




Research Article

Growth trajectories and ages of main tree species in dry Afromontane forest fragments of northern Ethiopia



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Abstract

Information on long-term growth rates, ages, and survival of dominant tree species is vital to understand forest dynamics. In this study, tree-ring analysis was used to reconstruct lifetime growth patterns and to examine age–diameter relationships of selected tree species from the dry Afromontane forest fragments in northern Ethiopia. Ring width measurements were based on increment core samples and stem discs collected from three tree species (*Juniperus procera*, *Olea europaea* subsp. *cuspidata*, and *Podocarpus falcatus*). Standard dendrochronological methods were used for data collection and analysis. Overall, across species and sites, significant mean radial growth differences were found. *P. falcatus* trees showed the highest mean annual radial growth (2.45 mm/year), while *O. europaea* trees showed slow growth rates, with average annual growth ranging between 1.6 mm in Desa'a and 2.0 mm in Hugumburda. The mean ring width of an individual *J. procera* tree ranged between 1.8 mm/year (in Desa'a site) and 2.3 mm/year (in Hugumburda site). Many trees of the sampled species exhibited more or less sigmoid growth curves. Age variation is mainly determined by the variation in passage time through the smaller diameter classes (juvenile classes). In general, the results obtained in this study have important implications for understanding growth dynamics of tropical dry Afromontane forests and for planning conservation and restoration activities. This study has to be supported by eco-physiological studies to further understand the responses of these and related main tree species to the varied environmental gradients to better explain the dynamics in relation to emerging environmental changes.

Keywords Dendrochronology · Dry Afromontane forest · Radial growth · Tree age

1 Background

Understanding the effect of environmental changes (climate change in particular) on forest dynamics requires knowledge of the drivers of individual tree growth over their lifetime [1, 2]. Such an information is crucial to understand the mechanisms underlying changes in tree biomass and make inferences about environmental controls of tree biomass, which in turn influences bio-geochemical cycles, climate, and biodiversity across local to global scales [1]. Nonetheless, it has been difficult to directly observe the

complete lifespan of individual tree species in the tropics using only the prospective studies (measurements on permanent sample plots). This hindered understanding of the long-term responses and feedback of tropical forests to global changes (including climate change) [2, 3].

Obviously, individual trees of different species show variations in their growth trajectories [4, 5]. This can be attributed to the varying eco-physiological characteristics of the tree species coexisting in a given forest ecosystem [6]. It is, therefore, valuable to have knowledge on age and radial growth patterns of dominant tree species across

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their lifespans to understand forest dynamics and facilitate sustainable forest management [7–9]. Besides, information on the occurrence and frequency of periods of releases and suppressions is vital to understand differences in life histories among species [10, 11].

Most often, yield predictions use estimates of average diameter growth rates in a given population, ignoring variations among individual trees. However, studies show that the existence of strong and persistent growth differences among individual trees substantially affects predictions of future timber yield [4, 11]. And, these studies proved that tree-ring analysis is a powerful alternative to the short-term (often less than 20 years) tree growth measurements from permanent sample plots. Tree-ring analysis has increasingly been used to obtain accurate age estimates and insights in lifetime growth trajectories of many tropical tree species [5, 7, 11] although its application in this regard was limited due to the assumption that tropical trees do not form distinct annual growth rings [12, 13]. Therefore, the application of tree-ring analysis in forest management issues is still not well developed in the tropics [4].

Despite the long-lasting arguments whether trees in tropical forests form annual growth rings, evidence over the past few decades has already shown the potential of tropical trees in dendrochronological research. This is particularly true in areas with some degree of seasonality in rainfall [13, 14]. The formation of annual growth rings has been proved for many tropical tree species [15–23], implying that tree-ring analysis can be used to study lifetime growth patterns and ages of tropical trees in a more reliable and direct way [11]. In general, tree-ring research provides a strong basis for determination of age and growth patterns of tree species and thus has valuable applications for forest ecology and sustainable management [23–25]. The long-term information that can only accurately be reconstructed from tree-ring records allows for better understanding of the dynamics of dry tropical forests [9]. In this study, tree rings were used to reconstruct lifetime growth patterns of selected trees from dry Afromontane forest fragments in northern Ethiopia. The presence of distinct annual growth rings in selected tree species from the same site has allowed the study on the growth history of the selected tree species during their lifespan [cf. 26]. Thus, the present study aims at determining the lifetime growth patterns and ages of selected tree species from the remnant dry Afromontane forests, with an overall implication of supporting the sustainable management of the forest remnants in the region. The study further examined the growth characteristics (radial growth dynamics) within and among the study species, and between different growing conditions (sites). The study attempted to address the following research questions: (1) Do the main tree species

from the dry Afromontane forests of northern Ethiopia show differences in growth patterns over their lifespan? (2) Are these variations also evident between sites? (3) Is there an occurrence of suppression and release events (periods) in the growth trajectories of individual trees? (4) Does the frequency of these events vary among species? (5) Which size class is more responsible for the variations in ages among the study species?

2 Materials and methods

2.1 Study area

The study was conducted in Desa'a and Hugumburda forests, the two major dry Afromontane forest remnants in northern Ethiopia (Fig. 1). These forests are mainly located along the western escarpment of the Great Rift Valley facing the Afar depression [27]. The area falls in the semi-arid agro-ecological zone of Tigray region, northern Ethiopia, where the climate is influenced by topography and exposures to rain-bearing winds [28].

The regional climate shows a distinct seasonality in rainfall with a unimodal pattern. The mean annual rainfall was estimated at 532 mm in Desa'a [29] and 981 mm in Hugumburda [27]. The core rainy season occurs between June and September, while the remaining extended periods are more or less dry (Fig. 2).

Large areas of these forests are characterized by shallow soils and frequent rock outcrops. The dominant soil types are Leptosols, Cambisols, Vertisols, Regosols, and Arenosols [27]. The study sites are generally characterized by rugged topography.

Desa'a and Hugumburda forests are broadly classified as dry Afromontane forests, mainly characterized by dry climate (with an annual rainfall of less than 1000 mm). These forests are dominated by drought-tolerant tree species, such as *Juniperus procera* (mainly in the canopy) and *Olea europaea* subsp. *cuspidata* (in the understorey) [27, 30]. Other co-occurring tree species include *Dodonaea viscosa* Jacq, *Maytenus senegalensis* (Lam.) Exell, *Carissa edulis*, and species of *Euclea*, *Rhamnus*, *Rhus*, *Mythenus*, and *Podocarpus* (*Afrocarpus*) [27, 30].

The dry Afromontane forest fragments in northern Ethiopia are generally among the most threatened habitats. The existing forest fragments in the region are already dwindling at an alarming rate due to the continued pressures emanating from natural and anthropogenic factors. Vegetation regeneration in the study region is limited by the lack of suitable microclimate and edaphic factors. Plant growth and survival are largely hindered by the nutrient-poor soils and the water-deficit conditions which extend for longer periods. Climate change (global warming)

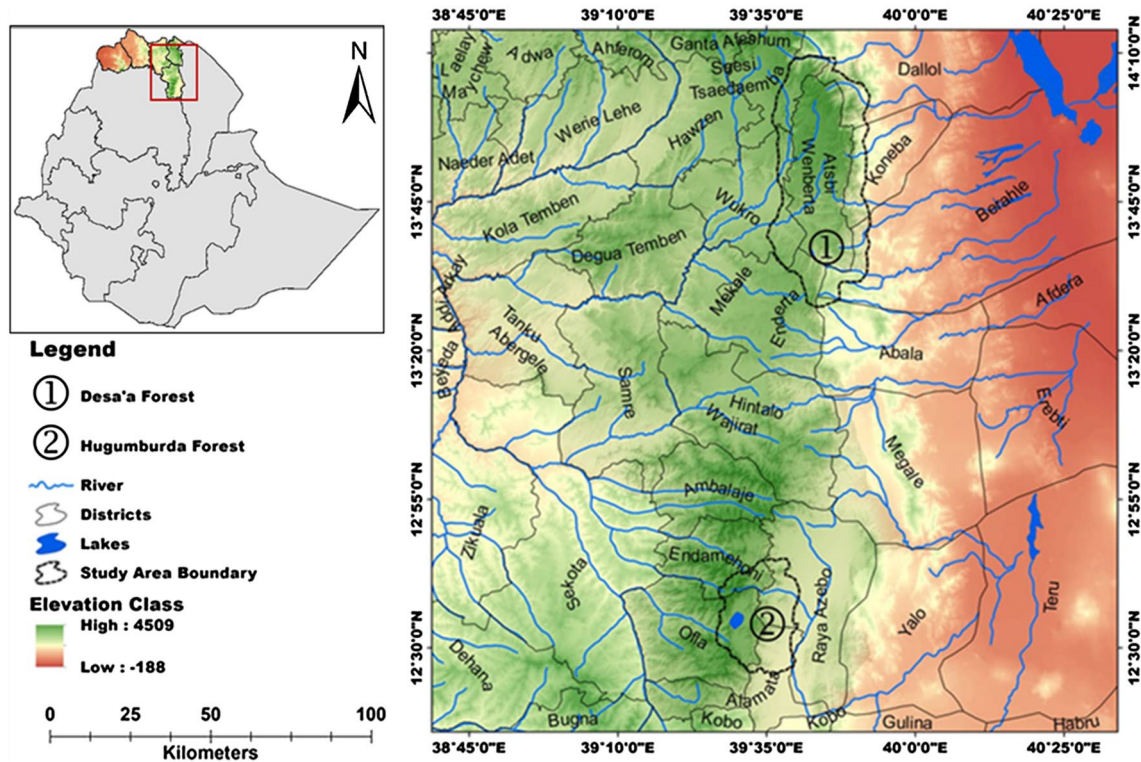


Fig. 1 Location of the study area

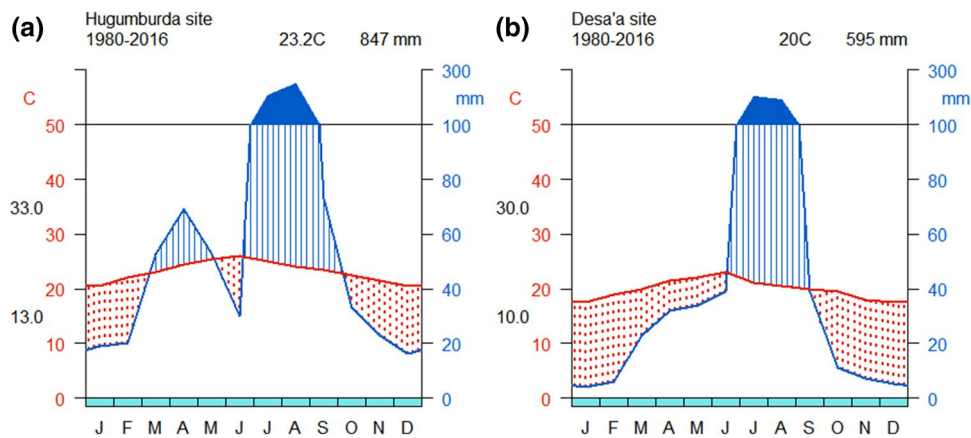


Fig. 2 Climate diagrams after Walter–Lieth Method for the two study sites: **a** Hugumburda and **b** Desa'a, in the dry Afromontane forest Remnants of northern Ethiopia. The blue line represents rainfall curve, and the red line represents temperature. Temperature and rainfall are scaled to 100 mm equivalence of 50 °C (ratio 1:2). This serves to mark months with arid (red dotted boxes) and humid (blue boxes) conditions. Monthly rainfall values above 100 mm are

shown in compressed forms. The average maximum temperature of the warmest month and the average minimum temperature of the coldest month are also indicated on the left side of each diagram for the two sites. The upper right corner of the diagrams shows annual averages of temperature and annual total rainfall for the two study sites

may also induce additional threats to the remnant tree population.

Although these remnant forests are included in the national forest priority area in Ethiopia, they are under

continued human-induced pressures. Illegal logging and free grazing are commonly practiced in these areas. In general, deforestation and habitat fragmentation attributed mainly to conversion to agricultural land use types

and overexploitation of the forest resources to satisfy food and energy demands of the ever-increasing population growth are among the major concerns seeking urgent management measures.

2.2 Sample collection and ring measurement

Samples (both cores and wood discs) were collected from two main species (*J. procera* and *O. europaea*) and one co-occurring species (*P. falcatus*) from two sites, namely Desa'a and Hugumburda, between April and June 2017. The samples were collected from a total of 106 trees belonging to the three species and considered different diameter classes (Table 1).

The cross-sectional wood discs were taken with a chain-saw, and increment cores were collected using an increment borer. Two increment cores were collected per tree from opposite directions at breast height (about 1.3 m from the base of all trees) from trees that have no sign of obvious rot and damage in the stem. In addition, diameter at breast height (DBH) of all sample trees was measured during the sampling.

The collected samples were carefully transported to and open air-dried at the wood-science laboratory of Wondo Genet College of Forestry and Natural Resources, Ethiopia. After air-drying, the cores and stem discs were sanded and polished progressively with sanding papers of grades ranging between 60 and 600 grits to improve the visibility of the growth ring boundaries and anatomical features [19, 31]. After sanding the stem discs, the growth rings were marked, counted, and measured in two to four radii and calculated annual diameter growth rates by averaging ring widths from those radii. Radii were chosen such that the average of the radii best corresponds to the calculated average diameter of the disc.

Ring widths were measured to the nearest 0.001 mm using LEICA MS 5 microscope coupled with LINTABTM5 digital measuring stage associated with TSAP-dos software [32]. Ring measurements were performed along the pre-determined radii in a straight line and perpendicular to ring boundaries. To ensure that each ring was assigned

to the correct calendar year of its formation, all series of a given tree species were crossdated and their quality was checked using the program COFECHA [33, 34]. Each tree-ring series was standardized using the dendrochronology program library in R programming language (dplR) [35, 36]. A cubic spline with a wavelength of 32 years and 50% cut-off was fitted to remove possible ontogenetic trends and low-frequency variation. Then, the growth patterns of the individual trees were analysed.

2.3 Assessment of growth trajectories and diameter–age relationships

Mean annual radial growth was calculated for each tree of the sampled species. Then, the lifetime growth trajectories per tree were established by summing the annual diameter growths [7, 11, 23]. The year of establishment of each sample tree was estimated by counting the number of rings from the outermost ring (near to the bark) to the inner ring (the pith) from the successfully dated series. For each study species, a regression model was fitted to relate tree size (DBH) to the estimated tree age [23]. Cumulative growth trajectories and mean annual radial increments derived from the tree-ring series can be used to estimate growth rates and growth variations in the entire lifespan of species [7, 11]. Accordingly, the general diameter–age relationship is represented by the cumulative growth curve (CGC). For this purpose, cumulative growth increments were established for the study species in relation to tree age for their complete lifetime. Annual diameter increment of each tree was calculated by averaging ring widths along the different radii and multiplying it by two and was used to reflect an approximate age–diameter relationship. The cumulative radial growth curves of each tree calculated over its lifetime were averaged to obtain mean growth curves for each species. However, it is worth mentioning that the ages presented here are calculated from the stem discs taken at the specified sampling height (ranging between 0.5 and 1.3 m), implying that the time required to grow from seedling to sampling height is not included. One-way analysis of variance (ANOVA) was used

Table 1 Study species and sample size in each study site

Study site	Species	Family	Sample distribution in each DBH class (cm)				Total class
			10–15	16–20	21–30	> 30	
Hugumburda	<i>Juniperus procera</i>	Cupressaceae	5	15	12	1	33
	<i>Olea europaea</i> (subsp. <i>cuspidata</i>)	Oleaceae	8	2	0	0	10
	<i>Podocarpus falcatus</i>	Podocarpaceae	6	5	3	4	18
Desa'a	<i>Juniperus procera</i>	Cupressaceae	2	14	12	4	32
	<i>Olea europea</i>	Oleaceae	0	7	5	1	13

to test if there is a significant difference in average radial growth rates among the study species. Besides, a two-way ANOVA was also used to compare growth rates between species and sites.

For all study species, the minimum, median, and maximum passage time (i.e. the number of years spent in a size class) was calculated through 10-cm-diameter classes. A Kruskal–Wallis test was used to test for differences between species in passage times in each size class. This enabled to identify size classes which are more important in determining the ages of the sampled trees [11].

2.4 Analysis of temporal growth patterns

The lifetime growth trajectories of individual trees were established to determine the differences in growth changes between different size classes. Then, percentage growth change (%GC) was calculated for each tree-ring series to test how the species differ in the way they grow to the canopy and to identify the potential growth responses to various disturbances and prolonged periods of suppression [11, 37]. A 10-year moving window was used to remove long-term age–size relations and the influence of short-term growth fluctuations associated with high variation in weather [38]. The per cent growth change for each year of the ring width series was calculated using the formula of [38] as:

$$\%GC_i = [(M_2 - M_1) / M_1] \times 100$$

where %GC_{*i*} is a percentage of growth change for year *i*, *M*₁ is mean annual diameter growth of the preceding 10-year period (including the year of change), and *M*₂ is mean annual diameter growth of the subsequent 10-year period. For instance, to obtain the %GC for the year 1972, *M*₁ was calculated as the mean growth rate over the period 1963–1972, and that of *M*₂ was calculated over the years 1973–1982.

For each species, the frequency of growth releases and suppressions were calculated based on criteria adapted from [38, 39]. Three levels of release thresholds were used: (1) major release (%GC ≥ 100%); (2) moderate release (%GC = 50–99%); and (3) minor release (%GC = 25–49%). The temporal growth patterns of the species were also compared using the number of consecutive years of slow and fast growth. To identify subsequent periods of slow and fast growth, species-specific radial growth threshold values were established from all ring width measurements of each species following the approach of [10]. Accordingly, the threshold values for slow and fast growth were calculated as the 25th and 75th percentile ring widths, respectively. Median and maximum of consecutive periods of slow and fast growth

were determined for each study species and were used as an indicator of the ability of species to survive periods of suppressed growth [40, 41]. Fast growth years are defined as years in which a tree is growing above a species-specific growth threshold (75th percentile growth rates), whereas slow growth years are defined as years in which a tree is growing below a species-specific growth threshold (25th percentile growth rates). A Kruskal–Wallis test was used to compare the median periods of fast and slow growth among the study species. R software (mainly in R commander) was used for all the statistical data analyses. Results are statistically significant at *p* < 0.05 unless stated otherwise.

3 Results

3.1 Results of tree-ring analysis

The results showed that all the sampled tree species form distinct growth boundaries; they were clear enough for marking, counting, and measuring. The study confirmed the formation of annual growth rings through successful crossdating and by correlating the growth rings with rainfall [cf. 26]. For each sampled species, a standardized tree-ring chronology was created using the dendrochronology program library in R programming language (dplR). The longest tree chronology, spanning from 1888 to 2016, was observed for *O. europaea* from Desa'a site, followed by that of *J. procera* from the same site which covered from 1905 to 2016. In Hugumburda site, however, the chronologies were relatively short due to the difficulties encountered to access very old trees, particularly for *O. europaea* and *P. falcatus* trees. The tree-ring chronologies of all the sampled species showed high year-to-year variability and common environmental signal as clearly indicated by the high values of mean sensitivity (0.43–0.63), standard deviation (0.59–0.66), series intercorrelation (0.51–0.57), and low values of average autocorrelation (0.04–0.20). The EPS (Expressed Population Signal) value for the study species ranged between 0.87 (*O. europaea*) and 0.93 (*J. procera*). This is indicative of the quality of crossdating among the tree-ring series, and there is a common environmental signal which drives tree growth in the region. Ring width of the studied tree species significantly correlated with rainfall: *J. procera* (*r* = 0.59, *p* < 0.001), *O. europaea* (*r* = 0.34, *p* < 0.05), and *P. falcatus* (*r* = 0.52, *p* < 0.001) from Hugumburda, and *J. procera* (*r* = 0.36, *p* < 0.05) and *O. europaea* (*r* = 0.35, *p* < 0.05) from Desa'a site. The results highlight the potential applicability of tree-ring analysis for reconstructing long-term growth patterns and ages of tree species from the study region.

Table 2 Summary of annual growth increment of the study species in each study site

Study site	Species	N	Age range (years)	DBH (cm)	Annual radial increment (mm)		
					Mean	Maximum	Minimum
Hugumburda	<i>J. procera</i>	33	23–65	12–42	2.31 ± 0.54	16.29 ± 3.01	0.25 ± 0.17
	<i>O. europaea</i>	10	28–47	10–19	2.01 ± 0.36	7.82 ± 1.55	0.36 ± 0.14
	<i>P. falcatus</i>	18	20–54	11–39	2.45 ± 0.58	12.75 ± 2.13	0.39 ± 0.24
Desa'a	<i>J. procera</i>	32	32–112	14–50	1.83 ± 0.57	12.68 ± 2.60	0.15 ± 0.18
	<i>O. europaea</i>	13	48–129	16–35	1.61 ± 0.20	6.44 ± 0.80	0.41 ± 0.09

N number of successfully dated series, DBH diameter at breast height (ranges), annual radial increment (mean, maximum and minimum) with standard deviations calculated from successfully crossdated tree-ring measurements

3.2 Radial growth rates

We estimated mean radial growth rates and ages of the study species using tree-ring analysis. The descriptive statistics associated with radial growth rates and ages of the study species across two different growing sites is presented in Table 2.

Considerable variations were found in ages and ring widths among the studied tree species across spatial and temporal scales. With an average ring width of 2.45 mm/year [95% CI, (2.21, 2.69)], *P. falcatus* trees showed the highest growth rate. The average ring width of an individual *J. procera* tree ranged between 1.83 mm/year [95% CI, (1.69, 2.06)] in Desa'a and 2.31 mm/year in Hugumburda [95% CI, (2.16, 2.52)]. *O. europaea* trees showed a relatively narrower ring width ranging between 0.36 and 7.82 with overall means of 1.61 mm/year [95% CI, (1.33, 1.90)] in Desa'a site and 2 mm/year [95% CI, (1.70, 2.35)] in Hugumburda site (Table 2). Of the studied tree species, *O. europaea* from Desa'a site had the longest lifespans (129 years), which were estimated at the sampling height, followed by *J. procera* (with 112 years). For *P. falcatus*, the sampled trees reached an age of 54 years (Table 2).

3.3 Comparison of radial growth rates

3.3.1 Radial growth within species

We used a one-way analysis of variance (ANOVA) to test whether there is difference in average radial growth among the sampled trees of each species in both sites. The results from the ANOVA model are presented in Table 3.

As shown in Table 3, significant differences were found among the sampled trees of each species ($p < 0.001$) in both study sites.

3.3.2 Radial growth among species

As illustrated in Fig. 3 (cf. Table 2), radial growth rates varied among species in both sites. *P. falcatus* trees showed

Table 3 Results from the generalized linear model (one-way ANOVA) showing the differences in mean radial growth among sampled trees of each study species in Hugumburda and Desa'a sites, northern Ethiopia

Species	Study site	df	F value	p value
<i>J. procera</i>	Hugumburda	32/1374	4.673	4.6×10^{-16}
	Desa'a	31/1700	10.27	2×10^{-16}
<i>O. europaea</i>	Hugumburda	9/348	3.724	1.76×10^{-4}
	Desa'a	12/980	4.879	7.41×10^{-8}
<i>P. falcatus</i>	Hugumburda	17/618	6.402	4.8×10^{-14}

df degrees of freedom; differences were tested with one-way ANOVA

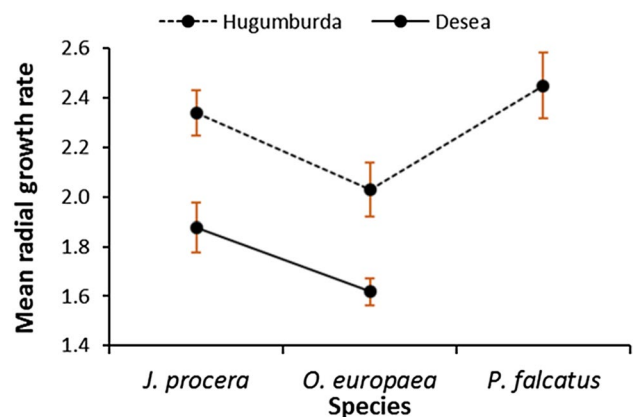


Fig. 3 Mean radial growth rates of the study species by study site

higher radial growth rates relative to the other tree species. On the other hand, *O. europaea* trees in Desa'a showed the narrowest ring width, reflecting its slow radial growth relative to the other species. In order to confirm the hypothesis that growth rates differed among tree species sampled from both sites, a two-way ANOVA was performed. Three species sampled from two different sites were considered in this analysis. The results showed statistically significant differences in radial

growth rates among the studied tree species (ANOVA, $F(2,101) = 3.258$, $p < 0.05$). To further evaluate the nature of the differences between the means, Fisher's LSD post hoc tests were undertaken. Results of the pair-wise comparisons showed statistically significant mean differences (at $p < 0.05$) among all the study species.

The relationships of ring width series among the study species in a given site were also evaluated (Fig. 4). The sampled trees in Hugumburda site showed better matches in annual variation in radial growth patterns, which can be explained in the higher correlations (ranging between 40 and 60%) among each other, while those in Desa'a site showed weaker correlations. Overall, the correlations among the established tree-ring chronologies for the common periods were not strong enough to be merged together to develop a common site-specific chronology. This suggests that the habitats in these dry Afromontane forest fragments are heterogeneous.

3.3.3 Radial growth between sites

Tree species which are commonly found in both sites were used to examine if radial growth rates of the study species differ between the study sites. It can be seen that tree species sampled from Hugumburda site showed higher mean radial growth rates compared to those from Desa'a site (Figs. 3, 5). A two-way ANOVA was employed using

tree species and site as independent variables. The site comparisons showed that growth rates of the studied tree species were significantly different between the two study sites (ANOVA, $F(1,101) = 11.965$, $p < 0.001$).

Overall, the comparisons of ring width series of the common tree species in both sites (*J. procera* and *O. europaea*) showed weaker correlations between the tree species. On the other hand, the fact that the detrended ring widths (ring width indices—RWI) of all the study species in each site were crossdatable reflects a common environmental forcing of growth patterns of the tree species. This has already been explained using the higher values of inter-serial correlation coefficients obtained in each site. The average inter-serial correlation coefficients ranged from 0.48 to 0.56 in Desa'a and 0.42 to 0.59 in Hugumburda for *J. procera*; 0.53 to 0.57 in Desa'a and 0.46 to 0.59 in Hugumburda for *O. europaea*; and 0.49 to 0.56 for *P. falcatus* in Hugumburda. This is indicative of the quality of crossdating among the tree-ring series.

3.4 Age–diameter relationships and growth trajectories

3.4.1 Age–diameter relationships

A simple linear regression model was used to determine the relationships between tree ages and stem diameters

Fig. 4 Comparisons of the ring widths among the study species from the remnant dry Afromontane forests in Hugumburda (a) and Desa'a (b) sites, northern Ethiopia

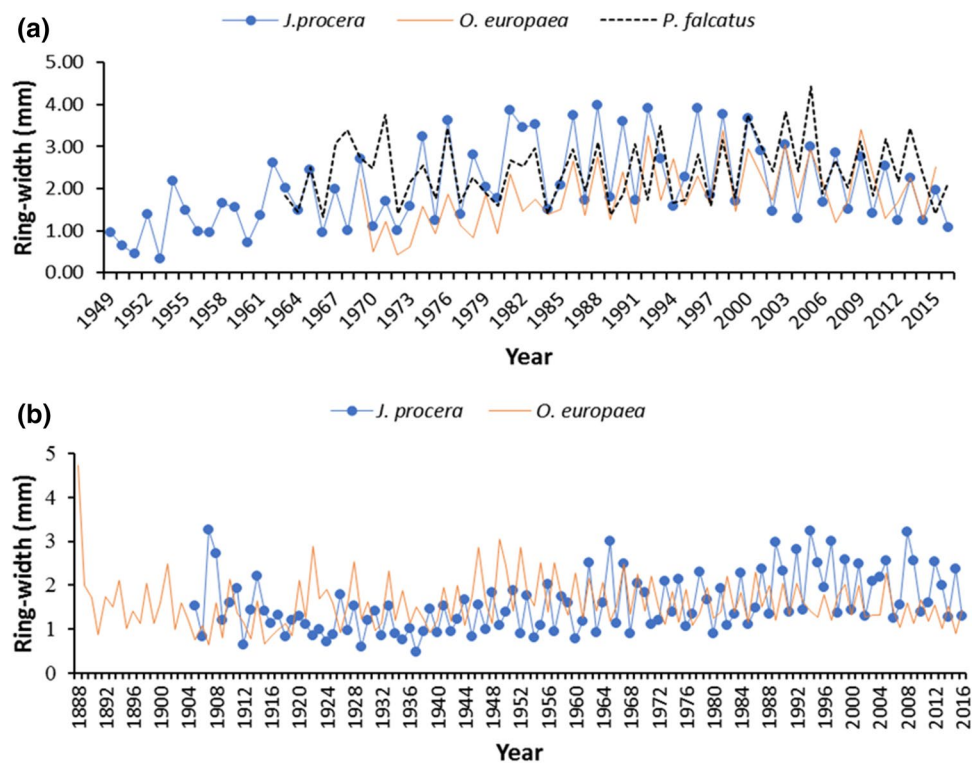
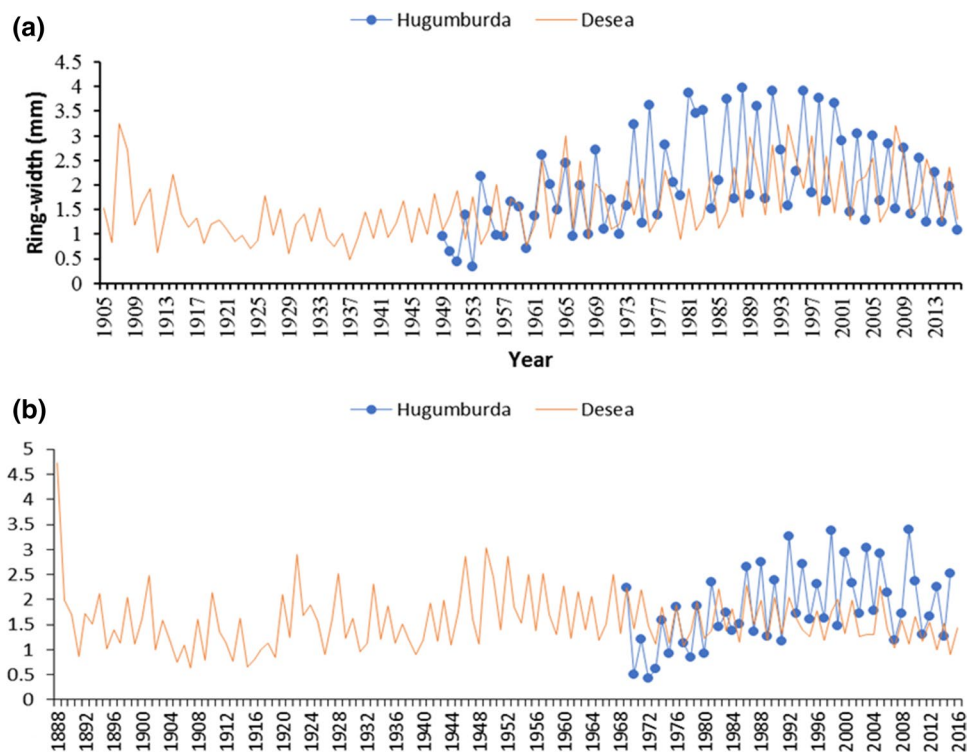


Fig. 5 Comparisons of the ring widths of *J. procera* (a) and *O. europaea* (b) between study sites, Hugumburda and Desa'a, from remnant dry Afromontane forests, northern Ethiopia



(DBH) for the study species. The established relationships and their statistical significance are presented in Fig. 6.

Results of the age–diameter relationships showed that age and stem diameter of all studied tree species were significantly related, implying that diameter increases with tree age. However, considerable variations were observed among the study species.

3.4.2 Cumulative growth increments

Large variability was observed in mean diameter increment (MDI) among the study species and between sites. The MDI was higher for *P. falcatus* (with an estimated value of 0.49 ± 0.11), followed by *J. procera*. A relatively lower MDI rates were observed for *O. europaea*. This variability was also evident between the study sites, with higher values observed in Hugumburda (Fig. 7).

Cumulative growth curves (CGC) were also constructed using the tree-ring width data of all sample trees accumulated from the innermost ring (pith) to the outermost ring (right before the bark). The individual ring width measurements from the different radii were doubled and accumulated to approximate the increment in total stem diameter for the study species. The growth curves and overall mean growth curves of the study species are presented in Figs. 8 and 9, respectively. It can be observed from the cumulative growth curves that mean annual increment increases with stem diameter until it reaches the maximum size class beyond which the increments start to decline.

In general, the lifetime growth trajectories varied among species and within species (Figs. 8, 9). As it is shown in the CGC, all the studied tree species showed comparable general growth trends at the initial stages (the juvenile phase) and appear to vary considerably in the later stages. The effect of site conditions on the growth patterns of the species is also vividly observed, where the growth rates of the tree species from Hugumburda remained higher over longer periods of time.

In all the studied species, many trees exhibited more or less sigmoid growth curves, i.e. a relatively slow initial growth rates that gradually increased at intermediate ages, decreasing again slightly for older trees. Considerable variations were observed in age–size relations of the study species across the two study sites, with increased age differences at larger diameters than at smaller diameters (Fig. 9).

3.4.3 Passage time and its implications

For all study species, the passage time (minimum, median, and maximum) was compared through 10-cm-diameter classes using the nonparametric Kruskal–Wallis test. In all cases, except for *O. europaea* from Desa'a site, significant differences were found in passage time in each of the size categories (Kruskal–Wallis tests, $p < 0.001$).

The highest median passage time was observed in the size class of 0 to 10 cm in diameter and decreased in

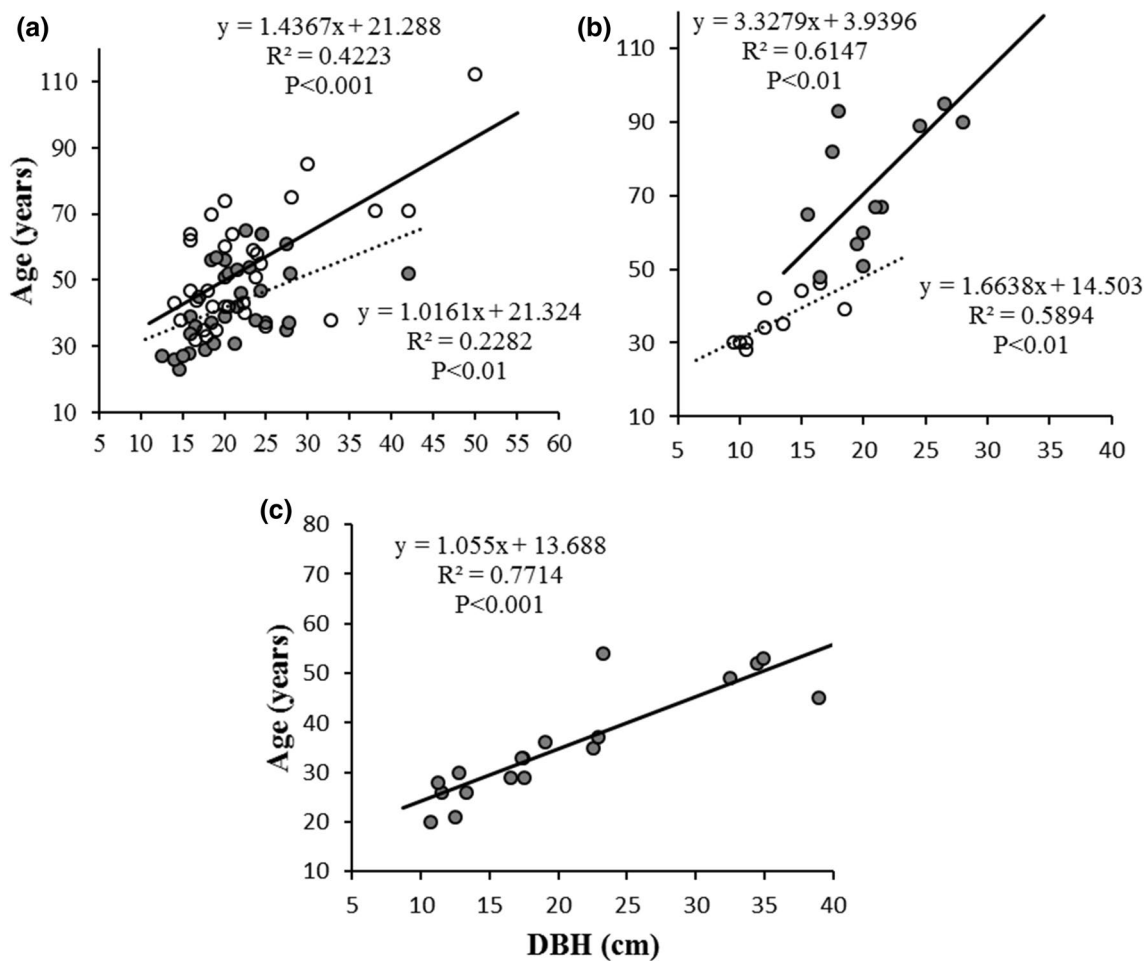


Fig. 6 Scatter diagram of relationships between stem diameter (DBH) and estimated tree age of the study species, *J. procera* (a), *O. europaea* (b), and *P. falcatus* (c), in Hugumburda (filled circles) and

Desa'a (open circles); regression fitted lines are indicated by continuous lines (Hugumburda) and dotted lines (Desa'a)

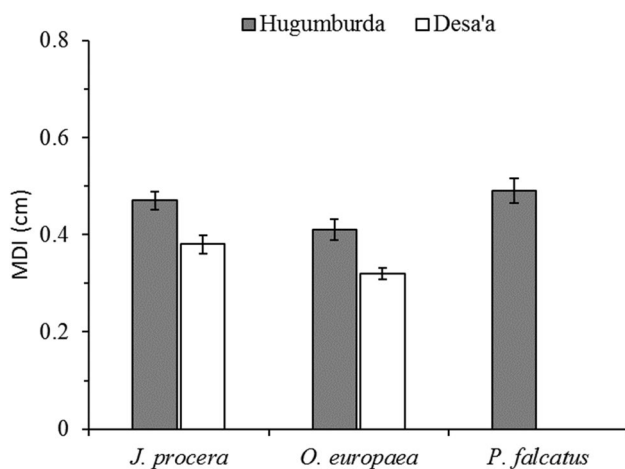


Fig. 7 Mean annual diameter increment (MDI) of the sampled species in each study site: Hugumburda and Desa'a, northern Ethiopia

subsequent size classes (Fig. 10). In general, large differences were found between the minimum passage time and maximum passage time for all the study species. The differences were larger at the first size class and decreased in the subsequent larger size classes in all species. These results indicate that the smaller size classes are more important in determining the ages of large trees.

3.5 Temporal growth patterns

The temporal growth patterns of individual trees of the main species in remnant dry Afromontane forests in northern Ethiopia were analysed to determine their lifetime growth dynamics. Percentage growth changes were calculated applying a decadal moving average to detect abrupt growth variations among the study species. Greater negative or positive values of the percentage growth changes (PGC) were used to indicate a suppression or

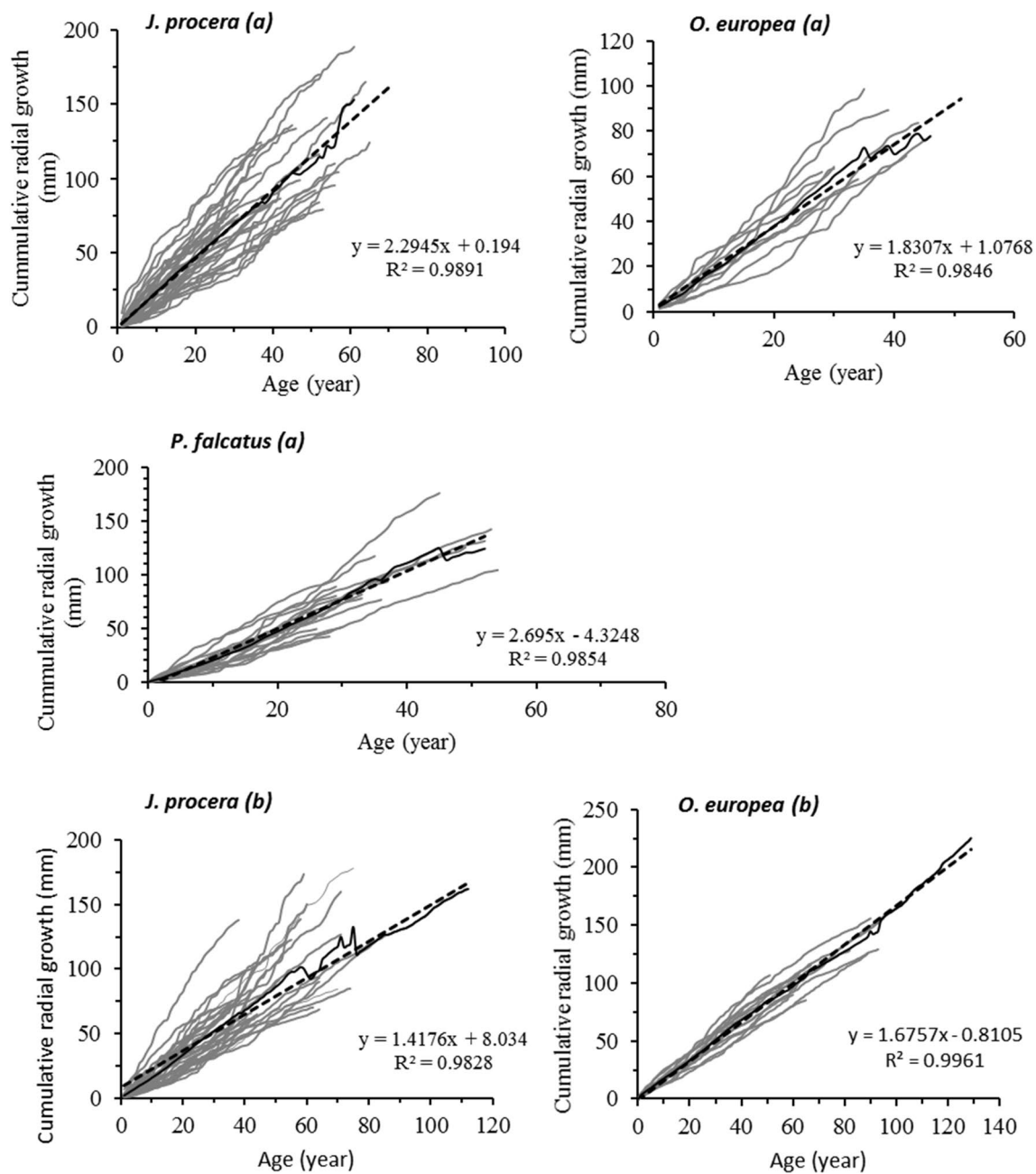


Fig. 8 Cumulative radial growth in relation to tree age for the study species in **a** Hugumburda and **b** Desa'a sites; each line (grey lines) represents an individual tree. The black line and dashed lines indi-

cate average cumulative radial growth and regression (prediction) line, respectively

release periods, which are more likely associated with various disturbance events. In all study species, release and suppression periods were observed in their lifespans, with PGC values ranging from 25% (minor) to more than 100% (major) (Table 4).

The distribution of the mean frequency of release and suppression events for each species is also shown in Fig. 11.

The study species also showed variations in terms of the occurrence of release and suppression events (Fig. 11). No systematic synchronicity was observed in the onset of suppression period and the time of release from the suppression across the studied trees. In all the study species, no major suppression event was found, i.e. the majority of the suppression events were minor. However, a varying degree of release periods was observed across species and sites. While no major release event was found for



Fig. 9 Mean cumulative stem diameter growth curves of the study species from the remnant dry Afromontane forests in Hugumburda (a) and Desa'a (b), northern Ethiopia; averages at a certain tree age were calculated only if at least ten trees of a species which reached that age were included

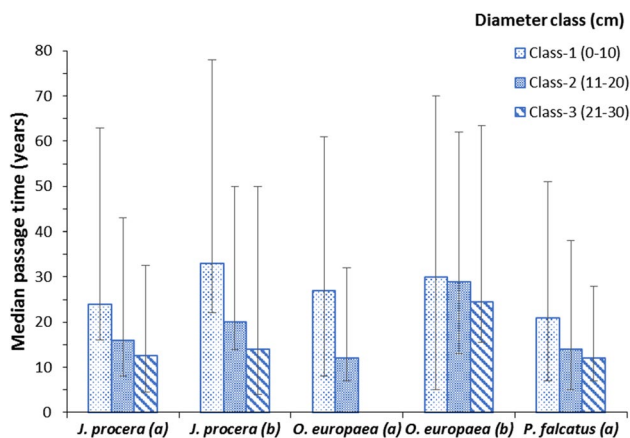


Fig. 10 Median passage time through 10-cm-diameter classes for the study species from remnant dry Afromontane forests in Hugumburda (a) and Desa'a (b) sites, northern Ethiopia; error bars represent differences between maximum passage time and minimum passage time. Sample sizes vary from 5 to 33 trees per class. Passage time differed ($p < 0.001$) between species in each of the size categories (Kruskal–Wallis tests)

O. europaea from Desa'a site, differing frequency of major release periods was observed for the other species.

Besides, the growth patterns of the species were compared in terms of the number of consecutive years of slow and fast growth. To identify subsequent periods of slow and fast growth, species-specific radial growth threshold values were established from all ring width measurements of each species (Table 5). Accordingly, the median and maximum duration of slow and fast growth periods were determined for each study species.

There was no statistically significant difference among the median length of consecutive years of slow growth

(Kruskal–Wallis Chi-squared = 5.65; $df = 4$, p value = 0.227). However, the tree species from Desa'a site had a relatively fewer median period of slow growth when compared to those from Hugumburda site. In the same vein, comparison of periods of fast growth among the study species showed no significant differences in the length of consecutive years of fast growth (Kruskal–Wallis Chi-squared = 6.06, $df = 4$, p value = 0.195). Figure 12 also shows that the number of consecutive years of fast growth was comparable in all the study species.

4 Discussion

Understanding the effect of environmental changes on forest dynamics demands consideration of the drivers of individual tree growth over their lifetime [1]. It has been difficult to directly observe the complete lifespan of individual tree species in the tropics using only prospective studies (measurements on permanent plots). Alternatively, tree-ring analysis yields direct annual growth data over the entire lifetime of individual trees (i.e. through retrospective growth measurements) and therefore produces more accurate data than the extrapolations from the short-term growth data by repeated diameter measurements from permanent sample plots (prospective growth measurements) [11]. However, examination of the historical dynamics of tropical tree species has been constrained by the presumptions that tropical trees lack distinct annual growth rings [12, 13]. The existence of only a few long-term datasets from tropical forests hindered the development of models of forest dynamics at longer temporal scales. As a result, we have relied heavily on forest models developed in the temperate regions [10]. Nowadays, however, tree-ring analysis is widely being used in studying long-term growth performances and recruitment dynamics of individual tropical tree species which form annual growth rings [17, 19, 22, 42, 43]. In this study, dendrochronological techniques were employed to unravel the long-term growth patterns and age–size relations of individual tree species from the dry Afromontane forest fragments in northern Ethiopia.

4.1 Radial growth

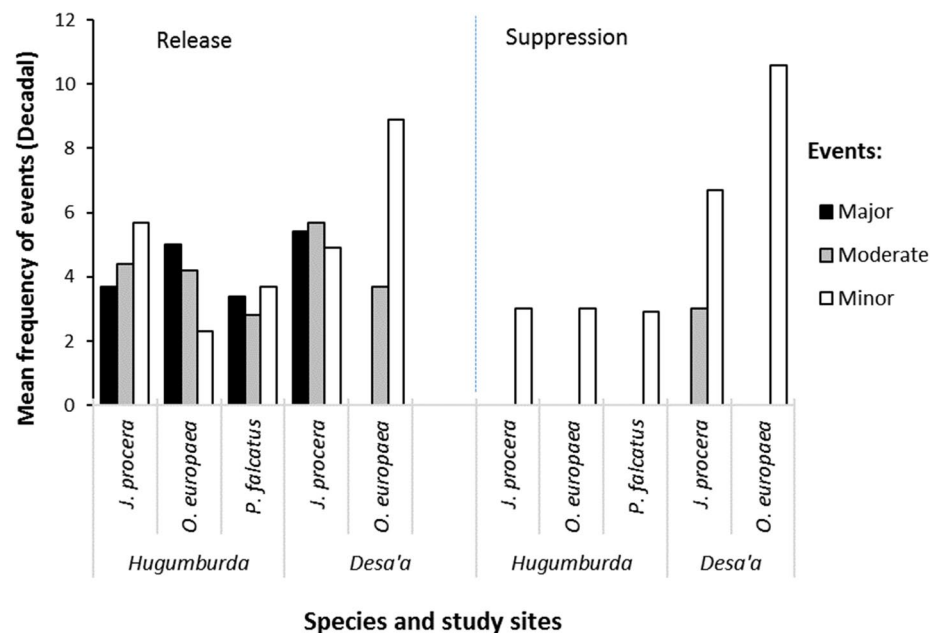
Across species and sites, significant mean radial growth differences were found. In all cases, the average ring widths, which express mean growth rates of the trees, varied considerably between years ranging from 0.15 to 16.29 mm for *J. procera*, 0.36 to 7.82 mm for *O. europaea*, and 0.39 to 12.75 mm for *P. falcatus*. Overall, *P. falcatus* trees showed the highest mean annual radial growth (2.45 mm/year), while *O. europaea* trees showed

Table 4 Frequency of release and suppression periods for the study species

Study site	Species	No. of %GC fluxes [and percentage of trees]		
		Major (%GC ≥ 100)	Moderate (%GC = 50–99%)	Minor (%GC = 25–49%)
Hugumburda	<i>J. procera</i> (N=33)			
	Release	57 [30%]	66 [45%]	57 [48%]
	Suppression	–	27 [27%]	187 [97%]
	<i>O. europaea</i> (N=10)			
	Release	15 [30%]	21 [50%]	16 [70%]
	Suppression	–	–	24 [80%]
Desa'a	<i>J. Procera</i> (N=32)			
	Release	92 [53%]	149 [81%]	134 [84%]
	Suppression	–	24 [25%]	195 [91%]
	<i>O. europaea</i> (N=13)			
	Releases	–	26 [55%]	107 [92%]
	Suppression	–	–	127 [92%]

Release (positive growth) and suppression (negative growth) periods are based on percentage growth changes calculated applying a running mean window of ten consecutive years (a decadal moving average). Three levels of release thresholds were used: (1) major release (%GC ≥ 100); (2) moderate release (%GC = 50–99%); and (3) minor release (%GC = 25–49%)

Fig. 11 Frequency of release and suppression events for each study species



slow growth rates, with average annual growth ranging between 1.6 mm in Desa'a and 2 mm in Hugumburda. The mean ring width of an individual *J. procera* tree ranged between 1.83 mm/year (in Desa'a site) and 2.31 mm/year (in Hugumburda site). Comparable average annual radial growth rates were reported for various tree species growing in the dry forests and woodlands of Ethiopia. For instance, [20] reported an average annual

radial growth rate of 1.81–2.53 mm for three deciduous acacia species and a co-occurring evergreen *B. aegyptiaca* growing in the dry land area of the central Rift Valley of Ethiopia. The mean annual radial growth rates of *J. procera* reported elsewhere showed considerable variations, ranging between 1.5 and 4.0 mm [21, 44–47]. Similar mean annual radial growth rates were also reported for various other tree species from elsewhere: 2.5 mm

Table 5 Species-specific radial growth thresholds (mm/year) for identifying the number of consecutive periods of slow and fast growth

Site	Species	Slow growth threshold	Fast growth threshold	Longest run of slow growth	Longest run of fast growth
Hugumburda	<i>J. procera</i>	1.08	3.00	3	6
	<i>O. europaea</i>	1.15	2.66	6	7
	<i>P. falcatus</i>	1.44	3.12	6	10
Desa'a	<i>J. procera</i>	0.93	2.30	13	14
	<i>O. europaea</i>	1.09	1.96	8	5

The threshold values for slow and fast growth were calculated as the 25th and 75th percentile ring widths, respectively, from all ring width measurements obtained for each species. The maximum periods (longest run) of fast and slow growth are the number of years in which radial growth was above (fast) or below (slow) the threshold value

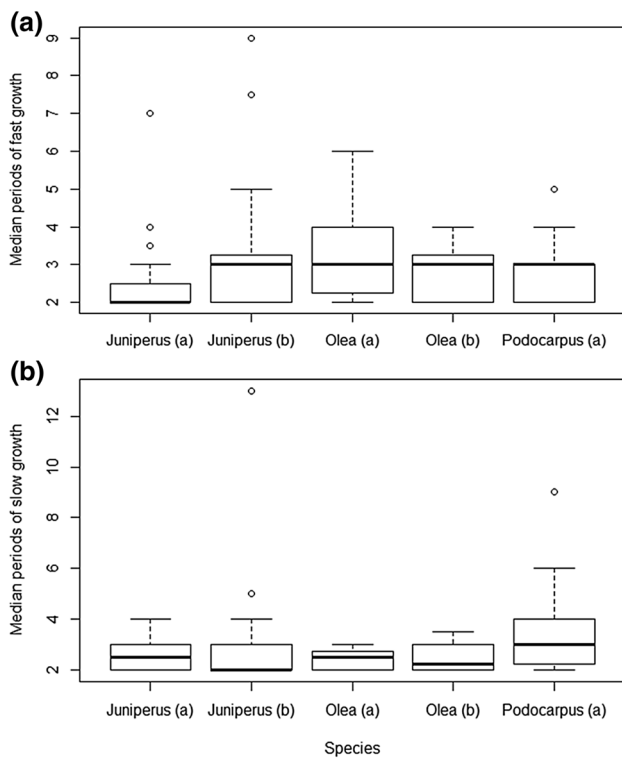


Fig. 12 Median periods of sequential years of slow and fast growth for the study species. Fast growth years (a) are defined as years in which a tree is growing above a species-specific growth threshold (75th percentile growth rates based on all the tree rings measured for each species). Slow growth years (b) are defined as years in which a tree is growing below a species-specific growth threshold (25th percentile growth rates based on all the tree rings measured for each species). Threshold values for slow and fast growth are given in Table 5. The boxes represent percentiles of the data (lower and upper box boundaries are 25th and 75th percentiles, respectively; the line in the box is the median value (50th percentile); the points above the boxes represent outliers)

for *B. neglecta* from the woodlands in southern Ethiopia [25], 1.5–2 mm for *Pterocarpus angolensis* from Miombo woodland of Zimbabwe [48], 1.75 mm for *P. angolensis* from Mozambique [42] and 1.9 mm from semi-deciduous

forest of Cameroon [17], and 1.05–1.88 mm for *Brachystegia spiciformis* from the Miombo woodland in south-central Africa [49]. Others reported much higher (e.g. 9.34 mm for *F. albida* from Malawi [50] and lower (e.g. 1.15 mm for *B. papyrifera* from the north-western woodlands of Ethiopia [23]) values of mean annual radial growth rates for many tropical tree species.

Such variations depict the fact that the growth behaviour of individual trees is not only sensitive to the amounts and distribution of rainfall but also is responsive to the extremely heterogeneous ecological conditions of the study sites and to the ontogenetic differences among species (e.g. the species-specific water use mechanisms and age-related effects). According to [51], the growth performance of tree species may partly be explained in relation to their water use strategies; some species are drought sensitive (drought avoiders), while others are drought tolerant. Accordingly, the avoidance mechanism and opportunistic use of water by the drought-sensitive plants may partially explain their growth reduction during drought years and enhance growth performances during moist years. On the other hand, the drought-tolerant species are conservative water users, and this is consistent with their lower growth performances in moist years compared to the former species [51]. During drought years, drought-sensitive species show reduced growth compared to drought-tolerant species but show enhanced growth during moist years.

In line with this study, previous studies elsewhere in Ethiopia witnessed huge variations in mean radial growth rates among individual *J. procera* trees and attributed it to differences in stand-level conditions (even within small-scale site conditions), including soil conditions (or water holding capacities) and tree-to-tree differences [21, 45, 47]. It was also reported that such between-site differences in radial growth rates of individual trees resulted from variability in rainfall distribution [21, 44]. Other similar studies from elsewhere in Africa, for instance for *Pterocarpus angolensis* D.C. from Southern Africa (Botswana, Mozambique, South Africa, Zambia, and Zimbabwe) [42], and for

various tree species from Cameroon [17], concluded that stand-level conditions are important in determining mean ring widths. In the present study, the considerable variations in individual tree-ring widths of all species around their respective means (which is presented by the standard deviations) were generally higher for the study sites, indicating the ecological heterogeneity of the study sites. Thus, in addition to its sensitivity to the overriding climatic factor (rainfall), tree growth tends to be determined by stand-level conditions in our study areas.

4.2 Lifetime growth trajectories and ages

In this study, the age–size relationships showed considerable variability among the study species. This finding is in agreement with several other studies [14, 17], which reported large variations in age–size relations among several tropical tree species. Although considerable variations were noted among the study species and across sites, this finding, generally, showed significant age–diameter relationships, which implies that diameter increases with tree age. Despite the strong correlation between the two variables, it is difficult to conclude that the largest tree in a population is necessarily the oldest tree. In line with this, other authors [17, 52] also found that trees of the same age could have a huge difference in their diameter or trees with similar diameter could significantly differ in their age. Such differences occur probably due to the high variation in growth rates among the individual trees as shown in the results of this study. This is typical of many tree species growing in tropical areas which are characterized by high variability in microsites, leading to varying growth rates among individual trees [17]. The observed variations in age–diameter relations suggest its instability and thus should be used cautiously as the diameter may not reflect the true age of a tree [53]. Previously, it has been suggested that there is a need to have additional information about the tree growth condition to obtain a reliable estimates of tree age [17, 54, 55].

As shown in the CGC (Figs. 8, 9), all sample trees of the study species showed comparable growth trends at the initial stages (the juvenile phase) and appear to vary considerably in the later stages. The effect of site conditions on the growth patterns of the species is also vividly observed, where the growth rates of the tree species from Hugumburda remained higher over longer periods of time than those of Desa'a site. In all the studied species, many trees exhibited sigmoid growth curves, i.e. a relatively slow initial growth rates that gradually increased at intermediate ages, decreasing again slightly for older trees.

To further analyse the lifetime growth dynamics of the species, the temporal growth changes were evaluated by calculating relative growth changes. The percentage

growth changes were calculated applying a decadal moving average and enabled us to detect release and suppression events. It was expected that the frequency and duration of release and suppression events would be synchronous among the study species. Results of the study showed evidence of release and suppression periods, varying from minor (%GC = 25–49%) to major (%GC ≥ 100%) events. In all species, minor and moderate release/suppression events were apparent, while major events were fewer. Even though variations were noted among species and between sites in regard to the median periods of slow and fast growth, the differences were not statistically significant (Kruskal–Wallis tests). In general, similar runs of slow and fast growth were found among the study species. This finding is similar to that reported by [10], who did not find major differences in the numbers of release/suppression events and in runs of slow and fast growth among five tree species from a seasonal tropical forest. The existence of a greater number of minor and moderate release/suppression events may be attributed to the varying intensities of disturbance factors across spatial and temporal horizons. Earlier studies have shown that the remnant dry Afromontane forests in northern Ethiopia have been shaped by such varying magnitude of disturbance factors [27, 56, 57].

In agreement with [10], it was argued that such disturbance factors may have shaped the growth dynamics of dry Afromontane forest species but are considered as 'noises' compared to the overriding climatic signal. In this study, no strong evidence was found that supports the claim that shade-intolerant tree species have longer runs of fast growth and shorter runs of slow growth than shade-tolerant tree species as reported by most studies of tropical forest growth dynamics [58, 59]. Following the approaches of [10], the study used the species-specific radial growth threshold values to compare growth patterns and to quantify release and suppression events. Using a community-based threshold value biases towards slow growth (due to the expected numerical dominance of small trees) thus provides little information on suppression and release events/patterns of fast-growing, shade-intolerant species [10]. Besides, it has been reported that species-specific threshold allows comparison of an individual's annual growth with the diameter growth potential for that species [60].

As shown in Table 6, more than 60% of the annual growth rings of all the study species were neither narrower nor wider than the specified species-specific threshold values of each species. For instance, 20% of the annual growth rings of *J. procera* from Desa'a site were narrower than the specific threshold size of 0.93 mm, while 16% of the annual growth rings were wider than the threshold size of 2.30 mm. The widths of the remaining growth rings

Table 6 Overall percentage of annual growth rings below or above the stated species-specific thresholds for slow and fast growth, respectively, for the study species

Study site	Species	Percentage of annual growth rings	
		Narrower than slow growth threshold	Wider than fast growth threshold
Hugumburda	<i>J. procera</i>	16	18
	<i>O. europaea</i>	15	17
	<i>P. falcatus</i>	7	20
Desa'a	<i>J. procera</i>	20	16
	<i>O. europaea</i>	16	24

Threshold values for slow and fast growth are given in Table 5

(about 64%) were between these two threshold values (between 0.93 and 2.30 mm). This confirms a sustained slow growth pattern of the studied tree species. In general, the considerable differences in tree growth trajectories reflect variation in growing conditions.

5 Conclusions

In this study, tree-ring analysis was employed to reconstruct the lifetime growth patterns of main tree species from dry Afromontane forest fragments in northern Ethiopia, with an overall implication of supporting the sustainable management of the forest remnants in the region. The dry Afromontane forest fragments in northern Ethiopia are among the most threatened habitats. Therefore, understanding the long-term growth dynamics of dominant tree species in the face of the changing climate is important for devising sustainable management options for the remnant resources (threatened species). This study examined the suitability of the dominant tree species for dendrochronological studies and quantified the long-term growth trajectories of the main tree species. The study demonstrated significant variations in annual radial growth rates within and among the different tree species, and between sites. Results of the study also suggest that the effect induced by climate change is species specific and also appears to be affected by different growing conditions. Overall, this study confirms the potential of tree-ring analysis in studying tropical forest dynamics and recruitment histories of individual tree species. Nevertheless, further research is required to properly understand the dynamics of the dry Afromontane forest remnants. In view of this, it is suggested that future work should address physiological plant responses to various edaphic factors, e.g. nutrient uptake, different levels of soil microbial activity, and the long-term

role of both processes in the establishment of tree seedlings in the forest remnants.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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