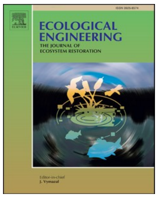
Ecological Engineering 217 (2025) 107662

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng



The potential of native tree species for forest restoration in the Central Congo Basin

Brice Yannick Djiofack [a,b,c,*], Nils Bourland [d], Hans Beeckman [a,c], Paolo Omar Cerutti [e], Collins Dzernyuy Fai [e], Martin Van Hulle [f], Mathilde Pierson [f], Jules Mayaux [f], Nestor Kashikija Luambua [c], Donatien Musepena [c,g], Basile Luse Belanganayi [a,c,h], Félix Laurent [a,b,c], Bhely Angoboy Ilondea [g,i], Jan Van den Bulcke [b], Wannes Hubau [a,b,c]

[a] *Royal Museum for Central Africa, Service of Wood Biology, Leuvensesteenweg 13, B-3080 Tervuren, Belgium*
[b] *Ghent University, Faculty of Bioscience Engineering, Department of Environment, Laboratory of Wood Technology (UGent-Woodlab), Coupure Links 653, B9000 Gent, Belgium*
[c] *Wood Laboratory of Yangambi, Yangambi, Congo*
[d] *Cerac.be, Avenue Galilée, 5/2, BE-1210 Brussels, Belgium*
[e] *Center for International Forestry Research (CIFOR), Kisangani, Congo*
[f] *Resources & Synergies Development Pte Ltd., Raffles Quay 16, #33-03 Hong Leong Building, Singapore*
[g] *Institut National pour l'Études et la Recherche Agronomiques (INERA), Kinshasa, Congo*
[h] *Forest Is Life, TERRA Teaching and Research Centre, Gembloux Agro Bio-Tech, University of Liège, Passage des Déportés 2, Gembloux, Belgium*
[i] *Université Pédagogique Nationale, BP 8815 Kinshasa, Ngaliema, Congo*

ARTICLE INFO

Keywords:
Forest restoration
Large-scale tree-plantation
Native species
Exotic species
Growth performance
Carbon sequestration
Yangambi landscape
Climate change

ABSTRACT

Decades of deforestation and unsustainable land use have created extensive areas of degraded and deforested land across the central Congo Basin, contributing substantially to climate change and biodiversity loss. Recently, nature-based solutions have gained increasing interest, particularly those focusing on forest restoration for long-term carbon sequestration and additional societal benefits for human well-being. Thus, forest restoration, especially with native species, offers a viable pathway to address environmental and social challenges while supporting local communities. However, both technical and scientific knowledge about many native species' performance in large-scale plantations, which could serve the current and future needs of central African countries, is currently lacking. To address these knowledge gaps, we established an experimental plantation in Yangambi, Democratic Republic of the Congo, to evaluate the potential of native tree species in comparison with the fast-growing exotic species *Acacia auriculiformis,* which is often planted in monoculture at a large-scale in the central Congo Basin. From 37 promising native species initially selected, the seeds of 19 were successfully harvested from the natural forest. Among these, 16 species yielded sufficient seedlings in the nursery and were planted in the field. After five years, five native species (*Pachyelasma tessmannii, Piptadeniastrum africanum, Irvingia smithii, Ongokea gore,* and *Canarium schweinfurthii*) demonstrated growth, survival, and carbon sequestration performance comparable to *Acacia auriculiformis*. This illustrates that local tree species are promising alternatives for exotic species. Nevertheless, further research is necessary to optimize the large-scale production of native seedlings, including improving seed conservation and nursery techniques. Drawing on the ongoing forest restoration initiatives in Yangambi, we emphasize the importance of integrating local knowledge and actively involving local communities to ensure the successful implementation and long-term sustainability of tree-planting efforts, benefiting both nature and human well-being.

---

* Corresponding author at: Royal Museum for Central Africa, Service of Wood Biology, Leuvensesteenweg 13, B-3080 Tervuren, Belgium.
E-mail addresses: briceyannick.djiofack@ugent.be (B.Y. Djiofack), nils.bourland@cerac.belgium.be (N. Bourland), hans.beeckman@africamuseum.be (H. Beeckman), P.Cerutti@cifor-icraf.org (P.O. Cerutti), c.fai@cifor-icraf.org (C.D. Fai), b.luse@doct.uliege.be (B.L. Belanganayi), Felix.Laurent@africamuseum.be (F. Laurent), jan.vandenbulcke@ugent.be (J. Van den Bulcke), wannes.hubau@ugent.be (W. Hubau).

https://doi.org/10.1016/j.ecoleng.2025.107662
Received 4 November 2024; Received in revised form 3 April 2025; Accepted 18 April 2025

1. Introduction

In recent years, central African countries have issued an impressive number of official pledges, policies and regulations (e.g. the recent CMR new Forest Law of July 2024, or countries' commitment to the Bonn Challenge; Lewis et al., 2019; Parr et al., 2024) to safeguard forest ecosystems. These initiatives aim to reduce biodiversity loss and support climate change mitigation (Sullivan et al., 2017; Lee et al., 2021), reflecting a recognition that integrated solutions are required to face the pressing challenges ahead(Seddon et al., 2020b). Among these, nature-based solutions (NBS) have recently gained increasing traction as one such integrated approach to address climate emergency and biodiversity loss while supporting sustainable development goals (Seddon et al., 2020a; Di Sacco et al., 2021). The International Union for the Conservation of Nature (IUCN) defines NBS as "actions to protect, sustainably manage, and restore natural or modified ecosystems that address societal challenges effectively and adaptively, simultaneously providing human well-being and biodiversity benefits" (Cohen-Shacham et al., 2016).

The intrinsic diversity of central African forests represent a key feature of the success of NBS in this region (Malhi et al., 2013; Abernethy et al., 2016). In contrast with currently proposed technological solutions (e.g. carbon dioxide removal (CDR) (Lefebvre et al., 2021; Callow, 2021); bioenergy with carbon capture and storage (BECCS)(Girardin et al., 2021; Callow, 2021), and others), NBS has the potential to tackle both climate mitigation and adaptation challenges at relatively low cost while delivering multiple additional benefits for people and nature (Seddon et al., 2019; Folkard-Tapp and Cavan, 2021). The mitigation potential of terrestrial ecosystems comes from three main pillars of the NBS: (i) ecosystem conservation, which aims to maintain their complexity and functions and thus reduce carbon release; this includes efforts to reduce deforestation; (ii) improved land management, to provide cleaner air and water, for timber, crops and grazing, to reduce carbon emissions, as well as to sequester more carbon; and (iii) restoration of ecosystems, such as wetlands and degraded lands, so that they increase their carbon sequestration potential (Zhang et al., 2020; Girardin et al., 2021; Di Sacco et al., 2021). Interventions involving NBS should also adhere to four high-level principles (Seddon et al., 2021). First, NBS should not be an alternative to decarbonization. Second, they need to include a wide range of ecosystems. Third, they should be designed in partnership with local communities, respecting indigenous and other rights. Fourth, they must support biodiversity, from the genetic to the ecosystem level (Seddon et al., 2019, 2021; Girardin et al., 2021). This paper focuses on the third pillar above, i.e., the restoration of ecosystems, with a special focus on the tropical forests of central Africa.

Over recent decades, forest restoration has been increasingly promoted on regional, national, and global scales as a primary NBS approach (Lamb et al., 2005; Zhang et al., 2020; Brancalion and Holl, 2020). It is defined as a planned process aimed at regaining (previously lost or degraded) ecological integrity and enhancing human well-being on deforested or degraded lands (Di Sacco et al., 2021). This approach helps to balance human needs and biodiversity by restoring a range of forest functions within a defined area, while recognizing and managing the inherent trade-offs (Lewis et al., 2019; Parr et al., 2024). For example, fire exclusion in an anthropogenic savanna over the long-term leads to the rapid disappearance of savanna specialist tree species but results in more tree biodiversity and greater carbon stock potential in the longer run (Deklerck et al., 2019a; Djiofack et al., 2024a, 2024b). However, multiple efforts by multilateral organizations, nongovernmental organizations, and the private sector have been launched to achieve large-scale restoration targets (Brancalion and Holl, 2020). Within Africa, 30 countries have committed to embracing the challenge of restoring significant portions of their degraded or lost forests by participating in the African Forest Landscape Restoration Initiative (AFR100; https://afr100.org/) (Vinceti et al., 2020; Parr et al., 2024). The AFR100 commitments adhere to international targets and agreements, such as the Bonn Challenge, and the African Union Agenda 2063 (Girardin et al., 2021; Parr et al., 2024), with an overall objective to restore 100 million hectares of land in Africa by 2030 (Brancalion et al., 2019; Parr et al., 2024). The restoration of intact forests in tropical and subtropical lands committed for forest restoration under the Bonn Challenge or national restoration schemes is predicted to store an additional 42 Gt of carbon by 2100 across 350 Mha (Lewis et al., 2019). About a quarter of this additional carbon would be stored in central Africa (Lewis et al., 2019), home to the vast majority of the globally suitable and available land for forest restoration initiatives (Brancalion et al., 2019; Lewis et al., 2019; Bastin et al., 2019; Djiofack et al., 2024a). Reaching these ambitious restoration commitments planned for the immediate future is more likely to be achieved through large-scale tree-planting.

Tree plantations have been established across tropical regions in the past decade for many reasons (Holl and Brancalion, 2020), including as part of the countries' restoration commitments (Brancalion and Holl, 2020; Seddon et al., 2021). Knowledge about exact areas and, most importantly, about the status and management conditions of such plantations in central Africa and beyond remain, however, scattered and incomplete, mainly due to poor national data-gathering and analysis conditions (Hall, 2008; Ndongo et al., 2009; De Ridder et al., 2010; Ngueguim et al., 2015). However, there seems to be a tendency toward monocultural plantations with fast-growing exotic species (Zhang et al., 2020). For example, in the Democratic Republic of the Congo (RD Congo), while deforestation and forest degradation impact about 0.5 million hectares each year (Potapov et al., 2012; Tyukavina et al., 2018; Kipute et al., 2023) – an effect larger than any other country in central Africa – plantations of fast-growing exotic species, notably to supply the country's wood-energy needs, remain poorly documented but reportedly focused on *Acacia auriculiformis, Eucalyptus* spp., and a few other species (Schure et al., 2015; Proces et al., 2018; Kasekete et al., 2022). Similar trends occur in other central African countries (Marien and Mallet, 2004; Palou et al., 2010; Bertaux et al., 2021). The vast majority of these plantations, for which data are indeed available, have not yet been the subject of scientific studies, especially regarding growth performances and the long-term carbon sequestration potential, socio-economic profitability, or the sustainability of their management (Schure et al., 2015; Kasekete et al., 2022). As monocultures are easily planted and are assumed to allow for maximizing biomass production and being cost-efficient, they have become a dominant global practice within major restoration initiatives (Liu et al., 2018; Chazdon and Brancalion, 2019; Holl and Brancalion, 2020; Zhu et al., 2023), though increasingly criticized, because they do not meet the fundamentals of NBS, notably biodiversity and human well-being (Holl and Brancalion, 2020; Seddon et al., 2021; Feng et al., 2022), and resilience to perturbations, which can compromise their long-term carbon storage ability, especially under future climate conditions (Bennett et al., 2021; Warner et al., 2023). Conversely, a growing body of evidence shows that such functional resilience is more efficient in multispecies tree plantations, especially when mixed or entirely based on native species (Callaway, 2007; Brancalion and Holl, 2020; Feng et al., 2022). Yet, both technical and scientific knowledge about many native species' performance in large-scale plantations, which could serve the current and future needs of central African countries, is currently lacking. More specifically, one of the primary knowledge gaps hindering the use of native species in large-scale tree-planting initiatives in central Africa is the lack of comprehensive data on their reproductive phenology (Couralet, 2010; Ilondea et al., 2019; Kearsley et al., 2024). Specifically, detailed information on the fruiting periods of native species is scarce, with precise data available for only a limited number of species in this region (Couralet, 2010; Meunier et al., 2015; Ilondea et al., 2019).

Therefore, to maintain healthy, resilient ecosystems that can continue to deliver benefits to people over the long-term, there is an urgent need to invest in finding well-performing native species for large-scale plantation initiatives in central Africa.

To this end, over the period from 2017 to 2023, we set up an experimental plantation starting from an initial set of 37 native tree species in the Yangambi landscape in the DR Congo, in the heart of the central African rainforest. We used this experiment – conducted both at nursery and plantation stages – to assess survival and growth performances, and the carbon sequestration potential of native species vs. the widely used exotic species *A. auriculiformis*, addressing four specific research questions:

(i) Which native species are suitable for large-scale tree-planting initiatives according to local foresters and considering the availability of seeds from the natural forest?
(ii) What is the success of the germination of the seeds of these species in the nursery?
(iii) What is the survival and growth performance of the seedlings once transplanted in the field?
(iv) How fast do plantations of these native species sequester carbon?

Therefore, the study defines performance as the growth, survival and overall health of tree species in a specific environment or under specific management practices. Performance is typically determined through metrics such as height and diameter growth, stem density (tree ha^{-1}), biomass accumulation and mortality rates over time (Piotto et al., 2003; Wishnie et al., 2007; Calvo-Alvarado et al., 2007; Fayolle et al., 2015; González-Tokman et al., 2018; Singh and Kumar, 2022). Performance assessments often consider the influence of various factors, including climatic conditions, soil characteristics and competition from other species (Callaway Mng'omba et al., 2007; Wishnie et al., 2007; González-Tokman et al., 2018), aiming to determine how effectively a species can thrive and contribute to reforestation or ecological restoration efforts (Singh and Kumar, 2022).

The next section will present the materials and methods used to set up and assess species performance in our experiment. The results will then be presented and discussed, and the last section will conclude.

2. Materials and methods

2.1. Study site

This study was conducted within the buffer zone of the UNESCO Man and Biosphere (MAB) reserve of Yangambi, approximately 100 km west of the city of Kisangani, in the Tshopo province of the Democratic Republic of the Congo (RD Congo) (0°45′28.3"N; 24°29′05.2″E) (Fig. 1). The Yangambi reserve covers an area of approximately 230,000 ha (Ebuy et al., 2011). Its vegetation consists of a semi-deciduous tropical rainforest with fragments of evergreen rainforest, transition forest, agricultural lands, fallow lands, and swamp forest (Kearsley et al., 2013; Van de Perre et al., 2018). According to the Köppen classification, the Yangambi region has an *Af*-type tropical rainforest climate, with an annual rainfall of 1837 mm, characterized by two dry seasons (December–March and June–July) alternating with two rainy seasons (April–May and August–November), and a consistent annual temperature of 25.1 °C (Kasongo et al., 2023; van Vliet et al., 2023). Soils in the Yangambi plateau are ferralsols primarily formed from aeolian sediments, composed mostly of quartz sand, kaolinite clay, and hydrated iron oxides (Kearsley et al., 2013).

2.2. Selection of initial focal species and seed harvest

The Yangambi research station has a long and illustrious history (Keay, 1956). During the colonial period, the focus of forestry research

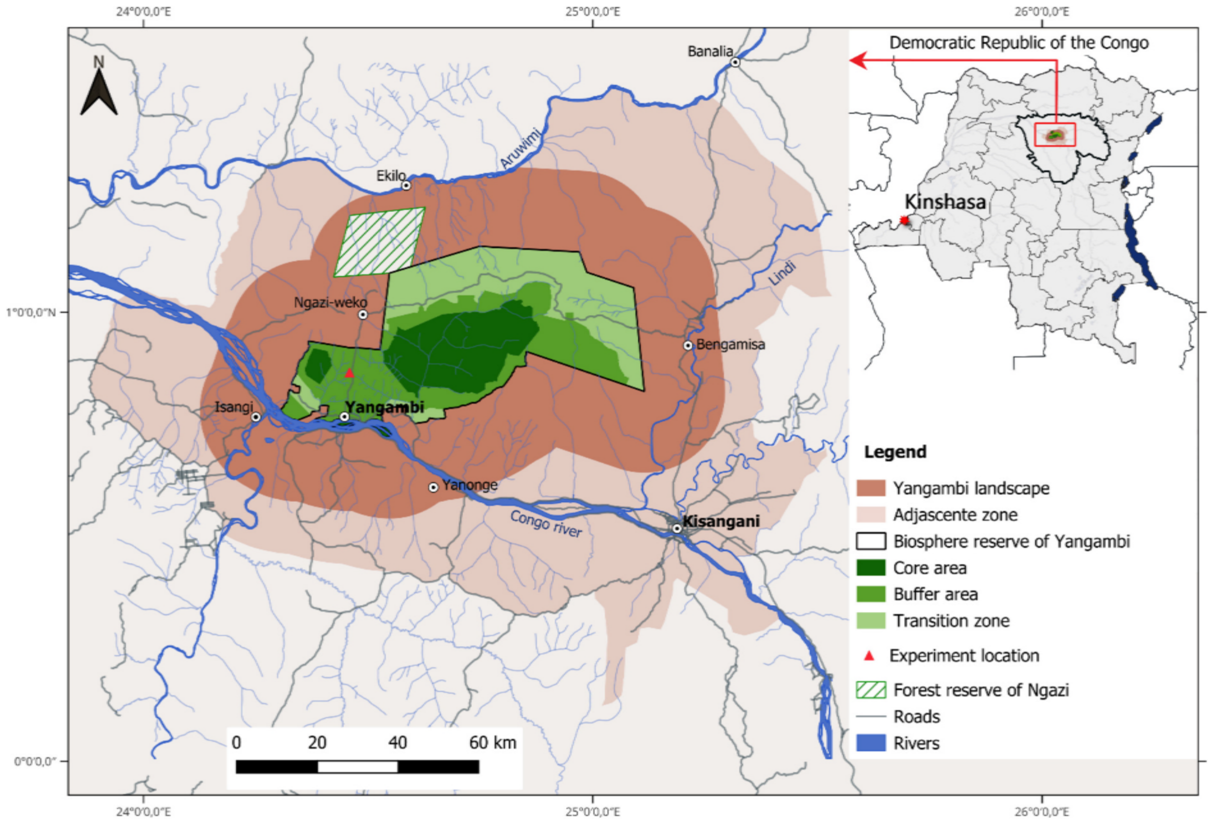


Fig. 1. Location of the study area. Maps showing: The limits of the Yangambi landscape with its adjacent area inside the red square within the DR Congo; the location of our plantations experiment (red triangle) within the buffer zone in the MAB reserve of Yangambi. Map lines delineate study areas and do not necessarily depict accepted national boundaries. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in Yangambi was particularly on silviculture and the promotion of commercially valuable timber species (Donis, 1956). The silvicultural experiments primarily aimed at eliminating competitive vegetation around target light-demanding species to stimulate their growth, incorporating both monoculture and mixed species plantations with up to six different native species. The historical plantation in Yangambi covered over 50 ha of experimental plots (Bauters et al., 2015). These plantations were rigorously monitored until the independence of Congo in 1960, an event that led to the loss of significant archives on the research experiments at Yangambi (Kearsley, 2015). Since then, the experimental sites have been under the responsibility of the *Institut national pour l'Etude et la Recherche Agronomiques* (INERA) (Ilondea et al., 2020). However, the loss of information from the monitoring period (up to 1960) and the scarcity of information from the end of the colonial period to the present day make their scientific evaluation and use complex. Hence, there is a dire need for new experimental plantations to increase interest in promoting native species in the large-scale tree-planting initiative in the Yangambi landscape (Fig. 1), as well as to generate knowledge which can again be used to support similar efforts across central Africa. To select a broad list of potential native species for this experiment, we used several sources. First, we used the available results from historical plantations to identify which species performed well (Ebuy et al., 2011; Bauters et al., 2015). We then collected local information through individual interviews with a total of 3064 heads of household representatives from all seven neighborhoods of Yangambi (CIFOR, 2024). We completed the list with information from the long-term experience of local scientists from the Forestry division of INERA-Yangambi and the Yangambi wood biology laboratory. Once the first tentative list of potential useful native species had been established, seeds from these proposed species were collected from the Yangambi Man and Biosphere (MAB) reserve (Data S1; Fig. 1) between August and December 2017. The seeds of *A. auriculiformis* were instead sourced from the Bateke Plateau in DR Congo (Schure et al., 2015; Proces et al., 2018).

In this study, we define performance as the growth, survival and overall health of tree species at different growth stages in a specific environment or under specific management practices. It is typically determined through metrics such as height growth, diameter increment, biomass accumulation and mortality rates over time. Performance assessments often consider the influence of various factors, including climatic conditions, soil characteristics and competition from other species (Wishnie et al., 2007; González-Tokman et al., 2018), aiming to determine how effectively a species can thrive and contribute to reforestation or ecological restoration efforts (Singh and Kumar, 2022).

2.3. Performance at the nursery stage

When seeds were found, they were brought to the nursery at the INERA-Yangambi research station for germination. Seedlings spent 12 months in the nursery before being transplanted. The seeds of *A. auriculiformis* spent four months in the same nursery alongside the native species. Not all species have the same ability to successfully germinate or thrive in the nursery because of the influence of many possible limitations inherent to each species or group of species (Daïnou et al., 2021). These limitations are quantified through the use of a 'nursery score' calculated using seed characteristics derived from the literature (Table S1). This nursery score serves as an indicator of a species' ability to successfully germinate and thrive in a nursery. The nursery score ranges from 5 to 19 and is composed of the sum of five sub-scores given to germination rate, seed conservation duration, seed dormancy, nursing time and number of seeds per kg (Table 1, Table S1). The lower the nursery score, the easier the species germinates and thrives in a nursery. Based on the species-specific nursery score (Table S1), each species was treated in the nursery using a customized protocol. Specifically, two different germination procedures were used to facilitate seed germination: In the case of recalcitrant seeds, the protocol required immediate planting after harvest in the forest. Recalcitrant seeds germinate rapidly and cannot withstand drying, which can significantly reduce their germination rate (Turner, 2004; Daïnou et al., 2021); In the case of orthodox seeds, they can be stored in the dormant state for relatively longer periods, usually at relatively low seed water content (Turner, 2004; Daïnou et al., 2021). For the seeds successfully collected from the Yangambi MAB reserve, we used either cold water, hot water, boiling water or manual scarification to break dormancy (Daïnou et al., 2021). The seeds germinated and thrived in the nursery without any special control conditions or measurable environmental parameters.

2.4. Planting

After 12 months in the nursery, all surviving seedlings were planted in November 2018. The planting sites were fallows located within the INERA-Yangambi research station. The planting design was a systematic single-species plot with 2 m × 2 m-grid spacing between individual seedlings, which resulted in a stem density of 2500 stems ha^{-1} just after planting (Zemp et al., 2019). The location of each single-species plot within the planting site was randomized (Calvo-Alvarado et al., 2007; Zemp et al., 2019). The total planted surface was determined by the available number of seedlings for each species (Table 2). At the time of planting, seedling height was around 60 cm for the native species and 40 cm for the exotic reference species *A. auriculiformis*, with a basal diameter of 0.5 cm for both categories.

2.5. Survival performance

Survival performance was quantified in the form of mortality rate, which is a fundamental descriptor of tropical forest tree dynamics (Lewis et al., 2004; Picard and Gourlet-Fleury, 2008). In this study, mortality was defined as death or disappearance (Picard and Gourlet-Fleury, 2008). We recorded three different states of seedling death: (i) a standing stem, (ii) a broken stem, and (iii) a vanished stem (stem not found and assumed to have rotten entirely) (Condit et al., 1995).

We first calculated stem density (in stems ha^{-1}) as a proxy for tree mortality. Stem density was calculated as the total number of alive stems recorded during the census of August–September 2023 divided by the planted plot size (in ha).

We then calculated the commonly used mortality rate (λ, unitless): $\lambda = (ln(N_0) - ln(N_t))/t$ (Eq. 1), where N_0 is the number of initial planted seedlings, N_t is the number of surviving trees after t years, and $ln(N)$ is the natural logarithm of N (Condit et al., 1995; Ligot et al., 2022).

We then used the *qbeta* function in R to calculate the lower and upper bounds of the confidence interval for the proportion of surviving trees (N_t) out of the initial planting of seedlings (N_0). This method uses the binomial distribution to model the probability of tree survival, while the beta distribution accounts for uncertainty in this probability. The beta distribution allows the model to adjust its estimates as new survival data is observed. The parameters of the Beta distribution are determined based on the observed data, with, $\alpha = N_0 - N_t + 1$ and $\beta = N_t + 1$, and the 2.5 % and 97.5 % quantiles of this distribution are used to estimate the 95 % credible interval for the proportion of surviving trees (Condit et al., 1995; Ligot et al., 2022).

2.6. Growth performance

After 5 years of growth (2017/2018 to 2023), we conducted dendrometric measurements on all plantations between August and September 2023. In each plantation plot of our studied species, all live stems were tagged. Each stem's basal diameter (i.e., diameter at 10 cm above the stem base) was measured using a diameter tape. We used a caliper for stems with basal diameter below 5 cm. The total height of each tree (i.e., height from the stem base to the highest living apical bud) was measured using a telescopic height measuring stick (Doucet et al., 2016; Wishnie et al., 2007; Zemp et al., 2019). For trees that were more

Table 1

Harvest success of 37 initially suggested native species for large-scale plantations in the Yangambi landscape. Guild traits consist of short-lived pioneers (SLP), long-lived pioneers (LLP), non-pioneer light demanders (NPLD), and shade-tolerant species (ST)(Luambua et al., 2021). Leaf phenology indicates leaf shedding behavior: deciduous (De) or evergreen (Ev) species. The average annual diameter increment (ADI, cm yr^{-1}) is obtained from various literature sources (references are given below the table). Wood density (WD, in g cm^3) is from the DRYAD repository. Dmax (in m) is the maximum diameter and Hmax (in m) is the maximum height from various literature sources. The literature nursery score combines various criteria and ranges from 5 to 19, with 5 being the best score (Table S1). Seed harvest success in the Yangambi landscape is indicated as “v” for species from which seeds were effectively found and collected in the forest in quantities that were sufficient to initiate nursery activities (“-“indicates that seeds were not found in sufficient numbers). A total of 19 native species were harvested successfully (their nursery success is quantified in Table 2).

Species	Family	Guild[3,6]	Leaf phenology 2,3,8	ADI 1,5,10,12	WD[4]	Dispersal mechanism[1,2,3,6,13]	Dmax[1,2,7,8,9]	Hmax[1,2,7,8,9]	Literature nursery score[1,2,9,14]	Harvest success in YBI	Main use[1,2,3,7]
Acacia auriculiformis A. Cunn. ex Benth. Φ	*Fabaceae*	*NPLD*	Ev	*1.23*	0.68	Unassisted	0.5	25	6	*	Charcoal, fuel wood
Afzelia bipindensis Harms	*Fabaceae*	*NPLD*	Ev	0.16	*0.73*	Terrestrial animals	1.5	*40*	7	–	Timber
Albizia adianthifolia (Schumach.) W. Wight	*Fabaceae*	*LLP*	Ev	*0.66*	*0.51*	Wind	0.7	*25*	6	–	Timber
Albizia adianthifolia (Schumach.) W. Wight	*Fabaceae*	*LLP*	Ev	0,45	*0.50*	Wind	0.8	*30*	6	–	Timber
Albizia laurentii De Wild.	*Fabaceae*	*NA*	Ev	*NA*	0.65	Wind	0.4	25	6	–	Timber
Albizia lebbeck (L.) Benth.	*Fabaceae*	NPLD	Ev	*NA*	0.54	Wind	2	25	6	–	Multi-purpose
Anonidium mannii (Oliv.) Engl. & Diels	*Annonaceae*	*ST*	Ev	*NA*	*0.29*	Terrestrial animals	0.80	30	7	v	Medicinal, fruits
Blighia welwitschii (Hiern) Radlk.	*Sapindaceae*	*ST*	*De*	*NA*	*0.79*	Terrestrial animals	1	40	NA	v	Timber
Brachystegia laurentii (De Wild.) Louis ex Hoyle	*Fabaceae*	*ST*	*Ev*	*NA*	*0.50*	Unassisted	1.5	45	NA	–	Timber
Canarium schweinfurthii Engl.	*Burseraceae*	*LLP*	De	0.41	*0.41*	Terrestrial animals	2	50	8	v	Multi-purpose
Celtis tessmannii Rendle	*Cannabaceae*	*NPLD*	*Ev*	*NA*	*0.65*	Terrestrial animals	1.5	40	10	–	Medicinal, fuel wood
Entandrophragma utile (Dawe & Sprague) Sprague	*Meliaceae*	*NPLD*	*De*	*0.39*	*0.54*	Wind	2	60	9	–	High-value timber
Erythrophleum suaveolens (Guill. & Perr.) Brenan	*Fabaceae*	*LLP*	*Ev*	0.36	*0.87*	Unassisted	1.5	*40*	10	v	Timber, bears edible caterpillars
Funtumia africana (Benth.) Stapf	*Apocynaceae*	*NPLD*	*NA*	*NA*	0.42	Wind	0.5	30	9	–	Timber
Gilbertiodendron dewevrei (De Wild.) J. Léonard	*Fabaceae*	*ST*	*Ev*	*NA*	*0.71*	Unassisted	2	40	11	v	Timber
Mitragyna stipulosa (DC.) Kuntze	*Rubiaceae*	*LLP*	*NA*	*NA*	*0.48*	Wind	1	35	NA	–	Charcoal
Hymenocardia ulmoides Oliv.	*Phyllanthaceae*	*LLP*	*Ev*	*NA*	*0.67*	Wind	0.6	30	NA	–	Timber
Irvingia smithii Hook. f.	*Irvingiaceae*	*NA*	*Ev*	*NA*	0.92	Terrestrial animals	1	30	8	v	NA
Klainedoxa gabonensis Pierre ex Engl.	*Irvingiaceae*	*LLP*	*Ev*	*NA*	*0.93*	Terrestrial animals	1	50	14	–	Multiple
Milicia excelsa (Welw.) C.C. Berg	*Moraceae*	*LLP*	*De*	0.57	*0.58*	Flying animals	1.5	*55*	8	–	High-value timber
Millettia laurentii De Wild.	*Fabaceae*	*NA*	*Ev*	*NA*	0.74	Unassisted	0.8	*30*	9	–	Timber, bears edible caterpillars
Ongokea gore (Hua) Pierre	*Olacaceae*	*ST*	*Ev*	*NA*	*0.75*	Terrestrial animals	1.25	50	8	v	Timber
Pachyelasma tessmannii (Harms) Harms	*Fabaceae*	*NPLD*	*Ev*	*NA*	*0.74*	Unassisted	2.5	60	11	v	Timber
Paramacrolobium coeruleum (Taub.) J. Léonard	*Fabaceae*	*ST*	*Ev*	*NA*	*0.68*	Terrestrial animals	0.6	*40*	8	v	Timber
Pentaclethra macrophylla Benth.	*Fabaceae*	*NPLD*	*Ev*	*NA*	*0.84*	Terrestrial animals	1	*30*	8	v	Timber and medicinal
Pericopsis elata (Harms) Meeuwen	*Fabaceae*	*LLP*	*De*	0.64	*0.64*	Wind	1.3	*40*	10	–	High-value timber
Petersianthus macrocarpus (P. Beauv.) Liben	*Lecythidaceae*	*NPLD*	*Ev*	*NA*	*0.68*	Wind	1.3	*40*	9	–	Timber, bears edible caterpillars
Piptadeniastrum africanum (Hook. f.) Brenan	*Fabaceae*	*NPLD*	*Ev*	0.75	*0.61*	Wind	2	*60*	9	v	Timber
Greenwayodendron suaveolens (Engl. & Diels) Verdc.	*Annonaceae*	*ST*	*Ev*	*NA*	*0.70*	Terrestrial animals	0.8	*35*	7	–	Multi-purpose
Prioria balsamifera (Vermoesen) Breteler	*Fabaceae*	*NPLD*	*Ev*	0,56	*0.41*	Wind	1.5	*55*	10	–	Timber

(*continued on next page*)

Table 1 (*continued*)

Species	Family	Guild[3,6]	Leaf phenology 2,3,8	ADI 1,5,10,12	WD[4]	Dispersal mechanism[1,2,3,6,13]	Dmax[1,2,7,8,9]	Hmax[1,2,7,8,9]	Literature nursery score[1,2,9,14]	Harvest success in YBI	Main use[1,2,3,7]
Pterocarpus soyauxii Taub.	*Fabaceae*	*NPLD*	*De*	0.61	*0.66*	Wind	1.5	*50*	9	v	Timber
Pycnanthus angolensis (Welw.) Warb.	*Myristicaceae*	*NPLD*	*Ev*	0.62	*0.41*	Terrestrial animals	1.5	35	9	v	Timber
Ricinodendron heudelotii (Baill.) Pierre ex Heckel	*Euphorbiaceae*	*LLP*	*De*	*NA*	*0.21*	Terrestrial animals	1.5	*40*	11	v	Medicinal, bears edible caterpillars
Scorodophloeus zenkeri Harms	*Fabaceae*	*ST*	*Ev*	*NA*	*0.72*	Unassisted	0.8	*40*	10	v	Medicinal, fruits
Terminalia ivorensis A. Chev.	*Combretaceae*	*NPLD*	*Ev*	*NA*	0.45	Unassisted	1.2	45	11	v	Timber
Treculia africana Decne.	*Moraceae*	*ST*	*De*	*NA*	*0.54*	Terrestrial animals	1	35	7	v	Medicinal/fruits
Tridesmostemon omphalocarpoides Engl.	*Sapotaceae*	*NPLD*	*NA*	*NA*	*0.74*	NA	0.7	35	NA	v	Timber
Trilepisium madagascariense DC.	*Moraceae*	*NPLD*	*Ev*	*NA*	*0.50*	Terrestrial animals	0.6	*40*	9	v	Multi-purpose

Φ Exotic reference species; 1 https://prota.prota4u.org, 2 (Meunier et al., 2015), 3 (Doucet et al., 2016), 4 (Zanne et al., 2009), 5 (Proces et al., 2018), 6 (Luambua et al., 2021), 7 (Doucet et al., 2022), 8 https://africanplantdatabase.ch/en, 9 (ICRAF, 2009), 10 (Nasi and Détienne, 2000), 11 http://www.tropicaltimber.info/fr/, 12 (Poulsen et al., 2001), 13 https://plants.jstor.org/, 14 (Daïnou et al., 2021).

Table 2
Nursery success of 19 harvested species in the Yangambi landscape. Number of planted seedlings and planted area (in ha). A total of 16 native species were raised successfully in the nursery and planted on fallow land in the Yangambi landscape in November 2018 using a spacing of 2 m × 2 m (growth and survival performance results are given in Table 3 and Table 4 below).

Species	Nursery success (nbr of seedlings)	Planted area (in ha)
Acacia auriculiformis Φ	5000	2.00
Anonidium mannii	1723	0.70
Blighia welwitschia	1085	0.43
Canarium schweinfurthii	1360	0.54
Erythrophleum suaveolens	57	0.02
Gilbertiodendron dewevrei	2035	0.81
Irvingia smithii	290	0.12
Ongokea gore	330	0.13
Pachyelasma tessmannii	2872	1.15
Paramacrolobium coeruleum	0	–
Petersianthus macrocarpus	0	–
Piptadeniastrum africanum	1112	0.44
Pterocarpus soyauxii	1285	0.51
Pycnanthus angolensis	330	0.12
Ricinodendron heudelotii	0	–
Scorodophloeus zenkeri	4880	1.95
Terminalia ivorensis	500	0.20
Treculia Africana	2042	0.82
Trilepisium madagascariense	1410	0.56
Tridesmostemon omphalocarpoides	1263	0.51

Φ Exotic reference species.

than 8 m high, we used a Nikon Laser Rangefinder Forestry Pro hypsometer (Kafuti et al., 2022).

To quantify species growth performance of a target species, we calculated the absolute growth rate (*AGR*) in height (height increment, in cm yr^{-1}), and the absolute growth rate in basal diameter (diameter increment, in cm yr^{-1}): $AGR = (\delta_t - \delta_0)/t$ (Eq. 2); with δ_t the height or diameter value at time *t*, and δ_0 the initial value of the planted seedlings (Fayolle et al., 2015; Zemp et al., 2019). We also calculated the relative growth rate in height (RGRh, in m m^{-1} yr^{-1}), and the relative growth rate in basal diameter (RGRd in cm cm^{-1} yr^{-1}) of each living stem over the period (t): $RGR = (ln(\delta_t) - ln(\delta_0))/t$ (Eq. 3).

2.7. Wood volume and carbon sequestration performance

We calculated the wood volume index (VI) for each individual tree as: $VI = \left(0.5\pi(BD)^2\right).(4H_t)^{-1}$ (Eq. 4), where DB is basal diameter (cm) and H_t is the total tree height (m) (Wishnie et al. Mng'omba et al., 2007). Plot-level VI (in m^3 ha^{-1}) was then obtained by summing VI across all individuals and dividing by the plot size (in ha). Given the young age of our experiment, we consider this metric to be a proxy for true tree volume estimate, as it does not consider a species-specific form factor (Wishnie et al., 2007).

Aboveground biomass (AGB, in Mg $stem^{-1}$) of each stem was estimated using an allometric equation for moist tropical forest (Chave et al., 2014): $AGB = \left(0.0673*\left(\rho*DB^{2}*H_t\right)^{0.976}\right)/1000$ (Eq. 5), where ρ is wood density (g cm^{-3}), DB is basal diameter (cm) and H_t is the total tree height (m). AGB values were then converted to aboveground carbon stock (AGC, in Mg C $stem^{-1}$) using the mean carbon fraction for tropical angiosperms (i.e., 45.6 %) (Martin et al., 2018). Plot-level AGC (in Mg C ha^{-1}) was then obtained by summing AGC across all individuals and dividing by the plot size (in ha). Basal diameter (DB) and total tree height (H_t) were obtained directly from the 2023 inventory (cfr. Section 2.5). Basic wood density (WD, g cm^{-3}) was determined using X-ray μCT scanning. A more detailed description of the wood density extraction process using X-ray μCT can be found in Data S1.

2.8. Statistical analysis

To evaluate the survival and growth performances at the species-level across the 17 species within our experiment, we used the *emmeans* function from the R package *emmeans* (version 1.9.0) to calculate estimated mean, standard errors (SE), and lower and upper confidence intervals (lower CI and upper CI) for each performance metric (Lenth, 2017; R Core Team, 2023)(Table 3; Table S2; Fig. 2). To compare the differences in mean wood density among species, we performed a non-parametric Kruskal–Wallis test, followed by the Dunn's test with the Benjamini–Hochberg adjustment to address the multiple comparison problem (Benjamini and Hochberg, 1995; Ostertagová et al., 2014). The non-parametric Kruskal–Wallis test was selected because the metric wood density at species-level did not meet the assumption of homogeneity of variances according to the Bartlett test ($p < .05$), nor the criterion of normality of residuals, following the Shapiro-Wilk test (Wu and Wong, 2003; Villasenor Alva and Estrada, 2009). The statistical significance level was set at $p < .05$. Apart from the estimated means and CI, no particular statistical tests were conducted for other performance metrics due to the experiment's limitations, specifically, having only one plot per species and relying on preliminary data from a single inventory campaign. All analyses and visualizations were performed in R (version 4.3.1), using the *ggplot* function from the R package *ggplot2* version 3.5.1 (R Core Team, 2023; Wickham et al., 2024).

3. Results

3.1. Initial species selection and harvest success

A total of 37 species with high potential for reforestation and native to the Yangambi landscape were initially listed, based on results of interviews with 3064 heads of local household representatives, results from old INERA plantations, and expertise of local scientists (Table 1). These species are suggested as potential alternatives to *A. auriculiformis* for achieving bioenergy production objectives and advancing the establishment of native species plantations that can contribute to long-term carbon sequestration and support local community needs (Fig. S3; Table S4). These species were searched in the Yangambi MAB reserve for 5 months, between August and December 2017. Not all species fructify during this limited period (Fig. S1); sufficient seeds were found to proceed to the nursery stage for only 19 out of the 37 proposed species (Table 2).

Table 3

Survival performance of 17 species from 5-year-old experimental plantations in the Yangambi landscape. Estimate (λ) and confidence intervals (CI) of the mortality rate (in %). Also shown is the initial number of trees planted for each species (N_0), the number of trees alive at the end of the last field measurement (N_t), the length of the period in years between planting and field measurement (t).

Species	N_0	N_t	t	λ	C I
Acacia auriculiformis Φ	5000	3228	4.8	9.1	8.7–9.6
Anonidium mannii †	1723	0	4.8	100	NA
Blighia welwitschii	1085	427	4.8	19.4	17.9–20.9
Canarium schweinfurthii	1360	533	4.8	19.7	18.3–21.0
Erythrophleum suaveolens	57	25	4.8	17.1	11.8–23.8
Gilbertiodendron dewevrei	2035	875	4.8	17.7	16.6–18.7
Irvingia smithii	290	219	4.8	5.8	4.6–7.3
Ongokea gore	330	113	4.8	22.3	19.3–25.5
Pachyelasma tessmannii	2872	2113	4.8	6.4	5.9–6.9
Piptadeniastrum africanum	1112	973	4.8	2.8	2.4–3.3
Pterocarpus soyauxii	1285	971	4.8	5.8	5.2–6.5
Pycnanthus angolensis	330	189	4.8	11.6	9.8–13.6
Scorodophloeus zenkeri	4880	2550	4.5	14.6	13.9–15.2
Terminalia ivorensis †	500	0	4.8	100	NA
Treculia africana	2042	790	4.8	19.7	18.6–20.8
Tridesmostemon omphalocarpoides †	1263	0	4.8	100	NA
Trilepisium madagascariense	1410	668	4.8	15.5	14.4–16.7

Φ Exotic reference species; † All the seedlings of these species died between November 2018 and September 2023.

3.2. Performance at the nursery stage

All seeds successfully harvested in the Yangambi MAB reserve were transported to the INERA-Yangambi station nursery, where they germinated. Out of 19 successfully harvested species, 16 successfully produced seedlings in the nursery. These seedlings were transplanted in the field in November 2018, together with *A. auriculiformis* (Tables 1 and 2). One successfully germinated species (*R. heudelotii*) was not planted in the field due to pests attacks that destroyed all seedlings, while two other species (*P. coeruleum* and *P. macrocarpus*) failed to germinate (Table 2). Together, we planted 27,574 trees, covering an area of 11.01 ha (Table 2).

3.3. Survival performance

Five years after planting, we measured 13,674 stems, corresponding to 49.6 % of the initially planted stems (Table 3). Species-specific mortality rate ranged from 100 % for *A. mannii, T. ivorensis* and *T. omphalocarpoides* to 2.8 % for *P. africanum*. In addition to *P. africanum*, four other species exhibited a mortality rate of less than 10 %: *P. soyauxii* and *I. smithii* with 5.8 %, *P. tessmannii* with 6.4 %, and *A. auriculiformis* with 9.1 % (Fig. 2, Table 3).

3.4. Growth performance

All individuals of three (out of 17) species totally disappeared (*A. mannii, T. omphalocarpoides, T. ivorensis*) (Tables 2 and 3). The largest stem among native species had reached 19.2 cm in basal diameter (vs. *A. auriculiformis* at 22.9 cm), and the tallest tree among native species had reached 9.5 m in height (vs. *A. auriculiformis* at 15.2 m). Absolute diameter increment ranged from 0.10 cm yr^{-1} for *S. zenkeri* to 1.86 cm yr^{-1} for *P. tessmannii.* Apart from *P. tessmannii*, four other studied native species showed an absolute diameter increment above 1 cm yr^{-1}, notably *C. schweinfurthii* (1.05 cm yr^{-1}), *O. gore* (1.08 cm yr^{-1}), *P. africanum* (1.35 cm yr^{-1}), and *Irvingia smithii* (1.54 cm yr^{-1}) (Fig. 3a, Table 4; Table S2). The average estimate of the absolute height increment of the exotic species *A. auriculiformis* was 1.45 m yr^{-1}, while all the studied native species showed an absolute height increment of less than 1 m yr^{-1}. The average estimates of the absolute height increment of these native species varied from 0.04 m yr^{-1} (*S. zenkeri*) to 0.88 m yr^{-1} (*P. tessmannii*). Apart from *P. tessmannii*, five other native species showed an absolute height increment above 0.5 m yr^{-1}, more specifically *E. suaveolens* (0.59 m yr^{-1}), *C. schwienfurthii* (0.61 m yr^{-1}), *O. gore* (0.62 m yr^{-1}), *P. africanum* (0.79 m yr^{-1}), and *I. smithii* (0.85 m yr^{-1}) (Fig. 3b; Table 4; Table S2). Relative growth rates (RGRd for diameter and RGRh for height), followed a similar trend to that observed with absolute diameter and height increment. *P. tessmannii* exhibited the highest RGRd (0.60 cm cm^{-1} yr^{-1}) followed by *I. smithii* (0.56 cm cm^{-1} yr^{-1}) and *A. auriculiformis* (0.56 cm cm^{-1} yr^{-1}). Regarding the RGRh, *A. auriculiformis* led with 0.68 m m^{-1} yr^{-1}, followed by *P. tessmannii* (0.63 m m^{-1} yr^{-1}) and *I. smithii* (0.60 m m^{-1} yr^{-1}). In contrast, *S. zenkeri* showed the poorest growth performance (Fig. 3c, d; Table 4; Table S2).

3.5. Wood volume and carbon sequestration performance

We computed the total AGC stock (Mg C ha^{-1}) sequestered by each studied species between November 2018 and September 2023. The highest total AGC stock sequestered by the native species within this period was 19.75 Mg C ha^{-1} for *P. tessmannii*, followed by 15.59 Mg C ha^{-1} for *P. africanum*, and 14.38 Mg C ha^{-1} for *I. smithii* (Fig. 4a; Table 4), vs. *A. auriculiformis* which sequestered 16.69 Mg C ha^{-1}. The lowest total AGC stock was sequestered by *S. zenkeri* (0.03 Mg C ha^{-1}), *B. welwitschii* (0.08 Mg C ha^{-1}), *T. madagascariense* (0.14 Mg C ha^{-1}),

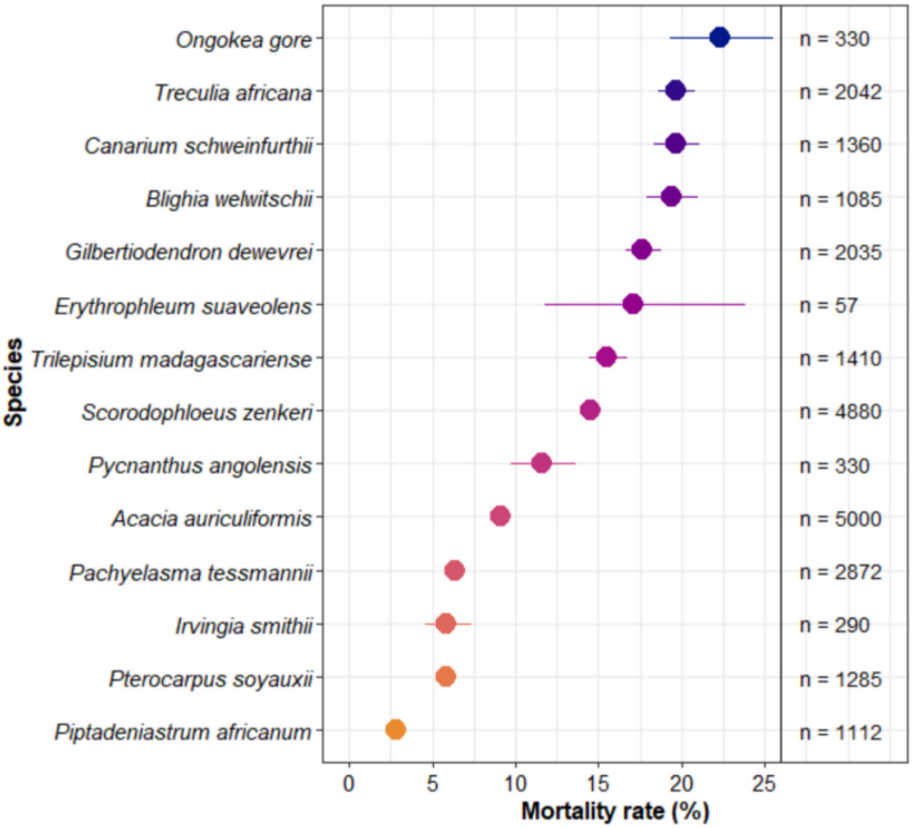


Fig. 2. Mortality rate of studied tree species from 5-year-old experimental plantations in Yangambi. The colour dots represent the estimated mortality rate (λ) over 5-years for each tree species presented on the y-axis. The horizontal lines extending from the dots represent the 95 % confidence intervals for the mortality rate (λ). The total number of initially planted seedlings per species is shown alongside the mortality rate on the right side of the graph. Species with the best survival performance are located toward the bottom of the graph. The graph does not show species with a 100 % mortality rate for visibility reasons.

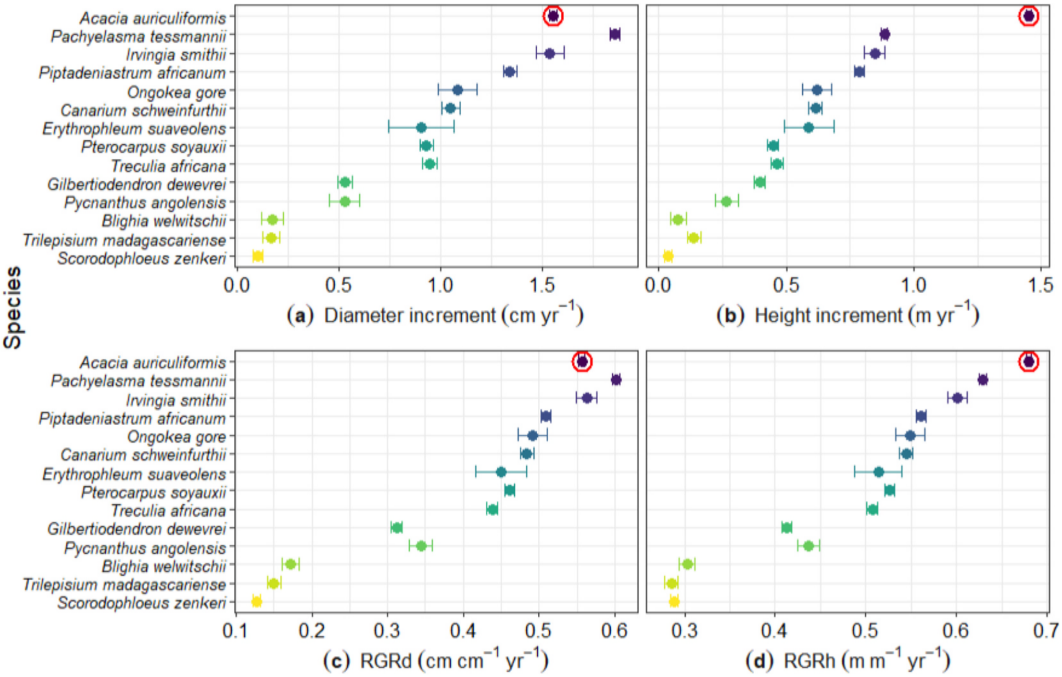


Fig. 3. Growth performance of a 5-year-old tree plantation experiment in Yangambi. (a) Absolute basal diameter increments in cm yr^{-1}. (b) Absolute height increment in cm yr^{-1}. (c) Relative growth rate in basal diameter in cm cm^{-1} yr^{-1}. (d) Relative growth rate in height in m m^{-1} yr^{-1}. For each growth performance variable, the points indicate the mean value at the species level. The error bars are 95 % confidence intervals around means. The red circle highlights the position of the exotic reference species *A. auriculiformis*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4

Growth performance, wood volume and carbon sequestration performance of 17 species from 5-year-old experimental plantations in the Yangambi landscape. Mean basal diameter increment (in cm yr^{-1}), mean height increment (in m yr^{-1}), mean relative growth rate in basal diameter (RGRd, in cm cm^{-1} yr^{-1}), mean relative growth rate in height (RGRh, in m m^{-1} yr^{-1}), mean wood density (WD, g cm^{-3}), total aboveground carbon stock (AGC, in Mg C ha^{-1}), Stem density (trees ha^{-1}), and the total volume index (VI, in m^3 ha^{-1}). WD was derived from core samples using the X-ray µCT scans.

Species	Diameter increment (cm yr^{-1})	Height increment (m yr^{-1})	RGRd (cm cm^{-1} yr^{-1})	RGRh (m m^{-1} yr^{-1})	WD (g cm^{-3})	Total AGC (Mg C ha^{-1})	Stem density (trees ha^{-1})	Total VI (m^3 ha^{-1})
Acacia auriculiformis Φ	1.55	1.45	0.56	0.68	0.60	16.69	1614	41.92
Anonidium mannii †	NA	NA	NA	NA	NA	0	0	0
Blighia welwitschii	0.17	0.08	0.17	0.30	0.85	0.08	993	0.13
Canarium schweinfurthii	1.05	0.61	0.48	0.54	0.56	2.48	987	6.45
Erythrophleum suaveolens	0.90	0.59	0.45	0.51	0.82	4.66	1250	8.29
Gilbertiodendron dewevrei	0.53	0.40	0.31	0.41	0.72	1.49	1080	3.05
Irvingia smithii	1.54	0.85	0.56	0.60	0.86	14.38	1825	24.78
Ongokea gore	1.08	0.62	0.49	0.55	0.78	2.79	869	5.19
Pachyelasma tessmannii	1.86	0.88	0.60	0.63	0.82	19.75	1837	35.78
Piptadeniastrum africanum	1.35	0.79	0.51	0.56	0.80	15.29	2211	30.89
Pterocarpus soyauxii	0.93	0.45	0.46	0.53	0.71	3.39	1904	6.86
Pycnanthus angolensis	0.53	0.27	0.34	0.44	0.60	0.76	1575	1.78
Scorodophloeus zenkeri	0.10	0.04	0.13	0.29	0.86	0.03	1308	0.04
Terminalia ivoirensis †	NA	NA	NA	NA	NA	0	0	0
Treculia africana	0.94	0.46	0.44	0.51	0.59	2.05	963	5.09
Tridesmostemon omphalocarpoides †	NA	NA	NA	NA	NA	0	0	0
Trilepisium madagascariense	0.16	0.14	0.15	0.29	0.57	0.14	1193	0.35

Φ Exotic reference species; † All the seedlings of these species died between November 2018 and September 2023.

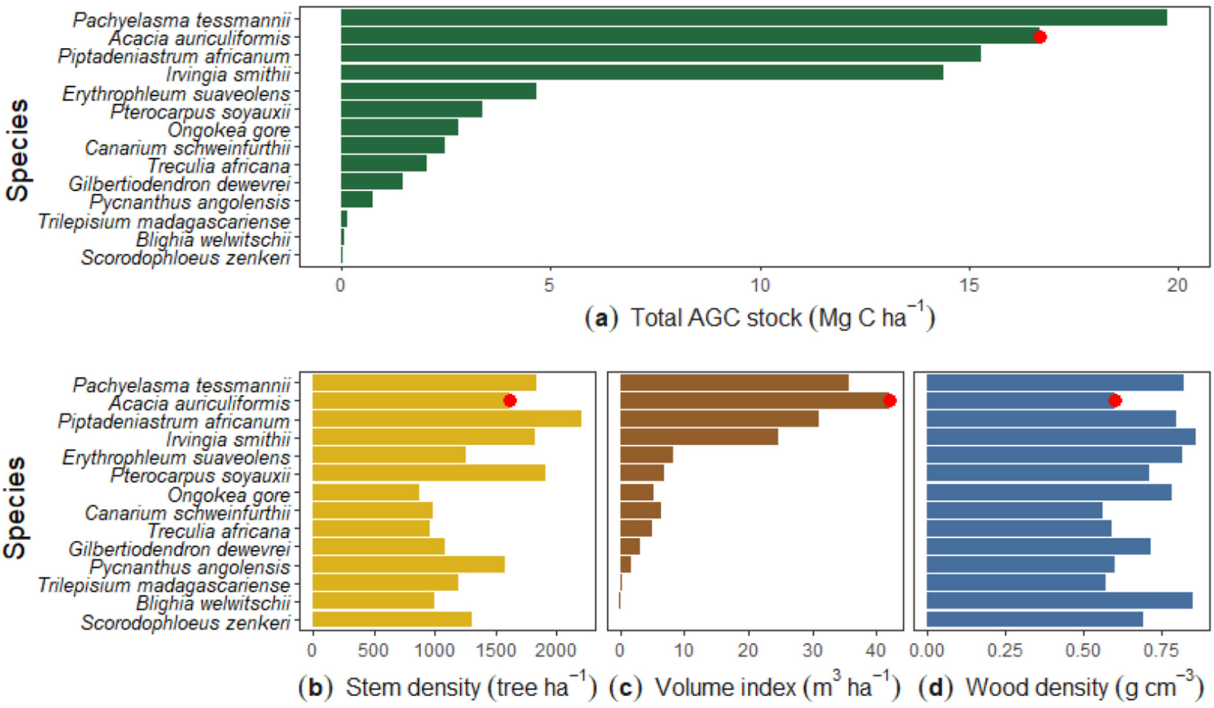


Fig. 4. Carbon sequestration and the related performance metrics for the studied tree species in 5-year-old plantations. (a) Total aboveground carbon stock (AGC, in Mg C ha^{-1}), (b) Stem density (tree ha^{-1}), (c) Total volume index (VI, in m^3 ha^{-1}), and (d) Wood density (in g cm^{-3}) extracted from the core samples using X-ray µCT scanning. The red dots on the graphs highlight the reference exotic species *A. auriculiformis*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and *P. angolensis* (0.76 Mg C ha^{-1}).

In addition to the total AGC, we calculated the stem density (trees ha^{-1}), the total volume index (VI, m^3 ha^{-1}), and the wood density (g cm^{-3}), which are three performance metrics that significantly influence the total AGC stock (Fig. 4b-c; Table 4). The stem density of each planted species after 5 years was calculated based on the initial planted size and the number of seedlings, allowing the expression of the remaining number of stems of each plot as equivalent per ha. (Fig. 4b). We found that *P. africanum* dominated with an equivalent of 2211 tree ha^{-1}, followed by *P. soyauxii* (1904 tree ha^{-1}), *P. tessmannii* (1837 trees ha^{-1}), *I. smithii* (1825 tree ha^{-1}), and *P. angolensis* (1575 tree ha^{-1}). The remaining native species accounted for less than 1500 tree ha^{-1}, with the lowest density recorded for *O. gore* (869 tree ha^{-1}). However, we observed a stem density of 1614 tree ha^{-1} for the reference exotic species *A. auriculiformis*.

We estimated the productivity of the studied species by calculating the wood VI (Fig. 4c). The total VI across the studied species was 170.4 m^3 ha^{-1}. The highest contribution of this total volume index came from *A. auriculiformis* (41.92 m^3 ha^{-1}), followed by *P. tessmannii* with 35.75 m^3 ha^{-1}), and *P. africanum* with 30.89 m^3 ha^{-1}. The species with the lowest performance in terms of productivity included *S. zenkeri* (with 0.04 m^3 ha^{-1}), *B. welwitschii* (with 0.13 m^3 ha^{-1}), *T. madagascariense* (with 0.35 m^3 ha^{-1}), *P. angolense* (with 1.78 m^3 ha^{-1}) and *G. dewevrei* (with 3.05 m^3 ha^{-1}). The total VI followed the same trend as the total AGC stock among studied species (Fig. 4c).

Wood density is a crucial structural and functional variable for the wood itself, but also a key variable in tree biomass estimation. We extracted the wood density from the wood cores of the studied species using an X-ray μCT scanning (Fig. 4d). The resulted wood density varied from 0.86 g cm^{-3} for both *I.smithii* and *S. zenkeri* to 0.56 g cm^{-3} for *C. schweinfurthii*. We observed a significant difference in wood density across studied species ($p < .001$). However, no significant difference in wood density was observed between *A. auriculiformis* and *P. angolense* ($p = .974$), between *P. soyauxii* and *G. dewevrei* ($p = .833$), and between *S. zenkeri* and *P. africanum* ($p = 1$) (Fig. S2; Table S3).

4. Discussion

In this study, we used an experimental plantation set up in the Yangambi landscape to compare the performance of one of the currently most used exotic species in large-scale plantations (*A. auriculiformis*) with a group of native species which could support future tree-planting initiatives as an NBS approach for climate change mitigation in central Africa and beyond. From an initial list of 37 potentially suitable native species, the seeds of 19 of them were successfully harvested in natural forests. Among these, 16 species produced sufficient seedlings in the nursery and were subsequently transplanted in the field. After 5 years, we found that 5 of these species demonstrated survival, growth, and carbon sequestration performance comparable to the fast-growing exotic species *A. auriculiformis*. We discuss these results in the context of the potential for carbon offsetting through large-scale tree planting as an NBS approach.

4.1. Harvesting success depends on knowledge of reproductive phenology

Globally, plantation-based restoration is the most prevalent strategy, with 45 % of global commitments involving monocultures of fast-growing species (Lewis et al., 2019). In central Africa, major tree-planting efforts have predominantly relied on a limited number of fast-growing exotic species, such as Acacia and Eucalyptus (Marien and Mallet, 2004; Bertaux et al., 2021; Kasekete et al., 2022). This preference for exotic species may be justified by substantial knowledge gaps on native species that could serve as viable alternatives (Höhl et al., 2020; Vinceti et al., 2020). In response to these crucial knowledge gaps, our study identified 37 potentially suitable native species based on local knowledge and seed availability from the natural forests of the MAB reserve of Yangambi. Of these, seeds from 19 species were successfully harvested from the natural forest (Table 1). Results confirm that, beyond local knowledge and local communities' involvement (see supporting Discussion Data S1), understanding the reproductive phenology of native species is indeed crucial. For example, among the 37 species identified in this study, information on fruiting periods was found in the literature for only 16 species (Fig. S1; Table 1). Furthermore, almost half of these species with available fruiting information produce fruits annually between August and January (ICRAF, 2009; Meunier et al., 2015; Doucet et al., 2016; Daïnou et al., 2021) (Fig. S1). Additionally, some species may demonstrate supra-annual fruiting, producing fruits every 2–3 years under similar ecological conditions (Bourland et al., 2012). An example is *P. elata* (Bourland et al., 2012; Ouédraogo et al., 2018), which appears to be a good candidate for large-scale tree-planting mainly for its significant long-term carbon storage potential (Table 1). Although limited information is available (Couralet, 2010; Menga et al., 2012; Bourland et al., 2012; Ilondea et al., 2019), the scarcity of data on fruiting periods represents a significant bottleneck to incorporating native species into large-scale tree-planting initiatives, which is essential for achieving major restoration objectives (Lewis et al., 2019; Brancalion and Holl, 2020; Parr et al., 2024).

The following sub-section discusses results in the same order as they were presented in the previous section.

4.2. Performance at the nursery stage

Of the 19 species whose seeds were successfully harvested from the natural forest, 16 produced sufficient seedlings in the nursery and were subsequently planted in the field. While the high species richness of the central Africa forests offers a significant advantage for including native species in large-scale tree-planting initiatives, the variability in seed germination among these species introduces an important uncertainty when considering them for such efforts in this region (Daïnou et al., 2021). Previous research in tropical regions has focused on improving germination and conservation techniques for various native species seeds (Sanogo et al., 2013; Chandima et al., 2022; Quispe-Melgar et al., 2024). In our study, the nursery germination success of our selected species was evaluated using a nursery score calculated from existing literature on seed characteristics (Table 1, Table S1). For a given native species, the germination rate is among the key components for seed success in the nursery (Table 1, Table S1). This component of the nursery score is strongly linked to the conservation duration of the seed following its collection in the forest. The seed conservation duration provides information on the decaying susceptibility of the seed and the loss of germination capacity, shorter for recalcitrant seeds and relatively longer for orthodox seeds (Daïnou et al., 2021). Another important nursery score component influencing nursery success is seed dormancy, the main characteristic of orthodox seeds (Chandima et al., 2022). Seed dormancy is defined as the failure of viable seeds to germinate naturally when conditions are favorable (Mng'omba et al. Mng'omba et al., 2007; Chandima et al., 2022). Breaking seed dormancy is necessary to trigger germination in the nursery. As observed in this study, the time required in the nursery from seed germination to the development of mature seedlings ready for field transplantation is typically longer for native species (about 12 months on average) compared to the fast-growing exotic species such as *A. auriculiformis* (approximately 4 months). This significant difference in nursery time may partly explain the widespread use of *A. auriculiformis* in many tree-planting initiatives in central Africa (Marien and Mallet, 2004; Proces et al., 2018; Bertaux et al., 2021). The last component considered in the nursery score calculation is the number of seeds per kilogram. This indicates the effort necessary to produce a given quantity of seedlings in the nursery, which may include nursery materials and the planting site capacity (nursery spaces, quantity and quality of nursing soil, quantity of nursing bags, etc.), as well as the number of workers per day (Daïnou et al., 2021).

4.3. Survival and growth performances

In natural conditions, shading is presumed to be the dominant driver of the high mortality rates of seedlings and understory plants (McDowell et al. 2018). However, during the early establishment phase in plantations, seedlings are also susceptible to insect and animal damage, as well as environmental factors like water availability and temperature, which might explain the differences in mortality rate observed among our studied species (McDowell et al. 2018; Zemp et al., 2019). Despite monitoring over 27,574 trees in a 5-year-old plantation, we observed 13,900 dead trees across 17 species, including our reference exotic species, *A. auriculiformis*. At the species-level, the plot size (range from 0.02 to 2 ha) and the 5-year monitoring duration were likely too small to confidently and statistically evidence differences in mortality rates across species (Ligot et al., 2022).

Existing studies on the performance of suitable native species for forest restoration through tree-planting are predominantly reported from central and south America (Montagnini and Ugalde, 2003; Piotto et al., 2003, 2004; van Breugel et al., 2011), contrasting with central Africa, where few studies focus on the performance of a limited number of commercial timber species in logging gaps (Ouédraogo et al., 2014; Fayolle et al., 2015; Doucet et al., 2016; Ligot et al., 2022). Furthermore, few studies have reported the growth performances of fast-growing exotic species plantations in central Africa (Proces et al., 2018; Kasekete et al., 2022), especially in comparison to a selection of native species. Regarding absolute increment and relative growth rate in height, *A. auriculiformis* performs significantly better than the studied native species (Fig. 3; Table 4). However, some native species demonstrated promising absolute increment and relative growth rate in height compared to *A. auriculiformis* (Fig. 3; Table 4; Table S2). In contrast, some native species, such as *S. zenkeri, B. welwitschii, T. madagascariense*, and *G. dewevrei,* show poor growth performance over 5 years in plantations (Fig. 3; Table 4; Table S2). However, contrasting results were reported in a plantation experiment with 12 species in Costa Rica. Most species with good initial growth maintained good growth rates over 15–16 years (van Breugel et al., 2011). Similarly, some species may show accelerated growth after poor growth in the first years (Piotto et al., 2003; van Breugel et al., 2011). Although climatic (temperature and rainfall) and edaphic conditions (e.g. soil texture, structure, composition, moisture, pH and nutrient availability) are known to influence species growth and productivity (Baker et al., 2003; Bauters et al., 2020; Kasekete et al., 2022), these variables were not determinants in this study. Additionally, while our study identifies promising native species as alternatives to the exotic species *A. auriculiformis*, many of the selected species exhibited poor seed harvest and nursery success, as well as suboptimal performance in plantations. This opens the door to a wide range of possible explanations, including the initial quality of the planting material, site conditions (elevation, exposure), resource availability (Baker et al., 2003), and pressure from insect herbivory or pathogens (Guidosse et al., 2024).

4.4. Performance in carbon sequestration

The literature is very scant on the carbon sequestration performance of native species in plantations compared to that of exotic species (Liu et al., 2018; Singh and Kumar, 2022). This knowledge gap persists because proxies for carbon stock in young plantations, such as wood density, are often lacking (Chave et al., 2014). The available global datasets of wood density include only large trees (DBH $\geq$ 10 cm)(Zanne et al., 2009). Therefore, this limitation hampers comparisons of carbon sequestration performance between young plantations of native species and fast-growing exotic species (e.g. *A. auriculiformis)* in large-scale tree-planting for long-term carbon sequestration in central Africa.

In a 5-year plantations experiment, we estimated the AGC stock of the studied species by extracting wood density values from core samples collected from our planted species using X-ray CT scanning (De Mil et al., 2016; Van Den Bulcke et al., 2019; De Mil and Van den Bulcke, 2023). The best-performing native species over 5 years that challenged the exotic species *A. auriculiformis* in terms of carbon storage was *P. tessmannii* (Fig. 3a; Table 4; Table S2). Consequently, *P. tessmannii* emerged as a principal alternative native species to the reference exotic species *A. auriculiformis* for large-scale tree-planting initiatives in the Yangambi landscape. This species is described as a “paradoxical” species (Deklerck et al., 2019b): on the one hand, it has a high wood density (0.82 g cm^{-3} vs. 0.60 g cm^{-3} from *A. auriculiformis*), which is characteristic of species with long-term carbon sequestration potential (Bastin et al., 2015); on the other hand, it shows excellent survival and growth performance over 5 years in plantations (Figs. 3 and 4). However, *P. tessmannii* is not among the 18 hyperdominant species that represent 50 % of the total AGB of the central African forests (Bastin et al., 2015); this may be due to its relatively low stem density (0.156 stem ha^{-1}; dbh, diameter at breast height $>$ 20 cm) in natural forests (Doucet et al., 2022). Yet, its excellent performance in the plantation, as found in this study, demonstrates its significant potential for long-term carbon sequestration in large-scale tree-planting initiatives in central Africa. In contrast, the monodominant *G. dewevrei* reported to contribute to over 20 % of the total AGB of the central African forests (Bastin et al., 2015), shows poor performance in plantations (Fig. 3; Table 4), underscoring the importance of forest conservation as another major pillar of NBS approach for long-term carbon sequestration (Folkard-Tapp and Cavan, 2021; Girardin et al., 2021). In addition, our results highlight other promising, well-performing native species with high carbon sequestration potential such as *P. africanum* and *I. smithii*. Although *A. auriculiformis* exhibits higher carbon sequestration performance than some native species, some authors (Shimamoto et al., 2014; Liu et al., 2018) reported that the carbon accumulation is closely related to the age and the species functional group (Hubau et al., 2019). It is well known that long-lived and slow-growing species have more time to grow and sequester carbon under appropriate conditions than short-lived and fast-growing species, which might affect long-term carbon accumulation (Shimamoto et al., 2014; Mendoza-Páez et al., 2024). Consequently, fast-growing monoculture plantations sequester carbon rapidly, but they may not maximize carbon storage in the long-term as they are more vulnerable to disease, pests, and climate extremes (Seddon et al., 2020a). Moreover, the difference in carbon sequestration performance among our studied native species can also be explained by variations in metrics such as wood density, stem density, and total volume index recorded of each species (Fig. 3; Table 4), which are proxies for the total AGC stock. For instance, most allometric models for biomass estimation are based on three variables: tree diameter at breast height, tree height and wood density (Fayolle et al., 2013; Chave et al., 2014). The latter refers to the oven-dry mass of a wood sample divided by its green volume (Williamson and Wiemann, 2010; Vieilledent et al., 2012). The first two variables serve to assess tree volume, while wood density allows the conversion of this volume into biomass (Chave et al., 2014; Sagang et al., 2018). While the tree diameter used to calculate the volume is often measured at breast height, in this study, we considered the tree basal diameter, given the young age of the trees in our experiment, which represents a potential limitation of our wood volume estimates. Additionally, the measurement of the basal diameter was subject to a potential source of error due to the relatively high proportion of the small size trees in our experiment, which could have, *in fine,* influenced our estimates of the volume. However, as the trees in our experiment will grow over the coming years, we will be able to measure the diameter at breast height rather than basal diameter, which will improve the estimate of our actual volume and, therefore, carbon sequestration performance.

However, the poor performance in growth rate and carbon sequestration of some native species in our experiment (e.g. *S. zenkeri, B. welwitschia, T. madagascariense,* and *P. angolensis*) suggest that they may not be suitable species for large-scale tree-planting initiatives under the conditions of our experiment in the Yangambi landscape. In contrast, under natural conditions in central Africa, slow-growing native species can experience long life spans in the understory, resulting in relatively low DBH at older ages (Memiaghe et al., 2016; Hubau et al., 2019). Their adaptations allow them to survive in the understory without the need to invest in rapid growth while contributing disproportionately to carbon sequestration compared to the limited contribution of the sub-canopy trees (Memiaghe et al., 2016; Hubau et al., 2019).

4.5. Limitations

Despite the importance of the topic of this study, we identified four major limitations that must be acknowledged and considered for future research. First, the local population was asked about the species and their preferences, but no thorough analysis and socio-economic assessment was conducted to assess whether selected species could fulfil, in the long-term, local needs in terms of biomass needs or income generation. Such an assessment is needed to maximize the potential benefits native species offer in forest restoration initiatives, ensuring they provide long-term incomes for the local population. Second, this research was constrained by the time horizon applied; five years is certainly sufficient to assess a series of variables as it was done in this paper, but more research and a longer time span are needed to conduct a more conclusive comparative assessment between exotic and native species. Third, land-tenure is acknowledged in the literature to be among the most important variables ultimately determining the good or bad outcomes of tree-based restoration, especially in the global south. This experiment was conducted in a semi-controlled environment, whereby tree plantations were established on a private concession (INERA's) with the local population (largely INERA's workers and their families) having partial use and access rights. More research is needed to assess each species' performance under full customary tenure, as is the case in the vast majority of degraded areas across central Africa. And finally, our experiment was conducted without considering any environmental parameters that might favor or hinder the performance of some species. Given the reported long-term resilience of native species vs. exotic species to climate change and the long-term benefits for people, care should be taken to include the influence of environmental factors on the performance of suggested native species in future research.

5. Conclusion

Our study identified promising native species such as *Pachyelasma tessmannii, Piptadeniastrum africanum Irvingia smithii, Ongokea gore, and Canarium scheinfurthii*. These species demonstrated growth, survival, and carbon sequestration performance comparable to *Acacia auriculiformis* over five years in plantations. This illustrates that local tree species are potential alternatives to exotic species for ecological restoration initiatives in the central Congo Basin. Overall, this suggests that substituting *Acacia auriculiformis* with native species will benefit the environment and local communities. Environmental benefits include long-term carbon sequestration, climate change mitigation, reducing the risk of biodiversity loss and reducing pressure on remaining intact forests. Additional benefits for local communities include maintaining a healthy water balance and producing forest and non-forest products such as wood and honey that substantially support sustainable local livelihoods. However, our findings are based solely on experimental plots of single-species plantations. Many studies (Piotto 2008; Feng et al., 2022; Warner et al., 2023) suggest that mixed-species plantations, especially in the case of native species, can significantly enhance growth and long-term carbon sequestration performance (Manson et al. 2013; Liu et al., 2018; Zhang et al., 2020; Feng et al., 2022; Zhu et al., 2023). Thus, we argue that a well-managed, multispecies plantation approach could have improved the performance of the species studied here. As an NBS approach, future large-scale tree-planting efforts with native species may benefit from combining fast-growing and slow-growing species, short-lived and long-lived species, light-demanding and shade-tolerant species, shallow-rooting and deep-rooting species, and nitrogen-fixing and non-nitrogen-fixing species to take advantage of their complementary effects (Callaway Mng'omba et al., 2007; Liu et al., 2018; Feng et al., 2022), alongside the development of a seed orchard to ensure regular seed production of selected tree species (Chaloupková et al. 2019; Ravichand and Gunaga 2021). However, to realize the potential benefits of increasing tree cover, large-scale tree-planting initiatives must include thorough goal setting, local community involvement, planning, and implementation, with a sufficient time scale for maintenance and monitoring.

Author contributions

Brice Yannick Djiofack: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Nils Bourland: Writing – review & editing, Supervision, Methodology, Conceptualization. Hans Beeckman: Writing – review & editing, Supervision, Methodology, Conceptualization, Funding acquisition, Project administration. Paolo Omar Cerutti: Writing – review & editing, Conceptualization, Funding acquisition, Project administration. Collins Dzernyuy Fai: Writing – review & editing, Methodology, Conceptualization. Martin Van Hulle: Investigation, Methodology, Conceptualization. Mathilde Pierson: Investigation, Methodology, Conceptualization. Jules Mayaux: Investigation, Methodology, Conceptualization. Nestor Kashikija Luambua: Investigation, Methodology, Conceptualization. Donatien Musepena: Investigation, Methodology, Conceptualization. Basile Luse Belanganayi: Investigation, Methodology, Conceptualization, Writing – review & editing. Félix Laurent: Project administration; writing – review and editing. Bhely Angoboy Ilondea: Investigation, Writing – review & editing. Jan Van den Bulcke: Writing – review & editing, Methodology, Validation, Supervision. Wannes Hubau: Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Project administration.

Funding sources

Belgian Directorate-General for Development Cooperation and Humanitarian Aid (DGD) via PilotMAB (2019–2023) and PilotMABplus (2024–2028) projects.

European Union (EU) via the Center for International Forestry Research (CIFOR); FORETS project (EEC40).

CRediT authorship contribution statement

Brice Yannick Djiofack: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Nils Bourland:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Hans Beeckman:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Paolo Omar Cerutti:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Collins Dzernyuy Fai:** Writing – review & editing, Methodology, Conceptualization. **Martin Van Hulle:** Writing – review & editing, Investigation, Conceptualization. **Mathilde Pierson:** Methodology, Investigation, Conceptualization. **Jules Mayaux:** Methodology, Investigation, Conceptualization. **Nestor Kashikija Luambua:** Methodology, Investigation, Conceptualization. **Donatien Musepena:** Methodology, Investigation, Conceptualization. **Basile Luse Belanganayi:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Félix Laurent:** Writing – review & editing, Project administration. **Bhely Angoboy Ilondea:** Writing – review & editing, Investigation. **Jan Van den Bulcke:** Writing – review & editing, Validation, Supervision, Methodology. **Wannes Hubau:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

This study was conducted within the framework of the PilotMAB and PilotMABplus projects, implemented by the Royal Museum for Central Africa (RMCA), with the financial support of the Belgian Directorate-General for Development Cooperation and Humanitarian Aid (DGD). The experiment was set up within the framework of the FORETS project (EEC40), led by the Center for International Forestry Research (CIFOR) and funded by the European Union. We thank Quentin Ducenne and Resources & Synergies Development Pte Ltd. (R&SD) for coordinating and providing logistical support for the nursery and experiment setup. Our gratitude extends to the technicians of INERA-Yangambi for their fieldwork contributions. We thank Toon Gheyle for his help during sample preparation and for supporting the scanning process and wood density extraction.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2025.107662.

References

Abernethy, K., Maisels, F., White, L.J.T., 2016. Environmental Issues in Central Africa. Annu. Rev. Environ. Resour. 41, 1–33. https://doi.org/10.1146/ANNUREV-ENVIRON-110615-085415/1.

Baker, T.R., Burslem, D.F.R.P., Swaine, M.D., 2003. Associations between tree growth, soil fertility and water availability at local and regional scales in Ghanaian tropical rain forest. J. Trop. Ecol. 19, 109–125. https://doi.org/10.1017/S0266467403003146.

Bastin, J.F., Barbier, N., Réjou-Méchain, M., et al., 2015. (2015) seeing Central African forests through their largest trees. Sci. Report. 51 (5), 1–8. https://doi.org/10.1038/srep13156.

Bastin, J.F., Finegold, Y., Garcia, C., et al., 2019. The global tree restoration potential. Science 364, 76–79.

Bauters, M., Ampoorter, E., Huygens, D., et al., 2015. Functional identity explains carbon sequestration in a 77-year-old experimental tropical plantation. Ecosphere 6, art198. https://doi.org/10.1890/ES15-00342.1.

Bauters, M., Meeus, S., Barthel, M., et al., 2020. Century-long apparent decrease in intrinsic water-use efficiency with no evidence of progressive nutrient limitation in African tropical forests. Glob. Chang. Biol. 26, 4449–4461.

Benjamini, Y., Hochberg, Y., 1995. Controlling the False Discovery Rate: a Practical and Powerful Approach to Multiple Testing. J. R. Stat. Soc. Ser. B Stat Methodol. 57, 289–300. https://doi.org/10.1111/J.2517-6161.1995.TB02031.X.

Bennett, A.C., Dargie, G.C., Cuni-Sanchez, A., et al., 2021. Resistance of African tropical forests to an extreme climate anomaly. Proc. Natl. Acad. Sci. USA 118, e2003169118.

Bertaux, P., Baltzer, C., Angulo, J., et al., 2021. Forest Plantations in Central Africa. Chapter 3, State of the Forests 2021. Cent Africa For Obs, p. 16.

Bourland, N., Kouadio, Y.L., Lejeune, P., et al., 2012. Ecology of pericopsis elata (fabaceae), an endangered timber species in southeastern cameroon. Biotropica 44, 840–847. https://doi.org/10.1111/J.1744-7429.2012.00874.X.

Brancalion, P.H.S., Holl, K.D., 2020. Guidance for successful tree planting initiatives. J. Appl. Ecol. 57, 2349–2361. https://doi.org/10.1111/1365-2664.13725.

Brancalion, P.H.S., Niamir, A., Broadbent, E., et al., 2019. Global restoration opportunities in tropical rainforest landscapes. Sci. Adv. 5, eaav3223. https://doi.org/10.1126/sciadv.aav3223.

Callaway, R.M., 2007. Positive interactions and interdependence in plant communities. Posit Interact Interdepend Plant Communities 1–415. https://doi.org/10.1007/978-1-4020-6224-7/COVER.

Callow, B.J., 2021. Characterising the Permeability and Structure of Fluid-Escape Conduits in Sedimentary Basins - Application to Geological Carbon Sequestration. University of Southampton.

Calvo-Alvarado, J.C., Arias, D., Richter, D.D., 2007. Early growth performance of native and introduced fast growing tree species in wet to sub-humid climates of the Southern region of Costa Rica. For. Ecol. Manag. 242, 227–235. https://doi.org/10.1016/J.FORECO.2007.01.034.

Chandima, B.R., Samarasinghe, P., Gehan Jayasuriya, K.M.G., et al., 2022. Seed dormancy and germination behaviour of tropical rainforest tree species from Sri Lanka. Seed Sci. Res. 32, 94–103. https://doi.org/10.1017/S0960258522000162.

Chave, J., Réjou-Méchain, M., Búrquez, A., et al., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Chang. Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629.

Chazdon, R.L., Brancalion, P., 2019. Restoring forests as a means to many ends. Science 364, 24–25. https://doi.org/10.1126/SCIENCE.AAX9539/ASSET/2448DFF3-0A82-4280-AA01-B51CCE39E2D4/ASSETS/GRAPHIC/365_24_F2.JPEG.

CIFOR, 2024. Yangambi Engagement Landscape - Our projects. https://www.cifor.org/yangambi/en/our-projects/. Accessed 6 Mar 2024.

Cohen-Shacham, E., Walters, G., Janzen, C., Maginnis, S., 2016. Nature-Based Solutions to Address Global Societal Challenges. IUCN International Union for Conservation of Nature.

Condit, R., Hubbell, S.P., Foster, R.B., 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. Ecol. Monogr. 65, 419–439. https://doi.org/10.2307/2963497.

Couralet, C., 2010. Community Dynamics, Phenology and Growth of Tropical Trees in the Rain Forest Reserve of Luki. Democratic Republic of Congo, Ghent University.

Daïnou, K., Tosso, D.F., Bracke, C., et al., 2021. Guide pratique des plantations d'arbres des forêts denses humides d'Afrique. Les presses agronomiques de Gembloux. Université de Liège - ULiège, Gembloux, Belgium, pp. 1–322.

De Mil, T., Van den Bulcke, J., 2023. Tree Core Analysis with X-ray Computed Tomography. J. Vis. Exp. 2023. https://doi.org/10.3791/65208.

De Mil, T., Vannoppen, A., Beeckman, H., et al., 2016. A field-to-desktop toolchain for X-ray CT densitometry enables tree ring analysis. Ann. Bot. 117, 1187–1196. https://doi.org/10.1093/aob/mcw063.

De Ridder, M., Hubau, W., Van Den Bulcke, J., et al., 2010. The potential of plantations of Terminalia superba Engl. & Diels for wood and biomass production (Mayombe Forest, Democratic Republic of Congo). Ann. For. Sci. 67, 501. https://doi.org/10.1051/forest/2010003.

Deklerck, V., De Mil, T., Ilondea, B.A., et al., 2019a. Rate of forest recovery after fire exclusion on anthropogenic savannas in the Democratic Republic of Congo. Biol. Conserv. 233, 118–130. https://doi.org/10.1016/j.biocon.2019.02.027.

Deklerck, V., De Mil, T., Kondjo, P., et al., 2019b. Sleeping beauties in materials science: Unlocking the value of xylarium specimens in the search for timbers of the future. Holzforschung 73, 889–897. https://doi.org/10.1515/HF-2018-0269/DOWNLOADASSET/SUPPL/HF-2018-0269_SUPPL.ZIP.

Di Sacco, A., Hardwick, K.A., Blakesley, D., et al., 2021. Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. Glob. Chang. Biol. 27, 1328–1348. https://doi.org/10.1111/GCB.15498.

Djiofack, B.Y., Beeckman, H., Bourland, N., et al., 2024a. Protecting an artificial savanna as a nature-based solution to restore carbon and biodiversity in the Democratic Republic of the Congo. Glob. Chang. Biol. 30, e17154. https://doi.org/10.1111/GCB.17154.

Djiofack, B.Y., Beeckman, H., Bourland, N., et al., 2024b. Natural forest regeneration through fire protection is a less imminent threat for truly stable savannas than afforestation. Glob. Chang. Biol. 30, e17370. https://doi.org/10.1111/GCB.17370.

Donis, C., 1956. La forêt dense congolaise et l'état actuel de sa sylviculture. Bull Agric Congo Belg 47, 261–289.

Doucet, J.-L., Daïnou, K., Ligot, G., et al., 2016. Enrichment of Central African logged forests with high-value tree species: testing a new approach to regenerating degraded forests. Int J Biodivers Sci Ecosyst Serv Manag 12, 83–95. https://doi.org/10.1080/21513732.2016.1168868.

Doucet, R., Doucet, J.L., Lejeune, P., et al., 2022. Wood description and timber use investigation of Pachyelasma tessmannii (Harms) Harms. Eur J Wood Wood Prod 80, 199–212. https://doi.org/10.1007/S00107-021-01758-3/TABLES/4.

Ebuy, J., Lokombe, J.P., Ponette, Q., et al., 2011. Allometric equation for predicting aboveground biomass of three tree species. J. Trop. For. Sci. 23, 125–132.

Fayolle, A., Doucet, J.L., Gillet, J.F., et al., 2013. Tree allometry in Central Africa: Testing the validity of pantropical multi-species allometric equations for estimating biomass and carbon stocks. For. Ecol. Manag. 305, 29–37. https://doi.org/10.1016/J.FORECO.2013.05.036.

Fayolle, A., Ouédraogo, D.-Y., Ligot, G., et al., 2015. Differential Performance between two Timber Species in Forest Logging Gaps and in Plantations in Central Africa. Forests 6, 380–394. https://doi.org/10.3390/f6020380.

Feng, Y., Schmid, B., Loreau, M., et al., 2022. Multispecies forest plantations outyield monocultures across a broad range of conditions. Science (80-) 376, 865–868. https://doi.org/10.1126/science.abm6363.

Folkard-Tapp, H., Cavan, E., 2021. Nature-based Solutions to tackle climate change and restore biodiversity. Artic J Appl Ecol. https://doi.org/10.1111/1365-2664.14059.

Girardin, C.A.J., Jenkins, S., Seddon, N., et al., 2021. Nature-based solutions can help cool the planet — if we act now. Nature 593, 191–194. https://doi.org/10.1038/d41586-021-01241-2.

González-Tokman, D.M., Barradas, V.L., Boege, K., et al., 2018. Performance of 11 tree species under different management treatments in restoration plantings in a tropical dry forest. Restor. Ecol. 26, 642–649. https://doi.org/10.1111/REC.12617/SUPPINFO.

Guidosse, Q., Biwolé, A., De Clerck, C., et al., 2024. Seedling ecology of Aucoumea klaineana Pierre, the most important timber species in Central Africa. For. Ecol. Manag. 569, 122221. https://doi.org/10.1016/J.FORECO.2024.122221.

Hall, J.S., 2008. Seed and seedling survival of African mahogany (Entandrophragma spp.) in the Central African Republic: Implications for forest management. For. Ecol. Manag. 255, 292–299. https://doi.org/10.1016/J.FORECO.2007.09.050.

Höhl, M., Ahimbisibwe, V., Stanturf, J.A., et al., 2020. Forest landscape restoration—what generates failure and success? For 938 (11), 938. https://doi.org/10.3390/F11090938.

Holl, K.D., Brancalion, P.H.S., 2020. Tree planting is not a simple solution. Science 368, 580–581. https://doi.org/10.1126/SCIENCE.ABA8232/SUPPL_FILE/ABA8232_HOLL_SM.PDF.

Hubau, W., De Mil, T., Van den Bulcke, J., et al., 2019. The persistence of carbon in the African forest understory. Nat Plants 5, 133–140. https://doi.org/10.1038/s41477-018-0316-5.

ICRAF, 2009. World Agroforestry Centre | agroforestree database 4.0. https://apps.worldagroforestry.org/treedb/. https://apps.worldagroforestry.org/treedb/. Accessed 15 Feb 2024.

Ilondea, B.A., Beeckman, H., Ouédraogo, D.Y., et al., 2019. Une forte saisonnalité du climat et de la phénologie reproductive dans la forêt du Mayombe : l'apport des données historiques de la Réserve de Luki en République démocratique du Congo. Bois Forets Des Trop 341, 39–53. https://doi.org/10.19182/BFT2019.341.A31753.

Ilondea, A.B., De Mil, T., Hubau, W., et al., 2020. Towards improving the assessment of rainforest carbon: Complementary evidence from repeated diameter measurements and dated wood. Dendrochronologia 62, 125723. https://doi.org/10.1016/j.dendro.2020.125723.

Kafuti, C., Van den Bulcke, J., Beeckman, H., et al., 2022. Height-diameter allometric equations of an emergent tree species from the Congo Basin. For. Ecol. Manag. 504, 119822. https://doi.org/10.1016/j.foreco.2021.119822.

Kasekete, D.K., Ligot, G., Mweru, J.P.M., et al., 2022. Growth, productivity, biomass and carbon stock in eucalyptus saligna and grevillea robusta plantations in North Kivu.

Democratic Republic of the Congo. Forests 13, 1508. https://doi.org/10.3390/F13091508/S1.

Kasongo, Y.E., Van Acker, J., Van de Vyver, H., et al., 2023. Ground-based climate data show evidence of warming and intensification of the seasonal rainfall cycle during the 1960–2020 period in Yangambi, Central Congo Basin. Clim. Chang. 176, 1–28. https://doi.org/10.1007/S10584-023-03606-0/TABLES/4.

Kearsley, E., 2015. Carbon storage and functional diversity of tropical rainforest in the Congo Basin, 199 pp.

Kearsley, E., de Haulleville, T., Hufkens, K., et al., 2013. Conventional tree height–diameter relationships significantly overestimate aboveground carbon stocks in the Central Congo Basin. Nat. Commun. 4, 2269. https://doi.org/10.1038/ncomms3269.

Kearsley, E., Verbeeck, H., Stoffelen, P., et al., 2024. Historical tree phenology data reveal the seasonal rhythms of the Congo Basin rainforest. Plant-Environment Interact 5, e10136. https://doi.org/10.1002/PEI3.10136.

Keay, R.W.J., 1956. African vegetation: meeting at Yangambi. Nature 178, 1273–1274. https://doi.org/10.1038/1781273A0.

Kipute, D.D., Mate, J.P., Sufo Kankeu, R., et al., 2023. Effectiveness of the Yangambi Biosphere Reserve in Reducing Deforestation in the Democratic Republic of the Congo. Hum. Ecol. 51, 75–87. https://doi.org/10.1007/S10745-022-00378-6/FIGURES/6.

Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628–1632. https://doi.org/10.1126/science.1111773.

Lee, W.J.T., Masudi, E.B., Ndongo, J.D., et al., 2021. Congo Basin rainforest — invest US $150 million in science. Nature 598, 411–414. https://doi.org/10.1038/d41586-021-02818-7.

Lefebvre, D., Williams, A.G., Kirk, G.J.D., et al., 2021. Assessing the carbon capture potential of a reforestation project. Sci. Rep. 11, 19907. https://doi.org/10.1038/s41598-021-99395-6.

Lenth, R.V., 2017. Emmeans: estimated marginal Means, aka Least-Squares Means. CRAN Contrib Packag. https://doi.org/10.32614/CRAN.PACKAGE.EMMEANS.

Lewis, S.L., Phillips, O.L., Sheil, D., et al., 2004. Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation and comparison when census intervals vary. J. Ecol. 92, 929–944. https://doi.org/10.1111/J.0022-0477.2004.00923.X.

Lewis, S.L., Wheeler, C.E., Mitchard, E.T.A., Koch, A., 2019. Restoring natural forests is the best way to remove atmospheric carbon. Nat 5687750 (568), 25–28. https://doi.org/10.1038/d41586-019-01026-8.

Ligot, G., Gourlet-Fleury, S., Dainou, K., et al., 2022. Tree growth and mortality of 42 timber species in Central Africa. For. Ecol. Manag. 505, 119889. https://doi.org/10.1016/j.foreco.2021.119889.

Liu, C.L.C., Kuchma, O., Krutovsky, K.V., 2018. Mixed-species versus monocultures in plantation forestry: Development, benefits, ecosystem services and perspectives for the future. Glob Ecol Conserv 15, e00419. https://doi.org/10.1016/j.gecco.2018.e00419.

Luambua, N.K., Hubau, W., Salako, K.V., et al., 2021. Spatial patterns of light-demanding tree species in the Yangambi rainforest (Democratic Republic of Congo). Ecol. Evol. 11, 18691–18707. https://doi.org/10.1002/ECE3.8443.

Malhi, Y., Adu-Bredu, S., Asare, R.A., et al., 2013. African rainforests: past, present and future. Philos Trans R Soc B Biol Sci 368. https://doi.org/10.1098/RSTB.2012.0312.

Marien, J.-N., Mallet, B., 2004. Nouvelles perspectives pour les plantations forestières en Afrique centrale. Bois Forêts des Trop.

Martin, A.R., Doraisami, M., Thomas, S.C., 2018. Global patterns in wood carbon concentration across the world's trees and forests. Nat. Geosci. 11, 915–920. https://doi.org/10.1038/s41561-018-0246-x.

Memiaghe, H.R., Lutz, J.A., Korte, L., et al., 2016. Ecological Importance of Small-Diameter Trees to the Structure, Diversity and Biomass of a Tropical Evergreen Forest at Rabi Gabon. PLoS One 11, e0154988. https://doi.org/10.1371/JOURNAL.PONE.0154988.

Mendoza-Páez, J.S., Giraldo, J.A., Mazo-Lopera, M.A., et al., 2024. Trends in planted native tree biomass established in a tropical Andes city water basins. Restor. Ecol. e14296. https://doi.org/10.1111/REC.14296.

Menga, P., Bayol, N., Nasi, R., Fayolle, A., 2012. Phénologie et diamètre de fructification du wengé, Millettia laurentii De Wild : implications pour la gestion. Bois Forêts des Trop 312, 31–41. https://doi.org/10.19182/BFT2012.312.A20501.

Meunier, Q., Moumbogou, C., Doucet, J.-L., 2015. Les arbres utiles du Gabon. Presses Agronomiques de Gembloux.

Mng'omba, S.A., Du Toit, E.S., Festus, Akinnifesi K., 2007. Tree and Forestry Science and Biotechnology Germination Characteristics of Tree Seeds: Spotlight on Southern African Tree Species. Tree For Sci Biotechnol.

Montagnini, F., Ugalde, L., 2003. Navarro C (2003) growth characteristics of some native tree species used in silvopastoral systems in the humid lowlands of Costa Rica. Agrofor. Syst. 592 (59), 163–170. https://doi.org/10.1023/A:1026351812036.

De, Madron L.D., Nasi, R., Détienne, P., 2000. Accroissements diamétriques de quelques essences en forêt dense africaine. bois forets des trop 263, 63–74. https://doi.org/10.19182/BFT2000.263.A20062.

Ndongo, P.A.O., Peltier, R., Linjouom, I., et al., 2009. Plantations de bois d'oeuvre en zone équatoriale africaine : cas de l'arboretum de l'Enef de Mbalmayo au sud du Cameroun. BOIS FORETS DES Trop 299, 37–48. https://doi.org/10.19182/BFT2009.299.A20421.

Ngueguim, J.R., Zapfack, L., Noiha, N.V., et al., 2015. Expériences sylvicoles au Cameroun : Croissance, mortalité et adaptabilité des espèces de bois d'oeuvre dans la station forestière de Mangombé (1964–2010). Int. J. Biol. Chem. Sci. 9, 2789–2807. https://doi.org/10.4314/IJBCS.V9I6.22.

Ostertagová, E., Ostertag, O., Kováč, J., 2014. Methodology and Application of the Kruskal-Wallis Test. Appl. Mech. Mater. 611, 115–120. https://doi.org/10.4028/www.scientific.net/AMM.611.115.

Ouédraogo, D.-Y., Fayolle, A., Daïnou, K., et al., 2014. Enrichment of Logging Gaps with a High Conservation Value Species (Pericopsis elata) in a Central African Moist Forest. Forests 5, 3031–3047. https://doi.org/10.3390/f5123031.

Ouédraogo, D.Y., Doucet, J.L., Daïnou, K., et al., 2018. The size at reproduction of canopy tree species in Central Africa. Biotropica 50, 465–476. https://doi.org/10.1111/BTP.12531.

Palou, M.O., Peltier, R., Balarabe, O., et al., 2010. Abandon ou extension des plantations d'acacias au Nord-Cameroun : tout dépendra du fonctionnement des filières gomme arabique. Bois Forêts des Trop.

Parr, C.L., Te, Beest M., Stevens, N., 2024. Conflation of reforestation with restoration is widespread. Science 383, 698–701. https://doi.org/10.1126/SCIENCE.ADJ0899.

Picard, N., Gourlet-Fleury, S., 2008. Manuel de référence pour l'installation de dispositifs permanents en forêt de production dans le Bassin du Congo. COMIFAC.

Piotto, D., Montagnini, F., Ugalde, L., Kanninen, M., 2003. Performance of forest plantations in small and medium-sized farms in the Atlantic lowlands of Costa Rica. For. Ecol. Manag. 175, 195–204. https://doi.org/10.1016/S0378-1127(02)00127-5.

Piotto, D., Víquez, E., Montagnini, F., Kanninen, M., 2004. Pure and mixed forest plantations with native species of the dry tropics of Costa Rica: a comparison of growth and productivity. For. Ecol. Manag. 190, 359–372. https://doi.org/10.1016/J.FORECO.2003.11.005.

Potapov, P.V., Turubanova, S.A., Hansen, M.C., et al., 2012. Quantifying forest cover loss in Democratic Republic of the Congo, 2000–2010, with Landsat ETM+ data. Remote Sens. Environ. 122, 106–116. https://doi.org/10.1016/j.rse.2011.08.027.

Poulsen, J.R., Clark, C.J., Smith, T.B., 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. J. Trop. Ecol. 17, 787–808. https://doi.org/10.1017/S0266467401001602.

Proces, P., Dubiez, E., Bisiaux, F., et al., 2018. Production d'Acacia auriculiformis dans le système agroforestier de Mampu, plateau Batéké, République démocratique du Congo. Bois Forets Des Trop 334, 23. https://doi.org/10.19182/bft2017.334.a31489.

Quispe-Melgar, H.R., Huayta-Hinojosa, L.D., Llacua-Tineo, Y.S., et al., 2024. Evaluating the performance of Polylepis incana seeds: reassessing their potential for restoration and conservation of high Andean forests. Restor. Ecol. e14276. https://doi.org/10.1111/REC.14276.

R Core Team, 2023. R: The R Project for Statistical Computing. https://www.r-project.org/. Accessed 10 Dec 2024.

Sagang, L.B.T., Momo, S.T., Libalah, M.B., et al., 2018. Using volume-weighted average wood specific gravity of trees reduces bias in aboveground biomass predictions from forest volume data. For. Ecol. Manag. 424, 519–528. https://doi.org/10.1016/j.foreco.2018.04.054.

Sanogo, S., Sacande, M., Van Damme, P., Ndiaye, I., 2013. Caractérisation, germination et conservation des graines de Carapa procera DC. (Meliaceae), une espèce utile en santé humaine et animale. Biotechnol. Agron. Soc. Environ. 17, 321–331.

Schure, J., Ingram, V., Arts, B., et al., 2015. Institutions and access to woodfuel commerce in the Democratic Republic of Congo. Forest Policy Econ. 50, 53–61. https://doi.org/10.1016/j.forpol.2014.06.010.

Seddon, N., Turner, B., Berry, P., et al., 2019. (2019) Grounding nature-based climate solutions in sound biodiversity science. Nat. Clim. Chang. 92 (9), 84–87. https://doi.org/10.1038/s41558-019-0405-0.

Seddon, N., Chausson, A., Berry, P., et al., 2020a. Understanding the value and limits of nature-based solutions to climate change and other global challenges. Philos Trans R Soc B Biol Sci 375, 20190120. https://doi.org/10.1098/rstb.2019.0120.

Seddon, N., Daniels, E., Davis, R., et al., 2020b. Global recognition of the importance of nature-based solutions to the impacts of climate change. Glob Sustain 3, e15. https://doi.org/10.1017/SUS.2020.8.

Seddon, N., Smith, A., Smith, P., et al., 2021. Getting the message right on nature-based solutions to climate change. Glob. Chang. Biol. 27, 1518–1546. https://doi.org/10.1111/GCB.15513.

Shimamoto, C.Y., Botosso, P.C., Marques, M.C.M., 2014. How much carbon is sequestered during the restoration of tropical forests? Estimates from tree species in the Brazilian Atlantic forest. For. Ecol. Manag. 329, 1–9. https://doi.org/10.1016/j.foreco.2014.06.002.

Singh, A.N., Kumar, A., 2022. Ecological performances of exotic and native woody species on coal mine spoil in Indian dry tropical region. Ecol. Eng. 174, 106470. https://doi.org/10.1016/j.ecoleng.2021.106470.

Sullivan, M.J.P., Talbot, J., Lewis, S.L., et al., 2017. Diversity and carbon storage across the tropical forest biome. Sci. Rep. 7, 39102. https://doi.org/10.1038/srep39102.

Turner, I.M., 2004. The Ecology of Trees in the Tropical rain Forest. Cambridge university press, the Edinburgh Building, Cambridge CB2 2RU, UK.

Tyukavina, A., Hansen, M.C., Potapov, P., et al., 2018. Congo Basin forest loss dominated by increasing smallholder clearing. Sci. Adv. 4, 2993. https://doi.org/10.1126/sciadv.aat2993.

van Breugel, M., Hall, J.S., Craven, D.J., et al., 2011. Early growth and survival of 49 tropical tree species across sites differing in soil fertility and rainfall in Panama. For. Ecol. Manag. 261, 1580–1589. https://doi.org/10.1016/j.foreco.2010.08.019.

Van de Perre, F., Willig, M.R., Presley, S.J., et al., 2018. Reconciling biodiversity and carbon stock conservation in an Afrotropical forest landscape. Sci. Adv. 4, eaar6603. https://doi.org/10.1126/sciadv.aar6603.

Van Den Bulcke, J., Boone, M.A., Dhaene, J., et al., 2019. Advanced X-ray CT scanning can boost tree ring research for earth system sciences. Ann. Bot. 124, 837–847. https://doi.org/10.1093/AOB/MCZ126.

van Vliet, N., Quintero, S., Muhindo, J., et al., 2023. Status of terrestrial mammals in the Yangambi Landscape, Democratic Republic of the Congo. Oryx 57, 799–810. https://doi.org/10.1017/S0030605322001569.

Vieilledent, G., Vaudry, R., Andriamanohisoa, S.F.D., et al., 2012. A universal approach to estimate biomass and carbon stock in tropical forests using generic allometric models. Ecol. Appl. 22, 572–583. https://doi.org/10.1890/11-0039.1.

Villasenor Alva, J.A., Estrada, E.G., 2009. A Generalization of Shapiro–Wilk's Test for Multivariate Normality. Commun Stat Methods 38, 1870–1883. https://doi.org/10.1080/03610920802474465.

Vinceti, B., Valette, M., Bougma, A.L., Turillazzi, A., 2020. How is forest landscape restoration being implemented in burkina faso? overview of ongoing initiatives. Sustain 10430 (12), 10430. https://doi.org/10.3390/SU122410430.

Warner, E., Cook-Patton, S.C., Lewis, O.T., et al., 2023. Young mixed planted forests store more carbon than monocultures—a meta-analysis. Front For Glob Chang 6, 1226514. https://doi.org/10.3389/FFGC.2023.1226514/BIBTEX.

Wickham, H., Chang, W., Henry, L., et al., 2024. Create Elegant Data Visualisations Using the Grammar of Graphics [R Package ggplot2 Version 3.5.1]. CRAN Contrib Packag. https://doi.org/10.32614/CRAN.PACKAGE.GGPLOT2.

Williamson, G.B., Wiemann, M.C., 2010. Measuring wood specific gravity…Correctly. Am. J. Bot. 97, 519–524. https://doi.org/10.3732/ajb.0900243.

Wishnie, M.H., Dent, D.H., Mariscal, E., et al., 2007. Performance of 24 tropical tree species in relation to reforestation strategies in Panama. Forest Ecology and Management. For. Ecol. Manag. 243, 39–49. https://doi.org/10.1016/J.FORECO.2007.02.001.

Wu, J., Wong, A.C.M., 2003. A note on determining the p-Value of Bartlett's Test of Homogeneity of Variances. Commun Stat - Theory Methods 32, 91–101. https://doi.org/10.1081/STA-120017801.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., et al., 2009. Data from: Towards a Worldwide Wood Economics Spectrum. Dryad Digital Repository.

Zemp, D.C., Gérard, A., Hölscher, D., et al., 2019. Tree performance in a biodiversity enrichment experiment in an oil palm landscape. J. Appl. Ecol. 56, 2340–2352. https://doi.org/10.1111/1365-2664.13460.

Zhang, J., Fu, B., Stafford-Smith, M., et al., 2020. (2020) Improve forest restoration initiatives to meet Sustainable Development Goal 15. Nat Ecol Evol 51 (5), 10–13. https://doi.org/10.1038/s41559-020-01332-9.

Zhu, H., Zhang, J., Cheuk, M.L., et al., 2023. Monoculture plantations impede forest recovery: evidence from the regeneration of lowland subtropical forest in Hong Kong. Front For Glob Chang 6, 1098666. https://doi.org/10.3389/FFGC.2023.1098666/BIBTEX.