THE FRANKINCENSE TREE OF ETHIOPIA

ecology, productivity and population dynamics

Abeje Eshete Wassie

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thesis committee

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

thesis co-supervisor
Dr. Ir. F. J. Sterck
Assistant professor at the Forest Ecology and Forest Management Group
Wageningen University

other members
Dr. T. Bekele, Ethiopian Institute of Agricultural Research, Addis Ababa, Ethiopia
Prof. Dr. L. Brussaard, Wageningen University
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Prof. Dr. B. Muys, Catholic University Leuven, Belgium

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To my father (Eshete Wassie) who passed before his dream comes true

To my mother (Bosena Alemu) who did more than enough for my life

Abstract

Combretum – Terminalia woodlands and Acacia – Commiphora woodlands are the two dominant vegetation types that cover large parts of the dry land areas in Ethiopia. Several of their tree and shrub species yield economically valuable products such as gum Arabic, frankincense and myrrh. *Boswellia papyrifera* provides the widely traded frankincense that accounts for >80% of the export revenues that the country is earning from gum and resin resources. Unfortunately, the Ethiopian dry woodlands and the *B. papyrifera* populations are disappearing rapidly due to the combined effects of over-harvesting gums and resins, overgrazing by livestock, recurrent fires, and excessive wood harvesting. The current lack of small saplings in the remaining populations of Boswellia suggests that the populations may not be sustained for the future.

The main objectives of this thesis were to determine diversity and production patterns in *B. papyrifera* dominated dry woodlands, to show the regeneration status in various *B. papyrifera* populations, and to evaluate the effects of environment, frankincense harvesting, and grazing on the population dynamics of *B. papyrifera*. The main research questions were: (1) how do environmental conditions affect the tree/shrub species richness and production of Ethiopian dry woodlands? (2) what factors determine the frankincense production by *B. papyrifera* trees? (3) how do the vital rates and population dynamics of *B. papyrifera* vary across habitats that differ in soil conditions and biotic factors? (4) What are the major bottlenecks in the life cycle of the trees that hinder the sustainability of the remaining populations? To address these questions, tree populations were studied in the highlands of Abergelle and the lowlands of Metema. Metema also has a longer wet season length, higher annual rainfall and better soil fertility status than Abergelle.

In total 36 and 22 tree and shrub species representing 20 and 9 families were recorded in Metema and Abergelle woodlands, respectively. The most dominant plant families were *Burseraceae, Fabaceae, Combretaceae* and *Anacardiaceae*. The vegetation at both sites was dominated by *B. papyrifera*. The two sites differed in species richness, diversity and production. Metema, the site with the longer wet season, had a higher species richness, diversity and production than Abergelle. The productivity of woodlands also increased with a higher clay content and greater soil depth. Populations structures indeed lacked the saplings, except for one very isolated population on a steep mountain slope.

The studied frankincense trees produced 41 to 840 gram of frankincense during a year with seven collection rounds, and 185 to 1826 gram of frankincense during a year with 14 collection rounds. The variation in frankincense production was large across individuals. Frankincense production increased with tree size, tapping intensity, and tapping frequency. The increase in production, however, levelled-off beyond a stem diameter of 20 cm, a tapping intensity of 9 spots, and a tapping intensity of 10 rounds. Growth rate, survival rate and fruiting probability varied across populations, but were not related to soil conditions or biotic factors. The growth rates of the 12 Metema populations varied between 0.86 to 0.98, suggesting that they were all decreasing. Matrix model analyses indicated that the mortality of adult trees was the major bottleneck for sustainable population growth, and that the lack of sapling recruitment was a second major bottleneck. These bottlenecks appear both in tapped and non-tapped stands. Remarkably, tapped stand showed higher growth rates than non-tapped stands, probably because productive stands were selected for harvesting resin.

All results suggest that the remaining populations of *B. papyrifera* will disappear in the near future if the current situation continues. Frankincense production is expected to halve in 15-20 years. Unexpectedly, tapping had no negative effect on vital rates, nor on population growth rates indicating that other factors are responsible for the decline of the populations. Adult mortality by insect infestation and windfall, and the negative impact of grazing and fire on the establishment of saplings need extra attention. Management should be directed towards releasing two major population bottlenecks (improve sapling regeneration, reduce adult mortability) to maintain the Boswellia populations and frankincense production in the future.

Keywords: *Boswellian papyrifera*, Frankincense tree, matrix model, population dynamics, population bottleneck, tapping.

Contents

Chapter 1

Introduction

SPECIES RICHNESS AND DIVERSITY OF TROPICAL DRY FORESTS

Tropical dry forests occur at a lower annual rainfall and stronger seasonality in rainfall than the wetter tropical rain forests . Tropical dry forests are poorer in species than rain forests (Gentry 1995), which has been attributed to a longer dry season and a lower annual precipitation. Dry forest are however very diverse and differ in the vegetation composition, structure, species richness and diversity due to different climates, soils, biogeographic histories and disturbance regimes across the globe or at more local scales (Murphy and Lugo 1986b). How and why the tropical forest productivity and diversity varies so largely at different spatial scales inspired ecologists for collecting large datasets of tropical forests (Gentry 1995), but the drier forest are relatively poorly know in this respect.

For tropical dry forests a number of variables have been identified that are associated with plant species richness and diversity. Variables affecting species richness include annual and seasonal distribution of precipitation, temperature, soil nutrients, habitat area and various forms of disturbance, such as fire, grazing and plant or plant product harvests by people. The amount of annual precipitation and a shorter dry season are correlate positively with species richness, but not anymore when the rainfall threshold has been reached that allows for a closed-canopy dry forest (Gentry 1988, Ter Steege et al. 2000). Soil nutrients also play a role, but the greatest plant species richness is observed at intermediate nutrient values (Huston 1979, Tilman 1982, Ashton 1992). With increasing altitude, the general trend is a decline in species richness (Wassie et al. 2010b, Gentry 1988, Lieberman et al. 1996). Anthropogenic disturbances is widely believed to influence species diversity in these dry forests (Connell 1978, Huston 1979). The intermediate disturbance hypothesis proposed that species richness peaks at intermediate disturbance level because superior competitor species monopolize resources and exclude other species at low levels of disturbance, whereas at high disturbance levels only the most damage resistant species survive (Grime 1973; Connell 1978). Several research studies tried to validated the hypothesis (Bongers et al. 2009; Molino & Sabatier 2001), but the empirical proof is not general for tropical forest and is particularly poorly known for dry forests (Mackay and Currie 2001).

TROPICAL DRY FORESTS PRODUCTS

Forests provide a great variety of products and services to human kind. The major economic value of forests comes from wood of trees, used or traded as lumber, plywood, fuel wood or charcoal. Other economic importance include food, medicines, fodder for livestock, natural gums, etc. The latter collectively called non-timber forest products (NTFPs) (Ros-Tonen et al. 1995). For tropical dry forests, NTFPs are a major source of livelihood and cash income for the majority of rural households and many urban households as well in developing countries (FAO 1989, Wollenberg & Ingles 1998 1998, Lemenih et al. 2003).

While less rich in species than wet forests, tropical dry forest provide habitats for a large number of tree species (Hegner, 1979; Murphy and Lugo, 1986a; Wassie et al., 2010a; White, 1983), many of them being used by local communities for a multitude of products and services. Countries that consist of large dry tropical forests, such as many countries in Africa, do not export timber in quantities as observed for countries with tropical rain forests (Dufournaud et al., 1995), but rather provide sources of fuel, construction, and furniture to local or international markets. Fuel wood provides >80% of the energy supply in most Sub-Saharan countries (Pearce and Turner, 1990). Dry forests also provide NTFPs like resins, gums, bark, leaves, grass, bamboo, fern, tubers, fruits, fungi, honey, bees wax, animal products etc, that are used for food and medicine and as sources for running a local cash economy. Some of NTFPs are widely traded in local, regional and international markets, such as natural gum and resins of dry forests running from east to west below the Sahel in Africa. Gum Arabic and Frankincense are traded in the greatest volumes and improve livelihoods of local communities in terms of products and income, and also provide national foreign exchange earnings (Lemenih et al. 2003, Chikamai 2002). Moreover, the trees that produce such product are also important as buffer against soil erosion and desertification (Pearce et al., 1990). In this thesis, I studied Ethiopian tropical dry forest, or woodland, dominated by the resin producing Frankincense trees.

ETHIOPIAN DRY FORESTS/WOODLANDS

Ethiopia's total surface area amounts 1.22 million km2. The country is ecologically very diverse owing to diverse physio-geographic features with high and rugged mountains, flat topped plateaux, deep gorges, incised river valleys and rolling plains. The altitudinal diversity ranges from 110 m below sea level to 4620 m above sea level. Ethiopia experiences a very high variation in macro and micro-climatic conditions that have contributed to the formation of diverse ecosystems inhabited with a great diversity of life forms of both animals and plants. The mean annual rainfall ranges from 500 to 2800 mm and with high variation in temperature (>30 oC and < 10 oC (Demissew and Nordal 2010, Such diverse ecological conditions enabled the country to inhabit > 7000 higher plants of which about 12% is considered to be endemic (Tewolde 1991).

While Ethiopia is considered a mountainous country, more than 70% of the land surface is considered lowland dry area (Tamire, 1997). The Institute of Biodiversity Conservation (IBC 2007) has grouped vegetation of Ethiopia into 10 categories based on the results of other studies and, more recently, Friss et al. (2010) classified the vegetation resources of Ethiopia into 12 vegetation types, out of which seven are encountered in dry lowland areas. The two dominant dry forest types in these dry land areas are the Combretum – Terminallia woodlands and the Acacia – Commiphora woodlands.

The Combretum–Terminalia woodland and wooded grassland vegetation that are located in the lowland dry areas occur in large parts of the lowland of north western and western parts (Gondar, Gojam Wellega, Illubabor) and south western region (Gamo Gofa, Kefa) of the country. This Combretum–Terminalia woodland vegetation is often dominated by a combination of *Boswellia papyrifera, Anogeissues leiocarpa, Terminalia brownii, Combretum collinum, Balanites aegyptiaca, Commiphora africana, Erythrina abyssinica, Stereospermum kunthianum, Gardenia lutea, Lannea schimperi, Piliostigma thonningii,* and *Lonchocarpus laxiflorus.* The species composition varies most strongly with altitude, ranging from 500 masl to 1.900 masl (Awas et al. 2001, Awas 2007). Eighty percent of the 199 woody species recorded here are considered endemic for this vegetation. This vegetation provide livelihood diversification, wood and food security, animal feed, human health care and environmental conservation to rural and urban households (Lemenih and Teketay 2003a).

The Acacia – Commiphora woodlands occur in the north, east, south and central parts of the country, mainly east of the highlands and in the rift valley (Friis et al. 2010). The common species in this vegetation type include species of the genera *Acacia, Commiphora, Zizyphus, Maerua, Cadaba, Boscia, Euphorbia, Aloe,* and *Sansevieria*. The most common species include *Acacia tortilis, A. etbaica, A. seyal, A. abyssinica, A. spirocarpa subsp. spirocarpa, A. mellifera, Ballanites eagyptica and Erythrina, Aerva spp., Acalypha spp.,* and *Barleria spp*. This composition also varies mainly with altitude, also running from 500 to 1900 m.a.s.l. Annual rainfall is however lower and ranges from 410 to 820 mm. Of the 565 species recorded, 286 (~53%) are considered endemic. The Combretum – Terminalia woodland and Acacia – Commiphora woodland are both dominated by gum and resin producing tree species, and the gums and resins in particular Arabic gum and Frankincense are economically very important non-timber forest products.

Frankincense: a major non-timber forest product of Ethiopia

The main sources of frankincense are tree or shrub species of the genera Boswellia (Burseraceae). The genera Boswellia is composed of about 20 species. The six Boswellia species of Ethiopia include *B. microphyllae, B. neglecta, B. ogadensis, B. rivae, B. papyrifera* and *B. pirrotae* (Vollesen, 1989). Of the three frankincense types Tigray, Ogaden and Borena, the Tigray frankincense type produced by *B. papyrifera* through tapping its bark is the most widely traded from Ethiopia and accounts for >80% of all gum and resin export (Eshete 2002, Tadesse et al. 2007). Organizations or local cooperatives are engaged in collecting, processing and marketing this product, but local communities may also harvest more locally. Moreover, people may benefit from the activities of the more commercial enterprises providing employment. Frankincense has been and is still used for religious rituals and the traditional coffee ceremony, as well as for yielding volatile oils, balsamic odours, which are used in perfumery industry (Lemenih and Teketay 2003b).

Adequate information is lacking on the potential as well as the actual production of gum and resin in Ethiopia (Tadesse et al. 2002, 2007). Fitwi (2000), however, indicated a potential of more than 300,000 metric tons of natural gum per year. While the actual maximum production was only 3,421 tons in 1994 during the period 1992-1999 (Fitwi, 2000) indicating that the resource is being underutilized. The major economic importance of gum and resin resources in Ethiopia is the generation of income to the government and foreign currency to the country. The total value of gum and resins exports from Ethiopia was US $34,138,670 for the period between 1998 to 2007 from the export of 25,192 tons, approximately an average of 2,519 tons per year (Lemenih and Kassa 2008). None the less, the total amount of gum and resins produced and exported in Ethiopia showed an increasing trend from 1976 to 1994, but after 1994 the production showed fluctuations due to several factors such as drought, prolonged cold weather, policy changes, security problem, and decrease in number of harvestable trees (Tadesse et al. 2002).

FRANKINCENSE PRODUCTION AND MANAGEMENT

Commercial production of gum and resin in Ethiopia is an old activity. Gum and resins in Ethiopia has been produced formally on a commercial bases by "Tigray Agricultural and Industrial Development Limited" (TAIDL) since 1948. TAIDL was then replaced by Natural Gum Processing and Marketing Enterprise (NGPME) during the Derg regime in 1977/78. NGPME was the sole governmental organization responsible for the collection, processing and marketing of gum and resin in Ethiopia until the dawn fall of the Derg regime in 1991. Since 1992, a free market economic policy was installed in the country that leads to the increase in the number of organizations that involve in the collection, processing and marketing of the gum and resins. At present, more than 15 organization involved in the business (Eshete 2002).

Kebede (2010) identified three kinds of gum and resin production system at the Metema, north western Ethiopia based on the nature of the organization involved in the production and marketing of gum and resins, how the production site is managed, how the employees (skilled or unskilled labourers) are arranged and capital resources of the organizations. The three systems are direct collection, concessions and farming-integrated. Under direct collection system, only one governmental organization (NGPME) is involved whereas in the other two systems a number of organizations (private or farmer cooperatives) are involved. In all cases, gum and resin are collected from natural stands that belong to the property of the state and the people. The collection of gum and resin resources in the south and south eastern of Ethiopia is mainly practiced by individuals that sell the products to licensed organizations. In the north, north western and western Ethiopia the collection of the products is practiced by licensed organizations. Very recently, farmers cooperatives start the collection, but are obliged to sell to the licensed organizations or to become business partner with licensed organization (Habebo et al. in preparation, Kebede 2010). Production license is issued by the Regional Commerce and Industry Bureau upon the request of the organization that full fill the requirements set by the Bureau (Eshete 2002; Kebede 2010). Licensed organizations shall apply to regional and local agricultural offices to lease production site on yearly bases that is subjected to renewal annually (Kebede 2010). The sustainable utilization of the gum and resin resources rests upon the licensed organization through written agreement with Regional bureau of Agriculture (personal communication).

CHALLENGES FOR SUSTAINABLE GUM AND RESIN PRODUCTION IN ETHIOPIAN WOODLANDS

The areas in which Combretum - Terminalia and Acacia - Commiphora woodland vegetation located are very hot, prone for malaria infestation, and inaccessible. As a result these areas were sparsely populated (Teketay 2000). Recently, the number of inhabitants increased due to population growth, migration of people from dry highlands and government resettlement programs (Eshete 2002). Today the vegetation is being cleared for agriculture by native inhabitants, temporary and permanent settlers, which are coming into the area through the national resettlement program. Thus, expansion of farmlands is one of the major threats for the vegetation. Moreover, these vegetations are the grazing areas throughout the year for the native people and seasonally (during the rainy season) for the nearby mid highlanders and highlanders (Eshete, 2002). The large livestock population of both the native inhabitants and nearby inhabitants degraded and is still degrading the vegetation. Today, there is heavy, unregulated and unmanaged grazing by large numbers of livestock. This even increased the already high pressure on the remaining vegetation resources (Tedla and Lemma 1998). Consequently, the increasing levels of disturbance by grazing might create a problem for the regeneration of this species, and threaten the persistence of the *B. papyrifera* populations and the Frankincense yield in the long run.

A second threat is the more intensive use of the remaining population for frankincense production by an increasing amount of people and, moreover, commercial companies. Tapping for frankincense impacts the trees negatively since they reduce the survival, growth and reproduction of trees (Ogbazghi, 2001; Rijkers et al 2006). The current tapping system has been condemned by several researchers impling that it is too intensive and damaging. So far there is no systematic effort to conserve these trees or to develop sustainable harvest systems for it (Gebrehiwot 2003). The current results suggest that the remaining populations of Frankincense trees are declining at an alarming rate and that tapping might be one of the major underlying causes.

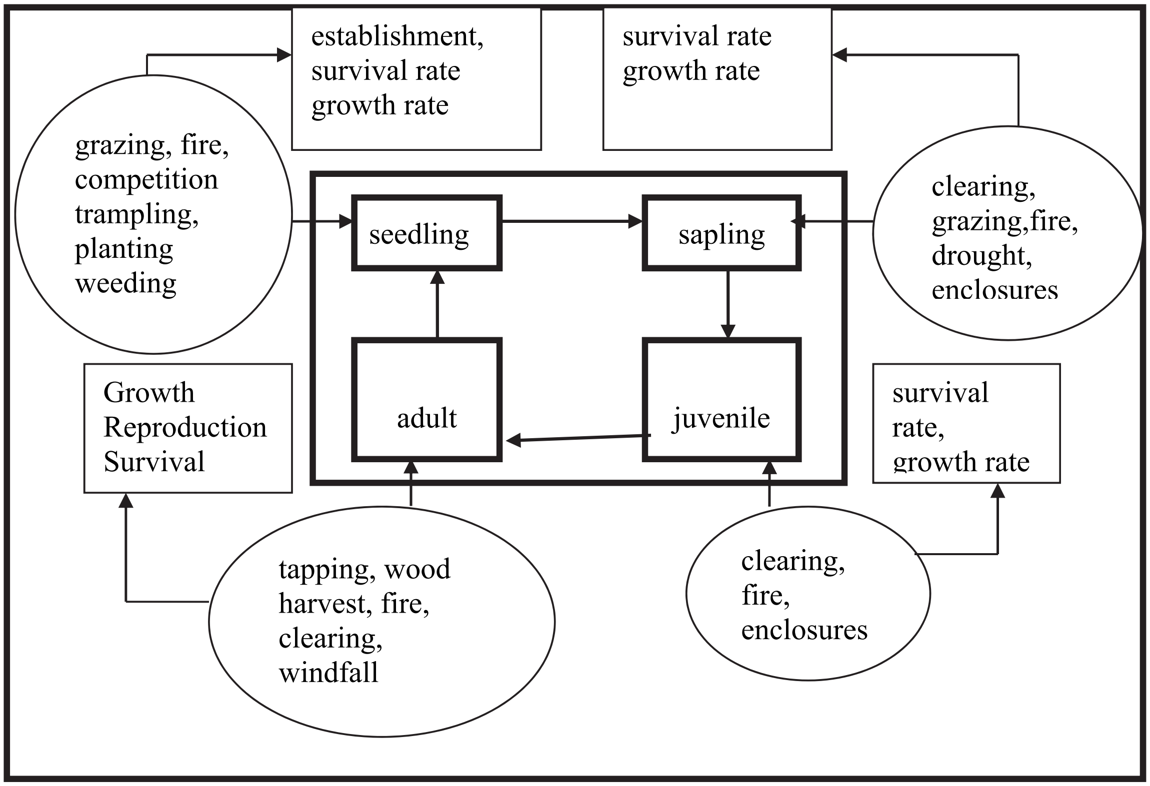
The challenge is to understand the overall impact of this mix of factors and thus predict the future of the remaining populations and, if possible, provide sustainable management actions for those populations. I provide the first study with extensive quantitative information over the entire life cycle of *B. papyrifera* trees, analyze their present and future productivity, and the impact of climate, soil, tapping regime and disturbance by grazing and other factors on the population dynamics, and on the productivity and diversity of the whole dry woodland communities.

LIFE CYCLE DYNAMICS OF *B. PAPYRIFERA* AND HUMAN IMPACTS

Overexploitation of the vegetation that harbors gum and resin bearing tree species has significantly increased since the arrival of humans in and around the vegetation through the national settlement programs. Inhabitants usually practice mixed agriculture which resulted in the conversion of large forested areas to agricultural fields. The forest vegetation is also subject to overgrazing throughout the year. Besides, fire is the most commonly used tool for various activities. Collection and marketing of natural gums as a source of income at household and national level has shown a remarkable increased in the last few decades. The organizations now employ a more intensive and greater frequency tapping regime. Hence, the present scale and extent of exploitation is different from the previous times, and with that the current impact of exploitation on population dynamics of gum and resin bearing tree species probably will be higher.

The focus of this thesis is to identify the specific life stage and demographic processes that act as a bottleneck to maintain the population of *B. papyrifera* and the anthropogenic factors that negatively affect the specific stages in the life cycle of the study species. For this purpose, the life cycle of *B. papyrifera* has been categorized into four stages: seedlings, saplings, juveniles and adult trees (Figure 1). The conceptual scheme in Figure 1 shows the anthropogenic factors that act on each of these four stage and the demographic processes that I expect to be affected by these factors.

Figure 1. A hypothetical scheme of anthropogenic influences on the life cycle stages of *Boswellia papyrifera*, and the demographic processes that are affected. The central box shows the life stages of the frankincense tree. The ovals encompass the anthropogenic factors that infuence life stages, and the rectangular boxes indicate the demographic processes that are expected to be impacted.



Grazing and recurrent fire limit the successful establishment, survival and growth of seedlings of the palatable and fire intolerant frankincense tree species. Besides, increased fire frequency and overgrazing of the vegetation could result in degradation of the habitat by decreasing its potential to maintain the tree population. This may lead to the decline of the frankincense tree population, an increase in the current population of fire and grazing tolerant species and an introduction of new tolerant tree species. Currently, *B. papyrifera* trees are being tapped improperly. The more intensive and greater frequency tapping regime that has been used recently is considered to impact tapped trees negatively.

At the other end of human intervention, the inhabitants as well as concerned governmental and non-governmental organization could play a significant role in maintaining the declining *B. papyrifera* populations and restoring the degrading ecosystems. This would be possible through implementing active management directed at encouraging natural regeneration, establishment of new seedlings of tree species that exhibited unstable population, or increased reproduction and survival of adult trees. This is a crucial process to develop a self-sustained population. These would be possible through removal of the indicated anthropological factors (i.e. installing enclosures) and improving the environmental conditions that help for successful establishment and increased survival and growth rate of established seedlings with the application of management practices, like cultivation of soil to improve the soil condition, weeding to reduce competition and providing adequate reproductive materials (seed and/or seedlings) and developing scientifically proved tapping methods. This thesis evaluated the likely effects on population growth rates of various management actions using population matrix models.

OBJECTIVES AND RESEARCH QUESTIONS

This thesis aims at (1) evaluating how environmental factors (climate and soil conditions) affect species richness, diversity and productivity of Ethiopian dry woodlands, (2) determining how the tapping regime impacts frankincense production by *Boswellia papyrifera*, and (3) identifying the bottleneck for sustainable population dynamics and resin yield, and forecasting the potential effects of various human interventions on those dynamics. This is crucial for development of long-term sustainability and use of these dry lowland woodlands . This thesis addresses the following research questions: (1) how dry tropical woodlands in Ethiopia vary in the production by woody plants and in woody plant richness and diversity? (2) what factors determine frankincense production by *B. papyrifera*? (3) what is the impact of tapping for frankincense production on vital rates and population dynamics of *B. papyrifera*? (4) How do vital rates (reproduction, stem growth, survival) and population growth rates of *B. papyrifera* populations vary among populations differing in soil conditions? and (5) What are the bottlenecks for achieving persistent *B. papyrifera* populations?

THESIS OUTLINE

This thesis consists of six chapters. In Chapter 2, I describe the species composition of Ethiopian dry woodlands and evaluate the effect of climate (wet season length) and soil conditions on the species richness, diversity and productivity of Ethiopian dry woodlands. In addition, the population structures of the community and *B. papyrifera* populations are described, showing the general lack of smaller frankincense individuals. In Chapter 3, I show how different factors affect the frankincense production by *Boswellia papyrifera*. In particular, it is evaluated how annual frankincense production depends on tree size and tapping methods differing in intensity and frequency. In Chapter 4, I deal with the effects of tapping for frankincense production on the vital rates and population dynamics of *B. papyrifera* populations at Metema. Matrix models are applied to analyze the population dynamics and identify the major bottlenecks for the maintenance or growth of *B. papyrifera* populations located at different management regimes. Subsequently, matrix models are used with 3 different human intervention scenarios to determine future *B. papyrifera* populations and frankincense production. In chapter 5, I show an analysis of the population dynamics of *B. papyrifera* across its habitat range and I evaluate the effects of soil conditions on vital rates on elasticity values and population growth of *B. papyrifera* populations. And finally, in Chapter 6, I summarize the main results of this thesis and provide a general discussion. Because each chapter was written in a paper format, some overlap could not be avoided in the introduction and methods section of the chapters.

STUDY SITES

This study was conducted in the lowland dry woodlands of Abergelle and Metema located in the northern and north western Ethiopia, respectively. The vegetation in these sites are known as the Combretum–Terminalia woodland vegetation (Friss et al. 2010, Teketay, 2000). These woodlands have been classified under "undifferentiated woodlands in Ethiopia and Sudan Republic" by White (1983). Such woodlands are often encountered in degraded sites with shallow soils, steep rocky slopes, lava flows or sandy river valleys (Fichtl and Admasu, 1994; Teketay, 2000) and are co-dominated by one or more tree species that produce gum or resin (Lemenih et al. 2003; Ogbazghi et al 2006b). The rainfall is characterized by a unimodal distribution in both sites with mean annual rainfall of 965 mm and 800 mm at Metema and Abergelle, respectively. The rainy season (>100 mm/month) lasts for 4 months from June till September at Metema and for 3 months from June to August at Abergelle. Diurnal minimum and maximum temperature per month are 19.6 and 35.7 ◦C and 14.2 and 29.3 ◦C at Metema and Abergelle, respectively. In both study areas the forest vegetation is dominated by the frankincense tree *Boswellia papyrifera*.

I established 18 permanent plots: 12 plots at Metema and 6 plots at Abergelle in August 2007. The size of each plot ranges from 1.6 ha to 2 ha and distance between plots ranged from 2.5 km to 30 km within a study site. Each permanent plot was divided into 20 m × 20 m subplots where all ≥1.5m tall trees and shrubs were systematically surveyed by identifying, measuring and coding them. I measured the stem diameter, using a diameter tape at breast height (1.3 m above the ground). Stem height (to the top of the crown) was measured using a telescopic pole up to 12 m, and with a Suunto clinometer for taller trees. Local names for tree and shrub species were recorded and individuals were identified to species level at the site. Altitude of all plots was also recorded. All trees and new recruits were re-measured in August 2008 and August 2009.

Chapter 2

Diversity and production of Ethiopian dry woodlands explained by climate- and soil-stress gradients

Abeje Eshete, Frank Sterck & Frans Bongers

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ABSTRACT

Dry woodlands cover about 14% of the total African land surface and represent about 25% of the natural vegetation. They are characterized by a seasonal climate, with a dry season of 4–7 months. Large parts of these ecosystems are degrading due to grazing, fire or exploitation by people. We studied species richness and productivity patterns of dry woodlands in Ethiopia. For such ecosystems, classic productivity and diversity hypotheses predict that species richness and productivity increase as the wet season length increases, and decrease when soil conditions create water stress. We inventoried and measured trees in 18 2-ha plots distributed in two sites, one higher altitude site with a shorter wet season than the lower altitude site. We found that the stand volume per hectare was lower in the site with a shorter wet season. Across all 18 plots we observed that stand volume decreased with soil water stress (estimated from texture and depth). This was in line with the prediction. The species richness was lower in the short-wet season woodlands, but was unaffected by variation in soil conditions. This suggests that climate driven constraints (wet season length) set the limits to species richness, and not soil conditions. As far as we know, this study is one of the first studies that evaluated these productivity and diversity hypotheses for dry African woodlands.

Keywords: Dry woodland, Ethiopia, Frankincense tree, Matrix model, Population dynamics, Productivity, Species composition, Species richness

INTRODUCTION

Dry tropical forests or woodlands once covered over 40% of the global tropical forest areas (Mayaux et al., 2005) and 14% of the total African surface. These forests however decline rapidly in area by the expansion of agriculture and pasture lands (Gerhardt, 1993; Janzen, 1988; Miles et al., 2006). About 97% of the remaining dry tropical forests are at the risk of being further fragmented and degraded by fire, fuel wood collection (Lerdau et al., 1991; Miles et al., 2006; Mittermeier et al., 1999) and grazing damage (Yates et al., 2000). Tropical dry forest, defined as frost-free regions with 500–2000 mm annual precipitation and a dry season of four to seven months (Bullock et al., 1995; Walter, 1971), differs significantly from wet tropical forests in structure, diversity, species composition, leafing phenology, and other functional aspects (Bullock et al., 1995). While less rich in species than wet forests, tropical dry forest provides habitats for a large number of tree species (Hegner, 1979; Murphy and Lugo, 1986a; Wassie et al., 2010a; White, 1983), often used by local communities for a multitude of products and services. In the present study, we investigate how dry tropical woodlands in Ethiopia vary in the production by woody plants and in woody plant richness and diversity.

The production in tropical dry forest is expected to be greater with a more extensive rainy season and more fertile and deeper soils where texture improves water availability. It is less obvious how species richness will vary along such environmental gradients. The classical theories that have been developed for explaining broad diversity patterns suggest that diversity peaks at intermediate levels of disturbance (Bongers et al., 2009; Connell, 1978) and abiotic stress (Huston, 1979; Michalet et al., 2006). For example, species diversity might be highest at intermediate productivity levels when only few species are able to survive at high stress levels, few rapidly growing competitors dominate at low stress levels, and both groups of species survive at intermediate stress levels. It is however not yet clear how this hypothesis holds for dry tropical woodlands, which have been poorly studied in this respect (but see Bongers et al., 2009). For tropical dry woodlands the long dry season obviously creates stressful conditions, while water shortage generally is inferior in wet tropical forests. Moreover, dry forests are more often disturbed by grazing and fires (Miles et al., 2006; Yates et al., 2000), which remove biomass frequently and hinder the dominance by few competitive species (cf. Grace and Jutila, 1999; Huston, 1979). For the tropical dry woodlands studied here we thus predict a higher species richness with lower abiotic stress, as provided by climatic or soil conditions.

In the present paper, we test these predictions for dry woodlands in northern Ethiopia, co-dominated by the Frankincense tree, *Boswellia papyrifera* (Del.) Hochst. We predicted that productivity (using tree size and stand volume as proxies) and species richness increase with wet season length and for deeper soils with a texture and composition that better supplies nutrients and water to plants. We explore predictions with a correlative field study of dry tropical woodlands in two contrasting areas in Ethiopia, and associated soil and vegetation properties across 18 dry woodland stands. The studied woodlands include the climatic extremes of the "Combretum–Terminalia woodlands", co-dominated by *B. papyrifera*, in the Horn of Africa.

MATERIALS AND METHODS

Study site

This study focuses on dry woodlands that are known as the Combretum–Terminalia or Acacia-Commiphora woodland vegetation (Teketay, 2000). Such woodlands are often encountered in degraded sites with shallow soils, steep rocky slopes, lava flows or sandy river valleys (Fichtl and Admasu, 1994; Teketay, 2000). These woodlands are co-dominated by one or more tree species that produce gum or resin (Lemenih et al., 2003; Ogbazghi et al.,2006b). The selected sites of this study were co-dominated by the Frankincense producing tree, *B. papyrifera*. These woodlands have been classified under "undifferentiated woodlands in Ethiopia and Sudan Republic" by White (1983). In Ethiopia, more than half of the country's land area is located in such dry areas and associated tropical dry forest (NCSS, 1993). Moreover, these woodlands extend in large areas in other parts of Africa, including Nigeria, Cameroon,Central African Republic, Chad, Uganda, Sudan and Eritrea (White, 1983). The forests consist of many species providing timber and non-timber products to local communities (FAO, 1995). Owing to high human pressure and migration programs, they are currently rapidly turned into permanent agricultural or pastoral lands and thus losing their potential role for producing their traditional non timber forest products.

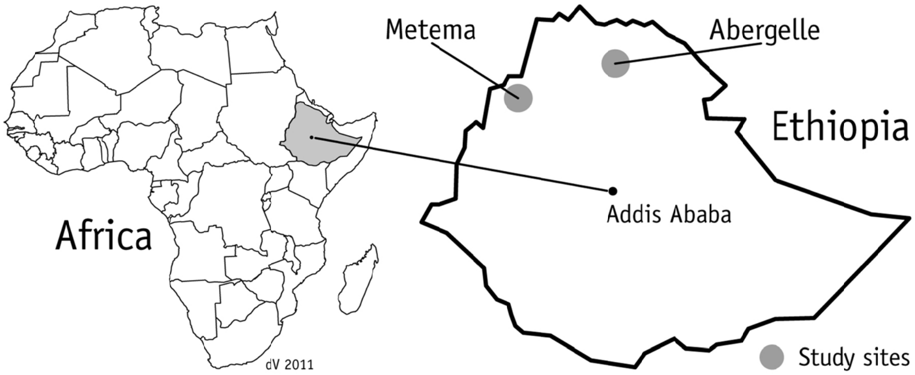


Figure 1. The locations of the two study sites in Ethiopia: Metema in the Amhara Region and Abergelle in the Tigray Region.

We established plots in the climate extremes for *B. papyrifera* dominated Combretum–Terminalia woodland types in northern Ethiopia (Fig. 1). The plots at Metema (North Gondar Zone of Amhara Regional State) were situated at an altitudinal range of 600–1200 m.a.s.l., and plots at Abergelle (central Tigray) between 1400 and 1650 m.a.s.l. At Metema, the annual rainfall ranged from 870 to 1390 mm (between 1988 and 2007) with mean annual rainfall of 965 mm and the rainy season (>100 mm/month) lasts for 4 months from June till September (Fig. 2). Diurnal minimum and maximum temperature per month are 19.6 and 35.7 ◦C, respectively. At Abergelle, the annual rainfall ranged from 400 to 1059 mm for the period from 1980 to 2008 and mean annual rainfall was 800 mm.The rainy season (>100 mm/month) lasts for 3 wet months from June to August. The diurnal minimum and maximum temperature per month are 14.2 and 29.3 ◦C, respectively (Fig. 2). The Abergelle site is inhabited since long and woodlands are considered heavily disturbed (Gebrehiwot et al., 2003). The Metema site is inhabited only for a few decades and their woodlands are considered one of the least affected wooded vegetations in Ethiopia (Teketay, 2000), but this situation is rapidly changing (Lemenih et al., 2007).

Plot establishment and sampling

A total of eighteen plots were established in August, 2007: 12 plots at Metema and 6 plots at Abergelle. The distance between plots ranged from 2.5 km to 30 km within a study site. At Metema more plots were established because dry woodlands covered a larger area and greater heterogeneity in soil and tree physiognomy. Both at Abergelle and Metema, the Combretum–Terminalia woodlands are dominated by *B. papyrifera* and are fragmented within a landscape of other dry woodland types and, in some cases, surrounded by agricultural lands. While we aimed at the establishment of 2 ha plots, some fragments were too small for a full 2 ha plot (Appendix A). Taking a minimum distance of 2.5 km between plots, we consider different plots as independent, approximate randomly selected replicates of the selected woodland types in both areas. However, since selected plots were at walking distance (<5 km) from existent roads and relatively easy to reach by people, we cannot exclude some bias to more disturbed conditions by, for example, grazing and fire or tapping regime. For Abergelle, such disturbances have a longer history (>50 years) than at Metema (<20 years), but at Metema the same disturbances are rapidly become more frequent and intense, owing to new settlements and new roads providing access to people. From that perspective, we expect that the historical effects of disturbance on Abergelle wood lands are nowadays acting in many areas of Metema woodlands, and certainly in the selected plots since they were accessible from the current road and walk track system.

Each permanent plot was divided into 20 m × 20 m subplots where all ≥1.5m tall trees and shrubs were systematically surveyed by identifying, measuring and coding them. For all stems, also for different stems of the few multiple-stemmed shrubs, we measured the stem diameter, using a diameter tape at breast height (1.3 m above the ground). Stem height (to the top of the crown) was measured using a telescopic pole up to 12 m, and with a Suunto clinometer for taller trees. Local names for tree and shrub species were recorded and individuals were identified to species level at the site according to The Flora of Ethiopia (Edwards et al., 1995, 1997, 2000; Hedberg and Edwards, 1989; Hedberg et al., 2003).

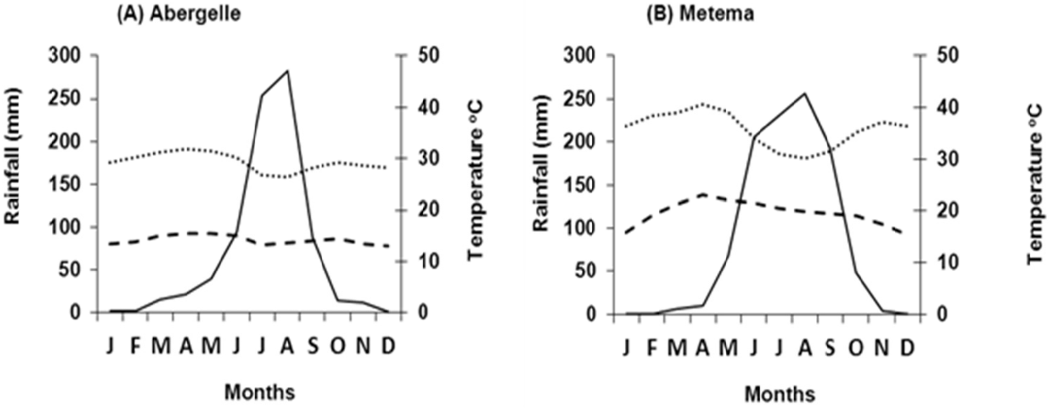


Figure 2. Climate variation over the year for the two study sites Abergelle (A) and Metema (B) in Ethiopia. Monthly rainfall (mm month^{-1}) is indicated by the solid line, mean diurnal maximum temperature per month (^{O}C) by the dotted line, and mean diurnal minimum temperature per month by the dashed line. The climatic data of Metema was obtained at the Gendwuha meteorological station (~25 km away from the study plots) for the period from 1988 to 2007. The annual rainfall ranged from 870 to 1390mm. Data for Abergelle was obtained at the Abi-adi station (~20 km away from the study plots) for the period from 1980 to 2007. The annual rainfall ranged from 400 to 1050 mm.

Individuals that could not be identified in the field were collected and identified at the National Herbarium in Addis Ababa University. Altitude of all plots was also recorded.

To quantify the soil variables per plot, soil samples were collected in three randomly selected 20 m × 20 m subplots as replicates per plot. In each of these subplots, three pits measuring 1 m × 1 m were dug, one at the center and two at diagonal corners. From each pit, soil samples were collected from the top 20 cm, or from a shallower soil volume when the bed rock was encountered at a depth <20 cm, and mixed to forma soil composite. This composite soil sample was divided into three equal parts and randomly one was selected as a working sample for further analysis. A total of 54 working soil samples, i.e. 36 from Metema woodlands and 24 from Abergelle woodlands were collected. The soil samples were then transported to Water Works Design and Construction Enterprise (WWDCE) soil fertility lab, Addis Ababa, Ethiopia for soil physical and chemical analysis. The soil parameters determined were the percentage mass of sand, silt and clay (%), using a hydrometer. The soil pH was measured using a 1:2.5 soil to water suspension. Cation exchange capacity (CEC) was determined, as well as the amount of exchangeable calcium (Ca2+), magnesium (Mg2+), potassium (K+) and sodium (Na+) in meq/100 g of soil. For this purpose, the cations were extracted from 2.5 g of soil sample in 50 mL of a molar solution of ammonium acetate (Thomas, 1982). The amount of organic C (%) was measured using the Walkley–Black method. The available P (in meq/100 g of soil) was measured using the Olsen method, and the amount of N (%) using the Kjeldahl method. Holes were dug to measure the soil depth as the vertical distance between the surface soil and the solid rocky parent material.

Data analysis

Differences in textural and chemical soil conditions and tree and stand structure and productivity measures between Abergelle and Metema were tested using a t-test, using the plots as replicates. Prior to each t-test available P and total cations were transformed using natural logarithm to meet the assumption of normal distribution. The proxies used for tree productivity included the median and maximum height (the 95 percentile) and the median and maximum stem diameter (the 95 percentile). The proxies used for the stand structure and productivity included the tree density (number of stems per hectare), the total basal area per hectare (m^2 ha−1), and the stand stem volume per hectare, assuming a cone stem shape (sum of stem volumes, with each tree volume equal to the product of the stem basal area, tree height and a form factor of 1/3). In addition to the community analysis, we also compared all those traits for the *B. papyrifera* populations separately. Vegetation structures are presented for Metema and Abergelle woodlands as frequency diagrams for different diameter classes, both for the whole plant community and for *B. papyrifera* populations separately. The Kolmogorov–Smirnov test was used to determine whether the distributions differed between sites.

For all 18 plots the floristic composition, species richness and species diversity were determined. We calculated individual density per species (where multiple-stem individuals count for one), basal area, stand volume, frequency (number of 20 m × 20 m subplots in which a species is present) and importance value index (IVI) of each species per plot. IVI of a species is defined as the sum of its relative abundance (number of individuals per hectare of a species divided by total number of individuals per hectare of all species), its relative dominance (total basal area for a species divided by total basal area for all species), and its relative frequency (frequency of a species divided by the sum of all frequencies of all species) (Kent and Coker, 1992).

To estimate the species richness and diversity of both sites, Rarefaction, Fisher's and Shannon' diversity indices and Shannon evenness were calculated on a plot basis. Since species richness and diversity are plot size and abundance dependent (Magurran, 2004), we calculated species richness estimates and species diversity indices based on values from a random selection of twenty five 20 m × 20 m subplots, which is the lowest number of subplots encountered in any plot, using EstimateS software version 8.2 (Colwell, 2006). The difference in species richness and diversity between Metema and Abergelle woodlands was tested using a t-test. We also constructed randomized species accumulation curves against number of individuals for each of the 18 plots and species rank-abundance curves based on logarithmic (base 10) transformed number of individuals for the two woodlands.

We computed the principal components (PCs) of the soil variables, and tested for soil-species richness and soil-productivity associations for the first two components. Stand volume of the community and of the *B. papyrifera* population and species richness (dependent variables) were related to soil PCs (independent variables), using a linear regression. We also used linear regression to explore whether individual soil characteristics determined stand species richness and our proxies for stand productivity and *B. papyrifera* productivity, using the stand volume as the best proxy for this. PASW Statistics 17 statistical software was used for these analyses.

RESULTS

Soils

The soils of the Metema woodlands differed from those at Abergelle in some but not all traits (Table 1). At Metema, woodlands occurred on deeper and more clayey soils than at Abergelle, but texture did not differ significantly. The cations Mg^{2+} and Na^{+} and the cation exchange capacity CEC were higher at Metema than at Abergelle, but N supply and soil pH were lower at Metema. P and K^+ supply did not differ between sites. Thus, except for N, the soils at Metema are generally more fertile in terms of nutrients.

The first two PCs of the soil variables from all plots described 56% of the variance (results not shown). The first axis is a fertility and acidity axis which shows a gradient from basic and less fertile to almost neutral and more fertile soils. The second axis is a textural and organic carbon content axis. These two PCs, clay content and soil depth affected community tree volume and *B. papyrifera* volume (Table 3).

Table 1. Soil properties at 0–20cm depth in dry woodlands at Metema (N= 12) and Abergelle (N= 6) in Northern Ethiopia. [a]Exchange rates. [b]Cation exchange capacity.

Variable	**Unit**	**Metema**	**Abergelle**	**t-value**	**P-value**
Physical					
Sand	%	39.22 ± 3.91	40.27 ± 7.24	0.141	0.890
Silt	%	23.91 ± 0.90	29.72 ± 3.18	1.755	0.131
Clay	%	36.86 ± 4.42	30.0 ± 4.28	0.982	0.341
Soil depth	cm	27.73 ± 3.58	15.30 ± 2.97	2.250	0.039
Chemicals					
[a]Ca^{++}	meq/100 g soil	27.95 ± 1.90	31.90 ± 2.46	1.236	0.234
[a]Mg^{++}	meq/100 g soil	17.85 ± 1.23	8.17 ± 0.68	5.310	0.000
[a]Na^+	meq/100 g soil	0.26 ± 0.02	0.19 ± 0.01	5.672	0.002
[a]K^+	meq/100 g soil	0.43 ± 0.11	0.29 ± 0.03	0.745	0.467
Total Cations	meq/100 g soil	46.54 ± 2.31	40.58 ± 2.82	1.669	0.115
[b]CEC	meq/100 g soil	48.27 ± 2.18	39.26 ± 2.86	2.440	0.027
C	%	2.58 ± 0.35	2.58 ± 0.32	0.008	0.994
N	%	0.19 ± 0.02	0.29 ± 0.04	2.241	0.040
P	mg /kg soil	13.86 ± 4.59	5.29 ± 0.85	1.303	0.211
pH		6.59± 0.09	8.28 ± 0.06	12.937	0.000

When each soil variable was tested separately, altitude, CEC, nitrogen and soil pH did not affect the stand volume of the community or of *B. papyrifera* alone (Fig. 5 and Table 3). Site had an effect on the following soil variables: PC2, clay, soil depth and CEC for community tree volume, and only PC1 and PC2 for *B. papyrifera* volume (Table 3). In all cases Metema had the higher tree volumes when controlling for the independent variable (Fig. 5). None of the soil variables significantly affected species richness (data not shown).

Population structure

At the community level, trees and shrubs were taller and had greater stem diameters at Metema than at Abergelle (Table 2). The mean abundance of trees and shrubs in Abergelle (range: 364–858 ha^{-1}) was higher than in Metema (range: 329–646 ha^{-1},t-test, P = 0.011), but mean basal area (range: 5.8–12.4 m^2 ha^{-1} for Abergelle and 7.6–16.4 m^2 ha^{-1} for Metema) did not differ significantly (P = 0.095). Because trees were taller in Metema (Table 2), stand volume was significantly higher at Metema (range: 21–57 m^3 ha−1) compared to Abergelle (range: 9–20 m^3 ha^{-1}).

B. papyrifera populations did not significantly differ in abundance and basal area between Abergelle (ranges: 117–401 ha^{-1} and 5.8–12.4 m^2 ha^{-1}, respectively) and Metema (ranges: 89–301 ha^{-1} and 7.6–16.4 m^2 ha^{-1}, respectively, Table 2). Because trees at Metema were taller than at Abergelle (Table 2), the Boswellia stand volumes tended to be larger at Metema (range: 7–38 m^3 ha^{-1}) than at Abergelle (range: 7–19 m^3 ha^{-1}), but this was not significant.

The whole tree community showed a bi-modal distribution with relatively large numbers of individuals in the lowest and middle diameter size classes (Fig. 4). Abergelle had a large proportion of individuals in the lowest classes (DBH≤5 cm); while in Metema the middle classes had the highest values. Abergelle had hardly any tree bigger than 33 cm while Metema showed higher numbers of such trees. In contrast to the bi-model distribution of the community, the diameter distribution of *B. papyrifera* showed a hump or uni-modal distribution in both woodlands without individuals in the lowest classes (Fig. 4). Larger *B. papyrifera* individuals were encountered at Metema than at Abergelle (Table 2).

Table 2. Species diversity and structural characteristics of dry woodlands in Metema (N= 12) and Abergelle (N= 6) sites in Northern Ethiopia.

Stand traits	Units	Metema	Abergelle	t-value	P-value
Diversity					
Rarefaction		16.96 ± 0.48	10.84 ± 1.28	5.5	0.000
Fisher's Alpha		3.47 ± 0.16	1.93 ± 0.30	5.1	0.000
Shannon		1.79 ± 0.07	1.26 ± 0.06	4.6	0.000
Evenness		0.61 ± 0.02	0.52 ± 0.01	2.4	0.030
Productivity					
Community					
Median diameter	cm	15.86 ± 0.72	9.77 ± 1.55	4.1	0.001
Maximum diameter	cm	30.91 ± 1.3	24.86 ± 0.74	4.0	0.001
Median height	m	7.65 ± 0.37	3.26 ± 0.21	10.3	0.000
Maximum height	m	11.96 ± 0.50	6.1 ± 0.13	11. 5	0.000
Abundance	ha^{-1}	438.93 ± 28.08	628.7 ± 76.29	2.9	0.011
Basal area	$m^2\ ha^{-1}$	12.19 ± 0.87	9.54 ± 1.2	1.8	0.095
Stand volume	$m^3\ ha^{-1}$	38.6 ± 3.79	15.38 ± 1.85	4.2	0.001
Boswellia populations					
Median diameter (cm)	cm	20.17 ± 1.14	18.56 ± 0.55	1.3	0.223
Maximum diameter (cm)	cm	31.33 ± 1.57	27.55 ± 0.9	2.1	0.054
Median height (m)	m	9.09 ± 0.4	4.94 ± 0.12	9.9	0.000
Maximum height (m)	m	11.66 ± 0.47	6.47 ± 0.14	10.5	0.000
Abundance		192.2 ± 20.48	281.29 ± 50.66	1.6	0.149
Basal area	$m^2\ ha^{-1}$	7.02 ± 0.92	7.38 ± 1.65	0.2	0.839
Stand volume	$m^3\ ha^{-1}$	22.60 ± 3.47	13.79 ± 1.91	1.7	0.107

The frequency distributions of both the whole tree community and *B. papyrifera* populations were statistically different between the two sites, both for shape ($P < 0.001$) and location of the DBH size distribution ($P < 0.001$).

Table 3. Testing for the effects of soil conditions on stand volume (m^3 ha^{-1}) and Boswellia population volume (m^3 ha^{-1}), while controlling for site (Abergelle and Metema) and site interaction effects. For unit of soil traits, see Table 1. Interactions are not shown since they were not significant. PCA-1 and PCA-2 are the major multivariate factors that result from a principal component analysis of all soil factors. Results are based on linear relation in relation to listed soil variables; test and significance (ns: $P \geq 0.05$, $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$).

[a] altitude, N and pH did not show significant trends for the whole community and Boswellia population, and CEC did not show a trend for Boswellia.

Variable	Intercept	slope	Site	F	P	R^2
Community [a]						
PCA-1	31.817	13.75**	Ns	18.141	0.000	0.67
PCA-2	14.813	ns	24.101***	12.782	0.001	0.58
Clay	−0.81	0.54**	19.553***	21.132	0.000	0.70
Soil depth	4.314	0.72**	14.261**	24.426	0.000	0.73
CEC	−3.372	ns	18.95**	9.837	0.002	0.51
Boswellia [a]						
PCA-1	30.837	14.26**	−16.764*	10.068	0.002	0.52
PCA-2	13.187	5.56*	9.711*	5.309	0.018	0.34
Clay	−2.014	0.53**	Ns	10.577	0.001	0.53
soil depth	2.961	0.71***	Ns	13.414	0.000	0.59

Species composition, richness and diversity

A total of 36 and 22 tree and shrub species representing 20 and 9 families were recorded in Metema and Abergelle woodlands, respectively. The most dominant plant families included the *Burseraceae, Fabaceae, Combretaceae* and *Anacardiaceae* (Appendix B). Vegetation at both sites were dominated by *B. papyrifera* and, in some cases, co-dominated by *L. fruticosa, Combretum collinum, Pterocarpus lucens* or *Lonchocarpus laxiflorus* (Appendix B). The species that occurred at both sites were *B. papyrifera*, *L. fruticosa, Stereospermum kunthianum* and *Dichrostachys cinerea*. The total number of observed species and also the estimated species richness was significantly higher for Metema than Abergelle (Table 2). At Metema, woodlands were also more diverse and species were more evenly distributed than at Abergelle (Table 2 and Fig. 3).

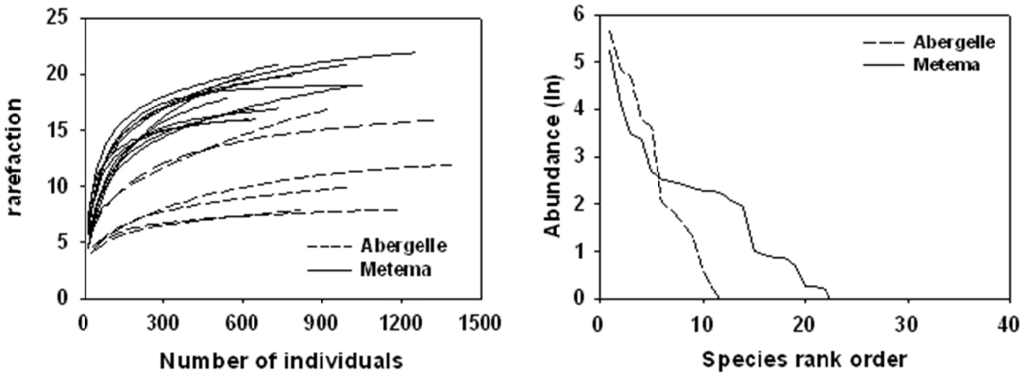


Figure 3. Species richness and diversity patterns of dry woodlands at Abergelle and Metema in Northern Ethiopia. (A) Rarefied species—effort curves, with accumulating amount of individuals per plot on the x-axis and (B) species dominance rank curves showing the relative abundance of species versus rank order for both sites.

DISCUSSION

Species composition and structure

In the present study we found that the species composition differed between the high altitude site Abergelle and the lower altitude site Metema. This difference in species composition might be associated with differences in precipitation and other climate conditions and soil characteristics between the two sites (Clark et al., 1998; John et al., 2007). Awas (2007) had also found similar results where soil variables significantly affect the species composition in lowland woodlands of western Ethiopia. Our woodlands were dominated by *B. papyrifera*, as were large areas in Ethiopia and Eritrea (Abiyu et al., 2010; Gebrehiwot, 2003; Ogbazghi et al., 2006b) and Sudan (Chikamai, 2002). This dominant species largely differed in population structure from the rest of the community. While the general community showed juvenile trees, this was not the case for the *B. papyrifera*. A lack of juvenile trees was also observed for *B. papyrifera* elsewhere in Ethiopia and Eritrea (Abiyu et al., 2010), and for other dry

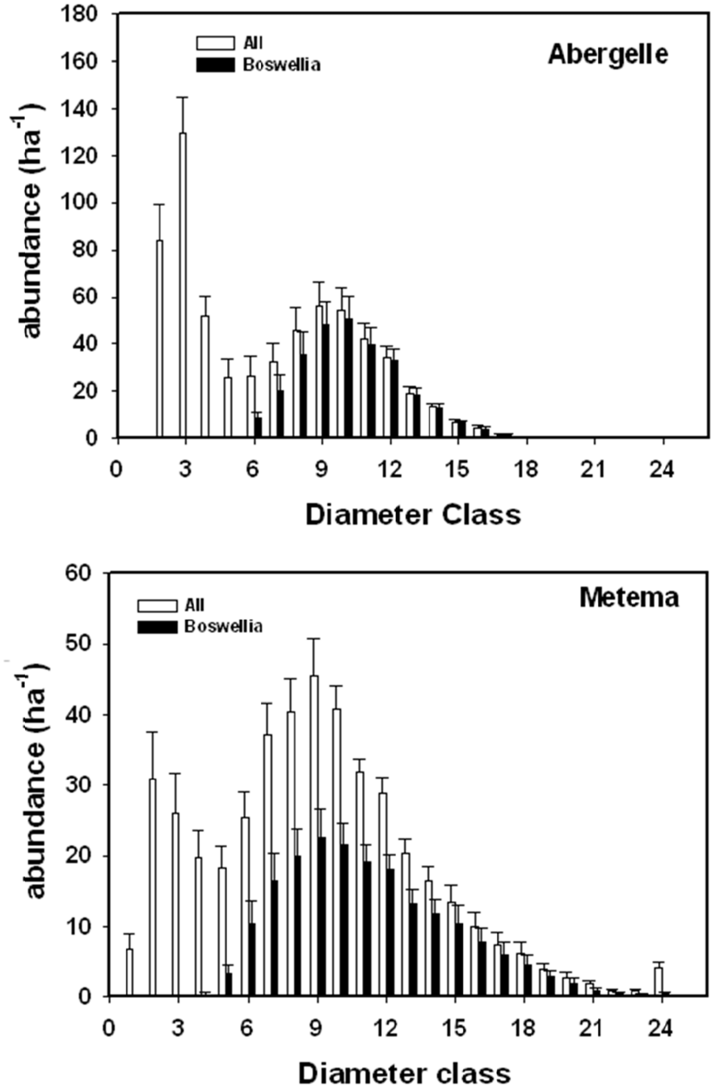


Figure 4. Size frequency distributions of dry woodlands at Abergelle (N= 6) and Metema (N= 12) in Northern Ethiopia. Results are shown for the whole tree community (white bars) and the populations of the most dominant species, *Boswellia papyrifera* (black bars). Abundance is the number of individuals per size class per hectare. DBH class 1 = 0–<1, 2 = 1–<3, 3 = 3–<5, 4 = 5–<7, . . ., 23 = 41–<43 and 24 ≥43 cm. Errors bars indicate ±1 standard errors.

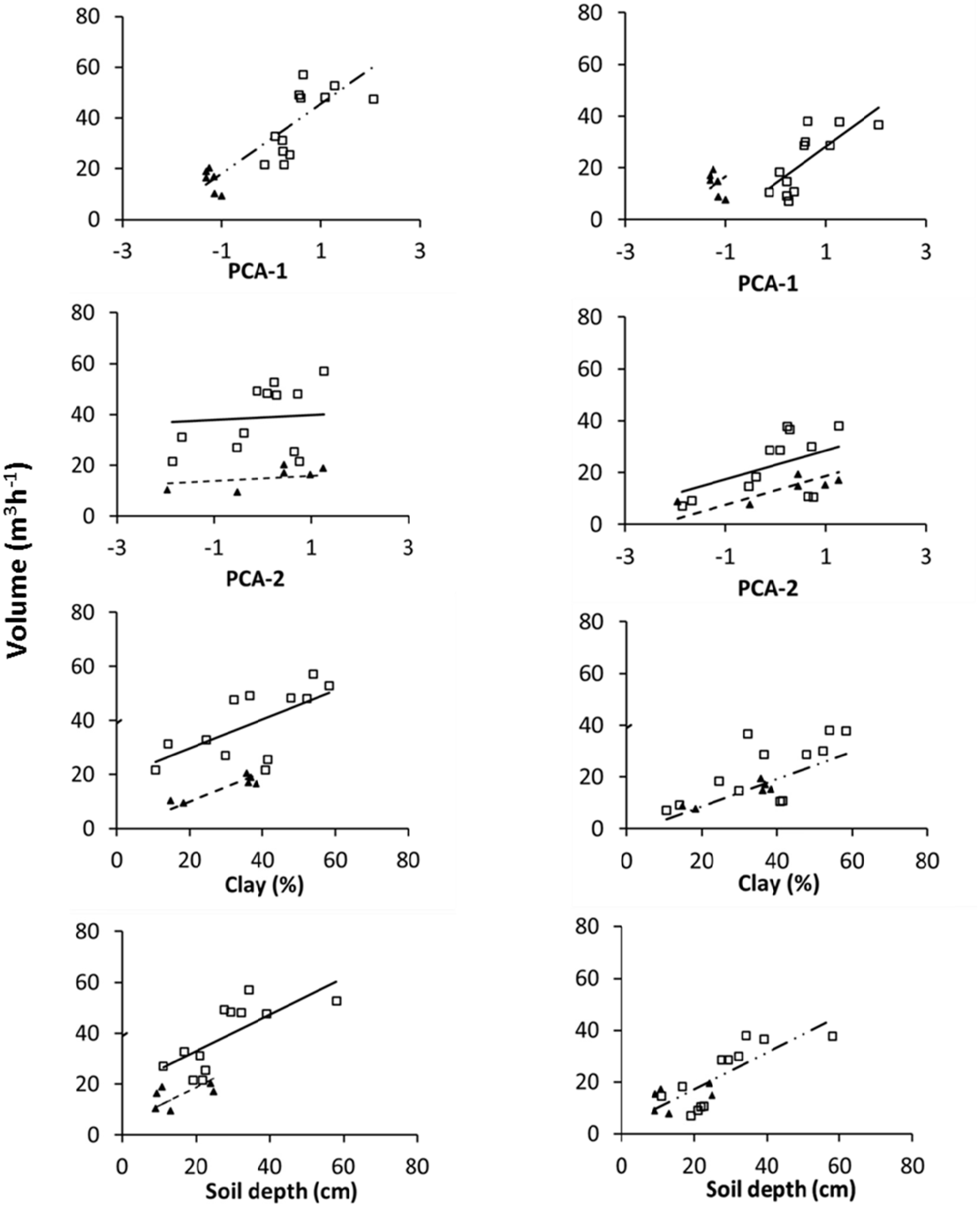


Figure 5. Significant trends between stand volume and soil properties for the community (left side) and the *Boswellia papyrifera* populations (right side). Solid lines shows a fitted line for Metema plots; dashed lines are fitted lines for plots in Abergelle, and dashed–dotted lines for both areas (no site effect). For statistics, see Table 3.

forest species, both in Ethiopia (Gebrehiwot, 2003; Sterck et al., 2010; Tesfaye et al., 2010) as elsewhere (Metcalfe et al., 2007). Population structures that lack juveniles are also found in other forest areas, notably in Ethiopian Afromontane systems, including Ethiopian church forest areas—small woodland remnants around churches and protected by church owners (Wassie et al., 2010a). The lack of regeneration in our case and those other cases is driven by land use changes, and increasing grazing intensity, fire frequency and clearing for agricultural purpose in particular (Belsky and Blumenthal, 1997; Fischer et al., 2009; Sagar et al., 2003; Shorrocks, 2007; Staver et al., 2009; Tesfaye et al., 2004; Wassie et al., 2010a). Our results suggest that the currently very dominant *B. papyrifera* will gradually be replaced by other species. Such changes in species composition have also been observed else- where, particular in relation to uncontrolled grazing (Yates et al., 2000).

Productivity

We predicted larger trees and higher stand volumes as proxies for stand productivity at lower abiotic stress levels. We indeed found that the wetter – lower altitude site – had larger tree and larger stand volumes than the drier – higher altitude – site, suggesting that wet season length and annual rainfall limit tree and stand productivity. At Metema, a longer wet season allows for longer leaf life spans and, in turn, for a greater potential for resource acquisition over a year. Probably, trees were therefore taller and had greater stem diameters and stand volumes were larger at Metema. Across all 18 plots, tree sizes and stand volumes increased with soil depth and soil clay content, but no trend was observed with nutrient supply. Since water stress becomes less with increasing soil depth as well as with increasing clay content, we expected that soil water stress drove the major variation in tree size and stand volume within the studied woodlands systems. This trend was observed for both whole tree communities and for *B. papyrifera* populations separately.

For *B. papyrifera*, we did not observe any difference in tree size or stand volume between the drier and wetter area at a given clay or soil depth content. In other words, annual rainfall and wet season length do apparently not explain the observed variation between those sites. From this observation, we suggest that production differences of B. *papyrifera* populations between the two studied geographic regions are driven by differences in texture (clay content) and soil depth, which drive soil water availability. In contrast, the productivity of the other species is much lower (Fig. 6) in the drier – high altitude – site at a given soil depth and clay content. Thus, the overall community productivity seems suppressed by low annual rainfall or a shorter wet season length.

Species richness

For the studied dry Ethiopian woodlands, we expected higher species richness with decreasing water stress (cf. Gentry, 1982, 1988; Hawkins et al., 2007; Holdridge et al., 1971). Despite considerable variation in soil properties, significant relationships between species richness and soil properties were not encountered. In line with our prediction, we did observe a higher species richness, diversity and evenness at the site that was characterized by a longer wet season (Metema). We cannot exclude other potential factors influencing species richness, such as for example altitude differing between the wetter (800m) and drier site (1600 m). The decline in species richness is thus also associated with increasing altitude, as was observed for church forests in the same region (Wassie et al., 2010b). These church forests however varied in altitude over a larger range (1800–3300m) and, remarkably, consisted of far more species, possibly owing to the forest policy of the church owners (Bongers et al., 2006; Wassie et al., 2010b). Qualitatively, our results and those of Wassie et al. (2010b) confirm those on other tropical forests showing that species richness and diversity generally decrease with altitude (Aiba and Kitayama, 1999; Hemp, 2006; Lieberman et al., 1996; Stevens, 1992; Vázquez and Givnish, 1998). For our expectation that species richness decreases with higher soil water stress (explained in terms of soil clay content and soil depth), we thus found no proof either. The tree size and stand volume analysis showed however that soil depth and clay content largely contributed to the productivity of sites. Knowing that these factors reduce water stress and possibly nutrient stress (Fernadez-Illescas et al., 2001; Knoop & Walker, 1985), we conclude that soil water stress did not contribute to variation in species richness in our study sites.

Both the study sites are exposed to anthropogenic disturbances, such as burning, grazing, and wood collection, which may also affect plant species richness and productivity of forests (Sabogal, 1992; Swaine, 1992; Maass, 1995). These effects would depend on the type and severity of the disturbance and the response of plant species to disturbances. Plant species richness is often hypothesized to be higher at intermediate disturbance level (Connell, 1978; Huston, 1979; Bongers et al., 2009). The argument is that species richness should be maximized under intermediate levels of disturbance because at low levels of disturbance superior competitor species monopolize resources and exclude other species, whereas at high disturbance levels only the most resistant species survive. The longer occupation of Abergelle site could actually result in a high disturbance in the dry forests compared to the recently inhabited Metema forests. Thus, in addition to the wet season length and soil variables, the longer and more intense disturbance history at Abergelle might also contribute to the observed variation in species richness and productivity between the two studied sites.

CONCLUSION

We found that the stand volume was lower if annual rainfall was lower and the wet season was shorter, and decreased with stronger soil water stress (estimated from texture and depth). This was in line with the prediction. The species richness was lower in the short-wet-season woodlands, but was unaffected by variation in soil conditions. This suggests that climate driven constraints such as wet-season length or factors related to altitude set the major limits to species richness, while soil conditions do not. Dry woodlands like the ones we studied are threatened by increasing pressure by local communities and, with them, increasing disturbances by grazing, fire and exploitation (e.g. Abiyu et al., 2010; Eshete et al., 2005; Miles et al., 2006). The increasing disturbance levels will probably negatively affect the species richness and productivity of these woodlands. In response to disturbance, changes are expected in species composition, such as the decline in the currently dominant *B. papyrifera* populations. Our results suggest that this latter species is particularly well adapted, or acclimated, to climate stressed conditions and that the loss of this species might result in a serious decline of the productivity at the most climate stressed sites.

Appendix 1.1 Location of the plots, plot size ha^{-1}, number of families and observed species, density (number of individuals ha^{-1}) and basal area of the plots studied in the *Boswellia papyrifera* dominated woodlands in northern Ethiopia (abundance is number of individuals ≥ 1.5 m in height).

Site	Plot no.	Altitude (m)	Plot size (ha)	No. family	Observed no. species	Abundance No. ha^{-1}	Basal area (m^2 ha^{-1})
Metema	1	793	2	10	19	540	14.6
	2	883	1.6	12	20	381.9	9.5
	3	880	2	13	21	329	8.0
	4	852	2	11	19	509	16.24
	5	851	2	10	20	407	14.2
	6	875	2	9	17	507.5	11.9
	7	593	2	10	16	332	7.6
	8	597	2	13	21	423	9.6
	9	782	1.8	8	16	354.4	13.7
	10	881	2	13	22	646	11.0
	11	823	1.8	11	18	366.7	14.6
	12	825	1.6	9	17	470.6	15.4
Abergelle	1	1636	1.8	5	8	682.8	10.6
	2	1635	1.8	6	12	789.4	11.9
	3	1660	1.6	7	16	858.8	12.4
	4	1656	1.6	9	17	596.3	10.7
	5	1580	1	7	10	481	5.8
	6	1575	1	5	8	364	5.9

Appendix 1.2.1. Scientific names of species, family names, abundance (number of individuals per hectare), basal area, frequency, and IVI (important value index) of species found in Metema site.

No.	Scientific names	Family name	Abundance	Basal area/ha	Frequency	IVI
1	*Acacia polyacantha* Willd. subsp. (unidentified)	Fabaceae	1.3±0.6	0.05± 0.02	2.0±0.8	1.7±0.6
2	*Acacia polyacantha* Willd. subsp. campylacantha (Hochst. ex A.Rich.) Brenan	Fabaceae	0.7±0.4	0.02± 0.02	0.9±0.5	0.8±0.5
3	*Acacia seyal* (Del.) Var. *Seyal*	Fabaceae	2.0±1.1	0.005± 0.002	2.6±1.2	1.7±0.8
4	*Acacia seyal* Del. var. fistula	Fabaceae	0.1±0.1	0.002± 0.001	0.3±0.3	0.2±0.2
5	*Accaia spp3.*	Fabaceae	0.5±0.4	0.001± 0.001	0.4±0.3	0.4±0.3
6	*Albizia malacophylla* (A. Rich.) Walp.	Fabaceae	0.1±0.1	0.004± 0.003	0.2±0.1	0.2±0.1
7	*Anogeissus leiocarpa* (DC.) Guill. & Perr.	Combretaceae	9.9±5.7	0.32± 0.2	5.9±2.7	8.3±4.4
8	*Balanites aegyptiaca* Del.	Balanitaceae	0.1±0.1	0.001± 0.001	0.2±0.2	0.1±0.1
9	*Boswellia papyrifera* (Del.) Hochst.	Burseraceae	192.2±20.5	7.0± 0.9	43.6±1.7	92.9±15.8
10	*Boswellia pirottae* Chiov.	Burseraceae	0.4±0.3	0.01± 0.01	0.6±0.4	0.6± 0.4
11	Chimlikie/Dimeto[a]	Unidentified	0.8±0.3	0.02± 0.01	1.5±0.5	1.2±0.4
12	*Combretum aculeatum* Vent.	Combretaceae	1.3±0.4	0.02± 0.01	2.0±0.7	1.4±0.5
13	*Combretum adenogonium* Steud. ex A.Rich.	Combretaceae	7.7±2.2	0.08± 0.02	8.6±1.9	6.2±1.4
14	*Combretum collinum* Fres.	Combretaceae	32.±12.9	0.2± 0.1	15.0±3.8	14.1±4.2
15	*Combretum molle* R.Br. ex G.Don	Combretaceae	9.8±4.2	0.1± 0.04	9.6±3.1	7.5±2.4
16	*Cordia africana* Lam.	Boraginaceae	0.1±0.1	0.001± 0.001	0.1±0.1	0.1±0.1
17	*Dalbergia melanoxylon* Guill. & Perr.	Leguminosae	6.9±4.1	0.03± 0.01	3.8±1.9	2.0±1.0
18	*Dichrostachys cinerea* (L.) Wight & Arn	Fabaceae	10.6±3.8	0.03± 0.01	4.4±1.2	3.7± 1.1
19	*Diospyros mespiliformis* Hochst. ex A.DC.	Ebenaceae	0.2±0.2	0.001± 0.001	0.1±0.1	0.1±0.1
20	*Ficus glumosa* Del.	Moraceae	0.4±0.4	0.01± 0.01	0.3±0.3	0.3±0.3

[a] Local name

Appendix 1.2.1 continued.

No.	Scientific names	Family name	Abundance	Basal area/ha	Frequency	IVI
21	*Flueggea virosa* (Roxb. ex Willd.) Voigt	Euphorbiaceae	12.4±8.4	0.01± 0.01	3.2±2.4	3.4±2.3
22	*Gardenia ternifolia* Schumach. & Thonn. .	Rubiaceae	0.3±0.2	0.001± 0.001	0.3±0.1	0.2±0.1
23	*Grewia bicolor* Juss.	Tiliaceae	0.1±0.1	0.001± 0.001	0.2±0.1	0.1±0.1
24	*Lannea fruticosa* (A.Rich.) Engl.	Anacardiaceae	60.1±5.5	1.3± 0.2	39.3±1.8	35.3±4.7
25	*Lonchocarpus laxiflorus* Guill.& perr.	Fabaceae	14.6±3.1	0.3± 0.04	16.3±2.0	13.3±2.3
26	*Maytenus senegalensis* (Lam.) Exell	Celasteraceae	2.5±1.6	0.01± 0.01	1.9±1.2	1.3±0.8
27	Mebrat Zaf[a]	Unidentified	0.1±0.1	0.003± 0.002	0.2±0.1	0.1±0.1
28	*Ochna leucophloeos* Hochst. ex A. Rich.	Ochnaceae	0.8±0.4	0.01± 0.01	1.4±0.6	1.1±0.6
29	*Pterocarpus lucens* Guill & Perr.	Fabaceae	28.8±12.3	1.0± 0.	19.5±3.4	18.9 ± 5.2
30	*Sterculia setigera* Del.	Sterculiaceae	9.1±2.0	1.2± 0.2	11.5±2.3	12.8±3.3
31	*Stereospermum kunthianum* (Cham, Sandrine. Petit)	Bignoniaceae	2.8±0.7	0.05± 0.01	4.4±0.9	2.8±0.6
32	*Strychnos innocua* Del.	Loganiaceae	2.4±0.8	0.1± 0.02	2.4±0.7	2.21±0.8
33	*Terminalia laxiflora* Engl. Ex Diels	Combretaceae	2.4±0.8	0.2± 0.05	3.5±1.1	3.8±1.3
34	*Ximenia americana* L.	Olacaceae	11.3±5.1	0.04± 0.01	4.8±1.	4.7±1.6
35	*Ziziphus abyssinica* Hochst. ex A. Rich.	Rhamnaceae	12.0±3.8	0.05± 0.02	8.1±2.2	6.2±1.8
36	*Ziziphus spina--christi* (L.) Willd.	Rhamnaceae	1.2±1.0	0.002± 0.002	1.1±0.9	2.1±1.5

[a] Local name

Appendix 1.2.2 Scientific names of species, family names, abundance (number of individuals per hectare), basal area, frequency (number of 20m×20m subplots in which a species is present), and IVI (important value index) of species found in Abergelle site.

No.	**Scientific names**	**Family name**	**Abundance**	**Basal area/ha**	**Frequency**	**IVI**
1	*Acacia abyssinica* Hochst. ex Benth	Fabaceae	3.8 ± 1.4	0.2 ± 0.1	3.7 ± 1.4	4.1 ± 1.7
2	*Acacia etbaica* Schweinf.	Fabaceae	125.3 ± 47.5	0.7 ± 0.3	22.8 ± 7.3	37.2 ± 12.9
3	*Acacia mellifera* (Vahl) Benth.	Fabaceae	0.4 ± 0.3	0	0.5 ± 0.3	0.4 ± 0.2
4	*Acacia oerfota* (Forsskal)Schweinf	Fabaceae	37.1 ± 13.6	0.3 ± 0.1	15.3 ± 3.3	21.7 ± 5.9
5	*Acacia spp1.*	Fabaceae	0.2 ± 0.1	0	0.3 ± 0.2	0.2 ± 0.1
6	*Acacia spp2.*	Fabaceae	7.7 ± 7.4	0.01 ± 0.01	1.7 ± 1.3	2.0 ± 1.7
7	*Boswellia papyrifera* (Del.) Hochst.	Burseraceae	281.3 ± 50.7	8.1 ± 1.2	33.3 ± 3.9	150.3 ± 7.7
8	*Capparis decidua* (Forssk.) Edgew.	Capparidaceae	0.9 ± 0.8	0	0.3 ± 0.2	0.5 ± 0.4
9	*Combretum hartmannianum* Schweinf.	Combretaceae	1.20± 0.7	0.02 ± 0.01	1.5 ± 0.8	1.2 ± 0.6
10	*Combtretum spp*	Combretaceae	0.1 ± 0.1	0	0.2 ± 0.2	0.1 ± 0.1
11	*Commiphora africana* (A.Rich.) Engl.	Burseraceae	0.3 ± 0.2	0	0.5 ± 0.3	0.4 ± 0.2
12	*Dichrostachys cinerea* (L.) Wight & Arn	Fabaceae	1.9 ± 1.2	0	1.7 ± 1.2	1.3 ±0.9
13	*Grewia erythraea* Schweinf.	Tiliaceae	0.2 ± 0.2	0	0.2 ± 0.2	0.2 ± 0.2
14	*Grewia villosa* Willd.	Tiliaceae	0.1 ± 0.1	0	0.2 ± 0.2	0.1 ± 0.1
15	*Ipomoea spp.*	Convolvulaceae	45.4 ± 10.1	0.03 ± 0.01	21.3 ± 1.9	24.8 ± 5.0
16	*Lannea fruticosa* (A.Rich.) Engl.	Anacardiaceae	5.1 ± 2.5	0.1 ± 0.04	5.2 ± 2.4	4.9 ± 2.2
17	*Lannea triphylla* (A. Rich.) Engl.	Anacardiaceae	0.1 ± 0.1	0	0.2 ± 0.2	0.1 ± 0.1
18	*Maerua angolensis* DC.	Capparidaceae	0.8 ± 0.6	0	1.00± 0.7	0.7 ± 0.5
19	*Salvadora persica* L.	Salvadoraceae	0.1 ± 0.1	0	0.2 ± 0.2	0.1 ± 0.1
20	*Senna singueana* (Del.) Lock.	Fabaceae	109.4 ± 29.1	0.2 ± 0.1	24.7 ± 3.3	41.6 ± 10.5
21	*Stereospermum kunthianum* (Cham, Sandrine. Petit)	Bignoniaceae	0.9 ± 0.5	0.01 ± 0.00	1.3 ± 0.8	1.0 ± 0.6
22	*Terminalia brownii* Fresen	Combretaceae	6.6 ± 2.0	0.1 ± 0.04	6.0 ± 1.8	7.1 ± 2.1

Chapter 3

Frankincense production by Boswellia papyrifera in Ethiopian dry woodlands

Abeje Eshete, Frank Sterck and Frans Bongers

ABSTRACT

Resins produced by trees can provide economically important products and their production has therefore been commercialized for, for example, rubber and Arabic gum. Highly esteemed resins, such as Frankincense, are however still exploited in more traditional ways. Remarkably, these traditional ways nowadays lead to weak trees and non sustainable resin production. We therefore investigated how frankincense yield is affected by different tapping intensities and frequencies, since both of them have been intensified recently. Moreover, these effects are considered for trees of different size, since larger trees probably provide more resources for resin production. These patterns were studied for 4 different populations of *Boswellia papyrifera*, in Northern Ethiopia.

We predicted that frankincense production would initially increase with tapping intensity and tapping frequency, but later level-off because of resin depletion. We indeed found that resin yield increased with tapping intensity, but not anymore beyond an intensity of 9 incision spots. We also observed that resin yield peaked at around the seventh collection round, but declined thereafter. Moreover, we found that resin yield increased with tree size, but not anymore for trees >20 cm DBH. These resin yield patterns were similar across populations on contrasting soils and in contrasting climates.

In conclusion, our result shows that management should take intensity and frequency of tapping, and tree size, into account because it allows for maximizing resin yield at intermediate levels of tree damage by tapping. Soil and climate did not effect this pattern. This study thus allows for developing less damaging and more commercial and sustainable management regimes of highly esteemed frankincense in threatened dry woodlands in the future.

Keywords: insect attack, resin canals, tapping frequency, tapping intensity, tree size.

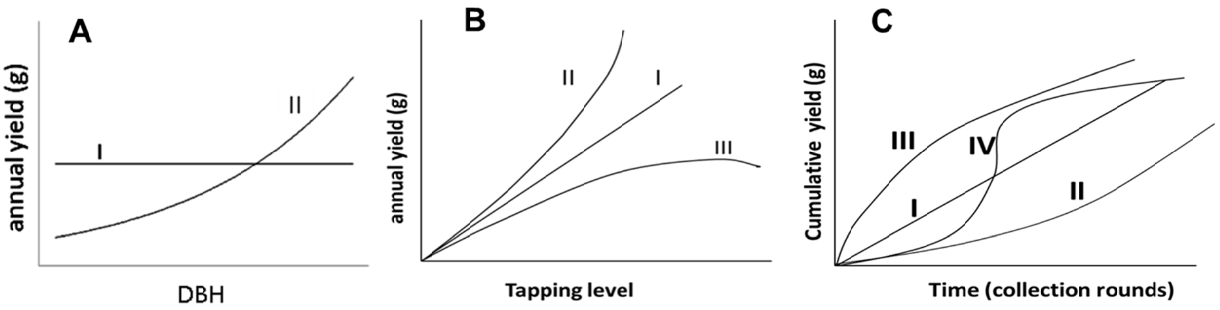
INTRODUCTION

Many trees produce gum and resin in response to wounding (Langenheim 2003) and thus seal the wounds and protect themselves against water loss, insect damage and pathogen invasion (Wink 1988). Some gum and resins are exploited since a long time and used for traditional or industrial purposes (Nussinovitch 2010). Sophisticated, commercialized, and sustainable harvest systems have been developed for, for example, rubber in rain forest areas (Cecil and Mitchell 2003), for different resins in dry Mediterranean or temperate forest areas (Coppen and Hone 1995), and for Arabic gum in the dry Sahel zone (Fagg and Allison 2004). Apart from Arabic gum, no such systems are available for the other gum and resin producing species of dry tropical woodland systems (Fagg and Allison 2004; Gebrehiwot 2003; Ogbazghi 2001). Recently, traditional harvesting systems for the resin (frankincense) production in those tropical dry woodlands are reported to have detrimental effects on tree vitality and reproduction (Rijkers *et al*. 2006). For such resin species, sustainability and optimization of resin production remains a major challenge.

The resin that is stored in small pockets, ducts or canals and seals wounds directly after wounding is called constitutive resin (Langenheim 2003). Resin production that is induced by enzyme activation after wounding is called induced resin. For rubber it has been shown that tapping and stimulants increase the production of latex by shifts in the carbohydrate allocation towards resin production (Sethuraj and Matthew 1992; Silpi *et al*. 2006). Some studies suggest that resin species can increase the resin production after wounding by the formation of newly formed traumatic resin ducts, which provides a particular form of induced resin (Langenheim 2003; Nussinovitch 2010). Such induced resin production is observed for most commercialized resin systems, including rubber, peach, Norway spruce and various pine species (Krokene *et al*. 1999; Nussinovitch 2010). In addition to such physiological processes, the resin production after tapping takes away resources from the plant. Since resource availability for resin production and plant growth depends on plant size and environmental conditions, resin prediction most likely differs between plants of different size or in different environmental conditions (Raddad & Luukkanen 2006). Moreover, the method of tapping influences the amount of resin produced (Coppen and Hone 1995; Lewinsohn *et al*. 1994; Tingey *et al*. 1980; Wekesa *et al*. 2009).

Figure 1 provides a conceptual framework and alternative hypotheses for the effects of tree size and method of tapping on resin production. For the effects of tree size, the growth-differentiation balance hypothesis (GDBH) predicts that the resin production increases with plant size (Herms and Mattson 1992, Fig 1A line II), because of higher resource acquisition rates (Lambers *et al*. 1998) and larger storage pools for secondary metabolites (Goralka *et al*. 1996). With increasing amount of tapping spots (Fig 1B), resin production is also expected to increase. When resin production is a local process and not limited by resources, it will increase linearly with the amount of injuries imposed on the tree or the amount of resin canals or - pockets opened (e.g. for *Pinus taeda* - Klepzing *et al*. 2005; Lombardero *et al*. 2000) (line I in Fig. 1B). If more injury induces new resin production from reserves, we could expect a curved linear increase in resin production with the increase in amount of tapping spot when resources for resin are not limiting (line II in Fig. 1B). However, under limited resource availability in the plant, the increase in resin production with tapping level may level-off because of resource exhaustion (type III, Fig. 1B). With an increasing number of tapping rounds, the resin production per tapping round may follow several pathways (Fig. 1C). Yield remains constant when environmental conditions are similarly limiting over time and when the resin-synthesizing proteins are present and remain active (line I in Fig. 1C). However, in seasonal climates, the proteins first may have to be synthesized to produce resin, causing a delay in resin production (line II in Fig. 1C). Resin production may also be exhausted after many injury rounds, i.e /when resin production is of constitutive nature and when resources for resin production are limiting (line III in Fig 1C). Finally, the response to injury may combine the last two patterns: the system requires induction until it reaches its peak but might show exhaustion for resin production later in the season (line IV in Fig. 1C). We thus have alternative predictions for resin production in response to individual factors.

Figure 1. Conceptual models of frankincense production. Hypothesized relationships for the effects of A) tree size, B) the number of tapping spots and C) the number of collection rounds during the dry season. For explanations, see introduction section.



The resin from *Boswellia papyrifera* (Del.) Hochst., frankincense, is traded at the local and international markets for thousands of years (Groom 1981). Despite its long history in the commercial market, studies on the resin system and on factors that determine resin production are scarce. Here we evaluate what factors determine the frankincense production by *B. papyrifera.* Specifically we address the following questions: (1) Does resin production increase with tree size? (2) Does resin production increase with tapping intensity and frequency? We predicted that resin production from *B. papyrifera* increases with tree size, with tapping intensity and frequency, but at higher intensity and frequency production would level-off. We tested these predictions for 4 populations growing in two sites that differ in macro-climate and soil conditions.

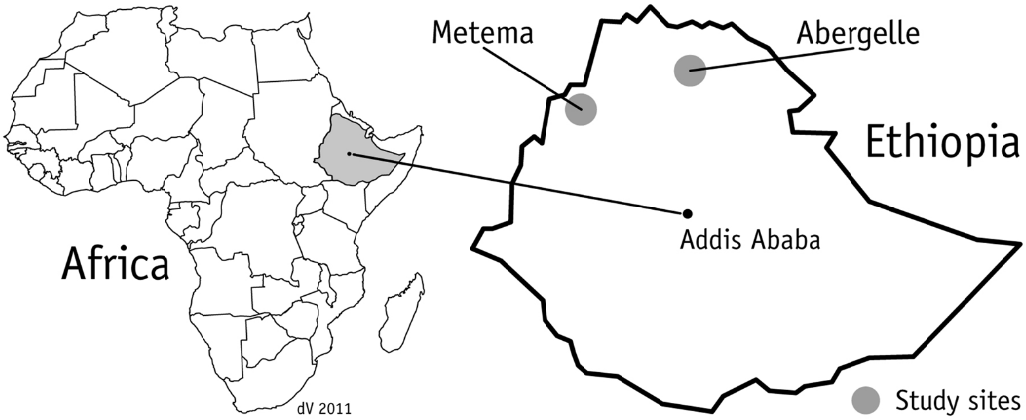


Figure 2. A map showing study sites in northern Ethiopia: Metema (Amhara Region) and Abergelle (Tigray Region) sites are shaded.

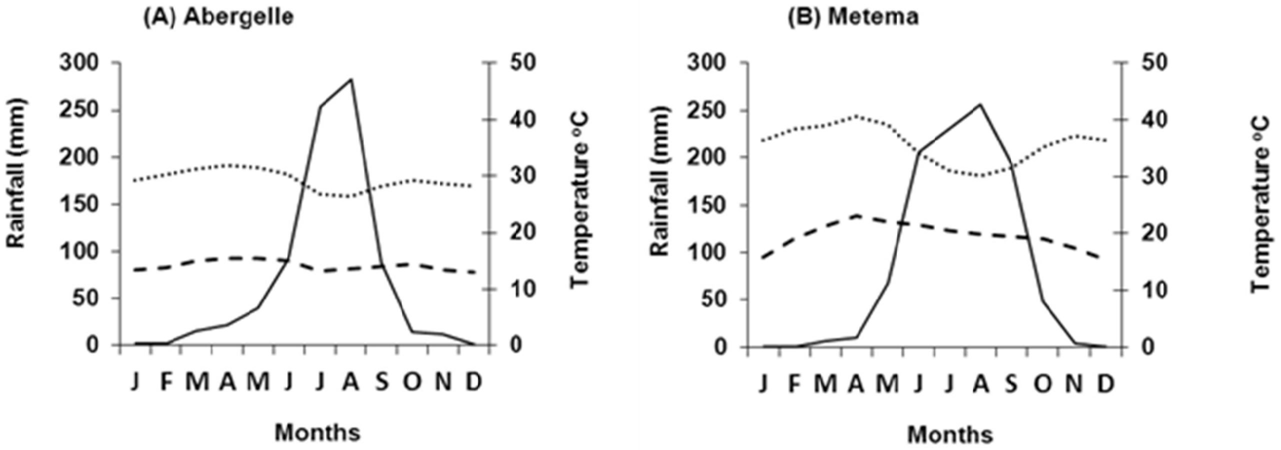


Figure 3. Climate variation over the year. Monthly rainfall distribution (mm year^{-1}) and mean maximum and minimum temperature (^{o}C) at Abergelle and Metema. The climatic data of Metema was obtained at Gendwuha meteorological station, 25 km away from the study sites for the period from 1988 to 2007. Data for Abergelle was obtained at Abi-adi station which is 20 km away from the study site for the period from 1980 to 2008.

MATERIAL AND METHODS

Study sites

We investigated the frankincense production of naturally growing *B. papyrifera* using experimentally controlled tapping techniques, in Abergelle (Tigray Region) and Metema (Amhara Region), located in northern Ethiopia (Fig. 2). The *B. papyrifera* forests cover an area of 330000 ha in Tigray and 604000 ha in Amhara, and are mostly found in deciduous woodlands occupying degraded sites with very shallow soils, steep rocky slopes, lava flows or sandy river valleys (Eshete 2002; Fichtl and Admasu 1994; Teketay 2000). The forests in Metema and Abergelle differ in species composition, diversity and structure (Eshete *et al*. 2011). The rainfall is seasonal in both areas with a wet season from June to September at Metema and from June to August at Abergelle. Metema (965 mm) receives more annual rainfall than Abergelle (800 mm) (Fig 3.). The mean annual maximum and minimum temperature is 35.7 and 19.6 ^{o}C in Metema and 29.3 and 14.2 ^{o}C in Abergelle, respectively. Both forested areas can be classified as dry tropical forests (Friis *et al*. 2010; Teketay *et al*. 2010; Walter 1973; White 1983). The abundance of trees and shrubs (≥ 1.5 m height) is 439 ± 28 individuals/ha in Metema and 629 ± 76 individuals/ha in Abergelle (Eshete et al. 2011). At both sites, the forests are dominated by our study species: the density of *B. papyrifera* is 192 ± 20 (accounting for 44% of total density) at Metema and 281 ± 50.7 (accounting for 51% of total density) at Abergelle (Eshete *et al*. 2011). We selected two populations at Metema and two populations at Abergelle for the present study.

Tapping techniques

Tapping of *B. papyrifera* trees involves removal of the bark, leaving the xylem intact, using a special tool locally called "Mengaff". Tapping starts in the first week of October (at the start of the dry season) and ends in the first week of June (just before the start of the rainy season). During this dry period, the tree has no leaves. Traditionally a tree is tapped 8-12 times (rounds, tapping frequency) per year (Gebrehiwot 2003). During the first tapping, a thin layer of the bark (~1 mm deep and ~2.5 cm^2 in area) is removed. The subsequent tappings deepen and enlarge the already established wounded spots . At the last tapping round the size of a tapping spot will be ~6 cm in horizontal direction, ~10 cm in vertical direction, and approximately 10-20 mm. deep. Using the traditional tapping technique all trees with a diameter of 10–30 cm are tapped at 6-8 spots (tapping levels) while trees with a diameter of >30 cm are tapped at 8-12 spots. During and after each tapping a white resin flows out of the bark, dries and becomes solid on top of the wound, and is collected by tappers before they start the next tapping round.

The present experiment was conducted in four *B. papyrifera* populations, two at Abergelle (named Abergelle-1 and Abergelle-2) and two at Metema (Metema-1 and Metema-2). We selected 125 trees per population and thus 500 tree in total. We allocated the 125 trees per population randomly to two treatments, where the tapping intensity treatment consisted of five levels (3, 6, 9, 12 and 16 spots) and the tree size treatment of five stem diameter classes (10–15 cm, 15-20 cm, 20–25 cm, 25–30 cm and >30 cm). We thus established a fully crossed 5x5 design, with five replications for every tapping intensity – tree size combination. For trees with three tapping spots, the spots were separated vertically by 50 cm at either the eastern or western side of the trunk. For trees with 6 tapping spots, the three spots were at the east side and three at the west side of the trunk. For trees with 9 tapping spots, three directions were used (3 E, 3 W and the remaining 3 in either N or S). Trees with 12 tapping spots are tapped in four directions (3 in each of the cardinal directions). Trees with tapping level 16 were tapped in four directions with 4 tapping spots above each other at each side. The vertical distance between two successive tapping spots was in all cases 50 cm.

Frankincense collection

The experiment was conducted for two production seasons. The first production season (October 2007 – June 2008) involved a low tapping frequency with only 7 frankincense collection rounds, similar to traditional tapping techniques. During the second production season (October 2008 – June 2009), the resin was collected for 14 rounds to show the possible exhaustion of frankincense production with increasing tapping frequency. The first frankincense collection round started at the second tapping round. Frankincense production per tree was determined by weighing the freshly harvested frankincense (locally called 'greazo') directly after collection, using a digital balance (0.01 g precision).

Data analysis

We used ANOVA to test for the predicted tree size and tapping intensity effects on frankincense production, and also included the population as a possible explanatory factor in the model. Two-way interactions of the main effects were also included in the model. The two seasons were analyzed separately. Yield differences resulting from each of the main effects were tested using Tukey test. A paired t-test was used to evaluate the difference between the first year 7-round collection and the first 7 collection rounds of the second year. Data were transformed to natural logarithm to meet the assumption of normal distribution. We used PASW Statistics 17.0 for all tests.

RESULTS

The annual frankincense production of trees ranged from 41 to 840 g in the first season with seven collection rounds, from 185 to 1826 g in the second season with 14 collection rounds. The production was in the same order of magnitude across the three populations but, the production at Metema-2 was lower than at the three other populations. (Table 1; Fig. 4). In all these

Table 1. Testing for the effects of population, diameter size and tapping level as well as the two way interactions on the mean annual frankincense yield in each production season. Results are based on a three-way ANOVA test (n = 500)

		2007/08 (7 collections)			**2008/09 (14 collections)**		
Variable	**df**	**MS**	**F**	**P**	**MS**	**F**	**P**
Corrected model	51	4.14	9.34	0.000	2.45	10.07	0.000
Population	3	5.62	12.74	0.000	1.36	5.57	0.001
DBH class	4	18.46	41.83	0.000	17.74	72.78	0.000
Tapping level	4	22.16	50.22	0.000	8.26	33.88	0.000
Site x tapping level	12	0.27	0.61	0.835	0.47	1.94	0.028
DBH class x tapping level	16	0.47	1.06	0.393	0.44	1.79	0.030
Site x DBH class	12	1.86	4.21	0.000	0.43	1.75	0.054

populations, frankincense production increased with tree size, but not anymore beyond 20 cm DBH (data not shown). This pattern was observed for both production seasons (Table 1; Fig. 5).

Frankincense production increased with a higher tapping level, but more than 9 spots did not add any net production anymore (Table 1; Fig. 5). Frankincense production did not differ between the two season when only 7 collection rounds were considered (paired t-test, df = 470; t= 4.591; p <0.386). However, because of more tapping rounds (higher frequency), the total annual frankincense production was much higher over the second production season (Fig. 4). Moreover, our analysis account for several interactive effects of population, size class and tapping level.

Frankincense production per collection round increased over the first 7 collection rounds, both for the first season and the second season (Fig. 6). This trend was consistent for different size classes, tapping levels and populations. After the 7th collection round in the second production season the frankincense production stabilized and then declined for different size classes, tapping levels and populations). The small sized trees declined more rapidly in resin yield after the 7th round than the larger sized trees. Remarkably, the trees that were tapped at different intensities showed very similar qualitative trends in initial increase and later decline in resin yield.

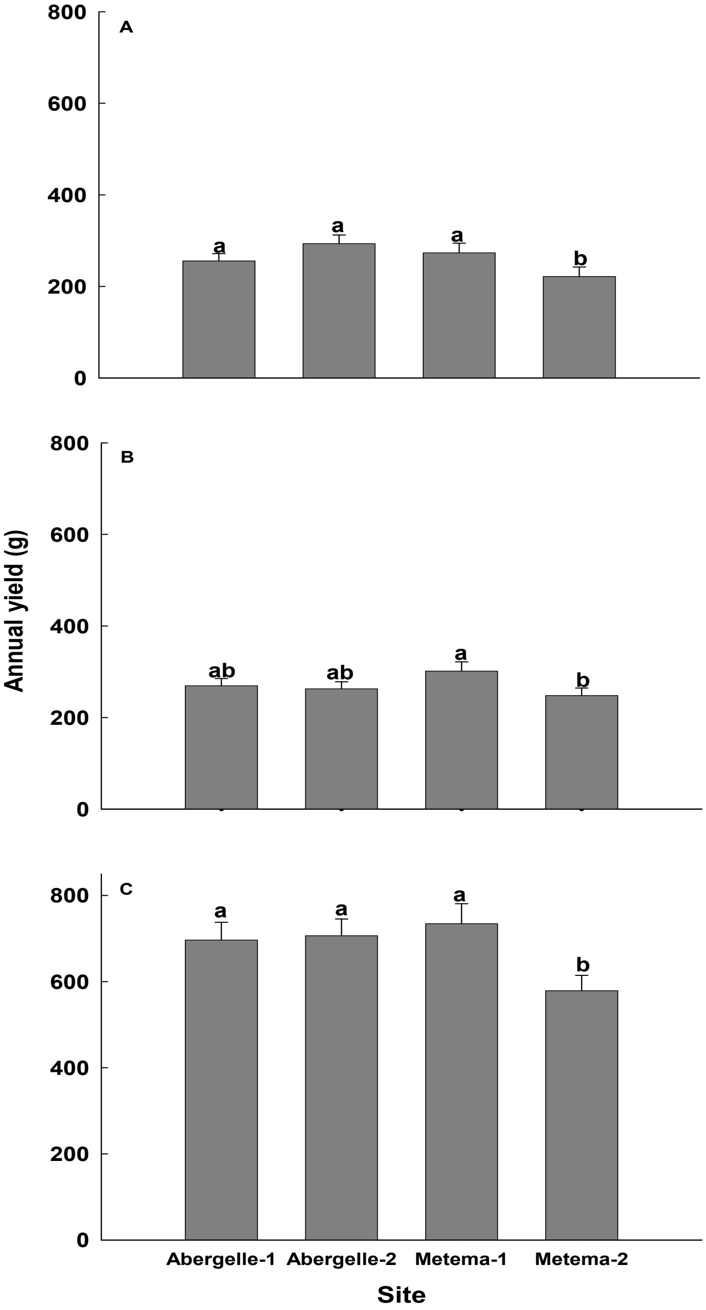


Figure 4. Mean annual frankincense production of *B. papyrifera* of the four populations during (A) the first year production season, (B) the second production season, the first 7 rounds only, and (C) the second season, all 14 collection rounds included. Yield data from all diameter classes and tapping levels were pooled in each population. Error bars are standard errors. Identical letters indicate means that are not significantly differentbetween sites following Tukey test ($p < 0.05$).

DISCUSSION

In this study we show how the frankincense yield in four Ethiopian *B. papyrifera* dry woodland populations varied with tree size, tapping intensity and tapping frequency. We evaluate our results in the light of the postulated hypotheses (see also Figure 1) and discuss their implications for sustainable frankincense yield, but first we compare the frankincense yield amongst the four populations.

For this study, we selected *B. papyrifera* populations at relative extreme and opposite climatic conditions, with the two Abergelle populations characterized by a higher altitude and a drier, colder and more intensively sun-lit site conditions than the two Metema plots. While the Abergelle plots and one Metema plot (Metema -2) were characterized by similarly poor soil conditions, the Metema-1 plots was characterized by much better soil conditions (Eshete et al. 2011). Remarkably, the two Abergelle plots on poor soils and the Metema plot on the richest soil did not differ in frankincense yield, whereas the Metema plot on a soil as poor as those plots at Abergelle exhibited a lower annual resin yield. Based on a parallel study on leaf and crown photosynthesis of these trees (Mengistu et al. in prep.), we suggest that high illumination and photosynthetic acclimation to those conditions at Abergelle might compensate for resource acquisition for resin production, despite rather poor soil conditions and a shorter wet season. The Metema plot on poor soil is characterized by less favorable irradiation conditions, and may not be capable to produce a similar amount of annual resin yield. These differences were small, however, suggesting that the selection for a sufficient amount of resin might be strong. Testing such hypothetical mechanisms for a lack of larger differences in resin yield between tree populations is however beyond the scope of the present study. The minor differences in resin yield nevertheless allowed us to pool the data of the four tree populations to show the much stronger trends in resin yield with tree size, tapping intensity and number of tapping rounds. Trends per population were very similar and are therefore not shown.

In line with our prediction (Fig. 1A Type II), bigger trees indeed produced more frankincense than smaller trees. Particularly, individual trees in the lowest diameter classes (10 – 15 cm DBH) gave lower amounts of frankincense (Figs. 5 & 6). This phenomenon was consistent over two production seasons, 5 tapping levels and 4 populations. Similar results were also reported for a number of Pinus species (Coppen 1995; Lombardero *et al*. 2000; Rodrigues *et al.* 2008) and for Protium (copal) trees (Neels 1996). Rodrigues and coworkers (2008), for instance, studying the effects of tree size on oleoresin yield of *Pinus elliottii* in Brazil, found bigger Pinus trees (22 – 23.5 cm DBH) to give 20-25% higher oleoresin yield than smaller trees (18 – 19.5 cm DBH). Higher yield in bigger trees may result from larger resin stocks, larger resource acquisition capacities that allow for more resin production, and more resin canals in the trunks of bigger trees (Coppen 1995; Ella and Tongacan 1992; Lambers *et al*. 1998). In rubber trees (*Hevea brasiliensis*), the rate of latex production was related to CO_2 assimilation capacity of the trees (Gomez 1983), which in turn depends on the crown size and leaf area of trees (Lambers *et al*. 1998). Gebrehiwot (2003) and Ogbazghi *et al*. (2006a) reported a linear relationship between stem diameter and crown diameter for *B. papyrifera* in Ethiopia and Eritrea, respectively. Thus, the higher frankincense production from bigger *B. papyrifera* trees observed in the present study may be the result of larger photosynthetic carbon acquisition capacity by bigger trees. This is consistent with the growth differentiation balance hypothesis (GDBH) that production of secondary producing structures and the metabolites produced, such as frankincense, increase with plant size (Herms and Mattson 1992; Goralka and Langenheim 1996; Goralka *et al*. 1996). However, beyond a stem diameter of 20 cm we did not observe any increase in resin yield.

In line with our expectation (Figure 1B type III), frankincense production increased with the number of tapping spots on the tree (Figure 5). A similar increase in gum arabic production by *Acacia senegal* with tapping intensity was reported in Sudan by Ballal et al. (2005).This increase however leveled-off beyond the 9th tapping spot on the trunk. The increase in frankincense production with the number of tapping spots is probably due to the fact that more resin canals are opened up (Trapp and Croteau 2001). A similar result was also reported for grand fir (*Abies grandis*) where the production of plant defense was proportional to the injury applied (Klepzig *et al*. 2005; Lewinsohn *et al*., 1991; Lombardero *et al*. 2000). In commercial production of resin from pine trees chemicals are used to simulate insect or fungal attack for maximizing resin production (Chaudhari *et al.* 1996; Coppen 1995; Klepzig *et al*. 2005; Rodrigues *et al.* 2008), but this is not yet the case for *B. papyrifera* where people only experimented with different numbers of tapping spots (Abiyu *et al*. 2010; Kebede 2010; Ogbazghi 2001). The leveling-off of the frankincense production after the 9th tapping levels is probably because the different tapping spots start to drain resin from the same pool. This result is in line with the results of *B. papyrifera* bark and wood anatomical studies (Menger 2010), suggesting that resin canals are

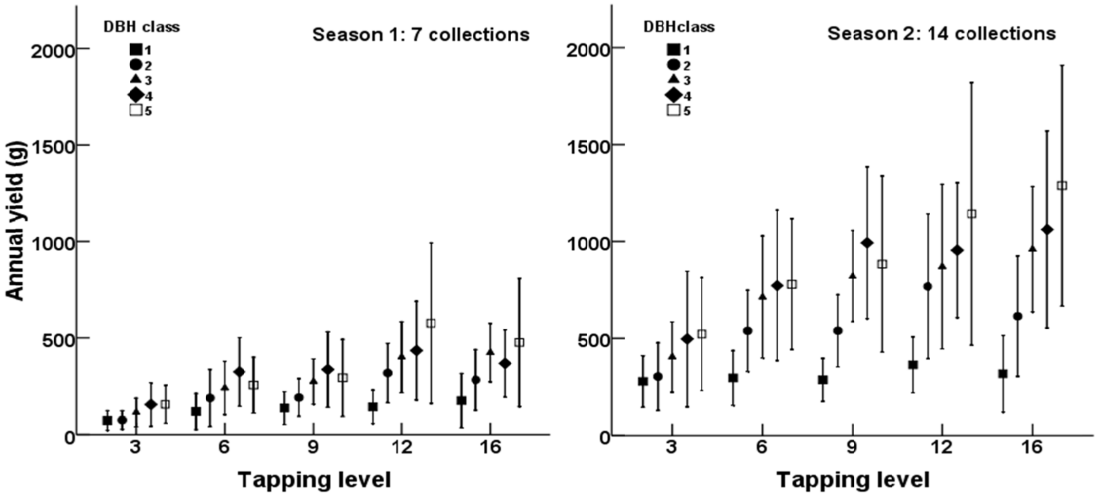


Figure 5. Effects of diameter and the number of tapping spots (tapping intensity) on the mean annual frankincense yield of *B. papyrifera*. Yield data of all individual trees from the four sites were pooled. Error bars are standard deviations.

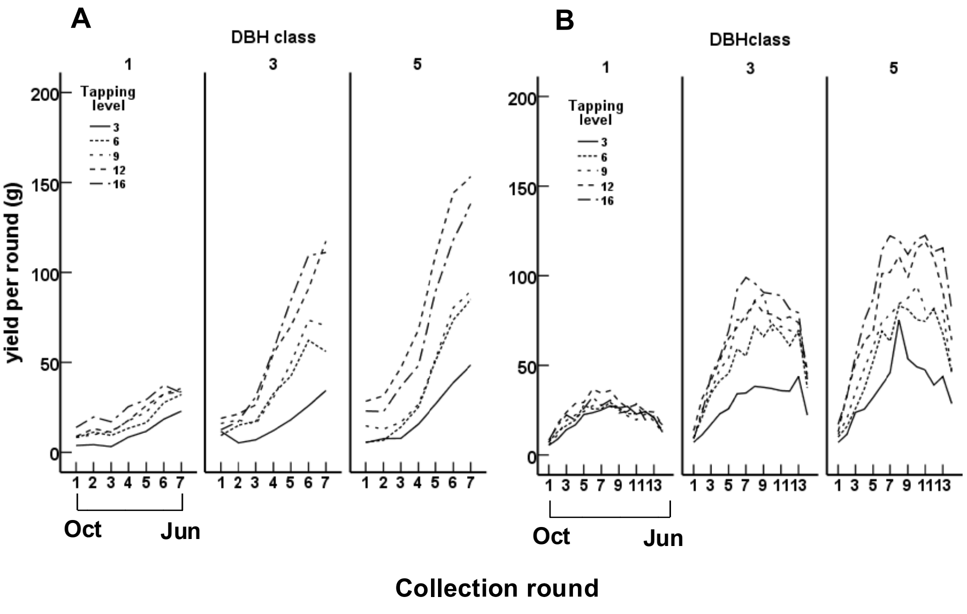


Figure 6. Mean annual frankincense yield per tree in relation to tapping level (3, 6, 9, 12, 16 tapping spots) and diameter size (10 – 15, 15 – 20, 20 – 25, 25 – 30 and > 30 cm DBH) in 2007/08 (A) and in 2008/09 (B). (Please note that the 7 collection during 2007/08 and the 14 collection during 2008/09 had the same time span, each start in the first week of October and end in the first week of June).

interconnected over longer distances than those between tapping spots, and thus allowing for draining frankincense from one spot by the other.

In line with our hypothesis, annual frankincense production increased with a higher tapping frequency (Figure 6). Frankincense production per tapping round increased over the first 7 collection rounds, then leveled-off, and ultimately decreased, which is in line with our prediction shown in Fig. 1C (type IV). The initial increase in frankincense production with tapping round may result from opening-up more resin canals (Trapp and Croteau 2001). Menger (2010) showed that indeed the density of resin canals increases from outer to inner side of the bark: more tapping rounds and getting deeper in the bark will open more resin canals. Moreover, frankincense production may also increase in response to a higher temperature (Wekesa *et al.* 2009). The decline in resin production at the end of the dry season in the second production season may indicate exhaustion of the resources for frankincense production (Ella and Tongacan 1987). Similar trends for resin yield per collection round were also obtained for *Pinus roxburghii* in India (Chaudhari *et al.* 1996) and *Protium copal* in Guatemala (Neels 1996). Remarkably, the decline was observed for all tapping intensity levels.

Implications for management

It is clear that smaller trees (10 -15 cm DBH) produce much less resin than large trees. We do not know if intensive tapping of small trees will negatively affect the production capacity of these trees when large: longer-term studies are needed to evaluate whether tapping has longer-term effects. However, studies of commercial resin production by Pinus species have led to obligatory minimum tree size limits for tapping (20 cm DBH in China and 20-25 cm DBH in other countries; Coppen and Hone 1995; Wang *et al.* 2006). In India a standard minimum diameter for tapping of *Pinus roxburgii* of 30 cm is used (Lohani 1970): tapping of trees smaller than 25 cm increased annual mortality rate from 1.1% to 29.3%. For *B. papyrifera*, Mengistu and coworkers (in preparation) showed that tapping reduced the photosynthetic capacity through a decrease in crown size. Given the rapid rise in resin yield in trees > 15 cm DBH, we therefore suggest a minimum tapping diameter of 15 cm for *B. papyrifera.*

Our results show how frankincense production varies with population, tree size, the amount of tapping spots, collection rounds and the frequency of tapping. Our study indicates that trees are clearly limited in resin production, and that the amount of tapping spots should be limited to 9 or less and the amount of tapping rounds should probably not exceed 10 in one production season (from October to June). Wounding without proper sealing will expose it to attacks by insects, fungi, or other pathogens (Trapp & Croteau 2001; Abiyu *et al*. 2010; Negussie 2008). Indeed, *B. papyrifera* trees in Tigray with more than 12 tapping spots had higher levels of insect attack (Negussie 2008). And in Metema the fate of insect affected trees is death: currently more than 65% of the dead *B. papyrifera* trees in this area were infested by the insect (Chapter 5). Extremely high numbers of tapping spots and collection rounds as currently found in some commercial production sites (up to 27 tapping spots – and 16 collection rounds - Kebede 2010) are therefore likely to result in high adult tree mortality and probably into the collapse of resin yield in a near future.

CONCLUSION

Resin production by trees is practiced in a sustainable commercialized way for a number of products and species, but not for most of the highly esteemed resins from tropical dry woodland trees. In this study, we evaluated how traditional methods drive the resin yield from Frankincense trees, inhabiting dry woodlands in the Horn of Africa (Ethiopia). Similar methods have probably been applied for millennia, but currently they result in non sustainable populations and resin yield. In this paper we show how frankincense yield changes with tapping intensity level and tapping frequency for trees of different size. We show that management should take these three factors into account, because that approach allows for maximizing resin yield at intermediate levels of tree damage by tapping. The presented detailed information of resin yield dynamics also suggests how physiological constraints limit the resin yield. Finally, we show that resin yield was relatively similar across populations on contrasting soils and in contrasting climates. From this we suggest that selection for a similar resin production capacity is strong across different populations. We consider our study the first broad scale study on the effects of alternative management regimes inspired by traditional practices, which allows for developing least damaging and more commercial and sustainable management regimes of the highly esteemed frankincense in threatened dryland woodlands in the future.

Chapter 4

Limitations to sustainable frankincense production: blocked regeneration, high adult mortality and declining populations

Peter Groenendijk, Abeje Eshete, Frank J. Sterck, Pieter A. Zuidema and Frans Bongers

ABSTRACT

Frankincense, an aromatic resin, is tapped from the bark of several *Boswellia spp.* (Burseraceae). Though important on local and international markets, exploited populations often suffer from poor regeneration. The demographic consequences of regeneration bottlenecks are poorly quantified and understood. Here we report on the first large-scale demographic study of frankincense-producing trees. We studied twelve populations of *Boswellia papyrifera* in Northern Ethiopia, distributed over an altitudinal and forest productivity gradient. Six of these populations had been exploited and were tapped during the study. Survival, growth and fecundity were determined for 4370 adult trees and 2228 seedlings and saplings, in a total of 22.8 ha over two years. Additionally an isolated population was studied to quantify growth and survival rates of missing sapling classes. Matrix models were used to project population growth and frankincense production based on observed dynamics and four management scenarios.

Population structures of both tapped and untapped populations show clear gaps. Small seedlings – which only appear above-ground during the rainy season – were abundant in the 12 main populations, but none developed into persistent saplings. Fire and grazing are likely causes of this regeneration bottleneck. Tapped populations presented higher diameter growth rates and fecundity compared to untapped populations, while survival rates did not differ. Faster growth in tapped populations probably resulted from non-random selection of exploited populations by tappers. Our matrix models projected an 87% decline in size of tapped populations over 50 years, and a 93% decline of untapped populations. Frankincense yields were projected to be halved in ~15 years. Scenario studies showed that stable populations could only be achieved when sapling recruitment was guaranteed and adult mortality was strongly reduced. Tapping does not appear to be the major driver behind these bottlenecks and field trials are needed to determine their causes and possible solutions to them. In conclusion, in addition to the conversion to agricultural land, the lack of regeneration and high adult mortality are causing raid decline of Frankincense-producing tree populations in Ethiopia. Current levels of frankincense production cannot be sustained unless these demographic bottlenecks are overcome.

Key *words*: population dynamics, tapping, managment actions, vital rates, frankincense, Ethiopia

INTRODUCTION

Resins are among the most valuable Non Timber Forest Products (NTFP) produced, particularly those tapped for fragrances and flavours. Frankincense, an oleo-gum resin tapped from several *Boswellia spp* of the Burseraceae family, is an important resin on the local and international market (Lemenih, Abebe & Olsson 2003b). For instance, in the Horn of Africa, frankincense is tapped from adult individuals of *Boswellia papyrifera* (Del.) Hochst. in natural woodlands and has several traditional, medicinal and ceremonial uses. On the international market it is an important commodity in the production of perfumes and incenses (Chikamai 2002; Lemenih & Teketay 2003b). *B. papyrifera* is a small deciduous tree, occurring from northern Nigeria to the highlands of Ethiopia and Eritrea, often on steep and rocky slopes with shallow soil in semi-arid conditions (Ogbazghi *et al.* 2006a). Tapping of resins can form a substantial sink of carbohydrates for a tree (Silpi *et al.* 2007) and reduce diameter growth (Silpi *et al.* 2006). In *Boswellia*, tapping was found to reduce seed production and viability (Rijkers *et al.* 2006), but its effects on growth of trees and populations are unknown.

Many populations of *B. papyrifera* are threatened by conversion into agricultural land and the lack of natural regeneration (Ogbazghi 2001; Gebrehiwot *et al.* 2003; Ogbazghi *et al.* 2006a). Natural *Boswellia* populations often present a hump-shaped population distribution, dominated by small seedlings and adult trees, lacking the sapling and treelet stages (Ogbazghi 2001; Gebrehiwot *et al.* 2003; Eshete, Teketay & Hulten 2005; Abiyu *et al.* 2010). This gap in the population structure may be caused by the low production and viability of seeds of tapped trees (Rijkers *et al.* 2006), recurrent droughts (Ogbazghi 2001), increased fire frequency, uncontrolled livestock grazing (Ogbazghi *et al.* 2006a) or a combination of these (Eshete, Teketay & Hulten 2005; Abiyu *et al.* 2010). Alternatively, the lack of regeneration may refer to unfavourable conditions during the recent past and to episodic recruitment, as sometimes encountered in arid environments (Crisp 1978; Walker 1993; Watson, Westoby & Holm 1997).

Blocked regeneration poses a threat to the maintenance of *Boswellia* populations and the production of frankincense on the long term. Understanding the effects of tapping and the blocked regeneration on population dynamics is crucial to assess the sustainability of current frankincense exploitation practices. Despite the economic importance of this species, virtually nothing is known about the population dynamical consequences of tapping and blocked regeneration in *Boswellia* populations. Such information can be obtained from stage-based population matrix models (Caswell 2001) which project population development. Matrix models are powerful tools to study population dynamics and have often been applied to study consequences of NTFP harvest (Ticktin 2004). They require relatively low data inputs for model parameterization and are suitable for sustainability analysis of NTFPs harvest (Boot & Gullison 1995).

Here we present a first study on the consequences of current frankincense exploitation for *Boswellia* populations and future frankincense production. This is also one of the first studies assessing the effects of resin tapping on population growth (Ticktin 2004). We hypothesize that tapped *Boswellia* populations will present stronger regeneration bottlenecks and lower rates of diameter growth, fecundity and survival compared to untapped populations. As a result, we expect lower population growth rates in tapped populations. We also expect that simulating full sapling regeneration in models for tapped and untapped populations will cause simulations to show growing populations.

We studied the dynamics in populations of six tapped and six untapped stands between 2007 and 2009. Data from another study area, where saplings and treelets are present, were used to quantify the vital rates of these size categories. We constructed matrix models for the pooled data of all tapped and all untapped populations, and used these to project population development. Using results from a yield study, we converted projected population sizes to projected frankincense yield. We also implemented various management scenarios, for increased regeneration and reduced adult mortality.

MATERIALS AND METHODS

Experimental sites and study species

Data collection was carried out in Metema districts, northern Ethiopia (12°33.58' – 12°41.53'N, 36°04.12' – 36°18.84'E). Stands were selected based on the presence of relatively intact *B. papyrifera* populations and to cover altitudinal and 'production' gradients (based on visual observations of stand characteristics and nearby cropland production). The region has a uni-modal rainfall, with the rainy season extending from June to the end of September. The annual rainfall in Metema ranges from (870-1390 mm (mean=965 mm), the mean minimum temperature is 19.6ºC and the mean maximum 35.7°C. The region is one of the main *Boswellia* growing areas in the Horn of Africa and has attracted several companies for the commercial extraction of frankincense (Eshete, Teketay & Hulten 2005). Population structure of *Boswellia* stands in the study area present only individuals in the classes above ca. 6 cm Diameter at Breast Height (DBH), except for small non-permanent seedlings (Eshete, Teketay & Hulten 2005; Abiyu *et al.* 2010). Additionally, a third site was selected near the village of Adi Arkay (13º27'N, 38º4'E), in the homonymous district, ca. 210 km Northeast of Metema. Located at an altitude of 1415 m, the area is characterized by steep cliffs with presence of *Boswellia* populations. In Adi Arkay, *B. papyrifera* regeneration of all sizes is present, presumably because the poor accessibility of the area prevents grazing and agricultural practices.

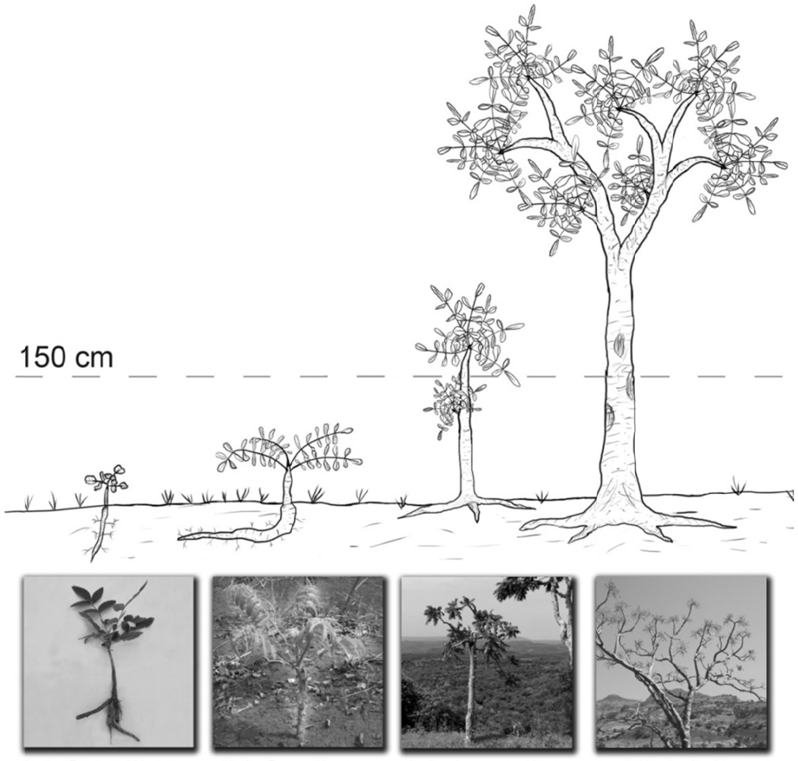
Boswellia papyrifera is a deciduous multipurpose tree found in woodlands and wooded grasslands with an altitudinal range of 800 – 1850 m (in Eritrea), often occurring on steep rocky slopes, sandy river valleys or lava flows (Ogbazghi *et al.* 2006b). In our study region, trees reached maximum height of 14–16 m, and a max DBH of 51.5 cm. The phenological cycle of the species is mainly controlled by the precipitation regime, characterized by a long dry season starting in mid-September to mid-May. Tapping for frankincense occurs during the dry season and coincides with the reproductive cycle of *Boswellia*. A special axe ('mengaff') is used to make incisions in the bark and trees are revisited periodically to collect the resin clumps and reopen tapping wounds. Tapping intensity (the amount of tapping spots) and frequency (the amount of rounds of frankincense collection) is variable among trees and tapping methods. The 'traditional' tapping intensity – which we applied in this research – implies 6-8 tapping incisions for trees of 10-30 cm DBH and 8-12 incisions for larger trees, after which frankincense is collected in 8-12 rounds (Ogbazghi 2001). Due to increasing demand, current commercial tapping is performed at much higher intensities, with up to 18 tapping spots on trees of 10-30 cm and up to 27 spots in trees > 30cm DBH (Kebede 2010).

Data collection

In Metema, 12 plots of 1.6-2.0 ha (total area 22.8 ha) were installed: six plots in areas where frankincense tapping is conducted (T1-T6) and six in untapped areas (U1-U6). Measurements took place during the rainy seasons (July) of 2007, 2008 and 2009.

During the first census, a total of 4370 trees >1cm DBH were found, tagged and their DBH measured. For all individuals under 150 cm height (n=2228), diameter at the stem base (hence called Root Collar Diameter, in short RCD) and height were measured. In the subsequent years, growth and survival status was registered for all individuals. To estimate reproductive status, we randomly selected 25 adult trees in each plot, stratified over all size categories, and recorded the status of fruit production (in December) and seed production (in January) in two years (2008 and 2009). A tree was considered to be reproductive if bearing seed-containing fruits.

A similar demographic study was carried out in the Adi Arkay plot to quantify growth and survival rates to be used as reference for the missing classes in the Metema plots. Here two plots (total of 2.4 ha) were installed and all individuals present (n=327) were measured in the rainy season from 2007 to 2009. Due to the difficult accessibility of plants in the plots, the smallest size class (small seedlings) was not included in the measurements. Reproduction was not measured in Adiarkay.



(a) Seedlings *(SC 1)* (b) Saplings *(SC 2-4)* (c) Juveniles *(SC 5)* (d) Adults *(SC 6-12)*

Figure 1. Life stages of *Boswellia papyrifera*: (a) seedlings with non-permanent stem (*Size Class 1*); (b) saplings (*Size Classes 2-4*); (c) juveniles (*Size Class 5*) and (d) adult trees (*Size Classes 6-12*).

In addition to the above demographic studies, we also conducted a tapping experiment to relate frankincense production per tree to its size (DBH). In two of the sites in Metema we selected ca. 5 trees per 10 cm DBH category just outside the plots and tapped them at an average intensity of 9 incisions in 2008 and 2009. Resin clumps produced by each tree were collected and their dry weight was measured.

Categorization and population structure

The population cycle of *Boswellia papyrifera* can roughly be split into seedlings, saplings, juvenile trees and adult trees (Figure 1). Seedlings are 0-2.0 cm RCD in size, with a height of 0-2.6 cm. In the Metema plots, we observed that these seedlings die back every dry season. It seems that these seedlings do not invest in height growth, forming only a rosette of leaves during the rainy period. Presumably, seedlings in this stage invest in roots and reserves. Several seedlings were dug out and even for small individuals, root systems of more than two meters in length were found (A. Eshete, *unpublished data* and P. Groenendijk).

It is unclear what triggers the switch from non-permanent seedlings to permanent sapling and we assume that this shift is made at approximately 2.0 cm RCD (Supporting Information Fig. S1). Saplings are all individuals between 2.0 cm RCD and 6 cm DBH, subdivided into three size classes: 2-4 cm RCD, from 4.0 cm RCD to 150 cm height and from 150 cm height to 6 cm DBH.

All individuals between 6-10 cm DBH were categorized as juvenile (non-reproductive) trees. Reproduction started at ~10cm DBH and individuals >10cm DBH were thus classified as adults and categorized in 7 DBH categories, from 10-14, 14-18, 18-22, 22-26, 26-30 30-35 and >35cm. Thus, a total of 12 categories were distinguished: one for seedlings, three for saplings, one for juvenile and seven for adult individuals (Fig. 1).

To obtain representative population structures for tapped and untapped populations based on a sufficiently large sample size in all categories, we pooled abundance data from the six tapped and untapped populations. We compared these population structures using a Kolmogorov-Smirnov test. We also tested for differences in adult and seedling densities (using plots as replicates) using a t-test.

Calculation of vital rates

We tested for relations between size on the one hand and growth, survival and reproduction on the other, using regression models. In these models, data of all size categories were combined. We used dummy variables to analyze differences between individual plots (tapped: T1-T6 and untapped: U1-U6) and interaction terms (plot*DBH) to check for differential relations across plots. To calculate the relation between growth rates and size we used linear regressions. For seedlings, the regression was computed between increment in root collar diameter (ΔRCD) and RCD for the period of 2008-2009. For saplings, we used growth data from Adi Arkay over two years (from 2007-2009). For adults, we used diameter increment (ΔDBH) over the period of 2007-2009. The relation between survival and diameter was analyzed using a multiple logistic regression. We also used a logistic regression to analyze the relation between reproduction and diameter and to calculate the probability of reproduction ($Prob\{\mathrm{f}\}_i$) per size class. We computed the regression for each year separately and calculated the $Prob\{\mathrm{f}\}_i$ per year for the six tapped and six untapped plots. Annual frankincense production per tree (in kg) was related to DBH by a linear regression.

Matrix model construction

We used stage based matrix models (Caswell 2001) to analyze the population dynamics of *B. papyrifera.* Matrix models are in the form: $n(t+1) = \mathbf{A} \times \mathbf{n}(t)$. Where $\mathbf{n}(t)$ and $\mathbf{n}(t+1)$ represent the population structure at time t and $t+1$, and **A** the square matrix containing the transition probabilities between categories for each time step (1 year). In our case, transition matrix **A** had 12 size categories.

We first parameterized one transition matrix for tapped and one for untapped stands based on the observed transitions in Metema (i.e. with blocked regeneration). These are hence called 'business as usual'. We then used these as a basis to create management scenarios with increased regeneration and reduced adult mortality (see below under *Scenarios*).

Matrix elements in **A** can be grouped into progression (G, in the sub-diagonal of the matrix), stasis (P, the diagonal of the matrix) and fecundity (F, the upper row except for the leftmost element). The progression elements represent the probability of an individual to grow from one size class (g_i) to the next and were calculated as $G_i = \gamma_i * \sigma_i$, where γ_i is the probability that a surviving individual in size class i grows to the next class (i+1) and σ_i is the annual survival probability in class i. We calculated γ_i as g_i/c_i, where g_i is the DBH or RCD growth rate for category i (in cm.yr^{-1} at its midpoint) and c_i is the category width (in cm). The stasis elements (P) represent the probability that a surviving individual stays in the same size class and were calculated as $Pi = \sigma_i - Gi$. The fecundity elements represent the seedling production per adult individual. Assuming that the number of new seedlings is equal for all reproductive individuals, we calculated F as $Fi = \sigma i \times Prob\{\mathrm{f}\}i \times fi$, where $Prob\{\mathrm{f}\}i$ is the probability for an individual in class i of being reproductive and fi the quotient of annual seedling recruitment per hectare divided by the abundance of reproductive adults per hectare.

To determine the vital rate value for every category, we used the regression equations of vital rates and size, by filling the size midpoint in the regression equation. For seedlings and trees >6 cm DBH, we calculated vital rates with data from Metema. The vital rates for saplings were calculated using data from Adi Arkay, and these were only used in transition models for the management scenarios (see below). The production of seedlings for each size class was calculated by multiplying the reproductive probability of that size class with the annual number of seedlings produced per reproductive tree.

Growth rates of seedlings presented high variation between individuals and an average negative growth rate, likely due to the annual die-back of non-permanent seedlings. We therefore used observed transitions from a different area to calculate the transition probability from seedling to sapling. Seedlings have been observed to continuously die-back yearly, even eight years after being planted (E. Birhane, *pers. communication*). We assumed that seedlings need at least 10 years to become permanent (growth rate of 0.2 cm.yr^{-1}) and used this growth rate in our simulation.

For the ‘business as usual’ models (Supporting Information Table S1) we calculated the vital rates for each of the six tapped and untapped plots using the regression models. Subsequently we took the average of each vital rate per size category from the six tapped and untapped plots. This procedure ensures that we obtain good and representative transition matrix for both tapped and untapped stands, in which plots that differ in environmental conditions and tree densities have an equal weight.

Scenario analysis

The business as usual models were used as the basis for several scenarios. Firstly, we used the vital rates from Adi Arkay to create transition matrices that included seedling-to-sapling transitions, for both for tapped and untapped populations ('REG' scenario, Supporting Information Table 1). Second, we also performed scenarios in which adult mortality was reduced, as this is an important vital rate which may be targeted by active management and protection in *Boswellia* populations. We simulated a 50% reduction in adult mortality (scenario REGMOR50) and a 75% reduction (scenario REGMOR75). Finally, to account for eventual effects of variation in seedling growth speed on the population growth, we also simulated variation in seedling growth by doubling (to 20 years) and halving (to 5 years) growth rates. We could thus test our hypotheses that population decline results from a lack of regeneration alone or also from the observed high adult morality rates.

Matrix model analysis

In matrix modelling, the dominant eigenvalue of a matrix (λ) represents the fixed population growth rate of the matrix once it has reached the stable stage distribution (i.e. the eigenvector of the matrix). Both eigenvalue and eigenvector are inherent characteristics of a matrix model (Caswell 2001). Although the eigenvalue is the most used measure for population growth, it is not realistic to apply it to a population with a blocked regeneration. Therefore we calculated the transient population growth rate over a period of 100 years (λ_{100}). Transient growth rates take the population structure at t=0 into account and were calculated as:

$$\lambda_{100} = \sqrt[100]{\frac{n_{100}}{n_0}}$$

where n_0 and n_{100} are the population sizes at t=0 and at t=100, respectively. We calculated λ_{100} for tapped and untapped populations in the 'business as usual' situation, as well as for the three management scenarios. These projections were combined with results of the yield experiment to calculate the development of frankincense yield over 100 years.

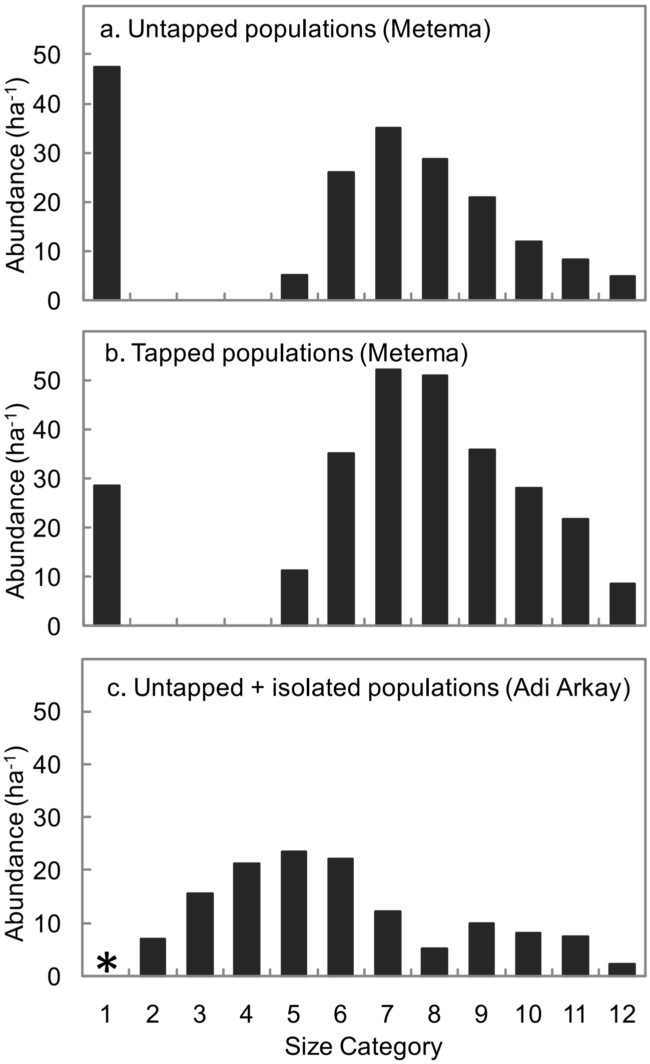


Figure 2. Population structure per hectare for the six untapped (*a*) and six tapped (*b*) stands in Metema and Adi Arkay (*c*) populations. Size category were grouped as seedlings: category 1 (0-2.0 cm Root Collar Diameter (RCD)); saplings: categories 2 and 3 (RCD 2-4 cm and 4 cm RCD–150 cm height); juvenile trees: categories 4 and 5 (150 cm height–6 cm Diameter at Breast Height (DBH) and 6-10 cm DBH); and adults: categories 6 to 12 (6-10, 10-14, 14-18, 18-22, 22-26, 26-30, 30-35 and >35 cm DBH). See Fig.1. In Adi Arkay, the first size class (*) was not measured.

RESULTS

Population structure

All tapped and untapped populations at Metema lack individuals in the size classes 2 till 4 and exhibit a hump-shaped distribution of adult trees (Fig. 2). Average seedling densities per hectare did not differ significantly between tapped and untapped populations, but individual plots varied largely in densities, ranging from 2 to 93 (average 28.5, tapped plots) and from 10 to 94 (average 47.4, untapped plots). The shape of the population structures did not differ between tapped and untapped populations (Kolmogorov-Smirnov p=0.85), but adult tree densities were higher in tapped (227.2±44.1 SD) compared to untapped stands (139.8±47.0 SD; T-test, P=0.003, T=3.319, df=10).

All stands presented new recruitment in both years, but seedlings were never observed to grow into persistent sapling phases. Annual seedling recruitment per reproductive tree was 0.39±0.55 SD in tapped and 0.79±0.57 SD in untapped stands.

Table 1. Different scenarios showing respective transient lambdas (λ_{100}) and frankincense production 'halftime' (½FR) for tapped [T] and untapped [U] stands. Scenarios: BAU (Business as Usual, i.e. measured vital rates in the field); REG (BAU + simulated regeneration); REGMOR50 (REG + adult mortality halved); REGMOR75 (REG + adult mortality reduced by 75%).

	Population growth (λ_{100})		**Frankincense halftime (½FR, years)**	
	Tapped	**Untapped**	**Tapped**	**Untapped**
Scenarios	**Population (T)**	**Population (U)**	**Population (T)**	**Population (U)**
BAU	0.937	0.934	17	15
REG	0.967	0.956	17	15
REGMOR25	0.993	0.984	51	43
REGMOR75	1.006	0.998	-	242

Vital rates

For adult trees, tapped plots T4 and T5 had higher annual growth rates than the reference plot (U1) and T1-T4 differed in the correlation between ΔDBH and DBH. Of the untapped plots, only plot U2 differed significantly from the reference. The average growth rate for the six tapped plots lumped was higher and presented a stronger relationship between ΔDBH and DBH than the average for untapped (Fig. 3).

Survival increased with tree size (method: forward Wald; Nagelkerke R^2=0.035). Due to the low explained variation, we choose to discard the model and to use the average annual survival rate of the 12 plots: 93.7% (±2.1%, n=12) for tapped and 93.3% (±3.8%, n=11) for untapped stands. One of the untapped plots (U7) had a very high (~25%) mortality rate from 2008-2009, caused by a windfall event. As we were interested in normal mortality rates, this plot-year was discarded.

For reproduction in the first year three tapped plots (T1, T3 and T6) and a single untapped plot (U4) differed from the reference plot (U1). For the second year, tapped plots T1, T3, T5 and T6 and untapped plots U7 and U8 differed from the reference plot. On average, individuals in tapped populations had a higher probability of being reproductive than in untapped plots (Fig. 3).

Seedling survival did not differ between plots, therefore we used the average of the six tapped and untapped plots over two years to calculate annual survival rates: 85.2% ±9.8% for tapped plots (n=10) and 84.4% ±13.1% (n=12) for untapped plots. For saplings (data from the Adi Arkay plot), growth rate and diameter were not correlated and the average growth rate was used for all sapling size classes (0.493 cm yr^{-1}, n=113). The probability of survival was significantly related to diameter (Nagelkerke R^2=0.238; $P<0.05$) and we used the logistic regression to estimate survival rates for the sapling classes.

Annual frankincense production increased with tree size (R^2=0.351, n=242; Fig. 3). The large variation in production is partially attributed to the different tapping intensities, which are not further considered here. The linear regression was used to estimate the yield at the midpoint of each size category.

Matrix model output and scenarios

Under the business as usual situation, growth rates λ_{100} were <1.0 for both tapped and untapped stands (~0.93), indicating population decline. As no regeneration was present and mortality was equal for all adult size classes, population growth in fact reflected adult survival rates (~93%). The projected frankincense yield based on the business as usual scenario showed a rapid decline, with tapped stands reaching half the initial production in 17 years and untapped in 15 years (Table 1).

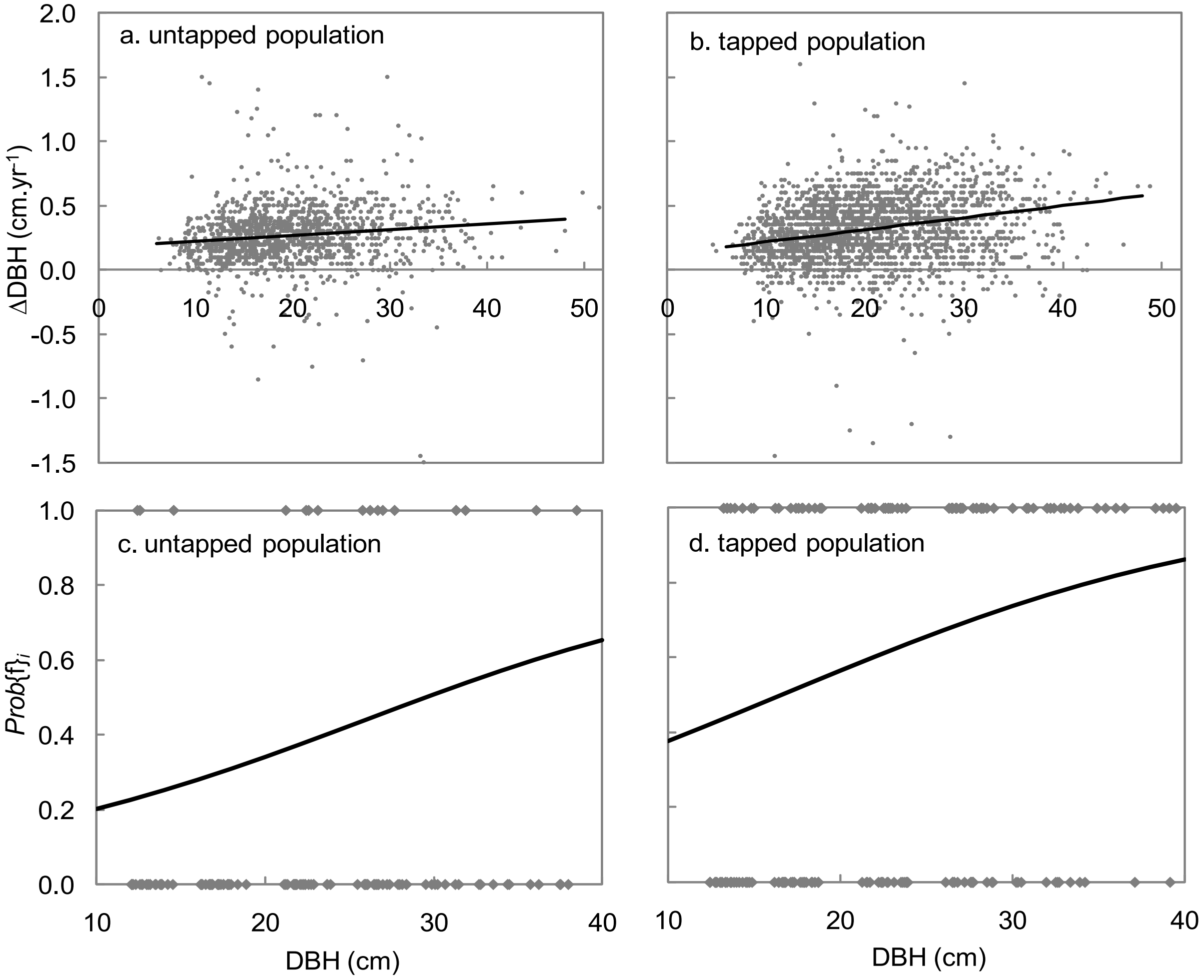


Figure 3. Relationship between annual growth rate (ΔDBH) and probability of being reproductive (*Prob*{f}$_i$) and DBH. *Black lines*: average for the six untapped and six tapped plots for ΔDBH (*a* and *b*, respectively) and *Prob*{f}$_i$ (*c* and *d*, respectively) against DBH. *Grey dots:* individual measurements.

In the REG scenario, λ_{100} increased to 0.967 for tapped and to 0.956 for untapped stands. These values still indicate a rapid decrease in population size. Values for halving frankincense production were the same as for the populations without regeneration. The high adult mortality caused frankincense production to be halved before regeneration was able to replenish the adult stock.

Reducing adult mortality by 50% (REGMOR50: changing survival rates from 93.4% to 96.7%), increased λ_{100} to 0.993 and enlarged the frankincense production halftime to 51 years for the tapped stands. For untapped stands, λ_{100} increased to 0.984 and the halftime to 41 years. Reducing adult mortality by 75% (REGMOR75: survival rates of 98.3%) resulted in approximately sustainable populations, with λ_{100} of 1.01 for tapped and 0.998 for untapped stands (Table 1). Doubling and halving seedling growth speeds in the regeneration scenario induced only small changes in population growth rate ($\Delta\lambda$ ~0.004)

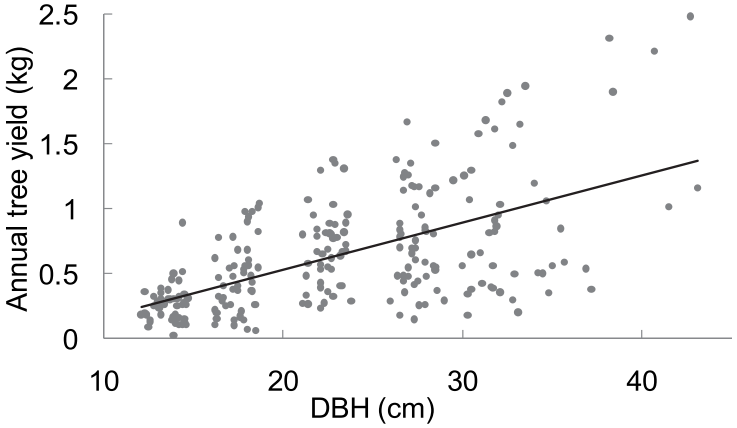


Figure 4. Correlation between annual yield of frankincense (in kg) and tree size (diameter at breast height, DBH in cm). *Grey dots*: individual measurements; *black line*: linear regression line.

DISCUSSION

Experimental studies have shown that resin tapping and lack of regeneration are potentially major threats for *Boswellia papyrifera* populations and for the sustainable exploitation of frankincense (Ogbazghi 2001; Rijkers *et al.* 2006). Here we present the first large scale study on natural population dynamics of *B. papyrifera.* Our results suggest that a lack in regeneration, but not resin tapping, is causing strong population decline. Our results also suggest that high rates of adult mortality in *Boswellia* populations also contribute to the rapid population decline. As a result, strong drops in frankincense production are predicted, indicated by a halftime of frankincense production rates of just ~15 years.

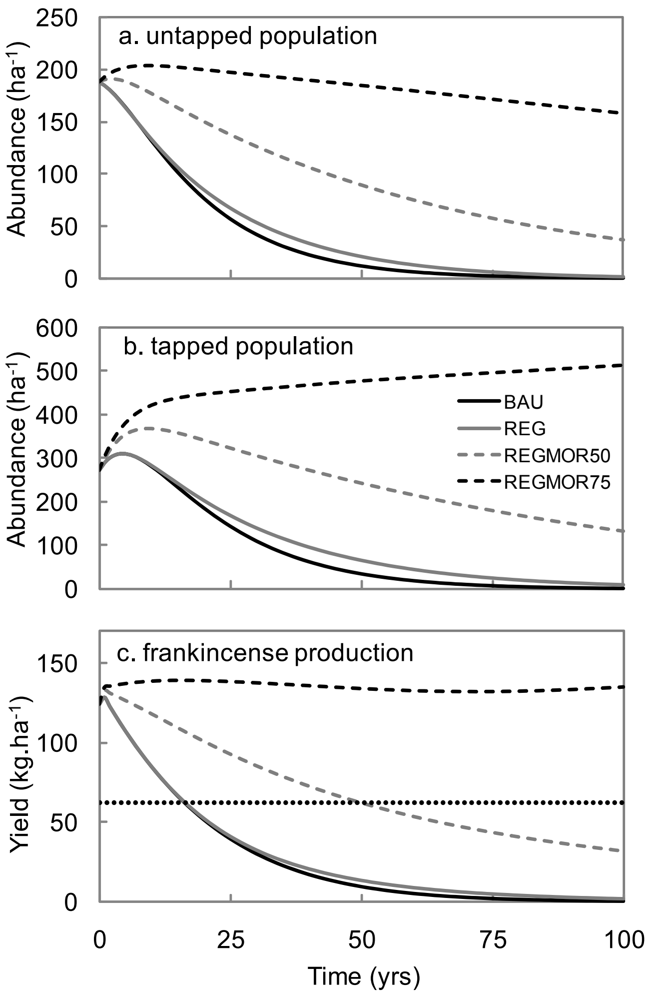


Figure 5. Matrix projection abundance of individuals for the untapped (*a*) and tapped (*b*) populations and frankincense yield projection (*c*, for tapped population only) under different scenarios: business as usual (BAU, *black line*), full regeneration (REG, *grey line*), 50% reduction in adult mortality (REGMOR50, *grey dashed line*) and 75% reduction in adult mortality (REGMOR75, *black dashed line*). The *horizontal dashed line* in *c* represents the 50% level of frankincense yield which is used to determine the yield halftime.

Vital rates and population dynamics in tapped vs untapped populations

We expected negative effects of resin tapping on tree growth, fecundity and mortality in *Boswellia papyrifera,* as the extraction of the resins leads to a significant loss of carbohydrates as well as a need for restoring damaged bark tissue. In the rubber tree (*Hevea brasiliensis*), the most widely tapped tree species globally, empirical studies showed that tapping indeed forms a substantial sink of carbohydrates (Silpi *et al.* 2007), with tapped trees presenting halved diameter growth (Silpi *et al.* 2006). To our surprise, tapped populations presented higher diameter growth rates and a higher proportion of reproductive trees compared to untapped populations. These results contrast with experimental studies on the effect of tapping. Rijkers et al. (2006) showed that tapping of *Boswellia* had a negative effect on reproduction, reducing flower and fruit production and increasing the proportion of non-viable seeds.

Why were diameter growth rates in tapped populations higher than those in untapped populations? There are two potential explanations for this finding. First, higher growth rates in tapped population may be found if diameter measurements are done close to the tapping spot, as increased bark formation may take place around the incisions (cf. Silpi *et al.* 2006). We do not expect that such measuring biases have influenced our data, as there were no signs of increased bark thickness or wound tissue at the measurement spots for diameter measurements. Second, tapped and untapped populations may differ in other respects than just the exploitation. In setting up our study, we choose to compare the demography of tapped and untapped populations instead of performing a large-scale tapping experiment in formerly untapped populations. We did so because such an experiment had been carried out before (Rijkers *et al.* 2006) and because it would not allow to evaluate the long-term effects of tapping that we were interested in. Farmers select populations for resin tapping based on their intuitive judgement of the potential resin production. This judgement is probably based on the average tree size and tree density but also on the distance to access roads and drinking water availability during the dry season when tapping is performed. Therefore, tapped populations constitute a non-random sample of *Boswellia* populations in the region and could possibly be located on more productive soils (Eshete, Sterck & Bongers , 2011) or with higher soil water capacity (Ogbazghi *et al.* 2006b). The higher adult tree density and higher diameter growth rates that we observed in tapped populations is consistent with the pattern that would be found if farmers would select tapping sites based on nutrient and water availability. We feel that it is likely that the observed differences are indeed due to the farmers' non-random selection of tapping populations. In this case, the more favourable conditions in tapped populations may have masked the negative effects of tapping.

Mortality rates did not differ significantly between tapped and untapped populations. Rijkers et al. (2006) suggested that resin tapping does not affect tree mortality, as long as it is performed at a moderate intensity. Tapping in our exploited populations was conducted in the traditional way, i.e. at these moderate intensities. More intensive tapping – involving more and deeper incisions or complete debarking and exposure of cambium – is known to occur in the region under high commercial pressure (Eshete 2002; Tadesse *et al.* 2002; Kebede 2010).

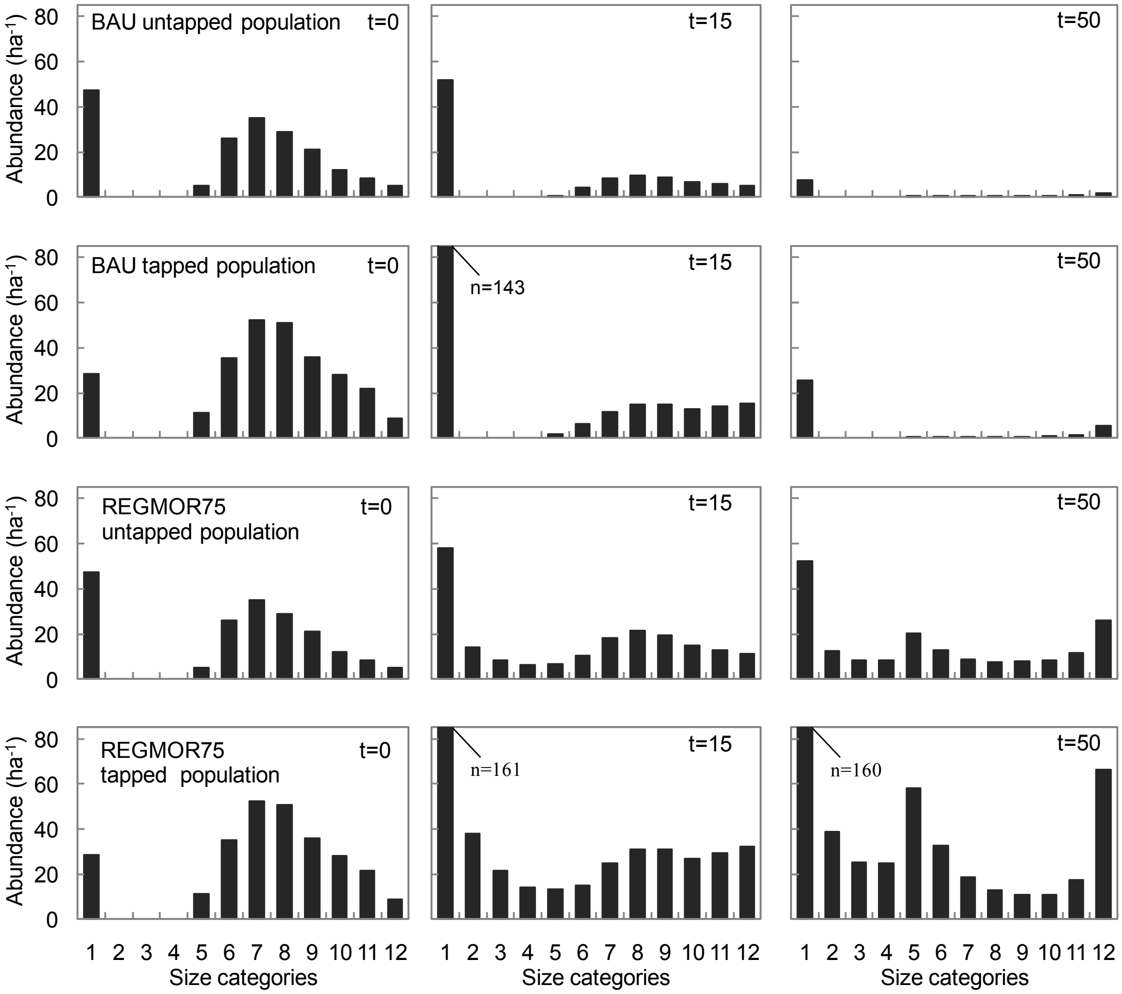


Figure 6. Population structure at time 0 (observed) and projected after 15 and 50 years for two scenarios: business as usual (*BAU*) and 75% reduction of adult mortality (*REGMOR75*). Results are shown for both tapped and untapped populations.

As a result of the higher rates of diameter growth and fecundity, tapped stands had a slightly higher population growth rate than untapped stands. The magnitude of this difference in population growth is much smaller than between the business as usual scenario (which led to strong population decline) and the most optimistic scenario with optimal regeneration and reduced adult mortality. Although this difference in magnitude of change needs to be interpreted cautiously, it suggests that factors other than tapping are importantly governing *Boswellia* populations in the study region.

Causes and consequences of failing regeneration

There were very clear regeneration bottlenecks in tapped and untapped populations. Population structures presented gaps in the sapling categories and none of the seedlings followed in our study (n=2228) grew into permanent saplings. Such gaps in population structure have been observed for tree species in both humid and dry tropical forests (Walker 1993; Poorter *et al.* 1996; Wassie *et al.* 2010b). In our study, only the isolated population (Adi Arkay) contained saplings and small juvenile trees. Applying the observed growth and survival of saplings of that population in our matrix models (REG scenario) yielded continuous population structures (results not shown) but populations were still projected to decline.

What are plausible explanations for the blocked regeneration in our study populations? First, apparent lack of regeneration may occur if regeneration occurs sporadically, e.g. during periods of favourable (climatic) conditions (Barton, Swetnam & Baisan 2001; Holmgren *et al.* 2001). Such erratic regeneration may be sufficient to replace the standing population and does not necessarily result in a decline in population viability (Wiegand, Jeltsch & Ward 1999; 2004). However, in our study region, there is no evidence of differences in temporal climatic variability between the Metema and Adi Arkay plots. In fact, regeneration events are likely to occur synchronously in both areas as well as in other sites across northern Ethiopia and Eritrea (cf. Abiyu et al. 2010). The continuous distribution over size classes in Adi Arkay suggests conditions have been favourable for regeneration. Thus, there is no evidence that gaps in population structure are the result of erratic sapling establishment in the other areas.

A second possible cause of regeneration failure is high seedling mortality due to fires or grazing. Natural fires occur occasionally in dry tropical forests and woodlands (Janzen 2002; Eriksson, Teketay & Granström 2003), are a major determinant of their dynamics (Swaine 1992;

Nangendo *et al.* 2010) and an important source of sapling mortality (Suresh, Dattaraja & Sukumar 2010). In *Boswellia*, non-permanent seedlings are likely not affected by fires as they do not possess aboveground structures at the time of fires (dry season). By contrast, growth and survival of permanent saplings may be severely impeded by fires as these maintain aboveground structures during the dry season. Grazing and browsing are known to affect natural regeneration in *Boswellia*: significantly higher seedling densities can be found in fenced compared to open areas (Ogbazghi 2001; Gebrehiwot *et al.* 2003). As *Boswellia* flushes just before the start of the rainy season, its leaves are an important sources of fodder for cattle, leading to severe damage of seedlings and saplings and high trampling risk (Gebrehiwot *et al.* 2003).

Farmers customarily burn grasses in the forest understory at the end of the dry season to stimulate nutrient-rich regrowth. It is likely that the incidence of fires and the intensity of grazing in our study area has increased over the last couple of decades. The region has seen large-scale immigration from the Ethiopian highlands (Eshete, Teketay & Hulten 2005) accompanied by an increase in cattle population. A large share of the forests with *Boswellia* that were previously relatively undisturbed, are now grazed and frequently burned. Studying the (changes in) fire frequency and the effects of fire and grazing on tree populations is of the utmost importance to assess the demographic changes taking place.

The role of high adult mortality

We observed high rates of adult mortality for *Boswellia* trees, in both tapped and untapped populations. Annual mortality rates for trees >10 cm DBH equalled 6-7%. These rates are almost ten times higher than those in an Indian dry forest (Suresh, Dattaraja & Sukumar 2010) and likely also substantially higher than in other dry forests. A large proportion of the studied trees were killed after having been attacked by the long-horn beetle (*Idactus spinipennis*) or by windfall (Eshete, A., *pers. obs.*). High infection rates (up to 85%) of *Boswellia* trees by larvae of this beetle have been reported for our study region (Metema) and elsewhere (Tigray, Kebede 2010). In this context, it is interesting to note that adult trees in the remote Adi Arkay population showed fewer signs of beetle attack (Eshete, A. *pers. obs.*) and presented lower rates of annual mortality (~3,6%; n=246). Clearly, there is a strong need to get clarity on the causes of the elevated adult mortality in *Boswellia* stands.

Our simulation results suggest that high adult tree mortality severely limits population growth and is one of the two main causes of the projected decline of *Boswellia* populations under the business-as-usual scenario. The modelling scenario in which adult mortality was reduced by 75% was the only one that projected growing populations. A high sensitivity of population growth to changes in adult mortality – as found for *Boswellia* – is typical for long-lived tree species (i.e. Zuidema *et al.* 2010) and forms an important focus point to achieve sustainability. The only scenarios yielding (theoretically) sustainable populations were those with strongly increased adult survival rates. Ensuring both the establishment of seedlings and enhancing adult survival rates are thus crucial steps to achieve sustainable populations and frankincense production.

Implication for management

This is the first study on the effects of frankincense extraction on the population dynamics and the first projections on the future prospects of frankincense populations. Our results show clear evidence for a regeneration bottleneck in *Boswellia* populations, leading to a rapid reduction of these populations and their potential for frankincense production. We also find indications for unusually high mortality rates of *Boswellia* adult trees, which are also projected to cause population shrinkage and reduced productivity. What can be done to reverse these processes? In the short run, it is essential to reduce adult mortality rates as this would allow to maintain existing populations and frankincense production. In the long run, maintaining populations and productivity requires successful establishment of persistent saplings. Thus, *Boswellia* management should focus on stimulating seedling and sapling establishment and reducing adult mortality. Stronger management incentives are needed to ensure sustainable management of these populations, and thereby safeguard future frankincense production.

Appendex 1. Annual transition matrices for *tapped* and *untapped* populations. Columns are stages at time *t* and rows at time *t* + 1. Highlighted cells represent estimated transition values. These transitions are absent in models without regeneration (the current situation).

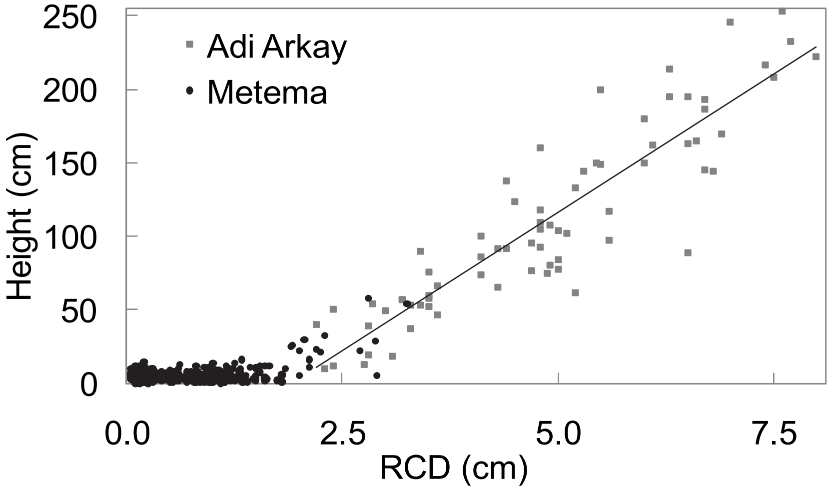
Tapped

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1	0.767	0.000	0.000	0.000	0.000	0.101	0.124	0.149	0.173	0.197	0.221	0.307
2	0.085	0.648	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3	0.000	0.161	0.752	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4	0.000	0.000	0.186	0.809	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
5	0.000	0.000	0.000	0.178	0.887	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6	0.000	0.000	0.000	0.000	0.050	0.878	0.000	0.000	0.000	0.000	0.000	0.000
7	0.000	0.000	0.000	0.000	0.000	0.059	0.869	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.068	0.860	0.000	0.000	0.000	0.000
9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.077	0.851	0.000	0.000	0.000
10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.086	0.842	0.000	0.000
11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.095	0.869	0.000
12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.068	0.937

Untapped

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1	0.759	0.000	0.000	0.000	0.000	0.062	0.078	0.098	0.119	0.141	0.166	0.211
2	0.084	0.648	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3	0.000	0.161	0.752	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4	0.000	0.000	0.186	0.809	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
5	0.000	0.000	0.000	0.178	0.883	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6	0.000	0.000	0.000	0.000	0.050	0.879	0.000	0.000	0.000	0.000	0.000	0.000
7	0.000	0.000	0.000	0.000	0.000	0.055	0.875	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.059	0.870	0.000	0.000	0.000	0.000
9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.866	0.000	0.000	0.000
10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.067	0.862	0.000	0.000
11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.071	0.882	0.000
12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.051	0.933

Appendix 2. Relationship between RCD and height for seedlings in Metema (*black dots,* RCD <3.3cm) and seedlings in Adi Arkay (*grey squares*, RCD >2.3 cm); *black line*: linear regression for Adi Arkay.



Chapter 5

The collapse of Frankincense tree populations and frankincense production is unaffected by soil conditions and biotic factors

Abeje Eshete, Frank Sterck, Pieter Zuidema, Tesfaye Bekele, Kindeya Gebrehiwot & Frans Bongers

Abstract

Regeneration of the frankincense producing tree, *Boswellia papyrifera* (Burseraceae) is scarce, in many studied populations threatening the dry woodlands and the highly valued frankincense production. Here we study the role of regeneration in the dynamics of 12 frankincense tree populations across its habitats in northern Ethiopia using a stage-classified matrix model. Growth, mortality and recruitment were recorded over two years in 12 permanent plots of 1.6 to 2 ha each. With population growth rates (λ) below 1 all 12 populations were declining. In spite of the high seedling recruitment in some of the populations none of the seedlings survived and grew to sapling stage. Overall mortality rate of juveniles and adults (7%) was high. Against our expectation, the elasticity analyses and scenario analysis showed that high recruitment and fast transitions of seedlings to saplings would not lead to a growing population. Instead, only higher large tree survival would imply population increase. The poor recruitment, high adult tree mortality and resultant low population growth rate were unaffected by soil fertility conditions and biotic factors (abundance, basal area, stand volume). Overriding disturbances by fire, grazing or herbivore attacks are probably responsible for the declines in tree abundance and the annual frankincense production capacity over the coming years.

Key words**:** Soil conditions, biotic factors, vital rates, population growth, Boswellia papyrifera, management actions

INTRODUCTION

Non timber forest products (NTFPs) are materials of biological origin derived from forests, including bark, roots, tubers, corms, leaves, flowers, seeds, fruits, gums, resins, honey, fungi, animal products and only excluding timber (de Beer & McDermott 1989, Ros-Tonen et al. 1995). NTFPs are a major source of livelihood and cash income for rural and urban households in developing countries (FAO 1989, Wollenberg & Ingles 1998, Lemenih et al. 2003). The extraction of NTFPs has been advocated as a land-use practice that integrates forest conservation and economic development of people living in forest areas (see, e.g., Nepstad and Schwartzman, 1992; Allegretti, 1990; Plotkin and Famolare, 1992). NTFP extraction is often thought to be economically viable, ecologically sound, and socially acceptable (Barbier 1987, Arnold & Ruiz-Perez 2001; Ticktin 2004). Unlike logging, the extraction of NTFPs usually shows no or limited signs of changes in forest structure, and is assumed to maintain forest environmental services and biological diversity, and provide opportunities of sound forest management (Peters 1996; Ros-Tonen 2000, Ticktin 2004**)**. More recently, however, it has been shown that exploitation of NTFPs may not always be sustainable (see a review by Hall and Bawa 1993), particular because the exploited trees decline in vigour, and recruitment and abundance may go down (e.g. Perez et al. 2003, Rijkers et al. 2006).

Sustainable extraction of non-timber forest resources can be implemented if periodic inventories show that strong negative impacts of NTFP extraction on tree numbers and NTFP production are negligible (Peters 1996; Hall and Bawa 1993;). Based on such inventories, matrix models can be parameterized (Caswell 2001, maybe a recent paper?) to assess the likely effects of various management strategies on population growth rates (Rist et al. 2010, Pinard & Putz 1992, Waite and Hutchings 1991, Aplet et al. 1994, Smith and Trout 1994, Maschinski et al. 1997,), or of natural or anthropogenic disturbances like fire, grazing, or harvesting (Silva et al. 1991, Nault and Gagnon 1993, O'Connor 1993, Pinard 1993, Bullock et al. 1994, Bastrenta et al. 1995, Olmstead & Alvarez-Buylla 1995, West 1995, Batista et al. 1998). Matrix models have also been used to document spatial and temporal variation in a species' vital rates (e.g., Horvitz and Schemske 1995, Oostermeijer et al. 1996, Kephart and Paladino 1997, Vavrek et al. 1997, Zuidema 2000; Svenning & Macia 2002). Sensitivity or elasticity analyses of these models can identify the life phases and vital rates that are most critical to the population growth (de Kroon et al. 2000, Zuidema et al. 2010), and these life phases should then receive particular attention in management programs (see also Verwer et al. 2008). Life table response experiments even more directly evaluate effects of environmental variation or management regime on the population (Caswell 2001).

Here we present a study on the effect of habitat characteristics (soil conditions), and biotic factors (abundance, basal area, standing volume) on population dynamics of the frankincense-producing tree species *Boswellia papyrifera* in Ethiopian dry woodlands. *B. papyrifera* occurs along a wide altitudinal range of 500-1600 m.a.s.l (Friis et al. 2010, Vollesen 1989, Eshete et al. 2011) in areas varying in geology, soil types, topography, climatic conditions (Gebrehiwot 2003, ILRI 2005), and in species composition and vegetation structure (Eshete et al. 2011). We recently showed that the population structure and biomass is mainly driven by variation in soil conditions, and probably less by the encountered climatic variation (Eshete et al. 2011). These populations are under pressure because the traditional frankincense tapping activities in the Horn of Africa have been intensified (Kebede 2010) and lead to reduced tree vigor (Rijkers et al. 2006). Moreover, unregulated grazing and recurrent fires prevent seedling and sapling establishment (Ogbazghi 2001; Gebrehiwot 2003; Abiyu et al. 2010), and land clearing for agricultural expansion degraded *B. papyrifera* dominated woodlands (Lemenih et al. 2007, Girma et al. inpreparation). These land and tree uses potentially threaten the existence of remaining populations, as confirmed by the missing recruitment class (Ogbazghi et al 2006a, Abiyu et al. 2010; Recently, we reported on the projected decline of populations in Northern Ethiopia, in both tapped and untapped areas (Chapter 4). This chapter examines to what extent habitat characteristics and biotic factors influence the dynamics of 12 tapped and untapped populations.

We use matrix models to predict the present growth rates of the twelve populations, and show how sensitive these population growth rates are to the vital rates in different life phases. Moreover, we explore whether the expected collapse of *B. papyrifera* populations is similar for populations differing in soil fertility or in frankincense tapping regime. More specifically we addressed the following research questions: (1) How do vital rates (reproduction, stem growth, survival) and population growth rates of *B. papyrifera* populations vary among populations differing in soil conditions? (2) What are the bottlenecks for achieving persistent *B. papyrifera* populations? We expect higher growth, survival and reproduction on more productive soils, which have a higher clay contents and deeper soil (Eshete et al. 2011). Since poor regeneration is the common feature of *B. papyrifera* populations (Abiyu et al. 2010), we expect that lack of recruitment (establishment and survival of seedlings) acts as a major bottleneck for the persistence of the populations. We will discuss our result in the light of the sustainable management of this species and the frankincense production, in areas where increasing numbers of people and organizations get involved in the harvesting, processing and marketing of frankincense (Lemenih et al. 2007, Eshete et al. 2005).

MATERIALS AND METHODS

Study species

Boswellia papyrifera (Del.) Hochst. (Burseraceae) is a deciduous tree that reaches a height of approximately 14 m, has a round crown, contains prominent vertical resin ducts in the bark, and has thick branches tipped with clusters of leaves (Azene Bekele *et al*. 1993, Eshete et al. 2011). The species is distributed in hot and arid areas, often on steep or exposed situations and on rocky slopes or in gullies. In Ethiopia, *B. papyrifera* is encountered in *Combretum-Terminalia* woodlands at altitudes of 600 - 1800 m.a.s.l. (IBC 2007, Friis et al. 2010), average temperature ranging from 20 to 25^{o} C and annual rainfall of 500 - 1000 mm (Eshete et al. 2011, Ogbazghi et al. 2006b). Beyond Ethiopia, this species is also encountered in Nigeria, Cameroon, the Central African Republic, Chad, Eritrea, Sudan, Somalia, and NE Uganda (Vollesen 1989; Azene Bekele et al. 1993). In Ethiopia, *B. papyrifera* provides both wood and non-wood forest products. Wood is important for local people to make household furniture and doors. Leaves are used as fodder for cattle, and honey is exploited (Eshete 2002). The highest economic value is provided by frankincense, a resin obtained by wounding the bark during the dry season. The tapping of frankincense is described elsewhere (Gebrehiwot 2003, Eshete et al. in preparation). Frankincense from *B. papyrifera* has been marketed since ancient times (Groom 1981). Ethiopia was and is still the major producer and exporter of this product. Gebrehiwot (2003) and Lemenih and Teketay (2003b) described the traditional and modern use of the frankincense.

Study site

The study sites are located in the Metema region in north western Ethiopia (12°33.58' – 12°41.53'N, 36°04.12' – 36°18.84'E). The climate is characterized by > 8 months dry season (Eshete et al. 2011). According to data from the nearest meteorological station, Shehidi, 25 km away from the study sites, the mean annual rainfall is 965 mm and the mean monthly minimum and maximum temperature are 19.6 and 35.7^{o}C, respectively. The altitude of the studied plots ranged from 595 to 920 m.a.s.l. The sites belong to the lowland dry areas where deciduous tree species dominate the vegetation. IBC (2007) and Friis et al. (2010) classify the vegetation in the study site as Combretum-Terminalia woodlands, dominated by gum and resin producing tree species .

Commercial harvesting of frankincense from *B. papyrifera* started long ago in Ethiopia, and since 1996 in the study site (Eshete 2002). We selected 12 populations in 1.6-2.0 ha plots for this study in August 2007. These plots varied in tree abundance (89–302 trees ha^{-1}), basal area (2.5–11.4 m^{2} ha^{-1}) and standing volume (7.3–38 m^{3} ha^{-1}) (Eshete et al. 2011). The plots also varied in soil texture and composition: the clay content ranges from 11 to 58%, organic matter from <1–5%, soil depth from 11. to – 58 cm, and available phosphorus from 1.84 to 50.21 ppm (Eshete et al. 2011). Six of the 12 studied populations were continuously tapped from 1995-2005, but not in 2006. Such a year without tapping is considered a “resting period”. From 2007 onwards the tapping was continued again. The other 6 populations were never exploited for frankincense because they were relatively inaccessible, did not provide water sources to workers, or were considered not sufficiently productive by local tappers (Eshete 2002). Also during our experiment, these populations remained untapped. Half of the tapped plots and of the untapped plots were fenced and protected from fire by creating vegetation free corridors.

Data collection

In each plot all individual plants of *B. papyrifera* (≥ one year old) were tagged and mapped at the start of the experiment (August 2007). Of all trees less than 1.5 m tall, height and root collar diameter (RCD) were measured, and of trees ≥ 1.5 m their height and stem diameter at breast height (DBH). Newly recruited individuals (at least 1 year old) were tagged and mapped. These new recruits were easy to distinguish from newly emerging seedlings(< 1 year seedlings), because the newly emerging seedlings had two cotyledons. Two plots (Plots 11 and 12) were established in October 2007 and thus new recruits were scored only for 2009. All trees and new recruits were re-measured in August 2008 and August 2009. Mortality was scored every six months starting at the time the plots were established. Trees were considered dead if they were debarked along a dry trunk during the dry season, or had no leaves during the rainy season. These dead trees were monitored also during later censuses to confirm their death. Tree damage (presence of fire scar or sign of insect attack) and possible death causes (due to fire, human cut, wind fall or insect attack) were recorded for dead trees.

For each plot the annual fruit production was determined on 5 trees for each of five diameter classes (diameter class 1 = 10 – 15 cm; 2 = 15 – 20cm; 3 = 20 - 25 cm; 4 = 25 – 30 cm; 5 = ≥ 30 cm). When fruits matured (December – January) the total number of fruit bearing apices per tree were counted. Of these, five apices were selected (one in each cardinal direction and one at the center of the crown) to count the number of fruit produced per apex (Rijkers 2006). From each plot a pooled soil sample (0-20 cm) was taken from three sub-plots (20 x 20 m) and soil physical and chemical variables were determined. Soil physical variables include, clay (%), sand (%), silt (%) and soil depth (cm). Soil chemical variables include: organic carbon, nitrogen, available phosphorus, basic cations (Na^+, Ca^{++}, Mg^{++}, K^+), cation exchange capacity, and soil pH. The methods employed to estimate each soil variable are described elsewhere (Eshete et al. 2011, Chapter 2). In that earlier study, we also showed that the stand volume correlated strongly with soil depth and clay %.

Data analysis

We divided the population into 4 stages and 18 size classes (Chapter 4, Fig. 1). The four stages were referred to as seedlings, saplings, juveniles and adults. The seedling stage that contained only the first size class were characterized by > 1 year age and < 2cm RCD. Plants in this stage class die back every dry season and do not produce a permanent shoot for at least 8 years. Seedlings needed about 10 years after establishment to produce permanent shoot and reach 2 cm RCD (field observation, Birhane, personal communication). The second stage includes the size classes 2, 3 and 4, and refers to saplings with a RCD of > 2 cm and a DBH of < 6 cm (size class 2= 2- 4cm RCD; 3 = 4 – 6 cm RCD; 4= 6 – 9 cm RCD). Juveniles are non-reproductive individuals and include only the 5th size class (DBH =6–10 cm). The adult stage includes all individuals that may fruit (DBH ≥ 10 cm). This stage was subdivided into 13 size classes (size class 6 = 10 – 12; 7 = 12 – 14; 8 = 14 – 16; 9=16 – 18; 10= 18 – 20; 11= 20 – 22; 12= 22- 24; 13=24 – 26; 14=26- 28; 15= 28 – 30; 16= 30 – 32; 17= 32 – 34; 18 = >34, inclusive of the lower bound of the interval).

Stand and population structure

Total plot tree abundance, basal area and standing volume were determined for each population. Abundance was determined as the number of individuals per hectare, basal area (G) was the sum of stem basal area scaled to a hectare (m^2.ha-1), and stand stem volume (V) was estimated assuming a cone stem shape and tree height H, using the equation,

$$V = G\,H/3 \qquad [1]$$

Vital rate calculations

For each population the annual vital rates of *B. papyrifera* were calculated based on the 2007-2009 field data. We therefore regressed fruiting probabilities, seed production per fruit, growth rates and survival rates per plot against size.

As mentioned before, the field measurements for fruiting probability and fruit production were collected from 25 trees in the 5 largest size classes (individual in adult stage) per plot. Proportion of fruiting trees per plot was calculated as the number of fruiting trees divided by the total number of study sample trees (i.e. 25). To analyze and determine size specific fruiting probability as well as fruit production per tree, the fruiting probability was regressed against DBH using logistic regression model, and the number of fruits per tree as a linear regression.

Survival rates were calculated for all size classes. For individuals in stage and size class 1 we calculated survival as,

$$S = 1 - m \qquad [2]$$

Where m is mortality rate defined as:

$$m = \frac{\ln (N_0) - \ln (N_t))}{t} \qquad [3]$$

where $\ln(N_0)$ is the natural logarithm of individuals at the initial time (2007) and $\ln(N_t)$ is the natural logarithm of individuals at *t* time (2009) (Condit et al. 1995). A two-way ANOVA was employed to test the importance of fencing and tapping on survival rate of seedlings. Logistic regression was used to analyze and determine size specific survival probability of individuals in all other stages and size classes. This analysis was performed for each plot.

Size specific annual growth rates of individual plants was calculated from growth curves obtained from the two years of field measurements. The growth curve was obtained using linear regression models where DBH or RCD and the square of DBH or RCD at year 0 was included as an independent variable. When no relation was observed between growth rates and tree size, average growth rates of the population was calculated.

Matrix model construction

Two transition matrices that differ in parameterization of matrix elements were constructed for each of the 12 populations: C_m and S_1. C_m matrices were based on the observed vital rates. It shows the population growth of each population under the current situation. S_1 is a transition matrix constructed based on important assumptions for some vital rates. First, we made an important assumption that individuals in the first class would take 10 years to join the second size class, thus growth rate of individuals in this size class would be 2 cm/10 years = 0.2cm per year. Second, as indicated in Chapter 4., the individuals in the 2nd, 3rd, and 4th classes were missing in all plots. But, we need to calculate the transition elements for the missing classes. Thus, we looked for another site (Adiarkay) where individuals of all size classes were present. In this site we monitored the survival and growth of individuals with root collar diameter of ≥ 2 cm to < 6 cm in diameter at breast height for similar number of years. The survival and growth rate as well as the growth and stasis elements of the these classes were estimated based on the two year data. The S_1 transition matrices were then used to analyze the dynamics of *B. papyrifera* populations based on the C_m and with transition elements of the missing classes estimated from the observed vital rates at Adiarkay site and assumed growth element of the first class ($G_{1} = 0.2$). Each matrix used a stage-classified transition matrix model to analyze the dynamics of *B. papyrifera* populations (cf. Caswell 2001). The transition matrix models took the form:

$$\mathbf{n}(t+1) = \mathbf{A}\,\mathbf{n}(t) \qquad [4]$$

where $\mathbf{n}(t)$ is a vector of the stage abundances at time t, and $\mathbf{A}$ is the matrix containing transition probabilities that describe the contribution of each stage to the population at the next time step. The intrinsic population growth rate is calculated as the dominant eigenvalue, $\boldsymbol{\lambda}$, of the matrix $\mathbf{A}$. The projection interval (from t to $t + 1$) was 1 year.

The matrix **A** contains matrix elements (a_{ij}): P*i*, G*ij*, and F_i. P*i* describe the probabilities of surviving and staying in same life stage (stasis), G*ij* describes the probabilities of surviving and growing from stage *i* to stage *j* during the time interval from *t* to *t* + 1; and; F*i* describe the fecundity value of the *i* stage class. The value of the growth element G_{ij} was calculated as $G_{ij} = g_i*\sigma_i*C_i^{-1}$, where g_i represents mean annual growth rate recorded in size class *i*; σ_i the survival rate of individuals in *i* class and C_i^{-1} represents the class width of *i* class. P*i* was calculated as P*i* = σ_i - G_i. Fecundity (F_i) was determined as $F_i = \sigma_i * \Pr\{f\}_i * f_i$, where $\Pr\{f\}_i$ is the probability that an individual in size class *i* is reproductive and f_i the number of offspring produced by a reproductive individual in size class *i*. The value of f_i was determined as the size-class specific fruit production, multiplied by the number of seedlings produced that emerged per fruit produced during the previous year.

To test if the population growth rate, λ, (from S_1 transition matrix) of each population is different from 1, confidence intervals for λ were calculated using the first-order approximation proposed by Caswell (1989), that depends on the sensitivity and variation of transitions matrix elements.

Elasticity analysis was used to get important information on the extent to which population growth rate depends on survival, growth and reproduction at different stages in the life cycle (de Kroon et al. 1986, Caswell 2001). The formula for elasticity, *e*, is given by:

$$e_{ij} = (a_{ij}/\lambda)\ (\delta\lambda/\ \delta a_{ij}) \qquad [5]$$

where $\delta\lambda/\ \delta a_{ij}$ is the sensitivity of the population growth rate to a small change in each transition probability. The elasticity analysis was carried for the two kind of matrices: C_m and S_1.

Effect of soil conditions and biotic factors on vital rates and population growth of *B. papyrifera*

To test the importance of soil conditions for vital rates we regressed different vital rates against each soil physical and chemical variables and tested for a significant slope. These tests were performed at two level. The first test was at plot level where the average vital rates per plot were used for the test. For the second test we used the vital rates of specific size class to avoid the error that would arise due to difference in size class distribution between plots (chapter 4). Similarly, vital rates were regressed against biotic factors (abundance, basal area and standing volume) To test the relationship between size specific vital rates and soil conditions as well as biotic factors, we chose 5 diameter classes (8 – 12) and the analyses was performed for each class separately. Similar test was performed for the population growth rate and elasticity at plot level. Here we choose clay % (the best proxy for soil productivity in the study sites, Eshete et al. 2011) to depict the results of the regression analysis.

Table 1. Vital rates for the 12 studied populations of *B. papyrifera* in the Metema region, North western Ethiopia. Means and standard error of means (SE) are only shown for growth because those values represent the averaged values per tree across the population. The other vital rates are population estimates. All data were obtained for juvenile and adult trees (>6 cm DBH) over a 2 year period (August 2007 - August 2009). Growth and survival rates are calculated on an annual basis and the proportion of fruiting trees and the annual recruitment are averages of the two years of study.

Plot	Tapping	Annual diameter growth rate (cm)		Annual survival rate	Proportion of fruiting trees (%)	Annual recruitment (no/ha)
		Mean	SE			
1	Untapped	0.26	0.03	0.96	38	65.3
2	Untapped	0.34	0.05	0.90	38	4.4
6	Untapped	0.24	0.02	0.95	45	7.0
7	Untapped	0.23	0.03	0.86	39	29.3
8	Untapped	0.25	0.02	0.93	26	24.0
9	Untapped	0.29	0.04	0.90	42	6.9
3	Tapped	0.39	0.02	0.95	79	4.3
4	Tapped	0.41	0.02	0.92	46	7.3
5	Tapped	0.43	0.03	0.92	70	95.8
10	Tapped	0.27	0.02	0.93	60	3.8
11	Tapped	0.13	0.03	0.95	72	133.1
12	Tapped	0.25	0.02	0.95	40	1.5

RESULTS

Fruiting and recruitment pattern

The percentage of fruiting trees ranged from 26 to 79% among the 12 populations For 6 of the 12 plots, fruiting probability increased with stem diameter and for all plots the number of fruits per tree increased with stem diameter. Tapped trees had a higher probability of fruit production than untapped trees (Fig 1). Approximately, 1/3 of all trees produced fruit in both years, ~1/3 in one of the two years and ~1/3 produced no fruit in both years. Trees of plot 5 produced much higher amounts of fruits than trees of other plots.

Seedlings recruited every year in all plots. The number of recruits per ha, however, varied from 1.5 (plot 11) to 133 ha^{-1} (plot 12) (Table 1). The recruiting plants originate from seeds in most plots. They, however, originated from root suckers in plots 2 and 6, even though trees were flowering and fruiting proliferically in these plots.

Survival

Survival rate of seedlings in fenced plots ranged between 0.81 and 0.98, and in open plots between 0.54 and 0.93. The overall average seedling survival rate was 0.85 (± 0.38 SE) across plots and was not significantly affected by fencing or tapping ($t= 0.961$, $p > 0.05$). Survival rate of saplings at Adiarkay site was 0.87. Initial root collar diameter showed a significant effect on the survival probability of saplings at Adiarkay site ($p < 0.05$, $R^2 = 0.24$). At population level survival rate of juveniles and adult individuals ranged from 0.86 to 0.96. And the overall mean annual survival rate of juvenile and adult individuals was 0.93 (± 0.01 SE) (Table 1, Fig. 1). Survival probability of juveniles and adult individuals showed positive (plot 7 and 9), negative (plot 5 and 8) or no relation (2, 4, 10 and 11) with initial diameter (Table 2, Fig. 1). Plot 1, 3, 6 and 12 showed an increase in survival probability for the first small diameter size then a decrease in survival probability with diameter size since the square of DBH was negative in the regression model. Insect attack, windfalls and human cut were the major sources of mortality accounting for 77%, 21% and 2%, respectively, of all deaths among juveniles and adults trees of > 6 cm DBH.

Growth

Seedlings died back during the dry periods of the two study years. The growth of root collar diameter as well as the height of re-shooting seedlings were not related to the initial root collar diameter or height (n= , $P > 0.05$). The linear regression test showed that growth of saplings at Adiarkay site was independent of initial root collar diameter ($p > 0.05$). Average growth rate of saplings was 0.5 cm/year. Average growth rate of juveniles and adults together ranged from 0.13 (plot 11) to 0.43 cm/year (plot 5). In 9 out of the 12 plots growth was affected by DBH, in most cases growth rates increased linearly with DBH (Fig. 1., Table 2)**.**

Table 2. Stem growth, survival and fruiting probability of *B. papyrifera* trees as a function of tree size for 12 populations at Metema, northern Ethiopia. Only trees > 6 cm diameter at breast height (DBH) were considered. Multiple linear regression results are shown.

Growth			**Survival**			**Fruiting probability (2007)**			**Fruiting probability (2008)**		
Constant	DBH	DBH^2	Constant	DBH	DBH^2	Constant	DBH	DBH^2	Constant	DBH	DBH^2
-0.212	0.053	-0.001	-0.25	0.26	-0.006	-2.143	ns	0.004	-0.944	ns	ns
0.31	0.02	Ns	1.493	ns	ns	-0.095	ns	Ns	-0.916	ns	ns
0.33	0.03	Ns	-1.196	0.334	-0.007	0.887	ns	Ns	1.946	ns	ns
-0.14	0.06	-0.001	1.7	ns	ns	-0.167	ns	Ns	-0.167	ns	ns
0.28	0.02	Ns	2.24	ns	-0.001	-1.966	ns	0.007	-1.232	ns	0.004
0.33	0.01	Ns	-2.417	0.555	-.015	-0.105	ns	Ns	-0.318	ns	ns
0.23	ns	Ns	-1.107	0.123	ns	1.224	ns	Ns	-	-	-
0.304	0.011	Ns	2.5	ns	-0.002	-3.634	0.168	Ns	-	-	-
0.29	ns	Ns	0.191	0.048	ns	-0.241	ns	Ns	-2.99	0.11	ns
0.152	0.025	Ns	1.892	ns	ns	0	ns	Ns	0.847	ns	ns
0.13	ns	Ns	2.226	ns	ns	-1.998	0.15	Ns	-2.287	0.141	ns
0.201	0.014	Ns	-0.712	0.269	-0.006	-0.405	ns	Ns	-5.473	0.211	ns

Note: ns = not significant

Matrix model output

The population growth rate λ of the 12 *B. papyrifera* populations ranged between 0.86 to 0.98 per year (average $\lambda = 0.92 \pm 0.03$ SD) in the period 2007 – 2009, indicating declining populations in all studied plots. The elasticity analysis showed that the most important matrix

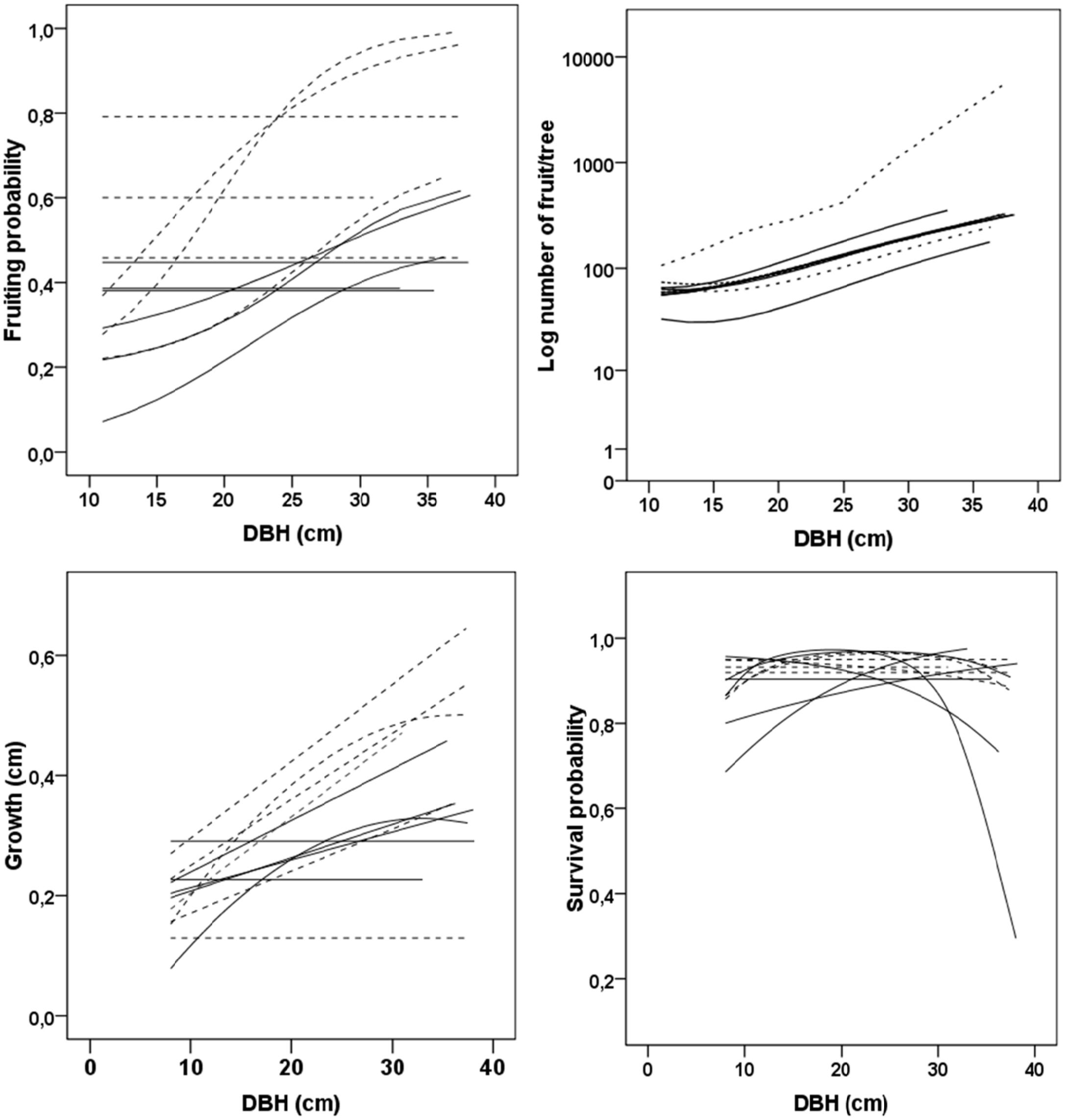


Figure 1. The relationship between vital rates and stem diameter in each of the 12 studied population of *B. papyrifera* at Metema, NW Ethiopia. Lines are regression lines according to stepwise multiple regression models for growth and fruit production and logistic regression for survival rate and fruiting production. Solid lines for untapped plots and dashed lines for tapped plots.

element is stasis, in particular the survival rate of the largest size class. This suggests that mainly the survival of the largest individuals is critical for the persistence of populations in the present conditions.

The adjusted matrix models (including regeneration and vital rates of saplings or missing classes in the study sites) showed population growth rates ranging from 0.90 to 0.98 (Fig. 2). Still all λ, except that of plot 11, were significantly lower than1 and thus indicated decreasing populations. Elasticity analysis for these adjusted matrix models in all plots showed that by far the largest proportion of total elasticity is contained in stasis elements (>92.9%), while growth (<6.6%) and fecundity (0.5%) elements had a very low contribution to λ (Fig. 3B). The elasticity analysis also showed that the survival rate of the adult stage was the most important vital rate in determining λ (Fig. 3A). The population growth rates were little affected by changes in the seedling vital rates in all plots.

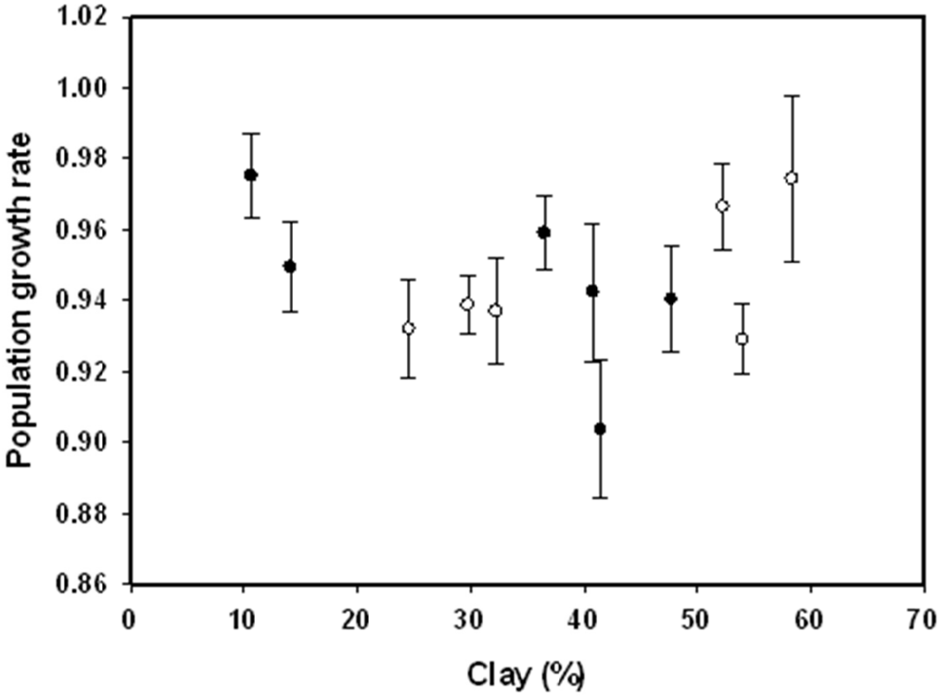


Figure 2. Population growth rate of the 12 *B. papyrifera* populations (calculated from Scenario 1 = with regeneration) in relation with soil clay content. Open circles are tapped plots, closed circles were not tapped. Error bars are standard error of the mean.

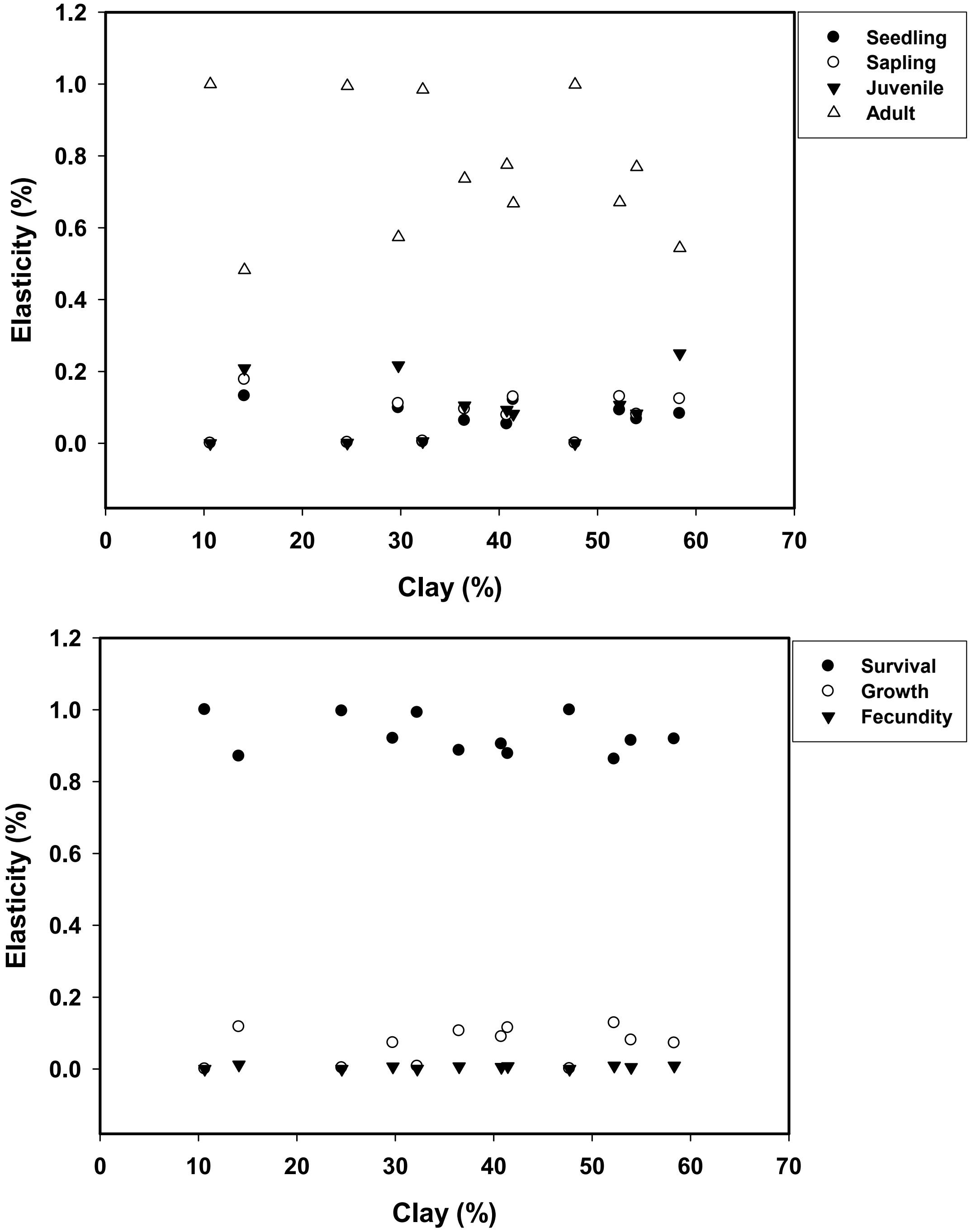


Figure 3. The proportion of total elasticity contained in different life phases (A) and matrix elements (B). to the population growth rate in relation with soil clay content.

Effect of soil conditions and biotic factors on population characteristics

We predicted higher growth rates, survival rates, and fruiting probability in populations growing on soil conditions with higher clay content, deeper soil depth and better soil fertility. We had also expected higher population growth rates for populations growing in better soil conditions. Contrary to our expectations, however, none of the vital rates (growth rate, survival and fruiting probability) were significantly related to soil conditions (clay content, soil depth and soil chemicals (Fig. 4) nor to biotic factors (abundance, basal area, and stand volume, data not shown). Similarly, population growth rates from the first model and elasticity values obtained from the second model were not also related to both soil conditions and biotic factors (data not shown).

DISCUSSION

This study evaluates if soil conditions and biotic factors affect demography (vital rates) of *B. papyrifera.* Based on earlier work (Eshete et al. 2011)where we showed that stand volume of *B. papyrifera* populations and of the whole woody plant community increased with soil fertility, we hypothesized that vital rates of *B. papyrifera* populations respond to soil fertility factors. We expected higher growth rates, survival and reproduction effort in response to higher soil fertility. Contrary to our expectations none of the vital rates were related to soil conditions, nor to the biotic factors evaluated. and biotic factors (abundance, basal area and standing volume).

Irrespective of soil conditions and biotic factors, all populations were characterized by lack of sapling regeneration and high adult tree mortality rates, and resulting in non-sustainable populations. We re-hypothesize that these factors are overruled by relatively recent and strong impacts of disturbance. In chapter 4, we showed that frankincense tapping regime is an unlikely candidate for explaining the decline in the growth rates of these populations, and fire and grazing are more likely candidates.

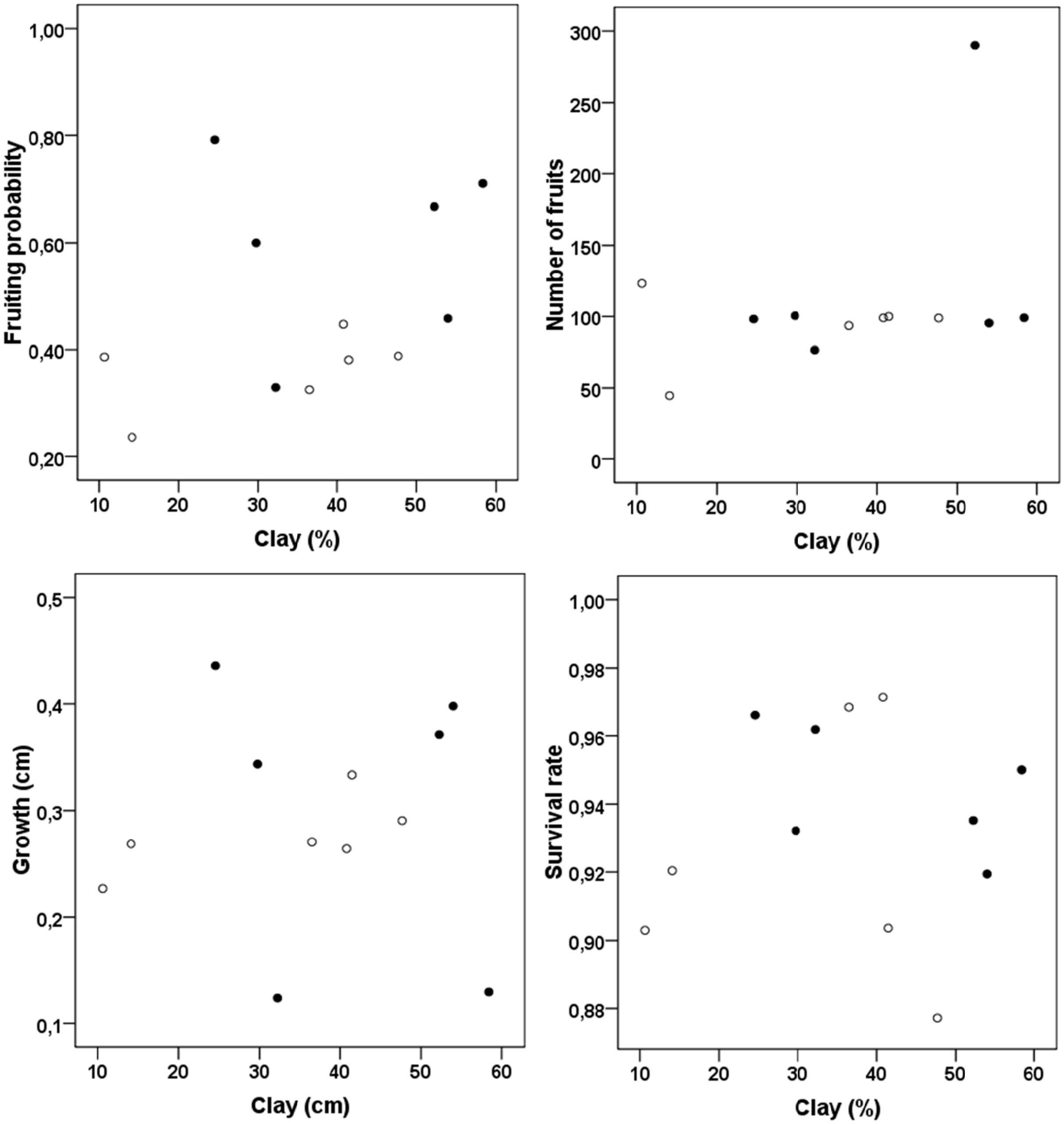


Figure 4. The relationship between vital rates and soil productivity, where clay content was taken as a proxy for soil productivity (Eshete et al. 2011.) Tapped populations are indicated by full circles and untapped populations by open circles. We did not find any significant correlation between vital rate (or growth rate) and clay content.

Vital rates of *B. papyrifera* across its habitat

Phenology

Soil conditions (water and nutrients availability) in tropical dry forests are essential resources that largely control phenological patterns (Bullock and Solis-Magallanes, 1990;) and seed production (Ray and Brown 1994). The study populations varied strongly in proportion of fruiting trees (26 – 79%), but this proportion was not related with soil conditions, in contrast to other findings. Valdez-Hernández et al. (2009) found differences in phenology within species between sites, with higher leaf, flower and fruit production at a site with better soil water conditions. Seghieri et al. (2009) showed fruiting probabilities to decrease with soil moisture in a dry Sahelian site and to increase in a wetter Sudanian site. That we did not find such relationships for *B. papyrifera* trees suggests that fruiting probability might be governed by other factors not considered here, like availability of pollinators and seed dispersers(Seghieri et al. 2009).

Mortality rate

Germination and regeneration of *B. papyrifera* seedlings at Metema occur from June to August during which seedlings have favorable soil water conditions. In the dry season (September to May) the established seedlings die back, probably to avoid desiccation (Fenshaw & Holman 1999; Rice et al. 2004).The mortality rate of established seedlings in the present study populations is low compared to the report made by Gebrehiwot (2003) and Ogbazghi (2001) who reported 86% and 67% of mortality rate of seedlings in Tigray, Ethiopia and Eritrea, respectively. Low mortality rates have sometimes been considered as an adaptive response to considerable climatic stress and disturbance (fire and herbivory) in order to enhance long-term persistence (Sukumar et al., 2005).

Fire and grazing are the commonly reported source of seedlings mortality in dry forests (Zida et al. 2007, 2009, Hoffmann & Solbrig 2003, Menaut et al. 1995), but we did not find differences in mortality rates across management regimes. Fencing had no effect on mortality in our populations, in contrast with findings of Ogbazghi (2001) and Gebrehiwot (2003). Fire also will not be the driver as it occurs during the dry season during which seedlings shed the aboveground and recurrent fire thus will not burn the seedlings. This die-back of seedlings is one of the strategies that dry forest tree species develop to avoid deleterious effect of drought and fire on their regeneration (Fenshaw & Holman 1999; Rice et al. 2004). Once seedlings grow to sapling stage and produce a permanent shoot fire and grazing could have negative effects. This confirms the lack of saplings in all studied populations and elsewhere (see Abiyu et al. 2010) At the Adiarkay site, sapling are present possibly because grazing and fire pressures are much lower (A. Eshete personal observation).

Mortality rates of juveniles and adult individuals in our populations (mean 7%, range 4-14%) are high compared to other dry forests. Annual mortality rates vary from 2.3% in a dry forest in Ghana (Swaine et al., 1990); via 2.9% in a mixed deciduous forest in Thailand (Marod et al., 1999) to 6.9% in dry forests in southern India (Suresh et al. 2010). Fire, grazing, drought, windfall, pest attack and senescence of old stems are considered to be the major causes of tree mortality in tropical dry forests (Sukumar et al., 2005). Some of these factors are related to soil moisture or soil water holding capacity (Condit et al., 1995). The mortality rates in our populations were high across both juveniles and adult stages and survival probability was independent of tree size in most populations. Insect attack followed by windfall were the main sources of juvenile and adult mortality. This result is similar to reports of Negussie (2008). He found that 65% and 85% of tapped *B. papyrifera* trees in Tigray were attacked by the long horn beetle named as *Idactus spinipennis* Gahan. In the present study, particularly insect attack was unexpectedly very common both in tapped and untapped populations and as a result mortality rates did not differ (chapter 4). The overall high mortality rates supported earlier speculations on alarming decline of *B. papyrifera* populations due to human disturbance (e.g, grazing, human cut, tapping, fire, insect attack) (Abiyu et al. 2010, Rijkers et al. 2006, Gebrehiwot 2003, Eshete 2002, 2005, and Tadesse et al. 2002)

Stem growth rates of a dry forest species vary among habitats depending on environmental factors (soil conditions). Water availability and soil conditions that exhibit spatial and temporal variability are the main drivers of tree growth (Ceccon et al. 2006, Mooney et al. 1995, Nath et al. 2006). Dry forest species in soil types that store water well (e.g. high clay% and deeper soil depth) may acquire great stature and biomass (Murphy and Lugo 1990; 1995). Soil fertility can also affect tree growth rate (Lu, et al. 2002; Malhi et al.2004) with better growth on more nutrient-rich soils (Russo et al. 2005, Toledo et al. 2011).

The average growth rate of *B. papyrifera* juveniles and adult individuals (range: 0.13 – 0.43 cm per year, Table 1) was within the reported range of growth rates of tree species in dry forest of Bolivia (Villegas et al. 2009). In Chapter 1 we showed that maximum diameter, maximum height, basal area and standing volume were related to soil conditions associated with water holding capacity (clay content as well as soil depth) (Eshete et al. 2011). Notwithstanding, tree growth rates were not related to soil conditions in the *B. papyrifera* populations examined, suggesting that stand or soil conditions do not govern tree growth rates, as was shown earlier for Amazonian forest (Viera et al 2004). This findings, however, contradicts the reports of Radda and Luukkanen (2006) who found a higher annual growth rate for *Acacia senegal* in soils with higher soil clay content. The absence of such relationship might indicate the presence of other overruling factors responsible for the observed variation in growth rates of *B. papyrifera* trees across its habitats.

Population dynamics of *B. papyrifera*

The population growth rate of *B. papyrifera* populations under the current situation varied spatially (range 0.86 to 0.98) but not directly related to soil conditions and biotic factors. population growth rate lower than 1 indicates population decline if vital rates remain unchanged. Similar population growth rates have been documented for other slow-growing, long lived tree species (Kwit et al. 2004, Silvertown et al. 1993). The low λ-values were the result of high mortality rate of juveniles and adults in all studied populations: the elasticity analysis showed that survival of adult individuals made the largest contribution to λ in all studied populations (Fig. 4). In contrast to our predictions *B. papyrifera* populations decline even under simulated successful establishment of seedlings. During the 2 years of study the decline of *B. papyrifera* populations in Ethiopia thus is not due to lack of recruitment (establishment and survival of seedlings), although the absence of sapling individuals suggest that the growth of established seedlings to sapling stage (< 6 cm DBH) was severely constrained in the recent past. This may be related to the start of inhabitation of the study area in the 1960s as a result of large scale re-settlement (Eshete 2002) Since then people living in and around these forest use fire for various purposes, like clearing for farming, regrowth of new grasses, to walk freely within the forest, and to keep away dangerous wildlife (Eshete 2002). The forests also became the main grazing area for the large herds of cattle of both local inhabitants and nearby highlanders (Eshete et al. 2005, Lemenih et al. 2007). In addition, tapping for frankincense has increased with negative reproductive effects (Rijkers et al. 2006, but see Chapter 4)

Given the results emphasized above, the question arises as to whether *B. papyrifera* populations may persist for long periods of time across its habitats. Our analysis does not allow a straight forward answer to this question given the limitations of our data set (only one area and two years were considered). However, our result showed that all populations experience a demographic decline through time associated with high mortalities of juveniles and adult individuals. Thus, the long term success of the species depend upon the reduction of the high mortality of large individuals and perturbations to seedling establishment, survival and growth would be less effective than those that target juveniles and adult survival (stasis). These results have important implications in terms of forest management: the heavy disturbance observed in the study sites (recurrent fire, heavy and unregulated grazing, improper tapping, Abiyu et al. 2010) that reduced the survival rate of large individuals could further lead to a decline in the abundance of the species. This information is needed for proper predictions regarding population dynamics under different scenarios of human impact, and the results of that for resin production and ecosystem status. As the first long-term study of tree population dynamics at Metema, our results have important implications also for the conservation prospects of this tree species. Furthermore, the nature of disturbance at Metema (e.g. cattle grazing, recurrent fire, improper tapping for frankincense production) is typical of many *B. papyrifera* populations and our results may therefore help inform management decisions in other disturbed *B. papyrifera* populations as well.

Chapter 6

Synthesis

Dry tropical forests once present over 40 % of the tropical forests worldwide, and cover 14 percent of the total African surface (Mayaux et al. 2005) and 71% of the land surface in Ethiopia (Hawando 1997). Large areas of the Ethiopian dry forests are dominated by the Combretum-Terminalia and Acacia-Commiphora vegetation (Friis et al. 2010, IBC 2007), where trees and shrubs of *Acacia, Boswellia* and *Commiphora* species produce economically valuable gums and/or resins, such as arabic gum, frankincense, and myrrh, respectively (Coppen 1995). These products have been harvested and traded since long in the Horn of Africa including Ethiopia (Ahmed 1982, EFAP 1993). These woodland resources make up a large part of the national export revenues in Ethiopia (Lemenih and Teketay, 2003a). With Somalia, Ethiopia acts as the major producer and trader of Frankincense to the global market (FAO 1995).

The Combretum–Terminalia woodlands and Acacia–Commiphora woodlands are currently degrading at increasing spatial scale owing to improper land use. These vegetations, and particularly their Frankincense tree populations are threatened by over-harvesting of gums and resins, overgrazing by livestock, excessive wood harvesting, lopping for fodder, expansion of farmlands and recurrent fire. (Ogbazghi 2001, Gebrewihot 2003). This has led to incomplete populations with missing sapling stages, as shown for *Boswellia papyrifera* (Ogbazghi 2001, Gebrewihot 2002, Abiyu et al. 2010). Because saplings are missing, saplings are considered the key bottleneck for stable population dynamics and sustainable resin yield. The prospects of these woodlands are also threatened by increasing human and livestock population pressure as a result of national migration programs, advancing degradation (Lemenih 2007). To come up with sustainable management strategies for these dry woodlands in general and *Boswellia papyrifera* populations in particular, the interactive effects of soil conditions, climate and disturbances by grazing, fire and human harvest (frankincense production need to be understood.

In this thesis, I studied the current structure, dynamics and resin production of Boswellia populations in Combretum - Terminalia woodlands, and predict their future based on population model projections and scenarios. I analysed the effects of potential bottlenecks for sustainable population dynamics and resin production and, in turn, provide alternative sustainable scenarios for those populations. I focussed on the possible bottlenecks posed by frankincense tapping, and grazing for the population dynamics and habitat characteristics (mainly soil conditions) in dry woodlands of Ethiopia. For this purpose, I established twelve 1.6 - 2.0 ha permanent plots in the relatively wet lowland of the Metema site, and six of those plots in the drier highlands of the Abergelle site in August 2007. The two study sites differ in soil conditions and wet season length, wherMetema has a longer wet season and a higher annual rainfall than Abergelle. Soil samples were collected and analyzed. The plots covered gradients in soil conditions. For each plot, all individuals > 1.5 m in height were identified, tagged and measured for diameter at breast height (1. 3 m height from the ground) and total height to the top of the crown in August 2007. All *B. papyrifera* individuals were re-measured twice per year till August 2009. Matrix population models were used to analyze the dynamics of *B. papyrifera* populations.

Stand structure and diversity of Ethiopian dry woodlands

The species composition, species richness and productivity of the dry woodlands of Ethiopia was addressed in the second chapter. I have shown that species composition of the two study sites strongly differ: only four common species were found in both sites. In line with the intermediate abiotic stress hypothesis (Huston, 1979), we predicted that species richness and diversity would be higher in dry woodlands with a longer wet season and with substrates that are characterized by higher nutrient supply, deeper soil depth and a better water supply texture. While the predicted higher species richness and diversity with wet season length was found true, the increase in species richness with soil fertility conditions was not observed. The findings of the present study are in agreement with previous studies that showed species richness to increase with precipitation (Gentry 1982, 1988, 1995, Givnish 1999, O'Brien 1993). The two study sites also differ in altitude and level of disturbance which are important factors that govern species richness in tropical forests. Metema is at lower altitude than Abergelle and the longer human occupation of Abergelle could actually result in a higher disturbance in the dry forests compared to the recently inhabited Metema forests. Species richness increase with a decrease in altitude (Givnish 1999). The classical intermediate disturbance hypothesis (stating that species richness peaks at intermediate levels of disturbance stress, Connell 1978, see also Bongers et al. 2009). Thus, the higher species richness at Metema might not only be due to the difference in precipitation (wet season length) but also due to altitude and level of disturbance or the combined effect of wet season length, altitude and disturbance.

As predicted, wet season length and soil conditions govern tree and stand productivity of Ethiopian dry woodlands in general and *B. papyrifera* dominated woodlands in particular. This is confirmed by the presence of bigger trees and larger stand volumes in Metema than in Abergelle, suggesting that wet season length and annual rainfall limit tree and stand productivity. The influence of soil conditions was evaluated in relation to soil water availability, which was assumed to increase with increasing soil depth and increasing clay content. Indeed, a positive relation was observed between stand volume and both soil clay content and soil depth. This trend was observed for both whole tree communities and for *B. papyrifera* populations separately. However, for *B. papyrifera*, at a given clay content or soil depth we did not observe any difference in tree size or stand volume between the drier and wetter area. In other words, annual rainfall and wet season length do apparently not explain the observed variation between those sites suggesting that differences in stand volumes of *B. papyrifera* populations are driven by differences in texture (clay content) and soil depth, which drive soil water availability.

Frankincense production

I employed 500 trees in four populations (125 trees per population) to evaluate the effect of tree size, tapping intensity and tapping frequency on frankincense production. Tapping intensity refers to the number of tapping spots per tree while tapping frequency refers to the number of collection rounds in one production season. Five levels of tapping intensity (3, 6, 9, 12 and 16 tapping spots per tree) and 5 diameter size classes (1: 5 – 10, 2: 15 – 20, 3: 20 – 25, 4: 25 – 30, 5: > 30 cm DBH) were used for this particular experiment in which 5 trees were assigned for each treatment combination. The study was continued for two production seasons (from October 2007 to June 2008 and from October 2008 to June 2009). The first production season involves 7 collection rounds while the second season involves 14 collection rounds. I quantified the frankincense production and evaluated the determinants of frankincense production by naturally growing *B. papyrifera* located in 4 populations. Such basic information is important to understand the production system which is needed for planning sustainable management and utilization of the species in the natural population. Tapping for frankincense production is done from trees with > 10 cm DBH while the 95 percentile DBH was 31.3 and 27.6 cm at Metema and Abergelle, respectively. In chapter 3 the hypothesises were that frankincense production would initially increase with tree size, tapping intensity and tapping frequency, but would level-off later on.

The hypotheses were accepted as frankincense production indeed increased with tree size, tapping intensity and tapping frequency. However, as predicted, no more increase was observed beyond a tree size of 20 cm DBH, a tapping intensity of 9 spots and after the 10th tapping round. Similarly, many studies showed that resin production is a function of tree size and amount of injury applied (Coppen 1995; Lombardero et al. 2000; Rodrigues et al. 2008; Klepzig et al. 2005;

Lewinsohn et al., 1991; Lombardero et al. 2000). The higher frankincense production from bigger trees could result from two factors. The first being larger resource acquisition capacities of bigger trees which in turn depends on the crown size and leaf area of trees (Lambers et al. 1998, Gomez 1983). Resin production in bigger trees is thus facilitated by the presence of large crown size and leaf area. The second factor is the availability of more resin canals in the trunks of bigger trees (Coppen 1995; Ella and Tongacan 1992). This is in line with the growth differentiation balance hypothesis (GDBH) which postulates that production of secondary producing structures and the metabolites produced, such as frankincense, increase with plant size (Herms and Mattson 1992; Goralka and Langenheim 1996; Goralka et al. 1996). The levelling of frankincense production beyond tapping intensity of 9 might be related to the anatomy of resin producing structure in *B. papyrifera* and resin production potential of individual trees. Menger (2010) reported that resin canals in *B. papyrifera* are interconnected. And production potential of each individual tree depends on its size suggesting that each tree production potential is limited. This potential production would be distributed to each tapping spot and thus, the flow of resin to tapped spots would be constrained by the number of tapping spots, as its anatomy would allow for drainage frankincense from one spot by the other.

Vital rates of *Boswellia papyrifera*

Growth

Stem growth rates of dry forest species vary among habitats depending on environmental factors (soil conditions and water availability). Dry forest species in soil types that store water well (e.g. high clay% and deeper soil depth) may acquire great stature and biomass (Murphy and Lugo 1990; 1995). Soil fertility can also affect tree growth rate (Lu, Moran & Mausel 2002; Malhi et al. 2004) with better growth on more nutrient-rich soils (Russo et al. 2005, Toledo et al. 2011). Thus, soil water availability and soil fertility are the main drivers of tree growth, but their availability varies spatially and temporally (Ceccon et al. 2006; Mooney et al. 1995; Nath et al. 2006). Despite such established facts no relation was found between soil variables and stem growth rate of *B. papyrifera* (Chapter 5). This might result either from the fact that the difference in the soil variables between habitats is too small to affect tree growth or due to the presence of other external factors that overruled the effect of soil variables or the combined effect of these two factors. Similar findings were also reported by Viera et al. (2004), who did not observe relationships between soil conditions and tree growth rate in Amazon rain forest. Generally, stem growth of juvenile and adult individuals of *B. papyrifera* increased with tree size (Chapter 4 and 5). Root collar diameter was also unimportant for the growth of saplings. Similarly, no effect of initial root collar diameter was found for the growth of seedlings as they died back during the dry season (September to June) in the two study periods. Seedlings of *B. papyrifera* die back for about 8 – 10 years before they start producing permanent shoots (A. Eshete unpublished data). Such a strategy is actually considered an adaptation for dry tropical species to avoid deleterious effect of drought and fire (Fenshaw & Holman 1999; Rice et al. 2004).

Survival

The results of the present study showed that the overall survival rate (0.93) of juvenile (6 – 10 cm DBH) and adult (>10 cm DBH) individuals (range 0.86 – 0.96) was lower than most commonly reported survival rates of juvenile and adult trees in dry tropical forests (Chapter 4 and 5). The relationship between survival probability of individuals with tree size varied between populations. In 7 out of 12 populations survival probability was not affected by tree size, in 2 populations survival probability increased with tree size, and in one population it decreased with tree size. Despite such variation in survival probability among populations, no relation was found between survival rates and soil conditions nor biotic factors suggesting that factors that govern survival rate of adult individuals are not site specific. Similarly, no clear pattern was observed for survival rate of established seedlings.

Reproduction

Boswellia papyrifera reproduced sexually and asexually through root suckers. Trees with a diameter of >10 cm produce flowers and fruits. At least 26% (range; 26 – 72%) of the adult individuals actually flowered and fruited in the two years of study. For those reproductive individuals, the number of fruits produced per year ranged from 111 to 1540 fruits per tree (chapter 5). Although proportion of fruiting trees in each study population showed high variation, no relation was observed between proportion of fruiting trees and soil conditions as well as biotic factors (Chapter 5, Table 1*).* The relation between tree size and production of fruits per tree as well as proportion of fruiting trees differed between populations. Number of fruits produced per tree increased with tree size in all populations while fruiting probability increased with DBH in four populations (plot 1, 5, 8 and 11) but showed no relation with tree size in the rest of the populations. The increase in number of fruits per tree size was similar to reports of the same species in Eritrea (Ogbazghi 2001, Rijkers et al. 2006).

Seedlings of *B. papyrifera* recruited every year almost in all study populations although the number of recruits varied among populations. Despite greater flowering and fruiting, only few seedlings established within some plots and no clear relation was observed between the proportion of fruiting trees and the number of recruits (Table 1 and 2). Earlier studies indicated that *B. papyrifera* does not enter dormancy (Gebremedihin 1997) and does not form a soil seed bank (Eshete et al. 2005), thus the current seed rain is the main source of seeds for the establishment of *B. papyrifera* seedlings. The lack of seed banks and absence of clear fruit production – recruitment relationships might be due to large across population variation in seed viability, abortion, seed predation, or the combination of these factors (Eshete et al (2005), Gebremedihin and Negash (2001) and Rijkers et al 2006 had reported 17, 19 and 25% of pre-seed dispersal predation. *B. papyrifera* seed disperse in the studied population from January to February. Germination and establishment of seedlings start in June when the rainy season starts. Dispersed seeds are thus exposed to seed predation for about 3 months, may dry out or may burn during the regular dry season fire. Seed predation or burning could limit the availability of seed and could be another reason for the low recruitment of seedlings in some populations (Fenner, M. & Kitajima, 1999). Moreover, in two of plots seedlings did not originate from seeds but from root suckers (Chapter 5).

What is the major bottleneck for population growth of B. papyrifera?

Boswellia papyrifera populations experience missing classes, particularly sapling stages in the regeneration profile (Abiyu et al. 2010). Due to this, lack of regeneration becomes a common feature for *B. papyrifera* populations in its natural habitat and is usually considered as a major bottleneck for population growth (Ogbazghi 2001, Gebrehiwot 2003). Population dynamics of *B. papyrifera* populations have been investigated using matrix models across the 12 studied populations in Metema of North Western Ethiopia. Individual plants were categorized into life stages and diameter size classes to meet the requirements of the model (Chapter 4 and 5). Vital rates of the species were quantified to estimate matrix elements that are used to construct the matrix model (Chapter 4 and 5). The outputs of the model were used to project the future development of the species.

Our population models based on two years of demographic data project declining *B. papyrifera* populations across its habitats (Chapter 5). The populations are therefore expected to be declining over time. No change in the growth of population was predicted through increasing the number of recruitments or allowing the growth of seedlings to saplings. Thus, output of the model contradicts earlier reports that considered lack of regeneration as a major bottleneck for the growth of population of the species. An elasticity analysis of the model showed that the survival rate of adult individuals was the most important for the population growth and contributed 86% to population growth. Thus, the observed low survival rate of adult individuals (range: 86 to 98%) is currently the major bottleneck for the growth of the studied *B. papyrifera* populations. Similar results have been found for other long-lived plant species. Rikhari et al. (1998) and Kwit et al. (2004) reported that efforts to increase seedling production and survival didn't increase population growth as these transitions had the lowest elasticities and minimal impact on population growth rates of *Taxus* species.

Many factors potentially influence population growth rates. For our study populations, we focussed on the possible effects of soil and climate conditions and disturbance by people. We did not find a significant impact of soil conditions on population growth rates. It can be speculated that the populations decline as a result of the increasing disturbance. Since the last three to four decades, these woodlands became re-settlement areas for people from dry and unproductive areas (Teketay 2000). In these woodlands they were allowed to produce their own food crops and graze their livestock regularly without any kind of regulation. As a result of these large areas were and are being converted to farmlands and Boswellia dominated woodlands became the main grazing area for large livestock populations throughout the year. Deliberate fire is set in the woodlands for farm clearing, to move freely in the forest, to keep away dangerous animals, to harvest honey, among others (Eshete 2002). Thus, the observed intensive and unregulated grazing and recurrent fire might be the responsible factors for the lack of saplings across the habitats through limiting the growth of seedlings to saplings.

Besides, following the interest of the current government to boost production of gum and resin products to increase the export, the number of organizations that involve in production, processing and marketing of the products such as Frankincense increased dramatically, and introduced more intensive tapping regimes than traditional tapping techniques. No scientific guideline is available for sustainable production of frankincense by *B. papyrifera*. Thus, individual trees are subjected to intensive tapping where each tree is tapped at more number of spots beyond the recommended number of spots by traditional tapping techniques. Resin production through tapping usually weakens the tree and may expose tapped trees for insect attack. Insect attack is now a common problem of *B. papyrifera* in both tapped and untapped populations (Chapter 5, Eshete et al. 2005, Negussie 2008). Insect attack and windfall were the main causes of adult tree mortality in study populations in which insect attack accounted for, on average, 65% of juveniles and adult mortality rate. This suggest that insect attack is an important factor for the death of adult individuals. Negussie (2008) reported similar observations where >65% of standings trees were affected by the long horn beetle named as *Idactus spinipennis* Gahan. in Tigray, Ethiopia. Under the current situation the *B. papyrifera* population are declining rapidly: only 50% of the population would remain after 17 years. In line with this the frankincense production potential of *B. papyrifera* would be halved in 17 years.

Effect of tapping on vital rates and population dynamics of *B. papyrifera*

Tapping is expected to divert reserves/resources to frankincense which otherwise could be used for other sinks (growth, reproduction, etc.) (Rijkers et al. 2006, Mengistu et al. in preparation). We hypothesized that tapping would decrease the rates of diameter growth, fecundity and survival compared to untapped populations. Consequently , we predicted lower population growth rates in tapped populations. We also hypothesized that tapping for frankincense production would affect regeneration capacity of the species and that tapped populations would present stronger regeneration bottlenecks.

In contrast to our expectation, we found that individual trees in tapped populations had relatively higher diameter growth rates and fruiting probability compared to individual trees in untapped populations (chapter 4). Survival rate of tapped individuals was slightly negatively affected. Similar positive effects on growth and reproduction potential of tapped trees was found for *Protium copal* in Guatemala (Neels 1996). However, Rijkers et al. (2006) reported a strong negative effect of tapping on reproduction potential of *B. papyrifera* in Ethiopia. Silpi et al. (2007) had also reported a strong negative effect of tapping for rubber on diameter growth of *Hevea brasiliensis*. The absence of such a negative effect of tapping on vital rates of *B. papyrifera* might be due to several reasons. First, the tapping intensity in the present study was moderate compared to some other populations that were more intensively tapped (> 27 tapping spots per tree, Kebede 2010). This moderate tapping intensity might have little effect on vital rates. Secondly, almost all tapped populations are located in a relatively better soil conditions (chapter 4) suggesting that producers select Boswellia stands that grow in a better soil conditions. Thus, such difference in soil conditions could have also precluded to see the effect of tapping. Thirdly, the cause of mortality in both tapped and untapped population was similar as > 65% of dead trees were insect affected in both populations. Thus, the high insect infestation in both populations might have overruled the effect of tapping on survival rate of individual trees.

Matrix populations model were constructed to assess the impact of tapping on the population growth of *B. papyrifera*. Six populations from tapped stands and 6 populations from untapped populations were used for the present study. The results showed that population growth rates of tapped populations were higher than those for untapped populations, but population growth rates of both populations were < 1 suggesting that *B. papyrifera* populations are declining under the current situation irrespective of management regimes. In both populations (tapped and untapped), the survival rate of adult individuals (which is comparable between the two populations) was the most important element for the maintenance and growth of *B. papyrifera* populations. Thus, the higher population growth rate of tapped populations is probably due to the higher fruiting probability and growth rate of adult trees in tapped than untapped populations.

Sustainable frankincense production scenarios

A number of past research reports documented that *B. papyrifera* populations are declining as a result of anthropogenic disturbance. Particularly, the lack of regeneration has been considered as the major bottleneck for the maintenance and/or growth of *B. papyrifera* populations. The outputs of our matrix models, however, indicated that the high mortality of juvenile and adult individuals were the major bottleneck for maintenance of the populations. The adult stages in particular contained the largest elasticities (86%). We simulated various management practices that target an increase in the regeneration as well as growth of seedlings to saplings and reduction of adult mortality. The reduction of adult mortality was simulated by lowering adult mortality first to 50% and then to 75% of the current observed mortality rate. The first set of simulations based on an increase in seedling regeneration and allowing the growth of seedlings to sapling stage are not likely to increase population growth under the current condition of high adult mortality. Similar results were reported for *Taxus* species where an increase in seedling production didn't bring change on population growth of the species (Hulme 1996, Rikhari et al. 1998, Kwit et al. 2004). The second set of simulation (seedlings grow to sapling and adult mortality reduced by 50%) results in a similar decline of *B. papyrifera* populations. When reduction of adult mortality by 75% was simulated, the growth rates of *B. papyrifera* populations become close to 1 for tapped and untapped stands (chapter 4) suggesting that *B. papyrifera* populations would be maintained or would probably grow if and only if the current mortality rate of adult individuals is reduced by 75%, i.e. when mortality rate is reduced from 7% to 1.75%.

A multiple-approach management will be needed to maintain *B. papyrifera* populations which are predicted to be in rapid decline as a result of anthropogenic disturbance. First, a scientific guideline for frankincense production shall be developed and implemented. The current intensive tapping is expected to weaken the tree and exposes them to insect attack. While reducing tapping intensity might to some extent decrease the mortality of adult individuals, it is certainly not sufficient to guarantee sustainable populations. Second, establishing enclosures to protect large areas against disturbance by grazing and fire would increase the chances of growth of most seedlings to sapling stage. Third, proactive management efforts that focus on generating environmental conditions that increase the survival and growth of established seedlings should be introduced. The low elasticities associated with seedlings and saplings should not preclude a long-term management focus on these stages. We propose that rapid actions are needed for sustainable production and conservation, since Boswellia populations are rapidly degrading to a state from which recovery might not be possible anymore.

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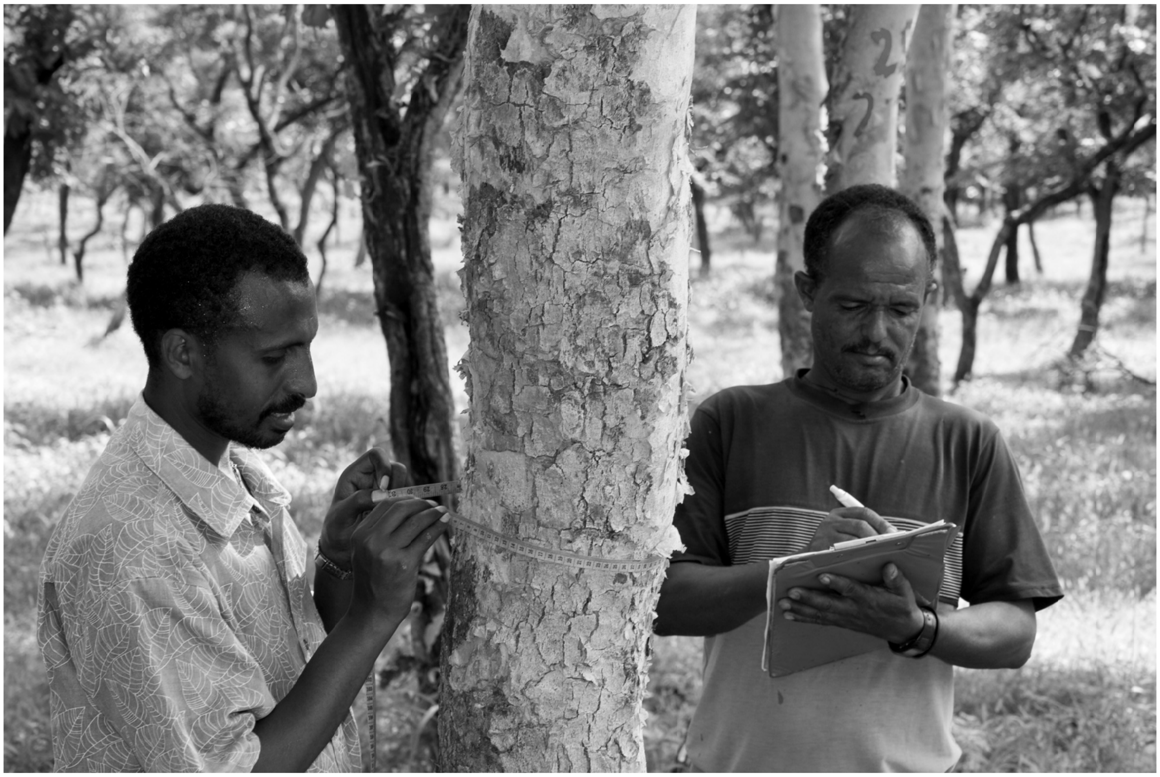

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Summary

Tropical dry forests cover large areas in the tropics, and 14% of the total African surface. Dry land areas of Ethiopia amount to 71% of the Ethiopian landmass, and are dominated by the Combretum–Terminalia and Acacia–Commiphora woodland types. Several tree and shrub species that inhabit these woodlands yield economically valuable products such as gum, frankincense (resin) and myrrh. *Boswellia papyrifera* provides the widely traded frankincense, which accounts for > 80% of the export revenues that the country is earning from gum and resin resources. Unfortunately, the Ethiopian dry woodlands and the *B. papyrifera* populations are disappearing rapidly due to the combined effect of over-harvesting gums and resins, overgrazing by livestock, recurrent fires and excessive wood harvesting. The lack of small saplings in populations of Boswellia suggests that these populations are not sustained for the future. The main objective of this thesis was to determine the diversity and production patterns in Ethiopian dry woodlands and the regeneration status of *B. papyrifera* in these woodlands. Moreover, the effects of climate, soil, harvesting and grazing for the population dynamics of *B. papyrifera* were evaluated. The following main research questions are addressed: (1) how do environmental conditions affect the tree/shrub species richness and productions of Ethiopian woodlands? (2) how do tree size and tapping regime influence the frankincense production by *B. papyrifera* trees? (3) how do the population dynamics of *B. papyrifera* vary across sites characterized by different environmental conditions, resin tapping regimes, and grazing levels? (4) What are the most important bottlenecks in the life cycle of the trees for achieving sustainable populations?

Tree species richness, diversity and production of dry woodlands as well as the production of frankincense by *B. papyrifera* was studied in the lowlands of Metema and the highlands of Abergelle, both in northern Ethiopia. The two study sites also differ in soil conditions and Metema has a longer wet season and higher annual rainfall than Abergelle. Soil samples were collected and analysed. In total eighteen 1.6-2.0-ha permanent plots were selected and established in August 2007, i.e. 12 plots in Metema and 6 plots in Abergelle. The plots were distributed along gradients in soil conditions. For each plot, all individuals >1.5 m in height were identified, tagged and measured for diameter at breast height (1.3 m height from the ground) and for total height to the top of the crown. All *B. papyrifera* individual were re-measured twice per year between August 2007 and 2009. For a subsample, fruit production was recorded. Matrix population models were used to analyse the population dynamics of the *B. papyrifera* populations.

In chapter 2, I address the question how climate and soil conditions affect woody plant species richness and production in Ethiopian woodlands. A total of 36 and 22 tree and shrub species representing 20 and 9 families were recorded in Metema and Abergelle woodlands, respectively. The most dominant plant families were the *Burseraceae, Fabaceae, Combretaceae* and *Anacardiaceae*. The vegetation at both sites were dominated by a single species, i.e. *B. papyrifera*. Metema, i.e. the site with a longer wet season, was characterized by a higher species richness, diversity and production than Abergelle. The production of woodlands increased with soil clay content and soil depth, but species richness was unaffected by soil conditions. This suggests that climate driven constraints (wet season length) and not soil conditions set the limits to species richness. Tree size distributions of the communities showed bi-modal distributions with relatively large numbers of individuals in the lowest and in the middle diameter size classes. The size distribution for *B. papyrifera* was hump-shaped without individuals in the lowest classes. Such distributions result from the disturbance history and indicate that many populations are locally disappearing.

In chapter 3 I determine the factors that affect frankincense production by *B. papyrifera* trees. Frankincense production by *B. papyrifera* increased with tree size, tapping intensity and tapping frequency. The increase in production, however, levelled-off beyond 20 cm diameter, 9 spots (tapping intensity) and 10 tapping rounds. The result of this particular study suggests that tapping for frankincense production at higher intensity and frequency doesn't pay off. Instead, such high tapping intensities and frequencies might weaken the tapped trees and make them more sensitive to diseases and insect attack.

In Chapter 4 I investigate the impact of tapping for frankincense production on the vital rates and growth of *B. papyrifera* populations. Additionally, I analysed the effects of human interventions on the future of *B. papyrifera* populations. Grazing and tapping had no influence on the establishment and survival of seedlings. Population matrix model output showed that tapped populations had a slightly higher population growth rate than untapped populations suggesting that tapping is not the major driving force for the rapid decrease of *B. papyrifera* populations. Human interventions that target an increase in seedling regeneration and allowing the growth of seedlings to sapling stage are not sufficient to increase the population growth to sustainable levels under the current conditions. Rather, the management actions should also reduce the current high adult mortality by 75% to maintain *B. papyrifera* populations.

In Chapter 5, I analysed the effects of soil conditions on the vital rates and growth of *B. papyrifera* populations. Growth rate, survival rate and fruiting probability of *B. papyrifera* population vary across sites, but no correlations were found between vital rates and physical or chemical soil variables, or between vital rates and the abundance, basal area and stand volume. Population growth rates of the Metema 12 populations ranged from 0.86 to 0.98 suggesting that *B. papyrifera* populations are declining in all studied plots. Matrix models also indicated that the contribution of survival of adult individuals (> 10 cm DBH) to the population growth rate was higher than the contribution of other stages and vital rates. This suggest that survival of adult individuals is crucial for the growth and maintenance of *B. papyrifera* populations. These findings contradict earlier reports that considered lack of regeneration as a single major bottleneck for the maintenance and growth of *B. papyrifera* populations. Reducing mortality of adult individuals and restoring sapling establishment are both urgently needed to maintain B. papyrifera populations.

In conclusion, climate (wet season length) is the driving factor for species richness and production of Ethiopian dry woodlands. Soil conditions affect production but not species richness. Tree size, tapping intensity and frequency are the main factors that determine frankincense production by *B. papyrifera*. *B. papyrifera* populations are decreasing in all studied plots irrespective of the variation in soil conditions and management regimes. Tapping had no negative effect on vital rates nor on population growth rates indicating that other factors might be responsible for the decrease of the populations. Despite a lack of saplings in the populations, the survival rate of adult individuals is the most critical bottleneck for the maintenance of the populations. *B. papyrifera* is expected to locally disappear in the near future if the current situation continues. Increasing regeneration and reducing mortality rates of juvenile and adult individuals should both be achieved to maintain *B. papyrifera* populations and frankincense production for the future.

Samenvatting

Tropische droge bossen domineren in grote delen van de tropen en bedekken 14% van het Afrikaanse landoppervlak en 71% van Ethiopië. In Ethiopië domineren de Combretum-Terminalia en Acacia-Commiphora bostypen. Verschillende inheemse boom- en struik- soorten leveren er economisch waardevolle producten. *Boswellia papyrifera* levert er hars dat als basis dient voor wierook. Wierook levert >80% van de export inkomsten uit rubber en hars in Ethiopië. Het areaal van de Ethiopisch droge bossen en de populaties van *B. papyrifera* nemen echter snel af als gevolg van de overexploitatie van hars, de overbegrazing door vee, en het frequenter voorkomen van bosbranden en houtkap. Jonge boompjes van Boswellia komen nauwelijks nog voor, en het lijkt erop dat de populaties niet duurzaam zijn.

De doelstellingen van dit proefschrift zijn de beschrijving van de diversiteit en productie van deze droge bossen van Ethiopië, het beschrijven van de status van de populaties van *B. papyrifera* en van de jonge bomen in het bijzonder, en het analyseren van de effecten van klimaat, bodem, harsoogst- en begrazing op de dynamiek van deze soort. De vragen zijn: (1) Wat zijn de effecten van klimaat en bodem op de rijkdom van boom- en struik- soorten en de productie in Ethiopisch droge bossen? (2) Hoe beïnvloedt de boomgrootte en het tapprotocol de productie van wierook door *B. papyrifera* bomen? (3) Hoe varieert de populatie dynamiek tussen gebieden die verschillen in klimaat, bodem, begrazing en tapprotocol? (4) Wat zijn de belangrijkste fases ("bottlenecks") in de levenscyclus die het voorbestaan van de populaties bedreigen?

Het onderzoek is verricht in populaties in de hooglanden van Abergelle en de laaglanden van Metema. Metema heeft ook een natter klimaat en langer regenseizoen dan Abergelle, en de verschillen in bodemcondities zijn ook onderzocht. In totaal zijn er 18 1.6-2.0 ha- permanente onderzoek locaties uitgezet, 12 in Metema en 6 in Abergelle. Deze locaties zijn gesitueerd langs een bodemgradiënt. Voor elk plot zijn alle individuen (hoger dan 1.5 m) geïdentificeerd, gelabeld en gemeten op diameter op borsthoogte (1.3 meter boven de grond, 'DBH') en totale hoogte.

Voor steekproeven van bomen is ook de reproductie (bloeiwijzen, vruchten en zaden) bepaald, en in subplots zijn alle kleinere individuen gevolgd. Alle individuen van *B. papyrifera* zijn twee keer per jaar gemeten tussen augustus 2007 en augustus 2009. Matrix populatie modellen zijn gebruikt om de populatie dynamiek van *B. papyrifera* populaties te analyseren.

In hoofdstuk 2 ga ik in op de vraag hoe klimaat en bodemgesteldheid de rijkdom van boomsoorten en de productie beïnvloeden in Ethiopisch droge bossen. In totaal zijn er 36 en 22 boom- en struik- soorten geregistreerd die 20 en 9 families vertegenwoordigen, respectievelijk in Metema en Abergelle. De dominante plantenfamilies zijn de Fabaceae, Burseraceae, Combretaceae en Anacardiaceae. Vegetaties op beide locaties worden door *B. papyrifera* gedomineerd. De bossen van Metema, met het langste regenseizoen, hebben een hogere soortenrijkdom, diversiteit en productie dan Abergelle. De productie van bossen neemt toe met kleigehalte en bodemdiepte, maar soortenrijkdom wordt niet door de bodem beïnvloed. De boomgrootte verdeling voor *B. papyrifera* laat zien dat er geen kleine individuen voorkomen. Deze verdeling duidt op verstoringen in het verleden en op het risico dat populaties gaan verdwijnen in de toekomst.

In hoofdstuk 3 bepaal ik de factoren die de productie van wierook door *B. papyrifera* beïnvloeden. Wierook productie door *B. papyrifera* neemt toe met boomgrootte, met de intensiteit van het tappen van wierook en de frequentie van het tappen. De toename in productie stabiliseert echter boven een stamdiameter van 20 cm. De productie neemt niet meer toe bij meer dan 9 littekens om te tappen, en vlakt af bij meer dan 10 taprondes per jaar. De resultaten van deze studie suggereren hoe de tapschade binnen de perken gehouden kan worden, terwijl de productie op niveau blijft. We kunnen echter niet uitsluiten dat ook deze lagere tapintensiteiten de bomen verzwakt en bloot stelt aan ziektes en insectenaanvallen.

In hoofdstuk 4 onderzoek ik de invloed van het wierook tappen van *B. papyrifera* op de populatie dynamiek. Begrazing en tappen lijken nauwelijks de vestiging of overleving van zaailingen te beïnvloeden. Populatie modellen geven aan dat getapte populaties van *B. papyrifera* iets hogere groei hebben dan niet getapte populaties. De simulaties laten ook zien dat alle populaties binnen minder dan 2 decennia halveren. Om deze situatie te keren zou de regeneratie van zaailingen en de groei van zaailingen tot kleine boompjes bespoedigd moeten worden, en moet de hoge sterfte bij volwassen bomen terug gebracht worden.

In hoofdstuk 5 analyseer ik het effect van bodemgesteldheid op de dynamiek van de populaties van *B. papyrifera* in Metema. Er werden echter geen effecten gevonden. De groei van de 12 onderzochte populaties in Metema varieerde tussen de 0.86 en 0.98. Dit suggereert dat de populaties geleidelijk aan afnemen in dichtheid en wierookproductie. De populaties blijken vooral zeer gevoelig te zijn voor de hoge sterfte van de volwassen bomen. Dat wijst erop dat de overleving van de volwassen bomen, naast de regeneratie van zaailingen, de kritische bottleneck is voor het behoud en de groei van *B. papyrifera* populaties.

Het klimaat beïnvloedt de soortenrijkdom en productie van de Ethiopisch droge bossen, en bodemgesteldheid heeft invloed op de productie maar niet op soortenrijkdom. Boom grootte, tapintensiteit en tapfrequentie zijn de belangrijke factoren die de productie van wierook door *B. papyrifera* bepalen. De populaties van *B. papyrifera* dunnen uit in alle onderzoeklocaties, ongeacht de verscheidenheid in bodemgesteldheid en beheer. Tappen heeft geen aantoonbare effecten op de populatie groei, wat aangeeft dat andere factoren verantwoordelijk kunnen zijn voor de afname van de populaties. *B. papyrifera* populaties zullen waarschijnlijk binnenkort verdwijnen wanneer de huidige situatie aanhoudt. Verbetering van de aanwas van jonge bomen en het drastisch verminderen van sterfte bij jonge en volwassen individuen zijn noodzakelijk om *B. papyrifera* populaties en de wierook productie te behouden voor de toekomst.

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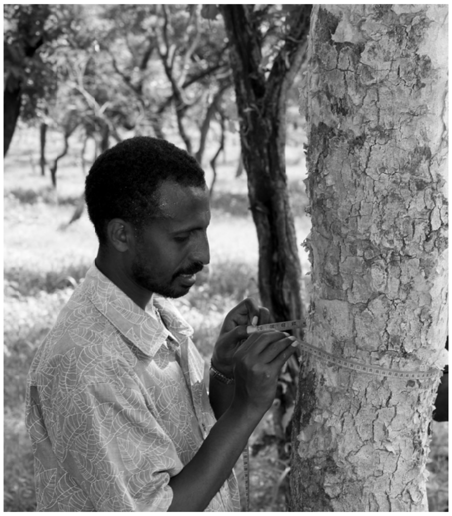
Short biography

Abeje Eshete Wassie was born on November 4, 1972 in Azezo (Gondar), Ethiopia. He joined Alemaya University of Agriculture in September 1990. He studied Forestry Science and obtained his BSc. degree in August 1993. He started working as the head of the District Natural Resources Development and the Environmental Protection Office in June 1994. In June 1996, he joined the Ministry of Agriculture as an expert for forestry and agroforestry development. In October 2001 he joined the Swedish University of Agricultural Science and studied farm forestry. He obtained his MSc degree in July 2002. He studied the regeneration status, soil seed bank and socio-economic importance of *Boswellia papyrifera*, a key dry land species in Ethiopia for his MSc. thesis. From August 2002 to June 2003, he worked as the head of the Natural Resources Team at the Ministry of Agriculture.

In July 2003, he joined the Forestry Research Centre of the Ethiopian Institute of Agricultural Research as an assistant researcher III. His main task was initiating research projects and implementing research projects when approved by the respective bodies. He was also a project coordinator for the Tree Seed Technology Project. In December 2006 he joined the Forest Ecology and Forest Management Group of Wageningen University as a PhD Student. During his PhD period, he further investigated the ecology, productivity and population dynamics of *Boswellia papyrifera*.



Publications

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Education Certificate

The C.T. De Wit
Graduate School
PE&RC
PRODUCTION
ECOLOGY
& RESOURCE
CONSERVATION

PE&RC PhD Education 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 (5 ECTS)

- Frankincense tree of Ethiopia: ecology, productivity and population dynamics

Writing of project proposal (5 ECTS)

- Frankincense tree of Ethiopia: ecology, productivity and population dynamics

Post-graduate courses (7.1 ECTS)

- Survival analysis (2007)
- Multivariate analysis (2007)
- Introduction to R (2009)
- Community ecology (2009)
- Ecophysiology of plants (2010)

Deficiency, refresh, brush-up courses (3 ECTS)

- Ecological methods I (2007)

Competence strengthening / skills courses (3.7 ECTS)

- PhD Competence assessment (2007)
- Writing grant proposal (2010)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.5 ECTS)

- PE&RC Weekend (2007)
- PE&RC Day (2009)
- PE&RC Day (2010

Discussion groups / local seminars / other scientific meetings (3.6 ECTS)

- Ecological Theory and Application (2007-2010)
- National Workshop on FRAME Program (2008)
- National workshop on wild fruit trees (2009)
- Training on gum production (2009)

International symposia, workshops and conferences (9 ECTS)

- Association of Tropical Biology and Conservation (oral presentation); Bali, Indonesia (2010)
- Student Conference on Conservation Science (oral presentation); Cambridge, UK (2011)
- Association of tropical Biology and Conservation (oral presentation); Arusha, Tanzania (2011)

Supervision of 2 MSc students; 130 days

- Population dynamics of Boswellia papyrifera
- Production systems of frankincense and market chain analysis

The FRAME project

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.