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Fencing improves the establishment and growth of *Boswellia papyrifera* (Del.) Hochst wildlings

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Abstract

Boswellia papyrifera (Del.) Hochst is a flagship species of semi-arid areas of the East African region with substantial economic, ecological and cultural values. However, its persistence is currently threatened by both anthropogenic and natural pressures. This calls for an immediate conservation action. Planting seedlings of *B. papyrifera* in natural habitats using nursery-grown seedlings from seed and cuttings has been little successful. Fencing of naturally regenerated seedlings (wildlings) established under the parent trees could be used as an alternative option. The objective of this study was to examine the effect of fencing on the seedling establishment and growth of *B. papyrifera* wildlings. The experiment was conducted using 36 plots in fenced and open conditions. The results showed that fencing significantly enhances the establishment and growth of *B. papyrifera* wildlings compared to the open areas. Fenced wildlings exhibited higher survival rates, increased height, greater leaf numbers, larger root collar diameters, larger leaf areas and higher leaf biomass compared to non-fenced wildlings. Therefore, the protection of *B. papyrifera* seedlings using a fencing intervention can improve the overall establishment and development of *B. papyrifera* seedlings, thereby contributing to the sustainable conservation and restoration of this valuable species.

1. Introduction

Dryland forests constitute the largest portion of Ethiopia's forest resources and are compositionally rich in endemic species (Lemenih & Kassa 2011). These forests are also rich in woody genera like *Boswellia*, *Commiphora* and *Acacia* comprising several indigenous tree species renowned for producing economically valuable oleo-gum resins, including frankincense, myrrh and gum arabica (Alemu *et al.* 2012; Tadesse *et al.* 2007; Yogi *et al.* 2017). The applications of these oleo-gum resins span various industries, including food, pharmaceuticals, perfumery, adhesives, ink and dye (Lemenih & Kassa 2011; Yogi *et al.* 2017). Moreover, these resins are internationally traded commodities, contributing significantly to the National Gross Domestic Product of several countries, including Ethiopia, Sudan, Somalia and Eritrea (Khamis *et al.* 2016; Lemenih & Kassa 2011).

The genus *Boswellia* has 24 tree species (Thulin 2020), of which only five produce tradable amounts of oleo-gum resins. Among them, *Boswellia papyrifera* (Del.) Hochst stands out for its globally tradable aromatic resin known as frankincense (Gebrehiwot *et al.* 2003). This product is distinguished by its high levels of octyl acetate and incensole acetate (DeCarlo *et al.* 2022). *B. papyrifera* is found in Ethiopia, Sudan, South Sudan, Eritrea, Uganda and Chad (Gebrehiwot *et al.* 2003). Beyond its economic significance, this species provides substantial ecological and cultural values in these regions (Canney-Davison *et al.* 2022; Moens *et al.* 2019). For instance, in 2014, Ethiopia exported approximately 8,000 tons of frankincense valued at 8.8 million US dollars, making the country a major global producer (Tadesse *et al.* 2020). The collection, processing and grading of frankincense also contribute to the livelihoods of many rural households (Mekonnen *et al.* 2013; Tilahun *et al.* 2011). Furthermore, the species is used for animal fodder, apiculture and soil and water conservation (Gidey *et al.* 2020; Mekonnen *et al.* 2013).

Despite the wider socio-economic and ecological values of *B. papyrifera*, its population is currently declining at an alarming rate due to over-exploitation, agricultural expansion and habitat degradation (Bongers *et al.* 2019; Bongers & Tennigkeit 2010; Canney-Davison *et al.* 2022; Derero *et al.* 2018; Eshete *et al.* 2021; Ogbazghi *et al.* 2006). In addition, the species is now associated with a lack of natural regeneration and little recruitment due to over-exploitation and habitat degradation across its growing areas in Ethiopia, Eritrea and Sudan (Eshete *et al.* 2011; Gidey *et al.* 2020; Groenendijk *et al.* 2012; Khamis *et al.* 2016; Ogbazghi 2001). As a result, the remaining natural stands of the species consist mainly of old trees, with few seedlings and saplings distributed across a significant part of its range (Bongers *et al.* 2019). While temporary establishment and survival of *B. papyrifera* seedlings were reported elsewhere (Hizikias 2011; Negussie *et al.* 2008; Ogbazghi 2001), their transition into the sapling stage was hindered by several factors, including overgrazing, drought, fire, erosion and insect and pests attacks (Abiyu *et al.* 2010; Eshete *et al.* 2005; Gidey *et al.* 2020; Groenendijk *et al.* 2012; Negussie *et al.* 2008). Grazing is a major contributing factor to the limited regeneration and recruitment of trees in many tropical areas (Adam & El Tayeb 2008; Giday *et al.* 2018; Gidey *et al.* 2020; Liu *et al.* 2019) and temperate forests (Husheer *et al.* 2006; Löf *et al.* 2021; Long *et al.* 2012).

Seedlings of *B. papyrifera* are likely to establish better in inaccessible areas where pressure from animals is expected to be low (Ogbazghi *et al.* 2006). A grazing exclusion strategy has been shown to enhance seed viability, regeneration and seedling development in *B. papyrifera* woodlands (Alemu *et al.* 2012; Eshete *et al.* 2012; Tilahun *et al.* 2011). Based on this, we hypothesised that the protection of *B. papyrifera* wildlings from anthropogenic disturbances (such as grazing and browsing) would improve their survival, seedling growth and biomass under field conditions. Furthermore, we expected that the effect of this strategy would increase with time of fencing. The objectives of this study were to examine: (1) the survival, growth, biomass and plant characteristics of *B. papyrifera* wildlings in fenced and non-fenced field conditions; and (2) the growth and biomass allocation of *B. papyrifera* wildlings over time with varying fencing durations.

2. Methods

2.1 Study area

The field experiment was conducted at Jijike site, Abergelle, Tigray region, northern Ethiopia (Fig. 1). The site lies at 13°26'34" to 13°33'01" N and 38°48'05" to 38°53'33" E. Within the study site, the altitude varies from 1400 to 1650 metres above sea level (Negussie *et al.* 2008). The monthly average temperature of the study area was estimated at 25.3°C, with an average total annual rainfall of 445 mm mainly raining between mid–June and August (Mengistu *et al.* 2012). The dominant soil types of the study area are *Cambic arenosols, Chromic cambisols* and *Leptosols* (Hizikias 2011). The vegetation of the study area is characterised as *Combretum-Terminalia* and *Acacia-Commiphora* woodland dominated by *B. papyrifera, Ipomea spps, Acacia etbaica and Senna singueana* (Gidey *et al.* 2020).

2.2 Study plots and seedling identification

The field experiment was conducted under natural conditions of the study site to observe the survival, growth and dry biomass of naturally regenerated *B. papyrifera* seedlings. A reconnaissance survey was conducted to identify the study experimental plots in *B. papyrifera* dominated woodlands. For homogenisation of the variability of the experimental plots, soil type, slope, aspect, vegetation cover, stoniness and distance from the canopy of trees were thoroughly considered. A total of 36 rectangular study plots, each measuring 1 m × 1.5 m, were established for monitoring the survival and growth of naturally regenerated *B. papyrifera* seedlings (referred to as wildlings). During the rainy season, 5–10 seedlings of *B. papyrifera* were randomly selected and marked with permanent tags in each plot, resulting in a total of 305 identified seedlings across all plots. Eighteen plots were enclosed with mesh wire to protect the seedlings from browsing by both domestic and wild animals. The growth and survival of the *B. papyrifera* seedlings were monitored over five growing seasons and four consecutive years, specifically at 3, 12, 24, 36 and 48 months, using the established permanent plots.

2.3 Data collection

Data related to seedlings' survival and performance were collected from both fenced and open (non-fenced) plots. Binary seedling survival data (dead = 0, live = 1) were recorded from marked seedlings in these plots. Additionally, seedling height and root collar diameter (RCD) were measured using a graduated metre and a digital calliper, respectively. The number of fully developed leaves and number of apices were also counted for each seedling. In both fenced and open plots, One to two seedlings per plot were uprooted every growing season to measure the leaf area and biomass of the sampled seedlings. These uprooted seedlings were then transported to the Forestry Laboratory, Mekelle University, Ethiopia for further analysis. At the Laboratory, the leaf area was measured using an AM 100 Leaf area metre (ADC Bioscientific Ltd.), and then the seedlings were divided into leaves, stems and roots sections and allowed to oven-dry at a temperature of 65°C until a constant weight was attained (Mokria *et al.* 2018). The leaf, stem and root dry biomass fractions of each seedling were measured using an electronic balance called the laboratory balance PCE (PCE Instruments Ltd.).

2.4 Calculations and statistics

Specific leaf area, leaf size and specific stem density were measured following the methods of Cornelissen *et al.* (2003). Seedling ratios (e.g., leaf area ratio, leaf weight ratio), absolute growth rates in sizes (e.g., seedling height, root collar diameter), dry weights (e.g., leaf, stem and root) and specific leaf weight were also calculated according to Hunt (1990). Seedling survival was analyzed using the generalised linear mixed-effect models (GLMM) with logit link function and binomial distribution (glmer function from the R package "lme4"): Logit (seedling survival) ~ Management + (1| Plot-ID/Site); where management and site are factors.

To explore the statistical mean differences in seedling performance between the fenced and non-fenced plots, non-parametric tests were employed for various seedling attributes. These attributes included RCD, height, leaf number, leaf area, number of apices, stem dry mass, root dry mass and shoot dry mass as the data did not normally distribute. Moreover, to satisfy the assumptions of normal distribution and homogeneity of variances, the leaf dry mass and seedling dry mass data were natural logarithmic (ln)-transformed before conducting statistical analyses. Specifically, the Mann-Whitney U test and T-test were employed to assess mean differences in seedling size and biomass between the fenced and non-fenced plots. For data analysis, both Statistical Package for the Social Sciences software (version 20) and R software were utilised.

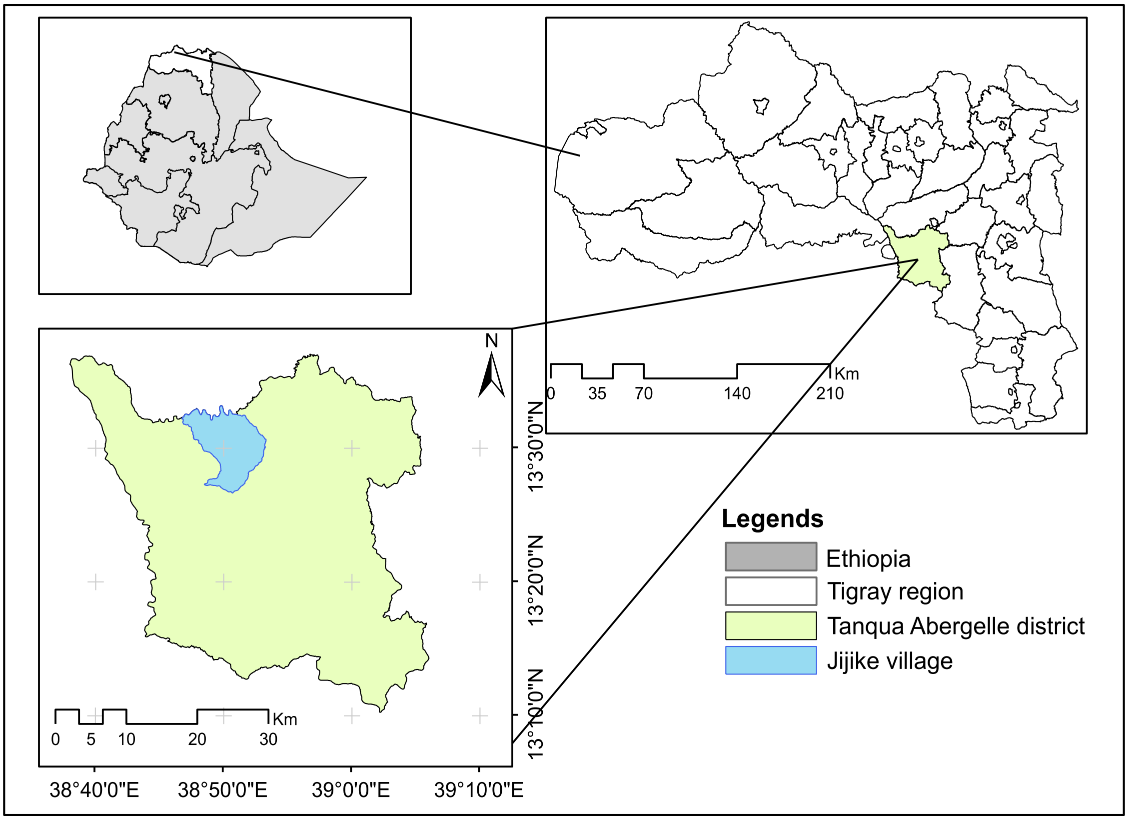

Figure 1. Location of the study area.

3. Results

3.1 Effect of fencing on seedling survival and diebacks

The likelihood of seedling survival was significantly lower in the open areas (Log odds ratio = 0.33, $P < 0.05$) compared to fenced plots; the odds of survival are reduced by 67% in open plots (Table 1). The statistical analysis employed GLMM, which considered the hierarchical structure of the data – specifically, the nesting of plot factors within site factors. This approach enhances the accuracy of assessing the relationship between management practices and seedling survival.

During the wet season (i.e., during the four months of the growing period), *B. Papyrifera* seedlings exhibited active growth in both above-ground and below-ground traits. However, during the dry period (which spans eight months of growth), *B. papyrifera* seedlings experienced contrasting responses in their above-ground (shoot) and below-ground (root) growth. While the shoots dried up, the roots remained active and viable as depicted in Fig. 2. This phenomenon likely contributes to the observed higher dry biomass of roots compared to shoots in the fenced and open areas (Fig. 3).

3.2 Effect of fencing on seedling size

Seedlings in the fenced and non-fenced plots differed in almost all seedling growth parameters (Table 2). *B. papyrifera* seedlings grown in the fenced plots exhibited significantly greater values for RCD, height, leaf numbers, leaf area and number of apices as compared to those in non-fenced plots (Table 2).

Dry matter of seedlings grown in the fenced areas was significantly higher in all biomass-related parameters than the seedlings grown in the open environment (Table 2). Seedlings in the fenced plots were 31% higher in total plant dry biomass, 33% in stem biomass, 29% in root biomass, 36% in leaf biomass and 35% in shoot biomass compared to those grown in non-fenced plots conditions. Most of the dry biomass was allocated to roots in both the fenced and non-fenced pots: 77% in the case of fencing and 80% in non-fencing (Table 2).

3.3 Effect of fencing time on seedling size

The size of *B. papyrifera* seedlings was higher in fenced plots than in the open plots in most fencing times and increased with the fencing time (Fig. 4). Seedling height was significantly different between the fenced and non-fenced plots at 3 and 48 months of fencing times. Besides, the leaf numbers were significantly higher in fenced plots at 36 and 48 months of fencing times. RCD was statistically higher in the fenced plot at 3, 24 and 48 months of fencing times. Seedlings grown in fenced plots also showed significantly higher leaf areas at 3, 36 and 48 months of fencing times (Fig. 4).

The dry biomass (of most biomass variables) of *B. papyrifera* seedlings was higher in fenced compared to the non-fenced plots along the growing seasons, and generally, the difference increased with the time of fencing (Fig. 5).

3.4 Effect of fencing on seedling growth rates

Growth rates of *B. papyrifera* seedlings were higher in the fenced plots compared to the non-fenced plots for most growth variables (Table 3). Specifically, seedling growth rates, including RCD,

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Table 1. Results of generalised linear mixed-effect models with logit linked function showing the relationships of seedling survival between fenced and open plots in Abergelle, Tigray region, northern Ethiopia

Parameters	Survival odds ratio (S.E)	95% CI
Intercept	11.00*** (0.43)	4.77 – 25.37
Management = open	0.33** (0.49)	0.03 – 0.87
Random effects		
σ2	3.29	
τ00 Site: Plot_ID	0	
τ00 Plot_ID	0	
N Site	2	
N Plot_ID	3	

Note: ***Significant at $p < 0.001$ level and **Significant at $p < 0.05$ level in the generalized linear mixed-effect models for factors affecting the survival of *B. papyrifera* wildlings. SE: Stnadard error.

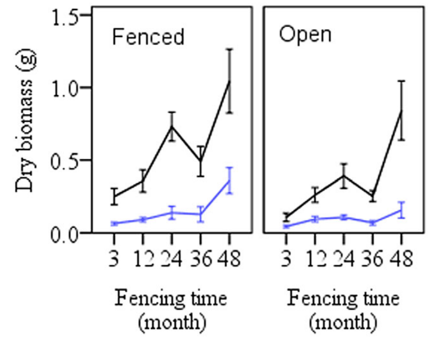

Figure 3. Dry biomass of root (black lines) and shoot (blue lines) of *B. papyrifera* seedlings.

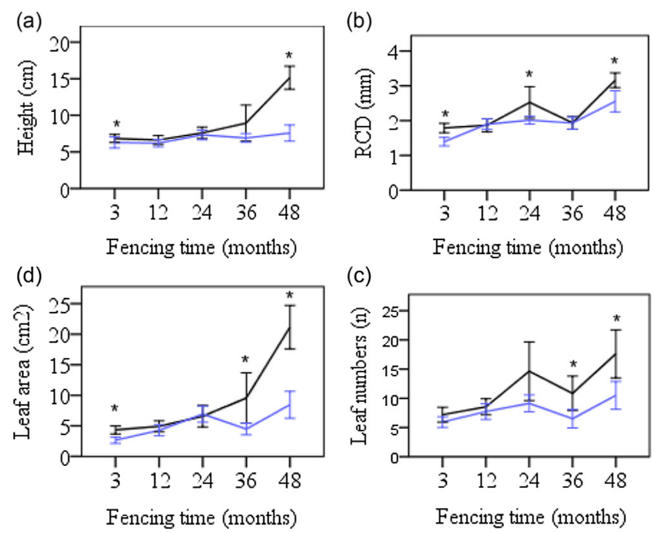

Figure 4. Changes in seedling size traits of *B. papyrifera* seedlings (Ns = 305) with time of fencing. Height (a), RCD (b), leaf numbers (c) and leaf areas (d) in the fenced (black lines) and open (blue lines) plots (Pn = 36). Means significantly different between fenced and open plots are indicated with an asterisk (*) (p < 0.05).

Table 2. Mean values of seedling size and biomass *of B. papyrifera* (Ns = 305) after 4 years under fenced and open experimental plots (Np = 36) in Abergelle, Tigray region, northern Ethiopia

		Mean values (mean±SE)		
Category	Parameters	Fenced	Open	p-value
Seedling size	Root collar diameter (mm)	2.44±0.08	1.95±0.05	0.000
	Height (cm)	10.06±0.44	6.84±0.17	0.000
	Leaf number (n)	12.85±0.95	7.92±0.37	0.000
	Leaf area (cm^2)	11.27±0.90	5.31±0.33	0.000
	No of apices (n)	4.22±0.26	3.10±0.25	0.001
Seedling dry biomass	Stem (g)	0.05 ±0.00	0.02±0.00	0.000
	Root (g)	0.66±0.05	0.36±0.03	0.000
	Shoot (g)	0.19±0.02	0.09±0.01	0.000
	Leaf (g)	0.15±0.02	0.07±0.01	0.000
	Plant (g)	0.85±0.07	0.46±0.03	0.000

Note: **t-test** was used to test the mean differences between leaf dry biomass and plant dry biomass, whereas the **Mann-Whitney U** test was used to test mean differences of all other growth parameters, and tests are significant at P < 0.05.

height, leaf numbers and leaf areas, were approximately 1.04 to 6.6 times greater in the fenced plots than in the non-fenced plots. Likewise, the growth rates in dry biomass variables were nearly 1.1 to 3.8 times higher for the fenced plots compared to the non-fenced plots (Table 3).

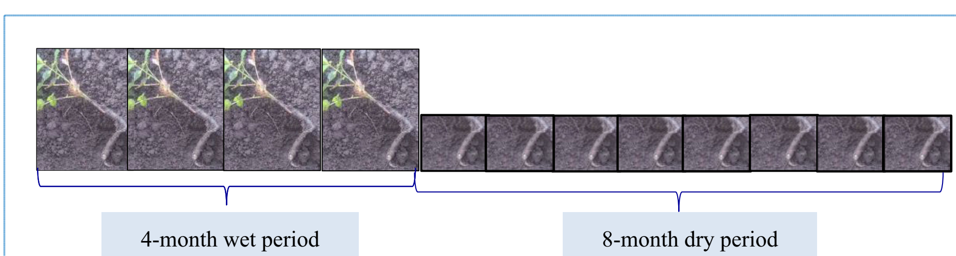

Figure 2. Schematic presentation of dieback behaviour of *B. papyrifera* seedlings.

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Table 3. Absolute growth rates (in size and biomass) of *B. papyrifera* seedlings under fenced and non-fenced experimental plots in Abergelle, Tigray region, northern Ethiopia

		Absolute growth rates (month^{-1})	
Category	Growth variables	Fenced	Open
Seedling size	Root collar diameter (mm)	0.029	0.028
	Height (cm)	0.172	0.026
	Leaf number (number)	0.226	0.108
	Leaf area (cm^2)	0.354	0.132
Seedling dry biomass	Leaf (g)	0.0048	0.0023
	Stem (g)	0.0015	0.0004
	Root (g)	0.0173	0.0164
	Shoot (g)	0.0063	0.0027
	Plant (g)	0.0236	0.0191

Table 4. Ratios and traits of seedlings in the fenced and open plots

	Mean values (mean±SE)		
Parameters	Fenced	Open	P-value
Specific leaf area (cm^{2}g^{-1})	101.07±5.30	117.12±13.71	0.668
Leaf area ratio (cm^{2}g^{-1})	15.56±0.91	15.06±.75	0.715
Leaf size per individual (cm^2)	0.756±0.25	0.753±0.06	0.024
Root weight ratio (gg^{-1})	0.776±.009	0.749±.011	0.078
Stem weight ratio (gg^{-1})	0.053±.003	0.073±.005	0.001
Leaf weight ratio (gg^{-1})	0.172±0.008	0.178±0.01	0.724
Specific leaf weight (gcm^{-2})	0.014±.001	0.015±.002	0.600
Stem-specific density (gcm^{-3})	0.843±.064	0.818±.048	0.277
Root-to-shoot ratio (R:S)	6.065±0.714	4.926±0.430	0.079

Mann–Whitney U test was used to test mean differences of the parameters, and tests are significant at $P < 0.05$.

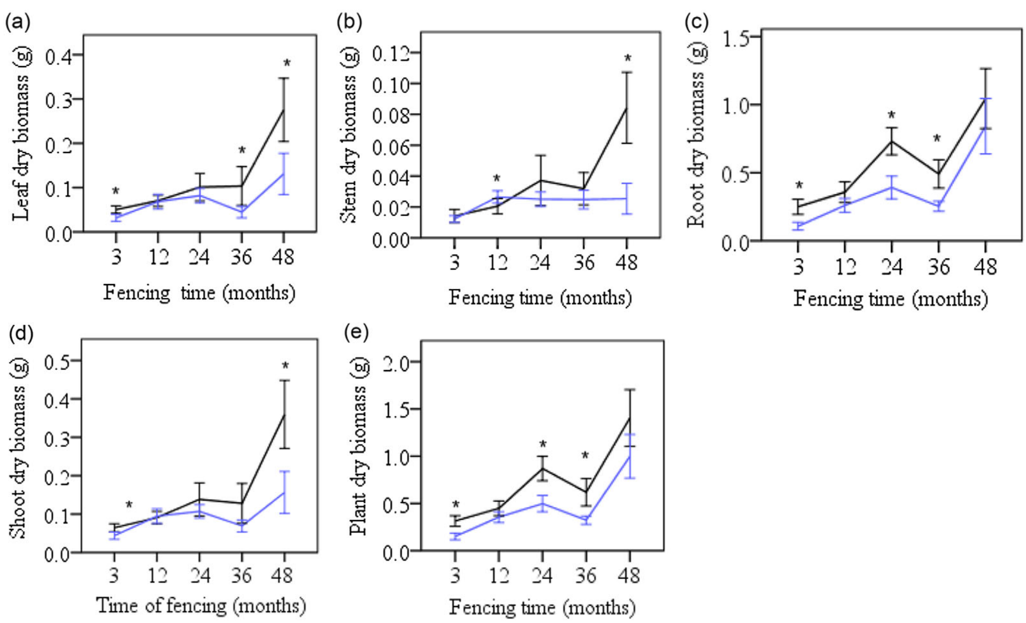

Figure 5. Dry biomass traits of *B. papyrifera* seedlings (Ns = 305) in the fenced (black lines) and non-fenced (blue lines) plots (Np = 36) during four years of fencing. Leaf (a), stem (b), root (c), shoot (d) and plant (e) dry biomasses. Means significantly different between fenced and open plots are indicated with an asterisk (*) ($p < 0.05$).

3.5 Seedling functional traits and ratios

The fenced seedlings exhibited greater biomass allocation than the non-fenced counterparts (Table 4). Significantly higher stem weight ratios were recorded in the non-fenced plots compared to the fenced plots. Although the biomass allocation, as reflected by Root:Shoot ratio (R:S), did not show significant differences between the fenced and open plots, the mean R:S ratio of the fenced plots was 10% higher as compared to the non-fenced plots (Table 4).

4. Discussion

We conducted an experiment to assess the effect of fencing on the survival and growth of *B. papyrifera* wildlings. We established permanent experimental plots under field conditions and monitored them for four consecutive years. We hypothesised that the sustained protection of the seedlings from various anthropogenic disturbances (such as grazing and browsing) would improve their survival and growth, ultimately contributing to the natural regeneration of the species in its native habitat. We found that fencing of *B. papyrifera* wildings did indeed lead to improved seedling survival and performance in terms of size and biomass, leaf area and higher root and leaf biomasses and absolute growth rates.

In agreement with the study results, a positive effect of fencing on *B. papyrifera* seedling density, recruitment and health conditions was found in exclosures (Moges & Kindu 2006). Long *et al.* (2012) also reported significantly higher root and stem dry biomasses of red oak (*Quercus rubra* L.) seedlings within the fenced plots compared to open plots. This enhancement likely facilitated improved water and nutrient uptake, leading to

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increased growth rates (Bacon 2009). Besides, a higher regeneration, survival rate, RCD and seedling height for several other dryland trees were also found in fenced areas as compared to open systems (Giday *et al.* 2018; Long *et al.* 2012; Mengistu *et al.* 2005; Ruo *et al.* 2018; Wassie *et al.* 2009). For example, Omondi *et al.* (2017) counted a higher number of seedlings and saplings of *Acacia senegal* in slightly disturbed populations compared to highly disturbed ones. This could be associated with the lower browsing and trampling of animals on seedlings in the slightly disturbed areas due to their restricted movements (Omondi *et al.* 2017; Wassie *et al.* 2009). Our study results are also consistent with other studies conducted in dryland regions elsewhere. For instance, Habrova and Pavlis (2017) observed an increasing rate of seedling survival and development for *Dracaena cinnabari* with increasing time of their exclosure on the Firmihin Plateau, Socotra Island, Yemen. Similarly, Löf *et al.* (2021) reported a significant height increment in both planted and naturally regenerated *Quercues robur* seedlings within fenced areas compared to non-fenced areas.

In our study, we observed that the size of the seedlings at the end of the study period (*i.e.,* in the 4th year) remained small. This may be attributed to various factors, such as moisture stress. Plant species in the deciduous dry woodlands have peculiar structural and functional traits that enable them to survive under high disturbance levels such as water deficits and fires (Pulla *et al.* 2015). Under seasonal water deficit conditions, plants either tolerate drought or avoid drought by, for example, dropping leaves to limit transpiration during the dry season. This adaptation allows them to thrive in dry environments. However, in certain regions, for instance, in the African dry woodlands, the intensity and frequency of rainfall can vary considerably even within the short-wet season itself, implying that deciduous trees may face drought stress (Bullock *et al.* 1995; Murphy & Lugo 2010). *B. papyrifera* copes with dry seasons through a conservative strategy using aboveground plant dieback – it dries out during the dry season and experiences re-growth during the wet season (Birhane *et al.* 2012). Strong variability in rainfall and the occurrence of extended dry spells (water stress) may have significant effects on the annual carbon gain and allocation patterns of *B, papyrifera* seedlings, affecting their survival in dry areas (Mengistu 2011). Browsing of the leaves during the wet period reduces the production of photosynthates and thereby the number of reserves in the plant and repeated browsing over the years will reduce the strength of the plant in terms of resprouting capacity (Mengistu 2011).

Overall, the study findings confirm the beneficial effects of sustained fencing on the survival and growth performance of *B. papyrifera* seedlings in their natural habitats. Fencing interventions could improve seedling survival and growth, thereby contributing to sustainable conservation of *B. papyrifera* woodlands. Future research should prioritise investigating the effects of more extended fencing interventions or exclosures (e.g., lasting over 5 years) on *B. papyrifera* seedlings (and saplings). Furthermore, additional efforts should concentrate on the mechanisms of periodic seedling dieback, and influence of soil moisture and animal browsing thereon.

There is already well established evidence that the sustainability of *B. papyrifera* woodlands and its renowned product–frankincense, is at greater risk (Bongers *et al.* 2019). Several population assessments of *B. papyrifera* have revealed evidence of the species population and regeneration collapse throughout its natural ranges, necessitating urgent conservation action to manage its regeneration in natural woodlands (Abiyu *et al.* 2010; Alemu *et al.* 2012; Eshete *et al.* 2005; Gebrehiwot *et al.* 2003; Gidey *et al.* 2020; Groenendijk *et al.* 2012; Ogbazghi *et al.* 2006; Tolera *et al.* 2013). Several factors contribute to this decline, including overgrazing, reckless tapping for frankincense, fire, land use conversion and insect infestation and damage. These challenges affect the species' regeneration and seedling performance, and triggered the high adult mortality of the species in Ethiopia (Abiyu *et al.* 2010; Eshete *et al.* 2005; Negussie *et al.* 2008, 2021), Eritrea (Ogbazghi *et al.* 2006) and Sudan (Khamis *et al.* 2016). *B. papyrifera* seedlings are sensitive to trampling, browsing and fire, among others. To address this, management options that promote adequate regeneration and long-term sustainability of populations are crucial. Regulated frankincense harvest and intensive population management strategies are essential for the natural stands. The future of this flagship species remains extremely unstable, emphasizing the need for coordinated efforts from all stakeholders to enhance its natural regeneration and preserve its myriad socio-economic and ecological roles (Bongers *et al.* 2019; Gidey *et al.* 2020; Lemenih *et al.* 2014; Lemenih & Kassa 2011). Based on the results of this study, we suggest the following measures: (i) sustained protection: implement fencing interventions to safeguard the remnant *B. papyrifera* woodlands, and (ii) restoration: actively restore degraded areas in integration with protection efforts.

In this context, there is well established evidence that converting communal grazing lands into exclosures, primarily using physical fences, offers several conservation benefits. These benefits include vegetation restoration, improvement in soil nutrient status and erosion reduction (Mekuria *et al.* 2007; Shimelse *et al.* 2020; Welemariam *et al.* 2018). Besides, the positive roles of exclosures are widely recognised and supported by local communities in dryland areas in Ethiopia, particularly in the Tigray region, northern Ethiopia (Birhane *et al.* 2017; Gebregziabher and Soltani 2019; Mekonen *et al.* 2022). However, the sustainability and success rate of the intervention are challenged by several factors, including biophysical and institutional factors (Birhane *et al.* 2017). Although fenced/exclosure areas primarily benefit local communities through biodiversity enhancement, soil and water condition improvements, and other ecological aspects, the livelihood improvements often receive less attention. Therefore, for the intervention to be both feasible and sustainable, it is crucial to consider the socio-economic and cultural context of the local communities. In light of this, exclosures established using social fences are widely regarded as more favourable in terms of ecology and social acceptance (Birhane *et al.* 2017). Ensuring active community participation from the selection of intervention areas to the establishment and management of exclosures is vital. Simultaneously, implementing benefit-sharing mechanisms and strategies among the custodians will contribute to the long-term success of these conservation efforts.

In the same manner, ensuring the sustainable and effective restoration of *B. papyrifera* woodlands through this intervention necessitates a transition from physical fencing to social fencing in the long term. The feasibility of the intervention for this particular tree species is supported by the fact that the tree species is highly valued by the local community for its versatile roles and that it is highly threatened and in immediate need of conservation actions. In addition, the remaining populations of this tree species are found in mostly inaccessible areas, areas not directly needed for agricultural practices, providing an ideal setting for establishing exclosures to safeguard this flagship species. Although armed conflict currently exerts another strong pressure on the Boswellia forests (Johnson & Bongers 2024), the success of this intervention hinges on full community participation at all stages. By engaging local stakeholders, we can ensure the long-term success of this vital conservation endeavour.

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Publishing ethics. The data and manuscript are our own original work.

References

Abiyu A, Bongers F, Eshete A, Gebrehiwot K, Kindu M, Lemenih M, Moges Y, Ogbazgh W and Sterck FJ (2010) *Incense woodlands in Ethiopia and Eritrea: regeneration problems and restoration possibilities*. In *Degraded Forests in Eastern Africa: Management and Restoration*: Earthscan, pp. 133–152. https://doi.org/10.4324/9781849776400

Adam AA and El Tayeb AM (2008) A comparative study of natural regeneration of *B. papyrifera* and other tree species in Jebel Marra Darfur; Sudan. *Research Journal of Agriculture and Biological Sciences* **4**, 94–102.

Alemu A, Pretzsch J, El-Sheikh T and Omar Y (2012) Population status of *Boswellia papyrifera* (del.). Hochst in the dry woodlands of Nuba mountains, South Kordofan state, Sudan. *Agriculture and Forestry* **54**, 41–50.

Bacon M (2004) *Water Use Efficiency in Plant Biology*. Oxford, UK: Blackwell.

Birhane E, Sterck FJ, Fetene M, Bongers F and Kuyper TW (2012) Arbuscular mycorrhizal fungi enhance photosynthesis, water use efficiency, and growth of frankincense seedlings. *Oecologia* **169**, 895–904. https://doi.org/10.1007/s00442-012-2258-3

Birhane E, Mengistu T, Seyoum Y, Hagazi N, Putzel L, Rannestad MM and Kassa H (2017) Exclosures as forest and landscape restoration tools: lessons from Tigray Region, Ethiopia. *International Forestry Review* **19**, 37–50. https://doi.org/10.1505/146554817822330498

Bongers F, Groenendijk P, Bekele T, Birhane E, Damtew A, Decuyper M, Eshete A, Gezahgne A, Girma A, Khamis MA, Lemenih M, Mengistu T, Ogbazghi W, Sass-Klaassen U, Tadesse W, Teshome M, Tolera M, Sterck FJ and Zuidema PA (2019) frankincense in peril. *Nature Sustainability* **2**, 602–610. https://doi.org/10.1038/s41893-019-0322-2

Bongers F and Tennigkeit T (eds.) (2010) *Degraded Forests in Eastern Africa: Management and Restoration*. London, UK: Earthscan, Ltd.

Bullock S, Mooney H and Medina E (eds.) (1995) *Seasonally Dry Tropical Forests*. Cambridge: Cambridge University Press.

Canney-Davison S, Bongers F and Phillips D (2022) The future of frankincense: understanding the plant's diversity is key to its conservation. *Herbalgram* **133**, 40–59.

Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, Steege HT, Morgan HD, Van Der Heijden MGA, Pausas JG and Poorter H (2003) A hand book of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**, 335–380. https://doi.org/10.1071/BT02124

DeCarlo A, Agieb S, Johnson S, Satyal P and Setzer WN (2022) Inter-tree variation in the chemical composition of *Boswellia papyrifera* Oleo-Gum-Resin. *Natural Product Communications* **17**, 1–6. https://doi.org/10.1177/1934578X221117411

Derero A, Worku A and Kassa H (2018) Genecological zones and selection criteria for natural forest populations for conservation: the case of *Boswellia papyrifera* in Ethiopia. *Journal of Forestry Research* **29**, 515–524. https://doi.org/10.1007/s11676-017-0466-8

Eshete A, Kassa H and Livingstone J (2021) *Inclusive Frankincense Value Chain Development in Ethiopia. A Historical Perspective on Forest Governance and Reforms for Better Livelihoods and Conservation Outcomes*. Ede, The Netherlands: PENHA, Addis Ababa, Ethiopia and Tropenbos International.

Eshete A, Sterck F and Bongers F (2011) Diversity and production of Ethiopian dry woodlands explained by climate and soil-stress gradients. *Forest Ecology and Management* **261**, 1499–1509. https://doi.org/10.1016/j.foreco.2011.01.021

Eshete A, Teketay D and Hulten H (2005) The socio-economic importance and status of populations of *Boswellia papyrifera* (Del.) Hochst. In northern Ethiopia: the case of North Gonder Zone. *Forests, Trees and Livelihoods* **15**, 55–74. https://doi.org/10.1080/14728028.2005.9752507

Eshete A, Teketay D, Lemenih M and Bongers F (2012) Effects of resin tapping and tree size on the purity, germination and storage behavior of *Boswellia papyrifera* (Del.) Hochst. Seeds from Metema District, northwestern Ethiopia. *Forest Ecology and Management* **269**, 31–36. https://doi.org/10.1016/j.foreco.2011.12.049

Gebregziabher D and Soltani A (2019) Exclosures in people's minds: perceptions and attitudes in the Tigray region, Ethiopia. *Forest Policy and Economics* **101**, 1–14. https://doi.org/10.1016/j.forpol.2019.01.012

Gebrehiwot K, Muys B, Haile M and Mitloehner R (2003) Introducing *Boswellia papyrifera* (Del.) Hochst and its non-timber forest product, frankincense. *International Forestry Review* **5**, 348–353. https://doi.org/10.1505/IFOR.5.4.348.22661

Giday K, Humnessa B, Muys B, Taheri F and Azadi H (2018) Effects of livestock grazing on key vegetation attributes of a remnant forest reserve: the case of Desa'a Forest in northern Ethiopia. *Global Ecology and Conservation* **14**, e00395. https://doi.org/10.1016/j.gecco.2018.e00395

Gidey T, Hagos D, Juhar HM, Solomon N, Negussie A, Crous-Duran J, Oliveira TS, Abiyu A and Palma JH (2020) Population status of *Boswellia papyrifera* Woodland and prioritizing its conservation interventions using multi-criteria decision model in northern Ethiopia. *Heliyon* **6**, e05139. https://doi.org/10.1016/j.heliyon.2020.e05139

Groenendijk P, Eshete A, Sterck FJ, Zuidema PA and Bongers F (2012) Limitations to sustainable frankincense production: blocked regeneration, high adult mortality and declining populations: sustainable frankincense production. *Journal of Applied Ecology* **49**, 164–173. https://doi.org/10.1111/j.1365-2664.2011.02078.x

Habrova H and Pavlis J (2017) Dynamic response of woody vegetation on fencing protection in semi-arid areas; Case study: Pilot exclosure on the Firmihin Plateau, Socotra Island. *Saudi Journal of Biological Sciences* **24**, 338–346. https://doi.org/10.1016/j.sjbs.2015.09.030

Hizikias EB (2011) Mycorrhizal symbiosis and seedling performance of the frankincense tree (*Boswellia papyrifera*). PhD thesis Wageningen University and Research, Wageningen, The Netherlands.

Hunt R (1990) *Basic Growth Analysis: Plant Growth Analysis for Beginners*. Dordrecht: Springer. https://doi.org/10.1007/978-94-010-9117-6_8

Husheer SW, Robertson AW, Coomes DA and Frampton CM (2006) Herbivory and plant competition reduce mountain beech seedling growth and establishment in New Zealand. *Plant Ecology* **183**, 245–256. https://doi.org/10.1007/s11258-005-9036-9

Johnson S and Bongers F (2024) Armed conflict as an underappreciated driver of conservation outcomes in frankincense (*Boswellia* spp.). *Trees, Forests and People* **15**, 100490, 1–7. https://doi.org/10.1016/j.tfp.2023.100490

Khamis M, Siddig E, Khalil A and Csaplovics E (2016) Changes in forest cover composition of *Boswellia papyrifera* (Del.) Hochst. Stands and their consequences, South Kordofan, Sudan. *Mediterranean Journal of Biosciences* **1**, 99–108.

Lemenih M, Arts B, Wiersum KF and Bongers F (2014) Modelling the future of *Boswellia papyrifera* population and its frankincense production. *Journal of Arid Environments* **105**, 33–40. https://doi.org/10.1016/j.jaridenv.2014.02.006

Lemenih M and Kassa H (eds.) (2011) *Opportunities and Challenges for Sustainable Production and Marketing of Gums and Resins in Ethiopia*. Bogor, Indonesia: CIFOR. https://doi.org/10.17528/cifor/003478

Liu J, Bian Z, Zhang K, Ahmad B and Khan A (2019) Effects of different fencing regimes on community structure of degraded desert grasslands on Mu Us desert, China. *Ecology and Evolution* **9**, 3367–3377. https://doi.org/10.1002/ece3.4958

Löf M, Barrere J, Engman M, Petersson LK and Villalobos A (2021) The influence of fencing on seedling establishment during reforestation of oak stands: a comparison of artificial and natural regeneration techniques including costs. *European Journal of Forest Research* **140**, 807–817. https://doi.org/10.1007/s10342-021-01369-w

Long RP, Brose PH and Horsley SB (2012) Responses of northern red oak seedlings to lime and deer exclosure fencing in Pennsylvania. *Canadian Journal of Forest Research* **42**, 698–709. https://doi.org/10.1139/x2012-025

Mekonen MK, Hailu AA and Abitew AA (2022) Social and institutional status of area exclosure in North Wollo and Waghemira Zones, Northeastern Ethiopia. *International Journal of Forestry Research* **2022**, 1–12. https://doi.org/10.1155/2022/9368955

Mekonnen Z, Worku A, Yohannes T, Bahiru T, Mebratu T and Teketay D (2013) Economic contribution of gum and resin resources to household livelihoods in selected regions and the national economy of Ethiopia. *Ethnobotany Research & Applications* **11**, 273–288.

Mekuria W, Veldkamp E, Haile M, Nyssen J, Muys B and Gebrehiwot K (2007) Effectiveness of exclosures to restore degraded soils as a result of overgrazing in Tigray, Ethiopia. *Journal of Arid Environments* **69**, 270–284. https://doi.org/10.1016/j.jaridenv.2006.10.009

Mengistu T (2011) Physiological ecology of the frankincense tree. PhD thesis, *Wageningen University and Research, Wageningen, The Netherlands*. ISBN: 978-90-8585-927-7.

Mengistu T, Sterck FJ, Anten NPR and Bongers F (2012) Frankincense tapping reduced photosynthetic carbon gain in *Boswellia papyrifera* (Burseraceae) trees. *Forest Ecology and Management* **278**, 1–8. https://doi.org/10.1016/j.foreco.2012.04.029

Mengistu T, Teketay D, Hulten H and Yemshaw Y (2005) The role of enclosures in the recovery of woody vegetation in degraded dryland hillsides of central and northern Ethiopia. *Journal of Arid Environments* **60**, 259–281. https://doi.org/10.1016/j.jaridenv.2004.03.014

Moens T, Jacob M and Lanckriet S (2019) *Boswellia Incense in the Giba River Gorge*. In J. Nyssen, M. Jacob, & A. Frankl (eds.), *Geo-trekking in Ethiopia's Tropical Mountains*, pp. 293–300: Springer International Publishing. https://doi.org/10.1007/978-3-030-04955-3_19

Moges Y and Kindu M (2006) Effects of fencing and ground cultivation on natural regeneration of *Boswellia papyrifera* in Metema Wereda, Ethiopia. *Journal of the Drylands* **1**, 45–51.

Mokria M, Mekuria W, Gebrekirstos A, Aynekulu E, Belay B, Gashaw T and Bräuning A (2018) Mixed-species allometric equations and estimation of aboveground biomass and carbon stocks in restoring degraded landscape in northern Ethiopia. *Environmental Research Letters* **13**, 1–14. https://doi.org/10.1088/1748-9326/aaa495

Murphy P and Lugo A (2010) *Dry forests of Central America and Caribbean*. In H. Stephen Bullock, Harold A. Mooney and Ernesto Medina (eds.), *Seasonally Dry Tropical Forests*, pp. 9–34: Cambridge University Press. https://doi.org/10.1017/CBO9780511753398

Negussie A, Aerts R, Gebrehiwot K and Muys B (2008) Seedling mortality causes recruitment limitation of *Boswellia papyrifera* in northern Ethiopia. *Journal of Arid Environments* **72**, 378–383. https://doi.org/10.1016/j.jaridenv.2007.06.009

Negussie A, Gebrehiwot K, Yohannes M, Norgrove L and Aynekulu E (2021) Continuous resin tapping for frankincense harvest increases susceptibility of *Boswellia papyrifera* (Del.) Hochst trees to longhorn beetle damage. *Heliyon* **7**, e06250. https://doi.org/10.1016/j.heliyon.2021.e06250

Ogbazghi W (2001) The distribution and regeneration of *Boswellia papyrifera* (Del.) Hochst. in Eritrea. PhD thesis, Wageningen University and Research. Wageningen, The Netherlands, 131. ISSN: 0926-9495.

Ogbazghi W, Rijkers T, Wessel M and Bongers F (2006) Distribution of the frankincense tree *Boswellia papyrifera* in Eritrea: the role of environment and land use. *Journal of Biogeography* **33**, 524–535. https://doi.org/10.1111/j.1365-2699.2005.01407.x

Omondi SF, Odee DW, Ongamo GO, Kanya JI and Khasa DP (2017) Effects of anthropogenic disturbances on natural regeneration and population structure of gum Arabic tree (*Acacia senegal*) in the woodlands of Lake Baringo ecosystem, Kenya. *Journal of Forestry Research* **28**, 775–785. https://doi.org/10.1007/s11676-016-0349-4

Pulla S, Ramaswami G, Mondal N, Suresh H, Dattaraja H, Parthasarathy N, Ramesh B and Sukumar R (2015) Assessing the resilience of global seasonally dry tropical forests. *International Forestry Review* **17**, 91–113.

Ruo G, Weldegebrial B, Yohannes G and Yohannes G (2018) The impact of fencing on regeneration, tree growth and carbon stock in Desa Forest, Tigray, Ethiopia. *Biomedical Journal of Scientific & Technical Research* **12**, 8900–8916. https://doi.org/10.26717/BJSTR.2018.11.002183

Shimelse S, Bekele T and Nemomissa S (2020) *Area exclosure as a strategy for climate change mitigation: Case Study from Tigray Region, Northern Ethiopia*. In W. Leal Filho (ed.), *Handbook of Climate Change Resilience*. Cham: Springer. https://doi.org/10.1007/978-3-319-93336-8_123

Tadesse W, Dejene T, Zeleke G and Desalegn G (2020) Underutilized natural gum and resin resources in Ethiopia for future directions and commercial utilization. *World Journal of Agricultural Research* **8**, 32–38. https://doi.org/10.12691/wjar-8-2-2

Tadesse W, Desalegn G and Alia R (2007) Natural gum and resin bearing species of Ethiopia and their potential applications. *Investigación Agraria: Sistemas y Recursos Forestales* **16**, 211. https://doi.org/10.5424/srf/2007163-01010

Thulin M (2020) The genus "Boswellia" (Burseraceae): the frankincense trees. *Symbolae Botanicae Upsalienses* **39**, 1–149, Uppsala Universitet. http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-405908

Tilahun M, Muys B, Mathijs E, Kleinn C, Olschewski R and Gebrehiwot K (2011) Frankincense yield assessment and modeling in closed and grazed *Boswellia papyrifera* woodlands of Tigray, Northern Ethiopia. *Journal of Arid Environments* **75**, 695–702. https://doi.org/10.1016/j.jaridenv.2011.03.005

Tolera M, Sass-Klaassen U, Eshete A, Bongers F and Sterck FJ (2013) Frankincense tree recruitment failed over the past half century. *Forest Ecology and Management* **304**, 65–72. https://doi.org/10.1016/j.foreco.2013.04.036

Wassie A, Sterck FJ, Teketay D and Bongers F (2009) Effects of livestock exclusion on tree regeneration in church forests of Ethiopia. *Forest Ecology and Management* **257**, 765–772. https://doi.org/10.1016/j.foreco.2008.07.032

Welemariam M, Kebede F, Bedadi B and Birhane E (2018) Exclosures backed up with community-based soil and water conservation practices increased soil organic carbon stock and microbial biomass carbon distribution, in the northern highlands of Ethiopia. *Chemical and Biological Technologies in Agriculture* **5**, 12. https://doi.org/10.1186/s40538-018-0124-1

Yogi RK, Kumar A and Jaiswal AK (2017) *Lac, Plant Resins and Gums Statistics 2015: At a Glance*. https://doi.org/10.13140/RG.2.2.14630.73282