameter of resin canals is an important resin canal trait which is related to resin yield (Baier et al., 2002). Hence, differences in diameter of resin canals might partly contribute to observed differences in frankincense yield among trees of the same diameter class as described for *B. papyrifera* from our study area (Tadesse et al., 2004; Eshete et al., 2012a).

Previous studies showed that yield of frankincense per tree increases during the first 5-7 tapping rounds and then declines when more tapping rounds are added later in the dry season (Eshete et al., 2012a; Tilahun et al., 2011). In the context of the result from this study this initial increase in resin yield can be related to the fact that in case of successively deeper cuts into the bark, the tapping proceeds into the inner zones with a high density of resin canals and an intact three-dimensional network of functional resin canals. The decline in yield after 7 rounds of tapping (Eshete et al., 2012a) suggests depletion of resin as it is drained through the well-structured network in the intact part of the inner bark. The strong reduction of resin yield towards the end of the tapping season most likely indicates depletion of the trees' carbon stock (Mengistu et al., 2012).

The anastomoses of resin canals facilitate long-distance resin transport and presumably work like a draining system in case of wounding, here specifically tapping. This may lead to a conclusion that larger wounds might not necessarily yield more resin while introducing more stress to the tree as it has to close the wound by production of wound tissue and wood to overgrow the wound (Shigo, 1984; Pearce, 1996). This is supported by results from Tadesse et al. (2004) who showed that enlarging the size of wounds for tapping *B. papyrifera* trees does not pay off in resin yield. Other results showing that resin yield per tree initially increases, then levels off and starts to decline with increasing number of tapping spots (Eshete et al., 2012a; Tilahun et al., 2011) can also be explained by the findings of this study. The decline of resin yield beyond a certain number of tapping spots may occur because wounds drain resin from the same pool.

The presence of interconnected canals (Raffa and Berryman, 1982; Lewinsohn et al., 1990) coupled with our observation of immediate flow of resin from the bark when the tree is wounded indicate that frankincense is present in the secretory system as a preformed resin. Therefore, it could be beneficial to drain all the preformed resin with a first deep cut into the intact part of the inner bark, i.e. to the depth that is usually reached during the tapping round that yields the maximum yield (i.e. 7th tapping round, Eshete et al., 2012a). Although the flow of resin will eventually be blocked by drying frankincense on the wound surface and the wound has to be re-opened to drain all preformed resin, the amount of labour required for production of frankincense could be reduced. This strategy would moreover be less harmful for the tree than initiation of multiple wounds to drain the same pool. The consequences of such one big deeper cut for frankincense yield as well as the related physiological processes require further research. We recommend additional specific experiments on different levels of cutting depths and on optimum distances between tapping wounds based on tree size.From earlier studies, it is evident that tapping increases adult mortality (Varghese and Ticktin, 2008), reduces reproductive effort (Rijkers et al., 2006; Mengistu et al., 2012), reduces growth of trees (Silpi et al., 2006; Mengistu, 2011) and exposes the trees to insect attack (Herms and Mattson, 1992; Abiyu et al., 2010). The current decline in populations of *B. papyrifera* across large areas in Ethiopia (Groenendijk et al., 2012; Eshete, 2011) and Eritrea (Ogbazghi et al., 2006) can partly be attributed to over-tapping (Abiyu et al., 2010; Mengistu, 2011). This indicates that the current tapping strategies need to be improved. One of the strategies under discussion is reducing the number of tapping rounds per season and reducing the number of tapping spots per tree (Abiyu et al., 2010; Eshete et al. 2012a; Mengistu et al., 2012). Our findings on the bark anatomy and distribution and architecture of resin secretory structures of *B. papyrifera* will stimulate new experiments aimed at improving tapping techniques. This contributes to the development of a more sustainable frankincense production that enhances the contribution of frankincense to rural livelihoods and the national economy.

Chapter 5

Frankincense yield is related to tree size and resin-canal characteristics

Motuma Tolera, Ute Sass-Klaassen, Abeje Eshete, Frans Bongers, Frank J. Sterck

Abstract

Boswellia papyrifera Hochst. is an important global source of frankincense. Tree numbers are rapidly decreasing in many populations of *B. papyrifera* in Ethiopia, where most of the internationally traded frankincense comes from. Improper tapping is among the frequently mentioned reasons for this decrease in populations. We still lack sustainable techniques for frankincense tapping, and these techniques are not yet tuned to individual trees since we are unaware how tree characteristics influence frankincense yield. This study investigates the relationships between different tree characteristics and their relation to frankincense yield. We measured DBH, tree age, number of leaf apices, radial growth, bark thickness, total resin-canal area, and total number of resin canals in a cross-section. Regression and path analysis were used to unravel the cause-effect relationships between tree characteristics and frankincense yield. Frankincense yield increased with increasing total resin-canal area in the bark, stem diameter, tree age, and the number of leaf apices, but was independent of the actual radial stem-growth rate. The variation in total resin-canal area was mainly driven by the size of individual canals, but also by resin canal density and bark-cross-section area.We show that frankincense yield by trees is not only a simple function of tree size. Remarkably, trees that grew slower over their whole life history (those that were older for the same given DBH) produced more frankincense, suggesting an intra-specific tradeoff in growth rate and frankincense production. In addition, the positive impacts of leaf apices on yield imply that trees are carbon limited for the frankincense production. Overall, this study thus shows that frankincense production is the result of complex plant trait networks and long term tree life properties.

Keywords: *Boswellia papyrifera*; Frankincense; Path analysis; Resin canals; Tree characteristics.

Introduction

The tree *Boswellia papyrifera* Hochst. is the major source of frankincense. Tree numbers and frankincense production are rapidly decreasing in many populations of this species, in Ethiopia (Negussie et al., 2008; Groenendijk et al., 2012) as well as in Eritrea (Ogbazghi et al., 2006) and Sudan (Abtew et al., 2012). Conversion to agricultural land (Gebrehiwot et al., 2003; Lemenih and Kassa, 2011), frequent fires, overgrazing and insect infestation (Abiyu et al., 2006) are major causes of the decline (Abiyu et al., 2010). In addition, improper tapping is frequently mentioned as one of the reasons for the decline of the populations (Abiyu et al., 2010; Eshete et al., 2012a). From earlier studies, it is evident that tapping for frankincense reduces reproductive effort (Rijkers et al., 2006; Mengistu et al., 2012) and exposes the trees to insect attack (Abiyu et al., 2006; 2010). Seeds from tapped *B. papyrifera* trees also showed lower germination success as compared to seeds from untapped trees (Rijkers et al., 2006; Eshete et al., 2012b). Similar effects of tapping were reported for other tree species (Silpi et al., 2006; 2007; Varghese and Ticktin, 2008; Chantuma et al., 2009). Developing more sustainable tapping strategies that reduce the risk of over-tapping is among the crucially important inputs for planning sustainable management of the remaining frankincense resources of species such as *B. papyrifera*. Possibly, frankincense tapping can be tuned in relation to the potential for frankincense yield of each individual tree. This approach however requires more knowledge on the relation between frankincense yield and various tree characteristics (Tadesse et al., 2001).

Frankincense yield considerably varies between trees (Gebrehiwot et al., 2003; Tadesse et al., 2004). In two different studies the annual frankincense yield per tree ranged between 0.4 and 1.8 kg y^{-1} (Eshete et al. 2012a), and between 0.1 and 1.7 kg y^{-1} (Tilahun et al., 2011). This large difference in annual frankincense yield per tree can potentially be attributed to many factors, including both tree characteristics (size, physiology) and external factors (e.g. tapping regimes and micro-site conditions). It was shown that frankincense yield is not related to soil fertility and soil-moisture holding capacity (Eshete et al., 2012a). Similarly, Lombardero et al. (2000), reported that resin yield of *Pinus taeda* is not related to drought and fertilization. On the other hand, Wekesa et al. (2009), reported a strong correlation between yield of Gum arabic and soil moisture and soil temperature. The intensity of tapping has a strong effect as variation in the number of incisions per tree and/or the number of tapping rounds per season leads to high yield variation (Gebrehiwot et al., 2003; Tadesse et al., 2004; Tilahun et al., 2011; Eshete et al., 2012a). Also tree characteristics, such as diameter, tree height and crown size (Tadesse et al., 2004; Tilahun et al., 2011; Eshete et al., 2012a) have a large effect. Similar relationships between tree characteristics (e.g. diameter and height) and resin yield were reported for *Pinus elliotti*, (Zheng and Xu, 1992, Wang and Zhu, 1994), *Pinus taeda* (induced resin; Lombardero et al., 2000) and *Pinus halepensis* (Spanos et al., 2010). In contrast, *Pinus pinaster* (Tadesse et al., 2001) and *Picea abies* (Baier et al., 2002) did not show such trends.

In addition to tree size, resin yield can also be directly related to characteristics of the resin-secretory structures that are responsible for the synthesis, storage and transport of resin (DeAngelis et al., 1986; Blanche et al., 1992; Baier, 2002). Diameter of internal lumen of resin canals (hereafter diameter of resin canals), density of resin canals and number of epithelial cells are among the commonly mentioned characteristics of resin-secretory structures that determine resin yield (DeAngelis et al., 1986; Blanche et al., 1992; Tolera et al., 2013a). These features are closely related to tree size and ontogeny (Blanche et al., 1992; Wimmer and Grabner, 1997; Levanic, 1999; Wainhouse et al., 2005; Wang et al., 2006; Fabasiak and Czajka, 2011). Moreover, both tree morphology and resin-secretory structures may be affected by climate and soil conditions (Reid and Watson, 1966; Blanche et al., 1992; Wimmer and Grabner, 1997; Levanic, 1999). In addition to tree and resin-canal characteristics, genetic variation related to physiological production capacity can also account for inter-tree variation in resin yield (e. g. Tadesse et al., 2001; Roberds et al., 2003; Spanos et al., 2010). However, it remains a major challenge to show how these networks of correlated tree and resin canal characteristics interact and ultimately drive the variation in frankincense yield of a tree.

In a previous study, we described and quantified resin-secretory structures of *B. papyrifera,* and showed differences in resin-canal characteristics among trees (Tolera et al., 2013a). We reported that resin canals of *B. papyrifera* are predominantly found in the bark and the density and diameter of axial resin canals are 0.8 mm^{-2} and 113 µm respectively. As resin canals form the source of frankincense, their size and density are assumed to be related with frankincense yield. Mengistu (2011) speculated that bark thickness and total area of resin canals could be strongly related to frankincense yield. In addition, resin-canal features are most likely related to tree size characteristics, such as stem diameter, tree height, bark thickness, as well as total leaf area, and possibly also recent radial growth. More sustainable management strategies aim at selecting specific tapping procedures for individual trees. These should be based on a better understanding of the combined effects of resin canals and different other tree characteristics on frankincense yield, but yet such studies have never been done for *B. papyrifera.* This study aims at unraveling the relationships between resin-canal characteristics, tree morphological and ontogenetic characteristics and frankincense yield, in order to understand what drives frankincense yield.

We hypothesize that total resin-canal area (labeled as "Resin area" in Figs. 1 and 3) increases with stem diameter, because the bark cross-sectional area increases with stem diameter (Wainhouse et al., 2005; Sonmez et al., 2007). In addition, we expect that a high resource acquisition rate (Mengistu et al., 2011), expressed by a large number of leaf apices and high radial growth rate (labeled as "Growth" in Figs. 1 and 3) positively impacts the frankincense yield of trees. We added tree age as a potential additional factor of influence on total resin canal area and expect that age has a negative impact on frankincense yield particularly at senescence. We summarized this hypothesized network of impacts on annual frankincense yield in a path diagram (Fig. 1), which we tested in the current study.

Materials and Methods

Study species

B. papyrifera produces the widely traded white incense and occurs in Ethiopia, Eritrea, Nigeria, Cameroon, Central African Republic, Sudan, Chad, and North East Uganda (Vollesen, 1989). In Ethiopia, *B. papyrifera* grows in dry *Combretum - Terminalia* woodlands and wooded grasslands in the northern and north-western parts (Bekele et al., 1993; Gebrehiwot et al., 2003; Eshete et al., 2011). It is a deciduous tree that usually dominates on steep and rocky slopes and shallow soil (Gebrehiwot et al., 2003; Ogbazghi et al., 2006; Abtew et al., 2012). In north-western Ethiopia, it grows on a relatively flat terrain and deeper soil depth (Eshete et al., 2011). It grows to a height of about 12m (Ogbazghi et al., 2006; Eshete et al., 2011).

Study site

The study area is located near the village of Lemlem Terara, Metema district, North-Western Ethiopia (12°39´ to 12°45´ N, 36°17´ to 36°23´ E). The data for this study was collected from trees growing in open woodland located at 870 m a.s.l. Based on data from National Meteorological Agency of Ethiopia, for the period of 1971 to 2009, annual rainfall in Metema ranges from 665 to 1380 mm, with a mean annual rainfall of 965 mm. The study area receives an average monthly rainfall of above 50 mm from May to October. The mean annual minimum and maximum temperatures are 19 °C and 36 °C respectively. The study site is dominated by clay soil and its average soil depth is 27.7 cm (Eshete et al., 2011).

Data collection

In October 2011, study trees were selected from tapped *B. papyrifera* populations (Eshete et al., 2011). Bark samples were collected using a TREPHOR (Cortina, Italy) of 140 mm long and 5 mm in diameter (Rossi et al., 2006) from 53 trees with circular bole shape. The sample trees range between 13 and 34 cm in stem diameter at breast height (DBH) and covers the DBH range of the whole population (Eshete et al., 2011). Two bark samples were collected from non-tapped spots of each sample tree to prevent influence of wound reactions on the bark structure. From the same trees, two increment cores were collected from opposite sides at similar direction and height (0.4-0.5 m) above the ground. DBH was recorded for all sample trees. All living leaf apices of the sample trees were counted. The total number of leaf apices was used as a proxy for total crown leaf area which is significantly related to assimilation rate (Mengistu, 2011). For frankincense yield, we used data collected from the 53 sample trees during the tapping season from October 2009 to June 2010. Frankincense was collected by making six incisions (tapping spots) from which the resin was tapped in 14 tapping rounds (Eshete et al., 2012a). Tree age, and radial growth of the recent five years were determined from the increment cores (Tolera et al., 2013b).

Resin-canal characteristics were measured from transversal micro-thin sections prepared from the two bark samples collected per tree following the protocol by Schweingruber et al. (2006). We measured the thickness and width of the inner bark (Tolera et al., 2013a) of each bark sample to estimate the surface area of each bark sample. All axial resin canals in the inner bark were marked, counted and their diameters were measured. All measurements were done using the image-analysis software ImageJ (http://rsbweb.nih.gov/ij/) version 1.44p.

The density of axial resin canals per bark sample (mm^{-2}) was calculated from the number of all resin canals counted on each bark sample and area of the inner bark and averaged for the two bark samples per tree. Similarly, the average diameter of axial resin canals per tree was calculated from the diameter of all axial resin canals of each bark sample and averaged for the two bark samples. This average diameter of resin canals was used to estimate the average surface area of a single axial resin canal (= π $(d/2)^2$) where d represents the average resin canal diameter for each sample tree. In line with our observations, we assumed all resin canals to be circular in cross-section.

The total number of resin canals at cross-section of the sampling height of each sample tree was estimated from the product of average density and the estimated average bark cross-section area. The total resin-canal area of each sample tree was calculated as the product of the number of resin canals and the estimated average surface area occupied by a single resin canal.

The relationship between resin-canal characteristics (total number of resin canals and total resin-canal area) and bark thickness, DBH, total number of leaf apices, age and RADIAL growth was explored using simple linear regression. The cause-effect relationship between tree and resin-canal characteristics and frankincense yield was determined using a path analysis model (e.g. Sterck et al., 2008). χ^2 and P values were used for testing the validity of the model using PASW–statistics, Amos18.0.

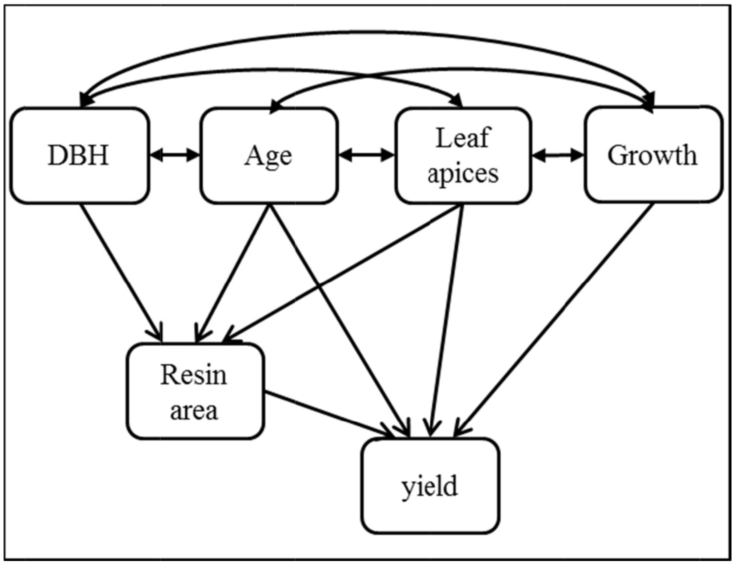

Figure 1. A conceptual framework for the causal relationship of tree and resin canal characteristics with frankincense yield. Cause–effect paths are indicated by single headed-arrows and correlation paths by double headed-arrows.

Results

Relationship between resin-canal and tree characteristics

The average density of resin canals per tree in the inner bark is 0.86 mm^{-2} (s.d. = 0.25, n = 53) and ranges between 0.35 and 1.51 mm^{-2}. The average resin-canal diameter of all axial resin canals measured from 53 trees is 0.11 mm (s.d. = 0.01, n = 2472, axial resin canals) and ranges between 0.02 and 0.23mm. The average number of resin canals at the cross-section area of the sample trees is 9887 and ranges between 1704 and 22979 per tree (s.d. = 4746; n = 53). The average total resin-canal area in the whole cross-section of the bark is 93mm^2 and ranges between 16 and 267 mm^2 (s.d. = 56; n = 53).

Most tree characteristics correlated significantly with resin-canal characteristics (Table 1). Larger DBH trees have more resin canals (Pearson correlation, r = 0.75, $P < 0.01$, n = 53) and a larger total resin-canal area (Pearson correlation, r = 0.81, $P < 0.01$, n = 53). Among the tree characteristics, growth is not correlated to either number (Pearson correlation, r = 0.20, P = 0.119, n = 53) or total area (Pearson correlation, r = 0.21, P = 0.133, n = 53) of resin canals.

Table 1. Bivariate relationship (Pearson correlations) among different tree and resin-canal characteristics of 53 trees of *B. papyrifera,* Ethiopia. Units are only shown in column titles.

Variables	**DBH (mm)**	**Inner bark thickness (mm)**	**Total resin-canal area (mm^2)**	**Age**	**Number of leaf apices**
Inner-bark thickness	0.617**				
Total resin-canal area	0.806**	0.642**			
Age	0.546**	0.370**	0.320*		
Number of leaf apices	0.703**	0.480**	0.728**	0.310*	
Radial stem growth	0.191	0.122	0.209	-0.132	0.155

**. Correlation is significant with $P < 0.01$

*. Correlation is significant with $P < 0.05$

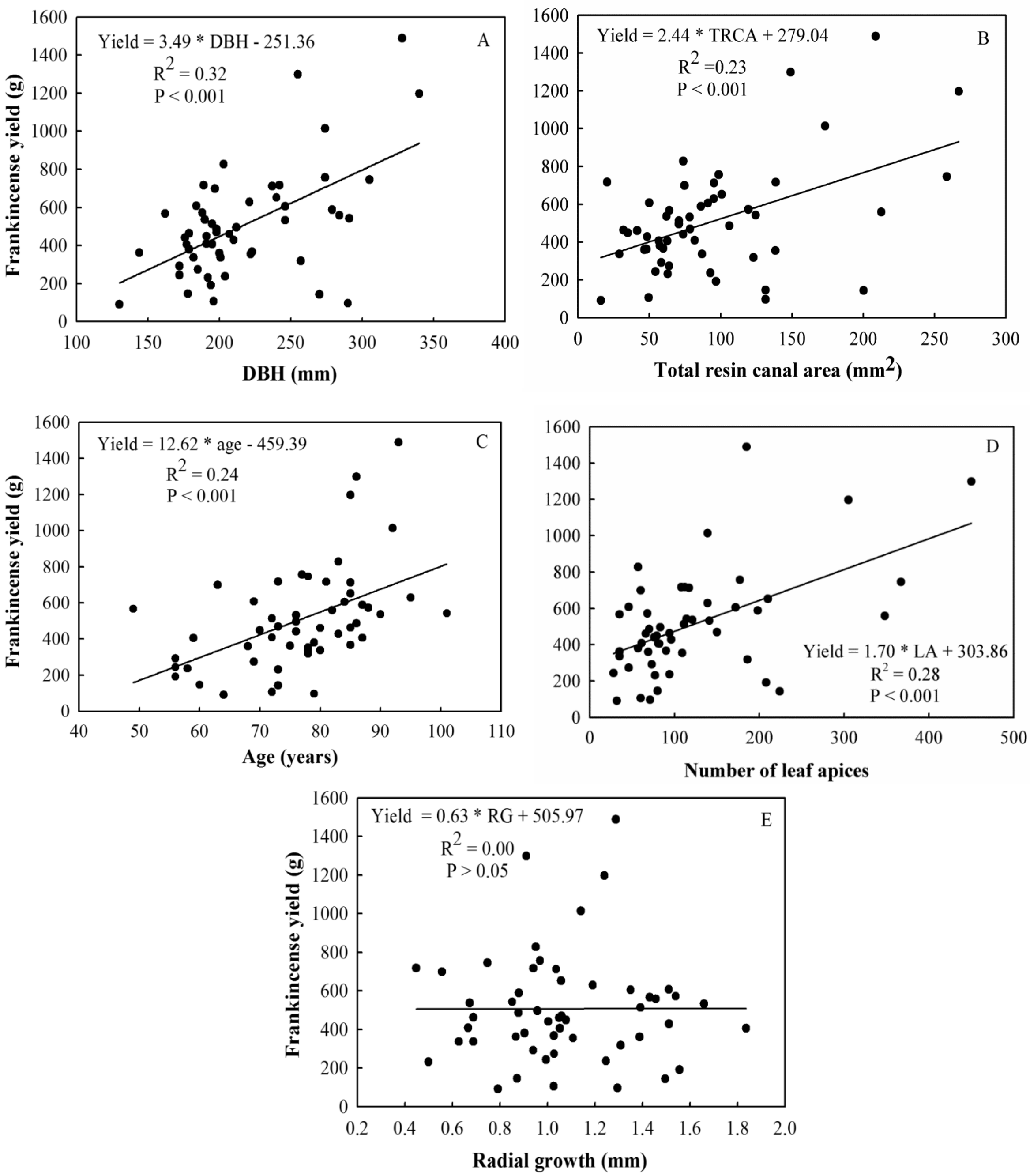

Figure 2. Scatter diagram of relationships between frankincense yield and tree and resin canal characteristics. TRCA in the model of (B) refers to total resin canal area, LA in (D) refers to number of leaf apices and SG in (E) refers to radial stem growth.

Effects of tree and resin-canal characteristics on frankincense yield

Annual frankincense yield increased with all tree and resin-canal characteristics, and correlation strengths were remarkably similar (Pearson correlation coefficient (r) ranging from 0.43-0.56, $P < 0.01$, Fig. 2). Surprisingly, annual frankincense yield was unaffected by radial growth.

Path analysis was used to unravel possible cause-effect relationships of different tree and resin-canal characteristics with annual frankincense yield (Fig. 3). The hypothesized conceptual model (Fig. 1) explains 46% of the variation in frankincense yield ($\chi^2 = 1.287$, df = 2, $P = 0.525$, Fig. 3A). The predicted impacts of number of leaf apices on total area of resin canals and radial growth on frankincense yield were not significant. Removing these non-significant cause-effect relationships resulted in a fit and simpler model that explains 44% of the variation in frankincense yield ($\chi^2 = 2.75$, df = 2, $P = 0.253$; Fig. 3B). It shows that the total number of leaf apices had the expected direct positive impact on frankincense yield. DBH had no direct effect on annual frankincense yield but an indirect effect through its strong direct effect on total resin-canal area. In contrast to our expectation, age had a direct positive impact on annual frankincense yield but at the same time a direct negative impact on total resin-canal area. Total resin-canal area had the expected positive direct effects on frankincense yield.

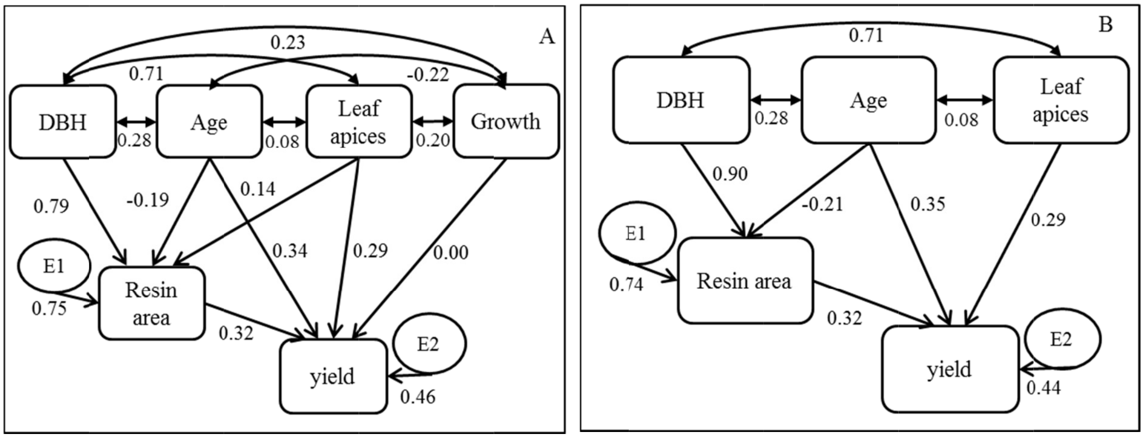

Figure 3. Path analysis of effects of resin canal and tree characteristics on frankincense yield of *B. papyrifera*, Ethiopia. A) shows cause-effects of the hypothesized model and B) shows the results for the model trimmed from insignificant paths. The boxes represent the variables considered in the model. Double headed arrows (curved and straight) in this model show correlative relationships. Single headed arrows show direct effects from one variable to the other and the direction of the arrow shows direction of effect. Values below the error term indicate variation in that variable explained by the model.

.Discussion

Our results show that tree size, bark thickness, and resin-canal characteristics are significantly correlated and frankincense yield is determined by all these interrelated tree and resin-canal characteristics. The recent radial growth level was the only tree characteristic that did not correlate with resin-canal characteristics and neither with frankincense yield.

Resin-canal and tree characteristics

Tapped *B. papyrifera* trees had similar resin-canal characteristics as observed earlier in non-tapped trees (Tolera et al., 2013a). Comparable to untapped trees the average diameter of all axial resin canals amounts to 0.11 mm (s.d. = 0.03) with a similar range (0.02 and 0. 23 mm for tapped trees and 0.03 to 0.23 mm for untapped trees) and similar average density of resin canals of 0.86 mm^{-2} for tapped and 0.82 mm^{-2} for untapped trees (Tolera et al., 2013a). This similarity in resin-canal attributes between tapped and untapped trees shows that tapping does not cause or stimulate general adaptations in the resin-secretory structure, such as traumatic resin canals (Nagy et al., 2000; Langenheim, 2003), at least at some distance from the tapping spots. As bark samples were collected at different heights along the stem, i.e. at 0.5 m in this study versus 1.3 m in Tolera et al. (2013a), we hypothesize the resin-canal characteristics to be relatively similar over the lower bole of *B. papyrifera* trees.

Most tree morphological and ontogenetic characteristics correlated significantly with resin-canal characteristics. As expected, trees with higher stem diameter had a thicker inner bark and a larger inner-bark surface which results in the presence of more resin canals and a larger total resin-canal area per tree. In an earlier study, we showed that resin canals of *B. papyrifera* are predominantly concentrated in the inner bark (Tolera et al., 2013a). The current study shows that inner-bark thickness linearly increased with stem diameter (Table 1). Similar observations were reported for whole-bark thickness in *Picea orientalis* (Sonmez et al., 2007) and *Pinus sylvestris* (Wainhouse et al., 2005). It thus seems that different species share an increase in bark thickness with increasing stem thickness.

In our study, we found no relationship between recent radial growth and the size and number of resin canals or the total resin-canal area in the inner bark. This is in agreement with results reported from wood of *Pinus contorta* (Reid and Watson, 1966), *Picea abies* (Wimmer and Grabner, 1997) and *Pinus sylvestris* (Fabisiak and Czajka, 2011). In other studies, however, radial growth was positively correlated with the number of resin ducts in the bark of *Picea* *glauca* (Alfaro et al., 1997) and with the number of resin ducts in wood of *Pinus taeda* (DeAngelis et al., 1986), but negatively in another study in the wood of the same species (Blanche et al., 1992). Baier (2002), also reported negative relationship between radial growth and number of resin ducts in the secondary phloem of *Picea abies*. There is thus no support for a generic role of radial growth in the amount of resin-producing tissues formed at the same time in the inner bark.

In contrast to our expectation, we observed an increase in the number of resin canals and the total resin-canal area with increasing tree age (Table 1). For other species, tree age correlated negatively with the number of resin canals in wood, for example for *Pinus nigra* (Levanic, 1999). We thus also lack support for a generic role of tree age in the amount of resin-producing tissues.

Effects of tree and resin-canal characteristics on frankincense yield

As predicted, the total resin-canal area in the bark had a positive impact on annual frankincense yield. This total resin-canal area in the bark is determined by the average resin-canal area, resin-canal density and the bark-surface area (Table 2). Earlier studies showed that total resin-canal area is positively related to number of epithelial cells which are responsible for the synthesis of resin (Braier, 2002), thereby partly explaining the positive relationship between resin-canal area and resin yield (Rosner 1998; Braier, 2002; Rosner and Hannup, 2004). These results are in agreement with results from wood of *Pinus taeda* (Blanche et al., 1992).

Table 2. Multiple regression showing effects of average density of resin canals (mm^{-2}), average diameter of resin canals (mm^2) and surface area of bark (mm^2) on total area of resin canals (mm^2). Underlined coefficient values are significant

Parameters	**Wald Chi-Square**	***P-value***
Intercept	$\underline{9.50}$	0.002
Average density of resin canals	2.52	0.112
Average size of resin canals	$\underline{10.08}$	0.001
Surface area of bark	$\underline{6.54}$	0.011
Average density x Average size	2.44	0.118
Average density x Surface area of bark	$\underline{41.15}$	0.000
Average size x Surface area of bark	$\underline{7.99}$	0.005

We hypothesized positive impacts of stem diameter on annual frankincense yield because trees with thicker stems will have more resin-canal area in the bark. The path analysis result shows that stem diameter increased the frankincense yield through its strong effects on the total resin-canal area in the bark (Fig. 3). This may also explain the higher frankincense yield in larger trees as observed in earlier studies (Tadesse et al., 2004; Tilahun et al., 2011; Eshete et al., 2012a), and the higher resin yield with tree size observed in *Pinus halepensis* (Spanos et al., 2010).

We observed that the total number of leaf apices, a good proxy of total leaf area, had no direct effect on the total resin-canal area in the stem, while it had a direct positive effect on frankincense yield. This implies that the greater carbon gain with a larger total leaf area (Ruel et al., 1998; Spanos et al., 2010; Mengistu, 2011) contributes to the ability of trees to produce more frankincense. The reported lack of significant effects of crown leaf area on frankincense yield (Mengistu et al., 2012) may be related to the limited size range (with tree stem diameters between 17–22 cm) considered in that study. Since resin is harvested during the dry season, we expect that the extra carbon, stored as starch, serves as a major source for the frankincense production during the dry season (Mengistu, et al., 2012). Additionally, the presence of bark chlorophyll (Girma et al., 2013) suggests that bark photosynthesis (Aschan and Pfanz, 2003) could also contribute to the frankincense production in the dry season. The lack of any direct effect of stem diameter on frankincense yield, however, implies that the role of bark photosynthesis in frankincense yield is limited.

We predicted larger radial growth rates, as indicator for high whole-tree vitality, to manifest greater potential for frankincense yield, but our results did not support this. Blanche et al. (1992) also reported that resin flow and radial growth were unrelated for *Pinus taeda*. Mengistu et al. (2012), speculated that *B. papyrifera* trees have the strongest demands for assimilates posed by maintenance respiration, foliage establishment and resin production and that radial growth has a low priority when compared to frankincense production. Such trade-offs in carbon-allocation pattern to different sinks may pose constraints on plants in a stressed environment (Chapin, 1991; Herms and Mattson, 1992; Kleczewski et al., 2010), and possibly decouples a direct link between radial growth and frankincense yield.

The path analyses suggested two unexpected age impacts. First, age had a negative indirect impact on frankincense production via a negative effect on the total resin-canal area. This implies that, among trees of similar size, older trees tend to make less total resin-canal area than younger trees. Maybe, the older trees are growing under resource-limited condition with lower relative growth rate (Herms and Mattson, 1992) and consequently also have a thinner bark that leads to lower total area of resin canals (Table 2). This is in agreement with the observation that trees can show long periods with persistently low or high growth rates over their whole life history, both for *B. papyrifera* (Tolera et al., 2013b) and other tree species (Brienen and Zuidema, 2005). This may reflect persistent differences in resource availability, resulting in persistent growth-rate differences amongst trees (Herms and Mattson, 1992).

The second age effect is a direct positive effect on frankincense yield: thus older trees produce more resin than younger trees of the same size. It implies that an average resin canal in an older tree produces more resin compared to such a canal in a younger tree of the same size. This implies an intraspecific tradeoff between growth rate potential and frankincense yield, since older and slower growing trees can thus compensate the loss in frankincense yield resultant from a smaller total resin-canal area in the stem by more productive resin canals. Yet, for *Picea abies*, no age effects on resin yield were observed (Baier et al., 2002), which questions the generality of our result. A meta-analysis on the ontogeny and plant defense showed that such studies are limited for woody plants (Barton and Koricheva, 2010), and that generalizations are premature.

Implications for sustainable production of frankincense

The results of this study shows that DBH, age, total resin-canal area and total number of leaf apices jointly determine frankincense yield. These findings indicate that these tree characteristics can be used in the field to identify trees with higher potential for frankincense yield. Some of these characteristics (like total resin-canal area and age) are difficult to evaluate in the field. However, the fact that these characteristics are highly correlated to each other enables to use other easily identifiable tree characteristics to estimate the tree characteristics that cannot be quickly measured in the field. For instance, the stem diameter of the tree can be regarded as a proxy for the total resin-canal area (Table 1 and Fig. 3B). Age estimations are also useful as it explains a significant amount of the variation in frankincense yield observed among trees of similar size (Tadesse et al., 2004 and this study). The strong relation between stem diameter and frankincense yield supports previous recommendations of lowering the number of tapping spots of trees of smaller size (e.g. Eshete et al., 2012a), because such trees are more limited in frankincense yield. The results can also be used for selection and propagation (e.g. Haile et al., 2011) of trees which are well suited for frankincense production. This study thus contributes to management regimes that minimize the damage to trees, while maximizing the benefits in terms of frankincense yield. Besides tree-size related characteristics, additional knowledge on the relation between frankincense yield and genetic variability (Tadesse et al., 2001; Spanos et al., 2010) is considered important to improve sustainability in frankincense production.

Chapter 6

General discussion

Introduction

Boswellia papyrifera grows in the *Combretum- Terminalia* deciduous woodlands (Friis et al., 2011) of Ethiopia and other dry tropical forests of Sub-Saharan Africa (Vollesen, 1989). This species has important economic, social and ecological benefits (Gebrehiwot et al., 2003; Abiyu et al., 2010; Tilahun et al., 2011; Woldamanuel, 2011). It produces frankincense which is globally used for church ceremonies and as raw material in pharmaceuticals, fragrances, flavours, detergents, soaps, and lotions (Lemenih et al., 2003; Coppen, 2005). Frankincense accounted for 90% of 29,340 tons of gum and resin exported from Ethiopia to the world market between 1998 to 2008 (Lemenih and Kassa, 2011). In addition to its use as a source of foreign currency, its employment opportunity contributes to the economy of many households (Tilahun et al., 2007, 2011; Woldeamanuel, 2011). *B. papyrifera* is also used to meet the demand for wood products such as firewood and construction materials. This species is adapted to a range of altitudes and may grow on more rocky sites and harsher environments than most other species (Ogbazghi et al., 2006; Abiyu et al., 2010; Lemenih and Kassa, 2011). Like many other species of tropical dry forests (Stern et al., 2002; Miles et al., 2006; Chidumayo and Marunda, 2010), *B. papyrifera* is currently facing severe challenges from different stress factors (Abiyu et al., 2010; Ogbazghi et al., 2006; Abtew et al., 2012). These stress factors include clearance for agriculture, overgrazing, fire, insect damage, and improper tapping (Gebrehiwot et al., 2003; Abiyu et al., 2006; 2010; Eshete et al., 2012a; Lemenih et al., 2012; Mengistu et al., 2012). Its growth and population dynamics may also be affected by climate change (Lloyd and Farquhar, 2008; Bogino et al., 2009; Lewis et al., 2009; Scheiter and Higgins, 2009; Timberlake et al., 2010; Feeley et al., 2012). As a result of these natural but mainly anthropogenic stresses, the current populations of *B. papyrifera* lack trees of smaller diameter (i.e. <10 cm; Ogbazghi et al., 2006; Negussie et al., 2008; Eshete et al., 2011; Abtew et al., 2012) and face high adult mortality (Groenendijk et al., 2012). It is also shown that tapping exposes the trees to more damage from fire and insect attacks (Abiyu et al., 2006), reduces reproductive effort (Rijkers et al., 2006) by lowering seed viability and germination success (Ogbazghi et al., 2006; Eshete et al., 2012b), and reduces photosynthetic carbon gain (Mengistu et al. 2012). Similar effects of tapping have been reported for other species, such as *Hevea brasiliensis* and *Canarium strictum* (Silpi et al., 2006; 2007; Varghese and Ticktin, 2008).

Due to the lack of regeneration and decline in tree numbers in the remaining tree populations, frankincense production is estimated to be reduced to less than 50% in the next 20 years

(Groenendijk et al., 2012). These results and those of previous studies highlight the urgent need to take measures for sustainable management of this globally valuable resource. This study focused on how tapping and land-use changes, expressed as clearance, grazing and fire, in combination with climate as natural factor impact the age structure, growth dynamics and frankincense production in trees and populations of *B. papyrifera* in Ethiopia (Fig. 1).

While the general relationship between tapping regimes and tree size on frankincense yield has been investigated in earlier studies (Fig. 1-broken arrow; Tadesse et al., 2004; Rijkers et al., 2006; Eshete et al., 2012a; Mengistu et al., 2012), no knowledge was available on the anatomy of resin-secretory structures in *B. papyrifera.* As resin-secretory structures are the key to synthesis, storage and transport of resins (Raffa and Berryman, 1982; DeAngelis et al., 1986; Lewinsohn et al., 1991; Blanche et al., 1992; Baier, 2002; Langenheim, 2003) this study aimed at a basic understanding of where frankincense is produced in the tree and how resin-canal traits and frankincense yield change in relation to tree morphology and ontogeny. The results were discussed in light of the potential for improving tapping practices that aim at sustainable management of this resource (Fig. 1). At the population level, the structure of the remaining *B. papyrifera* populations was studied. The results were used to identify stress factors related to past changes in growth and establishment of *Boswellia* trees. This synthesis chapter highlights the major findings and discusses two questions; (1) How do environmental stresses influence the growth, population dynamics, and frankincense yield of *B. papyrifera* (Fig. 1. broken rectangle, top panel)? And, (2) how can these results guide us in achieving sustainable management of *B. papyrifera* populations and their frankincense production (Fig.1. solid rectangle, bottom panel)?

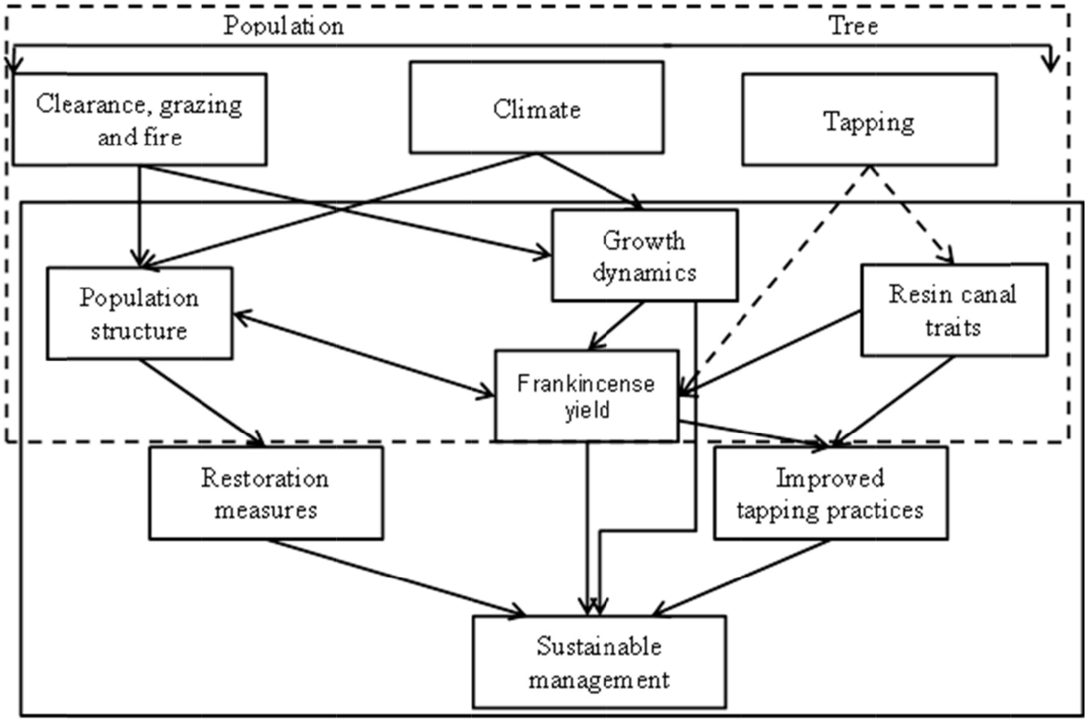

Figure 1. A conceptual diagram that captures the possible impacts of environmental stresses on factors operating at tree and population level and, in turn, the implications of these impacts for possible options to achieve sustainable management of the remaining resources.

Growth-ring formation of **B. papyrifera**

The potential of growth-ring formation and hence suitability for dendrochronological studies for tree species growing in Ethiopia was initially assessed by Briffa and Russell-Smith (1986) focusing on *Juniperus procera* and *Podocarpus falcatus*, the two most important indigenous timber species in Ethiopia. Subsequent studies built on this assessment and used *J. procera* for different dendroclimatological and dendroecological studies (Couralet et al., 2005; Sass-Klaassen et al., 2008; Wils et al., 2009). Krepkowski et al. (2011) also focused on species from the dry afromontane forest, when studying the dynamics of wood formation in the central highland of Ethiopia. Studies in the dryland of the Central Rift Valley area mainly included deciduous *Acacia* species (Eshete and Ståhl, 1999; Gebrekirstos et al., 2008, 2009). Most studies confirmed the presence of annual growth rings in their studied species, but also documented that crossdating of ring-width series was a challenge due to occurrence of missing rings (Eshete and Ståhl, 1999; Gebrekiristos et al., 2008; Sass-Klaassen et al., 2008) and/or multiple growth rings per year (Wils et al., 2009).

This study showed that *B. papyrifera* forms distinct growth rings. The annual character of these growth rings was proved by pinning, i.e. by introducing artificial markers to trace seasonality of wood formation (Sass et al., 1995; Seo et al., 2007; Lisi et al., 2008). The presence of annual rings was in line with expectations about growth ring formation in *B. papyrifera* since these trees experience an extended dry season which also induces leaf shedding and a leafless period for the majority of the months in a year. However, like in other dry-forest species, presence of missing and wedging rings as well as ontogenetic differences in distinctness of growth ring boundaries were challenges for crossdating *B. papyrifera.* The specific site conditions with presence of multiple natural and human-caused disturbances suggest that ring-width patterns of *B. papyrifera* trees carry a complex environmental signal. Thorough visual crossdating on multiple discs enabled the development of reliable mean time series, independently for two sites, that were subsequently used to adjust and crossdate ring-width series from core samples of almost 80 trees to end up with a large crossdated sample set which allowed the construction of site chronology for *B. papyrifera* from NW Ethiopia (February and Stock, 1998; Sass-Klaassen et al., 2008).

One of the ultimate tools to verify the reliability of multi-decadal site chronologies is crossdating with growth-ring records from the same or other species which contain a similar environmental signal. However, both the network of conducted ring-width chronologies and the network of environmental records in Ethiopia are not dense enough to link ring-width chronologies of *B. papyrifera* to other records. Besides geographical distance, a link with other ring-width chronologies was not expected as this study was carried out in a different climate zone and a different vegetation system, as well as on a different species, as compared to the previous dendrochronological studies conducted in Ethiopia (Briffa and Russell-Smith, 1986; Eshete and Ståhl, 1999; Couralet et al., 2005; Gebrekirstos et al., 2008; 2009; Wils et al, 2009; 2011; Sass-Klaassen et al., 2008; Krepkowski et al., 2011).

The presence of annual rings opened the possibility to apply dendrochronological techniques to investigate radial growth dynamics, age-diameter relationship, population-age structure and climate-growth relationships for *B. papyrifera* tree populations. By doing so, vital information related to recruitment failure, number of years to reach the minimum diameter for tapping, and relationship of tree age with frankincense yield and other tree and resin-canal characteristics was retrieved. This information is essential for understanding past changes in growth and population dynamics and for creating links with possible environmental factors related to the observed decline in populations of *B. papyrifera* and ultimately generate plans for sustainable management of *B. papyrifera* populations and resources gained from it.

Resin-secretory structures of **B. papyrifera**

Frankincense, an olio-gum resin, is produced by recurrently wounding the bark of *B. papyrifera* stems. The number of tapping spots (wounds) initiated per tree ranges between six and 12, depending on the diameter of the tree, and each wound is reopened and enlarged eight to 12 times during the dry season (Gebrehiwot et al., 2003; Tadesse et al., 2004; Eshete et al., 2012a). During each of these tapping rounds, the dried frankincense is collected from the wounds. Frankincense yield per tapping round increases during the first seven tapping rounds and decreases thereafter (Eshete et al., 2012a). Tilahun et al. (2011) reported that the yield of the first six tapping rounds explains about 88% of the variation in annual frankincense yield per tree. Such patterns in resin yield are most likely determined by the anatomy and functioning of resin-secretory structures (Bosshard and Hug, 1980; Raffa and Berryman, 1982; Lewinsohn et al., 1991; Langenheim, 2003).

Resin is produced by epithelial cells which are a special kind of parenchyma cells lining the inside of resin-secretory structures in the wood and/or bark of specific tree species (Langenheim, 2003). The resin is stored under pressure (Wiedenhoeft and Miller, 2002; Langenheim, 2003) and released during injuries (Trapp and Croteau, 2001; Baier et al., 2002; Franceschi et al., 2005; Pickard, 2008). Depending on the species, resins may be produced in resin canals or resin pockets (Langenheim, 2003). Tree species that possess resin canals depend mostly on constitutive (preformed) resins that can be transported over longer distances while trees with resin pockets rely on induced resins (Raffa and Berryman, 1982; Lewinsohn et al., 1991; Langenheim, 2003).

The results of this study indicated that *B. papyrifera* possesses axial and radial resin canals located predominantly in the inner bark (Fig. 1; Chapter 4). This has also been reported for other species in the Burseraceae family (Langenheim, 2003). For instance, resin-secretory structures of *Commiphora wightii* (Bhatt et al., 1989) and *Boswellia serrata* (Ghosh and Purkayastha, 1960) are most abundant in the bark. The wood of *B. papyrifera* contains only few radial resin canals that are connected to radial resin canals in the inner bark. There are direct and open connections, anastomoses (Bosshard and Hug, 1980), between the axial and radial resin canals. The axial resin canals are also connected tangentially forming a 3-dimensional network in the most recently formed intact zone (Fig. 1; Chapter 4) of the inner bark. The density of axial resin canals is highest in the intact zone close to the vascular cambium and decreases towards the outer bark. Besides, resin-canal traits (number of resin canals and total area of resin canals at cross-section of a stem) were found to be significantly correlated with tree size and age (Table 1; chapter 5). With path analysis we showed that stem diameter, age, number of leaf apices and total resin-canal area explain a high proportion of variation in the frankincense yield (Fig. 3B, chapter 5). Radial growth activity, i.e. the average ring-width of recently formed growth rings was not correlated with frankincense yield and a similar result was reported for *Pinus taeda* (Blanche et al., 1992). This suggests that stem growth in *B. papyrifera* has a low priority if it comes to assimilate allocation (Mengistu, 2011) as compared to competing sinks, such as maintenance respiration, reproduction and resin production for defence (Chapin, 1991; Herms and Mattson, 1992; Kleczewski et al., 2010). The findings of these studies (Chapters 4 and 5) have implications for frankincense yield resulting from the current tapping regimes (Gebrehiwot et al., 2003; Tilahun et al., 2011; Eshete et al., 2012a) and for explaining the variation in frankincense yield between trees of the same diameter (Tadesse et al., 2004). These findings are vital inputs for planning improved tapping strategies and sustainable production of frankincense.

***Climate-growth relationship of* B. papyrifera**

Growth and population dynamics of trees and forests in the dry tropics with a strong seasonality in rainfall are likely to be related to the amount of rainfall available especially during the rainy season (e.g. Couralet et al. 2010; de Ridder et al. 2013). Some of the studies reported a positive correlation between rainfall of the wet season and the growth of *J. procera* (Sass-Klaassen et al., 2008) and a positive correlation between annual rainfall and growth for *Acacia* species from Central Rift Valley area (Gebrekirstos et al., 2008). Krepkowski et al., (2011) reported that wood formation of *Podocarpus falcatus, Pinus patula, Prunus africana and Celtis africana* is initiated by rainfall. This implies that climate variability which is related to global climate change can potentially affect species in dry woodlands (Miles et al., 2006; Timberlake, 2010; Meir and Pennington, 2011) including those in Ethiopia. Tree-ring analysis (Dendrochronology) is an important tool to generate quantitative information on climate-growth relationships of trees (Fritts, 1976; Worbes et al., 2002; Rozendaal and Zuidema, 2011) and thereby offers an opportunity to predict the likely effects of climate change on growth of trees (Zuidema et al., 2012).

Our result shows that growth of *B. papyrifera* is increasing with higher rainfall and also with higher average and maximum temperatures during the growing season. The positive effect of rainfall was expected since rainfall and hence water availability drive physiological processes under periodically dry site conditions. This becomes obvious from the fact that rainfall triggers leaf phenology of *B. papyrifera* with the consequence of the trees being leafless for about six months during the dry season (Mengistu et al., 2012). The general positive relationship between growth and maximum temperature implies that light availability plays an important role and that is in line with the results of Mengistu et al. (2012). We however observed a negative impact of the minimum temperature, possibly because the respiration load, which is considerable for this tree species (Mengistu et al. 2012), increases with temperature. The future predictions show that both rainfall and temperatures increase in the study site and the rest of Ethiopia (Tadege, 2007), which may imply that stem growth rate limitations are released, when the negative impact of minimum temperature remains inferior.

How do environmental stresses influence the population dynamics, growth, and frankincense yield of* B. papyrifera *(broken rectangle, fig. 1)?

Lack of recruitment

This study (Chapter 2) shows that the trees in the remnant populations of *B. papyrifera* established continuously between 1903 and 1955. Within this period no incidental favourable recruitment peak years or peak periods (e.g. Moloney, 1986; Sato and Iwasa, 1993) were observed. The investigated remnant populations lack trees that have established during the last 55 years. Given the observation of massive small seedlings, this lack of regeneration is probably due to the inability of persistent sapling establishment (see also Groenendijk et al. 2012). This lack of successful recruitment coincides with the time when new human settlements were established in the area, i.e. early 1960s (Lemenih et al., 2007; 2012; Woldeamanuel, 2011). Since the start of the settlement, the human population of the study district has considerably increased (Central Statistical Authority (CSA), 1994, 2007; Eshete et al., 2005). From 1984 to 2007 an increase of human population from 12,887 to 110,231 was reported for Metema district CSA (1994; 2007). The establishment of settlements was accompanied by intensive clearance of forested land for agriculture, high grazing pressure, and increased demand for fire wood and wood products. The frequency of human-induced fire to open-up the forest for cultivation, initiate new grasses and chase wild-animals to reduce the threats to livestock, farmers working in their fields and also to frankincense tappers has also increased (Abiyu et al., 2006, 2010; Lemenih et al., 2012; Lemenih and Kassa, 2011). Additional pressure is caused by seasonal migration of livestock from four neighbouring districts to the study area. This already started between 1949 and 1958 and 84% of the households from the neighbouring districts started to take their livestock to the study area where they stay from May to October each year (Tegegne et al., 2009).

It is likely that these stress factors jointly influenced the population dynamics in the woodlands of the area during the last five decades by hampering seedling establishment and promoting clearance of saplings and young trees. Other studies also reported that tree recruitment can be hampered by grazing (Teich et al., 2005; Ogbazghi et al., 2006; Dufour-Dror, 2007; Auld and Keith, 2009; Tsegaye et al., 2009; Wassie et al., 2009; Abtew et al., 2012) and fire (Keith, 1996; Zida et al., 2007; Haubensak et al., 2009), which is a common phenomenon also for other tropical dry forests (Menuat et al., 1995; Miles et al., 2006; Chidumayo and Marunda, 2010).

Lack of seedling survival and development to sapling stage of *B. papyrifera* is not a local phenomenon. A similar lack of smaller trees was reported for other populations in our study area (>10 cm; Eshete et al., 2011), Northern Ethiopia (>10 cm; Gebrehiwot et al., 2003; Negussie et al., 2008; Eshete et al., 2011), Eritrea (>8 cm; Ogbazghi et al., 2006) and Sudan (>10 cm; Abtew et al., 2012). With the assumption of similar age-diameter relationships for all these *B. papyrifera* populations, this implies that successful recruitment of *B. papyrifera* might have failed over wide areas in East Africa over the last half century. Coupled with high adult mortality (Abtew et al., 2012), the lack of recruitment throughout such a long period of time may lead to extinction of the species within a few decades (Groenendijk et al., 2012).

B. papyrifera seedlings are assumed to follow a “waiting under the ground” strategy (Birhane et al., 2012), which has also been reported for other tropical dry forests species in Africa (Boaler, 1966; Stahle et al., 1999; Steenkamp et al., 2008). Such a strategy can help to increase the chance of survival once a seedling is emerging due to long-term investment in root development which enhances their potential to compete for moisture (Menuat et al., 1995). However, based on the age-diameter relationships, derived from this study, saplings or trees of *B. papyrifera* younger than 50 years were not encountered in the study populations. Inventories in other populations of the study area did also not record trees of <10 cm in the population structure (Eshete et al., 2011). Even if seedlings are assumed to use a “waiting under the ground" strategy, at least some seedlings were expected to have reached the sapling stage, unless the increased disturbance leads to seedling mortality or in the best case to a "waiting under the ground" age of more than 50 years. However, it is more likely that seedlings may not be able to get enough time to accumulate enough carbohydrate in their root (Abiyu et al., 2010) due to frequent fire, grazing, trampling and uprooting during grazing (Gebrehiwot et al., 2003). Based on our results and field observations we have to conclude, that it is unlikely that current populations will be refreshed by seedlings waiting under the ground under the current disturbance regime.

Implications for frankincense yield

B. papyrifera was found to be a slow growing species (Chapter 2) as compared to other dry woodland species in Ethiopia, such as *Acacia senegal*, *Acacia tortilis*, *Acacia seyal* and *Balanities aegyptiaca* (Geberekiristos et al., 2008) and other dry forests of Africa (Gourlay, 1995; Stahle et al., 1999; Therrell et al., 2007; Steenkamp et al., 2008). This means that it takes a while until a *Boswellia* tree grows from a seedling to an adult tree. This together with the predicted rapid decline of remnant *B. papyrifera* populations (Chapter 2, Groenendijk et al., 2012) implies negative consequences for the future production of frankincense. To minimize the pressure on smaller trees, Eshete et al. (2012a) suggested a diameter of 20 cm at breast height as a minimum tapping size. Based on our estimated age-diameter relationship (Chapter 2), a tree with an average radial growth rate will take about 73 years to reach a diameter of 20 cm. Previous studies indicated that the current population of *B. papyrifera* in the study area will be reduced to less than 10% of its current density in the next 50 years. The slow growth rate of *B. papyrifera* could then lead to a gap of about 20 years in frankincense production with an optimistic assumption that tree recruitment will be enhanced from now onwards.

The effect of different tapping regimes on frankincense yield, annual carbon gain and carbon stock has been studied (Tadesse et al., 2004; Eshete et al., 2012a; Mengistu et al., 2012). In this study (Chapter 4), patterns in frankincense yield through different tapping regimes (Tadesse et al., 2004; Tilahun et al., 2011; Eshete et al., 2012b) were linked to the distribution and architecture of resin-secretory structures (broken arrow, fig. 1). We showed that the density and the intactness of the network of axial resin canals increases from the outer bark across the different zones of the inner bark towards the vascular cambium. These anatomical patterns explain why frankincense yield increases during the first seven tapping rounds and declines in later tapping rounds (Tilahun et al., 2011; Eshete et al., 2012a). With successive deeper cuts in consecutive tapping rounds, the wounds reach the zones of the inner bark with higher resin-canal density and the intact network of resin canals with the consequence that more frankincense is drained. The yield declines with later cuts (>7) into the intact zone of the inner bark since most of the resin will be drained during the previous tapping rounds. The fact that axial resin canals are tangentially connected (anastomose) and hence form an efficient three-dimensional network could also explain why enlarging wound size does not pay off in frankincense yield (Tadesse et al., 2004). Due to the presence of the resin-canal network small wounds seem to be evenly effective in draining resins as wide wounds. For the same reason a higher number of tapping spots may not increase frankincense yield (e.g. Eshete et al., 2012a) since the wounds start to drain resin from the same pool. The results from the path analysis (Chapter 5) explain why trees of the same diameter have large variations in frankincense yield (Tadesse et al., 2004). The variation is due to difference in age which leads to variation in the total area of resin canals (Fig. 3; chapter 5). It is shown that large variation exists in the age-diameter relationship (Chapter 2) which implies that trees of the same diameter can vary in age and also in frankincense yield. Factors that explain frankincense yield are summarised in Table 1.

Table 1. Summary of previous and major findings of this study related to patterns of frankincense yield and the implications of findings of this study to improve tapping strategies for sustainable production of frankincense and sustainable management of *B. papyrifera* populations in North-Western Ethiopia.

Previous studies related to frankincense yield	**Major findings of this study linked to patterns of frankincense yield**	**Implication of the major findings in explaining the patterns of frankincense yield reported earlier**
Frankincense yield per tapping round increases with the first 6/7 tapping rounds and then declines (Tilahun et al., 2011; Eshete et al., 2012a).	The density and intactness of the 3-dimensional network of resin canals decreases from the cambium through the intact zone in the inner bark towards the outer bark.	Successively deeper cuts, reach the intact inner bark with an active 3-dimensional resin-canal network. Once the intact zone is reached, yield declines with later cuts.
Frankincense yield increases with 6-9 tapping spots (wounds) and then declines (Eshete et al., 2012a). Enlarging wound size does not pay-off in frankincense yield (Tadesse et al., 2004).	There is direct and open tangential and radial connections among the axial and between axial and radial resin canals.	Resin canals can drain resin from longer tangential and longitudinal distances. Hence, if many wounds exist, they start to draw resin from the same resource.
Frankincense yield is positively related to DBH (Tadesse et al., 2004; Tilahun et al., 2011; Eshete et al., 2012a)	Tree size (stem diameter) is strongly positively related to inner- bark thickness and to total area of resin canals in the cross-section of a stem.	Higher yield of frankincense per tree from trees with larger stem diameter is due to higher total area of resin canals.
Recommendation of minimum tapping size of 20 cm DBH (Eshete et al., 2012a)	Due to the slow growth rate of *B. papyrifera*, it will take on average 73 years to reach at diameter of 20 cm at DBH.	Coupled with the estimated decline in populations of *B. papyrifera* (Groenendijk et al., 2012), this may lead to a gap in frankincense production.

How can these results guide us in achieving sustainable management of **B. papyrifera** *populations and their frankincense production (solid rectangle, fig.1)?*

The lack of successful recruitment since about half a century coupled with high mortality rate of the adult trees (Groenendijk et al., 2012) puts the need for sustainable management of *B. papyrifera* at high priority. Without immediate interventions, the loss of this economically, socially, and ecologically valuable tree species within few years seems inevitable in large parts of Ethiopia. Interventions should target the stress factors that are leading to lack of recruitment and high mortality of the existing population; namely land-use change, overgrazing, fire, and improper tapping (Gebrehiwot et al., 2003; Lemenih et al., 2007; 2012; Abiyu et al., 2006; 2010; Rijkers et al., 2006; Ogbazghi et al., 2006;Abtew et al., 2012; Eshete et al., 2012a; 2012b; Mengistu et al., 2012). This study supports the idea that the lack of recruitment in the remaining *B. papyrifera* populations is associated with these disturbances in the study area. Hence, interventions suggested minimizing conversion of the woodland to agriculture, abolishing fire, and improved tapping practices (Abiyu et al., 2006; 2010; Eshete et al., 2012b; Lemenih et al., 2012) are highly important.

Most important is to sustainably maintain the remnant adult populations that bear the fate of possible future generation of this species. Protecting forested areas against grazing and fire (Aerts, et al., 2009) is probably most important for promoting successful development of seedlings to juvenile and adult stages. Such protection has been proved to be important to enhance tree recruitment (Dufour-Dror, 2007; Spooner and Briggs, 2008). It has also been practiced in Northern Ethiopia particularly to rehabilitate degraded areas (Birhane et al., 2006; Aerts et al., 2007; Tsegaye et al., 2009). Many trees that we studied increased stem growth over the recent 20 years showing the resilience-capacity of the species even in older trees (Chapter 3). Excluding livestock alone may not enhance recruitment (Aerts et al., 2007) and the rehabilitation activity may need to be supplemented with active rehabilitation measures like enrichment planting (Lemenih and Kassa, 2011), fire breaks and other fire control measures. High adult mortality is one of the reasons for the rapid decline of *B. papyrifera* populations (Groenendijk et al., 2012). This mortality is partly caused by insect attack (Abiyu et al., 2006, 2010) that uses the wounds of tapping as an inlet. Therefore detailed studies on the types of insects causing the damage, extent of damage and its management and control is urgently needed.

Global climate change is one of the stress factors threatening tropical dry forests (Timberlake et al., 2010; Meir and Pennington, 2011). In this study, we showed that climate-growth relationship for *B. papyrifera*, indicate a positive relation to precipitation and average and maximum temperature for trees in our study area, but a negative one with minimum temperature. For our study region, an increase in both temperature and rainfall is predicted based on the mid-range (A1B) CO_2 emission scenario (Tadege, 2007). This could have positive impacts on the stem growth of *B. papyrifera*. Yet, the relationships between climate variables and other vital rates (e.g. mortality and recruitment) that determine tree population dynamics are unknown. Therefore, further studies on the potential effect of climate factors on tree mortality and recruitment are important. Observations so far indicate that rainfall showed high annual variability and it is unpredictable in its seasonal distribution (Tadege, 2007; Funk et al., 2012). This may influence the agricultural productivity and increase dependence of local communities on forest resources. The expected warming might also aggravate fire occurrences in the woodland (Golding and Betts, 2008; Meir and Pennington, 2011). Therefore, the estimated positive effect on growth of *B. papyrifera* may be more than counteracted by the expected pressure through its socio-economic effects that may aggravate dependence on forest resources (e.g. income from tapping), fire occurrences, and land conversion. Consequently, it is not evident that changing climate conditions-even if favourable, have a direct positive effect on growth and population dynamics of *B. papyrifera*. Positive climate change impacts are probably overruled by negative impacts by aggravating fire intensity and frequency and land use-change which are already playing a major detrimental role for the decline of populations of *B. papyrifera*.

Sustainable management of *B. papyrifera* will also benefit from measures that reduce impacts of tapping. It is shown that the distribution and network of resin canals in the inner bark explains patterns of frankincense yield reported so far (Table 1). Based on the increasing density of resin canals and the intact three-dimensional network towards the intact zone of the inner bark (Fig. 1B, Chapter 4), it can be assumed that deeper cuts during the first few tapping rounds can drain most of the resin. This is on the assumption that frankincense is predominantly a preformed resin (Langenheim, 2003). The fact that *B. papyrifera* possess resin canals instead of resin pockets (Raffa and Berryman, 1982; Lewinsohn et al., 1991), similarity in resin canal attributes between untapped (Chapter 4) and tapped (Chapter 5) trees and the immediate flow of resin from the bark when a tree is cut support the preposition that frankincense is indeed a preformed resin. The radial and tangential connections of resin canals also show that a smaller number of tapping spots can drain resin from a larger area (Table 1). These findings can be used as a basis to set experiments to reduce the number of tapping spots and tapping rounds per season (Taddesse et al., 2004; Eshete et al., 2012a; Mengistu et al., 2012) to minimize the stress posed by tapping at tree and population level (Abiyu et al., 2006; Ogbazghi et al., 2006; Rijkers et al., 2006; Varghese and Ticktin, 2008; Silpi et al., 2007; Eshete et al., 2012b;Mengistu et al., 2012). In addition, allowing resting periods from tapping and retaining some trees without tapping as mother trees for seed production will assist recovery of *B. papyrifera* trees and populations from stress. On top of efforts to understand mechanisms to enhance the natural recruitment process, it is also important to strengthen establishment of plantations from cuttings that has shown some success (Haile et al., 2011). The selections of potential mother trees and cuttings for establishing plantations for frankincense production can be guided by tree size and vitality (expressed in number of leaf apices, Chapter 5). These are some of the interventions that may secure sustainable management of *B. papyrifera* and its frankincense production.

Abiyu, A., Vacik, H., Glatzel, G., 2006. Population Viability Risk Management (PVRM) applied to *Boswellia papyrifera (Del.) Hochst* in North-eastern Ethiopia. Journal of the Drylands 1(2), 98-107.

Abiyu, A., Bongers, F., Eshete, A., Gebrehiwot K., Kindu, M., Lemenih, M., Moges, Y., Ogbazghi, W., and Sterck, F.J., 2010. Incense woodlands in Ethiopia and Eritrea: regeneration problems and restoration possibilities. In: Bongers F. and Tennigkeit T. (Eds). *Degraded forests in Eastern Africa: management and restoration*. Earthscan. pp 133-152.

Abtew, A.A., Pretzsch, J., Mohamoud, T., Adam, Y.O., 2012. Population status of *Boswellia papyrifera* (del.). Hochst in the dry woodlands of Nuba mountains, South Kordofan state, Sudan. Agriculture and Forestry 54 (08), 41-50.

Aerts, R., Negussie, A., Maes, W., November, N., Hermy, M., Muys, B., 2007. Restoration of Dry afromontane forest using pioneer shrubs as nurse-plants for *Olea europaea* Ssp. *Cuspidata*. Restoration Ecology 15, (1), 129-138.

Aerts, R., Nyssen, J., Haile, M., 2009. On the difference between ‘‘exclosures’’ and ‘‘enclosures’’ in ecology and the environment. Journal of Arid Environment 73, 762-763.

Alfaro, R.I., F. He, F., Tomlin, E., Kiss G., 1997. White spruce resistance to white pine weevil related to bark resin canal density. Canadian Journal of Botany 75, 568-573.

Aschan, G., Pfanz, H., 2003. Non-foliar photosynthesis–a strategy of additional carbon acquisition. Flora 198, 81-97.

Attorre, F., Taleb, N., Sanctis, M.D., Farcomeni, A., Guillet, A., Vitale, M., 2011. Developing conservation strategies for endemic tree species when faced with time and data constraints: *Boswellia* spp. on Socotra (Yemen). Biodiversity Conservation 20,1483-1499.

Auld, T.D., Keith, D.A., 2009. Dealing with threats: integrating science and management. Ecological Management and Restoration 10, 579-587.

Awas, T., 2007. *Plant diversity in Western Ethiopia. Ecology, ethnobotany and conservation*. PhD thesis, University of Oslo, Norway.

Baier, P., Führer, E., Kirisits, T., Rosner, S., 2002. Defence reactions of Norway spruce against bark beetles and the associated fungus *Ceratocystes polonica* in secondary pure and mixed species stands. Forest Ecology and Management 159, 73-86.

Baillie, M.G.L., Pilcher, J.R., 1973. *A simple cross-dating program for tree-ring research. Tree Ring Bulletin* 33, 7-14.

Baker, P.J., 2003.Tree age estimation for the tropics: a test from the Southern Appalachians. Ecological Applications 13(6), 1718-1732.

Baker, P.J., Bunyavejchewin, S., Oliver, C.D., Ashton, P.S., 2005. Disturbance history and historical stand dynamics of a seasonal tropical forest in western Thailand. *Ecological Monographs* 75, 317-343.

Bannan, M.W., 1936. Vertical resin ducts in the secondary wood of the Abietineae. New Phytologist 35, 11-46.

Barnes, M.E., 2001. Seed predation, germination and seedling establishment of *Acacia erioloba* in northern Botswana. Journal of Arid Environments 49, 541-554.

Barton, E. K., Koricheva, J., 2010. The ontogeny of plant defense and herbivory: characterizing general patterns using meta-analysis. American Naturalist 175, 481-493.

Battles, J.J., Robards, T., Das, A., Waring, K., Gilless, K., Biging, G., Schurr, F., 2008. Climate change impacts on forest growth and tree mortality: a data-driven modelling study in the mixed conifer forest of the Sierra Nevada. California. Climatic Change 87, 193-213.

Bhatt, J.R., Nair, M.N.B., Ram, H.Y.M., 1989. Enhancement of oleo-gum resin production in *Commiphora wightii* by improved tapping technique. Current Science 58, 349-57.

Bekele, A., Birnie, A., Tengas, B., 1993. Useful trees and shrubs of Ethiopia: identification, propagation, and management of agricultural and pastoral communities. Technical Hand Book N^{o} 5. Nairobi. Regional Soil Conservation Unit, Nairobi, pp. 474.

Berryman, A.A., 1972**.** Resistance of conifers to invasion by bark beetle-fungus associations. BioScience 22**,** 598-602.

Birhane, E., 2011. *Mycorrhizal symbiosis and seedling performance of the frankincense tree (Boswellia papyrifera).* PhD thesis, Wageningen UR, The Netherlands.

Birhane, E., Sterck, F.J., Fetene, M., Bongers, F., Kuyper, T.W., 2012. Arbuscular mycorrhizal fungi enhance photosynthesis, water use efficiency, and growth of frankincense seedlings under pulsed water availability conditions. Oecologia 169(4), 895-904.

Blanche, C.A., Lorio, P.L., Sommers, R.A., Hodges, J.D., Nebeker, T.E., 1992. Seasonal cambial growth and development of loblolly pine: xylem formation, inner bark chemistry, resin ducts, and resin flow. Forest Ecology and Management 49, 151-165.

Boaler, S.B., 1966. The Ecology of *Pterocarpus angolensis* D.C. in Tanzania. Ministry of Overseas Development, London. Overseas Research, Publication No. 12, pp. 128.

Bogino, S., Fernández, Nieto, M.J., Bravo, F., 2009. Climate effect on radial growth of *Pinussylvestris* at its southern and western distribution limits. Silva Fennica 43(4), 609-623.

Borchert, R., 1999. Climatic periodicity, phenology, and cambium activity in tropical dry forest trees. IAWA Journal 20(3), 239-247.

Bosshard, H.H., Hug, U.E., 1980. The anastomoses of the resin canal system in *Picea abies* (L.) Karst., *Larix decidua* Mill. and *Pinus sylvestris* L. Holz als Roh- und Werkstoff 38, 325-328.

Bräuning, A., Homeier, J., Cueva, E., Beck, E., Günter, S., 2008. Growth dynamics of trees in tropical mountain ecosystems. Ecological Studies 198, 291-302.

Brienen, R.J.W., Zuidema, P.A., 2005. Relating tree growth to rainfall in Bolivian rain forest: a test for six species using tree ring analysis. Oecologia 146, 1-12.

Brienen, R.J.W., Zuidema, P.A., 2006. Life time growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. Journal of ecology 94, 48-493.

Brienen, R.J.W., Zuidema, P.A., During H.J., 2006. Autocorrelated growth of tropical forest trees: Unravelling patterns and quantifying consequences. Forest Ecology and Management 237, 179-190.

Brienen, R.J.W., Zuidema, P.A., 2007. Incorporating persistent tree growth differences increases estimates of tropical timber yield. *Frontiers in Ecology and the Environment* 5, 302-306.

Brienen, R.J.W., Lebrija-Trejos, E., van Breugel, M., Pérez-García, E.A., Bongers, F., Meave, J.A., Martínez-Ramos, M., 2009. The potential of tree rings for the study of forest succession in southern Mexico. Biotropica 41, 186-195.

Briffa, K.R., Russell-Smith, A., 1986. Dendroclimatic pilot study in Ethiopia. Climatic Research Unit, University of East Anglia, Norwich, pp. 26.

Buckley, B.M., Duangsathaporn, K., Palakit, K., Butler, S., Syhapanya, V., Xaybouangeun, N., 2007. Analyses of growth rings of *Pinus merkusii* from Lao P.D.R. *Forest Ecology and Management* 253, 120-12

Caro, T.M., Sungula, M., Schwartz, M.W., Bella, E.M., 2005. Recruitment of *Pterocarpus angolensis* in the wild. Forest Ecology and Management 219, 169-175.

Chantuma, P., Lacointe, A., Kasemsap, P., Thanisawanyangkura, S., Gohet, E., Clément, A., Guilliot, A., Thaler, P., 2009. Carbohydrate storage in wood and bark of rubber trees submitted to different level of C demand induced by latex tapping. Tree physiology 29, 1021-1031.

Cherubini, P., Gartner, B.L., Tognetti, R., Bräker, O.U., Schoch, W., Innes, J.L. 2003. Identification, measurement and interpretation of tree rings in woody species from mediterranean climates. *Biological Reviews* 78: 119-148.

Cherubini, P., Humbel, T., Beeckman, H., Gärtner, H., Mannes, D., Pearson, C., Schoch, W., Tognetti, R., Lev-Yadun, S., 2013. Olive Tree-Ring Problematic Dating: A Comparative Analysis on Santorini (Greece). PLoS ONE 8 (1). e54730. doi:10.1371/journal.pone.0054730.

Chidumayo, E., Marunda, C., 2010. Dry Forests and Woodlands in Sub-Saharan Africa: Context and Challenges. In: Chidumayo, E. N., Gumbo, D. J. (Eds.), *The dry forests and woodlands of Africa: managing for products and services.* pp . 1-10.

Chapin FS., 1991. Integrated Responses of Plants to Stress. BioScience 41(1), 29-36.

Clark, D.A, Clark, D.B., 1994. Climate-induced annual variation in canopy tree growth in a Costa Rican tropical rain forest. *Journal of Ecology* 82 (4), 865-872.

Clark, D.A., Piper, S.C., Keeling, C.D., Clark, D.B., 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences* 100(10), 5852-5857.

Cochrane, M.A., Laurance, William. F., 2002. Fire as a large scale edge effect in Amazonian forests. Journal of Tropical Ecology 18, 311-325.

Cook, E.R., 1985. *A time-series analysis approach to tree-ring standardization*. Ph.D dissertation, The University of Arizona, Tucson.

Coppen, J.J.W., 2005. Overview of International Trade and Markets. In: Chikamai, B., Casade, E. (Eds.), Production and Marketing of Gum Resins: Frankincense, Myrrh and Opoponax. FAO/NGARA, Nairobi, Kenya, pp. 5-34.

Corlett, R.T., 2011. Impacts of warming on tropical lowland rainforests. *Trends in Ecology and Evolution* 27, 145-150.

Couralet, C., Sass-Klaassen, U., Sterck, F., Bekele, T., Zuidema, P.A., 2005. Combining dendrochronology and matrix modelling in demographic studies: an evaluation for *Juniperus procera* in Ethiopia. Forest Ecology and Management 216, 317-30.

Couralet, C., 2010. *Community dynamics, growth and phenology of tropical trees in the rain forest Reserve of Luki, Democratic Republic of Congo*. PhD thesis, Gent University, Belgium.

Couralet, C., Sterck, F.J., Sass-Klaassen, U., Acker V.J., Beeckman, H., 2010. Species-specific growth responses to climate variations in understory trees of a central African rain forest. Biotropica 42, 503-511.

Crawley, M.J., 1989. Insect herbivores and plant population dynamics. Annual Review of Entomology 34, 531-564.

CSA, 1994. The 1994 population and housing census of Ethiopia, results for Amhara region volume I: Part I statistical report on population size and characteristics. Addis Ababa. pp. 314.

CSA, 2007. Summary and statistical report of the 2007 population and housing census of Ethiopia, population size by age and sex. Addis Ababa. pp. 114.

Cunningham, S.C., Read, J., 2003. Do temperate rainforest trees have a greater ability to acclimate to changing temperatures than tropical rainforest trees? New Phytologist 157, 55-64.

DeAngelis, J.D., Nebeker, T.E., Hodges, J.D., 1986. Influence of tree age and growth rate on the radial resin duct system in loblolly pine (*Pinus taeda*). Canadian Journal of Botany 64, 1046-1049.

Dejene, T., Lemenih, M., Bongers, F., 2012. Manage or convert Boswellia woodlands? Can frankincense production payoff? Journal of Arid Environments. http://dx.doi.org/10.1016/j.jaridenv.2012.09.010.

Demisew, S., 1996. Ethiopia's natural resource base. In: Tilahun, S., Edwards, S., Gebre Egziabher, T. (Eds.), Important bird areas of Ethiopia. Ethiopian wildlife and natural history society, Semayata press, Addis Ababa, Ethiopia. pp. 36-53.

De Ridder, M., Trouet, V., den Bulcke, J.V., Hubau, W.,Van Acker, J., Beeckman, H., 2013. A tree-ring based comparison of *Terminalia superba* climate–growth relationships in West and Central Africa. Trees DOI 10.1007/s00468-013-0871-3.

Dong, S.X., Davies, S.J., Ashton, P.S., Bunyavejchewin, S., Nur Supardi, M.N., Kassim, A.R., Tan, S., Moorcroft, P.R., 2012. Variability in solar radiation and temperature explains observed patterns and trends in tree growth rates across four tropical forests. Proceeding of the Royal Society B 279, 3923-3931.

Dufour-Dror, J.M., 2007. Influence of cattle grazing on the density of oak seedlings and saplings in a Tabor oak forest in Israel. Acta Oecologica 31, 223-228.

Eckstein, D., Bauch, J., 1969. Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. Forstwissenschaftliches Centralbl 88, 230-250.

Enquist, B.J., Leffler, A.J., 2001. Long-term tree ring chronologies from sympatric tropical dry-forest trees: individualistic responses to climatic variation. Journal of Tropical Ecology 17, 41-60.

Esau, K., 1965. *Plant anatomy.* 2nd ed. John Wiley and Sons, New York.

Eshete A. 2011. *The Frankincense tree of Ethiopia: Ecology, Productivity and Population Dynamics*. PhD Thesis, Wageningen University and Research Center, Wageningen, the Netherlands.

Eshete, A., Teketay, D., Hulten, N., 2005. The socio-economic importance and status of populations of *Boswellia papyrifera* (del.) Hochst. In northern Ethiopia: the case of North Gonder zone. Forests, Trees and Livelihoods 15, 55-74.

Eshete, A., Sterck, F.J., Bongers, F., 2011. Diversity and production of Ethiopian dry woodlands explained by climate and soil-stress gradients. Forest Ecology and Management 261 (9), 1499-1509.

Eshete, A., Teketay, D., Lemenih, M., Bongers, F., 2012a. Effects of resin tapping and tree size on the purity, germination and storage behavior of *Boswellia papyrifera* (Del.) Hochst. seeds from Metema District, Northwestern Ethiopia. Forest Ecology and Management 269, 31-36.

Eshete A., Sterck F.J., Bongers, F., 2012b. Frankincense production is determined by tree size and tapping frequency and intensity. Forest Ecology and Management 274, 136-142.

Eshete, G., Ståhl, G., 1999. Tree rings as indicators of growth periodicity of acacias in the Rift Valley of Ethiopia. Forest Ecology and Management 116, 107-117.

Fabisiak, E., Czajka, M., 2011. The effect of annual ring width on density of axial resin canals in pine wood (*Pinus sylvestris*). Forestry and Wood Technology 74, 40-45.

Fahn A. 1988. Secretory tissues in vascular plants. New Phytologist 108 (3), 229-257.

Fahn A. 1979. *Secretory tissues in plants.* Academic Press, London.

Farah, M.H., 2008. *Non-timber forest product (NTFP) extraction in arid environments: land-use change, frankincense production and the sustainability of* Boswellia sacra *in Dhofar (Oman).*PhD thesis. University of Arizona.

Feeley, K.J., Wright, S.J., Supardi, M.N.N., Kassim, A.R., Davies, S.J., 2007. Decelerating growth in tropical forest trees. Ecology Letters 10, 461-469.

Fichtler, E., Clark, D.A., Worbes, M., 2003. Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and ^{14}C. Biotropica 35, 306-317.

Franceschi, V.R., Krokene, P., Christiansen, E., Krekling, T., 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New Phytologist 167, 353-376.

Funk, C., Rowland, J., Eilerts, G., Kebebe, E., Biru, N., White, L., Galu, G., 2012. A Climate Trend Analysis of Ethiopia. U.S. Geological Survey Fact Sheet, 2012-3053.

February, Ed.C., Stock, W.D., 1998. An assessment of the dendrochronological potential of two Podocarpus species. The Holocene 8 (6), 747-750.

Feeley, K.J., Rehm, E.M., Machovina, B., 2012. The responses of tropical forest species to global climate change: acclimate, adapt, migrate or go extinct? Frontiers of Biogeography 4(2), 67-84.

Fraver, S., White, A.S., 2005. Identifying growth releases in dendrochronological studies of forest disturbance. Canadian Journal of Forest Research 35,1648-1656.

Friis, I., Demissew, S., van Breugel, P., 2011. Atlas of the potential vegetation of Ethiopia. Addis Ababa University Press and Shama Books. pp 306.

Fritts, H.C. 1976. *Tree ring and climate*. Academic Press Inc, London.

Gärtner, H., Nievergelt, D., 2010. The core-microtome: A new tool for surface preparation on cores and time series analysis of varying cell parameters. Dendrochronologia 28, 85-92.

Gebrehiwot K, Muys, B,, Haile, M., Mitloehner R., 2003. Introducing *Boswellia papyrifera* (Del.) Hochst and its non-timber forest product, frankincense. International Forestry Review 5, 348-353.

Gebrekirstos, A., Mitlohner, R., Teketay, D., Worbes, M., 2008. Climate growth relationships of the dominant tree species from semi-arid savanna woodland in Ethiopia. Trees-Structure and Function 22, 63-641.

Gebrekirstos, A., Worbes, M., Teketay, D., Fetene, M., Mitlöhner, R., 2009. Stable carbon isotope ratios in tree rings of co-occurring species from semi-arid tropics in Africa: Patterns and climatic signals. Global and Planetary Change. 66, 253-260.

Ghannoum, O., & Way, D.A., 2011. On the role of ecological adaptation and geographic distribution in the response of trees to climate change. Tree Physiology 31, 1273-1276.

Ghosh, S.S., Purkayastha, S.K., 1960. Anatomical studies on the resiniferous system in *Boswellia serrata* Roxb. trees. Indian Forester 86, 684-695.

Girma, A., Skidmore, A.K., de Bie, C.A.J.M., Bongers, F., Schlerf, M., 2013. Photosynthetic bark: use of chlorophyll absorption continuum index to estimate Boswellia papyrifera bark chlorophyll content. International Journal of Applied Earth Observations and Geoinformation 23, 71-80.

Golding, N., Betts, R., 2008. Fire risk in Amazonia due to climate change in the HadCM3 climate model: Potential interactions with deforestation. Global biogeochemical cycles, 22, GB4007, doi:10.1029/2007GB003166, 2008.

Goldschmidt, C., 1970. Die Weihrauchstrasse: Zur Geschichte des ältesten Welthandelsweges. In: Lindner M. eds. *Petra und das Königreich der Nabatäer*. Abhandlungen der Naturhistorischen Gesellschaft, Nürnberg.

Gourlay, I.D., Grime, G.W., 1994. Calcium oxalate crystals in african acacia species and their analysis by scanning proton microprobe (spm). IAWA Journal 15 (2), 137-148.

Gourlay, I.D., 1995. Growth ring characteristics of some African Acacia species. Journal of Tropical Ecology 11, 121-140.

Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree -ring research 57(2), 205-221.

Groenendijk, P., Eshete, A., Sterck, F.J., Zuidema, P.A., Bongers, F., 2012. Limitations to sustainable frankincense production: blocked regeneration, high adult mortality and declining populations. Journal of Applied Ecology 49, 164-173.

Groom, N., 1981. *Frankincense and myrrh. A study of the Arabian incense trade.* Longman, London and New York.

Haile, G., Gebrehiwot, G., Lemenih, M., Bongers, F., 2011. Time of collection and cutting sizes affect vegetative propagation of *Boswellia papyrifera* (Del.) Hochst through leafless branch cuttings. Journal of Arid Environments 75, 873-877.

Han, Q., Kabeya, D., Hoch, G., 2011. Leaf traits, shoot growth and seed production in mature *Fagus sylvatica* trees after 8 years of CO_2 enrichment. Annals of Botany 107, 1405-1411.

Haubensak, K., D'Antonio, C., Wixon, D., 2009. Effects of fire and environmental variables on plant structure and composition in grazed salt desert shrublands of the Great Basin (USA). Journal of Arid Environments 73, 643-650.

Herms, D.A., Mattson, W.J., 1992. The dilemma of plants: to grow or to defend. The quarterly review of Biology 67, 283-335.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43, 69-78.

IPCC. 2007. Climate Change 2007. The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jacoby, G.C., 1989. Overview of tree-ring analysis in tropical regions. IAWA Bull. n. s. 10, 99-108.

Junikka, L., 1994**.** Survey of English macroscopic bark terminology**.** IAWA Journal 15(1), 3-45.

Kebede, T., 2010. *Current production systems of frankincense from B. papyrifera tree, its implications on sustainable utilization of the resource*. MSc thesis, Mekele University, Ethiopia.

Keith, D.A., 1996. Fire-driven extinction of plant populations: a synthesis of theory and review of evidence from Australian vegetation. In: Proceedings of the Linnean Society of NSW 116, pp. 37-78.

Kelly, D., Sork, V.L., 2002. Mast seeding in perennial plants: why, how, where? Annual Review of Ecology and Systematics 33, 427-447.

Kleczewski, N.M., Herms, D.A., Bonello, P., 2010. Effects of soil type, fertilization and drought on carbon allocation to root growth and partitioning between secondary metabolism and ectomycorrhizae of *Betula papyrifera.* Tree Physiology 30, 807-817.

Kolalite, M.R., Oskolski, A.A., Richter, H.G., Schmitt, U., 2003. Bark anatomy and intercellular canals in the stem of *Delarbrea paradoxa* (Araliaceae). IAWA Journal 24 (2)**,** 139-154.

Krepkowski, J., Bräuning, A., Gebrekirstos, A., Strobl, S., 2011. Cambial growth dynamics and climatic control of different tree life forms in tropical mountain forest in Ethiopia. Trees 25: 59-70.

Langenheim, J.H., 1995. Biology of Amber-producing trees: focus on case studies of *Hymenaea* and *Agathis*. In: Anderson KB. and Krelling CJ, eds. *Amber, Resinite and Fossil Resins.* American chemical society symposium series, No. 617. pp. 1-30.

Langenheim, J.H., 2003. Plant resins: chemistry, evolution, ecology and ethnobotany. Timber Press, Cambridge, UK. pp. 586.

LaPasha, C.A., Wheeler, E.A., 1990. Resin canals in *Pinus taeda:* longitudinal canal lengths and interconnections between longitudinal and radial canals. IAWA Bulletin 11(3), 227-238.

Lemenih, M., Teketay, D., 2003. Frankincense and Myrrh resources of Ethiopia II. Medical and industrial uses. Ethiopian Journal of Science 26(2), 16-72.

Lemenih, M., Feleke, S., Tadesse, W., 2007. Constraints to smallholders production of frankincense in Metema district, North-western Ethiopia. Journal of Arid Environments 71, 39-403.

Lemenih, M., Kassa, H., (Eds) 2011. Opportunities and challenges for sustainable production and marketing of gums and resins in Ethiopia. CIFOR, Bogor, Indonesia. pp. 106.

Lemenih, M., Kassa, H., Kassie, G.T., Abebaw, D., Teka, W., 2012. Resettlement and woodland management problems and options: a case study from north-western Ethiopia. Land degradation and development DOI, 10.1002/ldr.2136.

Levanic, T., 1999. Vertical resin ducts in wood of black pine *(Pinus nigra* Arnold) as a possible dendroecological variable. Phyton 39, 123-127.

Lev-Yadun, S., 2011. Bark. In: Encyclopedia of Life Sciences (ELS). John Wiley and Sons, Ltd. Chichester. DOI: 10.1002/9780470015902.a0002078.

Lewis, S.L., Lloyd, J., Sitch, S., Mitchard, T.A., Laurance, W.F., 2009. Changing Ecology of Tropical Forests: Evidence and Drivers. The Annual Review of Ecology, Evolution, and Systematics 40, 529-49.

Lewinsohn, E., Gijzen, M., Croteau, R., 1991. Defense mechanisms in conifers: differences in constitutive and wound-induced monoterpene biosynthesis among species. Plant Physiology 96, 44-49.

Lieberman, D., Lieberman, M., Hartshorn, G., Peralta, R., 1985. Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. Journal of Tropical Ecology 1, 97-109.

Lisi, C.S., Tomazello-Filho, M., Botosso, P.C., Roig, F.A., Maria, V.R.B., Ferreira-Fedele, L., Voigt, A.R.A., 2008. Tree-ring formation, radial increment periodicity, and phenology of tree species from a seasonal semi-deciduous forest in southeast Brazil. IAWA Journal 29(2),189-207.

Lloyd, J., Farquhar, G.D., 2008. Effects of rising temperatures and [CO_2] on the physiology of tropical forest trees. Philosophical Transactions of the Royal Society B 363, 1811-1817.

Lo, Y.H., J,A. Blanco., and J,P. Kimmins., 2010. A word of caution when planning forest management using projections of tree species range shifts. Forestry Chronicle 86, 312-316.

Lombardero, M. J., Ayres, M.P., Lorio, P.L., Ruel, J.J., 2000. Environmental effects on constitutive and inducible resin defences of *Pinus taeda*. Ecological Letters 3, 329-339.

Martin, D., Tholl, D., Gershenzon, J., Bohlmann, J., 2002. Methyl Jasmonate induces traumatic resin ducts, terpenoid resin biosynthesis, and terpenoid accumulation in developing xylem of Norway Spruce stems. Plant Physiology 129, 1003-1018.

Mayaux, P., P, Holmgren., F, Achard., H, Eva., H, Stibig., Branthomme, A., 2005. Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical*

Transactions of the Royal Society of London. Series B, Biological Sciences 360, 373-384.

Meir, P., Pennington, R.T., 2011. Climatic change and seasonally dry tropical forests. In: Dirzo, R., Youn g, H.S., Mooney, H.A., Ceballos, G. (Eds.), *Seasonally dry tropical forests*. Island press, London, UK. pp. 279-300.

Mengistu T., 2011. *Physiological ecology of the frankincense tree*. PhD Thesis, Wageningen University and Research Center, the Netherlands.

Mengistu, T., Sterck, F.J., Fetene, M., Tadesse, W., Bongers, F., 2011. Leaf gas exchange in the frankincense tree (*Boswellia papyrifera*) in the dry woodlands of Ethiopia. Tree Physiol. 31, 740-750.

Mengistu, T., Sterck, F.J., Anten, N.P.R., Bongers, F., 2012. Frankincense tapping reduced photosynthetic carbon gain in *Boswellia papyrifera* (Burseraceae) trees. Forest Ecology and Management 278, 1-8.

Menaut, J.C., Lepage, M., Abbadie, L., 1995. Savannas, woodlands and dry forests in Africa. In: Bullock, S.H., Mooney, H.A., Medina, E. (Eds.), *Seasonally dry tropical forests*. Cambridge University press, Cambridge, UK. pp. 64-92.

Miles, L., Newton, A.C., DeFries, R. S., Ravilious, C., May, I., Blyth, S., Kapos, V., Gordon, J. E., 2006. A global overview of the conservation status of tropical dry forests. Journal of Biogeography 33, 491-505.

Mitchell, T.D., Jones, P.D., 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. International Journal of Climatology 25, 693-712.

Miyazaki, Y., Hiura, T., Kato, E., Funada, R., 2002. Allocation of resources to reproduction in *Styrax obassia* in a masting year. Annals of Botany 89, 767-772.

Moloney, K.A., 1986. Wave and non-wave regeneration processes in a subalpine *Abies balsamea* forest. Canadian Journal of Botany 64, 34-349.

Mushove, P.T., Prior, A. B., Gumbie, C., Cutlerd D.F., 1995. The effects of different environments on diameter growth increments of *Colophospermum mopane* and *Combretum apiculatum*. Forest Ecology and Management 72, 287-292.

Nagy, N.E., Franceschi, V.R., Solheim, H., Krekling, T., Christiansen, E., 2000. Wound-induced traumatic resin duct development in stems of Norway spruce (Pinaceae): anatomy and cytochemical traits. American Journal of Botany 87, 302-313.

Nair, M.N.B., Subrahmanyam, S.V., 1998. Ultrastructure of the epithelial cells and oleo-gum resin secretion in *Boswellia serrata* (Burseraceae). IAWA 19(4), 415-427.

Nakagawa, M., Takeuchi, Y., Kenta, T., Nakashizuka, T., 2005. Predispersal seed predation by insects vs. vertebrates in six Dipterocarp species in sarawak, Malaysia. Biotropica 37(3), 389-396.

Negussie, A., Aerts, R., Gebrehiwot, K., Muys, B., 2008. Seedling mortality causes recruitment limitation of *Boswellia papyrifera* in northern Ethiopia. Journal of Arid Environments 72, 378-383.

Nowacki, G.J., Abrams, M.D., 1994. Forest composition, structure, and disturbance history of the Alan Seeger Natural Area, Huntington County, Pennsylvania. Bulletin of Torrey Botanical Club 121, 277-291.

Nowacki, G.J., Abrams, M.D., 1997. Radial-growth averaging criteria for reconstructing disturbance histories from pre-settlement origin oaks. Ecological Monographs 67, 225-249.

Nussinovitch, A., 2010. *Plant gum exudates of the world.* Taylor and Francis group, CRC Press.

Ogbazghi, W., 2001. *The distribution and regeneration of* Boswellia papyrifera (Del.). *Hochst. in Eritrea.* PhD Thesis, Wageningen UR, the Netherlands.

Ogbazghi, W., Rijkers, T., Wessel, M., Bongers, F., 2006a. The distribution of the frankincense tree *Boswellia papyrifera* in Eritrea: the role of environment and land use. Journal of Biogeography 33, 524-535.

Ogbazghi, W., Bongers, F., Rijkers, T.,Wessel, M., 2006b. Population structure and morphology of the frankincense tree *Boswellia papyrifera* along an altitude gradient in Eritrea. Journal of the Drylands 1(1), 85-94.

Oven, P., Torelli, N., 1999. Response of the cambial zone in conifers to wounding. Phyton (Horn, Austria) 39(3), 133-137.

Ow, L.F., Griffin, K.L., Whitehead, D., Walcroft, A.S., Turnbull, M.H., 2008. Thermal acclimation of leaf respiration but not photosynthesis in *Populus deltoides* x *nigra*. New Phytologist 178, 123-134.

Pearce, R.B., 1996. Antimicrobial defenses in the wood of living trees. New Phytologist 132, 203-233.

Pickard, W.F., 2008. Laticifers and secretory ducts: two other tube systems in plants. New Phytologist 177, 877-888.

Piovesan, G., Adams, J.M., 2005. The evolutionary ecology of masting: does the environmental prediction hypothesis also have a role in mesic temperate forests? Ecological Research 20, 739-743.

Raffa, K.F., Berryman, A.A., 1982. Accumulation of monoterpenes and associated volatiles following inoculation of grand fir with a fungus transmitted by the fir engraver *Scolytus ventralis* (Coleoptera: Scolytidae).Canadian Entomologist 114, 797-810.

Rauchfuss, J., Ziegler, S.S., 2011. Reconstructing canopy-disturbance history and recruitment patterns to inform management decisions at the Lost 40 in the Chippewa National Forest, Northern Minnesota. The Geographical Bulletin 52, 3-17.

Reid, R. W., Watson, J.A., 1966. Sizes, distribution, and numbers of vertical resin ducts in lodgepole pine. Canadian Journal of Botany 44, 519-525.

Rijkers, T., Ogbazghi, W., Wessel, M., Bongers, F., 2006. The effect of tapping for frankincense on sexual reproduction in *Boswellia papyrifera.* Journal of Applied Ecology 43, 1188-1195.

Rinn, F., 2003. TSAP-Win, Software for tree-ring measurement analysis and presentation. Rinntech, Heidelberg.

Roberds, J. H., Strom, B.L., Hain, F.P., Gwaze, D. P., McKeand, S. E., Lott, L.H., 2003. Estimates of genetic parameters for oleoresin and growth traits in juvenile loblolly pine. Canadian Journal of Forestry Research 33, 2469-2476.

Roosner, S., Hannup, B., 2004. Resin canal traits relevant for constitutive resistance of Norway spruce against bark beetles: environmental and genetic variability. Forest Ecology and Management 200, 77-87.

Rossi, S., Anfodillo, T., Menardi, R., 2006. Trephor: a new tool for sampling micro-cores from tree stems. IAWA Journal 27 (1), 89-97.

Rozendaal, D.M.A., Zuidema, P.A., 2011. Dendroecology in the tropics: a review. Trees 25, 3-16.

Rozendaal, D.M.A., Soliz-Gamboa, C.C., Zuidema, P.A., 2011. Assessing long-term changes in tropical forest dynamics: a first test using tree-ring analysis. Trees 25, 115-124.

Ruel, J. J., Ayres, M. P., Lorio, P.L., 1998. Loblolly pine responds to mechanical wounding with increased resin flow. Canadian Journal of Forestry Research 28, 596-602.

Ruffner, C.M., Abrams, M.D., 2002. Dendrochronological investigation of disturbance history for a native American site in Northwestern Pennsylvania. Journal of Torrey Botanical Society 129, 251-260.

Ruffner, C.M., Abrams, M.D., 2003. Disturbance history and stand dynamics along a topographic gradient in old growth Hemlock Northern hardwood forests of the Allegheny Plateau, USA. Natural Areas Journal 23(2), 98-113.

Sabaté, S., Carlos, A., Graciaa, C.A., Sánchez, A., 2002. Likely effects of climate change on growth of *Quercus ilex, Pinus halepensis, Pinus pinaster, Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region. Forest Ecology and Management 5906, 1-15.

Sánchez-Azofeifa, G.A., Portillo-Quintero, C., 2011. Extent and drivers of change of Neotropical seasonally dry tropical forests. In: Dirzo, R., Young, H.S., Mooney, H.A., Ceballos, G. (Eds.), *Seasonally dry tropical forests*. Island press, London. pp. 45-58.

Sass, U., Killmann, W., Eckstein, D., 1995. Wood formation in two species of Dipterocarpaceae in Peninsular Malaysia. IAWA Journal 16 (4), 371-384.

Sass-Klaassen, U., Couralet, C., Sahle, Y., Sterck, F.J., 2008. Juniper from Ethiopia contains a large-scale precipitation signal. International Journal of Plant Science 169, 1057-1065.

Sato, K., Iwasa, Y., 1993. Modeling of wave regeneration in subalpine Picea abies forests: population dynamics with spatial structure. Ecology 74 (5), 1538-1550.

Scheiter, S., and Higgins, S. I., 2009.. Impacts of climate change on the vegetation of Africa:an adaptive dynamic vegetation modelling approach. Global Change Biology 15, 2224-2246.

Schweingruber, F.H., 1988. Tree rings: basics and applications of dendrochronology. Kluwer Academic publishers, Dordrecht. pp. 276.

Schweingruber, F.H., Börner, A., Schulze, E.D., 2006. Atlas of woody pant stems: Evolution, structure and environmental modifications. Springer-Verlag, Berlin. pp 229.

Seo, J.W., Eckstein, D., Schmitt, U., 2007. The pinning method: From pinning to data preparation. Dendrochronologia 25, 79-86.

Schöngart, J., Orthmann, B., Hennenberg, K.J., Porembski, S., Worbes, M., 2006. Climate-growth relationships of tropical tree species in West Africa and their potential for climate reconstruction. Global Change Biology 12, 1139-1150.

Shigo, A.L., 1984. Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves. Annual Review of Phytopathology 22, 189-214.

Silpi, U., Thaler, P., Kasemsap, P., Lacointe, A., Chantuma, A., Adam, B., Gohet, E., Thanisawanyangkura, S., Améglio, T., 2006. Effect of tapping activity on radial growth of *Hevea brasiliensis* trees. Tree Physiology 26, 1579-1587.

Silpi, U., Lacointe, A., Kasemsap, P., Thanisawanyangkura, S., Chantuma, P., Gohet, E., Musigamart, N., Clement, A., Améglio, T., Thaler, P., 2007. Carbohydrate reserves as a competing sink: evidence from tapping rubber trees. Tree Physiology 27, 881-889.

Sonmez, T., Keles,S., Tilki, F., 2007. Effect of aspect, tree age and tree diameter on bark thickness of *Picea orientalis*. Scandinavian Journal of Forest Research 22(3), 193-197.

Spanos, K., Gaitanis, D., Spanos, I., 2010. Resin production in natural Aleppo pine stands in northern Evia, Greece. Web Ecology 10, 38-43.

Spooner, P., Briggs, S., 2008. Woodlands on farms in southern New South Wales: a longer-term assessment of vegetation changes after fencing. Ecological Management and Restoration 9, 33-41.

Stahle, D.W., Mushove, P.T., Cleaveland, M.K., Roig, F., Haynes, G.A., 1999. Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. Forest Ecology and Management 124, 217-229.

Steenkamp, C.J., Vogelb, J.C., Fulsb, A., Rooyena, N., Rooyen, M.W., 2008. Age determination of *Acacia erioloba* trees in the Kalahari. Journal of Arid Environments 72, 302-313.

Sterck, F.J., Zweifel, R., Sass-Klaassen, U., Chowdhury, Q., 2008. Persisting soil drought reduces leaf specific conductivity in Scots pine (*Pinus sylvestris*) and pubescent oak (*Quercus pubescens*). Tree Physiology 28, 529-536.

Stern, M., Quesada, M., Stoner, K. E., 2002. Changes in composition and structure of a Tropical Dry Forest following intermittent cattle grazing. Rev. Biol. Trop 50(3/4), 1021-1034.

Sunnichan, V.G., Ram, Y.M., Shivanna, K.R., 2005. Reproductive biology of *Boswellia serrata* , the source of salai guggul, an important gum-resin. Botanical Journal of the Linnean Society 147, 73-82.

Suzuki A., 2001. Resource allocation to vegetative growth and reproduction at shoot level in *Eurya japonica* (Theaceae): a hierarchical investment? New Phytologist 152, 307-312.

Tadege, A. (Ed.), 2007. Climate change national adaptation programme of action (NAPA) of Ethiopia. National Meteorological Agency. Addis Ababa, Ethiopia. pp 96.

Tadesse, W., Nanos, N., Aunon, F.J., Alfa, R., Gil, L., 2001. Evaluation of high resin yielders of *Pinus pinaster* Ait. For. Gen. 8, 271-278.

Tadesse, W., Feleke, S., Eshete, T., 2004. Comparative study of traditional and new tapping method on frankincense yield of *Boswellia papyrifera*. Ethiopian Journal of Natural Resources 6, 287-299.

Tegegne, A., Mengistie, T., Desalew, T., Teka, W., Dejen, E., 2009. Transhumance cattle production system in North Gondar, Amhara Region, Ethiopia: Is it sustainable? IPMS (Improving Productivity and Market Success) of Ethiopian Farmers Project. Working Paper No. 14. ILRI (International Livestock Research Institute). Nairobi, Kenya. pp. 74.

Teich, I., Cingolani, A., Renison, D., Hensen, I., Giorgis, M., 2005. Do domestic herbivores retard *Polylepis australis* Bitt. woodland recovery in the mountains of Córdoba, Argentina? Forest Ecology and Management 219, 229-241.

Therrell, M.D., Stahle, D.W., Mukelabai, M.M., Shugart, H.H., 2007. Age, and radial growth dynamics of *Pterocarpus angolensis* in southern Africa. Forest Ecology and Management 244, 24-31.

Tilahun, M., Olschewski, R., Kleinn, C., Gebrehiwot, K., 2007. Economic analysis of closing degraded *Boswellia papyrifera* dry forest from human interventions: A study from Tigray, Northern Ethiopia. Forest Policy and Economics 9, 996-1005.

Tilahun, M., Muys, B., Mathijs, E., Kleinn, C., Olschewski, R., Gebrehiwot, K., 2011. Frankincense yield assessment and modelling in closed and grazed *Boswellia papyrifera* woodlands of Tigray, Northern Ethiopia. Journal of Arid Environments 75, 695-702.

Timberlake, J., Chidumayo, E., Sawadogo, L., 2010. Distribution and characteristics of African dry forests and woodlands. In: Chidumayo, E. N., Gumbo, D. J. (Eds.), *The dry forests and woodlands of Africa: managing for products and services.* pp.11-41.

Tolera, M., Menger, D., Sass-Klaassen, U., Sterck, F.J., Copini, C., Bongers, F., 2013. Resin secretory structures of *Boswellia papyrifera* and implications for frankincense yield. Annals of Botany 111, 1-8.

Tolera, M., Sass-Klaassen, U., Eshete, A., Bongers, F., Sterck, F.J., 2013. Frankincense tree recruitment failed over the past half century. Forest Ecology and Management 304, 65-72.

Trapp, S., Croteau, R., 2001. Defensive resin biosynthesis in conifers. Annual Review of Plant Physiology and Plant Molecular Biology 52, 689-724.

Trockenbrodt, M., 1990. Survey and discussion of the terminology used in bark anatomy. IAWA Bulletin 2(2), 141-166.

Trouet, V., Coppin, P., Beeckman, H., 2006**.** Annual growth ring patterns in *Brachystegia spiciformis* reveal influence of precipitation on tree growth. Biotropica 38(3), 375-382.

Trouet, V.**,** Esper, J., Beeckman, H., 2010. Climate/growth relationships of *Brachystegia spiciformis* from the Miombo woodland in southern Africa. Dendrochronologia 28, 161-171.

Tsegaye, D., Moe, S.R., Haile, M., 2009. Livestock browsing, not water limitations, contributes to recruitment failure of *Dobera glabra* in semiarid Ethiopia. Rangeland Ecology and Management 62, 540-549.

Varghese, A., Ticktin, T., 2008. Regional variation in non-timber forest product harvest strategies, trade, and ecological impacts: the case of black dammar (*Canarium strictum* roxb.) use and conservation in the Nilgiri Biosphere Reserve, India. Ecology and Society 13(2), 11. http://www.ecologyandsociety.org/vol13/iss2/art11/.

Verheyden, A., 2004. Rhizophora mucronata *wood as a proxy for changes in environmental conditions:* A study of the wood anatomy, stable isotope chemistry and inorganic composition of a Kenyan mangrove species. PhD thesis, Vrije Universiteit Brussel. Belgium.

Verheyden, A., Kairo, J.G., Beeckman, H., Koedam, N., 2004. Growth rings, growth ring formation and age determination in the mangrove *Rhizophora mucronata*. Annals of Botany 94, 59-66.

Volland-Voigt, F., Bräuning, A., Ganzhi, O., Peters, T., Maza., H., 2011. Radial stem variations of *Tabebuia chrysantha* (Bignoniaceae) in different tropical forest ecosystems of southern Ecuador. Trees 25:39-48.

Vollesen, K., 1989. Burseraceae. In: Hedberg, I. and Edwards, S. eds. *Flora of Ethiopia*. Volume 3, Addis Ababa, Ethiopia, pp.442-478.

Wainhouse, D., Staley, J., Johnston, J., Boswell, R., 2005. The effect of environmentally induced changes in the bark of young conifers on feeding behaviour and reproductive development of adult *Hylobius abietis* (Coleoptera: Curculionidae). Bulletin of Entomological Research 95, 151-159.

Wang, G., Zhu, G., 1994. Factors on resin yield of *Pinus elliottii*. Journal of Forest Chemical Industry 1, 27-29.

Wang, Z.,Calderonb, M., Carandang, G., 2006. Effects of resin tapping on optimal rotation age of pine plantation. Journal of Forest Economics 11, 245-260.

Wassie, A., Sterck, F., Teketay, D., Bongers, F., 2009. Tree regeneration in church forests of Ethiopia: effects of microsites and management. Biotropica 41, 110-119.

Way, D.A., and R, F. Sage., 2008. Thermal acclimation of photosynthesis in black spruce [*Picea mariana* (Mill.) BSP]. Plant Cell Environ. 31, 1250-1262.

WBISPP, 2004. Forest resources of Ethiopia. Addis Ababa, Ethiopia. pp. 32.

Wekesa, C., Makenzi, P., Chikamai, B. N., Lelon, J.K., Luvanda, A. M., Muga, M., 2009. Gum arabic yield in different varieties of *Acacia senegal* (L.) Willd in Kenya. African Journal of Plant Science 3 (11), 263-276.

Wertin, T.M., McGuire, M.A.,Teskey, R.O., 2011. Higher growth temperatures decreased net carbon assimilation and biomass accumulation of northern red oak seedlings near the southern limit of the species range. Tree Physiology 31, 1277-1288.

Whipple, S., Dix, R., 1979. Age structure and successional dynamics of a Colorado Subalpine Forest. American Midland Naturalist 101(1), 142-158.

Wiedenhoeft, A.C., Miller, R.B., 2002. Brief comments on the nomenclature of softwood axial resin canals and their associated cells. IAWA Journal 23, 299-303.

Wils, T.H.G., Robertson, I., Eshetu, Z., Sass-Klaassen, U.G.W., Koprowski, M., 2009. Periodicity of growth rings in *Juniperus procera* from Ethiopia inferred from crossdating and radiocarbon dating. Dendrochronologia*,* 27, 45-58.

Wils, T.H., Robertson, I., Eshetu, Z., Koprowski, M., Sass-Klaassen, U.G.W., Touchan, R., Loader, N.J., 2010. Towards a reconstruction of Blue Nile baseflow from Ethiopian tree rings. The Holocene 20, 837-848.

Wils, T. H., Sass-Klaassen, U.G.W., Eshetu, Z., Bräuning, A., Gebrekirstos, A., Couralet, C., Robertson, I., Touchan, R., Koprowski, M., Conway, D., Briffa, K. R., Beeckman, H., 2011. Dendrochronology in the dry tropics: the Ethiopian case. Trees 25, 345-354.

Wimmer, R., Grabner, M., 1997. Effects of climate on vertical resin duct density and radial growth of Norway spruce *(Picea abies* (L.) Karst.). Trees 11: 271-276.

Woldeamanuel, T., 2011. *Dryland resources, livelihoods and institutions.* Diversity and dynamics in use and management of gum and resin trees in Ethiopia. PhD Thesis, Wageningen UR, The Netherlands.

Worbes, M., 1995. How to measure growth dynamics in tropical trees, a review. IAWA Journal 16, 337-351.

Worbes, M., 1999. Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. Journal of Ecology 87, 391-403.

Worbes, M., 2002. One hundred years of tree-ring research in the tropics-a brief history and an outlook to future challenges. Dendrochronologia 200, 217-231.

Worbes, M., Staschel, R., Roloff, A., Junk, W.J., 2003. Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. Forest Ecology and Management 173, 105-123.

Worbes, M., Fichtler, E., 2010. Wood anatomy and tree-ring structure and their importance for tropical dendrochronology. *In*: Junk, W.J., Piedade, M.F.T., Parolin, P., Wittmann, F., Schöngart, J. (Eds.): *Amazonian Floodplain Forests:. Ecophysiology, Biodiversity and Sustainable Management*. Springer Ecological Studies. pp. 329-346.

Worku, A., Lemenih, M., Fetene, M., Teketay, D., 2011. Socio-economic importance of gum and resin resources in the dry woodlands of Borana, southern Ethiopia. Forests, Trees and Livelihoods 20 (2-3), 137-155.

Wright, S.J., 2010. The future of tropical forests. Annals of the New York Academy of Sciences 1195, 1-27.

Xing, P., Zhang Q.B., Baker, P.J., 2012. Age and radial growth pattern of four tree species in a subtropical forest of China. Trees 26, 283-290.

Zheng, G., Xu, B., 1992. Economic analysis resin production from *Pinus elliottii* plantation. Chemistry and Industry of Forest Products 12, 11-13.

Zida, D., Sawadogo, L., Tigabu, M., Tiveau, D., Odén, P. C., 2007. Dynamics of sapling population in savanna woodlands of Burkina Faso subjected to grazing, early fire and selective tree cutting for a decade. Forest Ecology and Management 243, 102-115.

Zuidema, P.A., Brienen, R.J.W., Schöngart, J., 2012. Tropical forest warming: looking backwards for more insights. Trends in Ecology and Evolution 4, 193-194.

Summary

The majority of the landmass area of Ethiopia is covered by drylands characterized by strong seasonality in rainfall. These areas host woodlands and shrub lands that cover about 50% of the country. In those woodlands, many tree species produce gum and resin, and one of them is *Boswellia papyrifera*. This species dominates the *Combretum–Terminalia* deciduous woodlands of North-Western Ethiopia, and better survives on rocky sites and harsh environments than most other tree species. *B. papyrifera* is considered an economically, socially and ecologically important species and is particularly known for its production of frankincense. The historical value of frankincense is illustrated by the gifts of the three kings (frankincense, myrrh and gold) to Jesus Christ (Matthew 2:11). Nowadays, frankincense is globally used for church ceremonies and as raw material in pharmaceuticals and cosmetics. Ethiopia is a major producer and exporter of frankincense and it contributes to more than 90% of the volume of gum and resin products exported from Ethiopia. *B. papyrifera* is also used to meet the demand for wood products such as firewood and construction materials.

The area of woodlands dominated by *B. papyrifera* is declining. Currently, many of the remaining populations lack trees in smaller size classes (DBH <= 10 cm) and the remnant trees are facing high adult mortality. The main reasons for such rapid losses are land-use change, overgrazing, fire and improper tapping. Global warming may induce additional stress to the trees and populations of this species. Sustainable management of the remnant populations, including solutions for lack of successful recruitment, is crucial to ensure the maintenance of socio-economic and ecological services. The major objectives of this study are to (1) investigate the current status of *B. papyrifera* populations with respect to radial-growth dynamics, size and age structure and climate impacts and (2) characterize its resin-secretory system and evaluate how the structure of this system explains the current patterns in frankincense yield. The study was conducted in *B. papyrifera* populations located in the Metema district, North-Western Ethiopia. Growth-ring analysis was used as an essential tool to assess radial stem growth dynamics and age structure of this species.

This study shows that *B. papyrifera* forms annual growth rings. Consequently, it was possible to investigate radial-growth dynamics, age-diameter relationships, population-age structure and climate-growth relationships for *B. papyrifera* tree populations. We show the age structure of remnant trees of *B. papyrifera*, which implies that trees continuously regenerated during the period of 1903 to1955. The populations have never been refreshed with younger

trees for about the last half century. The lack of successful recruitment for such a long period of time is attributed to intensive grazing and fire associated with the escalating increase of human settlement in the area. These stress factors may also be aggravated by changes in climate. This study also shows that radial stem growth of *B. papyrifera* benefits from more rainfall and higher maximum and average temperatures, but may be negatively affected by increasing minimum temperature. From these results, it remains highly uncertain whether the predicted higher rainfall and higher temperatures will positively or negatively influence the stem growth of these trees in the future. As a consequence of mainly the lack in recruitment, rapidly declining populations resulting in strongly reduced frankincense production is expected.

In this study, patterns in frankincense yield under different tapping regimes reported by other studies were linked to the distribution and architecture of the resin-secretory system. We showed that the density and the intactness of the network of resin canals decreases from the vascular cambium across the different zones of the inner bark towards the outer bark. This explains why frankincense yield increases during the first tapping rounds and declines in later tapping rounds: with successively deeper cuts during the first tapping rounds, the tapping wounds get closer to the zones of the inner bark close to the cambium, where an intact network of resin canals in high density is present from which resin can be drained. Once most of the resin is drained, the yield will decline with later cuts into the intact zone of the inner bark.

This study also shows that frankincense yield is determined jointly by resin canal and other tree characteristics. Total area of resin canals, tree diameter, tree age and number of leaf apices jointly explain large variation in frankincense which can be yield from one tree. As expected, large and vital trees yield most frankincense. Based on this knowledge together with the insights gained on the resin-secretory system we discuss how to improve tapping strategies in order to maximize frankincense yield and minimize impact on the trees. The latter could be achieved by deeper cuts into the intact inner bark during the start of tapping season to efficiently drain more resin with fewer cuts. Based on the structure and resin-canal network we moreover discuss the strategy to reduce the number of tapping spots as a higher number of tapping spots may not necessarily increase frankincense yield due to the fact that they may drain resin from the same pool. These findings can be used as a basis to set experiments to reduce the number of tapping spots and tapping rounds per season to minimize the stress posed by tapping on the trees. Our results can also be useful to guide selection of cutting material for plantations that will lead to higher frankincense yield.

Finally, we conclude that active restoration measures are urgently needed to save this species and its economic, social and ecological benefits. Exclosures with active rehabilitation measures like enrichment planting, fire control, resting from tapping and introducing new tapping techniques that aims at minimizing the stress from tapping may serve as possible options to sustainably manage the resource.

Ethiopië omvat veel droge gebieden die gekenmerkt worden door een sterke seizoenvariatie in neerslag. Deze gebieden worden gedomineerd door bomen en struiken en nemen ongeveer 50% van het land in. *Boswellia papyrifera* is één van de vele boomsoorten die er hars produceren. Deze bladverliezende soort domineert in de zogenaamde *Combretum-Terminalia* vegetaties in Noord-West Ethiopië, en overleeft beter op de droge, rotsige bodems dan de meeste andere soorten. *B. papyrifera* is een belangrijke soort in economisch, sociaal en ecologisch opzicht en staat bekend om zijn productie van wierook. Handel in wierook heeft een lange traditie, en was één van de geschenken van de drie koningen na de geboorte van Jesus Christus (Matthew 2:11). Tegenwoordig wordt wierook gebruikt in kerkceremonies over de hele wereld, en dient als grondstof in de farmaceutische en cosmetisch industrie. Ethiopië is een belangrijk productie en exportland van gommen en harsen, en deze handel bestaat uit meer dan 90% uit wierook. *B. papyrifera* bomen worden ook gesnoeid of gekapt om te voldoen aan de vraag naar houtproducten, zoals brandhout en constructiematerialen.

De gebieden waarin *B. papyrifera* nog voorkomt nemen af in omvang. In de resterende populaties ontbreken vaak de jonge en kleine bomen (DBH<10 cm), en grotere, volwassen bomen lopen een verhoogd risico op sterfte. De belangrijkste oorzaken van deze situatie zijn veranderingen in landgebruik, overbegrazing, vuur en het onzorgvuldig oogsten ("tappen") van wierook. Globale opwarming kan extra stress opleveren voor deze bomen en populaties. Het duurzaam beheren van de resterende populaties, en het vinden van oplossingen om deze populaties te verjongen, zijn essentieel om de sociaaleconomische en ecologische waarden van deze soort te behouden. De doelstellingen van deze studie zijn daarom : (1) het beschrijven van de huidige status van *B. papyrifera* populaties met betrekking tot de stamgroei dynamiek, structuur in grootte en leeftijd, en de invloed van het klimaat. (2) het karakteriseren van de wierook producerende structuren en het evalueren hoe deze structuren de patronen in wierook productie bepalen. Boomringen zijn verzameld en geanalyseerd om de stam groei dynamiek en leeftijdsopbouw van populaties te beschrijven. Alle informatie betrof enkele *B. papyrifera* populaties gelegen in het district Metema, in Noord-West Ethiopië.

Deze studie toont aan dat *B. papyrifera* bomen jaarlijkse ringen vormen in het stamhout. Op basis hiervan kon het onderzoek beginnen naar de stam groei dynamiek, leeftijd-diameter relaties, leeftijdsopbouw van populaties en klimaat-groei relaties. De huidige leeftijdsstructuur laat zien dat jonge bomen van *B. papyrifera* succesvol opgroeiden in de periode van voor

1955, maar dat de verjonging volledig is gestopt gedurende de laatste 50 jaren. Het ontbreken van enige verjonging gedurende een dergelijke lange periode kan worden verklaard door de intensievere vormen van begrazing en branden met het vestigen van meer mensen in deze regio. Het klimaat zou ook een rol kunnen spelen. Dit onderzoek laat echter zien dat de stam groei van de bomen toeneemt met meer neerslag en hogere maximum temperaturen, maar afneemt met hogere minimum temperaturen. Het blijft dus uiterst onzeker wat de invloed zal zijn van de voorspelde toename in neerslag en temperatuur. Op grond van het ontbreken van verjonging wordt echter een snelle afname van de resterende populaties verwacht.

In mijn onderzoek probeer ik patronen in wierook opbrengst bij verschillende oogstregimes te verklaren vanuit de verspreiding en architectuur van het hars-producerend systeem. Het blijkt dat de dichtheid en functionaliteit van het harskanalen netwerk afneemt vanaf het vasculaire cambium, van de binnenste bast in de richting van de oudste bast. Dit kan de toename in wierook opbrengst verklaren gedurende de eerste tapronden en de afname tijdens latere tapronden: met diepere sneden gedurende de eerste tapronden komt de wond dichter bij het intacte weefsel in de binnenste bast, waar een dicht netwerk van harskanalen de toevoer van wierook verzorgt. Na het oogsten van de wierook uit deze zone neemt de productie af, omdat de aanvankelijk volle harskanalen leeggelopen zijn.

Wierook productie hangt niet alleen af van het harskanalen netwerk, maar ook van andere boomkarakteristieken. De enorme variatie in de wierookproductie tussen bomen wordt bepaald door het totale oppervlak van het harskanalen netwerk in een stamdoorsnede, de stam diameter, de boomleeftijd, en het aantal bladeren in de boom. Naar verwachting produceerden grote, vitale bomen, de meeste wierook. Op grond van deze informatie, en onze beschrijving van het hars producerend systeem, worden mogelijkheden besproken om taptechnieken te verbeteren om zo de wierook opbrengt te maximaliseren en de schade te beperken. Diepere sneden tijdens de eerste tapronden en het verminderen van het totaal aantal tapronden zouden kunnen helpen om hoge oogsten te bereiken en bomen minder te beschadigen. Deze eerste inzichten dienen als basis om experimenten op te zetten gericht op het verminderen van het aantal tapronden en de verwondingen. Onze resultaten kunnen ook bijdragen aan het selecteren van de beste bomen om staken te verzamelen, om vervolgens vitale bomen op te laten groeien in plantages en een hoge wierookproductie te verwezenlijken.

Op grond van deze studie constateer ik dat actieve restauratie urgent is om deze soort en haar economische, sociale en ecologische waarden te behouden. Het lijkt erop dat we daarvoor gebieden moeten beschermen tegen grazers, en met actieve rehabilitatie van deze bomen, waarbij geëxperimenteerd wordt met maatregelen zoals beplanting, brandpreventie, periode van rust (geen tappen), en nieuwe taptechnieken om de schade aan bomen binnen de perken te houden, en zo weer vitale populaties van deze soort te kunnen creëren.

Acknowledgement

This thesis has come to this shape through the contribution of many individuals to whom I am very grateful. First of all, I would like to thank my supervisors whose contribution from the beginning to the end was instrumental. I am fortunate to work with such team of supervisors. I am grateful to my promotor, Prof. Frans Bongers, for opening the door for this opportunity and his unreserved scientific contribution from the concept note development to this end and overall management of my study. My special thanks also goes to my co-promotors Dr. Ute Sass-Klaassen and Dr. Frank Sterck for their continuous encouragements and guidance throughout my study. I would like to thank Dr. Ute Sass-Klaassen for introducing me to the science of dendrochronology and also to the dendro scientific community during different TRACE conferences. The deadlines and critical comments from Dr. Frank Sterck have tremendously contributed to the timely accomplishment of this thesis. Dr. Mulugeta Lemenih, who was my mentor throughout my scientific career has played a great role starting from the initiation of this study. I am grateful to his continuous encouragements and all other supports during the whole period of the study.

I am grateful to the staff members and PhD students of the Forest Ecology and Management group of Wageningen University for the fruitful contributions to my thesis and all the nice times shared during different occasions. I would like to thank all staff members; Prof. Frits Mohren, Dr. Lourens Poorter, Dr. Jan den Ouden, Leo Goudzwaard, Dr. Marielos Pena Claros, Dr. Pieter Zuidema, Ellen Wilderink for all the assistances and contributions throughout my study. I also greatly appreciate the unreserved facilitation from Joke Jansen. I would like to thank all the encouragements from my colleagues: Corneille Ewango, Geovana Carreno, Paul Copini, Emiru Birhane, Abeje Eshete, Teshale Woldamanuel, Jean Damascene, Tefera Mengistu, Addisalem Bekele, Gustavo Schwartz, Lennart Suselbeek, Lucy Amissah, Peter van der Sleen, Peter Groenendijk, Monique Weemstra, Masha van der Sande, Mathieu Decuyper, Peter Schippers, Marlene Soriano Candia, Estella Quintero, Madelon Lohbeck, Catharina Jakovac and Mart Vlam. Special thanks go to Britta Eilmann, Paul and Ellen for assistance with lab work and also fruitful discussions and inputs. I also would like to thank Geovana Carreno for her assistance and comments on my draft propositions. It was a great pleasure to get inputs and share ideas with staff and students of the group.

I am grateful to the whole FRAME team and specifically would like to appreciate the encouragements from Dr. Wubalem Tadesse and Dr. Tesfaye Bekele. I also would like to thank Dr. Zewdu Eshetu for all the scientific discussions and encouragements during my study. I would like to acknowledge and thank Dr. Aster Gebrekirstos and Prof. Achim Bräuning for all the material support as well as the unreserved assistances during the whole period of my study. I would like to thank Buruh Abebe, David Menger, Prawindukasih Yogiswari, Muluken Beresa, Mindaye Teshome and Mulugeta Gemi for their collaborations during this study. I also would like to appreciate the field assistances from Abadi Tesfaye and Adane. The assistance in the laboratory from Woiynshet Afework, Mohammad Ali, and also support from Tsige Mekonnen is also highly appreciated. Fanta Yakob deserves a special thanks for all the assistances with Chainsaws in the field as well as other laboratory activities. I also would like to thank the people of Lemlem Terara for the inspiring time passed during the field work. I would like to specifically thank Jemal Seid, Selam Tsehay and Dejene Yirdaw for their assistance during field works and also nice organization of all my stays in Lemlem Terara. I am grateful to all the drivers; Ashenafi Talew, Alemayehu Abiso, Sisay Zewde, Milkiyas Safa and Arefayine G/Meskel who made the long travels to the field work more inspiring and effective.

I greatly thank Dr. Gert-Jan Reichart and other staff of the Laboratory of Geochemistry of Utrecht University for the support to analyse Carbon and Oxygen isotopes from tree rings. The contribution from Ellen Wilderink during this analysis was again very instrumental. The financial support from Schure-Beijerinck Popping Fund for the isotope analysis is also highly acknowledged. This work unfortunately has not become part of this thesis, but surely will be further developed in the near future.

I greatly thank Dr. Abdella Gure, Dr. Zebene Asfaw, Alemnega Degefa, Dr. Feyera Senbeta, Dirriba Nigussie, Dr Erik Karltun, Dr. Girma Mengesha, Dr. Fekadu Gemechu, Tola Gemechu, Megersa Debele, Dr. Bekele Lemma, Dr. Melaku Bekele, Habtamu Debele Dr. Tsegaye Bekele, Wondimu Aklilu, Ethiopia Kassa and Alemayehu Negasa for the encouragements and all the supports during this study.

I am very grateful to my wife, Tiki Wami, whose contribution was exceptional during all the journeys of my scientific career. She refrained from all the opportunities to give me the chance to grow in my scientific endeavours. I feel short of words to express her contribution in all regards. I would like to thank my sons Firaol and Nafyad and my daughter Meti for all their patience during my study. My parents who decided to send me to school as one of the few colleagues to enjoy such opportunity also deserve special thanks. I would like to appreciate the contribution from my father, Tolera Feyissa, who was also my first teacher for opening my eyes to education. My mother also took historic decision to take all the burdens to send me to school. Finally, I would like to thank my brothers Teshale, Tamena, Kabe and Gadisa and their families for all their encouragements.

Finally, I would like to thank and acknowledge the financial support of Wageningen University, Wondo Genet College of Forestry and Natural resources through its Sida grant and British Ecological Service (BES grant number 2732/3420). This research is also supported by the Dutch-Ethiopian FRAME programme ‘FRAnkincense, Myrrh and arabic gum: sustainable use of dry woodland resources in Ethiopia’, funded by NWO (WOTRO; W01.65.220.00).

Short biography

Motuma Tolera Feyissa was born on June 20, 1972 in Arsi Negelle district, South central Ethiopia from a farm family. He attended elementary and junior secondary school at Sogido Elemetary School in the same area of his birth place. He attended high school at Abiyot Kirs Senior Secondary School, Addis Ababa. He joined Haramaya University of Agriculture in September 1991 and graduated with BSc degree in forestry in July 1995. In June 1996, he joined Shashemene-Munessa state forest development and utilization project (now part of Oromiya Forest and Wildlife Enterprise) and worked as Block-ranger, Branch manager and Head of planning division for a total of five and half years. He considers the opportunity to work at the mentioned organization as a second school where he gained skills of working with practical challenges of forestry in Ethiopia. He then joined Wondo Genet College of Forestry and Natural Resources as a graduate assistant. With this capacity, he assisted and partly thought courses like Forest Management, Forest Mensuration and Plantation Establishment.

In September 2004, he joined MSc program at Wondo Genet College of Forestry and graduated in July 2006 in Farm Forestry. His research was on "Woody species diversity in a changing landscape in the south-central highlands of Ethiopia" and it is published in Agriculture, Ecosystems and Environment (Issue 128, pages 52-581). He was then given the opportunity to coordinate a development-oriented interdisciplinary action research project which was jointly run by Wondo Genet College of Forestry and Natural Resources and Swedish University of Agricultural Sciences for about three years. He was also involved in a research project entiltled "making soil quality last-participatory soil fertility management in the south central Ethiopia" collaborating with researchers from Swedish University of Agricultural Sciences. During this time, he coordinated more than 20 interdisciplinary research projects which involved more than 50 researchers. These opportunities have given him the chance to learn social research methodologies and closely work with farmers and other key stakeholders in forestry. During this period he was also involved in teaching of the courses such as Farming systems and Ethnobotany and Agrobiodiversity.

In June 2009, Motuma joined Wageningen University as a Sandwich PhD student at Forest Ecology and Forest Mangement group and studied dendrochronology of the frankincense tree. Motuma is married with Tikki Wami in 1996 and has three children.

List of Publications

1. **Tolera, M**., Sass-Klaassen, U., Eshete, A., Bongers, F., Sterck, F.J., 2013. Frankincense tree recruitment failed over the past half century. *Forest Ecology and Management* 304, 65-72.

2. **Tolera, M.,** Menger, D., Sass-Klaassen, U., Sterck, F.J., Copini, C., Bongers, F., 2013. Resin secretory structures of *Boswellia papyrifera* and implications for frankincense yield. *Annals of Botany* 111, 1-8.

3. Karltun, E., Lemenih, M., **Tolera, M**., 2013. Comparing farmers' perception of soil fertility change with soil properties and crop performance in Beseku, Ethiopia. *Land Degradation and Development,*24(3),228-235

4. Lemenih, M., Karltun, E., **Tolera, M.,** 2012.Crop yield and soil organic matter effects of four years of soil management interventions in Arsi Negele, South Central Ethiopia. In: Mulugeta Lemenih, Getachew Agegnehu and Tilahun Amde (eds.) Soils for sustainable development. Proceedings of the 12th ESSS conference, March 17-18, 2011, Addis Ababa, Ethiopia, pp. 97-107.

5. Chiwona-Karltun, L., Lemenih, M., **Tolera M.**, Berisso, T., Karltun, E., 2009. Soil fertility and crop theft: changing rural dimensions and cropping patterns. Proceedings of seasonality revisited: 8-9 July, Institute of Development Studies, UK.pp 3-18.

6. Karltun, E., Roing de Nowina, K., Chiwona-Karltun, L., Lemenih, M., **Tolera, M**., Berisso, T., 2008. Working with farmers and local institutions to improve soil quality in Sub-Saharan Africa. *Currents*, **43**:7-11.

7. Lemenih, M., **Tolera, M**., Karltun, E., 2008. Deforestation: Impact on Soil Quality, Biodiversity And Livelihoods in the Highlands of Ethiopia, In: Ilya B. Sanchez and Carl L. Alonso (Eds), *Deforestation Research Progress*. Nova Science Publishers, Inc. PP. 21-39.

8. **Tolera, M.**, Asfaw, Z., Lemenih, M., Karltun, E., 2008. Woody species diversity in a changing landscape in the south-central highlands of Ethiopia. *Agriculture, Ecosystems and Environment* 128: 52-581.

Education Certificate

PE&RC PhD Training Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)
- Potential of dendrochronology to study growth and population dynamics of the frankincense tree

Writing of project proposal (4.5 ECTS)
- Growth and population dynamics of ABC species in response to climate change in Ethiopia (2009)

Post-graduate courses (7 ECTS)
- Understanding global environmental change: processes, compartments and interactions; SENSE (2009)
- Generalized linear model for ecologists; SENSE (2009)
- Wood anatomy and tree ring ecology; WSL (2010)

Laboratory training and working visits (4.8 ECTS)
- Laboratory techniques of tropical dendrochronology; Tervuren, Belgium (2009)
- Isotope and trace element analysis; Utrecht University (2011)

Deficiency, refresh, brush-up courses (3 ECTS)
- Ecological methods I (2010)

Competence strengthening / skills courses (2.8 ECTS)
- PhD Competence assessment (2009)
- Training on R and SAGA-GIS; Hawassa University (2011)

PE&RC Annual meetings, seminars and the PE&RC weekend (3 ECTS)
- PE&RC PhD weekend (2009)
- Ecological theory and application (2009, 2011, 2012, 2013)
- PE&RC Day (2011)

Discussion groups / local seminars / other scientific meetings (4.4 ECTS)
- CIFOR workshops on dry land forests (2009, 2012)
- FRAME workshops (2011)
- Research review; Hawassa University (2012)

International symposia, workshops and conferences (4 ECTS)
- TRACE Conference; oral presentation; Potsdam, Germanay (2012)
- TRACE Conference; oral presentation; Viterbo, Italy (2013)

Supervision of 4 MSc Students
- Detection and periodicity of growth-rings in *Boswellia papyrifera*
- Resin producing structures in *Boswellia papyrifera* and the anatomical response on tapping for frankincense
- Age structure of *Boswellia papyrifera* populations in Metema, Northern Ethiopia
- Climate-growth relationship of the frankincense tree from Southern Ethiopia

FRAME: Frankincense, Myrrh and gum arabic: sustainable use of dry woodland resources in Ethiopia

More than half of the total land area in Ethiopia is covered by arid to semiarid woodlands with marginal agricultural potential. These woodlands are commonly overexploited for their natural resources, which reduces the local livelihood options for a rapidly expanding population. Climate change (e.g. drought) may intensify this negative trend. Consequently, there is an urgent need for improved land-use strategies that will make the vast arid and semiarid woodland resources optimally contribute to the livelihoods of local people and national development goals.

The dry woodlands in Ethiopia are not resource poor as they host several woody species that hold economically well recognized aromatic products such as gum arabic, frankincense and myrrh, which are widely used locally and in several of today’s commercial industries such as cosmetic, pharmacological and food industries. Frankincense and myrrh are among the oldest internationally traded commercial tree products. Ethiopia is worldwide the main producer of frankincense and myrrh, and exports much gum arabic. Gum/resin production could significantly contribute towards sustainable development of these dry woodland areas. However, the overexploitation of natural resources by intensive grazing and intensive resin/gum harvesting and the lack of land management threatens the sustainability of the woody vegetation, and as a result of that also the long-term gum/resin production. Local communities may also enhance the productive capacity of the natural vegetation by establishing protected enclosures and by cultivation of trees. Such production systems may have a lower status regarding biodiversity and natural ecosystem functioning, but maintain ecological buffering capacity and improve production for human benefit.

The FRAME program addresses the following main research question: in what way dry land forests in Ethiopia can be made productive while maintaining ecosystem integrity in terms of sustainability of production and vegetation cover, with special attention to resin and gum resources?

FRAME uses a multidisciplinary approach involving scientific disciplines ranging from landscape-level geo-information studies to village-level socio-economic studies, plot level ecological and harvesting technology studies to tree-level ecophysiological studies with a strong contribution of local knowledge in answering the central research question. FRAME thus establishes a scientific basis for the sustainable management, including cultivation, of gum and resin yielding tree species and their habitat, the dry woodlands in the Horn of Africa. FRAME is actually involved in development of long-term scenarios for proper use and selection of suitable areas of dry woodland resources in Ethiopia.

The current PhD thesis is part of this FRAME program. A large part of this integrated FRAME research program was financially supported by NWO-WOTRO (Netherlands Organization for Scientific Research- Science for Global Development), grant W01.65.220.00.