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Leaf phenology and vegetation period of European beech (*Fagus sylvatica* L.) forests in Bulgaria

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Abstract

This study investigates variations of two main phenological events of European beech (*Fagus sylvatica* L.) across geographical gradients in its range in Bulgaria between 2017 and 2023. We found that altitude is the primary driver of leaf unfolding date, which is delayed by approximately 2.52 days per 100 m of elevation gain. In contrast, leaf colouring date is less influenced by altitude and more strongly driven by latitude, with a delay of about 2.12 days per degree northward. Leaf colouring date appeared more abrupt and latitude-dependent, likely due to regional climate differences in separate mountains. A modest influence of longitude on phenology was also detected, possibly linked to changes in continental climatic conditions in the west-east direction. These findings contribute to understanding how complex of geographic gradients shape the timing of phenological events and duration of vegetation period in European beech under the current climate in Bulgaria. They could be used as a basis for impact forecasting of future climate scenarios in the south-eastern part of the distribution of European beech forests.

Key words: leaf colouring date, leaf unfolding date, length of vegetation period, plant phenology index.

Introduction

European beech (*Fagus sylvatica* L.) is one of the most widespread tree species in European forests (Durrant et al. 2016). During the last glacial period, the European beech was wiped out of the central part of the continent and survived mainly in relatively small refugial areas in the Submediterranean and Mediterranean zones, also in the Balkans. From there, it began its secondary colonisation of Cen-

tral and later Western and Northern Europe. (Comps et al. 2001, Magri 2008). According to Leuschner (2020) and Leuschner and Ellenberg (2017), European beech is a temperate late-successional tree species, which can achieve high dominance under favourable growing conditions due to its ability to form an extensive shade crown and tolerate very low light intensities in both juvenile and adult life stage. European beech is typical dominant tree species in the natural vegeta-

tion of the lower mountainous ranges in Central Europe, gradually ascending into the mountains as the latitude decreases (Stefanov and Ganchev 1953). Beech is drought- and heat-sensitive. In Central Europe, it has a precipitation threshold of 500 to 550 mm per year, below which it gradually loses its dominance over oak and other tree species (Bolte et al. 2007). According to Larcher (2003), the optimal temperature in Central Europe for European beech photosynthesis is 20 °C and varies with the altitudinal and latitudinal temperature gradients.

In Bulgaria, European beech is widely distributed, predominantly in the middle mountain zone (Stefanov and Ganchev 1953), where it forms part of forests across a significant range of latitudes and altitudes. The southernmost forests dominated by European beech are located near the Greek border around Veykata Peak in the Rhodope Mountains. At the same time, in the north, the species reaches as far as the Bozhuritza Reservoir above the village of Sinagovtsi in Vidin region, which is also its lowest-altitude site in Bulgaria (140 m a.s.l.) (Anev 2025). In the mountains, European beech often forms the upper forest boundary. In the easternmost parts of the Balkan Mountains and throughout southeastern Bulgaria, the European beech is often replaced by the Oriental beech (*Fagus orientalis* Lipsky) (Stefanov and Ganchev 1953). This broad range in latitude, longitude, and elevation corresponds to a considerable diversity of climatic conditions. The wide distribution of the European beech in Bulgaria shows that the species can successfully tolerate the climate of mountains under the influence of the temperate-continental region (e.g., the Balkan Mountains), as well as those under the transitional-continental (e.g., Osogovo) and the continen-

tal-Mediterranean climatic regions (e.g., the Rhodopes) (Anev 2025, Stefanov and Ganchev 1953), probably due to the higher precipitation rate in the elevated mountainous areas.

The absence of the European beech in the plains, despite the more continental climate compared to Italy and Spain, is attributed by some authors to the high summer temperatures and dry periods (Fang and Lechowicz 2006). At the north-eastern distribution range, it seems to be more a late frost limit (Bolte et al. 2007, Leuschner and Ellenberg 2017). According to Magri (2008), the European beech requires at least 140 favourable days per year for vegetation, which explains why it does not survive far north in Scandinavia. The European beech enters deep dormancy and withstands low winter temperatures well, but it is susceptible to late spring frosts (Stefanov and Ganchev 1953). Well-developed leaf buds allow it to delay leafing (Anev 2025), and in Bulgaria, leaf emergence occurs from the first week of April at the lower range boundary, to early May at the upper range boundary (Kuzmanova 2021; Tzvetkova and Anev 2014; Anev 2023, 2025). However, late spring frosts have a strongly adverse effect, especially on young individuals that have not yet developed resistance mechanisms and leaf out significantly earlier than mature trees. Slavov and Kazandjiev (2005) established a strong relationship between the individual phenological events in European beech, but not between unfolding and autumn colouration. Petkova et al. (2017) note that Bulgarian provenances of European beech have a longer growing season than German ones, but their early development makes them more sensitive to low spring temperatures.

Phenology can change with increasing altitude and latitude due to variations in

temperature, light, and other environmental factors (Čufar et al. 2012; Schieber et al. 2013; Gressler et al. 2015; Vilhar et al. 2018; Lukasová et al. 2020; Anev 2023, 2025; Skvareninova et al. 2024). According to Hopkins' law (Hopkins 1918), temperatures in temperate latitudes tend to decrease linearly with increasing elevation or distance from the equator. This can lead to delays in the timing of phenological events. For example, spring events like budburst, flowering, and leaf emergence may occur later at higher altitudes and latitudes than at lower ones (Dittmar and Elling 2005, Čufar et al. 2012, Schieber et al. 2013). Conversely, autumn events tend to occur earlier at higher altitudes and latitudes. Consequently, the growing season at higher altitudes and latitudes is often shorter due to colder temperatures, which affects the duration and timing of various phenological events (Vitasse et al. 2009b). Such a shorter growing season may compress the time available for plants to complete their life cycles, potentially impacting their growth and reproduction. Higher altitudes and latitudes are more likely to experience extended periods of snow cover during winter (Yue et al. 2022). Snow acts as an insulator, delaying ground warming in spring and further postponing the onset of spring phenological events. Altitudinal gradients can create a wide range of microclimates within a relatively short distance compared to latitudinal gradients. Local factors, such as slope, aspect, and topography can significantly influence the microclimate. As a result, variations in phenological timing can occur even within the same altitude range. Schuster et al. (2014) concluded that cold-air pools significantly impact the vegetation period of deciduous trees, with trees on mid-hillside slopes gaining advantages compared to those at lower elevations.

The role of chilling temperatures and the photoperiod in determining the budburst date for some late-unfolding species, including European beech, has been widely studied (Falusi and Calamassi 1990; Vitasse and Basler 2013; Kuzmanova 2015, 2021; Roberts et al. 2015; Flynn and Wolkovich 2018; Wang et al. 2022). In European beech, the budburst thermal time requirement and chilling duration are linearly related (Vitasse et al. 2009a). In another study, Vitasse and Basler (2013) caution that this relationship should be interpreted carefully because photoperiod may confound the relationship between warming temperatures (forcing) and chilling requirements. However, Vilhar et al. (2018) demonstrate that first leaf unfolding dates in beech can be satisfactorily predicted based on tree phenological phases observed at national phenological stations and recommend combining ICP Forests and NPN methodologies to improve the national phenological network.

Studied wild species spring phenology over decades, which mainly focused on temperate woody species, shows that three major cues underlie budburst and leaf unfolding: warm spring forcing temperatures, increasing photoperiod, and length and intensity of winter chilling temperature (Flynn and Wolkovich 2018). Variations in temperature sums for many phenological phases, especially temperate forests, have repeatedly explained interannual phenological dynamics (Roberts et al. 2015, Flynn and Wolkovich 2018, Melaas et al. 2018). Roberts et al. (2015) also found that European beech was less sensitive to spring forcing than other European tree species and pointed out the role of dormancy induction in spring phenology. Badeck et al. (2004) showed that interannual variation in the timing of phenological events can reach

up to one month. On the other hand, Vitasse and Basler (2013) establish that the bud burst date of European beech shows fewer temporal and spatial variations than most of the other deciduous tree species in Europe, which this species' late leaf unfolding could explain.

Phenology observations using remote sensing devices, such as satellite imagery and Unmanned Aerial Vehicles (UAVs), are promising techniques (Ciocîrlan et al. 2022). Remote sensing methods can determine phenological events by monitoring changes in vegetation greenness from a distance, often using satellites or airborne sensors (Kimball et al. 2004). These methods are based on the fact that different phenological stages cause distinct changes in the reflectance of light from vegetation, which can be detected and analysed using remote sensing spectral indices. According to Bucha and Koren (2017), researchers can identify shifts in phenological events by analysing the spatial and temporal changes in these spectral indices. Algorithms and statistical techniques can be applied to detect the timing of specific events.

This study aimed to evaluate the influence of altitude, latitude and longitude on leaf unfolding, autumn leaf colouration, and the duration of the growing season of European beech dominated forests in Bulgaria.

Object and Methods

The study was conducted in forests dominated by European beech throughout Bulgaria. The data and polygons were taken from the national forest inventory, which is available at <https://maps.iag.bg/>. Within the boundaries of the studied forests, symmetrical sample points ($n = 294,665$)

were generated in QGIS (v. 3.42.1), which were 100 m apart using the 'qgis:regular-point' tool (Fig. 1).

The average age of the studied forests is 104.7 (± 37.8 years standard deviation), ranging from 1 to 250 years. Despite this wide variation, 50 % of forests are between 80 and 130 years old, and 90 % are between 40 and 160 years old (Fig. 2A).

The 'native:rastersampling' tool was used to extract the altitude of points from the EuroDEM raster layer downloaded from EuroGeographics (2025). Based on the EuroDEM raster image, the 'grass:r.slope.aspect' tool (Grass GIS, v. 8.4.1) was used to calculate the slope and aspect of the terrain, on which the points are located. European beech forests are normally distributed by altitude with average elevation 1060.0 (± 249.1 m standard deviation) and 50 % of them fall between 888 and 1228 m, and 90 % are between 649 and 1482 m (Fig. 2B). Although European beech forests are distributed throughout the country in terms of latitude, fifty per cent of them are concentrated in the range $42.14^\circ - 42.87^\circ$ with an average of 42.53° ($\pm 0.57^\circ$ standard deviation), and 90 % are between 41.44° and 43.25° (Fig. 2C). Despite being more evenly distributed in longitude, studied forests are mainly in Western and Central Bulgaria. Fifty per cent of them are in the range $23.3^\circ - 24.9^\circ$, with an average value of 24.14° ($\pm 1.06^\circ$ standard deviation), and 90 % are between 22.6° and 26.0° (Fig. 2D). The phenological events in the studied forests were identified using data from the Copernicus Land Monitoring Service (WEKEO 2025). Analysis was based on the Seasonal Trajectory series of the Plant Phenology Index (PPI), as described by Jin and Eklundh (2014), Smets et al. (2022), and referenced in Anev (2023). The leaf unfolding dates (LUD) and autumn leaf colouration

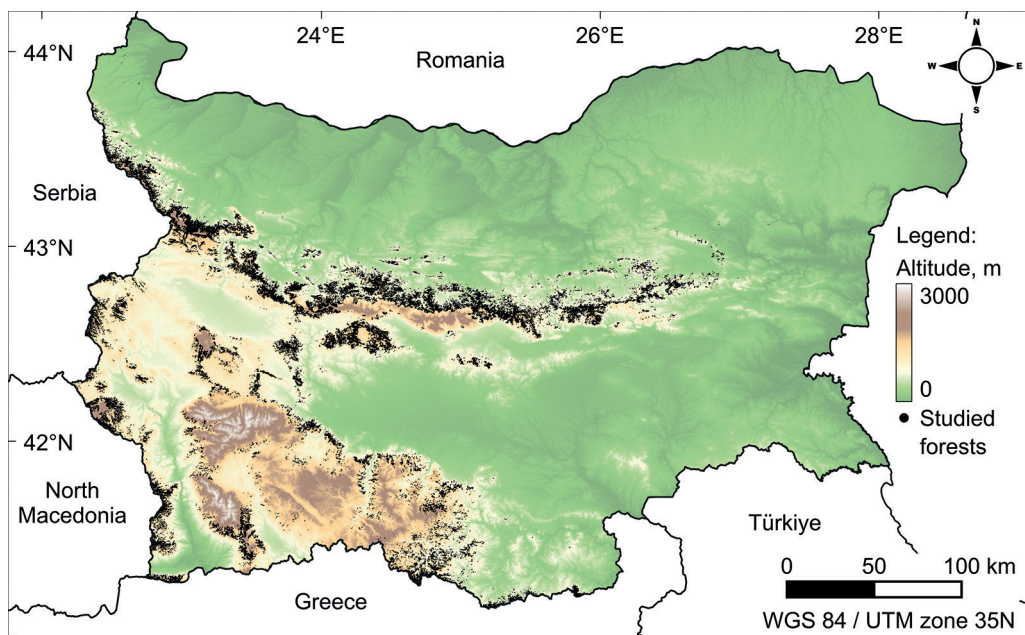


Fig. 1. Geographical distribution of European beech dominated forests in Bulgaria on a digital elevation map background.

Note: studied forests ($n = 294,665$), used for analysis, are shown with black solid dots.

dates (LCD), as well as the length of the vegetation period (LVP), were extracted with the 'native:rastersampling' tool from the raster images from the SOSD, EOSD and LOSD series, season 1, covering the territory of the studied beech forests. The collected information in the vector layer for the studied indicators was exported in csv-format with the 'gdal:gdal2xyz' tool (GDAL v. 3.10.2). In MS Excel (Office365, Microsoft), the data were statistically processed using the built-in functions and VBA-scripts (VBA v.7.1, Microsoft). One-way ANOVA with the Tukey test was used to compare phenological events in different years. Pearson's correlation coefficients were calculated between altitude, latitude, and longitude on the one hand, and LUD, LCD, and LVP, on the other. Multiple linear regressions were applied to calculate estimated indicator values of the

vegetation period according to changes in the complex geographical characteristics of sample points.

Results

Significant variation in the LUD were observed over the seven years studied. European beech opens the leaf buds and forms leaves from the end of March to the end of May. On average, during the study period, this event occurred on 26 April (± 11.4 days standard deviation), and in the 95th percentile, it varied from 03 April to 19 May (Fig. 3A).

LCD lasts from mid-September to mid-November. On average, during the study period, this event occurred on 19 October (± 15.7 days standard deviation), and in the 95th percentile, it varied from

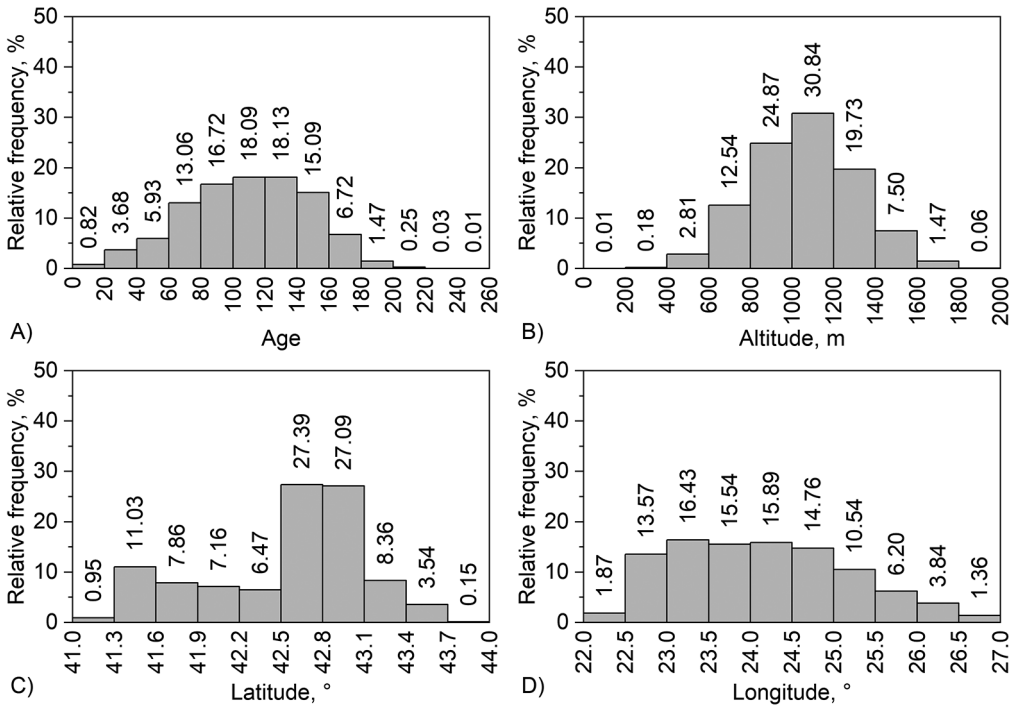


Fig. 2. Structure of studied European beech forests.

Note: the histogram's bins show the relative frequency (%) of European beech forests in each: A) age class (20 years), B) altitude (200 m), C) latitude (0.3°), and D) longitude (0.5°).

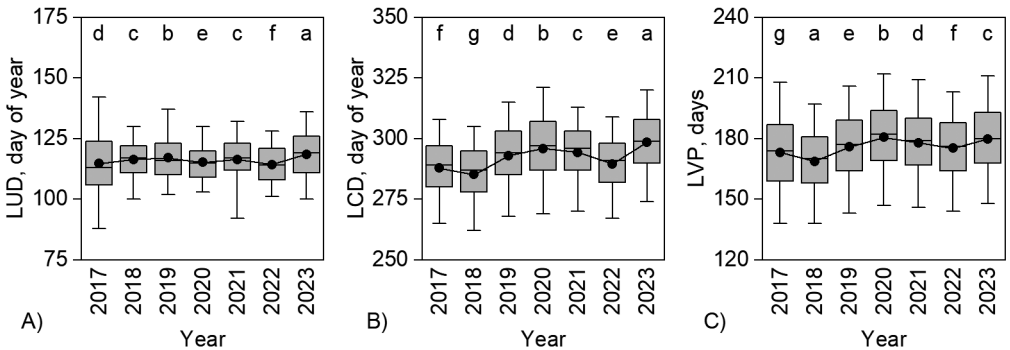


Fig. 3. Phenological events: A) Leaf unfolding date, B) Leaf colouring date, C) Length of vegetation period.

Note: Box plots present the distribution of phenological events. Mean values are shown with a solid dot, median with a line, box range presents 25–75 % quartiles, and whiskers present 5–95 % range. Means that do not share a letter differ significantly (one-way ANOVA with Tukey test, p -value < 0.05).

17 September to 16 November (Fig. 3B). Variations in LUD and LCD lead to variations in LVP. On average, during the study period, LVP lasts 176 days (± 15.8 days standard deviation). The shortest LVP was 169 days in 2018, while the longest was 181 days in 2020 (Fig. 3C).

The results of the correlation analysis between the geographical factors, altitude, latitude, and longitude, on the one hand, and the investigated phenological events, on the other, show a weak, albeit statistically significant relationship. The most substantial positive correlation was observed between LUD and altitude ($R = 0.519$, p -value < 0.001), while LCD correlates considerably less with altitude ($R = -0.061$, p -value < 0.001). The later start of the growing period with increasing elevation results in a negative correlation between LVP and altitude ($R = -0.339$, p -value < 0.001). The growing season is much less related to latitude. The correlation coefficients between latitude and LUD, LCD, and LVP are $R = -0.031$, $R = -0.057$, and $R = -0.026$, all with p -value < 0.001 . Similar and no longer so categorically negative is the correlation between

longitude and the studied indicators of the vegetation period – LUD ($P = -0.091$), LSD ($P = 0.017$) and LVP ($P = 0.064$), all with p -value < 0.001 .

The results of the multivariate linear regression show that leaf unfolding is the variable most strongly dependent on the geographical factors studied. Multiple regression coefficients for each factor show that unfolding of European beech is delayed by 2.519 (± 0.004 SE) days for every 100 m increase in altitude, by 2.197 (± 0.016 SE) days for every degree of northward shift, and by 1.581 (± 0.009 SE) days for every degree of eastward shift (Fig. 4A).

While altitude plays the strongest role in leaf unfolding, latitude is the leading factor in autumn leaf colouration. With a one-degree change to the north, the LCD happens earlier by 2.115 (± 0.038 SE) days, while with a 100-meter elevation increase it advances only by 0.073 (± 0.009 SE) days, and with a one-degree shift to the east it advances by 0.415 (± 0.022 SE) days (Fig. 4B). Thus, the growing period is shortened by 4.312 (± 0.045 SE) days for every degree of northward shift, by

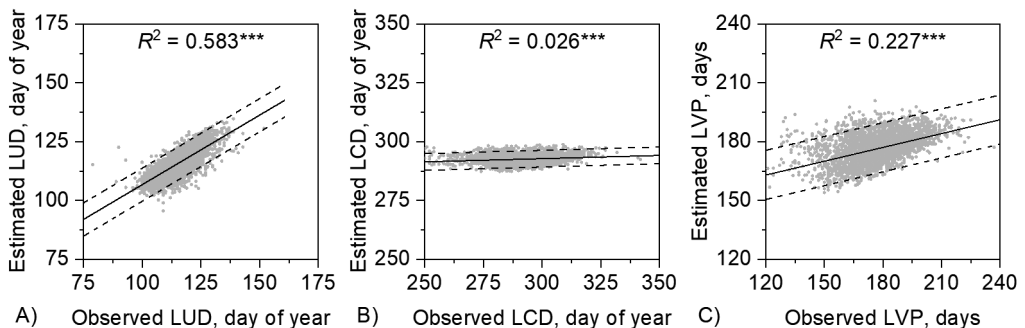


Fig. 4. Estimated vs. observed: A) leaf unfolding date, B) leaf colouring date, C) length of vegetation period.

Note: Grey dots represent estimated vs. observed LUD, LCD, and LVP values for all sample points ($n = 294,665$) and all seven years in the studied period ($N = 7 \cdot n = 2,062,655$). The solid line represents a multiple linear regression (MLR) trend; the dashed lines are the 95% prediction band. MLR's coefficients of determination (R^2) are shown above lines ($^{***} p$ -value < 0.001).

3.254 (± 0.011 SE) days for every 100 m higher altitude, and by 2.000 (± 0.026 SE) days for every degree of eastward shift (Fig.4C).

Discussion

We found that altitude is the leading factor in European beech's spring phenology, while latitude is the leading factor in its autumn phenology. Studied wild species spring phenology over decades, which mainly focused on temperate woody species, shows that three major cues underlie budburst and leaf unfolding: warm spring forcing temperatures, increasing photoperiod, and length and intensity of winter chilling temperature (Flynn and Wolkovich 2018). Bulgaria's 13-hour daylight duration occurs between 7 and 9 April and varies slightly due to the slight variation in latitude across the country. While the photoperiod is relatively independent of the geographical characteristics studied and has a well-pronounced seasonality, winter and spring temperatures are strongly influenced, especially by altitude. According to Marinova and Bocheva (2024), in the mountains temperature decreases with altitude by 0.3–0.4 °C per 100 m in January, by 0.6–0.7 °C per 100 m in April, by about 0.7 °C per 100 m in July, and by 0.5 °C per 100 m in October. Such a significant decrease in temperatures with increasing elevation, especially in spring, may explain the strong relationship between unfolding and altitude.

We predict that the LUD delay is 2.519 days per 100 m, or more than 49 days per the whole altitudinal diapason (1950 m) of European beech forests in Bulgaria. Our results are comparable to those of other authors who established the correlation between leaf unfolding of Euro-

pean beech and altitude. Similar results were reported by Čufar et al. (2012) for Slovenia, where the leaf unfolding shift is 2.6 days for every 100 m. Schieber et al. (2013) showed a 2.83–3.00 days shift in the onset of spring phenology per 100 m of an increase in altitude in the Inner Western Carpathians, Slovakia ($\sim 49^\circ$ N), while Skvareninova et al. (2024) showed a 2.2 days shift for the same region. Even more, Dittmar and Elling (2005) established a shift of two whole days per 100 m faster at the start of vegetation in South Bavaria with the Northern Alps and Bavarian Forest, compared to the northern regions of Bavaria, which they explain as unfavourable warmth and radiation conditions in the north. On the other hand, Vitasse and Basler (2013) establish that the bud burst date of European beech shows fewer temporal and spatial variations than most of the other deciduous tree species in Europe, which this species' late leaf unfolding could explain. Vitasse et al. (2010) found a linear relationship between spring phenology of European beech saplings and air temperature, with leaf unfolding occurring 5 days earlier for each degree higher mean annual temperature. At the same time, the relationship between autumn phenology and mean yearly temperature is hyperbolic, with leaf senescence occurring at the latest at temperatures of 8–9 °C (Vitasse et al. 2010).

The influence of altitude on autumn leaf colouration was significantly less. If spring phenological events occur slowly at different altitudes, autumn phenological events occur more expressively and spontaneously. We predict that the LCD delay is only by 0.073 days per 100 m, or less than 1.5 days per the whole altitudinal diapason (1950 m) of European beech forests in Bulgaria. Similar are the results of Skvareninova et al. (2024), who found a

significantly higher variation of the autumn phenology (1.1–2.9 days per 100 m) than the spring phenology. The expected influence of latitude on autumn leaf colouration is significantly greater, 2.115 days per one degree of northward shift. Lukasová et al. (2020) showed that on mid-altitude stands in the eastern part of Slovakia, the autumn phenology of European beech has a very significant positive effect on increasing temperature and heat waves. This effect is lost at lower and higher altitudes in the central and western parts of the country. As a major climatic factor, the latitude determines the levels of heat balance and, thence, the affiliation of the country to the regions with warmer climates in Europe (Marinova and Bocheva 2024). The European beech responds positively to climate warming in the eastern part of its range (Peters 1997, Fang and Lechowicz 2006, Bolte et al. 2007), probably because colder air masses from the northeast invade, strengthening the climate's continental character, which suggests strengthening the longitude factor at the expense of the altitude and latitude factors. However, we predict a delay of 1.581 days in the LUD and a two-day shortening of the LVP for each degree of eastward shift, which may be due to decreased precipitation and increased temperatures from west to east in Bulgaria (Marinova and Bocheva 2024).

Conclusions

The phenology of European beech forests in Bulgaria is closely related to the factors of latitude, altitude, and longitude. It is the visible manifestation of the environmental factors' influence on primary physiological processes, especially in transitional seasons. Spring phenological events show a stronger relationship with altitude than lat-

itude or longitude. In the autumn, the geographical latitude stands out as a limiting factor. Thus, latitude and altitude simultaneously impact the length of the growing season and even reinforce each other's influence. The dynamics of individual phenological events in different years, at various altitudes and different geographical latitudes and longitudes, show preserved potential for European beech acclimation to the current climate changes in the Bulgarian mountains. These findings contribute to understanding how complex of geographic gradients shape the timing of phenological events and duration of vegetation period in European beech under the current climate in Bulgaria. They could be used as a basis for impact forecasting of future climate scenarios in the south-eastern part of the distribution of European beech forests.

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Estimating carbon stock in litterfall of dominant vegetation on fallow land in Manokwari, West Papua

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Abstract

Litterfall plays a crucial role in transferring nutrients from vegetation to soil, particularly in the carbon and nitrogen cycles. This study aims to estimate and compare the carbon stock in it from dominant tree species in 15-year-old fallow land. Litterfall traps measuring 1×1 m were placed beneath the stands of dominant tree species *Pometia pinnata* J.R.Forst. & G.Forst., *Dracontomelon dao* (Blanco) Merr. & Rolfe, and *Octomeles sumatrana* Miq., with three replicates. Carbon stock was calculated using the drying method to achieve constant litterfall weight. The stock of carbon measurement data were analysed using one-way ANOVA, followed by the Least Significant Difference (LSD) test at a p level <0.05 . A significant difference was found in mean weekly carbon stock in litterfall between *P. pinnata* ($11.33 \pm 7.8 \text{ g} \cdot \text{m}^{-2} \cdot \text{week}^{-1}$) and *D. dao* ($19.50 \pm 8.8 \text{ g} \cdot \text{m}^{-2} \cdot \text{week}^{-1}$) and *O. sumatrana* ($18.85 \pm 7.1 \text{ g} \cdot \text{m}^{-2} \cdot \text{week}^{-1}$), but *D. dao* and *O. sumatrana* did not differ significantly. The difference in carbon stock production is due to peak leaf shedding of *D. dao* and *O. sumatrana* during the study period, whereas *P. pinnata* was not shedding leaves, leading to its lowest carbon stock production. Additionally, canopy height may influence litterfall capture in the trap. Estimates of annual carbon stock in it showed high values: $5.73 \text{ t} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for *P. pinnata*, $9.89 \text{ t} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for *D. dao*, and $9.37 \text{ t} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for *O. sumatrana*. Fallow land in Womnowi Village, Manokwari after 15 years, makes a substantial contribution to carbon stock. From the perspective of soil fertility for agricultural land, high carbon stock suggests that fallow land can be reutilised for agricultural purposes.

Key words: carbon estimations, *Pometia pinnata*, secondary forest, shifting cultivation, succession.

Introduction

Vegetation plays a role in increasing soil fertility through the transfer of nutrients to the soil in the form of litterfall (Lanuza et al. 2018, Sayer et al. 2020). Its production

plays a role in increasing organic carbon levels in the soil, especially the role of tree vegetation (Paul et al. 2022). Although most plants absorb organic carbon from the air in the form of CO_2 , carbon stock in plants (carbon sequestration) can con-

trol global warming (Ghale et al. 2022). In some cases of vegetation differences, dominant trees provide differences in carbon stock in various forest types (Gao et al. 2019, Schneidewind et al. 2019). The presence of dominant vegetation is the result of land management and climate control, both of which affect the balance of carbon and nitrogen stock (Gava et al. 2022, Okolo et al. 2023).

On a global scale, the balance of carbon and nitrogen can indicate high or low CO₂ emissions into the atmosphere. High N levels in the soil increase soil fertility so that vegetation becomes fertile, decomposition decreases, and the CO₂ fixation rate becomes high. If N increases, carbon stock becomes high (Eastman et al. 2021, Liu et al. 2024), so that the carbon stock stored in the plant body can be used to predict soil fertility. Land management is the main key in regulating carbon sequestration, for example secondary forests have low carbon stock but high N content (Gao et al. 2019). Cocoa monoculture planting systems can reduce carbon stock (Schneidewind et al. 2019), and group planting of N-fixing vegetation can increase carbon stocks in the soil (Rodríguez et al. 2022) and aboveground, but reduce plant diversity in secondary successional forests (Pati et al. 2025).

Traditional farming systems with fallowing to increase soil fertility are characteristic of land management in Papua (Allen and Filer 2015). Vegetation surrounding fallow land, especially fallow land that is more than 10-year-old, forms strata resembling primary forests in general (Budirianto and Ratnawati 2018, Susanto et al. 2018). Dominant tree vegetation indicating enriched fallow land in the lowland alluvial soil of Manokwari Regency was successfully identified by Susanto et al. (2018), as well as several aspects of dominant tree

litterfall production estimation (Susanto et al. 2019, 2020a). However, information on carbon stocks from litterfall in fallow land has never been studied.

Litterfall is known to be the main organic material contributing to carbon stock (Feng et al. 2019). Temporal information related from dominant tree litterfall production over a certain period of time is not available, especially in fallow lands in West Papua. In addition, the increasing human population and the problem of limited land, are expected to make fallow lands in Manokwari Regency increasingly short-lived and have the potential to become residential areas (Putri et al. 2024). This study aimed to quantify the weekly and estimated annual carbon stocks in litterfall from dominant tree species on 15-year-old fallow land in Womnowi Village, Sidey District, Manokwari Regency. Given the limited of research on carbon stocks in litterfall from dominant tree species in West Papua's fallow lands, this study sought to answer the question: What is the carbon storage potential of litterfall from dominant tree species in this specific ecosystem?

Method

Study site

The study was conducted in March–June 2018, divided into two activities, namely measuring litterfall production for three months and quantitative measurement of carbon stock. Measurement the production was carried out in the fallow land of Womnowi Village, Sidey District, Manokwari Regency, West Papua Province with sampling locations (0°48'17.20" – 0°48'23.20" S) (133°28'53.20" – 133°28'59.92" E), while the measure-

ment of carbon stock was carried out at the Botany Laboratory, Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Papua. The research location is crossed by two rivers, namely the Kali Womnowi from the south and the Kali Kasi from the west (Fig.1).

The climate of the research location is of the Af type (Peel et al. 2007) with rainfall above 1200 mm per year. The soil type is dominated by clay fractions with moderate to high soil fertility characteristics (Susanto et al. 2020b). The temperature and humidity conditions (under the vegetation canopy) for three months were recorded with an average temperature of 28.75 °C and humidity of 78.5 %. According to local meteorological data from

the Indonesian Meteorological, Climatological and Geophysical Agency (BMKG) in Rendani, Manokwari for 2018, the annual rainfall reached 2423.7 mm. The average temperature in 2018 was 27.5 °C, with relative humidity ranging from 80 to 84.5 % (BMKG 2018).

Tools and materials

GPS, litterfall traps made of 40 mesh nylon cloth (pore diameter/hole 0.5 cm) measuring 1 m × 1 m, thermohygrometer, plastic litterfall container, battery-powered analytical balance (Fortuno FAB 600, $\alpha = 0.01$), and Memmert Universal Oven UFB 400 were used. The materials were leaf litterfall of dominant trees measured weekly during March–June 2018.

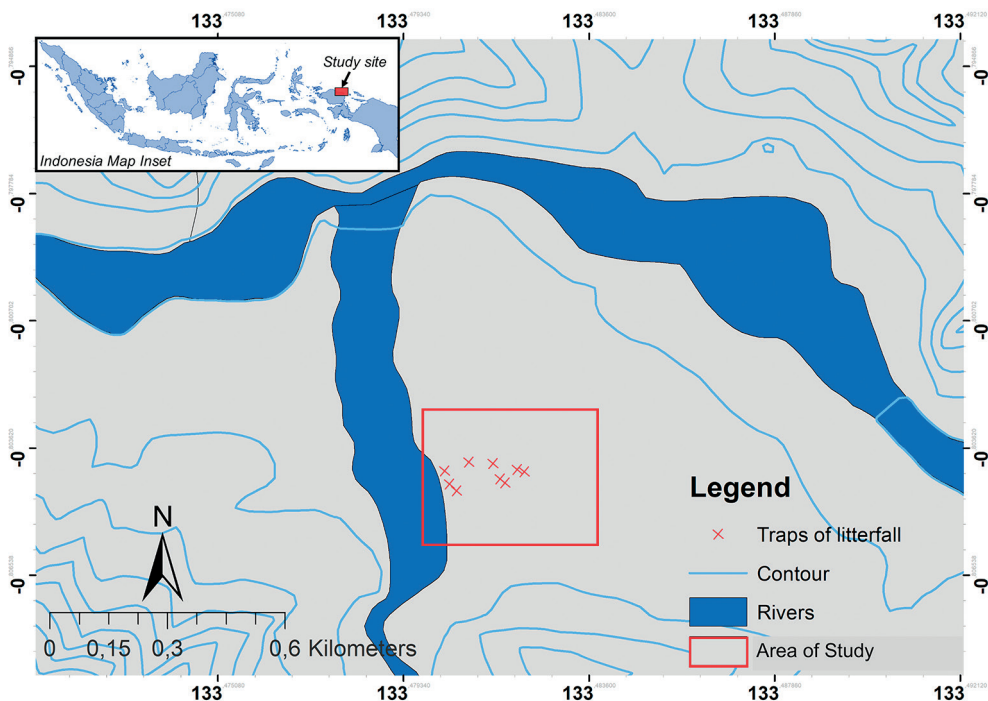


Fig. 1. Distribution of litterfall traps in fallow land in Womnowi Village, Sidey District, Manokwari Regency.

Research procedure

This study employed a completely randomised design, assuming the carbon stock from litter produced by three tree species as the treatment. Since the research was conducted only on 15-year-old fallow land, we assumed that all environmental factors studied were homogeneous. The independent variables were the dominant tree species, temperature, and air humidity under the canopy of these dominant trees. Meanwhile, the dependent variable was the carbon stock derived from the litterfall produced by these tree species.

The first step was to record the dominant tree vegetation. Dominant vegetation data were obtained from previous research by Susanto et al. (2018). In a total land area of 1 ha, the important value index (IVI) of dominant trees covering 15-year-old fallow land was *Pometia pinnata* J.R.Forst. & G.Forst. (48.97 %), *Dracontomelon dao* (Blanco) Merr. & Rolfe (43.89 %), and *Octomeles sumatrana* Miq. (36.53 %). Tree vegetation data were collected through a complete census conducted within a 1-ha plot. This study recorded all trees with DBH exceeding 20 cm. We assumed that trees with large diameters (e.g., *P. pinnata*, which can reach DBH >70 cm) and the highest and densest canopy strata are representative of the dominant species.

The next steps were measuring litter production. A total of three individuals of each dominant tree type were selected purposively to measure their litterfall production. Dominant vegetation litterfall was measured every week, using a 1 m × 1 m trap (Bhattarai and Mandal 2018, Gao et al. 2019). Litterfall traps were placed under the dominant tree vegetation stand at a height of 0.5 m from the ground surface (Schneidewind et al. 2019). The total number of traps used in the Womnowi fal-

low land, Sidey District, Manokwari, was 9 on a total area of 1 ha with a distribution as shown in Figure 1.

Carbon stock in litterfall was measured using the litterfall drying method at a temperature of 70 °C until its weight was constant, then continued with calculations based on standard equations referring to BSN (2011) and (Rusdiana and Lubis 2012). Carbon stock production was measured weekly and annually using the equation from BSN (2011) and Morffi-Mestre et al. (2020).

Data analysis

The first step to determine the carbon content in litterfall was to calculate its water content (%WC). It was calculated using the equation (1).

$$\%WC = \frac{WLW - DLW}{WLW} \cdot 100, \quad (1)$$

where: WLW is wet litterfall weight, kg; DLW is dry litterfall weight, kg.

Once the water content was known, the next step was to calculate the dry weight of the litter biomass as in equation (2).

$$DBW = WLW \cdot \left(1 - \frac{\%WC}{100}\right), \quad (2)$$

where: DBW is dry biomass weight, kg; WLW is wet litterfall weight, kg; %WC is water content, %.

Dry biomass weight (DBW) is the reference for calculating litterfall carbon stock estimates in this study. Meanwhile, the value of 0.46 is a conversion factor for calculating carbon stock in dry biomass. Therefore, after knowing the DBW based on formula (2), the carbon stock in the litter was then calculated using formula (3).

$$C = DBW \cdot 0.46. \quad (3)$$

Estimation of carbon stock from litterfall per hectare in a year was measured based on the equation developed by

Morffi-Mestre et al. (2020) and Susanto et al. (2020a) shown in equation (4).

$$C_n = \frac{C_x}{1000} \cdot \frac{10,000}{i} \cdot 52, \quad (4)$$

where: C_n is carbon stock in litterfall per hectare per year, $t \cdot ha^{-1} \cdot yr^{-1}$; C_x is average carbon stock in litterfall of each tree species, $kg \cdot m^{-2}$; i is area of litterfall trap, m^2 ; this study measured carbon stocks from litter weekly for 3 consecutive months, with 52 representing the number of weeks in a year.

Statistical analysis

Carbon stock production in litterfall per week of each dominant tree species was compared using ANOVA test at the $p < 0.05$ level, followed by the least significant difference (LSD) test at the $p < 0.05$ level. In addition, the effect of temperature and humidity on litterfall production which indirectly affects carbon stock, was analysed using the correlation r , Pearson method.

All data analysis was performed using SPSS v. 23.00 software (IBM Corp).

Results and Discussion

Litterfall carbon stock dynamics

Carbon stock in dominant tree litterfall in fallow land tends to fluctuate. Its per week was significantly different ($p < 0.05$) for *P. pinnata* ($11.33 \pm 7.8 g \cdot m^{-2} \cdot week^{-1}$) with *D. dao* ($19.50 \pm 8.8 g \cdot m^{-2} \cdot week^{-1}$) and *O. sumatrana* ($18.50 \pm 7.1 g \cdot m^{-2} \cdot week^{-1}$), but between *D. dao* and *O. sumatrana* there was no significant difference (Fig. 2).

The lowest carbon stock value in litterfall was found in *P. pinnata*, followed by *O. sumatrana* and *D. dao*. Although *P. pinnata* was the species with the highest IVI (Fig. 3), during 12 weeks of measurement it had the lowest carbon stock in litterfall, this due to the low value of litterfall production produced. Bhattarai and Mandal

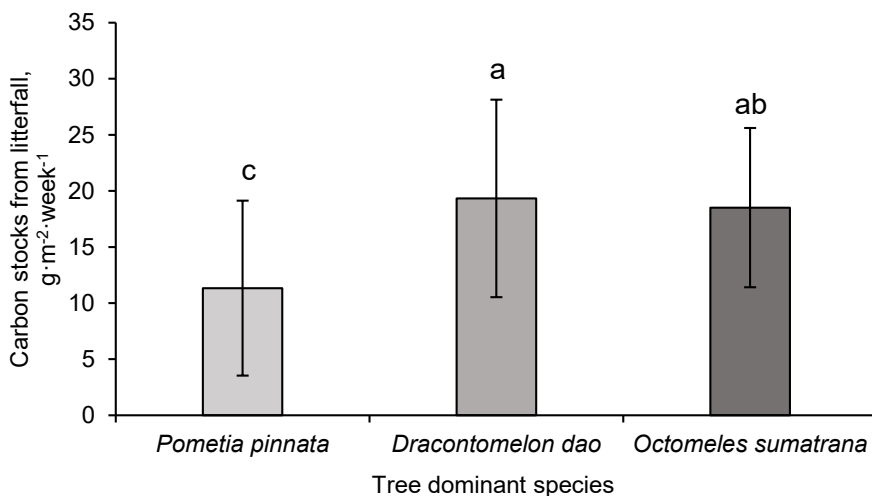


Fig. 2. Weekly carbon stock in litterfall of dominant tree vegetation on 15-year-old fallow land in Womnowi Village, Sidey District, Manokwari Regency.

Note: The same letters above the bars indicate no significant difference based on the least significant difference test.

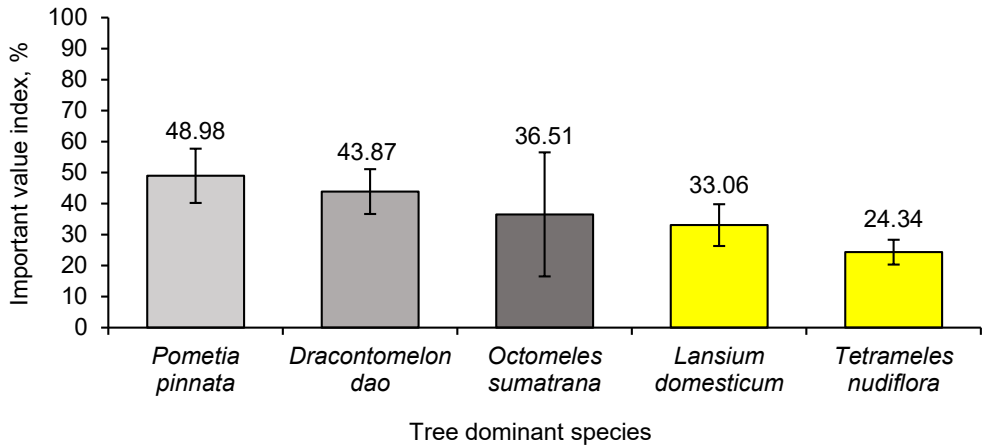


Fig. 3. The top five important value index of the highest trees in the fallow land of Womnowi Village, Sidey District, Manokwari Regency.

Note: The yellow colour indicates the types which litterfall production is not calculated (data adapted from Susanto et al. (2018)).

(2018) stated that carbon stock depends on the value of litterfall production, in addition the quality and quantity of dominant vegetation litterfall affect carbon stock (Singh et al. 2022).

This study shows that the importance value index of species (Fig. 3) does not affect the carbon stock value in litterfall during 12 weeks of measurement. However, it cannot be generalised that *P. pinnata* has the lowest carbon stock due to several reasons. Firstly, it has the highest tree density with 35 individuals per hectare, whereas *D. dao* and *O. sumatrana* have tree densities of 29 and 16 individuals per hectare, respectively. Logically, the higher the tree density, the higher the biomass estimate, especially litterfall (Sari et al. 2016, Kaushal and Baishya 2021), resulting in higher carbon potential. Secondly, the measurement period was too narrow, so when there was a peak leaf shedding from one species (in this case, *D. dao*), it affected the range of carbon stock from other species. Thirdly, there was interference from the canopy of oth-

er tree species that altered the direction of litterfall. For example, *P. pinnata* in this study can reach heights of over 30 m, so it is possible that when litter falls, it may be intercepted by the canopy of other trees below, preventing it from falling directly into the designated litterfall traps.

Canopy characteristics also affect litterfall production (Qiu et al. 2023), thus affecting carbon stock in it. *P. pinnata* is a species that has Koriba architecture (Budirianto 2011). A positive correlation between tree architecture models and high litterfall production is found in the tree architecture of Attims (*Ficus variegata*), Rauh (*Altingia excelsa* and *Scima wallichii*) and Roux (*Trema orientalis*) (Arrijani 2006). *D. dao* has a Stone architecture model (Naharuddin et al. 2016) which has a lower litterfall production value than the Attims, Rauh, and Roux models (Arrijani 2006). *O. sumatrana* has a Massar't tree architecture model (Hallé et al. 1978), with the characteristic of having a canopy that tends to be open compared to *P. pinnata* and *D. dao*. This architectural model

stores more water in the stem, and has a low soil water content. This is inversely proportional to *P. pinnata*, so that the litterfall production of *O. sumatrana* is higher than *P. pinnata*, but in terms of total biomass, *P. pinnata* stands have higher carbon stocks than *D. dao* and *O. sumatrana*.

Based on morphophysiological characteristics, *P. pinnata* and *D. dao* are compound-leaved plants capable of producing large numbers of leaves, whereas *O. sumatrana* is a single-leaved plant with wider leaves. In Papua New Guinea, *P. pinnata* is an indicator of mid-successional land with canopy cover exceeding 80 % (Burley et al. 2011). Notably, *D. dao*, *O. sumatrana*, and *P. pinnata* comprise 60–80 % of the canopy strata A and B in lowland areas near rivers on Papua Island, with tree heights reaching over 30 m (Paijmans 1976). Although specific studies on the phenology of these three species are lacking, it is likely that they exhibit

different leaf-shedding patterns, highlighting the importance of measuring carbon stocks from litter over an extended period.

Litterfall carbon stock estimations

Fallow land is classified as a secondary forest that is 15-year-old and shows a very high carbon stock estimate in litterfall ranging from 5.73–9.89 t·ha⁻¹·yr⁻¹ (Fig. 4). The use of an extrapolation equation for carbon stock per week to per year on 15–17-year-old succession land obtained a carbon stock in litterfall of 5.674 ± 0.274 t·ha⁻¹·yr⁻¹ (Morffi-Mestre et al. 2020). High carbon stock in litterfall on 15-year-old fallow land (secondary forest) is common, as in the results of a previous study by Moura et al. (2016) that the increase in carbon stock occurs until the succession reaches 37 years, then decreases. The estimated carbon stock from dominant tree litter in this study may

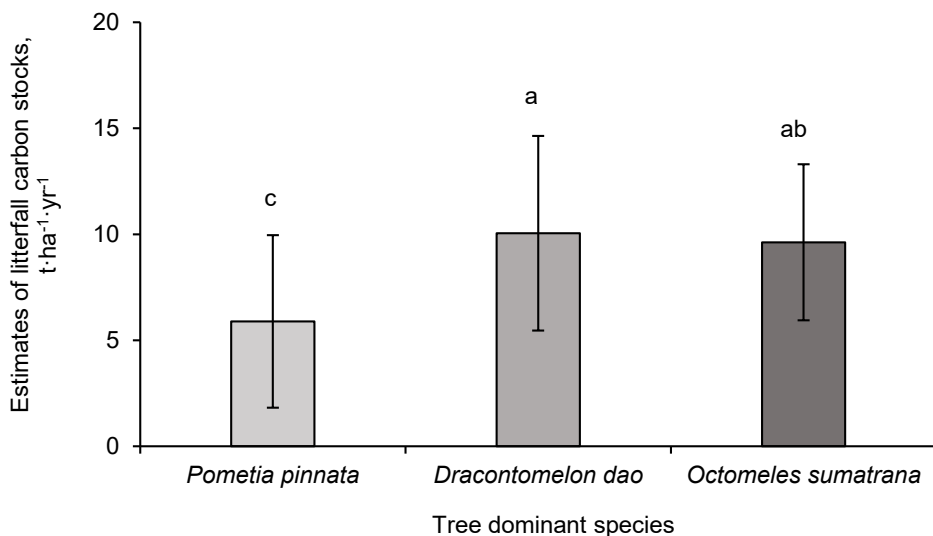


Fig. 4. Estimation of carbon stock in litterfall per year of dominant tree vegetation on 15-year fallow land in Womnowi Village, Sidey District, Manokwari Regency.

Note: The same letters above the bars indicate no significant difference based on the least significant difference test.

be highly dependent on climate and leaf senescence timing, resulting in variable values. Nevertheless, the high carbon estimates suggest a potential slowdown in litter decomposition rates, which is also influenced by soil nitrogen levels. High nitrogen levels in the soil can enhance vegetation growth, leading to increased biomass production and carbon stock (Song et al. 2024). This reasoning suggests that the nitrogen content in 15-year-old fallow land in Womnowi Village, Manokwari Regency, is likely sufficient to support traditional agricultural practices, indicating its potential for reuse.

The standard error (SE) values in Figure 4 provide an illustration that *O. sumatrana* is a species with relatively constant carbon stock from litterfall per week followed by *P. pinnata* and *D. dao*. These results are in line with the SE value of the estimated litterfall production value in a previous study (Susanto et al. 2020a). If the environmental control factor within a period of one year is relatively constant, then *O. sumatrana* is the species that contributes the most carbon to its litterfall followed by *P. pinnata* and *D. dao*. At the time of the study, *D. dao* was experiencing peak leaf shedding with high production of wet litterfall (especially leaves), so the estimated value of carbon stock per year in litterfall may be lower than the estimated value in Figure 4.

The estimated carbon stored from dominant tree litterfall in this study ranged from 5.73–9.89 t·ha⁻¹·yr⁻¹ (Fig. 4). This range is higher than the study by Schneidewind et al. (2019) on monoculture and conventional cocoa plantation ecosystems, namely 1.7–2.2 t·ha⁻¹·yr⁻¹. The correlation between canopy and litterfall volume is the reason for this difference in results. Tesfay et al. (2020) showed that the higher the canopy, the higher the litter-

fall production, so that carbon stock in the litterfall also increased. This study illustrates that 15-year-old fallow land with *P. pinnata*, *D. dao*, and *O. sumatrana* trees also contributed to storing carbon like forests in general when compared to monoculture farming systems.

Compared to several secondary forest ecosystems in tropical regions and fallow lands of similar age, the estimation of carbon stock from dominant tree litter in this study was notably higher. For instance, a study on secondary tropical forests aged 0–20 years, formerly plantations in hilly and lowland areas, reported a carbon stock range of 0.487 to 0.534 t·ha⁻¹·month⁻¹, equivalent to approximately 5.8–6.5 t·ha⁻¹·yr⁻¹ (Obando Guzman et al. 2023). In contrast, 15-year-old fallow lands dominated by shrubs such as *Chromolaena odorata* (L.) R.M.King & H.Rob. and *Imperata cylindrica* (L.) Raeusch. yielded carbon stocks below 1.5 t·ha⁻¹·yr⁻¹ (Toky and Ramakrishnan 1983). Similarly, 15-year-old fallow lands dominated by shrubs *Mimosa tenuiflora* (Willd.) Poir. in Caatinga dry forest ecosystem in Northeastern Brazil produced only 1.726 t·ha⁻¹·yr⁻¹ of carbon stock from litterfall (Moura et al. 2016). These findings suggest that fallow lands with dominant tree species such as *P. pinnata*, *D. dao*, and *O. sumatrana* contribute significantly higher levels of litter carbon stock. Furthermore, Gasheye et al. (2025) reported that ecosystem recovery in fallows from former shifting cultivation is accelerated when planted with tree secondary woody plants.

The carbon stock value of litterfall each week (Fig. 2) is never zero so that the carbon cycle runs well. The C and N content in an ecosystem is in a paired condition (Williams-Linera et al. 2021), if the N content is high, then soil fertility increases resulting in plants being able to absorb

large amounts of CO₂ to form biomass. When the fallow land was 15-year-old, the enriched fallow land in Womnowi Village, Sidey District, Manokwari Regency was indicated to have fertile soil. These results support the assumption of previous studies when tree vegetation was able to increase soil fertility (Budirianto et al. 2018).

Although shifting cultivation systems are a common problem found in tropical forests (Laskar et al. 2021), the subsequent succession process also contributes to storing carbon. The estimated value of carbon stock in litterfall is quite high per hectare in a year (Fig. 4), it is thought to remain constant because 52.75 % of 15-year-old fallow land in Womnowi Village, Sidey District, Manokwari Regency is dominated by the three types whose litterfall production was measured (Susanto et al. 2018). Windusari et al. (2012) found that natural succession areas dominated by transitional tree vegetation (70 %) provided the highest carbon stock in litterfall (3.14–3.08 t·ha⁻¹) in the PT Freeport Indonesia tailings deposition area. In addition, Behera et al. (2017) reported that dominant species growing in secondary forests generally have a greater number of individuals, thus potentially increasing litterfall production and carbon stocks. In line with this, in relation to the ability to

absorb carbon dioxide, secondary forests have a high carbon absorption potential due to the vegetation growth process and its photosynthesis capacity which continues to increase (Asmoro 2011, de Souza Almeida et al. 2021).

Litterfall carbon stocks and environmental parameters

Increases in temperature and humidity did not have a significant positive correlation ($p > 0.05$) with litterfall production (Table 1). *P. pinnata* wet litterfall production was independently affected by temperature and humidity, although it only had a correlation of c. 75 % ($p < 0.25$). *D. dao* and *O. sumatrana* tended to decrease litterfall production due to increased temperature. We assume that the time frame of our study was too narrow, and other environmental factors such as rainfall, humidity, and solar radiation intensity may have a greater influence on determining carbon stock production from litterfall of *D. dao* and *O. sumatrana*. According to BMKG data (2018), during the study period from March to June, rainfall reached 897 mm, accounting for approximately 38 % of the annual rainfall in 2018. Meanwhile, the annual temperature records from BMKG (2018) ranged from 27.2 to 27.8 °C. These

Table 1. Correlation values between temperature and humidity variables and litterfall production values.

No	Tree dominant species	Fresh litterfall production, g·week ⁻¹	Correlation with temperature (<i>r</i> , Pearson)	Correlation with humidity (<i>r</i> , Pearson)
1	<i>Pometia pinnata</i>	24.60	0.41 ns*	0.38 ns*
2	<i>Dracontomelon dao</i>	42.00	-0.22 ns	0.11 ns
3	<i>Octomeles sumatrana</i>	40.15	-0.42 ns	-0.06 ns
4	Average litterfall production of three tree species	35.58	-0.20 ns	0.18 ns

Note: The (-) sign indicates a negative correlation, ns – not significantly different $p < 0.5$, * – significantly different at $p < 0.25$ but not up to p -value 0.1.

data suggest that there is more variation in rainfall than in daily temperature, leading us to suspect that rainfall is a more significant factor influencing carbon stock production from litterfall in general.

Simultaneous increases in humidity tended to increase litterfall production (Table 1), so it is indicated that it has a greater effect on litterfall carbon stock than temperature factors. A year-long study by Souza et al. (2019) confirmed similar results, indicating that humidity was one of the factors determining 89 % of litter production and carbon stock. To understand the effect of temperature factors on carbon stock in litterfall, annual scale research is needed (Liu et al. 2024). A similar thing was expressed by Qiu et al. (2023), that annual temperature significantly affects 67 % of litterfall production in tropical ecosystems.

No research has specifically investigated the physiological characteristics of leaf shedding in *P. pinnata*, *D. dao*, and *O. sumatrana*. *P. pinnata* belongs to Sapindaceae family, while *D. dao* belongs to Anacardiaceae family, both of which exhibit periodic leaf shedding patterns. Anacardiaceae typically shed their leaves during the transition from the rainy to the dry season (Singh et al. 2020). Sapindaceae typically shed their leaves after fruiting (Thomson and Thaman 2006). Meanwhile, *O. sumatrana* belongs to the Tetramelaceae family, characterised by large leaf area and rapid growth (Jobin et al. 2024), and is thought to shed its leaves during the dry season. Therefore, further research on the phenology of these three plant species is necessary to better understand their leaf shedding patterns.

P. pinnata has a known wood density of $0.745 \text{ g}\cdot\text{cm}^{-3}$, has a biomass carbon stock of $156.6\text{--}164.4 \text{ t}\cdot\text{ha}^{-1}$ in $746 \text{ t}\cdot\text{ha}^{-1}$ (Asmoro 2011). In addition,

Budirianto (2011) showed that it stores more soil water content, so that water absorption is low. Low water absorption is thought to cause low stem water content and water content in litterfall. *P. pinnata* leaf litterfall has been reported to have a high C/N ratio of 25.2 (Rogers 2002) and has a dry litterfall weight percentage almost two times higher than *D. dao* and *O. sumatrana* leaf litterfall (Susanto et al. 2020a). Therefore, although the carbon stock in *P. pinnata* litterfall was the lowest, the low water content of this type of biomass indicates that it has the potential to store higher carbon in litterfall.

Conclusion

The 15-year-old fallow land in Womnowi Village, Sidey District, Manokwari Regency, dominated by *Pometia pinnata*, *Dracontomelon dao*, and *Octomeles sumatrana*, is estimated to produce litterfall carbon stock exceeding $5 \text{ t}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. The estimated carbon stock from litter production may vary if conducted over a longer period. Nevertheless, this research can serve as an initiator to study carbon stock in fallow land ecosystems, given the scarcity of such studies in Papua, Indonesia. The findings show that *P. pinnata* has an estimated annual litter carbon stock of $5.73 \text{ t}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, *D. dao* $9.89 \text{ t}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, and *O. sumatrana* $9.37 \text{ t}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. These results are inconsistent with expectations, as *P. pinnata*'s larger canopy cover should theoretically produce more litter and higher carbon stock. However, the opposite occurred, which may be attributed to the peak leaf senescence of *D. dao* and *O. sumatrana* during the study period, increasing their carbon stock.

Statistically, there is a significant difference ($p < 0.05$) in the carbon stock of *P.*

pinnata's litterfall compared to the other two species, while no significant difference ($p > 0.05$) exists between *D. dao* and *O. sumatrana*. Given the substantial carbon storage potential of the dominant tree species studied, it is highly recommended that local communities allow these tree groups to remain on their fallow lands. We predict that the estimated carbon stock in litterfall is close to the actual carbon stock, as more than 50 % of the cumulative relative dominance value at the research location is controlled by these three trees.

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Structure and chemical composition of birch and aspen fine roots growing at ash dumps

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Abstract

The aim of this study was to establish whether there are common peculiarities of root structure and ectomycorrhizas for two deciduous tree species growing on fly ash - artificial substrate with specific properties. The research was conducted in the southern taiga subzone of the Middle Urals at two ash dumps and typical zonal habitat. The roots of *Betula pendula* Roth and *Populus tremula* L. were studied. The following parameters were analysed: (i) soil concentrations of carbon (C), nitrogen (N), and phosphorus (P); (ii) micromorphological structure of fine roots and ectomycorrhizas; (iii) content of C and N in fine roots. The soils of ash dumps contained low amounts of N and high amounts of P compared with zonal soils. No species-specific features of fine root structure were detected for *B. pendula* and *P. tremula*. The size of roots, their vitality, the ratio of non-mycorrhizal and ectomycorrhizal roots, as well as the content and ratio of C and N did not differ between the trees of ash dumps and control area. Differences in the root structure between growing at ash dumps and in natural habitat *B. pendula* and *P. tremula* were generally low and affected only the features characterizing the size of the fungal mantle in ectomycorrhizas. The thickness of the mantle and its proportion in the total volume of ectomycorrhizae were less on the ash dumps than in the control habitat. Thus, the adaptation of the absorptive apparatus of *B. pendula* and *P. tremula* when living on fly ash occurs not due to autonomous rearrangements carried out by the plants, but probably by regulating the development of fungal symbionts.

Key words: artificial substrate, carbon, ectomycorrhizae, nitrogen, self-overgrowing, soil.

Introduction

Fine roots of plants are adapted to absorb water and nutrients in diverse habitat conditions. At the same time, most plants are not autonomous in terms of absorption of soil resources, since they interact

to varying degrees with different root symbionts, among which mycorrhizal fungi are the most common (van der Heijden et al. 1998, Wang and Qiu 2006, Brundrett 2009). The adaptation of plant roots and of the absorption function they perform under different edaphic conditions generally

occurs through three types of responses: (1) autonomous rearrangements carried out by the plant – reactions of the root system on the morphology level (Veselkin 2003, Veselkin et al. 2010, Roumet et al. 2016); (2) changes in the composition of the root symbionts with which they interact (Kikuchi and Futai 2003, Tedersoo et al. 2003, Saari et al. 2005, Ostonen et al. 2017); (3) alterations in the relationships among symbionts (Read et al. 2004, Chen et al. 2016, Konvalinková and Jansa 2016, Tedersoo and Bahram 2019).

We assumed that in order to study the mechanisms of absorptive root adaptation, it is necessary to analyse their structure in habitats with extreme or unfavourable conditions. One example of such environments is ash dumps – a special category of technogenic landscapes with a distinct substrate (Makhnev et al. 2002, Chibrik et al. 2011). The characteristics of technogenic ash substrates are generally unfavourable for plants due to: (1) low nitrogen content; (2) highly alkaline pH as a rule; (3) poor water-holding capacity due to sandy loam texture; (4) increased concentrations of some heavy metals (Pasinkova 1974, Makhnev et al. 2002, Gajic and Pavlovic 2018, Kostic et al. 2018, Uzarowicz et al. 2018, Nekrasova et al. 2020, Dergacheva et al. 2021, Nekrasova et al. 2022).

The areas of ash dumps that have not undergone recultivation become naturally overgrown, including by woody species. *Betula pendula* Roth and *Populus tremula* L. are pioneer tree species that frequently participate in the natural colonisation of ash dumps (Makhnev et al. 2002). The patterns of changes in the photosynthetic apparatus (Kalashnikova et al. 2021), as well as root morphology and biomass (Kalashnikova and Migalina 2012, Kalashnikova and Makhnev 2013),

have been studied among adaptations of trees of the genera *Betula* and *Populus* to ash dump conditions. To the best of our knowledge, the micromorphological and anatomical features of absorptive roots of boreal deciduous trees on such a specific substrate as fly ash were not studied previously. At the same time, it is possible that in the structure of the most active fine roots in terms of absorption, the features reflecting physicochemical characteristics of the substrates should be clearly visible.

According to the resource economics hypothesis (Grime 1977, Craine et al. 2009), plants at mineral-poor soils – such as ash substrates – are typically characterised by thick, long-lived, and slowly decomposed absorptive roots (Wahl and Ryser 2000, Perez-Ramos et al. 2012, Reich 2014). However, this expectation appears to conflict with empirical observations showing that many plants in such environments possess fine, short-lived absorptive roots (Ostonen et al. 2007, Holdaway et al. 2011, Prieto et al. 2015).

The rate of root turnover varies depending on the availability of soil resources. A common consequence of unfavourable soil conditions is an increase in the proportion of roots exhibiting cortex degradation (Spaeth and Cortes 1995, Visser et al. 1996, Schneider et al. 2017, Schneider and Lynch 2018). In poor soils, the biomass of ectomycorrhizal mycelium also tends to increase (Nilsson et al. 2005, Kjeller et al. 2012, Bahr et al. 2013), which increases soil volume exploited by plants (Smith and Read 2008) and, possibly, affect root morphological adaptations (Sun et al. 2010).

The content of C and N in the roots also varies depending on soil conditions (Elser et al. 2010, Tang et al. 2018). The roots in nutrient-poor soils are generally characterised by a long life and high C

content (Craine et al. 2005, Tjoelker et al. 2005, Roumet et al. 2016). The root life span is negatively correlated with the content of N in them (Reich 2014). The increased N content in fine roots of ectomycorrhizal trees is primarily associated with a large mycelial mass (Langley and Hungate 2003), which accounts for 10 to 40 % (Hogberg and Högborg 2002, Hobbie and Colpaert 2003, Ostonen and Lohmus 2003, Veselkin 2015). Non-mycorrhizal roots contain less N than mycorrhizal roots (Langley and Hungate 2003, Wurzbürger and Hendrick 2009).

The aim of this study was to establish the features of the structure of absorptive roots and ectomycorrhizas, as well as their C and N content for birch (*Betula pendula* Roth.) and aspen (*Populus tremula* L.) – dominant species naturally colonising ash dumps. We were interested in whether there are common to the two types of trees reactions of changes in the structure of roots and ectomycorrhizae, related to the characteristics of ash substrate. We made several assumptions about the structural features and chemical composition of roots and ectomycorrhizas that can be expected at ash dumps in contrast with nature soils: 1) smaller size (diameter) of roots and smaller thickness of the fungal mantle; 2) increased frequency of occurrence of roots with degraded cortex; 3) low content of N and high content of C.

Study Area

The study was conducted in the Middle Urals (Russia; 57°00'–57°20' N, 59°56'–60°27' E) within the southern taiga botanical and geographical district of the Sverdlovsk region. The moesorelief of the area is hilly and undulating with a predominance of altitudes of 300–350 m

a.s.l. The climate is moderately continental with long (5–6 months) cold winters and short (about 3 months) warm summers. The average annual temperature is +1.7...+2.4 °C, the average annual precipitation is 510–580 mm. The area is typically forested, with southern taiga pine and larch, less common pine-spruce and secondary birch and mixed forests. The forests have been repeatedly subjected to logging and fires.

Areas, habitats and sample site

The study was conducted in three areas: two technogenic ash dumps and a site with natural vegetation communities, which served as a control variant for the dumps.

Dump I (D I) is an ash dump of the Verkhnetagilskaya Power Plant (VPP, Verkhniy Tagil), formed between 1956 and 1965 because of fly ash storage after brown coal combustion. The dump area is 125 ha, its surface has been levelled. As a result of self-overgrowing of the ash surface in about 50 years, the areas with forest vegetation were formed on the dump. The samples were collected in deciduous forest area dominated by *Betula pendula* and *Populus tremula* with occasional occurrence of *Pinus sylvestris* L.; there are 26 species of vascular plants per 400 m² in the ground cover; the most abundant are *Pyrola rotundifolia* L., *P. minor* L., *Orthilia secunda* (L.) House, *Deschampsia cespitosa* (L.) P.Beauv. The names of plant species are given follow the WFO Plant List (2017). Young, poorly differentiated soils (technosols) have formed in the top 20 cm of the ash substrate in the studied community of dump I (Nekrasova et al. 2020).

Dump II (D II) is an ash dump of the Sredneuralskaya power plant (SPP, Sredneuralsk), formed between 1936 and

1968 because of fly ash storage from brown coal combustion. The area of the dump is 104 hectares, the surface has been levelled. As a result of natural overgrowth of the ash surface over 50 years, forest areas were formed. The samples were collected in mixed coniferous-deciduous forest dominated by *Betula pendula*, *Populus tremula* and *Pinus sylvestris* and young growth of *Salix caprea* L. and *Prunus padus* L.; there are 27 species of vascular plants per 400 m² in the ground cover, predominantly *Equisetum pratense* Ehrh., *Trifolium medium* L., and *Peperomia rotundifolia* (L.) Kunth. Young soils have formed in the forest community of dump II (Nekrasova et al. 2022).

Natural forest communities, designated as 'control' (Cont), were selected at 3–7 km from D I and about 50 km from D II. They were represented by birch forest with domination by *Betula pubescens* and *B. pendula*, with single trees of *Pinus sylvestris* and *Picea obovata* Ledeb. Forty-eight species of vascular plants per 400 m² were found in the ground cover, among them *Calamagrostis arundinaceae* (L.) Roth, *Aegopodium podagraria* L., and *Rubus saxatilis* L. predominated.

Methodology

Three sample plots of 20 × 20 m were established in each habitat of D I and D II and 2 sample sites of the same size – in the background area. In total, plant roots and soils were sampled from 8 sites.

Soil sampling and physico-chemical analysis

Three soil profiles were laid on each test site. The soils at the ash dump and con-

trol area were classified as Technosols and Retisols, respectively, according to the WRB criteria (IUSS Working Group WRB 2022). Soil sampling for analytical studies was done in detail, layer by layer, taking into account the visible boundaries of the forming soil horizons. The pH values were determined in an aqueous suspension at a soil-to-water ratio of 1:2.5 using an Anion 4100 potentiometer (Russia); the content of available phosphorus (P₂O₅) – according to Chirikov, using a UV Probe-1650 spectrophotometer (Japan); the content of total organic carbon (TOC) – by the wet combustion method according to Tyurin; total nitrogen (TN) – by the Kjeldahl wet combustion method (using the Heating Digestor DK 20 Velp and Dilation Unit UDK 127 Velp, Italy) finishing by titration (Arinushkina 1970). To establish the physico-chemical characteristics of the root layer of young soils (depth 0–20 cm), weighted means of indicators were calculated, considering the contribution of each horizon.

Plant sampling and chemical analysis

Sampling was conducted in July 2017 (D I and control sites) and 2018 (D II). The tree roots were excavated from a depth of 0–10 cm. Five root samples of each species were collected per site and washed from the soil in running water in the laboratory. Then the fine roots were selected for elemental analysis and microscopy according to the criteria outlined by McCormack et al. (2015). Absorptive roots of primary structure with a diameter of less than 0.5 mm were classified as fine roots, while all thicker roots were excluded from further analysis.

From two to five subsamples of approximately 5 g of fresh roots were prepared for each species on each site. One part

of each sample was fixed in 70 % ethanol to study the micromorphological features of the roots and mycorrhizal formation. Another part of the sample was dried for 48 h at 60 °C to determine the elemental composition. The content of C and N was determined in micro-samples of 3–5 mg in two analytical replicates using a CHNS analyser (EURO EA 3000 (EuroVector, Italy) at the N.N. Vorozhtsov Novosibirsk Institute of Organic Chemistry, SB RAS, with a determination accuracy <0.3 %.

Determination of root structure and ectomycorrhizae

Between 10 and 20 roots were taken from each sample to determine their micromorphological structure on thin cross sections. Thin sections with a thickness of 10–20 µm were made using a rotary microtome after freezing in water. The sections were analysed at ×200–450 magnification. The following parameters were recorded: presence or absence of a fungal mantle; root radius excluding the fungal mantle; mantle thickness; radius of the central cylinder. The following indicators were calculated: 1) Proportion of Mycorrhizal Roots (PMR); 2) Proportion of Mantle volume in Ectomycorrhizas (PME) – calculated according to Veselkin (2015); 3) Proportion of Fungal volume in Fine Roots (PFFR) – determined as the product of PMR and PME.

Data analysis

The mean value of each parameter per sample site was used as the unit of analysis for statistical evaluation. To compare mean values, one- and two-way analyses of variance (ANOVA) were applied, with pairwise differences assessed using

Tukey's test.

Results

Physico-chemical properties of soils

The soils of two ash dumps differed in their degree of acidity, but were similar in other parameters – the content of TOC, TN and available P. The soils of D I habitat differed in a more alkaline pH from the background (control) soils, whereas soils from the D II dump had pH values closer to those of the control soils, within a slightly acidic range (Fig. 1).

The TOC content in all studied soils ranged from 4 % to 6 %, with no significant differences among the various habitats. However, the TN content in the soils of the ash dumps was 2–3 times lower than in the control. The difference between the combined estimates for both ash dumps and the control area, according to one-way ANOVA, was statistically significant: $F_{(1,7)} = 25.08$; $P = 0.0016$. In contrast, the content of available P was an order of magnitude higher in the soils of both ash dumps compared to the control soils. The differences between the combined estimates for both ash dumps and the control ones were highly significant: $F_{(1,7)} = 50.96$; $P = 0.0002$. Thus, the main differences in the physico-chemical composition of ash dump soils, compared to those of the control, were their low availability of TN and high availability of P.

Micromorphological features of roots and ectomycorrhizas

The key question for our analysis of the micromorphological features of absorptive roots and ectomycorrhizas was – whether there were any taxon-specific peculiarities

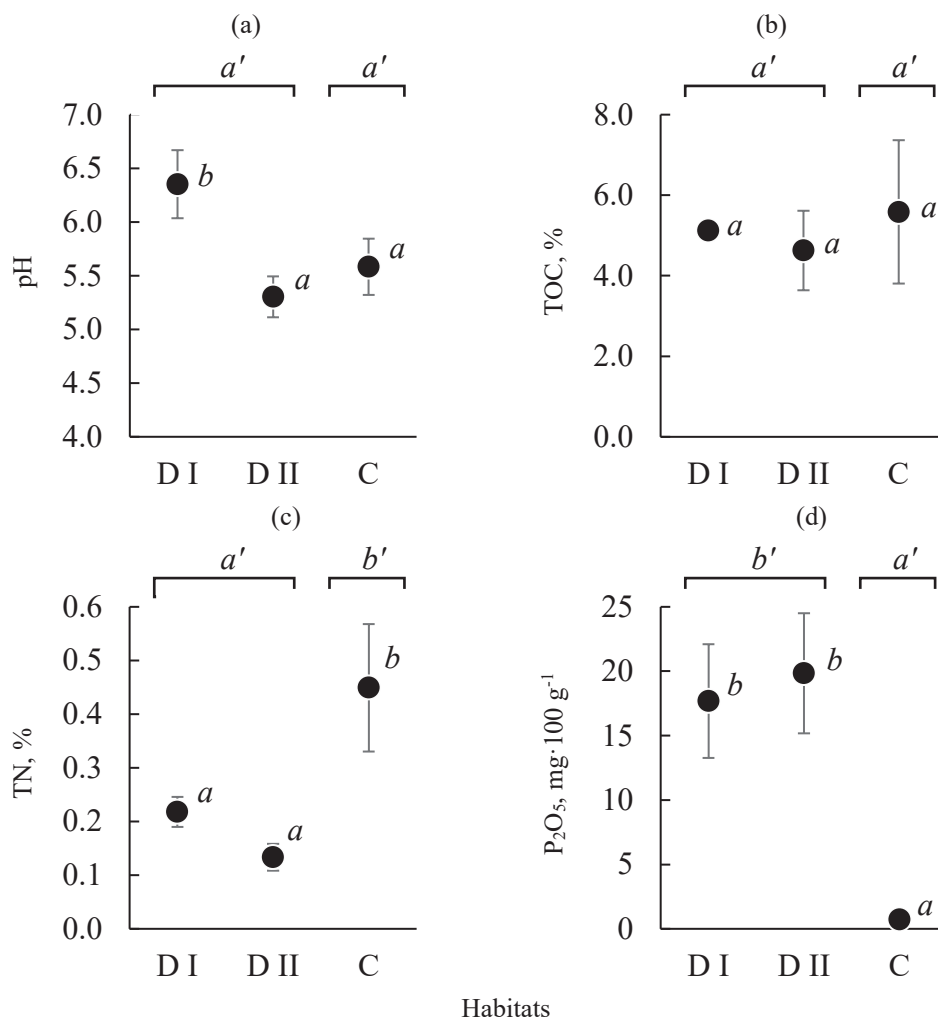


Fig. 1. Mean values of physico-chemical properties of soils in different habitats: (a) pH; (b) total organic carbon; (c) total nitrogen; (d) available phosphorus.

Note: Vertical lines represent the standard error of the arithmetic mean. Latin letters without an apostrophe next to the symbols indicate statistically homogeneous values of features according to Tukey's test for a separate analysis of three habitats: D I, D II, and control (C). Latin letters with an apostrophe, at the top of the diagrams indicate homogeneous values according to Tukey's test for a combined analysis, comparing the ash dumps (D I + D II) with the control (C).

related to tree species? To address this, a series of two-factor ANOVAs were conducted, with 'tree taxon' and 'habitat' as the factors (Table 1). No significant differences were found between *Betula pen-*

dula and *Populus tremula* in terms of the proportion of living roots, PMR, root size, fungal mantle thickness, or other features. Crucially, there was no significant interaction between the factors 'tree taxon' and

Table 1. Two-factor ANOVA results for root parameters.

Characteristics	Factors of root parameter variability						R^2_{adj}
	[1] – tree taxon; $dF = 1$		[2] – habitat; $dF = 2$		[1]×[2]; $dF = 2$		
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
Root structure and ectomycorrhizae characteristics							
Proportion of living roots	1.76	0.2179	2.55	0.1324	0.16	0.8550	0.07
Proportion of mycorrhizal roots	0.91	0.3644	2.93	0.1045	0.55	0.5950	0.12
Root radius in mycorrhizae	0.52	0.4882	4.10	0.0542	1.16	0.3566	0.24
Thickness of the fungal mantle	0.24	0.6342	8.82	0.0076	0.43	0.6650	0.54
Proportion of mantle volume in ectomycorrhizas	1.03	0.3373	6.96	0.0149	0.80	0.4795	0.51
Proportion of fungal volume in fine roots	0.05	0.8249	4.68	0.0405	0.33	0.7279	0.29
Characteristics of the elemental composition of roots							
C, %	2.16	0.1760	2.31	0.1552	1.39	0.2974	0.15
N, %	0.15	0.7110	6.99	0.0147	0.93	0.4305	0.45
C/N	0.02	0.9042	8.27	0.0091	0.73	0.5098	0.49

Note: The table presents the results of two-factor ANOVA assessing the effects of tree taxon and habitat on root structural traits, ectomycorrhizal characteristics, and elemental composition parameters. Values with a grey background are significantly different at $P < 0.05$.

'habitat'. This indicates that the root structure characteristics of *B. pendula* and *P. tremula* were consistent across different habitats. Based on these results, the samples from the two tree taxa were pooled for further analysis.

Among the micromorphological features of absorptive roots and ectomycorrhizas, habitat-dependent variability was observed only in traits related to fungal mantle development: specifically, mantle thickness (Fig. 2), and the PME and PFFR parameters (Fig. 3). Traits related to root vitality, the ratio of ectomycorrhizal to non-mycorrhizal roots, as well as root cross-sectional size did not vary significantly across habitats. No signs of cortical degradation were observed in 60–80 % of the roots from the combined *B. pendula* and *P. tremula* samples. On average, 45–60 % of the roots in different habitats were mycorrhizal, i.e. bear-

ing a fungal mantle, while 40–55 % were non-mycorrhizal. Based on the diagrams (Fig. 2), a slight trend towards reduced root vitality and lower PMR values at the ash dumps may be suggested; however, these trends were not statistically significant. Similarly, the mean root radius at the ash dumps was slightly lower than in the control area, but these differences were not statistically confirmed. Overall, the two explanatory factors used in the ANOVA (tree taxon and habitat) accounted for only a small proportion (from 7 to 24 %) of the total variability in root vitality, PMR, and root size.

At the same time, these two predictors accounted for more than 50 % of the variability in the characteristics of fungal mantle development, with this variability being primarily associated with the differences between habitats. The mean mantle thickness in *B. pendula* ectomycorrhizas was

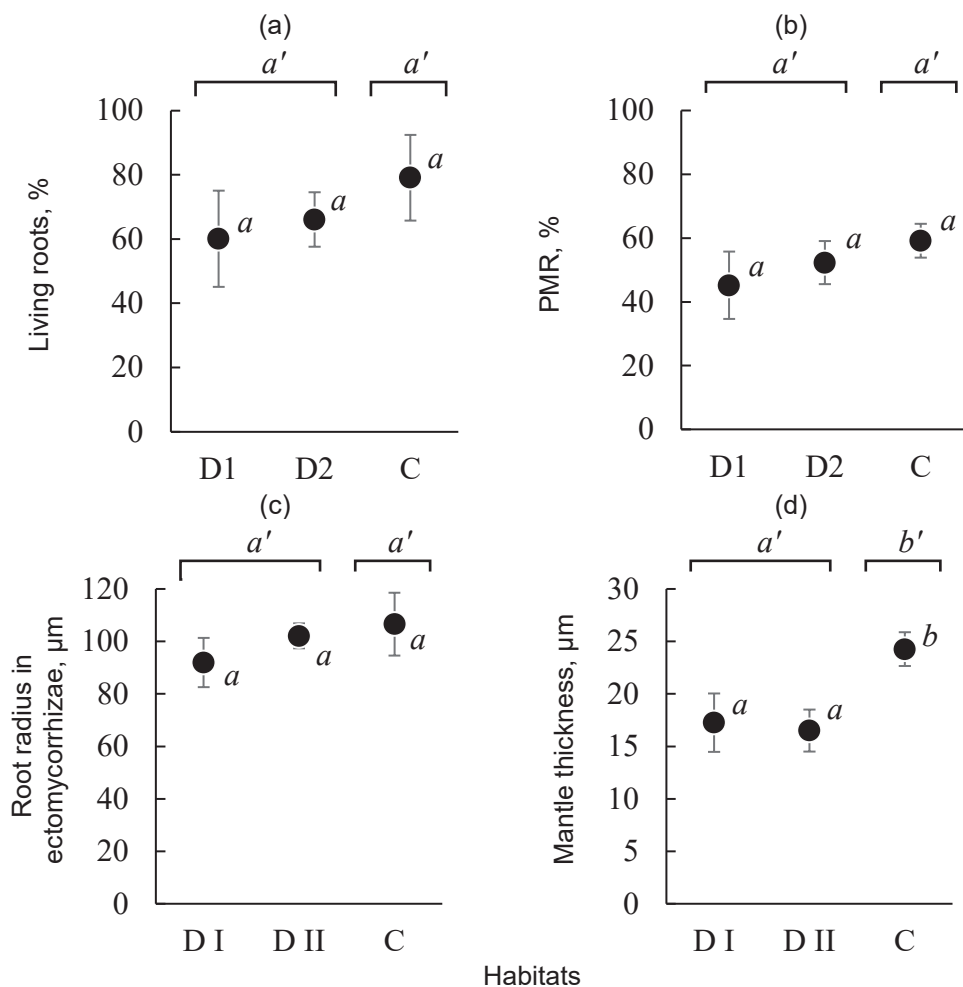


Fig. 2. Mean values of structural features of roots and ectomycorrhizas of *Betula pendula* and *Populus tremula* across different habitats: (a) living root share; (b) proportion of mycorrhizal roots; (c) root radius in ectomycorrhizae; (d) mantle thickness.

Note: See legend of Figure 1 for details on statistical notation and group comparisons.

16–18 μm at the ash dumps, compared with 25 μm in the control habitat. Similarly, in *P. tremula*, the mantle thickness at the ash dumps was 16–17 μm , while in the control habitat it reached 23 μm . These values indicate similar mantle thicknesses in the two deciduous tree species and a reduction of 27–35 % at the ash dumps compared with the control site.

The proportion of mantle volume in ectomycorrhizas in *B. pendula* and *P. tremula* was 26–29 % at the ash dumps and 31–35 % in the control habitat, with differences being statistically significant. The proportion of fungal volume in fine roots was 13–14 % at the ash dumps and 20 % in the control habitat, again with statistically significant differences.

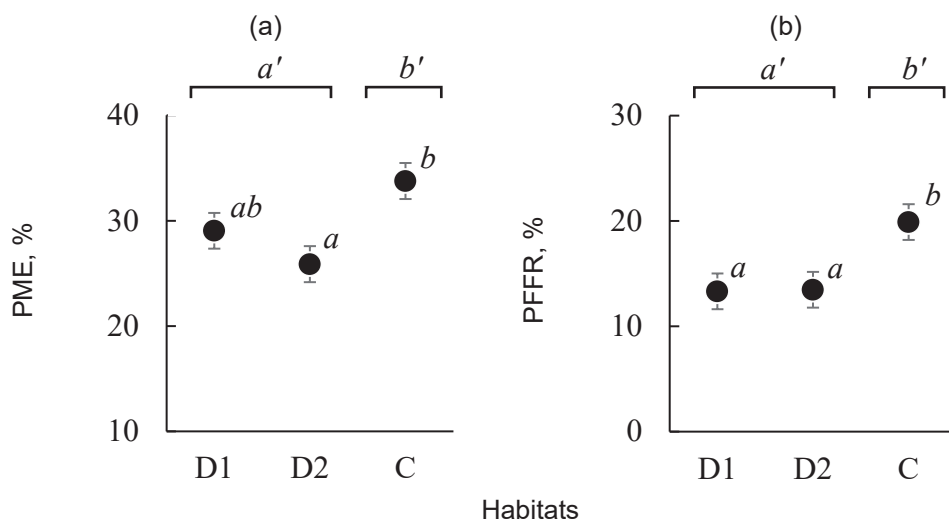


Fig. 3. Mean values across habitats for *Betula pendula* and *Populus tremula*: (a) proportion of mantle volume in ectomycorrhizas; (b) proportion of fungal volume in fine roots.

Note: See the legend of Figure 1 for details on statistical notation and group comparisons.

Elemental composition of roots

The carbon content in fine roots did not differ between *B. pendula* and *P. tremula* (Fig. 4). The observed range of variation in *B. pendula* was 42.3–47.2 % and in *P. tremula* – 40.9–47.1 %. No significant differences in root carbon content were detected between habitats. Similarly, nitrogen content did not differ between the two tree species. However, in contrast to carbon, the nitrogen content varied between habitats. In roots from ash dump D I nitrogen content ranged from 1.11 to 1.53 %, while in those from ash dump D II it was higher, ranging from 1.46 to 1.84 %. The nitrogen levels in roots from the control habitat were intermediate between the two ash dumps.

Discussion

N and P content in soils developing on ash dumps significantly differs from that in

zonal ones. Ash dump soils contain several times less N and several times more P compared to the control area. The recorded ranges of N and P content in the control soils correspond to the typical values reported for regional soils – 1.5–12.9 mg $P_2O_5 \cdot 100\text{ g}^{-1}$ and 0.21–0.35 % total N (Firsova and Rzhannikova 1972, Gafurov 2008). At the same time, the conclusion regarding N depletion and P enrichment in ash dump soils is well consistent with previously reported findings and is well substantiated (Nekrasova et al. 2020, Nekrasova et al. 2022).

Against the background of pronounced differences in the chemical composition of ash dump soils, the structural changes in fine roots of *Betula pendula* and *Populus tremula* found in these areas were relatively minor. Approximately half of all fine roots were colonised by ectomycorrhizas both at the dumps and in the control area, and the transverse root diameter did not differ significantly between habitats. However, the thickness of the fungal mantle,

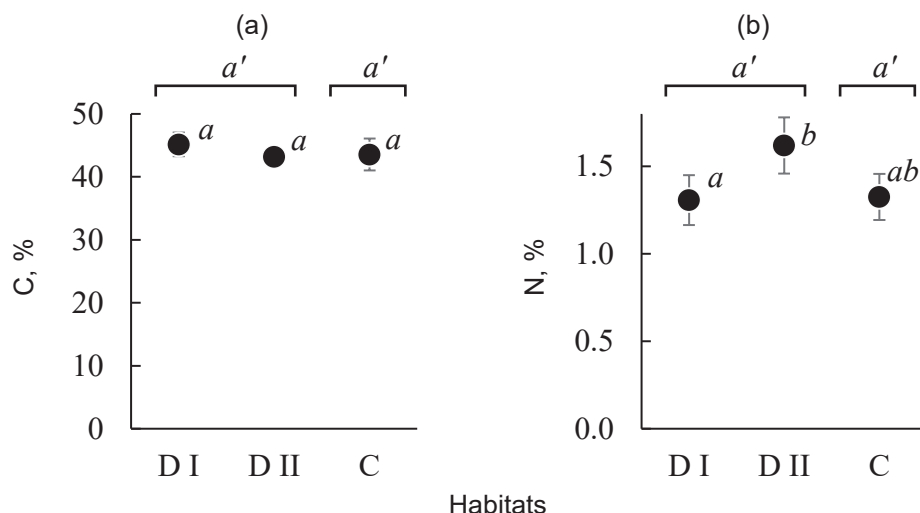


Fig. 4. Mean values of elemental composition parameters in absorptive roots of *Betula pendula* and *Populus tremula* across different habitats: (a) carbon content; (b) nitrogen content.

Note: See the legend of Figure 1 for details on statistical notation and group comparisons.

the relative mantle thickness, and the proportion of fungal volume in fine roots were all lower in the ash dump sites than the control habitat.

Based on published data (Huang and Eissenstat 2000, Garnett et al. 2009, Comas et al. 2012, Paz-Ares et al. 2022), we expected that variations in N and P availability would lead to changes in root thickness. This expectation formed part of our initial hypothesis. However, we did not observe such a response in our study. A possible explanation is that most of the published data refer to herbaceous species and tree species associated with arbuscular mycorrhizae, whereas our study focused on ectomycorrhizal trees.

The uptake of N and P is mainly regulated by the fungal component in ectomycorrhizal plants (Ostonen et al. 2011), by changing the amount of mycelium in particular (Zhu et al. 2023). Dominant fungal taxa (Ostonen et al. 2017) or the size of fungal mantle can change in environmen-

tal gradients (Veselkin 2008, Zaitsev et al. 2008, Sizonenko and Dubrovskiy 2018). We established a similar reaction, since we observed higher variability in the size of fungal mantle, but not in the size of tree roots.

Our second hypothesis, predicting an increased frequency of roots with degraded cortex at ash dumps, was not confirmed. The vitality of the absorptive roots of *B. pendula* and *P. tremula* did not differ in the considered range of conditions. This finding contrasts with several previous studies, where an increase in the proportion of roots with degraded cortex was interpreted as a consequence of unfavourable soil conditions (Veselkin et al. 2010, Schneider et al. 2017, Schneider and Lynch 2018).

The third hypothesis, which predicted a higher content of carbon (C) and a lower content of nitrogen (N) in the roots at ash dumps, was also not confirmed. No differences in the carbon content in tree roots

between habitats were found, although it is known that the C content in roots can change with changes in the C/N ratio in the soil (Craine et al. 2005, Tjoelker et al. 2005, Roumet et al. 2016).

The content of N in the roots of *B. pendula* and *P. tremula* varied more than C content and different between habitats. According to literature data, an increase in total N in the roots of ectomycorrhizal plants can be attributed either to a greater contribution of mycelium, which is relatively enriched in N compared to root tissues (Langley and Hungate 2003, Garnett et al. 2009), or to a high enzymatic activity of the parenchyma of the primary root cortex (Rivera Perez Carmen et al. 2022, Sun et al. 2023). However, we do not have sufficient data to discuss the validity of these explanations.

We did not identify species-specific features in the fine root structure of *B. pendula* and *P. tremula*. The features of root and ectomycorrhiza of *B. pendula* and *P. tremula* structure, as well as the characteristics of C and N content in them, had similar ranges of values and directions of changes depending on external conditions. It can be noted that the observed PME values of 26–35 % of the ectomycorrhizal volume in *B. pendula* and *P. tremula* generally correspond to a wide range of this parameter estimates in conifers: 3–7 % (Satomura et al. 2003); 14–28 % (Hobbie and Colpaert 2003, Osttonen and Lohmus 2003, Veselkin 2015) and 39–40 % (Fogel and Hunt 1979, Vogt et al. 1982).

Conclusion

The content of the main biogenic elements – N and P – in the soils on artificial substrate of ash dumps differed markedly

from their content in zonal soils. Despite these differences, root size, vitality, the ratio of non-mycorrhizal to ectomycorrhizal roots, as well as the C and N content and their ratio in tree roots at ash dumps did not differ significantly from those at the control site. Differences in the structure of *Betula pendula* and *Populus tremula* roots growing on ash were generally minor and affected only the features characterizing the size of fungal cover in ectomycorrhizas. The thickness of the mantle and its proportion in the total volume of ectomycorrhizas was less in the trees of ash dumps. Thus, established results in a broad sense can be interpreted as follows: the adaptation of absorptive apparatus of the trees to ash substrate occurs by regulating the development of fungal symbionts. To improve our understanding of the ways of underground tree organs adaptations to the conditions of ash dumps, it would probably be worthwhile to study the composition of ectomycorrhizal fungi in different habitats.

Fine plant roots and mycorrhizal fungal hyphae are important source of organic carbon in the root layer of soils. Our results showed that when C concentrations in roots cannot be empirically determined, interspecific (between *B. pendula* and *P. tremula*) and biotopic (between different habitats) variability can be ignored when calculating their contribution to the C balance, since they are not large. The situation with N concentration in the roots is different, therefore, when calculating their contribution to the balance of N, interspecific variability can be ignored, but biotopic variability should be taken into account. These conclusions are important for predicting the sequestration of C and N in young soils and for calculating carbon accumulation by forest carbon farms.

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Integrating GIS and traditional ecological knowledge for customary forest governance: a case study from Toro community, Indonesia

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Abstract

Indigenous forest governance has received growing recognition worldwide, yet its integration with modern spatial technologies remains limited in Southeast Asia. This study explores the integration of GIS with Traditional Ecological Knowledge (TEK) to analyse the structure and function of the Customary Forest Management Unit (CFMU) in Toro customary forest, Central Sulawesi, Indonesia. Toro community, renowned for its intricate customary zoning, faces contemporary challenges of tenure insecurity, external encroachment, and ecological pressure, creating an urgent need for hybrid governance approaches. A mixed-methods framework was employed, combining high-resolution satellite imagery, GIS-based Multi-Criteria Evaluation (MCE), GPS surveys, and participatory mapping with 35 community stakeholders, complemented by interviews and field observations. Toro forest, covering 20,276.98 ha, was classified into three functional categories: limited production forest (11,629.41 ha; 57.35 %), protected forest (6,292.22 ha; 31.03 %), and permanent production forest (2,355.35 ha; 11.62 %). MCE model achieved 88.7 % accuracy (Kappa = 0.83). Six customary zones were delineated – Wana Ngkiki, Wana, Pangale, Pahawa Pongko, Oma, and Balingkea – each serving distinct ecological and socio-cultural purposes. Overlay analysis revealed strong congruence: more than 90 % of core zones (Wana Ngkiki and Wana) coincide with steep slopes and intact forests, while over 70 % of peripheral zones (Oma and Balingkea) correspond with agroforestry mosaics. Findings confirm that Toro's concentric zoning is not only a cultural construct but also ecologically rational, simultaneously safeguarding biodiversity in core areas and supporting diversified livelihoods through agroforestry and non-timber forest products. This dual outcome underscores the role of customary governance as both an ecological safeguard and a foundation for green economic pathways. Beyond its local relevance, Toro case contributes to global discourses on biocultural conservation and sustainable development. By demonstrating how TEK and GIS can be synergistically integrated, this study provides a replicable and adaptive model for strengthening indigenous forest governance, enhancing tenure security, and embedding cultural values within contemporary conservation frameworks.

Key words: forest management unit, participatory mapping, spatial analysis, sustainable forest, traditional ecological knowledge.

Introduction

To Ngata Toro community of Central Sulawesi has sustained its forest ecosystems for generations through traditional ecological knowledge (TEK). Yet contemporary pressures – socio-economic transitions, agricultural intensification, demographic shifts, and policy interventions – now threaten this system. These pressures generate land-use conflicts, encroachment, biodiversity loss, and risks of unsustainable exploitation. While customary governance relies on oral traditions and communal norms, it lacks tools to address such complex changes. Hence, there is a need for an approach that combines TEK with GIS to strengthen local legitimacy, secure tenure recognition, and improve adaptive management. Toro illustrates the gap: TEK ensures cultural authority but lacks spatial precision, whereas GIS provides analytical capacity but is rarely adapted to indigenous contexts.

Forests are vital ecosystems supporting biodiversity, regulating climate, sustaining hydrological cycles, and providing resources for human well-being (Savilaakso et al. 2021, Shekhar and Dutta 2022). They harbour about 80 % of terrestrial biodiversity, store 2.4 billion tonnes of carbon annually, and support 1.6 billion people, many from indigenous and rural communities (FAO 2020). Forest products and ecosystem services add major ecological and economic value (Maffi and Woodley 2010, Bettinger et al. 2013). Yet forests face global deforestation and degradation, with Indonesia losing about 684,000 ha annually, threatening both ecosystems and indigenous livelihoods (Larson et al. 2010, Zalles et al. 2024).

One of the persistent challenges in forest conservation lies in governance. Formal state-led forest management models

have often marginalised indigenous systems, resulting in tenure insecurity and the erosion of traditional stewardship practices (Toledo 1999, Dancer 2021). Indigenous peoples have historically managed forests sustainably through customary laws and TEK. However, the lack of formal recognition of these customary rights leaves indigenous territories vulnerable to external encroachments, commercial exploitation, and development-driven deforestation. In Indonesia, the Constitutional Court Decision No. 35/PUU-X/2012 represented a landmark shift by affirming that customary forests are distinct from state forests. The Constitutional Court clarified that customary forests (*hutan adat*) are no longer classified as state forests but as forests located within indigenous territories, contingent upon state recognition of the indigenous community and its customary boundaries. This ruling provides the legal basis for indigenous tenure claims and obliges local governments to formalise recognition. In Toro case, the decision is pivotal because geospatial evidence from participatory mapping, GPS-tracked boundaries, and local land-use zoning strengthens the recognition process and reduces tenure ambiguity. Yet, implementation remains limited, with more than 13 million ha of indigenous forests still awaiting formal recognition (Simarmata 2024).

Amid ongoing environmental and governance challenges, there is increasing recognition of the potential of indigenous forest governance as a viable pathway toward conservation and sustainable development. The integration of indigenous knowledge systems with contemporary technologies offers a promising approach to enhancing forest governance frameworks. Among these technologies, GIS has emerged as powerful tools for spatial analysis, natural resource mapping, and

participatory land-use planning (Bryan 2011, Chang 2019). GIS facilitates the documentation of traditional territories, supports conflict resolution, enhances land tenure claims, and improves forest monitoring systems. However, despite its potential, the application of GIS in customary forest contexts remains underutilised, especially in Southeast Asia (McCall and Dunn 2012).

Previous studies in various Indonesian indigenous communities have demonstrated the benefits of integrating customary knowledge with modern governance frameworks. In Rantau Kermas, Jambi Province, customary zoning systems have been revitalised through community mapping initiatives (Lega et al. 2024). Similarly, in Hutumuri Village, Ambon, institutional strengthening of indigenous forest groups has enhanced sustainability outcomes (Lelapary et al. 2024). In Lombok, the Wetu Telu community combines traditional spiritual practices with forest conservation, while in East Kalimantan, the Hemaq Beniung community exemplifies successful customary forest management amidst modern pressures (Rusdianto et al. 2023, Jayadi et al. 2024). Although these examples underline the resilience of indigenous management systems, the systematic integration of GIS as a decision-support tool in these contexts remains rare (McCall and Dunn 2012).

Toro community manages about 21,750 ha through six zones – Wana Ngiki, Wana, Pangale, Pahwa Pongko, Oma, and Balingkea (Golar et al. 2023, Palaguna et al. 2025). Each has ecological and socio-economic functions, reflecting sustainable land use. What distinguishes Toro is its proactive adoption of GIS not only for advocacy but also for planning, zoning optimisation, and long-term resource management. This provides an important

opportunity to test TEK–GIS integration for reinforcing governance, ensuring cultural integrity, and maintaining resilience.

Furthermore, Toro case carries significant implications beyond Indonesia. Globally, there is increasing emphasis on biocultural conservation approaches that recognise the inseparability of biological diversity and cultural diversity (Maffi and Woodley 2010, Gavin et al. 2015). The integration of indigenous governance with modern spatial planning aligns with emerging paradigms in landscape-scale conservation and the rights-based approach to natural resource management. This biocultural perspective emphasises the interdependence between Indigenous peoples and biodiversity, as thoroughly explored by Toledo (1999) in his foundational work on indigenous ecological knowledge. Methodological frameworks such as those developed by Tobias (2009) reinforce the relevance of combining traditional knowledge systems with spatial technologies.

Given this context, this study aims to design and implement a GIS-based CFMU tailored to Toro community's traditional system. By employing a mixed-methods approach that integrates rigorous spatial analysis with participatory mapping and qualitative inquiries into indigenous knowledge, this research seeks to: 1) classify Toro forest areas based on ecological and customary criteria, 2) develop a spatially explicit management framework rooted in local governance traditions, and 3) offer a replicable model for enhancing indigenous forest management practices through technological empowerment. The study contributes to the broader discourse on indigenous rights, sustainable forest governance, and biocultural conservation in an era of escalating environmental and social change.

Materials and Methods

Study area

The study was conducted in Toro customary forest, located in Ngata Toro Village, Kulawi Subdistrict, Sigi Regency, Central Sulawesi, Indonesia ($1^{\circ}25'21''$ S, $120^{\circ}01'39''$ E) (Fig. 1). Covering approximately 20,276.98 ha, Toro landscape comprises a heterogeneous mosaic of tropical montane forests, agroforestry systems, and secondary regrowth areas. The elevation ranges from 600 to 2,300 m a.s.l., characterised by steep slopes, diverse vegetation cover, and high annual rainfall exceeding 2500 mm (Golar et al. 2023).

Data collection

A mixed-methods approach was adopted, integrating quantitative spatial analysis with qualitative socio-cultural research. This triangulation design ensured rigorous data validation across both ecological and cultural dimensions (McCall and Dunn 2012, Creswell and Clark 2017).

Spatial data

High-resolution Sentinel-2A imagery (10 m, 2023) was processed using ArcGIS 10.8 to generate land-use and forest-function maps. Topographic maps (1:50,000) were obtained from the Geospatial Information Agency of Indonesia (Geospatial

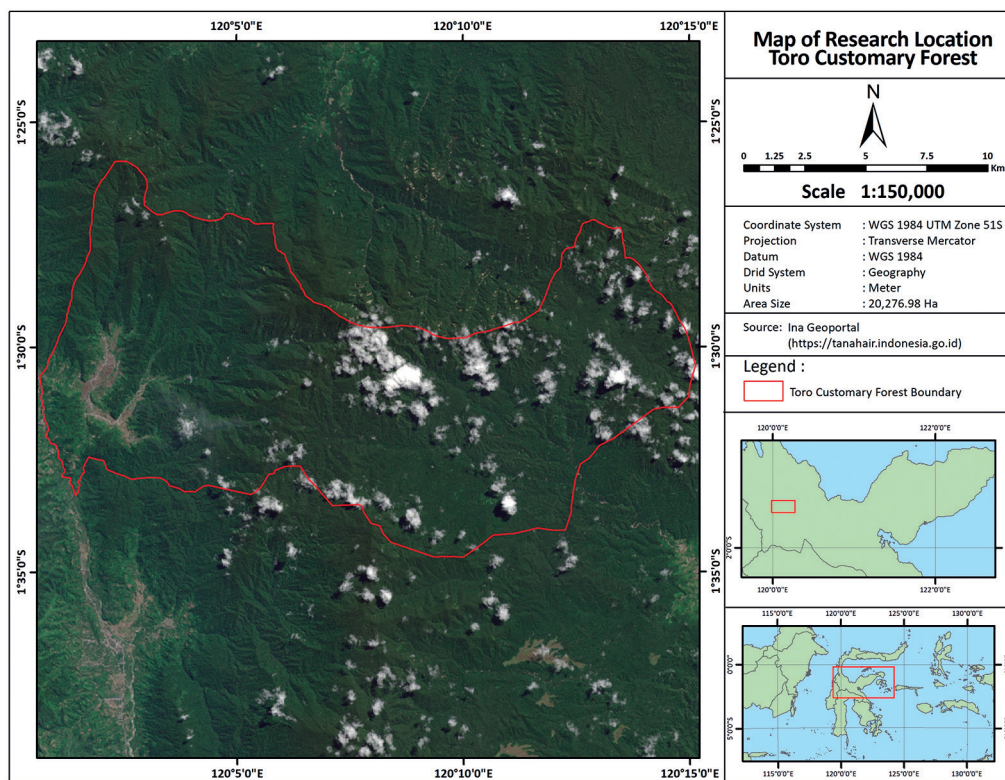


Fig. 1. Map of study area.

Information Board, BIG). Ground-truthing and GPS surveys were conducted between March and July 2024 to validate classifications and delineate boundaries. Ancillary datasets – slope, soil, and rainfall – were sourced from the Ministry of Environment and Forestry. All data were projected to WGS 84 / UTM Zone 51S (EPSG:32751) for spatial consistency.

Socio-cultural data

Purposive sampling identified 15 key informants, including customary leaders, elders, and forest users with knowledge of zoning and land use. This number was sufficient to capture both legitimacy and practical knowledge. Data collection involved semi-structured interviews, field verification using GPS, and participatory observation during rituals, harvesting, and patrols. Customary regulations, historical maps, and folklore archives were also reviewed. Agreement among respondents on land-use categories was calculated using formula (1):

$$\text{Agreement Index (\%)} = \frac{\text{Number of respondents agreeing}}{\text{Total respondents}} \cdot 100 \quad (1)$$

Interview data were coded and analysed using Miles and Huberman's (1994) interactive model, comprising reduction, display, and verification. This ensured both statistical rigour and cultural validity.

GIS spatial analysis

Forest functions were modelled using Multi-Criteria Evaluation (MCE) by overlaying four layers: slope, soil, vegetation, and rainfall. Each layer was assigned a weight: slope (30 %), soil (25 %), vegetation (25 %), rainfall (20 %), following established GIS decision methods (Malczewski 2006, Jayasinghe and Yoshida

2010). The suitability of the forest function classes was calculated using the formula (2):

$$S = 0.30 \cdot f(\text{slope}) + 0.25 \cdot f(\text{soil}) + 0.25 \cdot f(\text{vegetation}) + 0.20 \cdot f(\text{rainfall}), \quad (2)$$

where each factor $f(\cdot)$ was normalised (0–1), with higher values indicating higher protection priority. Based on Minister of Agriculture Decree No. 683/KPTS/UM/8/1981, three forest function classes were defined:

1. Protected forest: $S \geq 0.70$,
2. Limited production forest: $0.50 \leq S < 0.70$, and
3. Permanent production forest: $S < 0.50$.

The classification accuracy reached 88.7 % with a Kappa index of 0.83, indicating strong agreement. Spatial modelling was conducted using ArcGIS 10.8 software. Participatory mapping sessions complemented the GIS analysis, where printed satellite imagery was annotated by community members to delineate sacred zones, traditional forest boundaries, and resource extraction areas (McCall and Minang 2005).

Thematic qualitative analysis

Interview transcripts and observation notes were analysed using inductive thematic coding to uncover key socio-ecological values embedded in Toro's customary land-use practices. Emergent themes included customary harvesting norms, sacred site protections, knowledge transmission systems, and governance structures. These qualitative insights were integrated into the spatial planning framework to develop a Customary Forest Management Unit (CFMU) model. The model reflects both the ecological functionality of the landscape and Toro community's traditional zoning system, aligning with

co-management principles in biocultural conservation (Maffi and Woodley 2010, Gavin et al. 2015).

Data validation

To ensure data reliability, a three-step triangulation was conducted:

1. Field Verification – GPS data were cross-checked against remote sensing classifications for consistency.

2. Community Workshops – Participatory workshops with 35 local stakeholders validated preliminary zoning maps and thematic interpretations. A total of 35 participants were involved in the participatory mapping process. This number represents stakeholder representatives rather than random individuals. The selection was based on a purposive approach to ensure inclusion of all key groups relevant to customary forest management. Specifically, participants consisted of: (i) Toro customary council (Ngata Toro elders, *totua ngu-ku*), (ii) heads of the six customary zones, (iii) women and youth representatives, (iv) farmer group leaders, and (v) representatives from the village government and local forestry office. The number 35 was considered adequate to capture the diversity of perspectives without making the group too large, which could reduce the effectiveness of consensus-building discussions. The composition therefore ensured both legitimacy (through recognised community leaders) and inclusivity (through women and youth voices).

3. Expert Consultations – Academic researchers and local forestry officials reviewed outputs and provided technical recommendations.

This iterative validation approach strengthened the credibility and legitimacy of the final forest zoning, ensuring that both scientific and cultural knowledge sys-

tems were accurately represented (Bryan 2011).

Results

This study produced two principal outcomes:

1. the spatial classification of Toro customary forest based on biophysical parameters, and

2. the design of a CFMU structured according to traditional Toro zoning practices.

The integration of GIS spatial analysis with indigenous knowledge resulted in a detailed and culturally grounded forest management framework, aligning with contemporary models of biocultural landscape governance (Maffi and Woodley 2010, McCall and Dunn 2012).

Spatial classification of forest areas

Using GIS-based MCE, Toro customary forest, covering approximately 20,276.98 ha, was classified into three functional categories as presented in Table 1. As shown in Figure 2, the forest area is divided into protected, limited production, and permanent production classes based on ecological parameters.

Table 1. Functional classification of Toro customary forest.

Forest function	Area, ha	Share, %
Limited production forest	11,629.41	57.35
Protected forest	6,292.22	31.03
Permanent production forest	2,355.35	11.62
Total	20,276.98	100.00

This classification was based on a weighted ecological formula that integrated slope, soil type, vegetation cover, and

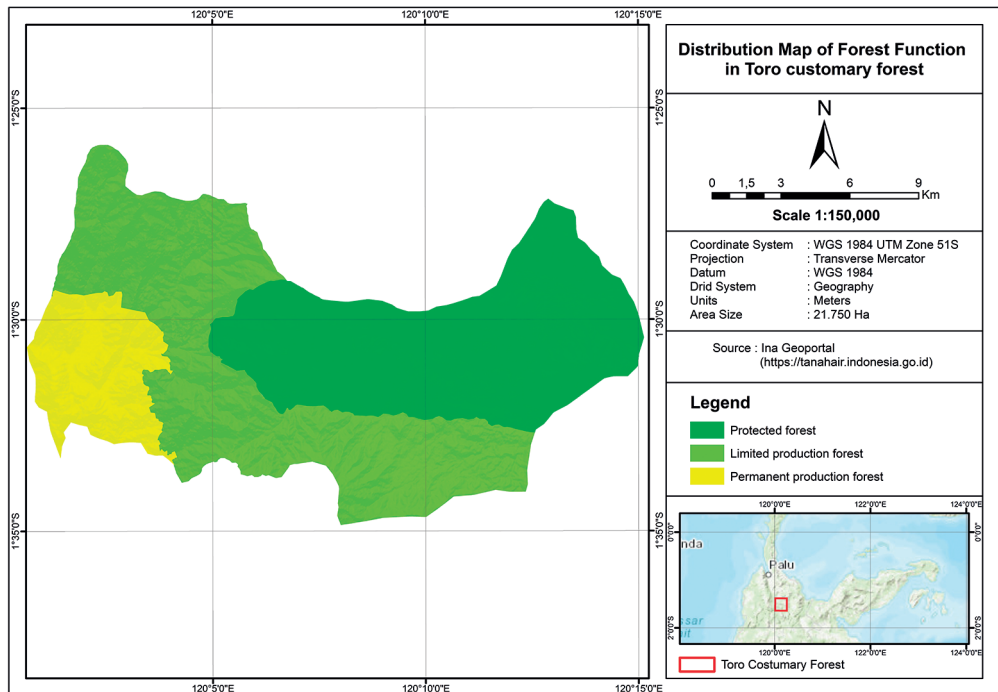


Fig. 2. Zoning map of Toro customary forest based on forest functions.

rainfall intensity – parameters adapted from national forest function standards (Ministry of Agriculture 1981) and supported by GIS-based MCE methodologies (Malczewski 2006, Jayasinghe and Yoshida 2010). The dominance of limited production forest suggests that timber harvesting remains a key livelihood strategy, albeit governed by ecological thresholds to ensure long-term sustainability (Awal et al. 2023).

Spatial analysis revealed strong correlations between protected forest zones and areas with steep slopes ($>40\%$) combined with high rainfall ($>2500\text{ mm}\cdot\text{year}^{-1}$), thus empirically validating Toro's customary zoning logic. Conversely, moderate slopes with lower erosion risk were classified as production forest, consistent with local practices of selective use.

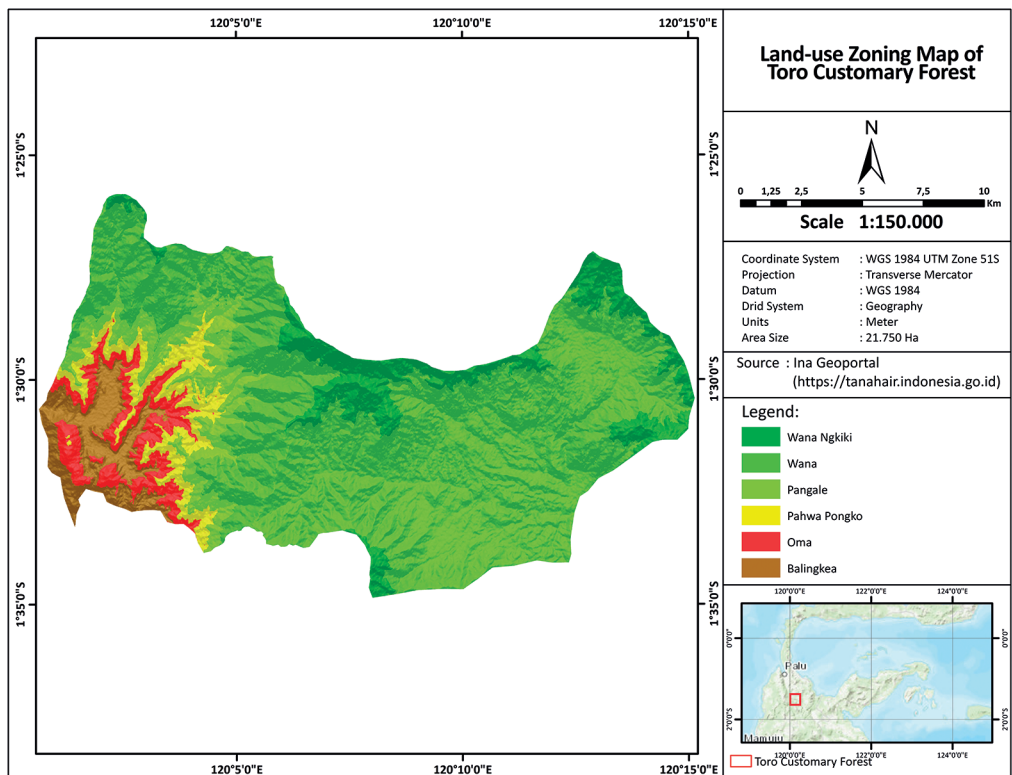
The overlay of biophysical maps with community knowledge (sacred zones, boundaries, and use areas) resulted in a hybrid classification framework that reflects both scientific rigour and cultural accuracy (Bryan 2011, McCall and Dunn 2012).

Design of customary forest management unit (CFMU)

Building upon the spatial classification results, a culturally grounded zoning system was delineated through participatory mapping sessions with Toro community. Table 2 presents the division of six customary forest zones, each with specific ecological and socio-cultural functions. Figure 3 then illustrates the spatial distribution of these zones across Toro customary forest.

Table 2. Division of customary forest zones.

Customary zone	Area, ha	Share, %	Primary function
Wana Ngkiki	2,300	10.57	Core conservation: sacred forest, steep terrain
Wana	11,290	51.91	Buffer zone; sustainable non-timber resource use
Pangale	2,950	13.57	Agroforestry, community gardens, selective timber use
Pahawa Pongko	1,460	6.71	Regrowth forest; previously cultivated areas
Oma	1,820	8.37	Permanent gardens; annual crops (e.g. cocoa)
Balingkea	1,930	8.87	Short-cycle cultivation: vegetables, maize, cassava
Total	21,750	100.00	

**Fig. 3. Distribution map of six customary zones in Toro customary forest.**

Note: The six customary zones are Wana Ngkiki (core), Wana (buffer), Pangale (limited use), Pahawa Pongko (fallow), Oma (gardens), Balingkea (settlement).

This zoning system reflects Toro community's traditional land classification, integrated with ecological functionality

through participatory GIS mapping.

The overlay analysis revealed clear ecological differentiation among the six

customary zones. Approximately 92 % of Wana Ngkiki and Wana coincide with slopes steeper than 40 % and intact, dense forest cover, validating their designation as strict protection areas. In contrast, over 70 % of Oma and Balingkea overlap with slopes below 15 % and agroforestry mosaics dominated by cocoa, coffee, candlenut, and mixed gardens. Pangale displayed a transitional profile, with around 54 % of its area characterised by forest regrowth interspersed with community gardens and selective timber plots. Pahawa Pongko, accounting for 1460 ha, corresponded largely to regrowth forests and previously cultivated fallow areas. These quantitative results demonstrate that Toro's concentric zoning is not only a cultural construct but also ecologically consistent with topographic gradients and land-cover distributions.

The slight discrepancy between the CFMU area (21,750 ha) and the GIS-analysed area (20,276.98 ha) reflects overlapping land-use classifications in transitional buffer areas – a common characteristic in dynamic customary systems.

Interpretation of zones

The following description summarises the ecological and socio-cultural roles of Toro zones:

1. Wana Ngkiki acts as the innermost sacred zone, equivalent to strict protection areas under global conservation frameworks (IUCN Category Ia).
2. Wana functions as a buffer, allowing regulated NTFP extraction, such as rattan and *Aquilaria* spp. (agarwood).
3. Pangale and Oma are designed for agroforestry and permanent garden systems, offering a balance between food security and canopy retention.
4. Pahawa Pongko indicates managed

fallow zones, showcasing Toro community's understanding of forest regeneration.

5. Balingkea supports short-cycle farming, fulfilling subsistence needs without compromising ecological function.

Spatial visualisation

The composite map of Toro customary zones (Fig. 3) illustrates a concentric zoning pattern, where Wana Ngkiki forms the inner core, followed by Wana, Pangale, Pahawa Pongko, Oma, and Balingkea outwardly. The concentric zoning pattern of Toro customary forest is reflected through the spatial arrangement of its six zones, which radiate outward from the most sacred and strictly protected core (Wana Ngkiki) to the more accessible and utilised periphery (Balingkea). This pattern was confirmed by participatory mapping exercises, where elders and zone heads delineated boundaries consistent with oral traditions and cultural norms. Spatial data from GPS tracks and overlay analyses further verified that each zone forms relatively concentric bands following watershed ridgelines and slope gradients. Field observations supported this structure: the innermost zones (Wana Ngkiki and Wana) correspond to steep, closed-canopy montane forest, while the outer zones (Oma and Balingkea) coincide with gently sloping lands used for agroforestry and settlement. Thus, the concentric pattern is not only cultural but also empirically supported by topographic and land-cover data. A principle shared with other indigenous mapping systems globally (Tobias 2009).

Significance of integration

CFMU demonstrates how indigenous spatial systems, when enhanced by GIS tools, can generate forest governance

models that are both culturally resilient and ecologically sound. Participatory mapping empowered the community to reaffirm customary rights and strengthen local institutions (McCall and Minang 2005). Notably, the strong alignment between Toro community's zoning and ecological risk zones (steep slopes, rainfall) offers empirical validation of TEK and its role in biodiversity stewardship (Toledo 1999, Gavin et al. 2015).

Discussion

TEK results

TEK findings revealed a nuanced understanding of customary forest zoning among Toro community. Local knowledge, passed down through generations, delineates zones such as Wana Ngkiki, Wana, Pangale, Pahwa Pongko, Oma, and Balingkea, each with distinct ecological functions and customary rules. Respondents emphasised the role of these zones in maintaining water sources, conserving biodiversity, and sustaining livelihoods. These insights align with studies showing that TEK can effectively complement scientific forest management approaches by providing spatially explicit cultural and ecological indicators.

GIS results

GIS-based spatial analysis corroborated much of the TEK, with high congruence between mapped customary zones and observed land-cover types. For example, Wana Ngkiki corresponded to high-elevation dense forest areas with minimal anthropogenic disturbance, while Oma and Balingkea overlapped with agroforestry and settlement zones. The integration

of GPS field data, satellite imagery, and land-use classification enhanced the precision of these delineations, confirming the ecological validity of the community-defined zones.

Integration of TEK and GIS

The consistency observed in the results – where over 90 % of core zones align with steep slopes and intact forest, and more than 70 % of outer zones overlap with agroforestry mosaics – provides empirical support for the integration of TEK and GIS. This alignment illustrates that Toro's concentric zoning is not only culturally legitimate but also ecologically and economically rational. Integrating TEK with GIS offers a powerful framework for enhancing forest management and biodiversity conservation. TEK provides deep, place-based ecological insights passed down through generations, while GIS offers spatial and analytical tools for mapping and modelling ecological processes.

The synergy between TEK and GIS merges scientific rigour with indigenous wisdom, offering a transformative framework for participatory governance and ecosystem resilience (McCall and Dunn 2012, Berkes et al. 2000). In real-world practice, TEK informs the cultural rationale behind zoning decisions, while GIS visualises and monitors these zones with spatial accuracy. This synergy leads to more adaptive, inclusive, and resilient forest management strategies (Johnson et al. 2016).

Comparison and broader implications

When comparing TEK, GIS results, and relevant literature, a strong convergence emerges in recognising the value of participatory mapping for sustainable forest

governance. Similar integrative approaches have been reported in other indigenous territories across Southeast Asia, where blending local knowledge with geospatial technologies has improved both conservation outcomes and community empowerment. Toro case reinforces the importance of co-producing spatial data, ensuring that forest zoning reflects not only ecological priorities but also cultural heritage and traditional rights.

Toro CFMU exemplifies a resilient social-ecological system, where GIS-derived ecological thresholds (e.g., slope >40 % for protected zones) are reinforced by customary institutions. For instance, the practice of *pamali* (taboos) in Wana Ngkiki prohibits extraction, mirroring IUCN Category Ia protections. This dual validation – scientific and cultural – enhances compliance, as observed in other indigenous systems (Berkes et al. 2000). However, climate-induced shifts in vegetation (Zalles et al. 2024) may challenge static zoning. Toro's adaptive response – evident in seasonal *pahawa pongko* (fallow rotations) – suggests TEK's capacity to accommodate ecological flux. Yet, formalising such dynamism in GIS models requires iterative community-scientist collaboration, as demonstrated in Canada's Indigenous Guardian programmes (Johnson et al. 2016).

The integration of TEK and geospatial technologies has emerged as a transformative approach in community-based forest management. Previous studies across different regions of the world demonstrate the potential of participatory GIS (PGIS) to strengthen indigenous land governance. For instance, in Rantau Kermas, Jambi Province, community mapping significantly reduced deforestation rates compared with state-managed forests (Lega et al. 2024). Similarly, in the Solomon Islands,

PGIS combined with species diversity surveys revealed that sacred sites supported substantially higher levels of biodiversity (Aswani and Lauer 2006). In Canada, participatory 3D LiDAR mapping enriched ecological knowledge by identifying seasonal use areas and microhabitats that had not been documented by conventional science (Johnson et al. 2016).

Compared with these experiences, Toro case contributes a distinct innovation. Toro community not only employ GIS for documentation or advocacy purposes, but also integrates it directly with a concentric zoning system rooted in cultural and ecological logic. The measurable congruence between Toro's core zones and steep, intact forests, and between its peripheral zones and agroforestry mosaics, highlights a unique alignment between cultural traditions and ecological indicators. Unlike other cases, where conservation or livelihood functions tend to dominate separately, Toro's hybrid model simultaneously ensures biodiversity protection in the core while sustaining diversified livelihoods in the periphery. This dual outcome positions Toro as a replicable model of biocultural governance, bridging indigenous wisdom with spatial technologies under contemporary conservation paradigms.

Challenges and institutional gaps

Despite advances, challenges persist. First, absence of a Forest Information System hampers monitoring and adaptive management, leaving community maps underutilised. Second, technical capacity remains limited; without sustained training, communities risk dependence on external facilitators. Third, legal ambiguity following Constitutional Court Decision No. 35/PUU-X/2012 leaves Toro and others vulnerable to encroachment. Address-

ing these gaps requires enabling policies, institutional support, and long-term investment. Methodologically, reliance on elder informants may underrepresent youth perspectives (Jayadi et al. 2024). Sacred zones such as Wana Ngkiki are rooted in oral histories, which 2D GIS captures poorly. New tools like 3D participatory mapping (Lega et al. 2024) could integrate spiritual narratives with spatial data.

Economic potential and sustainability pathways

Toro forest landscape offers considerable opportunities for green economic development through the sustainable utilisation of non-timber forest products (NTFPs) such as agarwood (*Aquilaria* spp.), damar (*Agathis dammara* Lamb.), Java pepper (*Piper cubeba* L.), and rattan (*Calamus* spp.). These commodities hold high market value, both locally and internationally. By engaging in participatory innovation platforms that promote value-added processing, market linkages, and inclusive decision-making, the community can strengthen NTFP value chains, improve livelihoods, and sustain ecological balance (Auch and Pretzsch 2020). The concentric zoning not only safeguards core conservation areas but also delineates peripheral zones (Oma and Balingkea) that provide tangible alternative economic resources. Overlay analysis confirmed that these outer zones are dominated by agroforestry mosaics (cocoa, coffee, candlenut, and mixed gardens) and settlements, while Pangale supports rattan, honey, and medicinal plants. Ground-truth surveys further validated these findings, demonstrating diversified land use in the periphery alongside intact forest conditions in the core.

These findings confirm that Toro zon-

ing system simultaneously secures conservation in the core zones and enables diversified livelihoods in the periphery. Such a dual outcome strengthens the argument that customary forest governance can function both as an ecological safeguard and as a foundation for community-based green economy initiatives.

Comparative perspectives from global Indigenous communities

Experiences from Indigenous territories worldwide illustrate how participatory GIS has become an essential tool for strengthening tenure, documenting land-use practices, and supporting ecological stewardship. In Brazil, Indigenous communities map *terra preta* sites to safeguard both cultural heritage and biodiversity (Winkler-Prins and Aldrich 2010). In Canada, participatory GIS approaches have helped First Nations integrate cultural values into planning and secure legal recognition of land rights (Turner and Berkes 2006, Tobias 2009). Similarly, in Africa, the Maasai use mapping techniques to protect sacred grazing lands, while in Papua New Guinea, community-driven GIS documentation of marine tenure systems has led to nationally recognised marine protected areas (Aswani and Lauer 2006).

These cases highlight a global trend where indigenous mapping bridges traditional ecological knowledge and modern spatial technologies. What distinguishes Toro, however, is the precision and ecological validity of its concentric zoning system. The measurable congruence between inner zones (steep, intact forests) and outer agroforestry mosaics demonstrates that customary rules align closely with biophysical indicators. This outcome contrasts with other examples where mapping primarily supports advocacy or

legal claims; in Toro, GIS is embedded directly within governance, reinforcing both ecological sustainability and cultural continuity.

By combining ecological data with spiritual and cultural logics, Toro offers a replicable model of biocultural governance. Its dual achievement – preserving biodiversity in the core while sustaining diversified livelihoods in the periphery – shows how Indigenous communities can adaptively manage landscapes within contemporary conservation frameworks.

Theoretical implications for biocultural conservation

This study contributes to the theoretical discourse on biocultural conservation, which emphasises that biological and cultural diversity are co-evolved and interdependent (Maffi and Woodley 2010, Gavin et al. 2015). Toro's hybrid governance system exemplifies this principle by embedding land-use rules in both ecological indicators and cultural meanings. The participatory use of GIS in Toro also illustrates the practice of *counter-mapping*, widely recognised as a political and legal tool to challenge dominant spatial narratives and assert indigenous territoriality (Peluso 1995, Bryan 2011). In this context, maps are not merely technical outputs but instruments for negotiation, recognition, and community-based planning.

Beyond counter-mapping, Toro case reflects an emerging model of hybrid governance where customary institutions, spatial technologies, and legal frameworks converge. This approach challenges the conventional dichotomy between 'traditional' and 'modern' management, offering instead a synergistic model that can inform national and global conservation policies. Furthermore, Toro's govern-

ance model aligns with the Sustainable Development Goals, particularly SDG 13 (climate action), SDG 15 (life on land), and SDG 16 (peace, justice, and strong institutions).

These theoretical insights are not abstract but are directly illustrated in Toro's concentric zoning system, where ecological data (slope, vegetation, rainfall) converge with cultural logics of sacredness and stewardship. This confirms that biocultural conservation is not only a normative framework but also an empirically demonstrable reality when TEK and GIS are combined.

Conclusions

This study demonstrates that the integration of Traditional Ecological Knowledge (TEK) and GIS provides a culturally grounded and scientifically robust framework for sustainable forest governance. The GIS-based Multi-Criteria Evaluation classified 20,276.98 ha of Toro customary forest into protected (31.03 %), limited production (57.35 %), and permanent production (11.62 %) categories, with a high overall accuracy (88.7 %; Kappa 0.83). These findings were further validated through participatory mapping with 35 community representatives, confirming the legitimacy of Toro's zoning system. Overlay analysis revealed that more than 90 % of core zones (Wana Ngkiki and Wana) coincide with steep slopes and intact forests, while over 70 % of peripheral zones (Oma and Balingkea) align with gentle slopes and agroforestry mosaics.

The results confirm that Toro's concentric zoning is not only a cultural construct but also ecologically consistent. This dual validation emphasises the capacity of customary governance to simul-

taneously safeguard biodiversity in core zones and sustain diversified livelihoods in peripheral areas through agroforestry and non-timber forest products. Such outcomes position Toro's zoning system as a living example of how ecological conservation and community-based green economy initiatives can be harmonised.

Nevertheless, institutional and structural challenges remain. Weak technical capacity, fragmented forest information systems, and the slow implementation of Constitutional Court Decision No. 35/PUU-X/2012 continue to limit the full recognition and consolidation of customary forests. Strengthening institutional support, ensuring continuous training, and advancing legal recognition are therefore critical to sustaining Toro Customary Forest Management Unit (CFMU) and embedding it within broader forest governance frameworks.

Beyond its local significance, Toro case contributes to global discourses on biocultural conservation. It illustrates that cultural logics and ecological indicators can be effectively aligned through participatory GIS, creating adaptive governance models that reconcile indigenous stewardship with contemporary conservation paradigms. In this sense, Toro's CFMU represents not only a replicable model for empowering indigenous communities but also a theoretical contribution to the practice of biocultural conservation, where ecological resilience and cultural continuity advance hand in hand.

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Land-use change driven by artisanal gold mining around Taï National Park, Côte d'Ivoire

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Abstract

Taï National Park (PNT) is drained mainly by Hana River, which rises outside it. It provides a source of water for the park's many animals and is an important ecosystem for maintaining Ivorian biodiversity. However, the river has been severely degraded by artisanal and illegal gold mining. It carries a load of pollutants into the Park from mining activities conducted upstream on the outskirts of the PNT. The general objective of this study is to study the development of land use, in particular, the dynamics of illegal artisanal gold panning in Hana River source area between 2021 and 2024 to improve park management. To achieve this, the methodology relies on the processing of Sentinel-2 satellite images. The classification of these images was carried out using the Random Forest algorithm and validated with several performance tests. Analysis of land-use change showed a significant increase in artisanal gold panning and food crops, with annual increases of 120.5 % and 14.1 % respectively. However, fallow land and water areas experienced a decrease in surface area, with regression rates of 21.7 % and 28.5 % respectively. The study highlighted the risks and dangers of illegal artisanal gold panning for Taï National Park. To preserve this natural heritage, it is imperative to prohibit gold panning activities in the peripheral zone of the Park and to implement measures for the ecological restoration of abandoned sites.

Key words: artisanal gold panning, cocoa farming, Hana River, spatio-temporal, sustainable management, water pollution.

Introduction

Taï National Park (PNT) in south-west Côte d'Ivoire is the largest forest massif in

West Africa (Fauret et al. 2018). It contains over 1800 plant species, 54 % of which are endemic to the Guinean Rainforest (Yeo et al. 2020). PNT contains more

than 140 mammal species, including 12 endemic to West Africa, 234 bird species, 56 amphibian and 42 reptile (OIPR 2015). Owing to its ecological and biological significance, it was designated a UNESCO Biosphere Reserve in 1978 and inscribed on the World Heritage List in 1981. This Park, which is one of the pillars of Côte d'Ivoire's biodiversity conservation policy, is drained by tributary streams of Cavalily River not shown on the map below F1. The most important of these is Hana River, which rises outside the PNT, beneath cocoa plantations, and crosses it from east to west (OIPR 2006). Hana River is thus the main source of water for animals and provides important ecosystems for maintaining biodiversity.

Research carried out around the headwaters of this river, on the periphery of the Park, has shown that the landscape has been severely degraded, mainly as a result of uncontrolled artisanal gold mining (OIPR 2021). Artisanal mining operations in this area are considered informal and/or illegal due to the lack of regulation. As a result, ore is mined clandestinely on a small scale. Indeed, artisanal miners use rudimentary mineral processing and extraction processes (Hilson et al. 2017). This poor practice actively contributes to deforestation, soil and water pollution from the chemicals used to recover gold (World Health Organization 2017, Kinyondo and Huggins 2021). The river drains a load of pollutants from artisanal gold mining upstream into the Park (Diarrassouba et al. 2020). As practiced, mining poses a real danger to the many known and lesser-known fauna in Taï National Park.

To combat this phenomenon and ensure better quality water entering the Park, we need to understand the spatio-temporal dynamics of artisanal gold mining in the landscape around the source of

Hana River. Detecting artisanal gold mining sites in PNT peripheral zone remains a major challenge not only for park protection officers, but also for scientists. Today, there is a wide range of solutions for monitoring changes in forest cover, deforestation, regeneration or artisanal gold mining. Earth observation data and tools offer solutions for measuring and detecting these changes reliably and repeatedly over large areas (Jofack Sokeng et al. 2019). Indeed, institutions such as the United States Geological Survey (USGS) and the European Space Agency (ESA) have developed approaches to detect, map, monitor, and analyse the expansion of artisanal gold mining across various regions (LaJeunesse Connette et al. 2016, Snapir et al. 2017, de Lucia Lobo et al. 2018, Forkuor et al. 2020). In Côte d'Ivoire, the work of Ngom et al. (2022) demonstrated the capacity of Sentinel-2 imagery to map illegal mining sites.

Mapping the land-use dynamics of Hana River landscape could provide managers with the data they need to develop and implement a strategy for preserving and monitoring it in order to sustainably safeguard the biodiversity of the Taï National Park. The present study aims to understand the evolution of land-use, in particular, the dynamics of illegal artisanal gold mining in the landscape of the source of Hana River between 2021 and 2024. To achieve this objective, the methodology relies on Sentinel-2 satellite images and the Random Forest algorithm.

Materials and Methods

Study area

The study area is located in south-western Côte d'Ivoire, on the outskirts of the

Taï National Park. It covers an area of 4013 ha between 05°54'00" and 05°58'48" north latitude and 06°55'22" and 06°51'21" west longitude (Fig. 1). Hana River rises in this area, beneath agricultural plantations. Point O (Latitude: 5°54'37" N and Longitude: 6°53'01" W) is the entry point of Hana River into the Park.

Data collection

Satellite images for the years 2021–2024 were obtained from the European Space Agency (2021–2024) using Google Earth Engine (GEE) based on a vector file of the study area. The images were acquired

by Sentinel-2A sensor. Monthly composites were generated. This frequency was chosen because artisanal gold mining sites can appear and expand rapidly, and a monthly temporal resolution allows for timely detection of such short-term changes while minimising the impact of cloud cover. Spectral bands with a spatial resolution of 10 m (Blue, Green, Red and Near Infrared) were utilised. In addition, spectral indices were calculated to better exploit the spectral richness of Sentinel-2 data. These indices include the Normalised Difference Vegetation Index (NDVI), which is sensitive to vegetation; the Normalised Difference Water Index

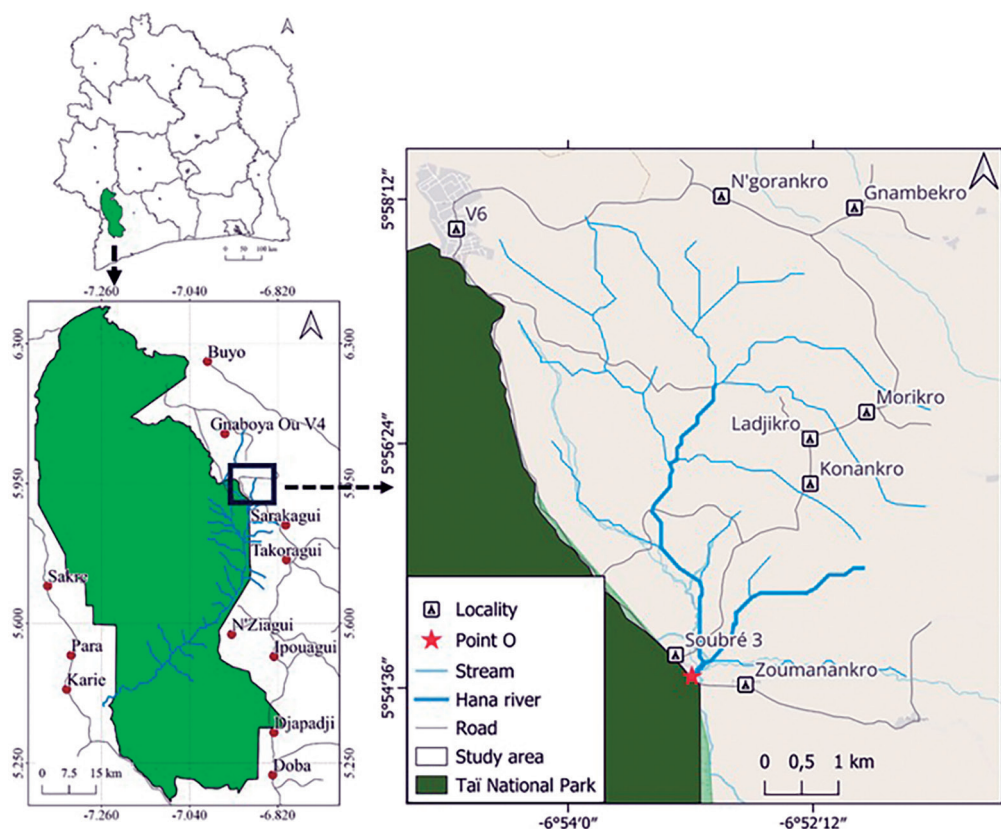


Fig. 1. Location of study area.

Note: left – Taï National Park and surrounding area; right – Hana River.

(NDWI), which is sensitive to soil moisture; and the Redness Index (RI), which is sensitive to soil brightness. According to Ngom et al. (2022), these bands and indices provide improved discrimination of artisanal gold mining sites.

Field survey and delineation of training samples

Based on a colour composition of the 2024 satellite image, areas of different colouration, texture and shape were identified and visited during the field verification mission, organised from 30 November to 8 December 2024. This mission enabled land-use types to be defined for mapping purposes. During the field mission, identification points and GPS plot delineations were carried out. They covered all types of land use, the main ones being cocoa-coffee plantations, rubber (*Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg.), artisanal gold mining, and food crops.

The delineation of training data was carried out through photo-interpretation based on field knowledge, with particular emphasis on the boundaries of training zones. Other sources of information were also used, including High Spatial Resolution (HSR) images available on Google Earth and data from field verification surveys. Seventy per cent of the data collected in the field were used to delimit the training plots, while the remaining 30 % were reserved for validation.

The advantage of this plot delineation technique is that it enables the algorithm to identify appropriate thresholds for distinguishing between land cover classes, thereby ensuring high-quality results (Niculescu et al. 2018). In fact, the accuracy of classification outcomes is closely linked to the quality of the training data (Grinand et al. 2013, Rakotomala 2015).

The training data were generated using QGIS version 3.28 software and stored in a dedicated database for the calibration of the classification algorithm.

Image classification and accuracy assessment

In this study, the Random Forest classification algorithm was employed to map land-use types. It was trained using field-based data corresponding to the seven land-use categories identified during the field survey. The input variables for classification are the Sentinel-2 spectral bands and indices (pixels sampled from the training dataset). After calibrating the model, the algorithm was applied to produce the raw land-use map. This map was made iteratively, producing 10 land-use maps for each date. Back-fitting of the training data and calibration resulted in the best version of the map. Processing was carried out using R software version 4.2.3 and the random Forest package (Liaw and Wiener 2002).

To assess map quality, cross-validation was carried out using the tools available in the 'Random Forest' package (Liaw and Wiener 2002). This tool was used to calculate the overall accuracy and confusion matrix from randomly selected test sample corresponding to 30 % of the field dataset (Bylander 2002). This assessment of map quality is useful for understanding the origin of confusion (Ouattara et al. 2021). In addition, model accuracy indicators (overall accuracy, Kappa coefficient, user accuracy, and producer accuracy) were calculated from the confusion matrix obtained by cross-validation. This validation method provides an unbiased estimate of the error rate when the model is extrapolated to the entire study area (Chehata et al. 2015).

The post-classification stage 'cleans'

the raw classification image through a filtering operation to reduce errors while eliminating isolated pixels. The ‘sifting’ operation adjusts the image to meet the Minimum Mapping Unit (MMU) requirements. MMU adopted to produce the land-use map corresponds to MMU of the minimum surface area of artisanal gold mining sites observed in the study area during the field mission, which is 0.1 ha. This MMU value was applied to all land-use types. For cartographic rendering, the raster files resulting from image classification were imported into QGIS software.

Land-use change analysis

Land-use change analysis was carried out using the transition matrix (in percent) and the rate of change of land-use types (in percent) over the study period. The transition matrix highlights the different land use conversions between two dates and quantifies these changes (Barima et al. 2016, Ouattara et al. 2021). Annual evolution rates were calculated using the standardised formula (1) proposed by Puyravaud (2003):

$$Tv = -\frac{1}{t_2 - t_1} \cdot \ln\left(\frac{S_2}{S_1}\right) \cdot 100, \quad (1)$$

where S_1 and S_2 represent the areas of the land-use type at dates t_1 and t_2 , respectively.

Results and Discussion

Evaluation of map quality

The land-use maps for the years 2021–2024 achieved overall accuracies of 94 %, 95 %, 95 %, and 96 %, respectively, with Kappa coefficients all exceeding 0.90. The confusion matrices of the images processed for each date show high values of user accuracy (PU > 80 %) for all land-use types. No major confusion was observed between land-use types in either matrix (tables 1, 2, 3, and 4). The low level of confusion between land-use types could be explained by a good description of land-use categories and quality data collection during the field mission. This result may also reflect the capability of Sentinel-2 images to map gold panning sites at small scales (Ngom et al. 2022).

Table 1. Confusion matrices and accuracy metrics for 2021 land-use map (in number of pixels).

Reference/ Classified	Fallow	Cocoa/ coffee	Food crops	Rub- ber	Artisanal gold mining	Wa- ter	Bare soil	Total	UA
Fallow	785	29	0	41	0	0	0	855	0.92
Cocoa/coffee	15	647	18	21	0	0	0	701	0.92
Food crops	0	25	911	0	0	0	11	947	0.96
Rubber	22	15	0	552	0	0	0	589	0.94
Artisanal gold mining	0	16	0	0	555	0	0	571	0.97
Water	0	0	0	0	0	322	0	322	1
Bare soil	0	0	0	0	0	0	430	430	1
Total	822	732	929	614	555	322	441		
PA	0.95	0.88	0.98	0.90	1	1	0.98		

Note: UA – User accuracy; PA – Producer accuracy.

Table 2. Confusion matrix and accuracies metrics for 2022 land-use map (in number of pixels).

Reference/ Classified	Fallow	Cocoa/ coffee	Food crops	Rub- ber	Artisanal gold mining	Water	Bare soil	Total	UA
Fallow	715	92	0	21	0	0	0	828	0.86
Cocoa/coffee	70	696	30	10	0	0	0	806	0.86
Food crops	0	20	803	0	0	0	1	824	0.97
Rubber	10	0	0	452	0	0	0	462	0.98
Artisanal gold mining	0	0	1	0	378	0	0	379	1
Water	0	0	0	0	0	357	0	357	1
Bare soil	0	0	4	0	15	0	302	321	0.94
Total	795	808	838	483	393	357	303		
PA	0.90	0.86	0.96	0.94	0.96	1	1		

Note: UA – User accuracy; PA – Producer accuracy.

Table 3. Confusion matrix and accuracy metrics for 2023 land-use map (in number of pixels).

Reference/ Classified	Fallow	Cocoa/ coffee	Food crops	Rub- ber	Artisanal gold mining	Water	Bare soil	Total	UA
Fallow	657	31	0	13	0	17	0	718	0.92
Cocoa/coffee	106	744	21	8	0	0	0	879	0.85
Food crops	0	1	536	0	0	0	1	538	1
Rubber	3	24	0	485	0	0	0	512	0.95
Artisanal gold mining	0	1	0	0	333	0	0	334	1
Water	3	0	0	0	0	266	0	269	0.99
Bare soil	0	1	22	0	0	0	213	236	0.90
Total	769	802	579	506	333	283	214		
PA	0.85	0.93	0.93	0.96	1	0.94	1		

Note: UA – User accuracy; PA – Producer accuracy.

Table 4. Confusion matrix and accuracy metrics for 2024 land-use map (in number of pixels).

Reference/ Classified	Fallow	Cocoa/ coffee	Food crops	Rub- ber	Artisanal gold mining	Wa- ter	Bare soil	Total	UA
Fallow	523	53	0	22	0	0	0	598	0.87
Cocoa/coffee	119	707	45	10	0	0	0	881	0.80
Food crops	0	7	430	0	0	0	0	437	0.98
Rubber	0	30	0	348	0	0	0	378	0.92
Artisanal gold mining	0	1	4	0	490	0	2	497	0.99
Water	0	2	1	11	0	331	0	345	0.96
Bare soil	0	1	1	0	50	0	307	359	0.86

Reference/ Classified	Fallow	Cocoa/ coffee	Food crops	Rub- ber	Artisanal gold mining	Wa- ter	Bare soil	Total	UA
Total	642	801	481	391	540	331	309		
PA	0.81	0.88	0.89	0.89	0.91	1	0.99		

Note: UA – User accuracy; PA – Producer accuracy.

Land-use dynamics in the periphery of Taï National Park

Visual analysis of the land-use maps for the years 2021–2024 (Fig. 2) reveals an absence of dense forest and a dominance of cocoa and/or coffee plantations in this zone. These covered 77.2 % (3098.9 ha) in 2021, 79.7 % (3197.3 ha) in 2022, 83.1 % (3336.5 ha) in 2023, and 79.1 % (3173.4 ha) in 2024 (Fig. 3). The area occupied by artisanal gold mining sites, initially the smallest at 6.1 ha (0.2 %) in 2021, increased to 6.7 ha (0.2 %) in 2022, 24.6 ha (0.6 %) in 2023, and 28.2 ha (0.7 %) in 2024.

The dominance of cocoa and coffee trees reflects the high intensity of these perennial crops on the periphery of Taï National Park. Indeed, as the south-west of Côte d'Ivoire is an area of high cocoa production, cocoa is the main source of agricultural income for people living in the area (Konaté et al. 2024). The presence of the park also favours rainfall in this part of the country, creating environmental conditions that appear to be optimal for cocoa cultivation. The absence of dense forest in the area around the source of Hana River can be explained by the high intensity of cocoa plantations. This crop is generally planted on land that was previously forested (Assiri et al. 2009) which contributes significantly to deforestation in Côte d'Ivoire (Barima et al. 2016). Also, the relocation of certain communities for the creation of the park would have accentuated a strong demand for arable land on the periphery of this protected area. The

low rate of evolution of cocoa plantations in contrast to the other classes can also be explained by a lack of land suitable for the installation of new cocoa plantations due to the absence of forests. The transition matrix highlights the conversion of cocoa farms to fallow and food crops, with proportions of 3.60 % and 5.99 % respectively. This conversion from cocoa to food crops and fallow is explained by the ageing of orchards observed in this zone (Kpangui et al. 2021, Konan et al. 2023). Food crops such as groundnuts and beans observed in cocoa plantations are grown primarily for food and, ultimately, to enrich the soil with a view to reintroducing cocoa trees (Assiri et al. 2009). Similar results were obtained by Koua et al. (2020) in Biankouma department.

Expansion of artisanal gold panning on the periphery of Taï National Park

Analysis of changes in land-use types over the period 2021 to 2024 (Fig. 4) shows a significant increase in artisanal gold panning sites, with an annual growth rate of 120.5 %. During the study period, cocoa and/or coffee trees recorded an annual growth rate of 0.8 %, food crops 14.1 %, rubber 1.8 %, and bare soil and habitats 6.8 %. However, fallow land and watered areas declined by 21.7 % and 28.5 %, respectively.

The surface area of gold panning sites increased considerably during the study period. From 6.11 ha in 2021, they will increase to 6.73 ha in 2022, 24.62 ha in

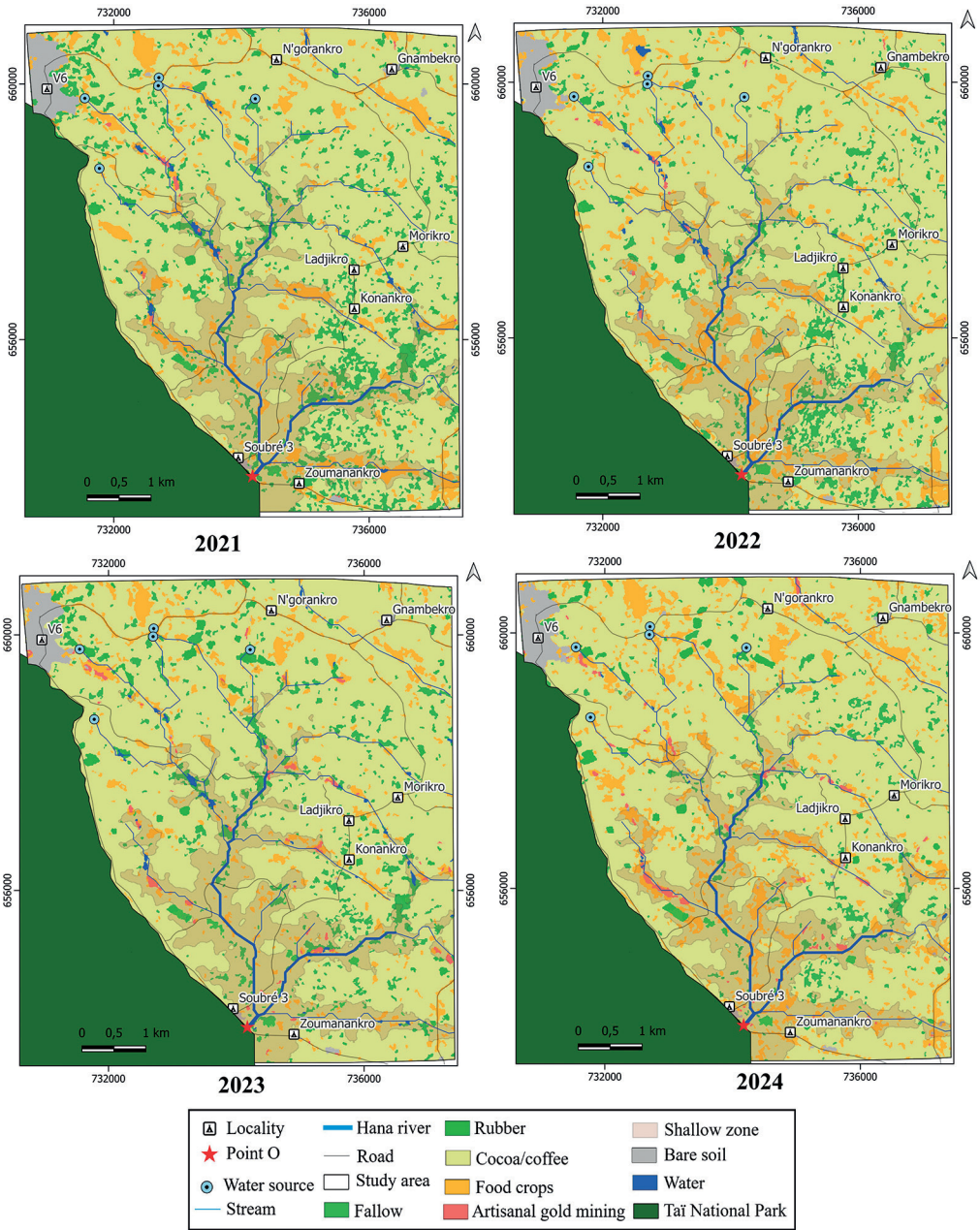


Fig. 2. Land-use maps of the study area for years 2021–2024.

2023, and 28.19 ha in 2024. This expansion of artisanal gold panning is observed in other regions of Côte d'Ivoire (Ngom et

al. 2022) and can be explained by several economic, political, and social factors. Economically, ageing cocoa plantations

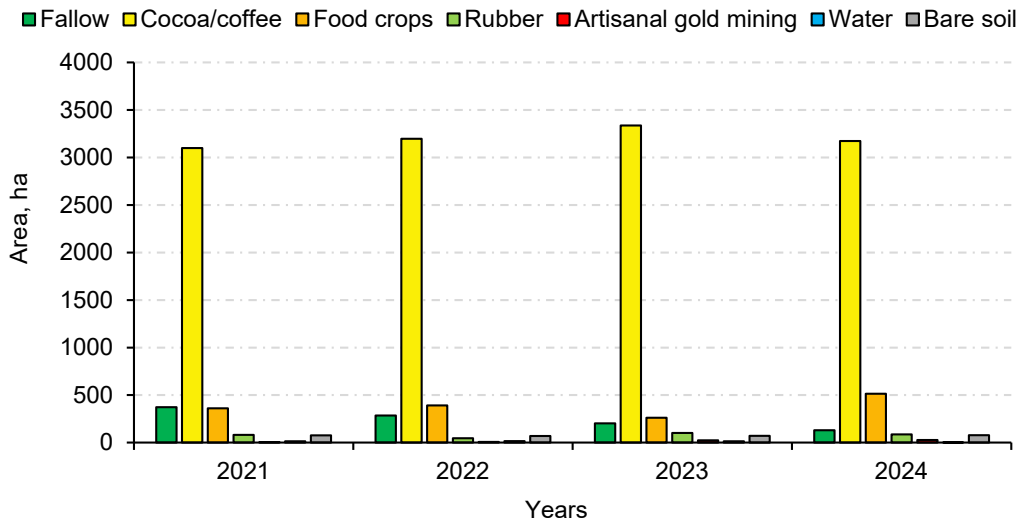


Fig. 3. Area of land-use types.

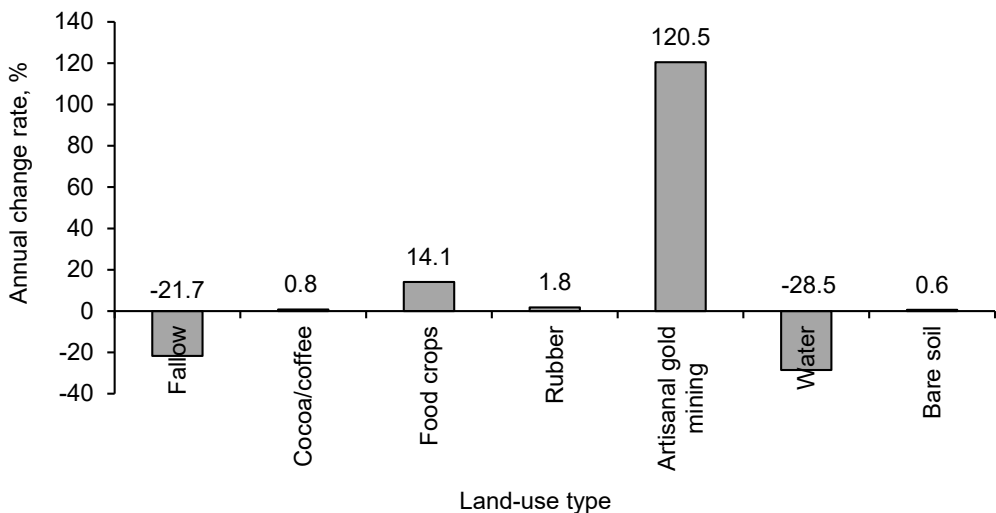


Fig. 4. Evolution of land-use areas from 2021 to 2024.

and declining yields have led farmers to turn to artisanal gold panning to the detriment of their traditional agricultural activities. Indeed, in times of agricultural crisis, gold panning can generate immediate profits that are sometimes much higher than farming (Hilson et al. 2017). Also, the

high demand for gold in recent decades has driven up prices on the global market. According to Ngom et al. (2022), the price of an ounce of gold rose from USD 280 to USD 1800 between 2000 and 2021 – an increase of 600 %. This rise in prices has led to the development of artisanal

mining in West Africa (Abass Saley et al. 2021). On the legislative and social front, mining regulations in Côte d'Ivoire are not in favour of local populations, who generally do not benefit from industrial mining revenues (Soko 2019). The government understood the economic importance of this activity and sought to re-organise and regulate it. Thus, many laws and policy frameworks aimed at reforming, restructuring, and legalising the artisanal gold mining sector. The cumbersome nature of the licensing process encourages the proliferation of illegal gold mining in rural areas.

Gold panning sites are located mainly in and around Hana riverbed and in the low-lying areas of the study zone. This pattern has resulted in the conversion of food crops and watercourses into gold-panning sites over the periods 2022–2023 and 2023–2024. The presence of gold panning sites in the lowlands can be explained by the alluvial gold formation method used by artisanal gold miners. Alluvial gold results from the weathering of gold-bearing rocks. These particles are transported by runoff or rivers water and deposited in river meanders, valley bottoms, or sandy banks (Melun and Bihan 2020). Artisanal gold mining typically involves on-site ore extraction and washing. Since gold washing requires substantial water, miners favour working in low-lying zones along watercourses. This activity alters water quality, discolours water bodies, and may even dry them up due to the formation of large excavated pits in and around riverbeds, which obstruct water flow during the dry season (Soko 2019).

In the study area, gold panning sites can be found in low-lying zones and within cocoa plantations. This situation shows the extent of gold panning and its preference over agriculture. For some local

communities, gold panning is perceived as more profitable than cultivating cocoa or coffee. Establishing cocoa or coffee plantation is a long-term investment, whereas gold panning provides faster returns. Furthermore, gold is sold more quickly and is available all year round, unlike agricultural products.

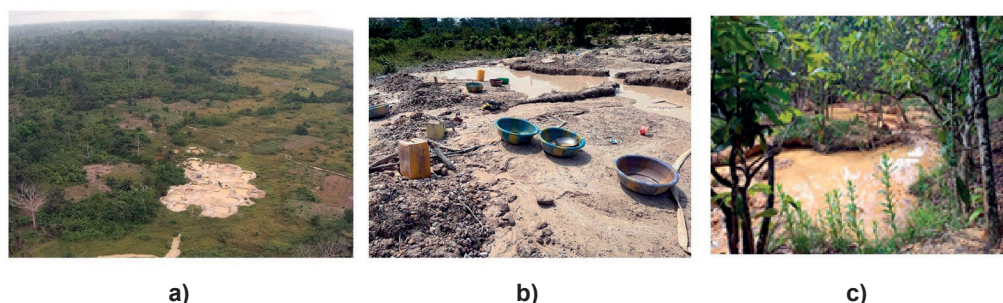
Transition matrices were used to analyse land-use conversions in greater detail. Over the three periods (2021–2022, 2022–2023, and 2023–24), the greatest conversions were to cocoa and/or coffee. Between 2021–2022, 51.97 % of fallow land was converted to cocoa and/or coffee. This conversion of fallow land to cocoa and/or coffee was 60.69 % and 57.94 % for the periods 2022–2023 and 2023–2024. Also, food crops were converted to cocoa and/or coffee at proportions of 44.81 %, 66.69 % and 32.01 % respectively over the periods 2021–2022, 2022–2023, and 2023–2024 (Table 5). Analysis of the transition matrices shows that the types of land use that have been converted to artisanal gold panning sites are water and food crops. Between 2021 and 2022, 3.35 % of water was converted to artisanal gold mining. 1.41 % and 8.55 % of water were converted to gold panning sites over the periods 2022–2023 and 2023–2024 respectively. The greatest conversion of food crops to gold mining sites was observed in the 2022–2023 and 2023–2024 periods, with 1.85 % and 1.66 % conversion respectively.

Artisanal gold panning and the integrity of Taï National Park

In 2021, there were 16 artisanal gold-panning sites (Fig. 5) covering a total area of 6.11 ha. Over time, both the number and size of these sites have increased, primarily in the lowlands of the study area. The

Table 5. Land-use transition matrix.

From \ to	Fallow	Cocoa/ coffee	Food crops	Rubber	Artisanal gold mining	Water	Bare soil
2021–2022							
Fallow	44.00	51.97	1.69	1.56	0.03	0.56	0.20
Cocoa/coffee	3.60	89.96	5.99	0.32	0.04	0.08	0.01
Food crops	0.07	44.81	53.14	0.01	0.22	1.14	0.62
Rubber	8.83	52.37	1.05	37.75	0.00	0.00	0.00
Artisanal gold mining	0.00	13.58	8.02	0.00	62.36	12.11	3.93
Water	2.12	44.05	0.21	0.00	3.35	49.59	0.68
Bare soil	0.32	3.35	8.17	0.01	0.45	0.14	87.54
2022–2023							
Fallow	33.93	60.69	1.05	3.34	0.53	0.37	0.09
Cocoa/coffee	3.22	90.27	4.22	1.66	0.42	0.15	0.05
Food crops	0.07	66.69	29.01	0.72	1.85	0.26	1.39
Rubber	5.06	17.82	0.28	76.84	0.00	0.00	0.00
Artisanal gold mining	1.19	15.75	37.00	0.00	24.96	18.13	2.97
Water	2.75	37.92	24.56	0.18	1.41	32.47	0.70
Bare soil	0.00	3.99	4.12	0.21	0.51	0.20	90.98
2023–2024							
Fallow	38.43	57.94	1.91	1.45	0.27	0.01	0.00
Cocoa/coffee	1.62	87.29	9.76	0.79	0.41	0.01	0.13
Food crops	0.05	32.01	63.25	0.53	1.66	0.04	2.46
Rubber	0.75	37.15	6.97	54.79	0.26	0.00	0.09
Artisanal gold mining	0.37	31.93	31.60	0.16	32.74	0.65	2.56
Water	1.53	73.78	6.43	0.00	8.55	9.72	0.00
Bare soil	0.37	2.32	4.48	0.03	0.29	0.00	92.51

**Fig. 5. Traces of artisanal gold panning in Hana River landscape.**

Note: a) Aerial view of a gold panning site (latitude 5°54'46"; longitude 6°52'37"); b) soil stripping with presence of pits (latitude 5°56'48"; longitude 6°52'55"); c) artisanal gold panning site in a cocoa plantation (latitude 5°57'38"; longitude 6°54'47").

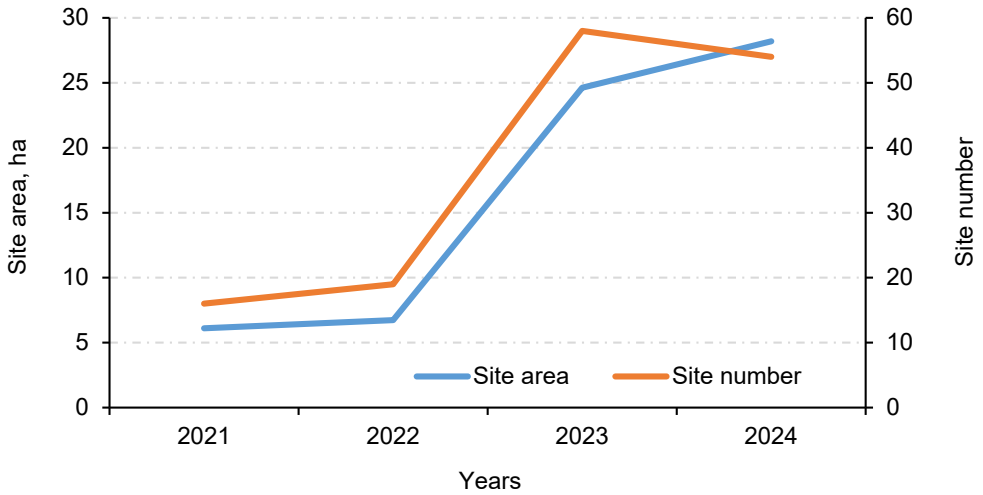


Fig. 6. Evolution of area and number of gold panning sites.

number of sites rose to 19 in 2022, 58 in 2023, and 54 in 2024, with corresponding surface areas of 6.73 ha, 24.62 ha, and 28.19 ha respectively (Fig. 6). Between 2022 and 2023, there was an increase in both the surface area and number of gold panning sites. However, during the 2023–2024 period, while the surface area of the sites continued to grow, the number of sites slightly decreased.

Our results show the conversion of watercourses into artisanal gold-panning sites in the area around the source of Hana River, located on the periphery of PNT. This situation bears witness to the risks and dangers of mining activities for the Park, which is classified as a Biosphere Reserve and World Heritage Site. Indeed, artisanal gold miners use chemicals such as mercury, cyanides and acids to recover gold (World Health Organization 2017). Hana River, which flows from east to west through PNT and has long served as a vital water source for wildlife, has now become a source of pollution, disease, and ecological degradation. Despite efforts by PNT protection officers to

step up surveillance and raise awareness among local communities, illegal artisanal gold panning persists in the peripheral zone. To preserve this natural heritage, it is imperative to prohibit gold panning in the entire peripheral zone of the Park and to involve local populations more closely in the sustainable management of resources by setting up income-generating activities. In addition, realistic and reliable ecological restoration measures adapted to the local context need to be implemented at the various abandoned sites. In addition, an early warning and monitoring system for illegal artisanal gold panning using remote sensing should be set up to ensure the long-term protection of Tai National Park.

Conclusion

This study analysed the change of land-use in Hana River source area between 2021 and 2024. Processing of Sentinel-2 satellite images showed that the landscape at the source of it is dominated by

cocoa plantations and a total absence of dense forest. Analysis of the evolution of land-use types over the period 2021 to 2024 showed a sharp increase in the surface area of artisanal gold panning sites, at an annual rate of 120.5 %. However, fallow land and water areas saw their surface area decline by 21.7 % and 28.5 % respectively. Between 2021 and 2024, the most significant conversions were to cocoa and/or coffee plantations.

In short, artisanal gold panning has increased and is practised in the bed and shallows of Hana river headwaters, on the periphery of the Park. This activity is the main cause of degradation of Hana River. For the sustainable management of Taï National Park, it is urgent to ban all gold panning activities, including the issuance of exploration and mining permits in the peripheral zone of the Park, and to involve local communities more closely in the protection through the creation of lucrative activities for young people. Realistic and reliable ecological restoration measures adapted to the local context must be applied to former gold mining sites, to enable the population to have access to arable land. In addition, an early warning and monitoring system for illegal artisanal gold panning using remote sensing should be set up to ensure the long-term, semi-automated protection of Taï National Park.

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Environmental drivers of reproductive allocation in Atlas cedar (*Cedrus atlantica*): morphometric insights from Belezma National Park under Saharan climatic pressures, Algeria

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Abstract

Atlas cedar, *Cedrus atlantica* (Endl.) Manetti ex Carrière, a cornerstone of North African forests, is increasingly threatened by habitat fragmentation and desertification in its southern range. This study aims to assess how morphological traits of cones, seeds, and needles vary among provenances to infer local adaptation to contrasting environments. Understanding local adaptation is therefore crucial for conservation. This study evaluates morphometric variation in cones, seeds, and needles among three Algerian provenances (Oued Tider, Ain Kerrouch, Talmét) within Belezma National Park, where Saharan influences constrain regeneration. From each provenance, 10 cones were sampled from 10 trees and analysed for weight, length, diameter, and scale number. For each cone, the total number of seeds was counted, and individual seeds were measured for weight, length, diameter, and thickness. In addition, seed-to-cone mass ratio was calculated to quantify reproductive efficiency. Besides, needle length and diameter were also measured. Results revealed significant provenance differences in cone weight, length, diameter, and scale count. Talmét cones were the largest and seed weight highest, followed by Ain Kerrouch and Oued Tider. Seed length and diameter were also greater in Talmét, while needle length peaked in Ain Kerrouch. Strong allometry emerged among cone dimensions and between cone and seed weight, but not with needles. These morphological patterns mirror local environmental gradients; Oued Tider's wetter climate favoured smaller cones and seeds, Talmét's harsher soils and aridity promoted larger reproductive investment, and Ain Kerrouch displayed intermediate traits with longer needles. Overall, provenance-specific contrasts in seed size and yield highlight environment-driven shifts in reproductive allocation, supporting evidence of local adaptation to semiarid gradients. These findings highlight adaptive divergence among provenances, offering critical guidance for seed-source selection under advancing desertification.

Key words: desertification, local adaptation, provenance variation, Saharan influences, semiarid forests, vegetative and reproductive traits.

Introduction

Atlas cedar (*Cedrus atlantica* (Endl.) Manetti ex Carrière) is an emblematic conifer native to the Atlas Mountains of Algeria and Morocco, occupying elevations between 1,500 and 2,200 m a.s.l. in semi-arid montane conditions (Cheddadi et al. 2022). As a keystone species in North Africa's Mediterranean-type ecosystems, *C. atlantica* plays a critical role in watershed protection, carbon sequestration, habitat provision, and biodiversity (Navarro-Cerrillo et al. 2013). However, overexploitation, land-use change, habitat fragmentation, climate change, and increasing drought stress have resulted in substantial population fragmentation and genetic erosion throughout its natural range (Bobo-Pinilla et al. 2022). In Algeria, the most extensive remaining cedar stands lie within Belezma National Park, which is increasingly threatened by advancing desertification and Saharan intrusions (Yahi et al. 2008). Effective conservation and restoration strategies require a comprehensive understanding of intraspecific variation in life-history traits across environmental gradients, as such variation underpins local adaptation to heterogeneous climatic and edaphic conditions.

Intraspecific variation in reproductive morphology, particularly cone and seed traits, affects seed dispersal, germination, early seedling establishment and survival, and long-term population viability, thereby influencing population resilience under climate change (Moles and Westoby 2006). In Pinaceae, larger seeds generally produce more vigorous seedlings with greater drought tolerance, but at the expense of reduced seed numbers (Rehfeldt et al. 1999). Cone phenology, size, and scale number are similarly adaptive, reflecting local patterns of resource al-

location and trade-offs between growth and reproduction (Jaramillo-Correa et al. 2015). Although *C. atlantica* has received attention regarding genetic diversity and conservation in some Mediterranean regions (Bobo-Pinilla et al. 2022, Fady et al. 2022), few studies have quantified provenance-level differences in cone and seed morphology within Algeria's montane landscapes. Furthermore, the timing of cone development and seed maturation in Atlas cedar typically spans two growing seasons; pollination occurs in autumn, while full seed ripening and cone disintegration take place during the second autumn (Cheddadi et al. 2022). This biennial reproductive cycle is particularly sensitive to climatic anomalies during the summer, when embryo enlargement depends on moisture availability. Understanding how such environmental constraints shape reproductive allocation among Algerian provenances remains critical for effective restoration planning.

The Algerian Saharan Atlas harbours distinct, fragmented cedar populations that differ in altitude, aspect, soil substrate, and precipitation. Moreover, Belezma National Park lies at the interface of Mediterranean and Saharan climates, where desertification fronts increasingly threaten cedar regeneration (Arar et al. 2019). These environmental pressures are expected to shape local adaptation in reproductive traits, yet empirical data are lacking. Without quantitative assessments of cone and seed morphology across these sites, restoration efforts risk selecting maladapted seed sources, thereby undermining long-term stand resilience. Understanding this adaptation is crucial for guiding seed transfer and preserving adaptive potential amid climate change and rising aridity (Jaramillo-Correa et al. 2015).

In semiarid conifers, cone scale number often correlates with cone mass and seed output, reflecting resource availability during cone development (Losada and Leslie 2018). Similarly, needle morphology can indicate site-specific water-use strategies, though its relationship with reproduction is frequently decoupled (Kuusk et al. 2018). Evidence from *Pinus sylvestris* L. and *P. pinaster* Aiton shows that needle length can be phenotypically plastic in response to microclimate, whereas seed traits remain under stronger genetic control (González-Martínez et al. 2001, Ramírez-Valiente et al. 2021). Whether *C. atlantica* populations conform to these patterns under Algeria's complex topography remains untested.

In response to these challenges, the present study adopts a morphometric approach integrated with silvicultural and climatic characterisation to explore variation in reproductive allocation among three Algerian provenances of *C. atlantica* from Belezma National Park, a region under Saharan climatic influence. Specifically, it seeks to (i) characterize and quantify variation in cone morphology, (ii) analyse seed morphological traits, (iii) assess variability in needle traits as indicators of site-specific adaptation, (iv) explore allometric relationships through multivariate trait covariation, and (v) relate morphological differentiation to local climatic and edaphic gradients to infer adaptive strategies in semiarid montane environments affected by desertification. This integrative, morphometric and environmental approach aims to preserve genetic diversity and provide ecologically sound guidance for seed-source selection and provenance-based restoration of Algerian Saharan Atlas cedar forests.

Materials and Methods

Study sites

Three natural populations of *C. atlantica* were selected from Belezma National Park (Algeria) based on geographical isolation, ecological fragmentation, and environmental heterogeneity (in climate, topography, soils, and stand structure). Two populations (Ain Kerrouch and Talmet) are situated in the Belezma Massif, while the third (Oued Tider) belongs to the Chélia Massif. All sites span an altitudinal gradient and experience differing climatic regimes within the Saharan Atlas (Fig. 1). Climatic and soil data were obtained from the National Meteorological Office of Algeria (ONM) and existing pedological studies of Belezma National Park (Arar et al. 2019).

Oued Tider (Chélia Massif) lies at elevation of 1,890 m on west-south-west-facing slopes, with a mean annual temperature of 14.3 °C (minimum of the coldest month 0.5 °C, maximum of the warmest month 21.4 °C), summer precipitation of ~40 mm, and total annual precipitation of ~440 mm. Soils are calcareous limestone (pH 7.0–7.5) on ~35 % slopes. *C. atlantica* dominates this forest, co-occurring with *Juniperus oxycedrus* L. The climate is temperate with dry summers (Csb, Köppen-Geiger classification; Kottek et al. 2006), averaging 12.3 °C annually with ~439 mm of precipitation (Fig. 2).

By contrast, Talmet and Ain Kerrouch (Belezma Massif) occur between 1,700 and 2,040 m a.s.l. on north- and north-west-facing slopes. The Ain Kerrouch population is located in Oued El Chaâba (35°30' N, 6°21' E), while Talmet lies further north. The Oued Chaâba meteorological station (1,278 m a.s.l.) is the closest

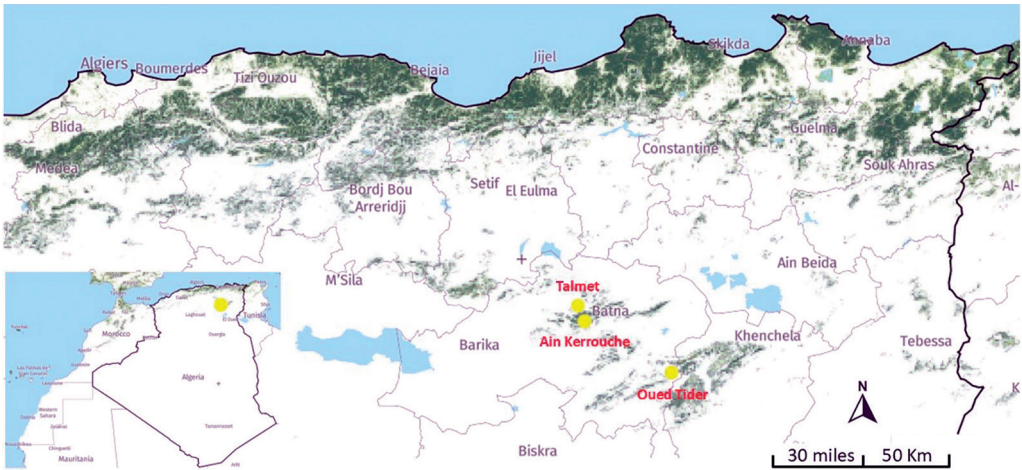


Fig. 1. Location of the study region.

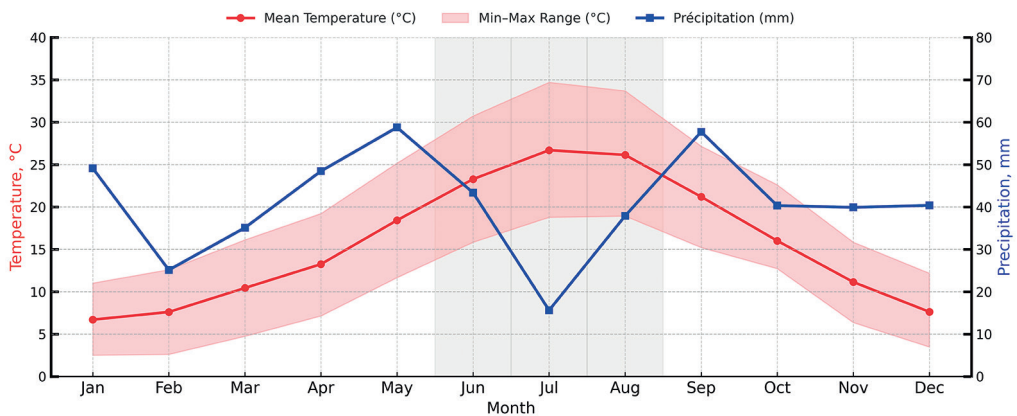


Fig. 2. Ombrothermic diagram of Bagnouls and Gaussen (1953) for the Chélia Massif.

available station and provides representative data for the regional climate of the Belezma Massif. Climate data from Oued Chaâba station indicate a semiarid cold steppe climate (BSk, Köppen-Geiger classification; Kottek et al. 2006), with an average annual temperature of 14.5 °C and 322 mm of precipitation (Fig.3). Mean annual temperature is ~15.6 °C (coldest-month minima -1.5 °C at Talmat, -1.0 °C at Ain Kerrouche; warmest-month

maximum ~34.9 °C in both sites), with summer precipitation of ~42 mm and low annual rainfall (260–320 mm). Both sites rest on marl-calcareous substrates (pH ~7) with 25–50 % slopes. The Belezma Massif includes Triassic, Jurassic, and Cretaceous formations. Soils range from calcareous brown soils on marl-limestone (1,400–1,600 m a.s.l.) to weakly calcareous brown soils on sandstone (1,600–2,000 m a.s.l.) and dolomitic rendzinas

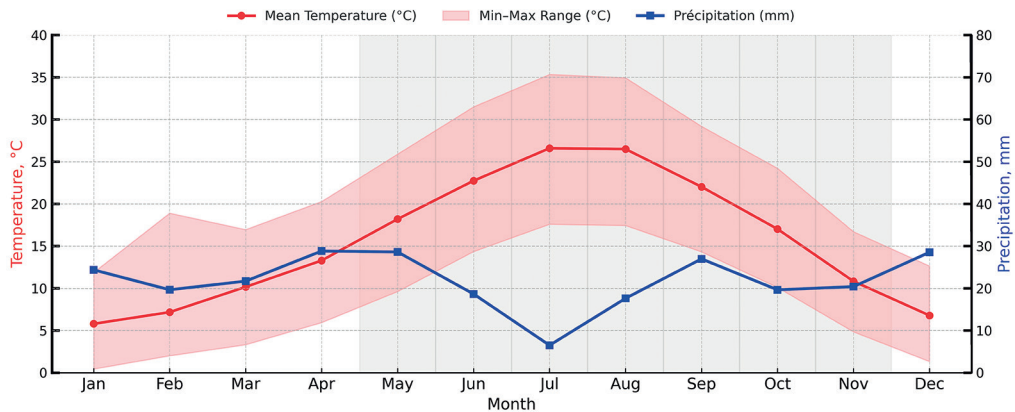


Fig. 3. Ombrothermic diagram of Bagnouls and Gaussen (1953) for the Belezma Massif.

on steep slopes. Vegetation includes pure or mixed stands of *C. atlantica*, often with *Quercus ilex* L., *Juniperus oxycedrus* L., *Ilex aquifolium* L., and other species, depending on altitude and exposure.

Sampling strategy

Sampling was conducted after cone maturation in late September 2022, following a year of average precipitation and temperature for the region, which ensured typical cone maturation (Fady et al. 2003). Tree selection followed a stratified random design (minimum inter-tree distance ≥ 100 m to minimise relatedness). Ten adult trees were selected to represent the full range of diameter at breast height and height observed within the stand. In each population, 10 dominant or co-dominant trees with well-formed crowns and no visible signs of disease or damage were selected to represent the average model tree for each site.

From each tree, 10 mature cones were collected from sun-exposed crown positions and placed in sealed plastic bags to preserve initial moisture. Immediately after collection, cones were transported

to the laboratory and stored in a cool, dry room (20 ± 2 °C, 45–50 % RH) for processing. Simultaneously, 10 needle fascicles were sampled from the same trees, stored similarly, and kept at ~ 20 °C until measurement.

Morphological measurements

For cones, fresh weight (g), length (cm), diameter (cm), and number of scale rows were recorded. Seeds were analysed for number per cone, fresh weight, length, diameter, and thickness. All instruments were calibrated at the start of each measurement session. Fresh weight was measured on a precision balance (Mettler Toledo AB204; ± 0.001 g). Dimensions were measured with a digital caliper (Mitutoyo Absolute Digimatic; ± 0.01 mm), following International Seed Testing Association (ISTA 2022) protocols for seed measurement.

Scale-row counts per cone were performed under natural light. In addition to individual seed dimensions, two integrative parameters were calculated to characterize reproductive allocation efficiency. The total-seed weight (TSW, g) was ob-

tained by multiplying the mean individual seed weight by the total seed number. The seed yield (% seed-to-cone mass ratio) was computed as the total mass of seeds extracted per cone divided by the total cone mass, multiplied by 100. This index reflects the proportion of cone biomass allocated to seeds and provides insight into reproductive efficiency among provenances (Leslie 2012, Leslie et al. 2017). The weight of 1000 seeds was also calculated for each provenance based on ten replicates of 100 seeds each.

Cone drying and seed extraction procedures followed controlled protocols to preserve initial moisture content. Cones were air-dried at 25 °C for 48 h in ventilated paper bags, then manually disintegrated. Seeds were separated from scales, cleaned with compressed air, and weighed immediately after extraction.

Needle traits, included length and diameter, were measured on five randomly selected needles per fascicle. Fascicles were examined under a stereomicroscope (Olympus SZ61) with an ocular micrometre.

Statistical analyses

Trait variation within and among populations was assessed using ANOVA, followed by Tukey's Honestly Significant Difference (HSD) post-hoc tests to identify statistically homogeneous groups. Pearson correlation was used to evaluate relationships between morphological traits and environmental factors. Multivariate analyses, including factorial discriminant analysis (FDA) on standardised data and Ward's hierarchical clustering based on Euclidean distances, were used to examine trait covariation and population structure (Taïbi et al. 2015, Boussaid et al. 2018). Results are reported as means $\pm$

standard deviations.

Results

Comprehensive ANOVA outcomes for all morphological parameters (cone, seed, and needle) are summarised in Table 1, while population means $\pm$ SD are presented in Table 2.

Cone traits

Cone weight, length, and diameter varied significantly among populations (one-way ANOVA; weight: $F = 27.82$, $p < 0.0001$; length: $F = 18.46$, $p < 0.0001$; diameter: $F = 11.12$, $p < 0.0001$) (Table 1). Talmet cones were largest in every dimension (80.5 ± 18.2 g weight; 75.8 ± 9.5 mm length; 50.2 ± 7.2 mm width; $n = 93$), followed by Ain Kerrouch (69.2 ± 13.5 g; 71.3 ± 8.7 mm; 48.1 ± 6.1 mm; $n = 76$) and Oued Tider (61.9 ± 12.7 g; 68.5 ± 8.2 mm; 44.9 ± 5.8 mm; $n = 75$) (Table 2). All pairwise comparisons were highly significant ($p \leq 0.003$), with Talmet > Ain Kerrouch > Oued Tider for each trait dimension.

The average number of scales per cone differed among populations ($F = 3.79$, $p = 0.02$), with Talmet cones (28.7 ± 3.5) exceeding both Ain Kerrouch (27.2 ± 3.1 ; $p = 0.038$) and Oued Tider (27.1 ± 3.3 ; $p = 0.03$), whereas Ain Kerrouch and Oued Tider did not differ ($p = 0.985$). Thus, Talmet trees combined larger cone dimensions with higher scale counts and greater per-tree cone output, yielding the largest overall seed biomass among sites.

In addition, the 1000-seed weight showed a significant population effect ($F = 12.05$, $p < 0.001$), mirroring the pattern in individual seed weight, and confirming stronger biomass investment at Talmet.

Table 1. ANOVA summary for cone, seed, and needle traits.

Trait	Source	df	SS	MS	F	p
Cone weight, g	Population	2	10,743	5,371.5	27.82	< 0.0001
	Residual	241	46,540	193.2		
Cone length, mm	Population	2	29,455	14,727.6	18.46	< 0.0001
	Residual	241	192,367	798.2		
Cone diameter, mm	Population	2	1,611.2	805.6	11.12	< 0.0001
	Residual	241	17,457	72.45		
Scale count	Population	2	73.60	36.80	3.79	0.024
	Residual	241	2,339.4	9.71		
Seed number per cone	Population	2	112.8	56.4	0.08	0.92
	Residual	168	118,487	705		
Seed weight, g	Population	2	0.0129	0.00645	12.28	< 0.0001
	Residual	168	0.0883	0.00053		
1000-seed weight, g	Population	2	8,213	4,106.5	12.05	< 0.001
	Residual	168	57,293	341.0		
Seed yield, %	Population	2	49.02	24.51	8.47	< 0.001
	Residual	168	486.15	2.89		
Needle length, mm	Population	2	63.37	31.69	14.72	< 0.0001
	Residual	33	71.02	2.15		
Needle diameter, mm	Population	2	0.058	0.029	1.85	0.17
	Residual	33	0.520	0.016		

Table 2. Variation of cone, seed, and needle traits by population (means $\pm$ SD).

Trait	Ain Kerrouch	Oued Tider	Talmet
Cone weight, g	69.2 $\pm$ 13.5 ^b	61.9 $\pm$ 12.7 ^c	80.5 $\pm$ 18.2 ^a
Cone length, mm	71.3 $\pm$ 8.7 ^b	68.5 $\pm$ 8.2 ^c	75.8 $\pm$ 9.5 ^a
Cone diameter, mm	48.1 $\pm$ 6.1 ^b	44.9 $\pm$ 5.8 ^c	50.2 $\pm$ 7.2 ^a
Scale count	27.2 $\pm$ 3.1 ^b	27.1 $\pm$ 3.3 ^b	28.7 $\pm$ 3.5 ^a
Seed number per cone	117.6 $\pm$ 15.2 ^a	118.2 $\pm$ 16.4 ^a	117.4 $\pm$ 15.2 ^a
Seed weight, g	0.068 $\pm$ 0.019 ^c	0.072 $\pm$ 0.019 ^b	0.079 $\pm$ 0.021 ^a
1000-seed weight, g	68.0 $\pm$ 19.0 ^c	72.0 $\pm$ 18.5 ^b	79.0 $\pm$ 21.0 ^a
Seed yield, %	12.14 $\pm$ 0.96 ^a	12.55 $\pm$ 0.84 ^a	9.97 $\pm$ 0.99 ^b
Seed length, mm	11.25 $\pm$ 0.52 ^a	11.24 $\pm$ 0.60 ^a	11.42 $\pm$ 0.64 ^a
Seed diameter, mm	5.30 $\pm$ 0.34 ^b	5.19 $\pm$ 0.35 ^c	5.41 $\pm$ 0.41 ^a
Seed thickness, mm	2.52 $\pm$ 0.28 ^b	2.55 $\pm$ 0.30 ^b	2.63 $\pm$ 0.33 ^a
Needle length, mm	17.1 $\pm$ 0.4 ^a	15.4 $\pm$ 1.1 ^b	15.9 $\pm$ 0.9 ^b
Needle diameter, mm	0.71 $\pm$ 0.06 ^a	0.65 $\pm$ 0.07 ^b	0.71 $\pm$ 0.08 ^a

Note: Superscripts denote significant differences among populations ($p < 0.05$).

Seed traits

The number of seeds per cone did not differ significantly among populations ($F = 0.08$, $p = 0.92$), indicating that reproductive output per cone was comparable across sites. However, both individual seed weight and 1000-seed weight differed highly among sites ($F = 12.05$, $p < 0.001$). Thus, inter-population variation in reproductive allocation was expressed primarily through seed size rather than seed number.

Seed weight showed a highly significant population effect ($F = 12.28$, $p < 0.0001$). Talmat seeds were heavier (0.079 ± 0.021 g; 79 ± 21 g per 1000 seeds), followed by Oued Tider (0.072 ± 0.019 g; 72 ± 18.5 g per 1000 seeds) and Ain Kerrouch (0.068 ± 0.019 g; 68 ± 19 g per 1000 seeds). By the same, seed yield (seed-to-cone mass ratio) varied significantly among populations ($F = 8.47$, $p < 0.001$), ranging from 9.97 ± 0.99 % in Talmat to 12.55 ± 0.84 % in Oued Tider. Despite producing the heaviest seeds, Talmat exhibited the lowest seed yield, reflecting a higher structural investment per cone and lower proportional allocation to seeds. In contrast, Ain Kerrouch and Oued Tider displayed higher reproductive efficiency (greater seed yield), consistent with milder moisture stress.

Significant differences emerged for seed length ($F = 3.81$, $p = 0.024$) and seed diameter ($F = 3.17$, $p = 0.045$). Talmat seeds (11.42 ± 0.64 mm long) were slightly longer than those from Ain Kerrouch (11.25 ± 0.52 mm; $p = 0.035$) and Oued Tider (11.24 ± 0.60 mm; $p = 0.028$). For seed diameter, Talmat (5.41 ± 0.41 mm) exceeded Oued Tider (5.19 ± 0.35 mm; $p = 0.004$) but was not significantly different from Ain Kerrouch (5.30 ± 0.34 mm; $p = 0.09$). Seed thickness did not vary

significantly among the three populations ($F = 2.29$, $p = 0.10$).

Needle traits

Needle length differed strongly among populations ($F = 14.72$, $p < 0.0001$). Ain Kerrouch needles (17.1 ± 0.4 mm) were longer than those of Oued Tider (15.4 ± 1.1 mm; $p = 0.0003$) and Talmat (15.9 ± 0.9 mm; $p = 0.011$). No significant differences occurred in needle diameter ($F = 1.85$, $p = 0.17$). Mean diameters were 0.71 ± 0.06 mm (Ain Kerrouch), 0.65 ± 0.07 mm (Oued Tider), and 0.71 ± 0.08 mm (Talmat). The low within-population variability of needle diameter contrasts with higher inter-population variability in cone and seed morphology, suggesting stronger genetic control of reproductive than vegetative traits.

Inter-trait correlations

Pearson correlation analysis revealed strong positive relationships among cone traits, with cone weight correlating highly with length ($r = 0.82$, $p < 0.0001$) and diameter ($r = 0.76$, $p < 0.0001$), and a moderate correlation between length and diameter ($r = 0.69$, $p < 0.0001$). Scale count showed moderate associations with cone weight ($r = 0.42$), length ($r = 0.38$), and diameter ($r = 0.29$), suggesting that larger cones tend to bear more scales. Among cone-seed associations, cone weight had the strongest correlation with seed weight ($r = 0.68$), followed by cone length ($r = 0.62$) and diameter ($r = 0.59$; all $p < 0.0001$). Scale count and seed weight were moderately correlated ($r = 0.31$, $p < 0.001$). Weaker but significant associations were found between cone weight and seed length ($r = 0.34$), diameter ($r = 0.28$), and thickness ($r = 0.21$). No

significant correlations emerged between needle traits and any cone or seed parameter ($p > 0.05$), indicating an apparent decoupling of vegetative and reproductive morphology.

Environmental drivers of morphological variation

Oued Tider population produced the smallest cones and lightest seeds (61.9 ± 12.7 g; 0.072 ± 0.019 g, respectively). In contrast, Talmet yielded significantly larger cones and heavier seeds (80.5 ± 18.2 g; 0.079 ± 0.021 g; both $p < 0.001$), while Ain Kerrouch occupied an intermediate position (69.2 ± 13.5 g; 0.068 ± 0.019 g), differing significantly from both ($p \leq 0.035$).

Strong positive correlations among cone mass, size, scale count, and seed weight ($r = 0.59\text{--}0.82$, $p < 0.0001$) suggest greater per-seed investment under arid, thermally extreme conditions, while the more mesic Oued Tider favours lower-cost seeds. In contrast, needle length peaked at Ain Kerrouch ($p < 0.001$ vs. Oued Tider; $p = 0.011$ vs. Talmet) and showed no significant association with reproductive traits ($p > 0.05$), confirming independent adaptation of foliage to microclimate.

Multivariate analyses

The FDA correlation circle illustrates the structure of trait covariation among *C. atlantica* provenances. The first two discriminant axes, F1 (69.69 %) and F2 (30.31 %), capture nearly all trait variation, indicating strong dimensional reduction and effective group discrimination. F1 primarily reflects variation in cone- and seed size-related traits, with cone diameter, cone length, cone weight, seed weight,

1000-seed weight, and seed length exhibiting strong, clustered loadings. This axis likely represents a gradient of reproductive investment or organ biomass, distinguishing individuals with larger and heavier reproductive structures (Fig. 4).

The second discriminant axis (F2) reflects a morpho-anatomical trade-off: it is positively associated with needle length, needle diameter, and seed diameter, and negatively with seed number per cone and seed thickness, possibly indicating divergent adaptive strategies to aridity. Along F1, Talmet individuals are clearly separated, characterised by larger cones and seeds, greater seed weight, and higher scale counts, traits defining a more investment-intensive reproductive profile. In contrast, Oued Tider and Ain Kerrouch populations overlap moderately near the origin, though Oued Tider trends toward negative F1 and F2 values, suggesting smaller reproductive organs and possibly a more conservative phenotype. Ain Kerrouch shows broader dispersion, especially along F2, hinting at greater phenotypic plasticity and a potential role as an ecological intermediary between the other provenances (Fig. 5).

Ward's clustering produced two clusters; the first contains Ain Kerrouch and Talmet while the second contains Oued Tider which confirms that Oued Tider, characterised by smaller cones, lighter seeds, and generally shorter dimensions, is morphologically distinct, whereas Ain Kerrouch and Talmet share a 'large-cone, heavy-seed, thick-needle' phenotype (Fig. 6).

Discussion

The present study demonstrates clear and consistent morphological divergence

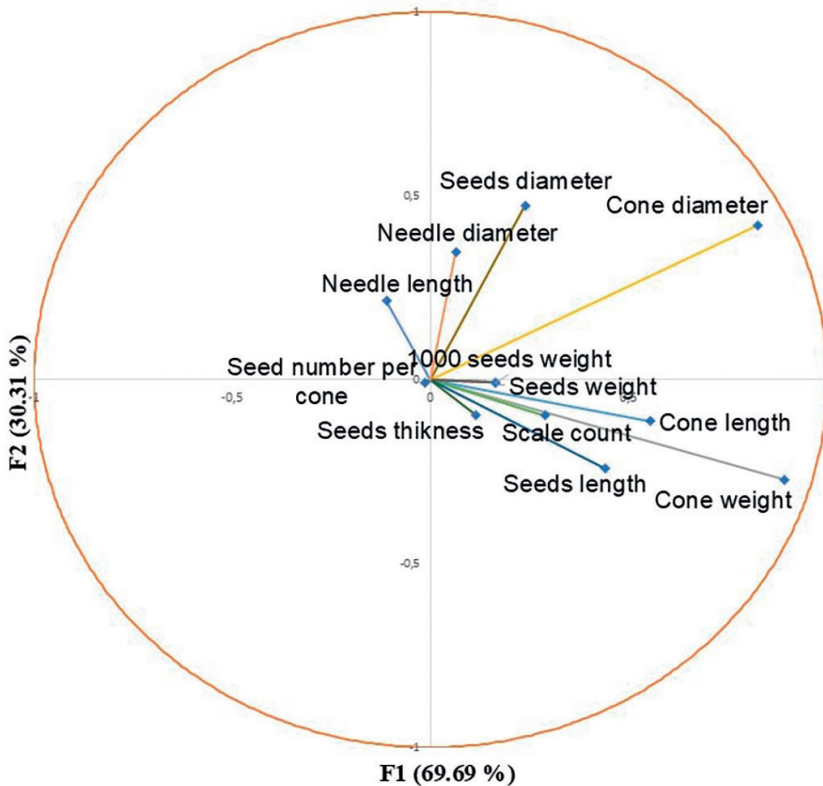


Fig. 4. PCA of cone, seed, and needle traits of the sampled populations of *C. atlantica*.

in reproductive and vegetative traits among the three *C. atlantica* provenances in Belezma National Park, aligned with local environmental gradients.

Reproductive allocation and local adaptation

Talmet trees exhibited the largest cones and heaviest seeds, significantly exceeding those of Ain Kerrouch and Oued Tider. In contrast, Oued Tider produced the smallest cones and seeds, while Ain Kerrouch was intermediate. These differences underscore a classic moisture-driven seed-size vs. seed-number trade-off: populations in arid, thermally extreme site of Talmet, allocate larger seeds with

greater nutrient reserves to enhance early seedling drought tolerance and buffer against episodic heat stress (Moles and Westoby 2006). Specifically, Talmet experiences low annual precipitation, extreme summer maxima and steep marno-calcareous slopes; under these constraints, investing more biomass per seed increases the probability of seedling establishment during brief moisture pulses (Greene and Johnson 1993, Leslie et al. 2017). By contrast, populations in milder, wetter site of Oued Tider enable a strategy of producing more cones and seeds at lower individual investment, given the more reliable moisture supply for germination (Moles and Westoby 2006). Provenances with larger seeds appear adapted to dri-

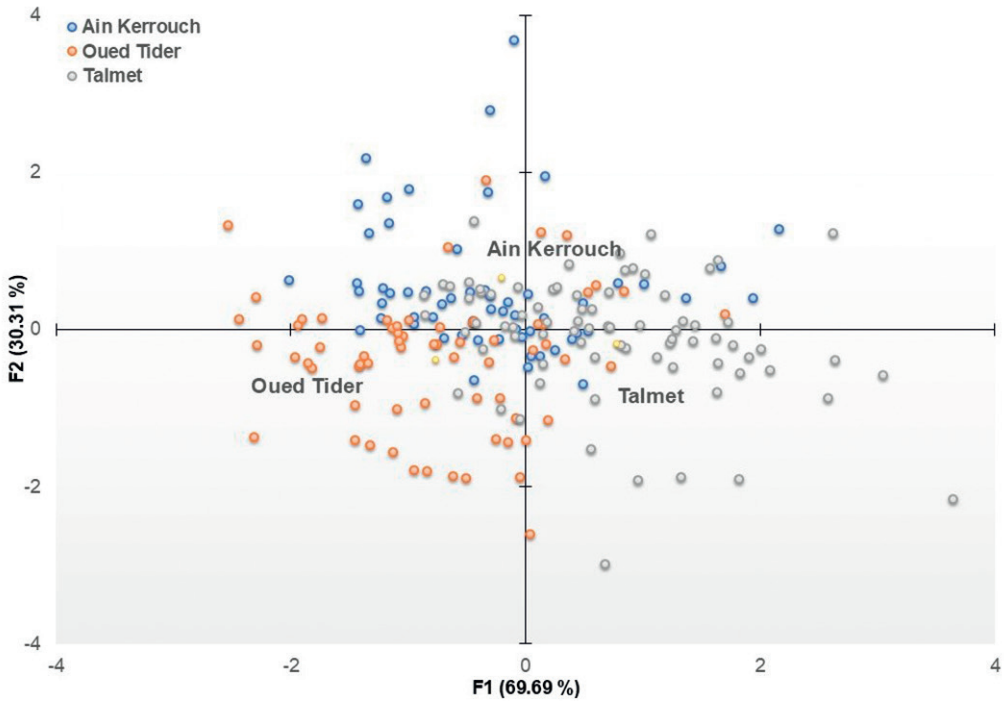


Fig. 5. FDA showing the morphological separation among the studied populations.

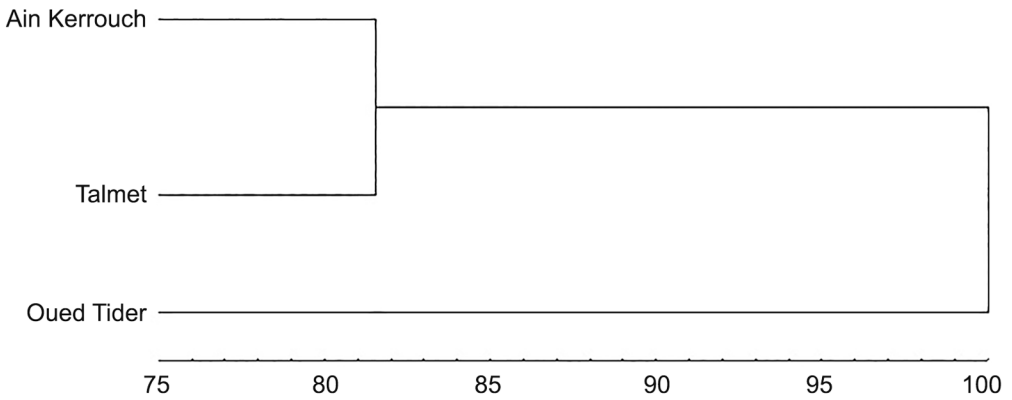


Fig. 6. Ward's dendrogram for all variables shows Ain Kerrouch and Talmet clustering together, separated from Oued Tider.

er environments, while those with smaller seeds may favour reproductive output under more favourable moisture conditions. Overall, within-population seed mass variation was moderate, indicating con-

sistent reproductive strategies within each provenance. Notably, the absence of significant seed-weight differences between Ain Kerrouch and Oued Tider, despite Ain Kerrouch's larger cones, suggests a com-

pensatory trade-off; greater cone biomass may be offset by reduced investment per seed, reflecting a balance between seed size and number (Snell et al. 2019).

Although the number of seeds per cone did not differ among provenances, seed mass and seed yield did. This pattern is consistent with a classic size–number allocation shift (Smith and Fretwell 1974), whereby reproductive investment is modulated primarily through per-seed provisioning rather than seed number. The lower seed yield observed at Talmét, despite heavier seeds, suggests proportionally greater investment in cone structural tissues (scales/bracts) and enhanced per-seed provisioning under harsher, arid conditions, an allocation pattern in line with conifer reproductive resource theory and cone–seed trade-offs (Leslie 2012; Leslie et al. 2014, 2017). Recent range-relevant work links larger cone scale area to heavier seeds in *C. atlantica* (Morocco), reinforcing the interpretation that cone architecture co-varies with per-seed investment (Trujillo-Ríos et al. 2025).

Allometric and trait relationships

Strong positive correlations among cone weight, length, and diameter ($r \geq 0.69$, $p < 0.0001$) confirm that these dimensions scale isometrically across provenances. The tight coupling between cone size and seed weight ($r = 0.68$) highlights a coordinated allocation strategy across provenances, ensuring that larger reproductive organs support better-provisioned seeds. Scale count correlated moderately with cone weight ($r = 0.42$, $p < 0.0001$), suggesting that cones with more annual scales accrue additional mass and length before abscission.

When paired with seed measures, cone weight explained a large fraction of seed weight variation ($r = 0.68$, $p < 0.0001$), aligning with other Pinaceae studies showing that cone size reliably predicts seed provisioning (Gao et al. 2023). Moderate correlations between cone weight and seed length ($r = 0.34$) or seed diameter ($r = 0.28$) further indicate that larger cones produce not only heavier but also physically larger seeds. The weaker but still significant correlation with seed thickness ($r = 0.21$, $p = 0.005$) suggests that thickness may be under slightly different developmental constraints (e.g. seed coat vs. embryo size) (Boccaccini et al. 2024). Overall, these allometric relationships echo findings in Scots pine and other montane conifers, where heavier cones consistently house larger seeds with proportional dimensional increases (Ramírez-Valiente et al. 2021, Parfenova et al. 2021). Such size-mediated reproductive allocation is critical for seedling vigour under semiarid conditions (Moles and Westoby 2006).

A clear association was also observed between site-specific climate-soil regimes and overall morphological differentiation. Oued Tider's wetter and milder environment corresponded with the smallest cones and lightest seeds, whereas Talmét's drier, hotter summers and marl-calcareous soils produced larger cones and heavier seeds. Ain Kerrouch, sharing Talmét's precipitation but occurring at slightly lower elevations and on north-facing slopes, displayed intermediate values. This cline of trait responses exemplifies local adaptation: heavy-seeded provenances are buffered against moisture scarcity and frost, whereas light-seeded populations maximize reproductive efficiency under reduced water stress.

Needle traits as indicators of site-specific adaptation

Needle traits exhibited less quantitative variation than reproductive traits, yet their spatial patterns clearly reflected site-specific environmental conditions. Needle length differed significantly among provenances (Ain Kerrouch > Oued Tider $\approx$ Talmet), whereas needle diameter remained relatively stable. This indicates that needle elongation is a more plastic trait influenced by local microclimate, while needle thickness is likely governed by stronger genetic constraints. The absence of correlation between needle and reproductive variables confirms that vegetative and reproductive organs respond to distinct ecological drivers operating at different spatial and temporal scales.

At Ain Kerrouch, where north-facing slopes receive less solar radiation and experience reduced evaporative demand, needles were significantly longer despite intermediate cone and seed sizes. This pattern suggests an adaptive adjustment that enhances photosynthetic efficiency by increasing surface area when water is relatively available (Jaramillo-Correa et al. 2015, El Bakkali and Amraoui 2022). In contrast, the shorter needles observed in Talmet and Oued Tider represent xeromorphic adaptations that minimize transpirational loss and maintain hydraulic safety under extreme heat and aridity (Bicego et al. 2025). These structural adjustments in foliage morphology demonstrate fine-scale acclimation to local temperature and moisture regimes, reinforcing the value of needle traits as sensitive functional indicators of microenvironmental adaptation.

In ecological terms, the independence of needle and reproductive traits should not be viewed as mere decoupling but as complementary expressions of multi-

dimensional adaptation. Vegetative traits buffer trees against short-term climatic variability through morphological plasticity, while reproductive traits reflect longer-term genetic adjustments to drought and temperature extremes. Together, these adaptive dimensions enable *C. atlantica* to persist across steep ecological gradients in Belezma National Park, maintaining population resilience at the arid margin of its natural range.

Environmental drivers of variation

The observed provenance patterns reflect adaptive strategies in semiarid montane forests. In low-rainfall stands, greater seed mass enhances seedling water reserves, improves drought tolerance, and may mitigate frost damage (Moles and Westoby 2006). Talmet's marno-calcareous substrates retain moisture better than pure limestone, but its steep slopes impose additional water stress, reinforcing selection for heavy seeds. Meanwhile, Oued Tider's freely draining limestone soils reduce the advantage of large seeds under higher rainfall. These intraspecific trends mirror other Pinaceae provenance trials in Mediterranean and montane contexts, where precipitation and temperature gradients drive seed size variation (Fady et al. 2022). For example, Scots pine populations at drier sites have around 20–30 % heavier seeds than those at wetter sites, with parallel differences in cone size (Savolainen et al. 2004, Parfenova et al. 2021). Similarly, maritime pine (*P. pinaster*) shows clinal variation in seed mass with climate across Iberian provenances (Solé-Medina et al. 2025).

Our results extend these insights to *C. atlantica*, underscoring that local hydric and thermal regimes are primary drivers of reproductive allocation in semiarid mon-

tane conifers. Documenting this adaptive trait variation has direct implications for *C. atlantica* conservation and restoration in Algeria. Seed transfer guidelines should incorporate local climate matching (Taïbi et al. 2014, 2015, 2016); Talmets-sourced seeds (large-seeded, drought-adapted) should be deployed on arid, low-rainfall sites to improve early survival, whereas Oued Tider seeds, with smaller seeds and lighter cones, are best suited to wetter, milder sites for higher sowing density and establishment. On intermediate-moisture or north-facing sites, incorporating Ain Kerrouch genotypes may balance drought resilience with growth vigour.

Conservation strategies and seed sourcing

It is advisable to define regional seed-transfer zones by overlaying these provenance trait profiles (seed mass, cone size, needle length) onto climatic maps, ensuring translocated seeds remain within environments matching their adaptive profile. Mixed-provenance seed orchards combining Talmets, Ain Kerrouch, and Oued Tider genotypes would hedge against interannual climate variability and preserve allelic diversity for long-term resilience. Furthermore, the decoupling of needle vs. reproductive traits implies that selecting fast-growing, long-needled genotypes may not compromise drought adaptation in reproduction (though field trials are needed to empirically validate such trade-offs under drought stress) (Jaramillo-Correa et al. 2015). Because *C. atlantica* faces escalating climate threats, prioritising genetically diverse, locally adapted germplasm is critical to maintain resilience (Fady and Scotti-Saintagne 2025).

Where future warming and aridification are projected, assisted migration should be considered, introducing Talmets-like germplasm beyond its current range under controlled trials to test survival and adaptive capacity. Ultimately, such recommendations must be validated via common-garden and reciprocal transplant experiments across climatic gradients. These trials will test seedling performance, refine safe transfer distances, and calibrate guidelines based on survival, growth, and observed phenotypic plasticity. By integrating these trait-driven guidelines into national reforestation programmes and seed certification standards, forestry managers can enhance restoration success, maintain local adaptation, and bolster the resilience of *C. atlantica* forests under future Mediterranean climates. Although our analysis revealed clear provenance-level differentiation, the absence of comparable, peer-reviewed morphometric datasets from other parts of the *C. atlantica* range prevents a direct assessment of whether Belezma populations represent typical or extreme expressions of the species' morphological diversity. This data gap underscores the value of the present findings as a first quantitative reference for Algerian provenances and highlights the need for coordinated, range-wide morphometric surveys to establish a broader context for evaluating local adaptation.

While our morphological survey reveals clear environment-driven trait divergence, it remains solely phenotypic. Future studies should integrate molecular analyses to confirm genetic adaptation and common-garden experiments to test the heritability and fitness consequences of these traits.

Conclusions

To conclude, semiarid climate gradients and edaphic differences clearly influence reproductive allocation in *C. atlantica*. This study demonstrates that Algerian cedar populations exhibit significant, environment-driven divergence in cone and seed morphology. Talmet's dry, extremely hot, marno-calcareous site selects for the largest cones and heaviest seeds, while Oued Tider's milder, wetter limestone site corresponds with smaller cones and lighter seeds. Although the number of seeds per cone was similar among provenances, seed yield varied significantly, revealing differences in reproductive efficiency consistent with local adaptation to water stress. Needle length varies independently and is greatest at Ain Kerrouch, suggesting differential allocation priorities among provenances. Notably, Ain Kerrouch, sharing rainfall with Talmet but on north-facing slopes, exhibits an intermediate reproductive outcome.

The absence of baseline data for comparison highlights the need for broader, range-wide study to better contextualise these findings within the species' phenotypic diversity. Another key limitation of this work is its exclusive focus on morphology; future genetic and experimental studies are needed to confirm that these trait differences confer true adaptive advantages. Overall, these findings provide a quantitative basis for seed transfer guidelines and conservation strategies in semiarid montane cedar forests, and emphasise the importance of incorporating local adaptation into germplasm selection under ongoing climate change.

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Comparative study of the distribution and phenology of *Quercus cerris*, *Quercus frainetto* and *Quercus petraea* in Bulgarian forests

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Abstract

This study examined the distribution and phenology of forests dominated by *Quercus cerris* L. (QC), *Quercus frainetto* Ten. (QF) and *Quercus petraea* sensu lato (QP) across Bulgaria. Ecological variables, including altitude, latitude, longitude, aspect and slope, were analysed to characterise species-specific habitat preferences. Phenological events, such as the start of the vegetation period (SVP), the end of the vegetation period (EVP) and the length of the vegetation period (LVP), were also compared. The results showed that QC and QF were more common on flat terrain, whereas QP preferred mountainous areas. QC tended to dominate shaded slopes, QF occurred mainly on sunny exposures, and QP was more evenly distributed across both. QC exhibited the latest leaf unfolding (20 April $\pm$ 4.8 days) and the earliest EVP (15 October $\pm$ 12.8 days), resulting in the shortest growing season (178.1 $\pm$ 13.8 days). In contrast, QF and QP began vegetation period almost simultaneously (16–18 April $\pm$ 4.8–6.6 days) and ended at similar times (20–23 October $\pm$ 9.4–12.9 days), with comparable vegetation periods (187–188 days). Observed features enhance our understanding of the ecological and phenological differences among the three oak species. They can be utilised to improve the efficient, evidence-based management of oak forests in Bulgaria, which may be crucial in the face of climate change challenges.

Key words: end of vegetation period, length of vegetation period, oak forests, start of vegetation period.

Introduction

Genus *Quercus* is one of the most significant groups of woody angiosperms in the Northern Hemisphere in terms of species diversity, ecological dominance and economic importance (Nixon 2006, Gil-Pelegrín et al. 2017). It comprises estimated 430 species of trees and shrubs

(Carrero et al. 2020), mainly deciduous, and occupies a variety of environments, including temperate, subtropical, and tropical regions (San-Miguel-Ayán et al. 2016). Few oak species are the most prevalent in Bulgarian hardwood forests – *Quercus cerris* L. (QC), *Quercus frainetto* Ten. (QF), and *Quercus petraea* sensu lato (QP), the latter of which includes

three sessile oak species recognised in Bulgaria: *Quercus petraea* (Matt.) Liebl., *Quercus dalechampii* Ten., and *Quercus polycarpa* Schur (Ganchev and Bondev 1966; Nicolescu et al. 2025). According to Stefanov (1943a,b, 1944), natural oak forests adapted to the plains and lower mountain slopes were extensively clear-felled in the past to meet agricultural needs, provide pasture, and supply fuel for nearby settlements. Despite historical logging pressures, stands containing these species still represent over a third of Bulgaria's forest area (Alexandrov and Tonchev 2024), with forests dominated by them covering 14.1% of the country's total forest area (NFI 2023). In many instances, the three species coexist in mixed oak forests, with different levels of dominance depending on site conditions. Stefanov and Ganchev (1953) also observed that oaks face significant challenges in colonising new areas due to their heavy seeds, limited germination viability, and high seed predation. Combined with their relatively slow growth, these characteristics emphasise the phytogeographic significance of oaks.

QC is distributed throughout southern Europe, from central and northern Spain to the Balkan Peninsula, extending to Switzerland in the north and Syria in the south (Stefanov 1934). Stefanov (1943a) notes that among all oaks found in Bulgaria, QC is notable for its widespread distribution. The author notes that among all oaks found in Bulgaria, QC is distinguished by its widespread distribution, except in mountainous regions (above 800–900 m a.s.l.) and in the Thracian plain. According to Vannini et al. (2022), it is more light-demanding than QP and susceptible to late spring frosts, but relatively tolerant of drought and air pollution. QF mainly occurs on the Balkan Peninsula

and in southern Italy (San-Miguel-Ayanz et al. 2016). Stefanov (1943a) emphasises that the species' distribution indicates adaptation to the continental climate and resilience to soil drought, which explains its widespread presence in Northern Bulgaria, particularly in the Northeast. Chatziphilippidis and Spyroglou (2006) describe it as a light-demanding, meso-xerophilous species typical of transitional climates between Mediterranean and continental areas, with hot summers and cold winters. QP is common throughout much of Europe, particularly in hilly and lower mountainous regions (Stefanov 1943a), which is why it is often called 'the oak of the mountains' (Nicolescu et al. 2025). It is regarded as drought-tolerant, often found on light, well-drained, rocky soils and acidic substrates, frequently on slopes and ridges (San-Miguel-Ayanz et al. 2016). Other authors, however, report that it flourishes in fertile, deep, and moist soils (Nicolescu et al. 2025) or limestone soils (Stefanov 1943a). Stefanov (1943a) attributes the species' absence in north-eastern Bulgaria and its sporadic presence in the Deliorman region to the limited number of humid localities in the area. High variability demonstrates its extensive phenotypic plasticity, which explains why some populations are classified as subspecies or even separate species in certain countries (Nicolescu et al. 2025). Nevertheless, this variability allows adaptation to different environments and enhances its resilience amid climate change (Sáenz-Romero et al. 2017).

The timing of phenological events is a significant determinant of the productivity and species distribution in temperate forests. Numerous studies (Vitasse et al. 2009, 2011; Čufar et al. 2012; Schieber et al. 2013; Gressler et al. 2015; Flynn and Wolkovich 2018; Peaucelle et al. 2019;

Piao et al. 2019; Lukasová et al. 2020; Ciocîrlan et al. 2022; Gafenco et al. 2022; Anev 2023, 2025; Skvareninova et al. 2024) indicate that the phenology of temperate deciduous trees varies with altitude and latitude due to differences in temperature, photoperiod and other environmental factors. According to Hopkins' bioclimatic law (Hopkins 1918), temperatures in temperate latitudes progressively decrease with elevation and distance from the equator, delaying spring phenophases, such as budburst, flowering and leaf unfolding, while advancing autumn events. This results in a shorter growing season at higher altitudes and latitudes, reducing the available time for growth and reproduction. Local factors, such as slope, aspect and topography create additional microclimatic variation, so phenological timing can vary even within the same altitude range. Schuster et al. (2014) found that cold-air pools significantly affect the growing season of deciduous trees, with individuals on mid-slope positions often having an advantage over those at valley bottoms. Long-term studies on temperate woody species demonstrate that three main cues govern budburst and leaf unfolding: spring forcing temperatures, increasing photoperiod, and the duration and intensity of winter chilling (Flynn and Wolkovich 2018).

Remote sensing techniques, such as satellite imagery and unmanned aerial vehicles, offer effective tools for monitoring phenology. Numerous studies (Bucha and Koren 2017, Lukasová et al. 2019, Gray and Ewers 2021, Soudani et al. 2021, Ciocîrlan et al. 2022, Grabska-Szwagrzyk and Tymińska-Czabańska 2024) demonstrate that the variations in vegetation's ability to absorb primarily red and infrared radiation, as measured by multispectral cameras, indicate distinct phenological

stages and can be quantified through spectral indices. These indices track variations over time and space in phenological events, with statistical algorithms aiding in determining their timing and relationship to environmental factors.

Although the ecology and biology of *Quercus* species in Europe have been broadly studied, some issues remain difficult to resolve. These issues relate to how long-lived organisms, like oaks, respond to changing climate conditions, which develop much faster than woody plants can adjust either in the short term through physiological changes or across generations in the long term.

This study aimed to improve understanding of the distribution and phenology of forests dominated by three of Bulgaria's most widespread oak species. The results are expected to deepen knowledge of their ecology and support evidence-based forest management strategies, which are essential in the face of climate change challenges.

Object and Methods

This study focuses on Bulgarian forests mainly composed of three common oak species: *Quercus cerris* L. (QC), *Quercus frainetto* Ten. (QF) and *Quercus petraea* sensu lato (QP). The latter includes three oak species recognised in Bulgaria: *Quercus petraea* (Matt.) Liebl., *Quercus dalechampii* Ten. and *Quercus polycarpa* Schur, all of which are listed in the national forest inventory as sessile oak. For the purposes of this study, and according to Welle et al. (2022), a forest stand was considered dominated by one of the species if at least 80% of the main tree layer consisted of that species.

Tree species composition and stand

polygons were sourced from the National Forest Inventory database, current as of 2022, and available at <https://iag.bg/> (Fig. 1). The polygons for the stands conformed to the boundaries outlined during the forest inventory. Before the analysis, a validity check algorithm was applied to the vector layer geometries, and no errors were detected.

The extent of QC-dominated forests is nearly the same as that of QP-dominated forests and surpasses the area of QF-dominated forests. The QP-dominated forests have the highest average age, while the QC-dominated forests are the youngest (Table 1).

The National Forests Inventory database and satellite raster imagery were processed using QGIS (v. 3.40.9). Mean stand coordinates (latitude and longitude)

Table 1. Area and age of studied forests

Variants	Area, ha	Area, %	Age, years $\pm$ SD
QC-dominated forests	183,684	4.83	56.8 $\pm$ 25.6
QF-dominated forests	169,690	4.46	60.5 $\pm$ 30.2
QP-dominated forests	183,872	4.83	67.2 $\pm$ 28.0

Note: The areas are presented both in hectares and as a percentage of the total forested area of Bulgaria.

were calculated using the 'native:meancordinates' tool. The EuroDEM raster layer (EuroGeographics 2025) was used to derive altitude, slope, and exposure. The raster was reprojected to EPSG:32635 with the 'gdal:warp' tool (GDAL v. 3.10.2), and slope and exposure rasters

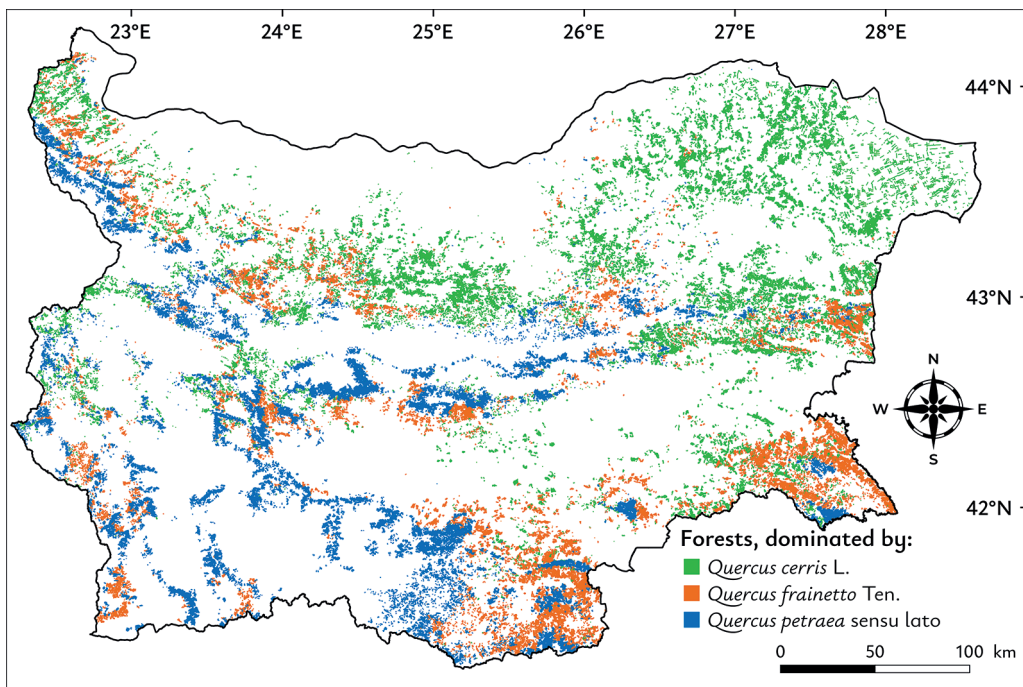


Fig. 1. Geographical distribution of forests dominated by *Q. cerris* (54,343 stands), *Q. frainetto* (40,684 stands) and *Q. petraea* (40,298 stands) in Bulgaria.

were generated with the 'r.slope.aspect' tool (GRASS GIS v. 2.12.99). Because the exposure raster represents circular data ($0^\circ = 360^\circ = \text{north}$), direct averaging would produce incorrect values. To address this, the exposure values were dissected into two components: 'Exposure_y', indicative of the north–south orientation through a cosine function, varying from $-1.0 = \text{south}$ to $1.0 = \text{north}$; and 'Exposure_x', indicative of the east–west orientation through a sine function, varying from $-1.0 = \text{west}$ to $1.0 = \text{east}$. Zonal statistics ('native:zonalstatisticsfb') were then used to compute average values ('Exposure_y_mean' and 'Exposure_x_mean') of these two rasters for each stand. The geographic angle of mean exposure was reconstructed using the function specifically created for this case:

CASE

WHEN degrees(atan2('Exposure_y_mean', 'Exposure_x_mean')) < 0

THEN degrees(atan2('Exposure_y_mean', 'Exposure_x_mean')) + 360

ELSE degrees(atan2('Exposure_y_mean', 'Exposure_x_mean'))

END

Phenological events were derived from the Copernicus Land Monitoring Service, using satellite imagery from the High-Resolution Phenology and Productivity series (WEkEO 2025) of the Copernicus programme (<https://land.copernicus.eu/>). The analysis used the Seasonal Trajectory of the Plant Phenology Index (ST-PPI) (Jin and Eklundh 2014; Smets et al. 2022), particularly the start of the season (SOSD), end of the season (EOSD), and length of season (LOSD) rasters for season 1 from the years 2017 to 2023. For each stand, the SOSD, defined as the spring day when the ST-PPI reaches 25 % of its maximum annual value, was used to estimate the average start date of

the vegetation period (SVP); EOSD, defined as the autumn day when the ST-PPI drops to 15 %, was used to estimate the average end date of the vegetation period (EVP); and LOSD, defined as the difference between EOSD and SOSD, was used to estimate the average length of the vegetation period (LVP) in days. Twenty-two raster images were analysed for each phenological event across each year from 2017 to 2023 ($N = 462$).

Images were reprojected using 'gdal:warp' and mosaicked with 'gdal:buildvirtualraster' (GDAL v. 3.10.2). Zonal statistics ('native:zonalstatisticsfb') were then employed to calculate mean values of phenological events for each stand's polygon. The final dataset, combining geographic and phenological attributes, was exported with the 'gdal:gdal2xyz' tool and transferred into MS Excel (Office 365, Microsoft) for visualisation and statistical analysis. Statistical processing was performed using built-in functions and VBA scripts (VBA v. 7.1, Microsoft). One-way ANOVA followed by Tukey's post hoc test was applied to compare geographic indicators and phenological events among the three oak-dominated forest types. The slope of the linear regression between latitude, longitude, and altitude, on one hand, and the SVP, EVP and LVP, on the other, was used to evaluate the impact of geographical coordinates on the timing of phenological events.

Results

Distribution

Species-specific variation in distribution by latitude and longitude was observed when comparing forests dominated by QC, QF, and QP. QC-dominated forests

were primarily located in North and East Bulgaria, while QP-dominated forests were mainly found in South and West Bulgaria. QF-dominated forests were spread throughout Bulgaria, except in the North-East. The distribution range in latitude was narrowest in QC and broadest in QF, and in longitude it was narrowest in QP and broadest in QC. QC and QF were more prevalent on flat terrain, whereas QP was mainly associated with mountainous regions (Fig. 2A,B).

Despite the notable difference in the average altitudes of forests dominated by QC and QF (mean $\pm$ SD: QC = 357.4 $\pm$ 205.6 m, QF = 380.0 $\pm$ 200.5 m), their similar ranges of variation (5–95 %: QC = 114.9–818.0 m, QF = 101.7–782.2 m) suggest comparable ecological importance for this indicator. Conversely, forests dominated by the QP (mean $\pm$ SD: 749.4 $\pm$ 334.7 m) are rarely (<5 %) found below 390 m a.s.l. (5–95 %: 392.3–1110.3 m),

which corresponded to the average altitude for forests dominated by QC and QF. In accordance with the vertical distribution patterns of these forest species, QC and QF were predominantly found on flat and gentle slopes, whereas QP was mainly located in sloped mountainous regions (Fig. 3A,B).

The distribution of forests dominated by the three studied species varied also with terrain exposure (Fig. 4A–C). While QC preferred shady exposures (56.8 %), this preference decreased in QP (51.9 %). In QF-dominated forests, the presence of sunny and shady slopes was nearly equal, and their tolerance for fully southern slopes was notable.

All three studied species tended to avoid western exposures, likely due to the prevailing westerly movement of air masses over Bulgaria. Nevertheless, while QC avoided slopes oriented west-southwest, QP avoided slopes oriented west-north-

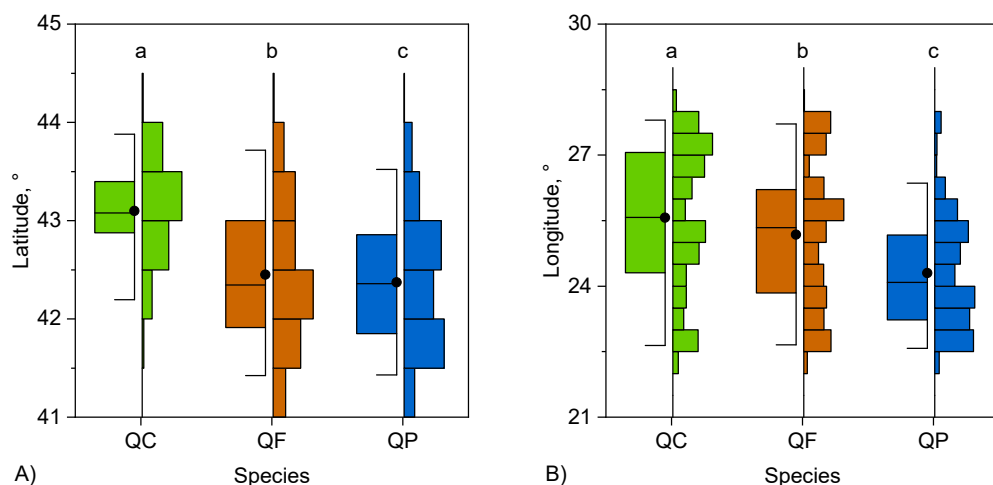


Fig. 2. Distribution extent of *Q. cerris* (QC), *Q. frainetto* (QF) and *Q. petraea* (QP) dominated forests by: A) latitude, B) longitude.

Note: Mean values are indicated by a solid dot, the median by a line, the box range shows the 25–75% quartiles, and the whiskers extend to the 5–95% range. Histograms display the distributions with a bin size of 0.5°. Means that do not share a letter differ significantly (one-way ANOVA with Tukey test, p -value < 0.05).

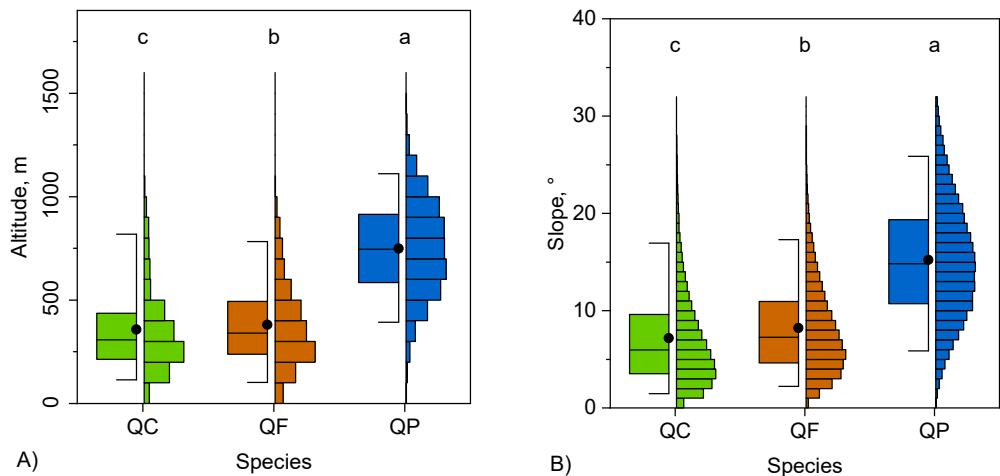


Fig. 3. Orography extent of *Q. cerris* (QC), *Q. frainetto* (QF) and *Q. petraea* (QP) dominated forests by: A) altitude, B) slope.

Note: Mean values are indicated by a solid dot, the median by a line, the box range shows the 25–75 % quartiles, and the whiskers extend to the 5–95 % range. Histograms display the distributions with a bin size of 100 m in altitude and 1° in slope. Means that do not share a letter differ significantly (one-way ANOVA with Tukey test, p -value < 0.05).

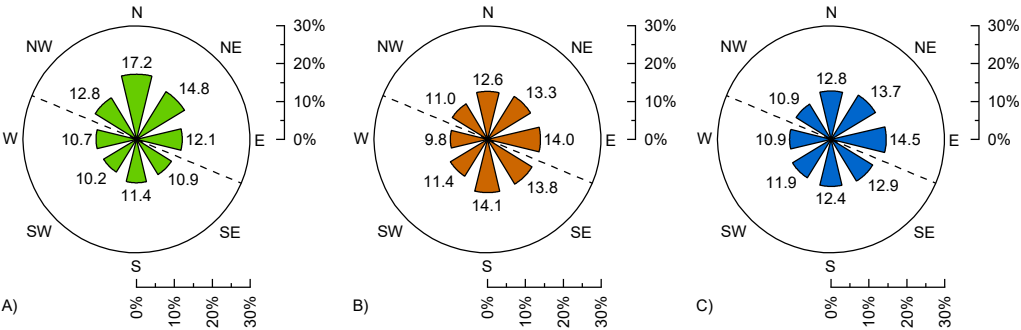


Fig. 4. Distribution of terrain exposures in forests dominated by A) *Q. cerris* (QC), B) *Q. frainetto* (QF) and C) *Q. petraea* (QP).

west, and the QF was least frequently observed on slopes directly exposed to the west.

Phenology

Within the noted disparities in the distribution of QC, QF, and QP-dominated forests, species-specific differences emerged both at the start and, more prominently, at the

end of the vegetation period (Fig. 5A–C).

In QC-dominated forests, the SVP occurred around 20 April (± 4.8 days), and the EVP occurred around 15 October (± 12.8 days), leading to a shortened LVP of 178.1 days (± 13.8). The longest LVP of 188.0 (± 12.4) days occurred in QP-dominated forests, primarily because of a later EVP on 23 October (± 9.4 days), rather than an earlier SVP on 18 April (± 6.6

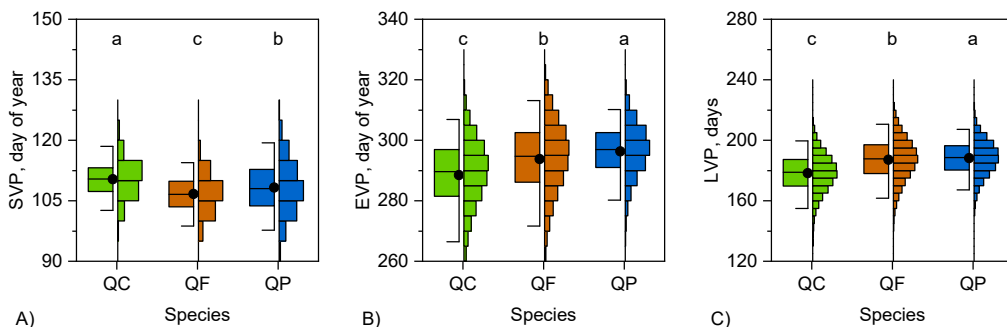


Fig. 5. Phenological events: A) start of vegetation period (SVP), B) end of vegetation period (EVP), and C) length of vegetation period (LVP) in forests dominated by *Q. cerris* (QC), *Q. frainetto* (QF) and *Q. petraea* (QP).

Note: Mean values are indicated by a solid dot, the median by a line, the box range shows the 25–75 % quartiles, and the whiskers extend to the 5–95 % range. Histograms display the distributions with a bin size of five days. Means that do not share a letter differ significantly (one-way ANOVA with Tukey test, p -value < 0.05).

days). The earliest SVP was observed in QF-dominated forests on 16 April (± 4.8 days). However, in these forests, EVP occurred earlier than in QP-dominated forests, on 20 October (± 12.9 days). This chronology resulted in an LVP of 187.1 days (± 14.7), which, despite being similar in length, remained slightly shorter than the LVP in QP-dominated forests.

In the two species most closely associated with plain conditions (QC and QF), SVP was reached relatively quickly, typically within two weeks, for 90 % of these forests. Conversely, in the more montane QP, SVP was significantly delayed, reaching nearly 22 days for 90 % of the forests dominated by this species. The EVP period was considerably longer than SVP, exceeding one month in the examined forests. EVP occurred most rapidly in forests primarily composed of the more mountainous QP species, around 30 days for 90 % of these forests. In contrast, for the more plains-adapted species, QC and QF, this period extended to 40–41 days.

Spring phenology at QC was most

strongly associated with latitude, with SVP occurring 2.3 days earlier per degree northward and 1.3 days later per 100 m increase in elevation, while longitude had no significant effect. Conversely, in QP, altitude had a greater influence, delaying SVP by 2.1 days per 100 m, whereas a one-degree northward shift advanced SVP by 1.8 days. The spring phenology in QF was not significantly influenced by latitude, longitude, and altitude, and occurred largely synchronously within its range in Bulgaria.

The autumn phenology in QC was significantly affected by geographical coordinates, with a one-degree eastward shift advancing EVP by 2.3 days, and a one-degree northward shift delaying it by 2 days later. Elevation had a minor effect on QC's autumn phenology, amounting to less than one day per 100 metres of elevation gain. In QF, longitude was the main factor, advancing EVP by 2.1 days per degree east. For QP, EVP occurred 1.5 days earlier per degree northward.

These trends were evident in LVP,

which increased by 4.3 days in QC with a degree shift to the north and decreased by 2.4 days with a shift to the east. In QF, longitude had the most significant effect, with a one-degree eastward shift reducing LVP by 2.4 days. In QP, LVP was most sensitive to altitude, shortening by 1.7 days per 100 m increase.

Discussion

This study confirmed that QC was associated with flatter conditions in Northern, Eastern, and especially Northeastern Bulgaria, and is nearly absent in southwestern Bulgaria due to the more mountainous terrain and higher altitude there. These findings align with those of other authors (Stefanov 1943a). QP preferred more mountainous areas in Southern, Western, and particularly Southwestern Bulgaria. Although QF exhibited a wide range across Bulgarian forests, it was most prominently dominant in hilly and flat regions within the northwestern-southeastern Bulgaria strip. Some authors, such as Mérian et al. (2011), suggested that the amount of precipitation during the active growth period (May to July) limits the distribution of QP. Perkins et al. (2018) and Peters et al. (2023) proposed that this may have resulted from the anisohydric traits of the species, which can lead to a more prolonged drought memory due to high investments in maintaining photosynthetic activity. In Bulgaria, the species' preference for southern and western regions appeared to be more closely associated with the mountainous terrain of these areas than with their hydrothermal regimes, as the species dominates forests from the Western Stara Planina to the Eastern Rhodopes and Strandzha. However, Šimková et al. (2023) highlighted

that droughts occurring in June and July mainly restrict the growth of QC, with temperature having only a minor influence. Stefanov (1943b) also notes that although it avoids terrain with high groundwater levels, the QP is sensitive to late spring droughts, which explains its preference for more mountainous, drained, but better periodically moistened areas by rain. Additionally, Móricz et al. (2021) observed that QP exhibited lower growth plasticity in response to drought compared to QC. The authors noted that QC responded dynamically to fluctuations in soil water availability, showing significantly decreased growth rates during droughts, a strategy that likely helps in conserving reserves for subsequent recovery and survival. The greater potential for recovery after a dry period in QC compared to QP was further confirmed by Mészáros et al. (2022). This, combined with better resistance to low temperatures due to later leafing, explains the more widespread presence of QC in Northern and especially in Northeastern Bulgaria. On the other hand, Stefanov (1943a) points out that, compared to other studied oaks, the QC has almost annual fruiting and significantly more successful natural regeneration, which may be responsible for its wide distribution. The preference for different terrain exposures in QC and QF probably reflects different strategies in water absorption, and therefore, differences in their geographical distribution. Although QF extends into the foothills of Northern Bulgaria, it is less dominant than QC in Northeastern part of Bulgaria, where the climate is likely too continental for this species. In the central and western parts of Northern Bulgaria, where both species coexist in mixed oak forests, they dominate slopes with different exposures – QF on south- and south-east-facing slopes, and QC on north- and

northeast-facing ones. It should be noted that, due to the preference for the flatter conditions of the QC and the QF, their distribution is heavily affected by human activity (Stefanov 1943b). The predominantly coppice forests (Alexandrov and Tonchev 2024) may regenerate through various mechanisms related to overcoming competition from grass and shrub vegetation, which in the QC could explain its stronger presence in shaded rather than sunny exposures. However, Popović et al. (1997) noted that QF has a narrower ecological range than QC in most aspects, especially concerning light and soil moisture, although it is more drought-tolerant and requires higher light availability.

The observed differences in phenological events were likely driven by ecological variations among the studied species and by the differing conditions of their respective forest habitats. As a more continental species (San-Miguel-Ayanz et al. 2016), QC emerged the latest, which probably enhanced its resilience to late spring frosts. Unlike European beech, in which the investment in winter bud formation begins in the middle of the previous year (Anev 2023, 2025), species within the genus *Quercus* do not show such preparatory processes. This creates a challenge for species that produce new leaves early, as they need to store more winter reserves in the xylem parenchyma to enable rapid leaf emergence. Conversely, species that unfolded earlier and over a longer period, such as QP, benefited from using assimilates produced by young leaves to support the later phases of leaf and shoot development. Numerous studies (Liepe 1993, Deans and Harvey 1995, Ducousso et al. 1996, Sáenz-Romero et al. 2017, Gafenco et al. 2022) conducted in comparative trials of sessile oak have shown that the budburst phenology varies with latitude,

with southern populations leafing earlier than northern ones. Gafenco et al. (2022) reported that budburst in sessile oak followed longitudinal and altitudinal tendencies rather than latitudinal ones, with lower-elevation eastern provenances leafing earlier than higher-elevation western ones, suggesting that less accumulated heat is required to trigger budburst. However, these findings contrasted with those of Jensen (2000), who found in comparative trials of sessile oak and pedunculate oak that northern provenances budded earlier than southern provenances, which agreed with our results. Nonetheless, certain studies have also documented similar clinal variations along altitudinal gradients (Alberto et al. 2011, 2013), which may be attributed to the species' high physiological tolerance to heat. The earliest leaf development observed in QF indicated a preference for more Mediterranean conditions and likely explained its weaker presence in Northeastern Bulgaria, where late spring frosts could disrupt the vegetation period. Across all species, EVP lasted longer than SVP. However, while in QP the difference between the two phenophases was only ten days, in QC and especially in QF, this difference exceeded two and a half times. The two species characterised by rapid and short SVP phases (QC and QF) had a slower and prolonged EVP, whereas, in contrast, the slow-developing QP completed the vegetation period quickly. This may reflect the more contrasting conditions in the mountain's habitats where QP predominates.

Conclusions

This study highlighted the distinct ecological and phenological features of the three most common oak species in Bulgarian

forests. Both QC and QF favoured flatter areas but differed in exposure preferences. Specifically, QC preferred shaded slopes, whereas QF was often found in sunny terrains. Meanwhile, QP occurred on steeper slopes, mountainous regions, reflecting its tolerance for cooler and more variable conditions. QC dominated the flat, low-lying areas of Northern and Eastern Bulgaria, exhibiting a broad longitudinal distribution and strong adaptation to continental conditions through late leaf unfolding and short vegetation periods. QF primarily inhabited hilly terrains across Southern Bulgaria, showing the widest latitudinal and longitudinal range, as well as earlier leaf development, reflecting adaptation to warmer, more Mediterranean climates, yet limiting its presence in the colder Northeast. QP prevailed in the mountainous regions of Southern and Western Bulgaria, displaying the widest altitudinal range and the most extended vegetation period due to delayed leaf senescence. Phenological rhythms varied geographically: QC was the most influenced by latitude and altitude, QP by altitude, and QF showed the least spatial dependence. These distinct ecological and phenological strategies shape distribution of studied oak species across Bulgaria and provide insights into their potential responses to future climatic shifts.

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Variability in drupe and seed traits of *Pistacia lentiscus* along a latitudinal gradient in Algeria

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Abstract

This study investigates drupe and seed traits, as well as seed viability, of *Pistacia lentiscus* L. across six sites distributed along a latitudinal gradient in Algeria. At each site, ten shrubs from wild populations were randomly selected for sampling. One hundred mature drupes per shrub were collected in 2018 and 2019 and analysed for various quantitative and qualitative traits. No significant differences were observed between years for quantitative traits, but significant variation was detected among sites. Drupes from the northernmost sites were heavier but contained smaller seeds compared to those from southern sites. Seed weight represented approximately 25 % of drupe weight. On average, seed viability was 18.94 %, although at two of the six sites it reached 35 to 47 %, with a few individuals showing up to 91 %. At the other sites, particularly in semi-arid areas, viability was low and sometimes zero. Principal Component Analysis (PCA) based on the drupe and seed features allowed discrimination between the two northernmost sites and the others. In contrast, qualitative traits such as colour, shape, and surface were relatively consistent across sites. This study provides the first evidence of geographic variation in reproductive parameters such as drupe and seed weight, seed size, and seed viability in *P. lentiscus* populations in Algeria. Such variation may influence the species' capacity to regenerate through seeds.

Key words: aridity, fruit traits, lentisk tree, Mediterranean region, phenotypic variation, seed viability.

Introduction

Pistacia lentiscus L. (lentisk tree) is a thermophilic shrub prevalent across diverse habitats in the Mediterranean region of Europe, North Africa, and the Levant. This species exhibits remarkable adaptations to harsh and arid environments (Verdú and García-Fayos 2001). It typically grows in warm regions at low altitudes, but it also thrives in sunny, sheltered areas at intermediate elevations. Resistance to early frost is closely linked to the timing of the end of the growing season (Pilar and Gabriel 1998, Palacio et al. 2005).

P. lentiscus is highly tolerant to drought and salinity (Alvarez et al. 2018) and is therefore valuable for the reforestation of eroded soils (Bouta et al. 2020) and for the restoration of fire-prone ecosystems due to its capacity to resprout after disturbance (Vallejo et al. 2012). In addition, its fruits play an important ecological role by providing food for frugivorous birds (Verdú and García-Fayos 2003).

Besides its ecological importance, *P. lentiscus* also has economic value, particularly through the mastic harvested from the wounded trunks of male trees. Various parts of the tree have been widely used in traditional medicine from ancient Greece to the present (Pachi et al. 2020, Başbayraktar and Yücedağ 2023). Recent studies have highlighted its biotechnological potential, particularly its antifungal (Al-Zaben et al. 2023), antioxidant (Bouakline et al. 2023), anti-inflammatory (Milia et al. 2021), and antimicrobial (Jara-dat et al. 2022, Djebbari et al. 2023) properties.

This species exhibits a mixed regeneration strategy, involving both resprouting and seed production. Regeneration by seeds is essential for maintaining plant genetic diversity (Grimsby et al. 2007).

Previous studies have emphasised the importance of seed traits for successful regeneration (Wang et al. 2014, Amimi et al. 2023). For example, seed size is recognised as a key factor in germination and seedling development. Traits such as seed morphology and germination directly influence recruitment, plant fitness, and persistence (Cochrane et al. 2015, Wu et al. 2018).

In Algeria, *P. lentiscus* is widely distributed across forests and scrublands, thriving under diverse edaphic and bioclimatic conditions ranging from coastal areas to inland regions and from lowlands to mountains (Ait Said et al. 2013, Doghbage et al. 2023). This study hypothesises that the broad geographical distribution of *P. lentiscus* may lead to significant variation in its reproductive traits, as previously evidenced for Moroccan populations (Bouta et al. 2020) and for other species (Wang et al. 2014, Diawara et al. 2024, Liu et al. 2025).

Despite the extensive ecological and biochemical research on *P. lentiscus*, few studies have examined intraspecific variation in its reproductive traits across contrasting environments. Information on how these traits respond to geographic gradients remains particularly scarce for North African populations, especially for Algerian ecotypes. To address this gap, the present study yields new insights into the quantitative and qualitative variability of drupe and seed traits among natural populations of *P. lentiscus*. These populations occur along a latitudinal transect which aligns with an aridity gradient in Algeria. Conducted over two years (2018–2019), the study also accounts for annual fluctuations in reproductive output. The findings provide essential data for understanding the species' adaptive potential and offer empirical support for conservation and

restoration strategies under changing Mediterranean climatic conditions.

Materials and Methods

Study area

Drupes were collected from six *P. lentiscus* populations located across a latitudinal-longitudinal gradient in northern Algeria, ranging from 34.80° N, 3.12° E (Ain Maâbed, Djelfa) to 36.89° N, 4.13° E (Tigzirt, Tizi Ouzou). The sampling sites span inland semi-arid zones to coastal humid areas, thus covering a wide bioclimatic range. Djelfa represents one of the most continental locations, whereas Tigzirt corresponds to the coastal extreme. Climatic data for the period 1979–2019 were obtained from the ERA5-Land dataset (Muñoz-Sabater 2019) (Table 1).

at each site (2.50 ± 0.50 m wide, 1.50 ± 0.50 m tall, and approximately 20–30 years old). From each shrub, 100 mature drupes were collected, yielding 1,000 drupes per site, for a total of 60 shrubs and 6,000 drupes harvested per year. The first harvest, hereafter referred to as the 2018 harvest, was conducted in December 2018, a period that coincides with drupe maturity according to earlier studies (Martínez-Pallé and Aronne 2000, Albaladejo et al. 2009). The second harvest was carried out in December 2019 at the same sites and on the same shrubs, which allowed assessment of the year effect. In the following, the sites are referred to by the name of their corresponding province, except for the two sites in Tizi Ouzou and for M'sila, which are referred to by the site name. Where relevant, the six sites are also designated by numbers in ascending order of latitude.

Field sampling of plant material

In 2018 and 2019, 10 shrubs from natural populations were randomly sampled

Quantitative measurements

For each shrub at each site, 100 drupe lots (DW, g) and the corresponding seed lots

Table 1. Geographic and climatic characteristics of the sampling sites.

Province	Site	Site code	Latitude °N	Longitude °E	Altitude, m	MAT, °C	MAP, mm	Bioclimate
Djelfa	Ain Maâbed	1	34.80	3.12	1048	16.72	276.62	Upper semi-arid
M'sila	Elhamel	2	35.00	4.08	772	17.10	322.50	Upper semi-arid
	Hemmam Dalâa	3	35.95	4.38	843	16.24	394.12	Lower semi-arid
Bouira	Haizer	4	36.40	3.99	682	16.50	667.16	Lower sub-humid
Tizi Ouzou	Tizi Gheniff	5	36.60	3.77	413	17.82	723.22	Upper sub-humid
	Tigzirt	6	36.89	4.13	18	18.10	827.54	Lower humid

Note: MAT – mean annual temperature, °C; MAP – mean annual precipitation, mm. Bioclimate classification is based on ERA5-Land data.

(SW, g) were weighed using an electronic balance (Carat GD603, Sartorius; accuracy: 0.001 g). The weight of 1,000 seeds was determined in accordance with ISTA (2018). This involved weighing 100 seeds from each of 10 replicates (shrubs). One hundred seeds per shrub were scanned and measured for length (SL, mm) and width (SWi, mm) using the trial version of Digimizer software, version 5.3.5 (2015 to 2019).

Seed viability (SV, %) was tested by the flotation method in water (Vasques et al. 2013, Daneshvar et al. 2017) on a single seed lot per shrub. Empty or poorly developed seeds floated, while filled seeds sank. Following this test, all seeds were dissected to confirm their content. This dissection verified that the sinking seeds were indeed filled, while the floating ones were empty. In the present study, we didn't distinguish whether viability loss was due to parthenocarp or embryo abortion. The percentage of viable seeds was calculated as the number of sinking seeds divided by the total number of tested seeds. The following variables were also calculated: seed-to-drupe weight ratio (SW/DW) and the seed width-to-length ratio (SWi/SL).

Measurements were based on 60 lots of 100 drupes, 1,000 seeds, 100 pericarp weights, and 100 seed viability assessments (total $n = 6,000$ for seed size).

Qualitative variables

Seed colour, surface texture, and shape were visually evaluated for the complete seed lot of each shrub at all sites.

Statistical analysis

Quantitative data were analysed using descriptive statistics and analysis of variance (ANOVA). For seed length and width,

ANOVA yielded identical results whether performed on the raw data or on shrub means; therefore, the latter approach was retained. A preliminary ANOVA showed no year effect for any quantitative trait. Consequently, data from the two years were pooled for each shrub within a site, and the site effect was tested using ANOVA. When significant differences among sites were detected, a multiple post hoc Tukey test was applied at a significance level of 5 %.

Pearson correlations and principal component analysis (PCA), including environmental conditions as supplementary variables, were also conducted on shrub means for drupe and seed traits ($n = 60$). The results were represented on the first two components. Qualitative data were summarised by site and year as percentages. All statistical analyses were performed using R software (version 4.3.2, R Core Team 2023).

Results

Quantitative traits

Statistical parameters (means per site, standard deviations, and homogeneous groups provided by the post hoc Tukey test) are summarised in Table 2 and figures 1–3.

The mean weight of 100 drupes was 6.17 g, with site-specific averages ranging from 3.53 (Site 1) to 8.76 g (sites 5 and 6). This pattern indicates a clear geographic trend, with drupe weight gradually increasing from southern to northern sites (Fig. 1A). The mean weight of 100 pericarps was 4.73 g, ranging from 2.67 g to 7.09 g per site (Fig. 1B, Table 2). These differences among sites were statistically significant, and mirrored the trend obser-

Table 2. Mean values (mean $\pm$ standard deviation) of *P. lentiscus* drupe and seed traits along a latitudinal gradient.

Traits	Southern sites				Northern sites	
	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
DW ₁₀₀ , g	3.52 ± 0.62 d	4.60 ± 0.43 c	5.41 ± 1.19 bc	6.16 ± 0.57 b	8.76 ± 1.18 a	8.56 ± 0.85 a
PW ₁₀₀ , g	2.67 ± 0.83 d	3.20 ± 0.40 c	4.04 ± 1.08 bc	4.78 ± 0.61 b	7.09 ± 1.07 a	6.94 ± 0.77 a
SW ₁₀₀₀ , g	12.20 ± 1.90 c	14.00 ± 0.90 b	13.70 ± 2.40 bc	13.70 ± 1.60 bc	16.70 ± 2.00 a	16.20 ± 2.40 ab
SW/DW	0.35 ± 0.06 a	0.30 ± 0.02 b	0.26 ± 0.05 c	0.22 ± 0.03 cd	0.19 ± 0.02 d	0.20 ± 0.02 d
SL, mm	4.02 ± 0.18 b	4.61 ± 0.37 a	4.71 ± 0.26 a	4.51 ± 0.18 a	3.66 ± 0.33 c	3.28 ± 0.17 d
SWi, mm	3.34 ± 0.17 b	3.85 ± 0.22 a	3.63 ± 0.22 ab	3.71 ± 0.30 a	2.80 ± 0.33 c	2.51 ± 0.26 c
SWi/SL	0.83 ± 0.03 a	0.84 ± 0.06 a	0.77 ± 0.02 a	0.82 ± 0.07 a	0.77 ± 0.04 a	0.77 ± 0.07 a
SV, %	1.25 ± 1.29 b	8.55 ± 9.55 b	8.00 ± 11.49 b	12.75 ± 20.75 b	47.15 ± 16.67 a	35.00 ± 25.06 a

Note: DW₁₀₀ is drupe weight per 100 pieces, g; PW₁₀₀ is pericarp weight per 100 pieces, g; SW₁₀₀₀ is seed weight per 1,000 pieces, g; SW/DW is seed-to-drupe weight ratio; SL is seed length, mm; SWi is seed width, mm; SWi/SL is seed width-to-length ratio; SV is seed viability, %. Means followed by different letters differ significantly at $\alpha = 0.05$ (Tukey's test).

ved for total drupe weight. Overall, the results suggest that in northern populations, *P. lentiscus* allocates a larger proportion of biomass to the pericarp.

The mean weight of 1,000 seeds was 14.40 g, with site-specific values ranging from 12.20 g to 16.70 g (Fig. 1C). The analysis of variance revealed statistically significant differences among sites, with the two northernmost sites producing heavier seeds than the southern sites. This trend indicates a lower allocation of weight to seeds in the southernmost site (Site 1). The seed-to-drupe weight ratio averaged 0.26 (range 0.19–0.35), indicating that most drupe biomass is devoted to the pericarp rather than the seeds (Fig. 1D). Significant differences were observed among sites: Site 1 had the highest proportion of biomass allocated to seeds (0.35), while sites 5 and 6 had

ratios not exceeding 0.20. Taken together, these values show a gradual decrease in the seed-to-drupe ratio from south to north.

Seed dimension also varied significantly among sites. Seed length averaged 4.14 mm, with values ranging from 3.28 mm to 4.71 mm. Four homogeneous groups were identified: sites 2, 3, and 4 had the longest seeds (4.51–4.71 mm); Site 1 had with intermediate length (4.02 mm); Site 5 had shorter seeds (3.66 mm); and Site 6 had the shortest seeds (3.28 mm) (Fig. 2A, Table 2). Seed width averaged 3.31 mm, with significant differences among sites. They were grouped into three categories: three sites with wider seeds (3.63–3.81 mm), the two northernmost sites with narrower seeds (2.51–2.80 mm), and the southernmost site with an intermediate mean value

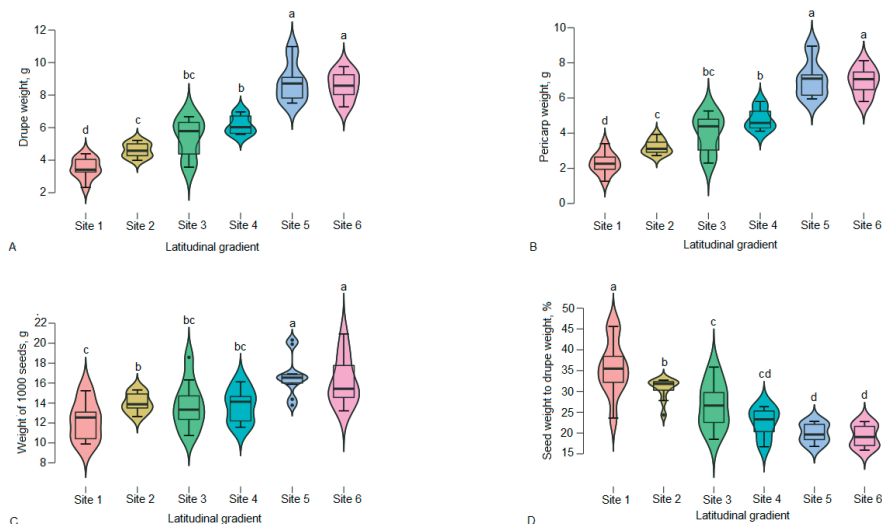


Fig. 1. Drupe and seed weights of *P. lentiscus* according to sites.

Note: A – weight of 100 drupes, B – weight of 100 pericarps, C – weight of 1,000 seeds, and D – seed-to-drupe weight ratio. Each violin box plot displays the kernel density plot outlines, median, Q1–Q3 range, Min–Max range. Letters above the boxes indicate significant differences among sites based on Tukey's post hoc test at $\alpha = 0.05$.

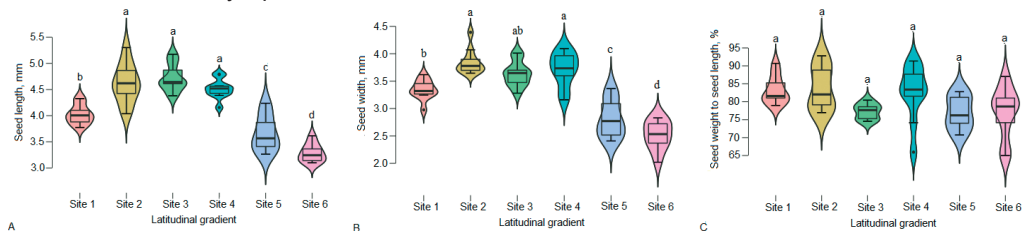


Fig. 2. Seed size of *P. lentiscus* according to sites.

Note: A – seed length, B – seed width, and C – seed width-to-length ratio. Each violin box plot displays the kernel density plot outlines, median, Q1–Q3 range, and Min–Max range. Letters above the boxes indicate significant differences among sites based on Tukey's post hoc test at $\alpha = 0.05$.

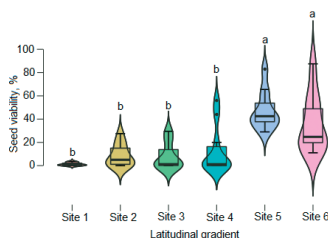


Fig. 3. Seed viability rate of *P. lentiscus* according to sites.

Note: Each violin box plot represents the kernel density plot outlines, median, Q1–Q3 range, and Min–Max range. Letters above the boxes indicate significant differences among sites based on Tukey's post hoc test at $\alpha = 0.05$.

(3.34 mm) (Fig. 2B, Table 2). The seed width-to-length ratio averaged 0.79 (range 0.77–0.84) and did not differ significantly among sites, suggesting similar seed shapes across the study area (Fig. 2C).

Seed viability averaged 18.94 %, with values ranging from 1.15 % to 47.15 % (Table 2). Differences among sites were statistically significant. Sites 1 to 4, with viability ranging between 1.15 % and 12.75 %, formed a single homogeneous group, whereas sites 5 and 6, with viability between 35 % and 47.15 %, formed a distinct group (Fig. 3). Thus, low seed viability was observed at the southern sites (1–4), while higher viability characterised the two northernmost sites (5 and 6).

Pearson correlations between traits

The correlation matrix revealed strong allometric and positive relationships among drupe traits, including drupe weight, pericarp weight, and seed weight. The correlation was particularly high between total drupe weight and pericarp weight ($r = 0.99$), reflecting the fact that approximately 74 % of drupe weight is allocated to the pericarp. In contrast, seed length and seed width were negatively correlated with drupe and pericarp weight, suggesting trade-offs between plant investment in fruit mass and seed size.

Sites 5 and 6, which had the heaviest drupes, produced the smallest seeds compared to the other sites. Seed viability was positively correlated with drupe traits (drupe weight, pericarp weight, and seed weight) but negatively correlated with the seed-to-drupe weight ratio. For instance, Site 1, with the highest seed-to-drupe weight ratio (0.35), exhibited the lowest viability (1.25 %), whereas Site 5 with the lowest ratio (0.19), with the highest seed viability (47.15 %).

Principal component analysis

The principal component analysis (PCA) of drupe and seed traits showed that the first two axes accounted for 84.30 % of the total variance, with 68.29 % explained by the first axis and 16.01 % by the second axis (Fig. 4).

All variables contributed significantly to axis 1, which displayed strong positive correlations ($R \geq 0.70$) with drupe weight (DW), pericarp weight (PW), seed weight (SW) and seed viability (SV), and strong negative correlations ($R < -0.75$) with seed length (SL) and seed width (SWi). Axis 2 was mainly explained by seed width (SWi) and seed length (SL), showing moderate correlations ($R = 0.50$ – 0.55). Environmental variables were associated only with axis 1, showing positive correlations with latitude (Lat), mean annual temperatures (MAT), mean annual precipitations (MAP) and negative correlations with altitude (Alt) (Fig. 4A).

Figure 4B illustrates the segregation of sites along the first PCA axis into two distinct groups. The first group comprised sites 5 and 6, located at northern latitudes and corresponding to upper sub-humid and lower humid bioclimates, respectively. The second group included the remaining four sites distributed along an increasing latitudinal gradient under various bioclimates: sites 1 and 2 in upper semi-arid conditions, Site 3 in a lower semi-arid zone, and Site 4 in a lower sub-humid environment.

The northern group (sites 5 and 6), positioned on the positive side of axis 1, was characterised by heavier drupes, heavier seeds, heavier pericarps, higher seed viability, and smaller seed size, whereas the southern group (sites 1 to 4) was characterised by lighter drupes, lighter pericarps, lighter seeds, lower seed viability, and

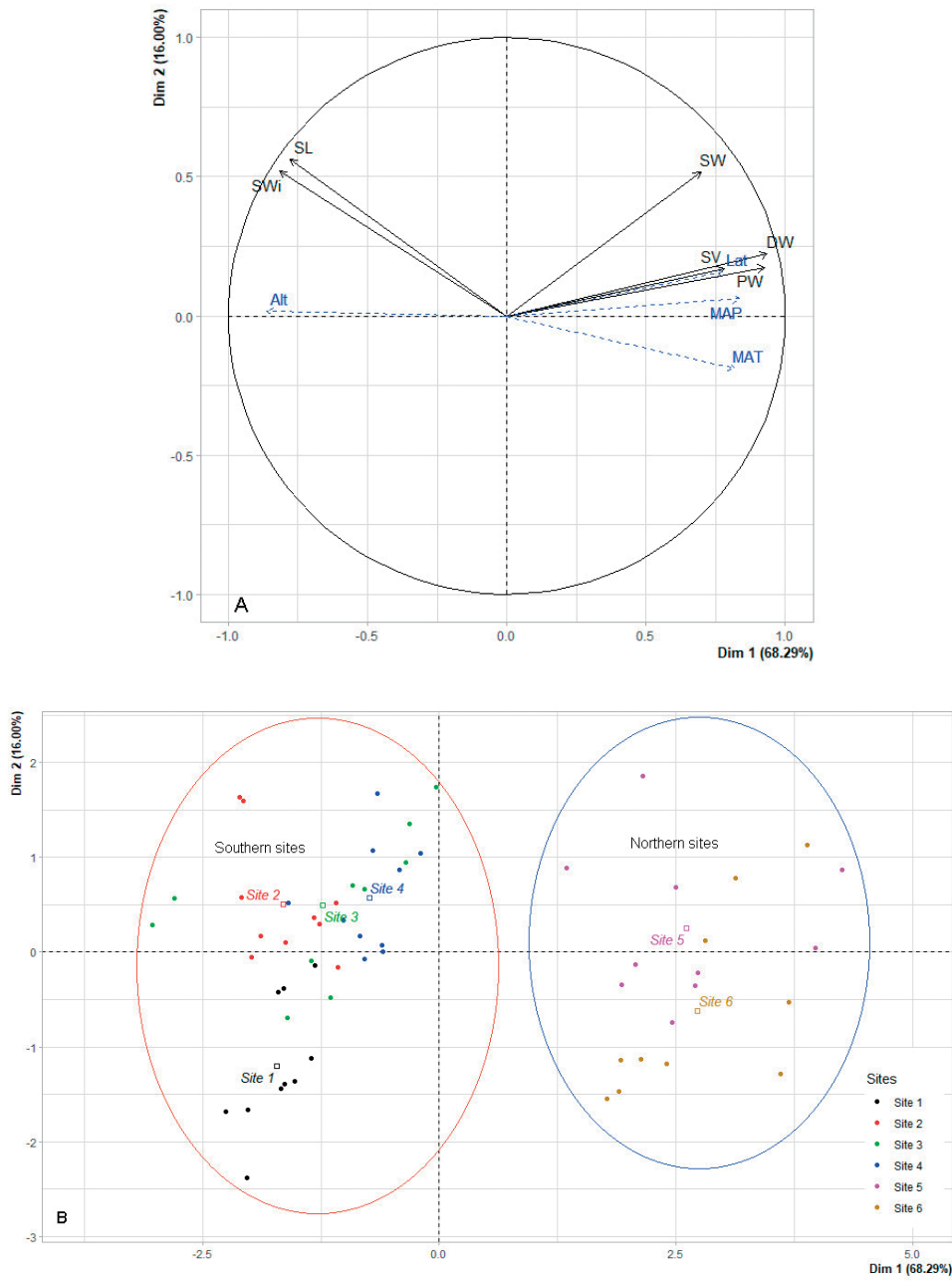


Fig. 4. Results of the PCA.

Note: A – correlation circle of axis 1 and axis 2; B – two-dimensional PCA plot depicting segregation between sites. For each axis, the values in brackets indicate the percentage of variance explained (eigenvalues). See Table 2 footnote for full variable names.

relatively larger seeds (Fig. 4B, Table 2). The clear separation between these two groups along axis 1 indicates that this axis primarily represents a drought gradient, which also aligns with the latitudinal gradient. Axis 2 contributed mainly to within-group variation.

Qualitative seed traits

Overall, two seed colours were observed: blackish-brown and light brown, with blackish-brown being dominant in both years (83.33 % in 2018 and 71.66 % in 2019). Two seed shapes were recorded, rounded and oval, with rounded seeds prevailing in both years (83.33 % in 2018 and 78.33 % in 2019). Seed surface was classified into two categories: soft and wrinkled, with wrinkled surfaces being the most frequent in both years (81.67 % in 2018 and 90 % in 2019) (Table 3).

Discussion

In this study, drupe and seed traits of *P. lentiscus* along a latitudinal gradient in Algeria were analysed. Significant differences were observed among sites for the weight of 100 drupes, the corresponding weights of 100 pericarps and 1,000 seeds, seed size (length, width, and the seed width-to-length ratio), and seed viability. No significant year effect was detected for any of these traits. The mean weight of 100 drupes remained constant across the

two sampling years but varied significantly among provenances. Similar interpopulation variation has been reported for *P. lentiscus* in other Mediterranean regions, with Bouta et al. (2020) documenting drupe weights of 36.60 to 52.30 mg in Morocco, and Mulas et al. (1998) recording 30 to 120 mg in Italy. The trend observed in Algeria suggests a clinal increase in drupe weight from south to north, with Djelfa, the southernmost site, producing the lightest drupes, while the two northernmost sites produced the heaviest. This geographic trend is most likely linked to environmental conditions, particularly bioclimate, which is arid in the south and sub-humid to humid in the north. These findings are consistent with García-Inza et al. (2014), who identified temperature as a key environmental factor influencing fruit weight.

The weight of 100 pericarps followed a pattern similar to that of total drupe weight across sites and years, confirming that most of the drupe mass (74 %) is allocated to the pericarp, while seeds account for only 26 %. The results also highlight a clear separation between the two northernmost sites and the remaining sites with respect to seed size and fruit characteristics, indicating a more pronounced latitudinal gradient for fruit traits than for seed dimensions. These findings are consistent with Boudieb et al. (2019), who reported significant variation in the weight of 1,000 seeds of *P. lentiscus* across three zones in northern Algeria (46–98 mg), attributing this variation to climatic factors.

Table 3. Qualitative seed traits of *P. lentiscus* by sites.

Year	Seed colour, %		Seed shape, %		Seed surface, %	
	Blackish-brown	Light brown	Rounded	Oval	Soft	Wrinkled
2018	83.33	16.67	16.67	83.33	18.33	81.67
2019	71.66	28.34	21.67	78.33	10	90

Interpopulation variation in seed size and seed mass has also been documented in other Mediterranean species, including *Arbutus unedo* L. (Faïda et al. 2021), *Myrtus communis* L. (Aabdousse et al. 2021) in Morocco, and *Quercus ilex* L. in Tunisia (Amimi et al. 2023). Beyond the Mediterranean, a decline in seed size with increasing latitude has been reported for *Pistacia atlantica* Desf. in Iran (Rahmani et al. 2023), *Euptelea pleiospermum* Hook.f. & Thomson in China (Wu et al. 2018), *Anthyllis vulneraria* L. in Europe (Daco et al. 2021), and numerous other species (Moles et al. 2007). On a broader scale, Moles and Westoby (2003) demonstrated a strong negative relationship between seed mass and latitude across 2,706 species, with seed mass being significantly greater in tropical regions.

In this study, seed dimensions varied significantly among sites but showed an inverse pattern compared to both drupe traits and seed viability. The two northern sites, which had the highest drupe weights and seed viability values, also produced the smallest seeds, suggesting a possible trade-off between plant investment in fruit mass and seed size. Seed viability rates were generally lower than those previously reported for the species: 19.89–43.38 % over two consecutive years (Jordano 1988) and 35.40–48.80 % (Albaladejo et al. 2009), both from Spain. The high variability in seed viability of *P. lentiscus* observed in these earlier studies has been attributed to the harshness and unpredictability of Mediterranean environments (Jordano 1989).

More recently, Quintero et al. (2024) confirmed that seed viability in *P. lentiscus* from Spain is often low (approximately 34 %). Water availability during the period of fruit development and ripening has been suggested as a major determinant of

fruit set in *P. lentiscus* (Jordano 1988, Albaladejo et al. 2009). In addition, Milla et al. (2006) reported that the fruiting period of *P. lentiscus* coincides with the seasonal water deficit that occurs between July and September. This environmental limitation may also apply to populations in Algeria, which experience the influence of the Mediterranean-type climate characterised by hot, dry summers.

The studied sites located in upper sub-humid and lower humid bioclimates exhibited higher seed viability rates compared to those in semi-arid bioclimates. In particular, the Djelfa site showed almost null viability in both years. Previous research has indicated that populations in marginal environments often flower and mature later, producing a higher proportion of non-viable seeds due to underdeveloped embryos. For example, García et al. (2000) demonstrated that in *Juniperus communis* L., a species with a wide latitudinal range, seed viability was lower in southern populations than in northern ones, a pattern attributed to both seed predation and abortion. Similarly, Caron et al. (2014) reported that in *Acer platanoides* L., seed viability, closely associated with seed mass, was 38 % lower under the warmest than under the coldest conditions.

The findings also reveal considerable heterogeneity in seed viability among shrubs within two of the six sites, namely Tigzirt and Tizi Gheniff, where values ranged from as low as 2 % to as high as 90 %. These results are consistent with earlier findings for *P. lentiscus* in Spain (Martínez-Pallé and Aronne 2000, Albaladejo et al. 2009, Quintero et al. 2024) and for *Cedrus atlantica* (Endl.) Manetti ex Carrière in Algeria (Krouchi et al. 2004). Variation in seed viability of *P. lentiscus* at the level of the individual-plants level may

be influenced by several factors, including plant size, phenological asynchrony between male and female individuals, and increased distances between female and male plants (Jordano 1988).

Our data indicate that drupes are retained on *P. lentiscus* shrubs regardless of whether they contain filled or empty seeds, consistent with previous findings. Earlier studies have emphasised that empty or parthenocarpic drupes, which may result either from parthenocarpy (absence of pollination) or from embryo abortion (Jordano 1988; Martínez-Pallé and Aronne 2000), are retained on *P. lentiscus* shrubs as an adaptive strategy to reduce predation by birds (Verdú and García-Fayos 2001) and on *P. terebinthus* plants to minimise predation by wasps (Traveset 1993). With respect to qualitative seed traits, including colour, shape, and surface, no significant variation was detected across sites.

According to Al-Saghir and Porter (2012), *P. lentiscus* is divided into two subspecies: *P. lentiscus* subsp. *lentiscus*, which includes several varieties and forms distributed in the Canary Islands, southern Europe, Turkey, and the Middle East, and *P. lentiscus* subsp. *emarginata* (Engl.) Al-Saghir, which occurs in East Africa (Ethiopia, Somalia, Kenya, Uganda, and Tanzania). Several studies have highlighted significant genetic diversity within the species (Zografou et al. 2010, Bouta et al. 2022, Mezni et al. 2024). The highly significant discrimination observed in the PCA between southern and northern Algerian sites may therefore reflect not only phenotypic responses to contrasting environmental conditions but also suggest the presence of underlying taxonomic or genetic differentiation.

The fruits of *P. lentiscus* are increasingly valued for diverse socioeconom-

ic uses. Results from this study indicate that fruits from the northern sites exhibited higher seed viability, a trait that may be particularly relevant for reforestation programmes. In addition, these sites produced a larger proportion of fleshy fruit tissue, which represents a potential source of essential and fixed oils for pharmaceutical and ethnobotanical applications.

Conclusions

The findings highlight clear geographic variation among *P. lentiscus* sites in Algeria with respect to drupe and seed traits, with the northernmost sites producing heavier drupes and exhibiting higher seed viability. Results also indicate that most of the drupe biomass is allocated to the pericarp rather than to the seed. Given the wide distribution of the species across Algeria, particularly from west to east, future research should incorporate additional sites along longitudinal and altitudinal gradients to provide a more comprehensive understanding of variation in fruit and seed traits. Assessing the taxonomic and genetic diversity of these populations would likewise yield valuable insights.

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Radial variation modelling in physical and mechanical properties of *Falcataria falcata* from community forests in Yogyakarta, Indonesia

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Abstract

In Indonesia, wood from fast-growing tree species that are planted in community forests plays an important role in meeting the raw material demands of the wood industry. One of these is *Falcataria falcata* (L.) Greuter & R.Rankin. This study aimed to determine the radial variation of wood properties of *F. falcata* grown in a community forest in Indonesia by linear and nonlinear mixed-effect models. Based on radial variation modelling, the linear model was selected as the best model for basic density and compressive strength parallel to grain, indicating that these properties increase gradually from pith to bark. Meanwhile, the logarithmic model was fitted for radial shrinkage and modulus of elasticity (MOE), and the Michaelis-Menten model was selected for tangential shrinkage and modulus of rupture (MOR). Both of these models indicated that radial and tangential shrinkage at 1% moisture content, as well as MOE and MOR, increased from the pith and then became almost constant toward the bark. It can be concluded that the outer part of *F. falcata* shows potential for use in products requiring higher strength, such as lightweight structural components, panels, and raw materials for wood-based composites, although further validation is needed.

Key words: mixed-effects models, variation in wood properties, wood-processing industry.

Introduction

In Indonesia, wood supply as raw material for wood-based industries is largely obtained from plantation forests as part of a strategy to reduce the exploitation of nat-

ural forests (Pirard et al. 2017, Susilawati and Kanowski 2022). One of the types of plantation forest management that is developing and widely established in Indonesia is community forests, which are characterised by fast-growing tree species

(Pirard and Cossalter 2006, Putraditama et al. 2021). Fast-growing tree species are commonly planted in community forests because they have some advantages, such as high growth rates, short harvest periods, high productivity, and sustainable wood production (Adi et al. 2014, Cossalter and Pye-Smith 2003). Several fast-growing tree species are commonly cultivated and possess high commercial value in community forests, such as *Falcata falcata* (L.) Greuter & R. Rankin, *Acacia mangium* Willd., *Neolamarckia cadamba* (Roxb.) Bosser, *Ochroma pyramidale* (Cav. Ex Lam.) Urb., and *Gmelina arborea* Roxb. ex Sm. (Amirta et al. 2016; Pertiwi et al. 2017, 2018; Yuniarti et al. 2019; Ngadianto et al. 2020, 2022; Nandini et al. 2023; Oluwajuwon et al. 2024).

F. falcata is a fast-growing plant species that is most widely planted in Indonesian community forests (Cossalter and Pye-Smith 2003, Alamsyah et al. 2007, Oluwajuwon et al. 2024). It belongs to the Fabaceae family and is native to the eastern islands of the Malay Peninsula, Indonesia, Papua New Guinea, and the Solomon Islands (Hughes et al. 2024). This species is widely known for its lightweight wood, rapid growth, and ease of processing, making it suitable for particleboard, plywood, and lightweight construction (Jimenez et al. 2022, Marasigan et al. 2022). In Indonesia, the majority of *F. falcata* was planted in short rotations to provide raw material for the veneer and plywood industries (Sumardi et al. 2018).

Understanding wood properties is crucial for improving the quality of many wood products. Wood properties generally vary within the tree, for instance showing radial variation from pith to bark. The presence of juvenile wood, formed during the early stages of tree growth, is an important factor in this wood variation. Ju-

venile wood typically has lower density, a higher microfibril angle, and reduced mechanical strength compared with mature wood, which may reduce product performance if not properly considered for (Zobel and Sprague 1998). A relatively high proportion of juvenile wood is common in fast-growing species harvested on short rotations, such as *F. falcata*. Therefore, understanding radial variations in wood physical and mechanical properties influenced by juvenile wood is crucial for improving the utilisation of fast-growing wood resources.

Previous studies have investigated the radial variation in wood properties of *F. falcata* (Ishiguri et al. 2007, Fajriani et al. 2013). However, radial variation in wood properties of *F. falcata* has been analysed without exploring statistical approaches, such as mixed-effect modelling. Evaluation of radial variation in wood properties using linear and nonlinear mixed-effects models in softwood as well as hardwood has been reported by several researchers (Auty et al. 2013, Kimura and Fujimoto 2014, Vega et al. 2020, Ngadianto et al. 2022). In a previous study, we modelled radial variation of physical and mechanical properties by intercept, linear, logarithmic, Michaelis-Menten, asymptotic, and quadratic models with distance from pith as the fixed effect and individuals as random effects in three fast-growing tree species: *Acacia mangium*, *Maesopsis eminii* Engl., and *Melia azedarach* L. (Ngadianto et al. 2022). We found that the logarithmic and Michaelis-Menten models were widely accepted for the physical and mechanical properties of wood in different species (Ngadianto et al. 2022). In addition, Vega et al. (2020) evaluated radial variation of wood density, microfibril angle (MFA), and modulus of elasticity (MOE) by linear and nonlinear models with cambial age as the

fixed effect and individual trees as random effects in 38 trees of *Eucalyptus nitens* (H.Deane & Maiden) Maiden grown in three sites in the south of Tasmania (Australia). They reported that the radial variation in wood density and MOE was best fit by the sigmoidal logistic model, while MFA was best fit by the asymptotic exponential model. However, compared to those studies, there are only a few reports of radial variation of *F. falcata* properties, and all of them relied on conventional statistical analyses rather than mixed-effects approaches, leaving a methodological gap in the literature. Moreover, no study has yet applied and compared various linear and nonlinear mixed-effects models to describe the radial variation in *F. falcata* wood properties cultivated in Indonesian community forests, particularly with regard to the role of juvenile wood. Thus, to acquire more extensive and accurate information, further investigation into *F. falcata* wood characteristics using linear and nonlinear mixed-effects modelling is required, which constitutes the novelty of this study. Although *F. falcata* is regionally distributed, it represents one of the most important fast-growing species in Southeast Asia, and the modelling approach applied here may be relevant for other tropical plantation species.

This study aimed to determine radial variation in physical and mechanical properties based on linear or nonlinear mixed-effects modelling for *F. falcata* grown in community forests in Indonesia. By using these models, the accuracy of within-tree variations in wood properties can be predicted, and it's important for better wood quality. The information generated is expected to provide more appropriate recommendations regarding the use of *F. falcata* from community forests, especially for practical applications

in the wood-processing industry, as it can guide the selection of suitable wood parts for structural applications and encourage the optimisation of the sustainable use of fast-growing wood resources. In addition, the relationships between measured properties were discussed in this study.

Materials and Methods

Materials

Four-year-old *F. falcata* were used in this study. A total of five trees were randomly selected from the same community forest plot located in Samigaluh, Kulon Progo, Yogyakarta, Indonesia ($-7^{\circ}40'28''$ S, $110^{\circ}7'3''$ E). The forest originated from naturally occurring *F. falcata* seedlings. The forest received no silvicultural treatments, including thinning, pruning, weeding, or fertilising. All samples were of the same age (4 years), with variation in growth characteristics reflecting the natural growth variability of *F. falcata* within the stand. Although the number of trees was limited, multiple radial measurements per tree provided sufficient data for modelling. The homogeneous age and site conditions also minimised the need for stratification, although the small sample size still restricts broader generalisation.

Growth characteristics

While the trees were still standing, stem diameter was measured at 1.3 m above ground using a diameter tape. Tree height was measured using a tape meter after felling the trees. After cutting down the trees, two types of disks (2 cm in thickness for measuring basic density and green moisture content and 50 cm in thickness for measuring mechanical properties and

shrinkage) were collected around 1.3 m above the ground. Growth characteristics, including stem diameter and tree height, of the five sample trees are presented in Table 1.

Table 1. Stem diameter and tree height of *F. falcata*.

Tree number	Stem diameter, cm	Tree height, m
1	29.0	28.9
2	22.5	23.7
3	21.8	20.7
4	28.5	20.9
5	21.0	13.8
Mean	24.6	21.6
Standard Deviation	3.9	5.5
Annual increment	6.2	5.4

Note: Annual increments of stem diameter and tree height were calculated by dividing the mean values divided by tree age (4-year-old of *F. falcata*).

Physical and mechanical properties

Figure 1 shows the procedures used for sample preparation. Basic density was measured on 2-cm-thick disks collected at 1.3 m above ground. Wedge-shaped specimens with 30° centre angles were cut from the disks at 1-cm intervals from pith to bark to assess radial variation of basic density. A total of 61 small specimens were obtained (10–15 radial positions per tree × five trees). Basic density was calculated by as the oven-dry weight divided by the green volume, determined using the water displacement method.

Shrinkage at 1% moisture content change in radial and tangential directions was measured using the Japan Industrial Standard (JIS) Z2101:2009 (Japanese Industrial Standards 2009). In the present study, radial and tangential shrinkage are considered as the most determining factors in industrial applications, where they affect the dimensional stabil-

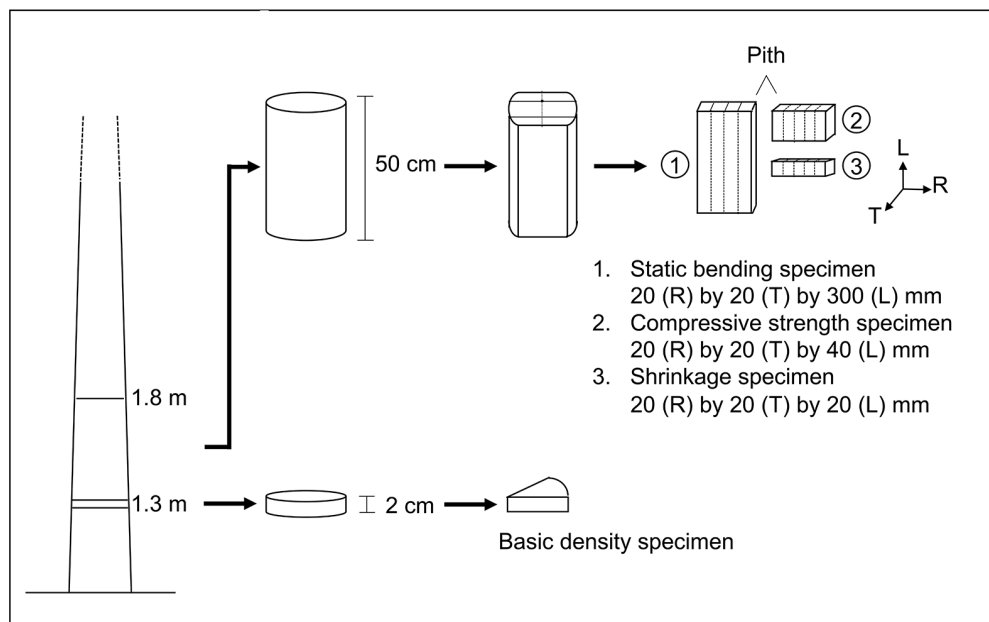


Fig. 1. Illustration of experimental procedure and sample preparations.

ity of wood during drying and processing (JIS Z2101:2009; Japanese Industrial Standards 2009). Small clear specimens (approximately 20 (R) × 20 (T) × 20 (L) mm) were prepared from radial boards obtained from 50-cm-long logs. We collected 22 specimens (four to five radial positions per tree × five trees). Radial and tangential dimensions of the specimens were measured under air-dry and oven-dry conditions using a digital screw gauge. Shrinkage at 1% moisture content change in radial and tangential directions was calculated according to the formulas described in our previous report (Ngadianto et al. 2022).

Mechanical properties, such as static bending and compressive strength parallel to the grain, were determined according to JIS Z2101:2009 (Japanese Industrial Standards 2009). Specimens were prepared from radial boards obtained from 50-cm-long logs. We collected 23 specimens (four to six radial positions per tree × five trees) for testing static bending and compressive strength parallel to the grain. The static bending and compressive tests were conducted using a universal testing machine. For static bending tests, a load was applied at the centre of the specimen on the radial surface, with a 280-mm span and a load rate of 5-mm·min⁻¹. Load and

deflection data were recorded using a personal computer to calculate the modulus of elasticity (MOE) and modulus of rupture (MOR). For compressive tests, a load rate of 0.5 mm·min⁻¹ was applied. Compressive strength parallel to the grain was calculated by dividing the maximum load by the cross-sectional area of the specimen. Static bending and compressive properties were calculated according to the formulas described in our previous report (Ngadianto et al. 2020).

Statistical analysis

All statistical analyses in this study were performed using R software (R Core Team 2023). Linear and nonlinear mixed-effects models were developed to evaluate the radial variations of wood properties, with each measured property as the response variable, the distance from the pith as a fixed effect, and individual trees as a random effect (Table 2). Modelling was carried out using the ‘lmer’ function in the ‘lme4’ package (Bates et al. 2015) and the ‘nlme’ function in the ‘nlme’ package (Pinheiro and Bates 2000). The best model among the several models developed was selected based on the Akaike information criterion (AIC; Akaike 1998), where the model with the minimum AIC value was

Table 2. Linear and nonlinear mixed-effects models used to evaluate radial variation in physical and mechanical properties of wood.

Formula	Model
$y_{ij} = \alpha_0 + a_j + \alpha_1 x_{ij} + \varepsilon_{ij}$	Linear
$y_{ij} = \beta_0 + b_j + \beta_1 \ln(x_{ij}) + \varepsilon_{ij}$	Logarithmic
$y_{ij} = \zeta_0 + z_j + \zeta_1 x_{ij} / (\zeta_2 + x_{ij}) + \varepsilon_{ij}$	Michaelis-Menten
$y_{ij} = \eta_0 + h_j + \eta_1 \eta_2^{x_{ij}} + \varepsilon_{ij}$	Asymptotic regression
$y_{ij} = l_0 + i_j + l_1 x_{ij} + l_2 x_{ij}^2 + \varepsilon_{ij}$	Quadratic

Note: y_{ij} is the measured value at the i th radial distance from pith to bark of the j th individual tree; x_{ij} is the i th radial distance from pith to bark of the j th individual tree; α_0 , α_1 , β_0 , β_1 , ζ_0 , ζ_1 , ζ_2 , η_0 , η_1 , η_2 , l_0 , l_1 , and l_2 are fixed effects; a_j , b_j , z_j , h_j , and i_j are random effects associated with α_0 , β_0 , ζ_0 , η_0 , and l_0 at the level of individual trees; ε_{ij} is the residual term.

considered the most suitable for describing radial variation. An intercept-only model was not developed, as some properties exhibited relatively constant values from pith to bark, which could be adequately represented by a linear model with a small slope. In addition, correlations between the measured wood properties were determined using Pearson's correlation coefficients via the 'cor.test' function.

Result and Discussion

Radial variations of physical and mechanical properties

The statistical values of the physical properties of *F. falcata* are presented in Table 3. The mean value of basic density was $0.28 \text{ g}\cdot\text{cm}^{-3}$. Previous studies reported mean basic densities of $0.32 \text{ g}\cdot\text{cm}^{-3}$ in 13-year-old *F. falcata* trees from Bogor, Indonesia (Ishiguri et al. 2007), $0.30 \text{ g}\cdot\text{cm}^{-3}$ in 7-year-old trees from West Java, Indonesia (Fajriani et al. 2013), and $0.32 \text{ g}\cdot\text{cm}^{-3}$ in 5-year-old trees from the west coast of Peninsular, Malaysia (Roslan et al. 2024). Mean shrinkage per 1% change in moisture content change in radial and tangential directions were 0.11 % and 0.19 %, respectively. When converted into total shrinkage, the mean values of total shrinkage in the radial and tangential directions were 3.30 % and 5.70 %, respectively. Reported mean total shrinkage values were 3.21 % in the radial direction and 6.11 % in the tangential direction for nine-year-old *F. falcata* grown in private forests in Yogyakarta (Listyanto 2018) and 3.07 % in the radial direction and 4.33 % in the tangential direction for seven-year-old *F. falcata* grown in the south-eastern Philippines (Marasigan et al. 2022). The values of basic density and radial and tan-

gential shrinkage obtained in this study were broadly consistent with those reported in previous studies (Ishiguri et al. 2007, Fajriani et al. 2013, Listyanto 2018, Marasigan et al. 2022, Roslan et al. 2024).

Table 3. Summary statistics for the physical and mechanical properties of *F. falcata*.

Property	<i>n</i>	Mean	SD	Min	Max
BD, $\text{g}\cdot\text{cm}^{-3}$	61	0.28	0.06	0.20	0.42
RS, %	22	0.11	0.02	0.08	0.15
TS, %	22	0.19	0.03	0.14	0.25
MOE, GPa	23	4.32	1.30	2.89	7.53
MOR, MPa	23	32.7	8.7	22.9	58.2
CS, MPa	22	21.6	5.0	16.3	33.9

Note: *n* – total number of radial positions in the five sample trees; SD – standard deviation; Min. – minimum; Max. – maximum; BD – basic density; RS and TS – shrinkages at 1% moisture changes in radial and tangential directions, respectively; MOE – modulus of elasticity; MOR – modulus of rupture; CS – compressive strength parallel to grain. The air-dry density and moisture content of static bending strength and compressive strength of specimens tested were $0.26 \text{ g}\cdot\text{cm}^{-3}$ and 12.0 %, respectively.

The statistical values of the mechanical properties of *F. falcata* are also shown in Table 3. The mean values of MOE, MOR, and compressive strength parallel to grain were 4.32 GPa, 32.7 MPa, and 21.6 MPa, respectively. The mean values of MOE, MOR, and compressive strength parallel to grain of 7-year-old *F. falcata* grown in the south-eastern Philippines were 4.94 GPa, 36.3 MPa, and 19.1 MPa, respectively (Marasigan et al. 2022). On the other hand, Alipon et al. (2021) find out that the mean values of 5-year-old *F. falcata* for veneer production that grew in the Philippines were 4.38 GPa, 33.7 MPa, and 18.5 MPa, respectively. The values of mechanical properties in this study were almost the same as those reported by oth-

er researchers (Alipon et al. 2021, Marasi-gan et al. 2022). Even in differences of growth sites and tree ages, this study's findings on the physical and mechanical properties of *F. falcata* were almost similar

to previous studies, indicating that the values might be utilised to assess the quality of *F. falcata* as raw materials for various wood-processing industry requirements.

Figure 2 shows the radial variations

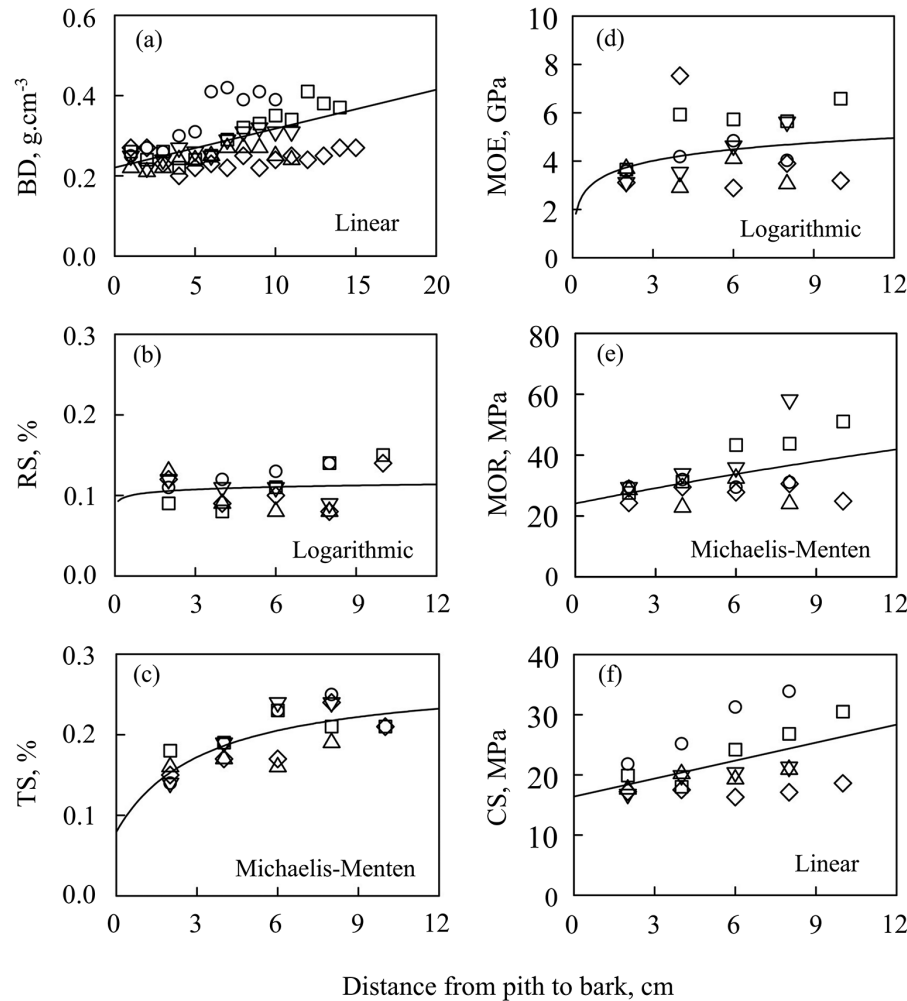


Fig. 2. Radial variations of wood properties in *F. falcata*.

Note: (a) BD – basic density; (b) RS – shrinkage at 1% moisture changes in radial direction; (c) TS – shrinkages at 1% moisture changes in tangential direction; (d) MOE – modulus of elasticity; (e) MOR – modulus of rupture; (f) CS – compressive strength parallel to grain. Squares, circles, triangles, diamonds, and inverted triangle indicate the data from trees Nos 1, 2, 3, 4, and 5, respectively. Regression lines or curves were fitted based on the fixed effects of the best model with the minimum AIC (Table 4) among those listed in Table 2, and the corresponding parameters are given in Table 5.

of wood properties of *F. falcata*. The best model was selected based on the AIC value (Table 4). The linear model was accepted for basic density and compressive strength parallel to grain. The model fitted predicted that basic density and compressive strength gradually increased from pith to bark. In addition, a non-linear model, such as the logarithmic model, was fitted for radial shrinkage and MOE, and the Michaelis-Menten model was adapted for tangential shrinkage and MOR. Both of these models indicated that radial and tangential shrinkage at 1% moisture content, as well as MOE and MOR, increased from the pith and then became almost constant toward the bark. In this study, a mixed-effects model was applied to measure multiple wood properties in radial variations on the trees, providing more reliable estimates of variation than simpler methods such as regression or ANOVA. The suitable models were selected based on AIC that was explained by previous studies. The Michaelis–Menten model used in this study shows more of a non-linear asymptotic equation that is able to describe the observed wood property patterns. The pragmatic use of the equation is consistent with modelling approaches reported by previous researchers (Vega

et al. 2020, Ngadianto et al. 2022).

The radial variations in physical and mechanical properties were also examined by several researchers (Ishiguri et al. 2007, 2012; Fajriani et al. 2013; Rahayu et al. 2014). They reported that wood density of *F. falcata* increased from the pith toward the bark (Ishiguri et al. 2007, Rahayu et al. 2014). On the other hand, Fajriani et al. (2013) reported that wood density increased from the pith and then became almost stable. Similarly, mechanical properties, such as MOR and compressive strength parallel to grain, increased from pith toward the bark (Ishiguri et al. 2012, Rahayu et al. 2014). Compared to previous studies, slight differences in results are likely due to differences in age, location, sample size, and methods used; for example, older or managed stands often exhibit higher densities and distinct radial variation patterns (Ishiguri et al. 2007, Marasigan et al. 2022). In contrast, studies based on smaller sample sizes have reported patterns closer to those described in our previous work (Ngadianto et al. 2022).

The restricted maximum likelihood estimates and standard errors of fixed-effect parameters and standard deviations of the random-effect parameters, for the

Table 4. Comparison of AIC values in the five constructed mixed-effects models for radial variation of wood properties in *F. falcata*.

Model	Wood properties					
	BD	RS	TS	MOE	MOR	CS
Linear	-240.301	-80.416	-77.994	81.261	141.583	98.060
Logarithmic	-198.555	-81.190	-81.142	78.976	149.983	117.230
Michaelis-Menten	-222.477	NC	-87.631	NC	130.857	116.876
Asymptotic regression	-225.475	NC	NC	NC	147.864	105.583
Quadratic	-225.389	-69.600	-64.751	88.183	155.706	123.943

Note: BD – basic density; RS and TS – shrinkage at 1% moisture changes in radial and tangential directions, respectively; MOE – modulus of elasticity; MOR – modulus of rupture; CS – compressive strength parallel to grain. Bold values indicate minimum AIC among five models. NC – model did not converge. The formulas of the models are provided in Table 2.

best-fitting models are presented in Table 5. The fixed effect parameters, or radial direction factor, for all models show significant values ($p < 0.05$), indicating that in the linear model, wood properties increase from pith to bark, and in the logarithmic and Michaelis-Menten models, wood properties show an increasing value followed by a stable pattern. This evidence indicates that the outer wood is of better quality than the inner wood. The model comparison not only found the best-fitting equations based on AIC value but also demonstrated that the mixed-effects approach was suitable for describing radial variation patterns of wood properties in *F. falcata*. The radial variation pattern of wood properties observed in this study was in accordance with the concept of juvenile wood to mature wood, where juvenile wood has unstable or fluctuating properties while mature wood has better or tends to have stable characteristics (Zobel and Sprague 1998). Due to the small number of sample trees, some parameter estimations showed large errors or non-significant values.

Table 5. Restricted maximum likelihood estimates and standard errors (S.E.) of fixed-effect parameters and standard deviation of random-effect parameters for the best model describing radial variation of each property in *F. falcata*.

Property	Model	Fixed-effect parameters				Random-effect parameters	
		α_0		α_1		a_j	ε_{ij}
BD		Estimate	S.E.	Estimate	S.E.		
	Linear	0.2207	0.0064	0.0097	0.0035	0.0075	0.0233
CS		16.3794	0.6302	0.9981	0.3847	0.8260	1.2320
Property	Eq.	β_0		β_1		b_j	ε_{ij}
		Estimate	S.E.	Estimate	S.E.		
RS	Logarithmic	0.1025	0.0148	0.0045	0.0089	1.40E-06	0.0230
MOE		3.2250	0.8202	0.7140	0.4955	0.3878	1.2143
Property	Eq.	ζ_0		ζ_1		ζ_2	
		Estimate	S.E.	Estimate	S.E.	Estimate	S.E.
TS	Michaelis-Menten	0.0781	0.1130	0.1952	0.0577	3.2198	6.2736
MOR		24.0740	9.6220	99.8170	1117.2220	55.7540	756.7300
						0.942	6.6565

Note: BD – basic density; CS – compressive strength parallel to grain; RS and TS – shrinkages at 1% moisture change in radial and tangential directions, respectively; MOE – modulus of elasticity; MOR – modulus of rupture. Formula for each model of radial variation of each property are shown in Table 2. p -values indicates the significance level for each fixed-effect parameter. α_0 , α_1 , β_0 , β_1 , ζ_0 , ζ_1 , and ζ_2 are fixed-effect parameters in the linear, logarithmic, and Michaelis-Menten models, respectively; a_j , b_j , and z_j are random effects parameters associated with the j th individual tree in the linear, logarithmic, and Michaelis-Menten models, respectively; ε_{ij} is the residual.

However, the overall pattern of fixed effects remained consistent with the radial variation in wood properties reported in previous studies.

Based on the results of the present study, it may be established that *F. falcata* shows an increase in physical and mechanical properties radially from the pith to the bark. Basic density, MOE, MOR, and compressive strength parallel to the grain increase from the pith to the bark, indicating that the outer part of the wood has better wood quality. Although the boundary between juvenile and mature wood could not be precisely determined, the consistent increase in density and strength toward the bark supports the interpretation that outer wood represents higher-quality material. This pattern is consistent with previous findings by Ishiguri et al. (2007) and Rahayu et al. (2014) and is supported by the modelling approach in this study. With these characteristics, the outer part of *F. falcata* shows potential for use in products requiring higher strength, such as lightweight structural components, panels, and raw materials for wood-based composites, although further validation is required.

Relationships between basic density and wood properties

Figure 3 shows the correlation coefficients between basic density and wood properties of *F. falcata*. Basic density showed significant positive correlations at the 1% level with tangential shrinkage ($r = 0.689$) and compressive strength ($r = 0.895$). On the other hand, significant positive correlations at the 5% level were found between basic density with radial shrinkage ($r = 0.506$) and MOR ($r = 0.455$). In addition, the MOE was also positively correlated with the MOR at the 1% level

($r = 0.634$). No significant correlation was found between basic density and MOE.

Roslan et al. (2024) find out that wood density has positive correlations with compressive strength, MOE, and MOR for *F. falcata*. In our previous study, significant positive correlations were found between air-dry density and compressive strength, MOE, and MOR for three species, such as *A. mangium*, *M. eminii*, and *M. azedarach* (Ngadianto et al. 2020). Another study found a positive correlation between wood density and compressive strength in *A. auriculiformis* (Chowdhury et al. 2009) and *A. mangium* (Makino et al. 2012). In addition, Duong and Matsumura (2018) reported that MOE has a high positive correlation with MOR in *M. azedarach*. Based on the results of the present study, with the minor exception of the MOE, basic density is considered to be a good indicator for predicting the physical and mechanical properties of *F. falcata*. Furthermore, the MOR also can be predicted by the MOE. These findings strengthen the understanding that wood density has an important contribution in assessing the structural performance of wood and can be used as an initial parameter in the selection of raw materials for engineering and industrial applications.

In the present study, anatomical properties (e.g., fiber length, microfibril angle, cell wall thickness) were not measured to determine the juvenile period of *F. falcata*. We focused on physical and mechanical properties that are directly relevant to industrial applications. This study was also limited to five trees, but each provided multiple radial measurements that allowed reliable model fitting. Further research including this aspect with larger samples is needed to complement and confirm these findings.

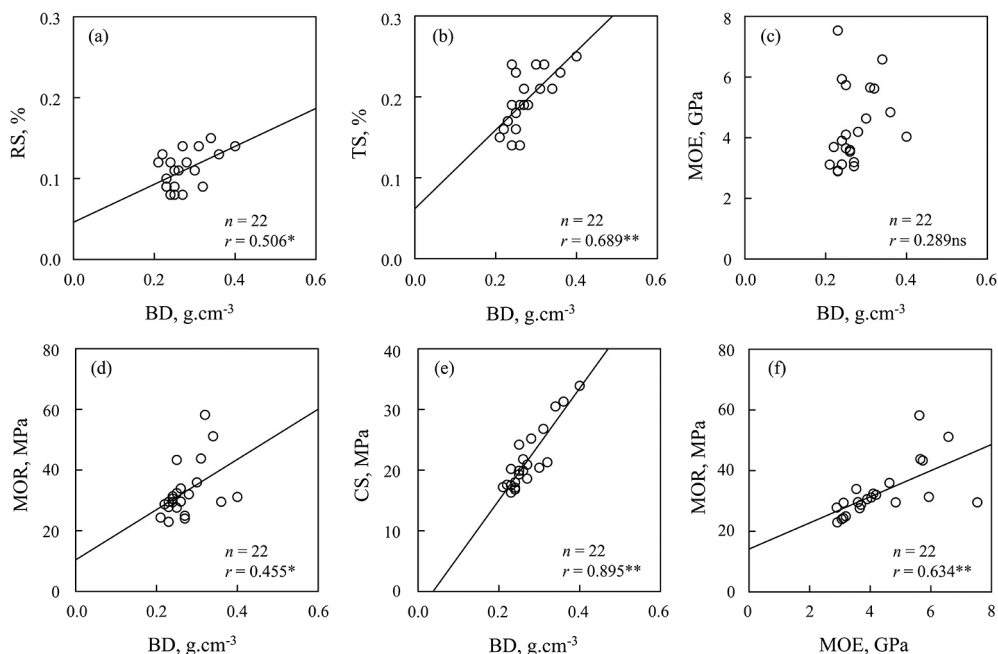


Fig. 3. Relationships between basic density and wood properties.

Note: n – total number of samples obtained from radial positions in the five sample trees; r – correlation coefficient; ** – significant at the 1% level; * – significant at the 5% level; ns – non-significant. Panels: (a) BD and RS – basic density and radial shrinkage at 1% moisture change; (b) BD and TS – basic density and tangential shrinkage at 1% moisture change; (c) BD and MOE – basic density and modulus of elasticity; (d) BD and MOR – basic density and modulus of rupture; (e) BD and CS – basic density and compressive strength parallel to grain; (f) MOE and MOR – modulus of elasticity and modulus of rupture.

Conclusions

In the present study, the physical and mechanical properties of *F. falcata* grown in community forests in Yogyakarta, Indonesia, were determined based on radial variation modelling using linear and nonlinear mixed effects models. The mean values of basic density, shrinkage at 1% moisture content change in radial and tangential directions, compressive strength parallel to grain, MOE, and MOR were 0.28 g·cm⁻³, 0.11 %, 0.19%, 4.32 GPa, 32.7 MPa, and 21.6 MPa, respectively. In the evaluation of radial variation of wood properties, the linear model was selected as the best

model for basic density and compressive strength parallel to grain, indicating that these properties increase gradually from pith to bark. Meanwhile, the logarithmic model was fitted for radial shrinkage and MOE, and the Michaelis-Menten model was adapted for tangential shrinkage and MOR. Both of these models indicated that radial and tangential shrinkage at 1% moisture content, as well as MOE and MOR, increased from the pith and then became almost constant toward the bark. These results indicate that the outer part (near the bark) of *F. falcata* shows higher physical and mechanical properties than the inner part (near the pith), suggest-

ing greater potential of outer wood for structural applications, although the real boundary from the pith could not be determined in this study. Further research including anatomical properties is needed to more precisely define the juvenile–mature wood transition and its utilisation implications. Regarding the relationship between basic density and wood properties, with the minor exception of the MOE, it can be concluded that basic density is considered to be a good indicator for predicting the physical and mechanical properties. The MOR also can be predicted by the MOE. These conclusions are limited to 4-year-old trees from one stand, and broader studies across ages and sites are required for confirmation.

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Age structure, growth rate and condition of *Alburnus mandrensis* (Leuciscidae) in the tributaries of the Mandra Reservoir

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Abstract

The Mandra shemaya is an endemic species of Bulgaria. It is found only in the Mandra Reservoir and in the rivers that flow into it. Information about its biology is important for its conservation and preservation. Due to the lack of detailed data on its population biology, we aimed to study certain population parameters of this species. This study investigates the age structure, growth rate, and condition of *Alburnus mandrensis* (Drensky, 1943) (commonly known as the Mandra shemaya) in two tributaries of the Mandra Reservoir: Sredetska and Rusokastrenska rivers. Field data were collected over four consecutive years (2020–2023), with a total sample of 334 individuals. The primary aim was to assess the species' growth characteristics and condition in its natural habitat. The majority of specimens were five to seven years old, with the most frequent length group ranging from 101–150 mm. Overall, total length varied between 77 and 223 mm, and total weight ranged from 3.1 to 100.9 g. The relationship between body length (L) and scale radius (S) was expressed as $L = 1.4187 \cdot S + 26.43$ ($r^2 = 0.96$), whereas the weight–length (WLR) relationship followed the equation $W = 0.0000007 \cdot L^{3.4919}$ ($r^2 = 0.99$). These results suggest a relatively slow growth rate for *A. mandrensis*. To date, this is the first detailed investigation of this endemic species within the Mandra Reservoir watershed.

Key words: growth parameters, Mandra shemaya, population biology.

Introduction

During the Middle Ages, Mandra was a bay located in the southern part of the Western Black Sea coast. At the beginning of 20th century, the connection to the sea remained in the form of a narrow strait, and the bay became a semi-saline coastal

lagoon (Fig. 1). The construction of a dam in 1963, which severed its connection with the Black Sea, made Mandra the largest freshwater reservoir (also referred to as a dam) in Bulgaria by area. The lake covers 38 km². Its maximum width is 1.3 km, its length is 8 km, and its depth varies between 0.75 and 5 m. It is fed by four rivers:

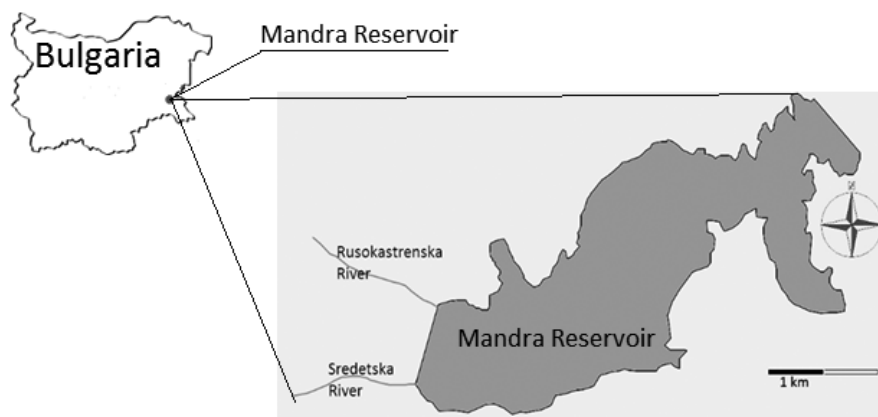


Fig. 1. Location and schematic map of the Mandra Reservoir.

Fakiyska, Sredetska, Rusokastrenska, and Izvorska (Karaivanov et al. 2011).

Two of the largest tributaries of the Mandra Reservoir are the Rusokastrenska and Sredetska rivers. The Rusokastrenska River is 65 km long, with a catchment area of 525 km², while the Sredetska River is 69 km long, with a catchment area of 985 km² (Hristova 2012). Both rivers flow into its western side. In summer, they often dry up almost completely, leaving only some small pools in the riverbeds and water retained in their estuarine extensions.

The Mandra shemaya (*Alburnus mandrensis* Drensky, 1943) is an endemic species found in the Mandra Reservoir basin (Kottelat and Freyhof 2007). It is currently listed as Endangered (EN) on the IUCN Red List (Freyhof and Brooks 2011). This pelagic, schooling fish feeds on terrestrial insects, zooplankton, and small fish, and typically does not exceed 30 cm in length. Spawning occurs in the spring, during April and May, in the reservoir and its tributaries, in places with running water and a rocky or gravel bottom. The fecundity of the species reaches 15,000–23,000 eggs. In the past, it was the subject of commercial fishing. The annual catch of Mandra

shemaya and Black Sea bleak (*Alburnus schischkovi* Drensky, 1943) taken together amounted to 3–5 t (Botev and Peshev 1985). By the end of the twentieth century, the density of the Mandra shemaya was estimated at 3,721 individuals per ha in the Sredetska River and 1,009 individuals per ha in the Rusokastrenska River, with species' biomass estimated at 3.78 kg·ha⁻¹ and 3.86 kg·ha⁻¹ in the respective rivers (Dikov et al. 1994). These data were most likely obtained during the breeding migration, when the species' abundance in the rivers is highest.

The Mandra shemaya is a species with a very limited distribution, restricted solely to the Mandra Lake system, and its biology is very poorly studied. The present study aims to clarify some aspects of the population biology of this valuable endemic of the Bulgarian ichthyofauna. For this purpose, the main growth parameters of the species were investigated.

Materials and Methods

A total of 334 individuals were collected for the study. All specimens were cap-

tured using a hook-and-line gear. Angling was carried out with 3-m telescopic poles, each equipped with one hook. J-hooks (He et al. 2021), size 16–22, were used. Maggot larvae were used as bait. A float method was employed.

Most of the fish were caught in the first two weeks of April 2022 in the Rusokastrenska River. This material was supplemented with catches from the Sredetska River made in the spring of 2020 and 2021 and the summer of 2022. Sampling was conducted at two designated sites (Table 1), and the fish were stored in a freezer. All specimens were processed in a laboratory.

Total length (L) and standard length (SL) were measured to the nearest 1 mm, while total weight (W) and gutted weight (GW) were recorded with an accuracy of 1 g. Fish age was determined by study of annual circles of scales, using an Olympus CX 31 microscope at 40× magnification. The scales were stored in paper bags and remain available in the laboratory.

The linear growth of the fish was assessed through back-calculation of total length (L) from the diagonal oral radius of the scale (S), following the method described by Ricker (1979) and Zhivkov (1981).

This relationship is expressed by linear equation (1):

$$L = a + b \cdot S, \quad (1)$$

where: L – the length of the fish, mm; S – diagonal oral radius of the fish scale (measured in eyepiece micrometre scales

divisions); a and b – equation coefficients.

Absolute annual linear increment was used as a measure of growth, following Zhivkov (1972), and was calculated using formula (2):

$$t = L_n - L_{n-1}, \quad (2)$$

where: t – absolute annual linear increment, mm; L_n, L_{n-1} – average length of fish in two consecutive years, mm.

The relationship between mass and length is expressed by a weight–length (W – L) regression, commonly formulated as shown in equation (3). The applied model was originally proposed by Ricker (1979) and has been widely employed:

$$W = a \cdot L^b, \quad (3)$$

where: W – body weight, g; L – fish length, mm; a is the intercept, and b is the slope of the logarithmically transformed relation.

To compare the linear growth of different populations, the method proposed by Zhivkov (1972) was used, whereby populations are ranked according to their mean length at a given age.

The condition of each population was assessed using three approaches:

1) Calculation of the classical condition coefficient (K_f) based on the Fulton equation (4).

$$K_f = (W \cdot L^{-3}) \cdot 100, \quad (4)$$

where: L – average length, mm; W – average weight, g;

2) By calculating the coefficient K_b , through the Fulton equation with exponent b from the W – L relationship (3);

3) By comparison of weight growth

Table 1. Sampling sites at the Mandra Reservoir tributaries.

Location	Geographic coordinates		Altitude, m a.s.l.	Month and year of sampling
	N	E		
Sredetska River	42°21'06"	27°10'07"	184	April 2020, April 2021, August 2023
Rusokastrenska River	42°25'29"	27°15'19"	388	April 2022

(W) of fish across different populations, following the method proposed by several authors (Goldspink 1979, Zhivkov 1999). The relationship is expressed by the equation (5).

$$W = a \cdot L^b, \quad (5)$$

where: W – weight of fish, g; L – length of fish, mm; a and b – equation coefficients.

To ensure comparability of W values derived from equation (3), pre-selected, rounded values of L (50, 100, 150 and 200 mm) were substituted into the equation (i.e. $L = 50$, $L = 100$, $L = 150$, $L = 200$). Applying equation (5) to these specified length values allows for the calculation of the corresponding weight estimates: $W_{L=50}$, $W_{L=100}$, $W_{L=150}$, $W_{L=200}$. These derived weight values for each studied population are subsequently compared (Zhivkov 1981, 1999; Raikova-Petrova and Zhivkov 1993). The strength of association between L and S , as well as between W and L , was assessed using the correlation coefficient (r^2). All data analyses were performed using MS-Excel 2010.

Results

Age and size composition

In both the Sredetska and Rusokastrenska rivers, the *Mandra shemaya* breeding herd comprised individuals ranging from one to twelve years of age (Fig. 2).

Some fish, as such as zero- and one-year-old individuals, were not susceptible to angling and were therefore not represented in the collected samples. The most abundant age groups were five-, six- and seven-year-old specimens, collectively accounting for approximately 70 % of the total catch. These cohorts represent a significant portion of the spawning popu-

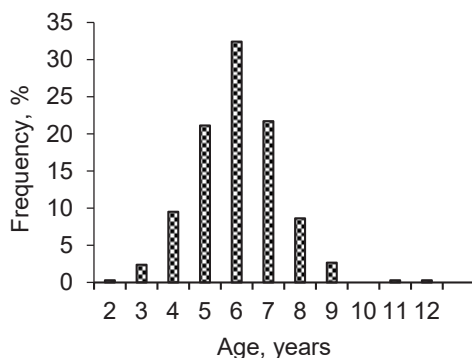


Fig. 2. Age structure of *Mandra shemaya*.

lation that migrates into the rivers during the spring and summer months. Notably, a considerable number of juvenile individuals were present in the sample, suggesting that immature fish also participate in the upstream migration.

Among the *Mandra shemaya* specimens, the largest recorded individual was a 12-year-old female measuring $L=215$ mm and weighing $W=101$ g. The average length and weight of the fish were $L=141 \pm 25$ mm and $W=24 \pm 19$ g, respectively. The most abundant size class comprised of individuals with L ranging from 126 to 150 mm. Specimens exceeding $L=200$ mm were rare, with only isolated individuals observed. Conversely, smaller size classes were also underrepresented, likely due to the selectivity of the fishing gear used (Fig. 3).

Growth in length

The relationship between L and scale radius S is described by equation (6) and illustrated in Figure 4.

$$L = 1.4187 \cdot S + 26.43, \quad r^2 = 0.96, \quad n = 334. \quad (6)$$

As shown in Table 2, *Mandra shemaya* exhibits a high growth rate during the first

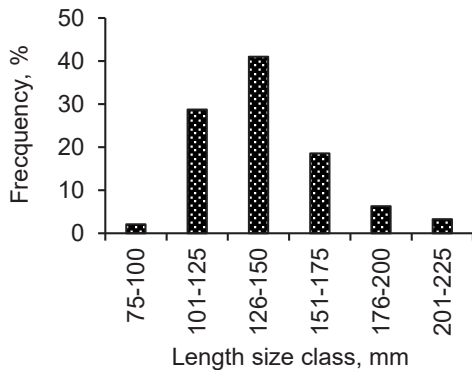
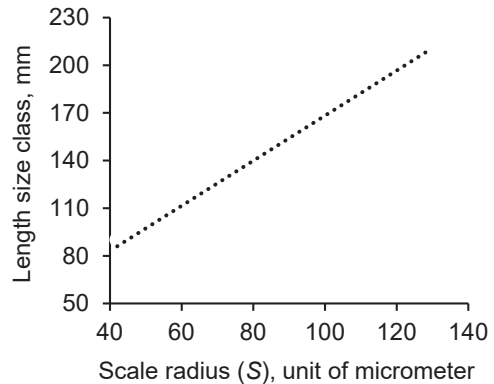
Fig. 3. Size structure of *Mandra shemaya*.

Fig. 4. Relationship between scale radius and length.

Table 2. Back-calculated length (*L*) of *Mandra shemaya*.

Age groups	<i>n</i>	Mean calculated <i>L</i> at age, mm											
		<i>L</i> ₁	<i>L</i> ₂	<i>L</i> ₃	<i>L</i> ₄	<i>L</i> ₅	<i>L</i> ₆	<i>L</i> ₇	<i>L</i> ₈	<i>L</i> ₉	<i>L</i> ₁₀	<i>L</i> ₁₁	<i>L</i> ₁₂
II	1	35	76										
III	8	48	58	86									
IV	32	48	60	76	104								
V	71	48	60	73	89	116							
VI	109	49	60	73	89	103	129						
VII	73	49	60	73	87	102	117	153					
VIII	29	48	59	75	86	102	116	131	148				
IX	9	49	62	75	89	103	114	130	144	168			
X	0	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.		
XI	1	48	59	76	93	104	114	131	143	161	178	195	
XII	1	52	65	72	83	96	114	126	140	157	174	188	208
Mean calculated <i>L</i> , mm	334	47	62	75	90	104	117	134	144	162	176	192	208
Mean observed <i>L</i> , mm		n.d.	82	101	117	127	139	155	168	191	n.d.	215	212
Annual increment, mm		47	15	15	16	14	16	19	14	20	17	16	20

year of life. In subsequent years, annual growth stabilises and remains relatively constant. The length increment in the first year is more than that observed in later years. By the fifth year, individuals typically reach double the length recorded at age one, and by the ninth year, their length is approximately three times greater. Specimens attain a length of 200 mm after the tenth year of life.

Growth in weight

Weight was calculated using the well-defined and nearly linear functional relationship between body length and weight (*W*–*L*), characteristic of the *Mandra shemaya*, as expressed in equation (7) and illustrated in Figure 5:

$$W = 0.0000007 \cdot L^{3.49}, r^2 = 0.99, n = 334. \quad (7)$$

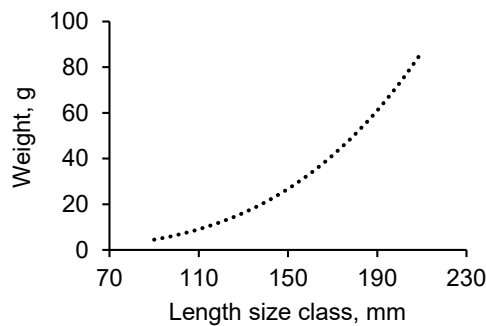


Fig. 5. Weight–length relationship of *Mandra shemaya*.

Given the slow linear growth of the *Mandra shemaya*, the corresponding in-

crease in weight is also very gradual (Table 3). Only exceptionally old individuals attain or exceed a weight W of 100 g. Notably, annual weight gain increases steadily with age, with nearly every subsequent year showing higher values, reaching a maximum in the oldest fish.

The coefficient of the weight–length relationship indicated positive allometric growth.

Calculating weight at fixed (standardised) length values provides a useful basis for comparing growth in weight within the same species across different water bodies, or between species of the same

Table 3. Back-calculated weight (W) of *Mandra shemaya*.

Age groups	n	Mean calculated W at age											
		W_1	W_2	W_3	W_4	W_5	W_6	W_7	W_8	W_9	W_{10}	W_{11}	W_{12}
II	1	0.2	2.6										
III	8	0.5	1.0	4.0									
IV	32	0.5	1.1	2.6	7.7								
V	71	0.5	1.1	2.2	4.5	11.3							
VI	109	0.6	1.1	2.2	4.5	7.5	16.4						
VII	73	0.6	1.1	2.2	4.1	7.2	11.7	29.8					
VIII	29	0.5	1.1	2.5	4.0	7.2	11.3	17.3	26.5				
IX	9	0.6	1.3	2.5	4.5	7.5	10.7	16.9	24.1	41.3			
X	0	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.		
XI	1	0.5	1.1	2.6	5.2	7.7	10.7	17.3	23.5	35.6	50.5	69.4	
XII	1	0.7	1.5	2.1	3.5	5.8	10.7	15.1	21.8	32.6	46.7	61.1	87.0
Mean calculated W , g	334	0.5	1.3	2.6	4.8	7.8	11.9	19.3	24.0	36.5	48.6	65.3	87.0
Mean observed W , g		n.d.	3.7	6.9	10.2	13.1	20.1	34.1	44.9	64.4	n.d.	100.9	97.1
Annual increment, g		0.5	0.8	1.4	2.4	3.4	4.7	8.3	7.3	13.3	14.5	16.7	25.9

Table 4. Weight calculated from the weight–length relationship at standardised lengths.

Rivers	Source	Equation for the total population	Average weights (W_L) calculated at the same rounded lengths (L , mm), g			
			W_{50}	W_{100}	W_{150}	W_{200}
Sredetska and Rusokastrenska	Our data 2025	$W = 0.0000007 \cdot L^{3.49}$	0.6	6.7	27.2	75.7

Note: W_L – weight of the fish at rounded length values (50 to 200 mm), W – total weight, g; L – total length, mm.

genus (Table 4).

Condition factor

The Fulton condition factor (K_f) and the modified coefficient K_b – calculated using the exponent from the population-specific weight–length relationship (equation 7) as the power parameter – were determined (Table 5). However, both coefficients are notably low, particularly K_b .

Table 5. The Fulton condition factor (K_f) and the modified coefficient K_b .

Coef- icients	Min	Max	Aver- age	Standard deviation	<i>n</i>
K_f	0.2	1.16	0.63	0.2	334
K_b	0.13	0.26	0.19	0.05	334

Discussion

Our observations showed that some of the largest breeding migrations of *Mandra shemaya* occur in the Sredetska and Rusokastrenska rivers. During the months of November and December, the rivers fill with water and some of the fish enter them in search of food. Some of these fish remain in the rivers until the start of reproduction, while others return to the Reservoir. The breeding migration begins in late March to early April. This is the period of the greatest influx of *Mandra shemaya* into the rivers. During this time, the fish occupy specific locations in the rivers for several days. Migrating fish schools are numerous and can often be observed with the naked eye. Once breeding is complete, most fish return to the Mandra Reservoir. As the summer dry season progresses and the water levels drop, all fish retreat into the Reservoir, except for a small part of the population, including young-of-the-year juveniles, which remain

in deep pools of the Sredetska River. Autumn and winter rains restore the migration path in the rivers. The relative number of fish entering each river varies annually, depending on weather conditions, water levels, and the timing of peak flow in one river versus the other. Because of this, the amount of migrating fish is different every year in the two rivers.

During the spring during migration, until the beginning of the fishing ban, which most often begins in mid-April, the *Mandra shemaya* is most actively caught by anglers. In addition, *Mandra shemaya* populations face pressures from piscivorous birds and illegal fishing practices (Dimitrov et al. 2024).

The absolute annual increase in length shows only a slight rise after the third year of life. However, when expressed as a percentage of body weight, the annual increase is greatest during the first three years, likely because most individuals reach sexual maturity after this age.

These calculations also confirm the very slow increase in weight of the *Mandra shemaya*. From the data on weight gain (Table 3), differences are evident between the calculated and directly measured average weights. This discrepancy is partly explained by the fact that about 40 % of the specimens in the sample were females with developed gonads, which increased their body weight. In addition, when weight is calculated from the increase in length (Fig. 5), such individual deviations are eliminated, revealing the general growth trend. Consequently, the weights obtained through this method are smaller, but more representative of the actual values.

The coefficient b of the weight–length relationship (WLR) is greater than three ($b = 3.49$), indicating positive allometric growth. This means that as the fish in-

crease in length and age, their bodies become proportionally deeper (Froese 2006). These data can be used in fish monitoring studies (Milošević and Mrdak 2016), as well as for estimating weight at age from the total reported catch weight and length and frequency distributions (Petrakis and Stergiou 1995).

The low value of the Fulton coefficient ($K_f < 1$) indicates poor condition of the fish. The K_b coefficient provides further evidence of insufficient nutrition and limited weight gain in this species. It is normal for a significant portion of nutrients to be allocated to the development of reproductive products at the beginning of the breeding season. However, it is possible that the low condition is related to the lack of food. After the construction of the Reservoir, the salinity of the water changed, which probably affected the invertebrate flora and fauna in it.

Conclusions

This study provides the first detailed assessment of the age structure, growth dynamics, and condition of the endemic Mandra shemaya in the tributaries of Mandra Reservoir. The breeding herd population has a slow but steady increase in length. The Mandra shemaya is characterised by positive allometric growth. Mature five-, six- and seven-year old fish dominate the breeding stock, while juveniles also appear among the migrating individuals. After 10 years of age, the fish can reach a length of nearly 20 cm. Growth in length is most pronounced during the first year of life, after which it stabilises at a slower, consistent rate. By the fifth year, individuals double their initial length, and by the ninth year, they triple it – highlighting the gradual but sustained

somatic growth over time. Only the oldest fish attain a weight of up to 100 g. The Mandra shemaya has an elongated body shape, which becomes deeper as they age. However, we have not registered a length of about 30–40 cm and a mass of 120–800 g, described in the literature (Botev and Peshev 1985, Karapetkova and Zhivkov 1995).

These findings enhance understanding of this endangered species' life history and are vital for informing conservation and habitat management strategies within the Mandra wetland system. Continued monitoring and further research into ecological interactions and food web dynamics are recommended to support effective protection measures.

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Author's statement

The present study was conducted in compliance with applicable national legislation.

Conflict of interest

The author declares that there is no conflict of interest.

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Agroforestry sustainability strategies in the Social Forestry region of Barru District, Indonesia: using the RAPFISH–AHP approach

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Abstract

Agroforestry systems in Social Forestry areas often face persistent challenges in achieving comprehensive sustainability, particularly in economic and socio-institutional dimensions. Despite their potential to enhance livelihoods and environmental resilience, limited studies have integrated multidimensional evaluations to identify the key leverage factors and policy priorities for sustainable agroforestry. This gap highlights the urgency of developing holistic strategies tailored to local institutional contexts. This study aims to formulate sustainable agroforestry strategies in Barru District, focusing on Social Forestry areas using the RAPFISH–AHP approach, and emphasising ecological, economic, and socio-institutional aspects. The sustainability assessment employed multidimensional scaling with the RAPFISH framework, complemented by the Analytical Hierarchy Process (AHP) to prioritise strategies derived from sensitive attributes identified through leverage analysis. The research involved 15 active members of the Mega Buana Forest Farmers Group in Pacekke Village through participatory observation and structured Likert-scale questionnaires. The results show that agroforestry in the study area is 'less sustainable' in economic (index 38.91) and socio-institutional (38.10) dimensions, and 'moderately sustainable' in the ecological dimension (47.56). The most sensitive factors influencing sustainability include the selling price of agricultural products, chemical fertiliser use, and the institutional role of Forest Farmer Groups. Based on AHP results, two key strategies were prioritised: (1) optimising local institutions and participatory technical assistance (67.4 %), and (2) developing downstream community-based agroforestry business models (32.6 %). These strategies provide an integrated policy framework to strengthen institutional capacity, enhance adaptive governance, and promote environmentally responsible practices within Indonesia's Social Forestry areas.

Key words: community-based land management, farmer participation, institutional resilience, multidimensional analysis, sustainability assessment.

Introduction

Agroforestry has gained global recognition for its critical role in enhancing land pro-

ductivity, improving livelihoods, and contributing to climate resilience (Khan et al. 2021). Globally, approximately 1.2 billion people depend on agroforestry systems,

covering nearly 1 billion hectares of land, and contributing to over 17 % of global agricultural landscapes (Nair and Garrity 2021, FAO 2022). In Indonesia, agroforestry covers around 6.5 million hectares within Social Forestry schemes, directly supporting more than 1.4 million households (KLHK 2023). However, despite this vast coverage and potential, the quantitative sustainability performance, particularly in economic and socio-institutional dimensions, remains poorly assessed and poorly integrated into local policy frameworks. As pressures on natural resources grow, this land-use model continues to evolve through innovations such as smart technologies and community-based digital tools, reinforcing its relevance in adaptive land management (Pantera et al. 2021). Recent research further confirms the importance of agroforestry strategies as a holistic solution to address environmental degradation, economic inequality, and the strengthening of social structures in forest communities (Junaedi et al. 2022, Arif et al. 2024).

In the Indonesian context, particularly in Barru District, the implementation of Social Forestry has encountered persistent challenges, including limited institutional capacity, market access constraints, and continued dependence on unsustainable farming inputs. Despite government support, forest farmer groups in the area often lack technical assistance, and their agroforestry activities are constrained by fluctuating product prices and inadequate organisational management. These site-specific issues highlight the urgent need for integrated sustainability strategies tailored to the local context.

However, most previous studies have focused on general assessments of agroforestry benefits or adoption drivers at national or regional scales, with limited

attention to how sustainability dimensions interact within specific Social Forestry schemes. Research in Indonesia has often emphasised biophysical or economic outcomes, leaving the institutional and socio-ecological linkages underexplored (Gebru et al. 2019, Amare and Darr 2020, Khan et al. 2021). Moreover, few studies have integrated the RAPFISH and Analytical Hierarchy Process (AHP) methods to provide a multidimensional and participatory evaluation framework suitable for Social Forestry regions such as Barru District. The mixed-method approach in this study combines RAPFISH for assessing ordinal sustainability performance across ecological, economic and institutional dimensions, and AHP for weighting stakeholder preferences and determining strategic priorities. This integration allows for both quantitative assessment and participatory validation, ensuring that sustainability strategies are analytically robust and socially grounded.

This study addresses these gaps by analysing the multidimensional sustainability of community-based agroforestry systems and identifying strategic priorities that link ecological, economic and socio-institutional factors. It provides a site-specific understanding of sustainability dynamics and practical strategies to enhance the adaptive capacity of Forest Farmers Groups within Indonesia's Social Forestry framework. In Barru District, the agroforestry model practised by the Mega Buana Forest Farmers Group typically integrates timber species such as teak (*Tectona grandis* L. f.), gamal (*Gliricidia sepium* (Jacq.) Kunth), and sengan (*Falcataria moluccana* (Miq.) Barneby & J.W.Grimes) with short-cycle agronomic crops including maize (*Zea mays* L.), cassava (*Manihot esculenta* Crantz), chilli (*Capsicum annuum* L.), and peanuts (*Ara-*

chis hypogaea L.). This combination reflects a multifunctional land-use approach aimed at ensuring ecological stability while supporting household food security and income diversification.

Technological innovations such as utilisation of smart technology, use of GIS and community-based digital management have strengthened agroforestry practices in various regions, including Barru District. In the context of Social Forestry, the agroforestry approach based on Forest Farmers Groups has gained increasing attention as an instrument for strengthening community capacity. This strategy includes the active involvement of farmers in planning and decision-making processes, the use of digital technology for product monitoring and marketing, and the incorporation of agronomic practices with local wisdom. This integrative model has been proven to increase the added value of agricultural products, improve supply chain efficiency, and strengthen the socio-economic structure of forest communities (Willmott et al. 2023).

Thus, this study aims to formulate a comprehensive agroforestry sustainability strategy for Barru District. It introduces an integrated evaluative framework that combines the RAPFISH and AHP methods while bridging local practices with data-driven technological approaches to support long-term system sustainability. The specific objectives of this study are to (i) quantify sustainability indices across ecological, economic and socio-institutional dimensions; (ii) identify key leverage attributes influencing sustainability performance; and (iii) prioritise policy strategies based on multi-stakeholder preferences. The findings are intended to inform the development of inclusive and adaptive Social Forestry policies that effectively respond to socio-ecological changes.

Object

Research site description

The study was conducted in Pacekke Village, Soppeng Riaja Sub-district, Barru District, South Sulawesi, Indonesia. The study site is located within an officially designated Social Forestry area managed under a community-based forest management scheme. The site was selected for its active agroforestry practices, supported by the Mega Buana Forest Farmers Group (FFG; locally known as Kelompok Tani Hutan, KTH), which has been consistently engaged in Social Forestry initiatives. According to the Meteorology, Climatology and Geophysics Agency (BMKG 2024), Barru District experiences a tropical humid climate with an average annual rainfall of 2,500–3,000 mm and a mean temperature ranging from 26 °C to 32 °C. The dominant soil type in the study area is Latosol, characterised by moderate fertility and good drainage, which supports diverse tree–crop combinations in agroforestry systems.

Observations and data collection

Observations and data collection focused on actively practising agroforestry farmers, ensuring both reliability and representativeness. Figure 1 presents a visual depiction of the research site and its administrative boundaries, highlighting its geographic context within Barru District's Social Forestry framework.

Methods

Sampling technique

A total of 15 respondents were selected through purposive sampling from

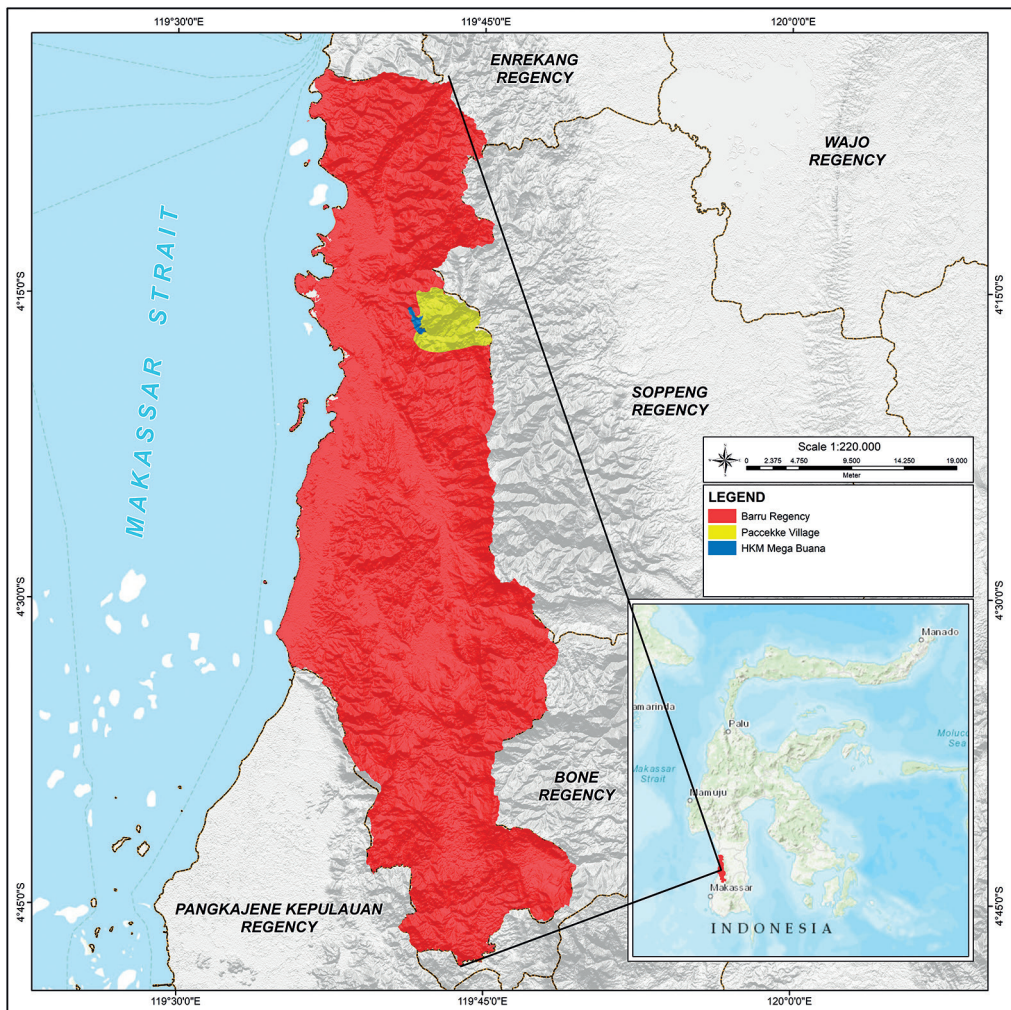


Fig. 1. Research location of the study area in Paccikke Village, Barru District.

the Mega Buana Forest Farmers Group (FFG) in Paccikke Village, Barru District. Paccikke Village was selected as an exploratory case study site due to its diverse agroforestry composition, where farmers cultivate a wide range of tree–crop combinations including timber, fruit and annual species representing the most active and varied Social Forestry practices in Barru District. Respondent selection followed specific criteria: active involvement in

agroforestry for at least three consecutive years under the Social Forestry scheme, formal membership of the FFG, and participation in extension or training activities related to community forestry.

This number represents the entire population of active and eligible agroforestry farmers in the study area at the time of data collection, making it adequate for a case-oriented sustainability analysis. The same 15 respondents participated in

all research stages, including field observation, the RAPFISH-based sustainability assessment and the Analytical Hierarchy Process (AHP). No external stakeholders were involved in the AHP stage to ensure that the prioritised strategies reflect the perspectives of local practitioners. Their consistent participation strengthened the internal validity and maintained the participatory, community-based character of this exploratory study.

Data collection

Data were collected in June 2025 through a closed-ended questionnaire designed using a five-point Likert scale. This questionnaire was used to measure respondents' perceptions of various agroforestry sustainability attributes. Each item was rated using a five-point Likert scale, following the method described by Sugiyono (2012). The scoring criteria are summarised in Table 1.

Table 1. Criteria for rating the questionnaire using a five-point Likert scale.

No	Description	Score
1	Very good	5
2	Good	4
3	Fair	3
4	Poor	2
5	Very poor	1

Note: Scoring criteria were adapted from Sugiyono (2012).

Data analysis

The data were analysed using a Multidimensional Scaling (MDS) approach with the RAPFISH method, adapted from Fauzi and Anna (2002) and Saida et al. (2011). The analysis consisted of three stages: (1) identification of sustainability attributes across ecological, econom-

ic and socio-institutional dimensions; (2) scoring of each attribute using a five-point Likert scale; and (3) ordination using MDS to generate sustainability indices. Attributes were defined through literature review, expert consultation, and field validation, ensuring contextual relevance to the Social Forestry framework in Indonesia. For example, ecological attributes included fertiliser use, crop diversity, and erosion control, while economic attributes covered income levels, input costs, and product marketing. Socio-institutional attributes assessed leadership, mentoring, and the role of women. Each attribute was operationalised as a questionnaire item to reflect farmers' perceptions. The validity of the results was analysed through Monte Carlo, and sensitivity through leverage analysis, as follows:

a) Scoring of each attribute. Each attribute in the Agroforestry sustainability dimension is given a score, ranging from 1 to 5 which is interpreted from bad to good; the greater the score, the more supportive the Agroforestry sustainability in the Social Forestry areas,

b) The sustainability index value of agroforestry farming, as used in this analysis, is categorised into four levels of sustainability status based on the method of Ruhimat (2015) (Table 2).

Table 2. Categories of sustainability status based on Ruhimat (2015).

No	Index value	Sustainability status
1	0–25.00	Not sustainable
2	25.01–50.00	Less sustainable
3	50.01–75.00	Moderately sustainable
4	75.01–100.00	Sustainable

c) Leverage analysis. Leverage analysis was conducted to identify the most sensitive attributes influencing the sustainability index of agroforestry practices. The Root Mean Square (RMS) value in

this analysis represents the magnitude of change in the sustainability index caused by the removal or variation of each attribute. In other words, RMS quantifies how strongly each attribute affects the ordination position in the RAPFISH multidimensional scaling plot. Attributes with higher RMS values indicate greater leverage or influence on sustainability performance. Following Ruhimat (2015), attributes with RMS values exceeding half of the x-axis scale are considered sensitive and thus have a substantial effect on sustainability outcomes. This approach helps determine priority factors that should be addressed to improve the sustainability status of agroforestry systems.

d) Monte Carlo analysis. The Monte Carlo simulation was conducted with 999 iterations at a 95% confidence level to test the stability and robustness of the RAPFISH ordination results. This procedure compares randomised iterations of the dataset with the original configuration to assess potential errors due to scoring variation or data entry. A difference value of less than 0.5 between the RAPFISH and Monte Carlo results indicates that the ordination is statistically stable and that

the sustainability index can be considered valid and reliable.

e) Analytical Hierarchy Process (AHP) method. After various steps or stages using MDS, these attributes were then used as input for the Analytical Hierarchy Process (AHP), which allowed respondents to perform pairwise comparisons in Expert Choice Ver. 11. The AHP results identified priority strategies, with consistency ratios below 0.1 considered acceptable (Oelvi-ani 2015).

Results and Discussion

Respondent identity

Understanding the demographic characteristics of respondents is essential to interpret the sustainability perceptions and decision-making patterns of community-based agroforestry practitioners. These characteristics – such as age, education level and household dependents – reflect socio-economic diversity and influence farmers' adaptive capacity within Social Forestry schemes. Table 3 presents a summary of these respondent profiles

Table 3. Respondent characteristics.

Aspects	Category	Number (persons)	Share, %
Age	30–40 years	3	20.0
	50–60 years	6	40.0
	>60 years old	6	40.0
Education	Not in school	2	13.3
	Elementary	6	53.3
	Junior high	1	6.7
	High school	3	20.0
	S1 (Bachelor's)	1	6.7
	S2 (Master's)	2	13.3
Family dependents	1 person	6	40.0
	2–3 people	5	33.3
	4–5 people	4	26.7

Note: Data derived from authors' field survey and analysis, 2025.

from the Mega Buana Forest Farmers Group ($n = 15$).

Age distribution of respondents

Most respondents were aged 50 years and above (40 %), with 40 % over 60 years old. This indicates that agroforestry is dominated by older, experienced farmers who possess extensive local ecological knowledge. However, the limited participation of younger individuals (20 %) highlights the need for youth engagement to ensure long-term sustainability and overcome constraints related to physical labour and technology adoption (Idris and Arafat 2019). Younger generations are generally more adaptive to digital tools, innovative farming systems and market-oriented practices, which are essential to revitalise agroforestry productivity and institutional continuity. Their involvement can bridge generational knowledge transfer while enhancing innovation and resilience within Social Forestry systems.

Education level

Over half of respondents (53.3 %) had only completed elementary school, while 13.3 % had no formal education. Only 20 % reached high school, with 6.7 % holding a bachelor's and 13.3 % a master's degree. This low educational background necessitates tailored outreach using visual aids, local language and practical methods. Educated individuals may serve as peer mentors to strengthen agroforestry literacy (Goparaju et al. 2020).

Number of family dependents

Respondents with one dependent made up 40 %, 33.3 % had two to three, and 26.7 % had four to five. More dependents

may increase labour capacity but also raise household economic burdens. A balanced family structure is essential for efficient agroforestry land management (Gebu et al. 2019).

Analysis of agroforestry sustainability in Mega Buana Forest Farmers Group

The MDS ordination analysis shows that the ecological dimension obtained the highest sustainability index (47.6), followed by the economic (38.9) and socio-institutional dimensions (38.1). These values indicate that agroforestry in the research area is categorised as moderately sustainable in the ecological dimension, while the economic and socio-institutional dimensions remain less sustainable (Fig. 2).

Our ecological sustainability index of 47.6 indicates a moderately sustainable condition, suggesting that the agroforestry system in Barru District performs relatively well in maintaining vegetation cover and intercropping diversity but remains constrained by low adoption of organic fertiliser and limited erosion control measures. This mixed performance reflects partial ecological resilience that has yet to reach the 'sustainable' threshold. Comparatively, similar studies in other Indonesian Social Forestry areas reported ecological indices ranging between 45 and 55, such as Rancah, West Java (Ruhimat 2015), and Jeneberang, South Sulawesi (Saida et al. 2011), showing that the ecological sustainability level in Barru is consistent with the national average.

Our economic index of 38.9 suggests that agroforestry in the study area remains less sustainable economically, reflecting limited market access, fluctuating product prices and low capital turnover. This pattern aligns with findings from ru-

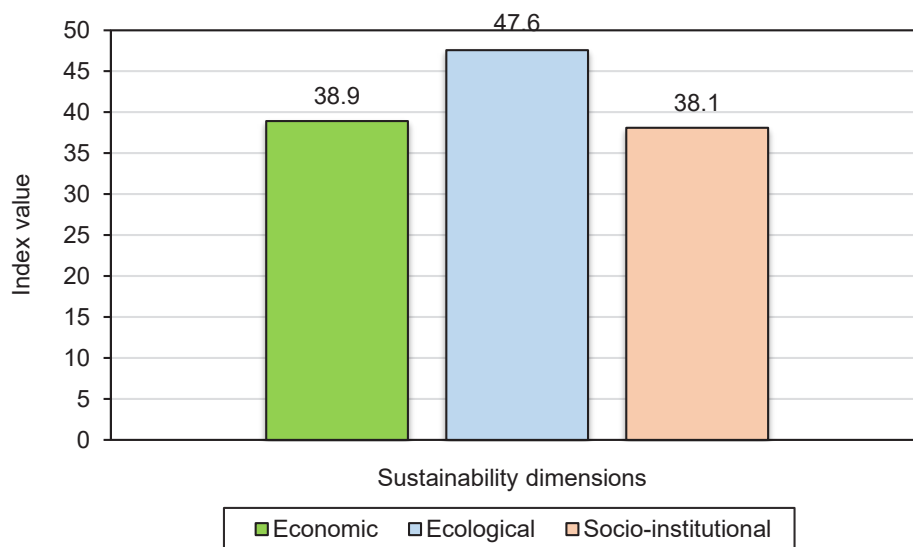


Fig. 2. Results of MDS ordination analysis of agroforestry sustainability in Barru District.

ral Social Forestry sites in Central Sulawesi and East Nusa Tenggara, where smallholder agroforestry also shows limited profitability due to low value-added production (Tega and Bojago 2023). Improving market connectivity and local enterprise capacity is therefore essential to strengthen economic resilience. Meanwhile, the socio-institutional dimension index of 38.1 suggests weak group organisation and limited participation in decision-making. This value is slightly lower than the 42.5 institutional index recorded in similar community forestry schemes in West Java (Ruhimat 2015), indicating that local institutional mechanisms in Barru are still developing. Strengthening forest farmer groups, mentoring schemes and participatory planning processes is crucial to improving institutional sustainability.

To better understand which attributes most affect these dimensions, a leverage analysis was conducted to identify sensitive factors influencing the sustainability scores, as presented in the following fig-

ure. The results of sensitivity analysis for the economic dimension are shown in the attributes that have the highest values in Mega Buana FFG, as illustrated in Figure 3.

The leverage analysis identifies the selling price of harvested products ($RMS = 2.78$) as most influential attribute within the economic dimension, as it significantly affects farmers' income and directly determines the profitability of agroforestry systems. This value exceeds the RAPFISH leverage threshold ($RMS > 0.95$), indicating that even small changes in product pricing can substantially shift the sustainability index. Other important factors include community income from agroforestry (1.24), availability of production inputs (1.22) and fertiliser affordability (1.14), all of which moderately affect sustainability. The least impactful is business capital support (0.38), suggesting its current limited role. To improve sustainability, enhancing market access, diversifying products, strengthening farmer institutions and pro-

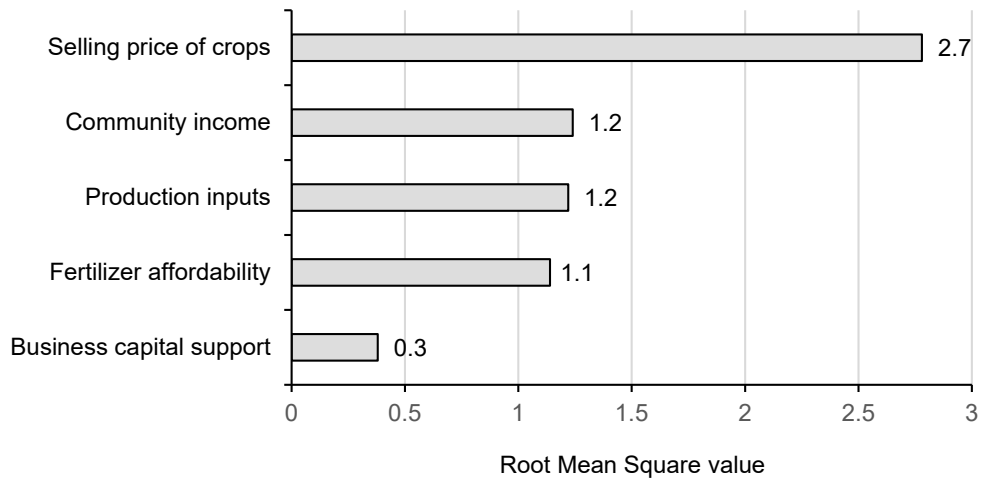


Fig. 3. Results of leverage analysis of the economic dimension in Mega Buana Forest Farmers Group.

viding training in marketing and financial literacy are essential strategies to raise crop prices and ensure long-term economic benefits (Tega and Bojago 2023).

The results of the sensitivity analysis for the ecological dimension are shown in the attributes that have the highest values

in the Mega Buana FFG, as illustrated in Figure 4.

The attribute with the highest leverage on ecological sustainability is the use of chemical fertilisers, with an RMS value of 3.1. This high value does not imply that chemical fertilisers improve ecological

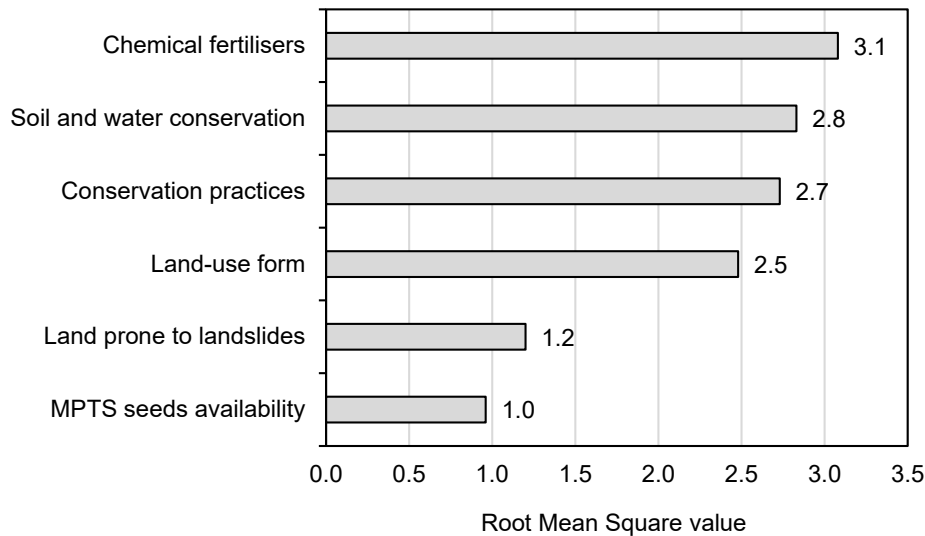


Fig. 4. Results of leverage analysis of the ecological dimension in Mega Buana Forest Farmers Group.

performance; rather, it indicates that this attribute exerts a strong influence, positive or negative, on the sustainability index. In the study area, persistent reliance on chemical inputs was observed during fieldwork, reflecting a critical ecological concern. Overapplication of synthetic fertilisers contributes to soil nutrient imbalances, reduced microbial diversity and long-term declines in soil fertility, thereby undermining ecosystem resilience (Guo et al. 2022, Maria et al. 2022). As such, the high RMS value reflects the sensitivity of this attribute; small adjustments in its use can substantially alter the ecological sustainability index in the RAPFISH ordination. This interpretation is supported by previous studies noting that input management plays a key role in agroforestry

sustainability (Gebbru et al. 2019, Do et al. 2020). Gradual substitution with locally available organic fertilisers, combined with continuous farmer training, is therefore essential to restore ecological balance and improve system sustainability.

The results of the sensitivity analysis for the socio-institutional dimension are shown for the attributes with the highest values in the Mega Buana FFG, as illustrated in Figure 5.

Leverage analysis of the socio-institutional dimension reveals that agroforestry sustainability is most strongly influenced by the institutional role of the Mega Buana Forest Farmers Group (FFG), with the highest RMS value of 3.70. In its current state, the group operates with limited organisational structure, inconsistent co-

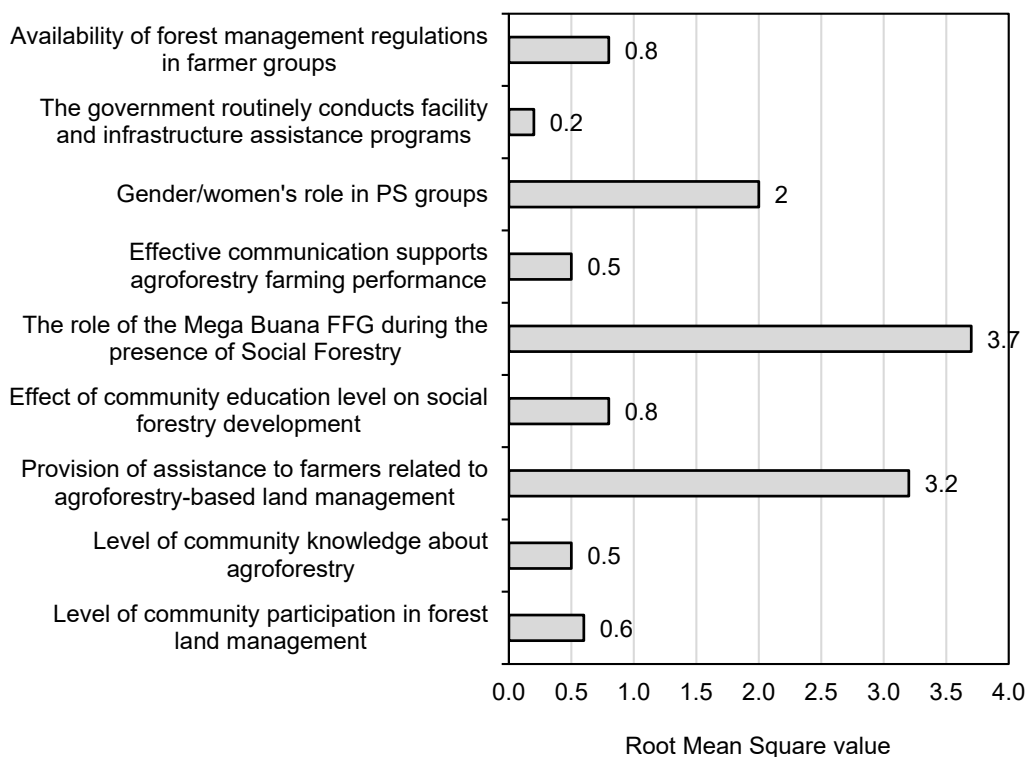


Fig. 5. Results of leverage analysis of the socio-institutional dimension in Mega Buana Forest Farmers Group.

ordination and minimal formalised roles – falling short of an ideal institution that would offer structured leadership, internal accountability and regular collective decision-making. Strengthening institutional capacity is thus critical to improving local resilience and management effectiveness.

Mentoring also emerged as a sensitive attribute (RMS = 3.27), yet remains irregular and project-dependent in practice. Ideally, consistent technical guidance would be embedded within extension services or peer-led networks to ensure the continued success of agroforestry practices and reduce technical failures. The role of women (RMS = 2.08) reflects moderate influence, as participation is currently limited to production tasks with minimal involvement in planning or leadership. In contrast, an inclusive system would actively promote gender equity in decision-making and benefit-sharing. Attributes such as education level (0.80), group regulations (0.83) and internal communication (0.51) also score low, indicating that knowledge access, rule enforcement and coordination mechanisms are underdeveloped compared to ideal participatory governance structures. To address these issues, targeted efforts to institutionalise mentoring, promote inclusive group structures, and invest in local capacity-building are necessary. As Amare and Darr (2020) highlight, sustainable agroforestry requires adaptive governance, strong local leadership and knowledge-sharing systems to effectively manage socio-ecological complexities.

The leverage analysis combines RAPFISH to assess sustainability status and Monte Carlo to test confidence levels. Value differences may result from procedural errors, scoring variation or data inconsistencies. These differences are summarised in Table 4.

Table 4. Difference between RAPFISH and Monte Carlo values at Mega Buana Forest Farmers Group in leverage analysis.

Results	Dimensions of sustainability		
	A	B	C
RAPFISH	38.91	47.56	38.10
Monte Carlo	38.65	47.29	37.95
Value difference	0.26	0.27	0.15

Note: A – economic dimension, B – ecological dimension, C – socio-institutional dimension.

The RAPFISH and Monte Carlo results for the Mega Buana FFG show only a slight value differences, indicating high confidence and validity in the MDS analysis. This confirms the reliability of the method for evaluating agroforestry learning outcomes (Do et al. 2020).

Agroforestry sustainability strategy

a. Hierarchical structure of criteria and alternatives

Based on the leverage analysis, several sensitive attributes were identified as key factors influencing agroforestry sustainability. These attributes were then structured into a hierarchical model using the AHP approach, which served as the basis for formulating sustainability strategies. The hierarchy comprises three main dimensions – economic, ecological and socio-institutional – each supported by critical attributes (Fig. 6).

The hierarchical structure highlights the priority issues that need to be addressed to enhance agroforestry sustainability within the Social Forestry areas of Barru District. In the economic dimension, the low selling price of harvested products and the low income of communities engaged in agroforestry are identified as major constraints. Within the ecological dimension,

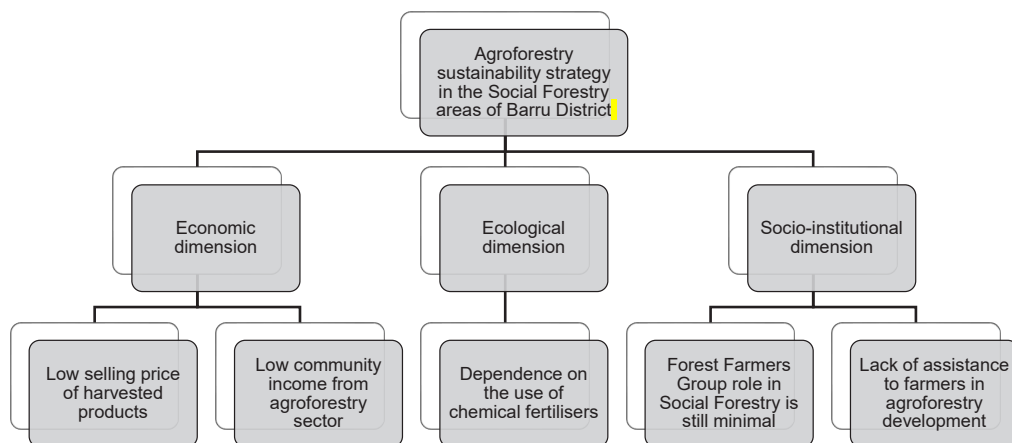


Fig. 6. Hierarchical structure used in the AHP analysis of agroforestry sustainability strategies in Barru District.

the reliance on chemical fertilisers emerges as a critical challenge. Meanwhile, the socio-institutional dimension reveals institutional weaknesses, reflected in the limited role of Forest Farmers Groups and the lack of adequate assistance to farmers in developing agroforestry practices. These findings provide the foundation for formulating targeted strategies to strengthen institutional capacity, improve ecological management and increase farmers' economic resilience.

b. Assessment criteria

Agroforestry sustainability in Barru's Social Forestry areas is assessed based on three main dimensions: ecological, eco-

nomic, and socio-institutional aspects. Sensitive attributes were identified using the RMS method with values exceeding half of the x-axis scale, and the criteria and sub-criteria applied in this study (Table 5) were adapted from Handayani (2015).

At this stage it is called the choice stage. This stage will be carried out a comparison of each criterion and alternative using the expert choice version 11 application. The first stage is Pairwise Comparison, which is a pairwise comparative assessment. Each factor in the form of objectives or criteria, sub-objectives and alternative decisions is determined by comparing pairs. This means that el-

Table 5. Assessment criteria affecting agroforestry sustainability.

No	Assessment criteria	Dimension category
1	Dependence on the use of chemical fertilisers	Ecological
2	Low selling price of harvested products from agroforestry commodities	Economic
3	Low community income from agroforestry sector	Economic
4	The role of Forest Farmers Group in Social Forestry is still minimal	Institutional
5	Lack of assistance to farmers in agroforestry development	Institutional

Note: Adapted from Handayani (2015).

ements are compared in pairs against a specified criterion. In the implementation using Expert Choice, it is often called the assessment process. This process begins by comparing in pairs starting from all predetermined criteria (Handayani 2015). The contribution of each sub-criterion to the overall sustainability objectives is shown in Table 6.

Expert Choice analysis, based on the authors' field data (2025), identifies five key priorities: lack of farmer assistance (20.2 %), low crop prices (19.5 %), weak roles of Forest Farmers Groups (17.5 %), reliance on chemical fertilisers (16.4 %), and low income (12.2 %). Addressing these requires sustained mentoring, institutional strengthening, value-added production, eco-friendly inputs and improved market access. Evidence from successful community-based agroforestry programmes in other regions supports these recommendations. In the context of this study, the assessed agroforestry systems predominantly represent a combination of agrisilviculture and silvopasture models. Farmers in Pacekke Village cultivate tree species such as *Gmelina arborea* Roxb., *Tectona grandis*, and *Gliricidia sepium* alongside seasonal crops such as maize (*Zea mays*), cassava (*Manihot esculenta*), and peanuts (*Arachis hypogaea*). In some cases, they also integrate small livestock grazing beneath the tree cover. This structure aligns with the theoretical agroforest-

ry frameworks described by Nair (2021) and Pantera et al. (2021), in which agrisilvicultural systems enhance land productivity through vertical and temporal complementarity, while silvopasture promotes soil fertility and livelihood diversification. Therefore, the sustainability indices and priority factors identified in this study reflect the performance of these integrated agroforestry models within the Social Forestry scheme in Barru District.

In Central Java, continuous mentoring combined with participatory training increased farmers' technical competence and institutional performance (Junaedi et al. 2022). Similarly, integrated agroforestry enterprises in South Sulawesi that focused on local product processing and cooperative marketing achieved higher profitability and reduced market dependency (Arif et al. 2024). In Ethiopia, the adoption of organic inputs and diversified tree-crop systems enhanced both ecological and economic sustainability (Gebbru et al. 2019).

c. Strategy prioritisation results

The Expert Choice analysis identified two core strategies for promoting sustainable agroforestry in Pacekke Village. These were formulated based on five key criteria and expert insights, integrating various supporting actions to enhance farmer welfare. The five criteria include: (i) lack of technical assistance to farmers, (ii) low selling price of agroforestry products,

Table 6. Contribution of each criterion to the achievement of the sustainability objective.

Assessment criteria	Weight (normalised)	Share, %	Pri- ority
Lack of assistance to farmers in the development of agroforestry	0.202	20.2	1
Low selling price of harvested products from agroforestry commodities	0.195	19.5	2
Minimal role of Forest Farmers Group in Social Forestry	0.175	17.5	3
Dependence on the use of chemical fertilisers	0.164	16.4	4
Low community income from the agroforestry sector	0.122	12.2	5

(iii) limited role of Forest Farmers Groups, (iv) dependence on chemical fertilisers, and (v) low household income from agroforestry. These criteria represent the main constraints identified through the RAP-FISH leverage analysis, reflecting ecological, economic and socio-institutional challenges within the Social Forestry system. Each criterion thus served as a decision variable in the AHP model to determine the most effective strategic priorities for improving overall sustainability. The contribution of each strategy to the overall objectives is summarised in Table 7.

To address the sustainability challenges in agroforestry, an integrated strategy combining technical, institutional and economic approaches is required. Two complementary strategies were formulated to guide policy and field-level interventions. The first focuses on optimising the role of local institutions – particularly Forest Farmers Groups – by improving managerial capacity, access to information and adaptive technical support. This approach promotes structured, multi-stakeholder assistance to enhance sustainable agroforestry practices, reduce chemical input dependency, and raise environmental awareness while supporting local economic development (Fauvelle and Garcia 2018). This first strategy is prioritised because institutional strengthening directly influences both ecological and economic outcomes, serving as a foundation for

long-term system improvement. Without effective institutions, downstream business development cannot be sustained, making this strategy the most critical lever for ensuring lasting agroforestry sustainability.

The second strategy targets the development of downstream schemes and community-based agroforestry business models. It seeks to strengthen farmers' economic institutions – such as marketing cooperatives and processing units – while integrating agroforestry systems with more profitable market schemes. This strategy aims to improve farmers' bargaining power, streamline supply chains, and create opportunities for income diversification through high-value products (Meter et al. 2022). Comparable best practices have been documented across Southeast Asia. In northern Thailand, Farmer Field Schools improved coordination between government agencies and forest communities, strengthening local organisations and adaptive capacities (Rout 2018). In Indonesia, effective interaction between smallholders and extension services proved critical for the long-term success of agroforestry systems (Achmad et al. 2022). However, this second strategy received a lower priority weight (33 %) compared to the first (67 %) because its successful implementation depends on the existence of strong local institutions, sufficient market access and stable production

Table 7. Strategy prioritisation scale.

No	Alternative	Weight (normalised)	Share, %	Prior- ity	Level of inconsis- tency
1	Optimising the role of local institutions and participatory technical assistance schemes	0.674	67.4	1	0.02
2	Development of downstream schemes and community-based agroforestry business models	0.326	32.6	2	

capacity – all of which are currently limited in the study area. While it provides significant long-term economic benefits, its impact is conditional on the prior strengthening of institutional and technical capacities. Therefore, the strategy is considered a complementary rather than foundational action, reinforcing the outcomes of institutional optimisation rather than replacing them.

Conclusions

This study found that agroforestry sustainability in Barru's Social Forestry areas remains constrained, particularly in the economic and socio-institutional dimensions, which scored 38.91 and 38.10 respectively, classified as 'less sustainable'. The ecological dimension scored higher (47.56), yet still falls within the 'moderately sustainable' range. While agroforestry contributes to environmental conservation, it has not yet translated into meaningful improvements in farmer welfare or institutional resilience. Key limiting factors include low crop prices, overdependence on chemical fertilisers, and weak performance of farmer group institutions. To address these challenges, two strategic priorities were identified through Analytical Hierarchy Process analysis: (1) optimising local institutions and participatory technical assistance, and (2) developing community-based agroforestry business models. These strategies can be translated into concrete actions such as conducting leadership and financial management training for farmer group administrators, integrating participatory mentoring into regular extension services, and establishing multi-stakeholder coordination platforms involving local government, NGOs, research bodies, and private sector ac-

tors. Additionally, strengthening farmer field schools, facilitating access to green finance, promoting product diversification, and incentivising organic input adoption are critical for supporting both institutional and economic improvements. To measure the success of these strategies, key performance indicators (KPIs) are proposed, including: (i) an improvement in the economic sustainability index to > 55 (moderately sustainable category), (ii) a 30% reduction in chemical fertiliser use through organic input substitution, and (iii) an increase in active Forest Farmers Group (KTH) membership to > 80% participation rate. These quantifiable targets provide a practical framework for monitoring progress and ensuring that strategy implementation contributes to long-term agroforestry sustainability within Indonesia's Social Forestry framework.

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Reproductive biology of *Alburnus mandrensis* in the Mandra Reservoir basin, Bulgaria

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Abstract

This study provides the first quantitative estimates of key reproductive parameters for the endangered Mandra shemaya (*Alburnus mandrensis* Drensky, 1943) (IUCN Red List) from two tributaries, the Rusokastrenska and Sredetska rivers, of the Mandra Reservoir in Bulgaria. Samples were collected during four years, from 2020 to 2023. Of the 334 fish captured by angling, 184 were with developed gonads. The youngest mature individual was a three-year-old female (96 mm, 5.3 g). Absolute fecundity ranged widely from 190 to 75,565 eggs, with a mean of 8,859 eggs, and showed a strong positive correlation with fish standard length, gutted weight, and age. Fecundity increased until the ninth year, after which a decline was observed in the older (11- and 12-year-old) fish. The average relative fecundity was 351 eggs per gram of gutted weight. These results establish an important baseline for understanding the reproductive biology of this endemic species and are instrumental for its future conservation and management.

Key words: absolute fecundity, endemic species, Mandra shemaya, population structure, relative fecundity, reproductive biology.

Introduction

The Mandra shemaya (*Alburnus mandrensis* Drensky, 1943) is one of the few species of the genus *Alburnus* native to Bulgaria. This gregarious, planktonic fish is endemic to Mandra Reservoir, Bulgaria (Kottelat and Freyhof 2007). In addition to plankton, its diet includes insect and fish larvae. It reaches a maximum length of 19 cm and a weight of 100 g. Spawning occurs in April and May in the rivers and backwater areas of the Reservoir (Peshev et al. 2000). The fecundity of the species

reaches 15,000–23,000 eggs (Botev and Peshev 1985). Historically, this species was abundant (Dikov et al. 1994) and supported commercial fishing. Currently, it is primarily targeted by anglers (Botev and Peshev 1985). As an endemic species, the biology of the Mandra shemaya is relatively understudied. Existing literature provides general information on three species of the genus *Alburnus*, two inhabiting coastal water bodies in Bulgaria (*Alburnus mandrensis* and *Alburnus schischkovi* Drensky, 1943) and one from the Bulgarian section of the Danube River

(*Alburnus sarmaticus* Freyhof & Kottelat, 2007). Given its ecological and regional significance, this study aims to improve understanding of the reproductive biology of *Mandra shemaya* by examining key reproductive parameters in detail.

Study area

Lake Mandra is one of three lakes located along the southern part of the Bulgarian Black Sea coast. It lies in a well-defined river valley, oriented transversely to the coastline, and extends close to the southern edge of Burgas (Fig. 1). The southern shore of the lake borders the northernmost slopes of the Strandzha Mountains. The Rusokastrenska, Sredetska, Fakiyska, and Izvorska rivers flow into Lake Mandra. In 1963, a dam wall was constructed in the eastern part of the lake, separating it from the sea and transforming it into a reservoir. Subsequently, a canal was dug to reconnect the reservoir to the sea. The maximum depth of Mandra Reservoir is 5 m, with an average depth of approximately 1 m. The reservoir spans 8 km in length, has a maximum width of 1.3 km,

and covers a surface area of 38.8 km². Water salinity varies from 1 to 12 ppm. The climate of the region is temperate with warm, with Mediterranean influences. Mandra Reservoir is home to 16 fish species from six families.

The study sites are located in the Rusokastrenska and Sredetska rivers, which flow into the western part of Mandra Reservoir (Fig. 1). The Rusokastrenska is 64.8 km long, and the Sredetska is 69 km long. Both rivers traverse flat and hilly terrain, primarily covered by agricultural areas and, to a lesser extent, oak forests. The riverbeds of both rivers are typically dry during the summer. Their mouths have been widened and deepened, and a second Reservoir wall has been constructed between them.

Materials and Methods

The study draws on a comprehensive dataset collected over several years. A total of 334 fish were sampled: the majority (251 individuals) were caught in April during 2020, 2021, and 2022, followed by 12 specimens in August 2023 and 71 in-

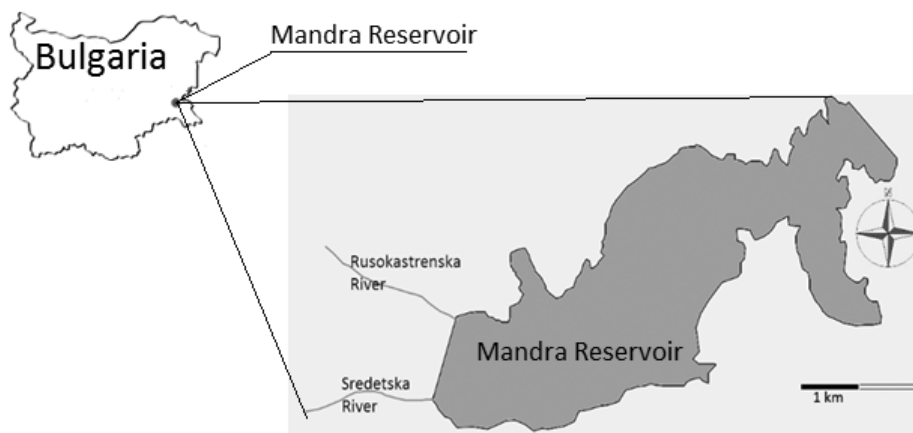


Fig. 1. Schematic map of Mandra Reservoir.

dividuals in December 2023. All fish were captured by angling in the Rusokasterenska and Sredetska rivers. Angling was carried out with 3 m telescopic poles, each equipped with a single hook. J-hooks (He et al. 2021), sizes 16–22, were used. Maggot larvae were used as bait, and a float fishing method was employed. Specimens for this study were collected from four sampling sites (Table 1).

The standard length (L) of the fish was measured to the nearest 1 mm, and the gutted weight (W) was measured to the nearest 1 g. Fish age was determined by counting the annual rings on scales. Fecundity (the number of eggs) was estimated using the gravimetric method: a 1 g subsample of gonads was taken, and the eggs (oocytes) within it were counted using a counting chamber under an Olympus CX31 microscope at 40× magnification. The sex of the specimens was determined by dissection.

The maturity stage of the gonads was assessed using coefficient b from equation (1), which describes the relationship between gonad mass and the gutted weight of the fish (Morozov 1964, Zhivkov 1985, Yankov 1988).

$$g = a + b \cdot W \quad (1)$$

where: g is gonad mass, g; W is gutted weight, g; a is proportionality coefficient; b is gonadosomatic index coefficient.

Relative fecundity was calculated as the ratio of absolute fecundity (F) to gutted weight (W) (Spanovskaya and Grigorash

1976). A second method for determining relative fecundity was also applied, based on the linear relationship between absolute fecundity and gutted weight. The coefficients a and b were calculated from equation (2), the relationship between F and W was described using a linear regression (Zotin 1961):

$$F = a + b \cdot W \quad (2)$$

where: F is absolute fecundity, number of eggs; W is gutted weight, g; a is intercept; b is slope.

The study also incorporated a method proposed by Zhivkov (1999), which allows for the comparison of fecundity across different fish populations by calculating the absolute fecundity for a standardised fish weight.

These morphometric and fecundity analyses were conducted to comprehensively assess the health and reproductive status of the studied Mandra shemaya populations.

The results provide detailed insights into the reproductive dynamics of Mandra shemaya, highlighting the influence of age, size, and weight on fecundity in the Rusokasterenska and Sredetska rivers.

Results

The age and sex composition of the Mandra shemaya sampled from the Rusokasterenska and Sredetska rivers are presented in Table 2. The sample encom-

Table 1. Sampling sites in the Mandra Reservoir tributaries.

Location	Geographic coordinates		Altitude, m a.s.l.	Month and year of sampling
	N	E		
Sredetska River	42°21'06"	27°10'07"	184	April 2020, April 2021, August 2023
Rusokasterenska River	42°25'29"	27°15'19"	388	April 2022
Rusokasterenska River	42°25'29"	27°15'19"	388	December 2023

Table 2. Age and size structure of Mandra shemaya.

Size class, mm	Age, years											
	II		III		IV		V		VI		VII	
	*	♂	*	♂	*	♂	*	♂	*	♂	*	♂
50-99	1		6	♂	1							
100-149			4		24	♂	5	♂	88	♂	16	♂
150-199					1		2		7		14	
200-250											2	
Σ	1	0	10	0	24	0	5	18	96	16	32	7
%	0	0	3	0	7	0	1.5	5.4	28	5	9.55	1.2
Sex ratio (♀:♂), %	0	100	100	100	100	78	76	61	73	66	100	100

Note: * – specimens of indeterminate sex; ♀ – females; ♂ – males; n – number of individuals; % – proportion of total sample.

passed ten distinct age groups, though individuals belonging to the 0, 1, and 10-year-old cohorts were absent.

Ten-year-old fish were absent from our samples, while nine-, eleven-, and twelve-year-old individuals were rare. The breeding cohort was predominantly composed of five-, six-, and seven-year-old specimens, which collectively constituted approximately 70 % of the sample. The length of most spawning individuals ranged from 100 to 150 mm. A single sexually mature female was recorded in the third age group. All individuals within the eleven- and twelve-year-old age groups were female.

The relationship between absolute fecundity and standard length is shown in Figure 2.

This relationship was best described by a power regression model (equation 3), which demonstrated a high degree of reliability (e.g., high R² value). The model indicates a strong positive correlation, where absolute fecundity increases significantly with standard length.

$$F = 0.000007 \cdot L^{4.1817}, R^2 = 0.98, n = 127 \tag{3}$$

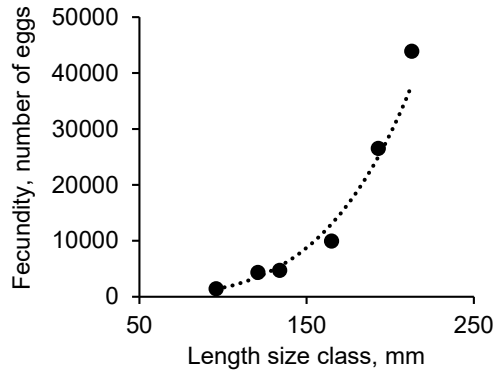


Fig. 2. Relationship between absolute fecundity and standard length of Mandra shemaya from the Rusokastrenska and Sredetska rivers.

The average absolute fecundity of the Mandra shemaya across different size classes is presented in Table 3. Average fecundity increased uniformly with

higher length classes. As the standard body length of fish increased from 100 to 200 mm, absolute fecundity increased nearly tenfold.

Table 3. Variation in the absolute fecundity (*F*) of *Alburnus mandrensis* by length class.

Length class, mm	Average length, mm	Range of fecundity, number of eggs	Average absolute fecundity, number of eggs	<i>n</i>
75–100	96	1401	1,401	1
101–125	121	980–14991	4,306	22
126–150	134	190–18952	4,689	68
151–175	165	1,602–23,460	9,915	21
176–200	193	3,232–48,450	26,505	9
201–225	213	30,549–75,565	43,886	6

As fish age increases, total fecundity also increases, as shown in Figure 3. This strong correlation is supported by a linear equation derived from the data (4), with a high degree of reliability.

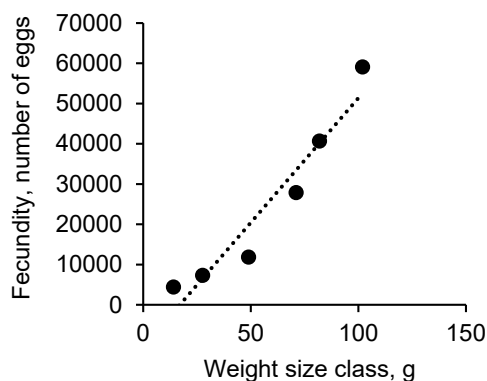


Fig. 3. Relationship between fecundity and average weight of the Mandra shemaya from the Rusokastrenska and Sredetska rivers.

$$F = 619.02 \cdot W - 10507, R^2 = 0.92, n = 127 \quad (4)$$

The absolute fecundity of Mandra shemaya at four fixed values of female fish weight is shown in Table 4. These calculations were performed using the method described by Zhivkov (1999).

The absolute fecundity of Mandra shemaya in the Rusokastrenska and Sredetska rivers increases with age (equation 5). The relationship between fecundity (*F*), number of eggs and age (*t*), years is presented in Figure 4.

$$F = 64.347 \cdot t^{2.6924}, R^2 = 0.95, n = 118 \quad (5)$$

Relative fecundity is an important indicator of reproductive potential and is widely used in comparative studies of fish species with different growth rates and body sizes. The relative fecundity of Mandra shemaya as the number of eggs produced per unit body weight is reflected

Table 4. Absolute fecundity, eggs of Mandra shemaya calculated for several standard values of weight, g.

River	W-L relation	Fifixed weight values, g				Source
		25	50	75	100	
		Absolute fecundity in different weight classes, number of eggs				
Rusokastrenska and Sredetska	$F = 619.02 \cdot W - 10,507$	4,969	20,444	35,920	51,395	Our data, 2025

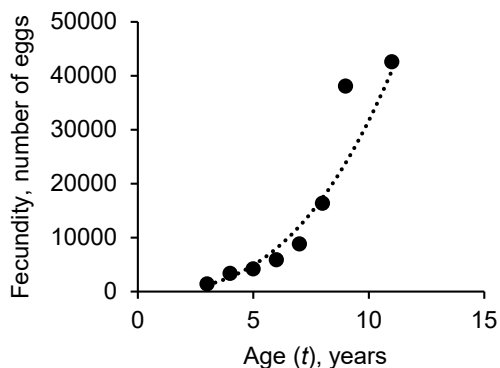


Fig. 4. Relationship between fecundity and age for *Mandra shemaya* in the Rusokastrenska and Sredetska rivers.

in Table 5.

Discussion

Studies by Kolev (2021) on *Barbus cyclolepis* (Heckel, 1837) and by Hamwi (2005) on *Squalius cephalus* (Linnaeus, 1758) showed that relative fecundity in both species is inversely proportional to linear growth. This pattern implies that younger, lighter individuals invest more intensively in reproduction relative to their body mass, while larger, older fish allocate more energy toward somatic growth and maintenance.

The sample of *Mandrenska shemaya* is characterised by a highly uneven distri-

bution of fish body weight. Approximately 70 % of the individuals fall into the first weight class (≤ 20 g; Table 5). This size class is the most representative and best characterises relative fecundity. The number of fish in the remaining weight classes is very small. These data indicate a tendency towards increasing relative fecundity with increasing body weight. However, limited sample size in the higher weight classes does not allow firm conclusions to be drawn regarding the dynamics of relative fecundity in this species.

Sex composition, age and length at first maturity

The population was predominantly composed of five-, six- and seven-years-old fish. Owing to the sampling method, young-of-the-year and one-year-old fish were absent from the sample. As the material was collected at different times of the year, it was not possible to determine the sex structure of the population. However, the data allow identification of the youngest age at sexual maturity in females and estimation of their fecundity.

Relationship between fecundity and body size

Absolute fecundity in *Mandra shemaya* increased significantly with standard length,

Table 5. Relative fecundity of *Mandra shemaya* by length class in the Rusokastrenska and Sredetska rivers.

Weight class, g	Average weight, g	Range of fecundity number of eggs	Relative fecundity, eggs g ⁻¹	n
0–20.9	13.0	12–1332	364	88
21.0–40.9	31.3	17–629	262	19
41.0–60.9	48.7	116–627	329	10
61.0–80.9	67.5	420–710	552	8
81.0–100.9	84.5	492–917	704	2

body weight, and age, a pattern consistent with many other fish species such as the Maritsa barbel (Rozdina 2009, Kolev 2021), Chub (Hamwi 2005), and Zander (Raikova-Petrova 1992). This measure ranged from 190 to 75,565 eggs, with a mean individual fecundity of 8,859 eggs ($n = 127$; length range: 65–185 mm). The maximum recorded fecundity (75,565 eggs) was from a nine-year-old female measuring 174 mm and weighing 82 g. The minimum (190 eggs) was from a six-year-old specimen of 107 mm and 12 g.

A strong positive correlation was observed between fecundity and both standard length (equation 5) and body mass. For instance, fecundity increased approximately tenfold as gutted weight increased from 25 g to 100 g (Table 4). This supports the assertion that weight gain is a primary factor driving increased fecundity (Nikolsky 1965, 1974; Zhivkov 1999). This trend is likely linked to ontogenetic shifts, where older, larger fish have access to a broader and more enriched nutritional spectrum, leading to better somatic condition and greater energy allocation to reproduction.

The maximum absolute fecundity of the Mandra shemaya is three times higher than the combined range of 15,000–23,000 eggs reported for three *Alburnus* species (*A. sarmaticus*, *A. schischkovi*, and *A. mandrensis*) (Botev and Peshev 1985). However, the average fecundity of the Mandra shemaya is below the maximum values reported in the literature (Table 3). Future studies on reproductive parameters are likely to reveal differences among these three species, as they inhabit water bodies with distinct hydrochemical characteristics. Additionally, the climate of northern Bulgaria, where the Danube River supports *A. sarmaticus*, differs significantly from that of the Mandra Reservoir region.

Conclusions

This study provides the first comprehensive dataset on the reproductive biology of the Mandra shemaya in the Rusokastrenska and Sredetska rivers. The results indicate that females reach sexual maturity by their third year. During the breeding season, the observed sex ratio was 2.6:1 (female:male). Absolute fecundity exhibited substantial individual variation, ranging from 190 to 75,565 eggs, with a mean of 8,859 eggs, while mean relative fecundity was 351 eggs per gram.

The data confirm that absolute fecundity is significantly influenced by fish size and age, increasing with standard length, gutted weight, and age until a peak in nine-year-old individuals. This set of reproductive parameter estimates provides a scientific foundation for assessing the population status and reproductive potential of the Mandra shemaya. The results are integral to informing effective conservation strategies and ensuring the sustainable management of this protected Bulgarian endemic.

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