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From roots to canopy: Ecological drivers of *Aucoumea klaineana* Pierre monodominance in Central African forests

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FROM ROOTS TO CANOPY: ECOLOGICAL DRIVERS OF *AUCOUMEA KLAINEANA* PIERRE MONODOMINANCE IN CENTRAL AFRICAN FORESTS

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Abstract

Okoumé (*Aucoumea klaineana* Pierre), “Gabon’s green gold”, is the most economically important timber species in Central Africa, accounting for more than one-third of the region’s annual production. This species is considered pioneer, light-demanding, and capable of forming monodominant stands. Although previous work has suggested the possibility of water and nutrient exchanges between neighboring individuals, the mechanisms involved have remained poorly characterized and have never been quantified. Understanding these processes is essential for developing sustainable management strategies that reconcile productivity with long-term sustainability of populations.

This thesis addresses three research questions inspired by the mechanisms proposed to explain monodominance in tropical forests: (**i**) Do light conditions play a decisive role in the establishment and persistence of Okoumé populations? (**ii**) Do the root-associated fungal communities exhibit assemblages that could influence nutrient exchanges or competition among neighboring trees? (**iii**) Can root grafts between individuals contribute to such exchanges?

The research was conducted in the FSC-certified forest concession allocated to “*Precious Woods-Concession Équatoriale des Bois”* in Gabon and in the Luki Biosphere Reserve (DRC).

Chapter 1 provides the contextual and theoretical foundation of the thesis. It introduces forest management practices in Central Africa and reviews the phenomenon of monodominance, summarizing the main ecological hypotheses that may apply to Okoumé.

Chapter 2 presents a comprehensive synthesis of research on Okoumé over the past 35 years, highlighting the gaps that limit our understanding of its ecology and regeneration dynamics. The analysis also shows that the “Vulnerable” conservation status currently assigned by the IUCN is not justified.

To clarify the environmental conditions enabling Okoumé to regenerate in cohorts, an 18-month semi-controlled experiment examined the effects of light and biotic pressure on 210 seedlings (**Chapter** 3). Survival remained remarkably high (97%) across the entire light gradient (1-100% of relative irradiance). This ability to survive, but not to grow, in deep shade supports the idea that seedlings can persist for at least several months while awaiting canopy disturbances. However, biotic pressure strongly reduced health and growth, mainly due to infestations by psyllids (93%) and the development of black canker (23%). Overall, regeneration success therefore appears to be initially more limited by biotic pressure than by light availability.

To identify any root-associated fungal communities involved in stand monodominance and/or suppressed tree survival, **Chapter** 4 first describes methodological improvements for molecular analyses, including the addition of activated charcoal during DNA extraction and bovine serum albumin during PCR.

These refinements enabled the first high-throughput sequencing of fungal communities in Okoumé fine roots. The analysis revealed diverse and variable communities dominated by saprotrophic fungi, with absent ectomycorrhizal associations and arbuscular mycorrhiza consistently present but not abundant. This high variability does not explain the remarkable persistence of shaded individuals, indicating that root-fungi interactions likely play a limited role in structuring stands or maintaining monodominance.

To observe root grafting, excavations and mapping of root systems were carried out in three monodominant stands (**Chapter** 5). This revealed that root grafts are frequent, particularly among dominant and co-dominant trees, and can also involve suppressed individuals, which tend to perform better when grafted. Such interconnected networks likely contribute to the persistence of monodominant stands by enhancing resource distribution, reducing competition, and allowing the survival of light-deprived trees. Nevertheless, precisely quantifying the functional role of grafting remains challenging due to uncertainties in tree age and growth rates, as annual rings are often indistinct. Despite these limitations, the data indicate that root grafting, potentially in combination with other facilitative processes such as litter accumulation, contributes to structural cohesion, resilience, and the long-term stability of Okoumé-dominated forests.

Finally, **Chapter** 6 integrates the thesis findings to propose a multifactorial explanation for Okoumé monodominance, involving shade tolerance, resilience to biotic stress, and root interactions between individuals. The study highlights the importance of population ecology approaches for sustainable management and conservation of tree populations. It offers new insights into tropical forest dynamics and demonstrates how Okoumé employs a unique strategy to shape and dominate its own forest ecosystems.

Résumé

L'Okoumé (*Aucoumea klaineana* Pierre), l'« or vert du Gabon », est l'essence commerciale la plus importante d'Afrique centrale, représentant plus d'un tiers de la production annuelle de la région. Cette espèce est considérée comme pionnière, héliophile et apte à former des peuplements monodominants. Bien que des travaux antérieurs supposent des échanges d'eau et de nutriments entre individus voisins, les mécanismes impliqués restent peu caractérisés et jamais quantifiés. Comprendre ceux-ci est pourtant essentiel pour développer des stratégies de gestion durable conciliant productivité et maintien des populations sur le long terme.

Cette thèse aborde trois questions de recherche, inspirées des mécanismes proposés pour expliquer la monodominance en forêt tropicale : (**i**) les conditions lumineuses jouent-t-elles un rôle déterminant dans l'installation et la persistance d'une population d'Okoumé ? (**ii**) Les communautés fongiques associées aux racines présentent-elles des assemblages susceptibles d'influencer les échanges de nutriments ou la compétition entre arbres voisins ? (**iii**) des greffes racinaires entre individus peuvent-elles, quant à elles, participer à de tels échanges ?

Les travaux ont été réalisés dans la concession certifiée FSC attribuée à « *Precious Woods-Concession Equatoriale des Bois* » au Gabon et dans la Réserve de biosphère de Luki (RDC).

Le **Chapitre** 1 fournit le cadre contextuel et théorique de la thèse. Il introduit le concept d'exploitation forestière en Afrique centrale et passe en revue le phénomène de la monodominance, en résumant les principales hypothèses écologiques pouvant s'appliquer à l'Okoumé.

Le **Chapitre** 2 propose ensuite une synthèse complète des recherches sur l'Okoumé au cours des 35 dernières années, mettant en évidence les lacunes limitant la compréhension de son écologie et de sa dynamique de régénération. Cette analyse montre également que le statut de conservation « Vulnérable » attribué par l'UICN n'est pas justifié.

Pour élucider les conditions environnementales permettant à l'Okoumé de se régénérer par cohorte, une expérience de 18 mois en conditions semi-contrôlées a évalué les effets de la lumière et de la pression biotique sur 210 plantules (**Chapitre** 3). La survie est restée remarquablement élevée (97 %) sur toute la plage lumineuse (1-100 % d'éclairement relatif). Cette capacité à survivre, mais pas à croître dans l'ombre soutient l'idée que les plantules peuvent attendre des perturbations de la canopée pendant plusieurs mois au moins. Cependant, la pression biotique réduit fortement la santé et la croissance des plantules, principalement en raison des infestations de psylles (93 %) et du développement du chancre noir (23 %). Dans l'ensemble, le succès de la régénération semble donc initialement davantage limité par la pression biotique que par la lumière.

Afin d’identifier d’éventuelles communautés fongiques associées aux racines et impliquées dans la monodominance des peuplements et/ou dans la survie des arbres dominés, le **Chapitre** 4 présente d’abord des améliorations des méthodes moléculaires existantes, grâce à l’ajout de charbon actif lors de l’extraction de l’ADN et de l’albumine sérique bovine lors de la PCR. Ces améliorations ont permis le premier séquençage à haut débit des communautés fongiques des racines fines d’Okoumé. L’analyse a révélé des communautés diverses et variables, dominées par des champignons saprotrophes, tandis que les associations ectomycorhiziennes étaient absentes et que les mycorhizes arbusculaires étaient présentes mais peu abondantes. Cette variabilité ne permet pas d’expliquer la persistance remarquable des individus dominés dans l’ombre, indiquant que les relations champignons-racines ne jouent probablement pas un rôle majeur ni dans la structuration des peuplements, ni dans le maintien de la monodominance.

Pour observer les greffes racinaires, des excavations et une cartographie des systèmes racinaires ont été réalisées dans trois peuplements monodominants (**Chapitre** 5). Cela a révélé que les greffes racinaires sont fréquentes, en particulier entre les arbres dominants et codominants, et peuvent inclure des individus dominés, qui tendent à mieux se développer lorsqu’ils sont greffés. Ces réseaux interconnectés favorisent probablement la persistance des peuplements monodominants en améliorant la distribution des ressources, en réduisant la compétition et en permettant la survie des individus privés de lumière. Cependant, quantifier précisément le rôle du greffage racinaire reste difficile en raison des incertitudes sur l’âge des arbres et leur rythme de croissance, les cernes annuels étant souvent indistincts. Malgré ces limites, les données indiquent que le greffage racinaire, potentiellement en combinaison avec d’autres processus facilitatifs tels que l’accumulation de litière, contribue à la cohésion structurelle, à la résilience et à la stabilité à long terme des peuplements monodominants d’Okoumé.

Enfin, le **Chapitre** 6 intègre les résultats de la thèse pour proposer une explication multifactorielle de la monodominance de l’Okoumé, impliquant la tolérance à l’ombrage, la résilience face aux stress biotiques et les interactions racinaires entre individus. L’étude souligne l’importance des approches liées à l’écologie des populations pour assurer la gestion durable et la conservation des essences commerciales, offrant de nouvelles perspectives dans la compréhension de la dynamique des forêts tropicales et montrant comment l’Okoumé utilise une stratégie unique pour façonner et dominer ses propres écosystèmes forestiers.

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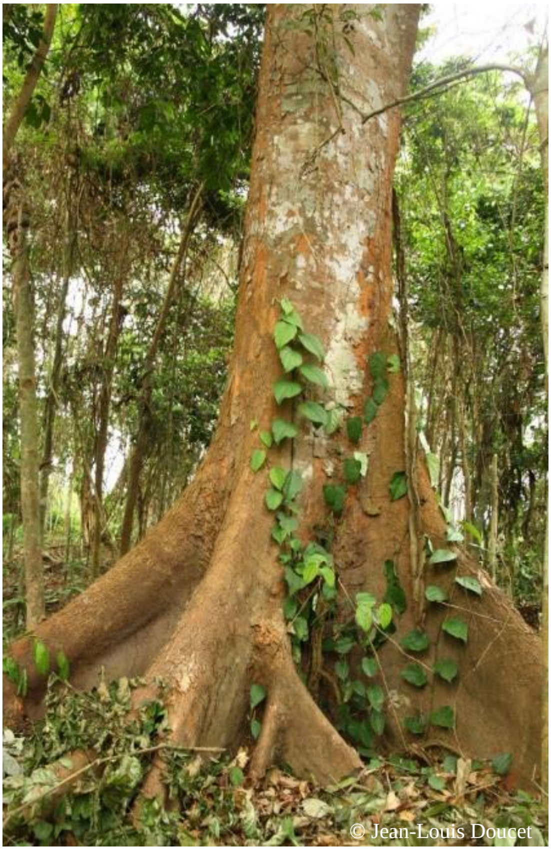
Chapter 1

General Introduction



Okoumé bole and buttresses

1 Central African forest

Central Africa's forest constitutes the second-largest tropical rainforest block in the world after the Amazon forest. It spans 184 million hectares and covers six countries: Cameroon, the Central African Republic, the Republic of Congo, the Democratic Republic of Congo (DRC), Equatorial Guinea, and Gabon (Vancutsem et al., 2021). It is part of the Guineo-Congolian center of endemism, an area of about 2.8 million km² stretching from the Guinean coast to the eastern part of the DRC, and interrupted in its central part by the Dahomey Gap, a dry corridor located in Benin (White, 1983).

This immense region hosts a wide range of forest types that differ in their structural and functional characteristics. Such diversity arises from variations in climatic conditions (e.g., humidity, temperature, evapotranspiration, rainfall), soil types, and topography, as well as from their long biogeographic and anthropogenic history. Overall, Central Africa is composed of a complex mosaic of forest ecosystems. Réjou-Méchain et al. (2021) identified ten forest types based on the community-weighted means of three key functional traits: wood density, deciduousness, and maximum diameter (Figure 1) :

(1) Atlantic highland evergreen, (2) Atlantic coastal evergreen, (3) Atlantic inland evergreen, (4) Margin semideciduous, (5) Evergreen-semideciduous on sandstone, (6) Semideciduous, (7) Central evergreen, (8) Mixed evergreen, (9) Degraded semideciduous, and (10) Semideciduous-evergreen transition. This typology captures

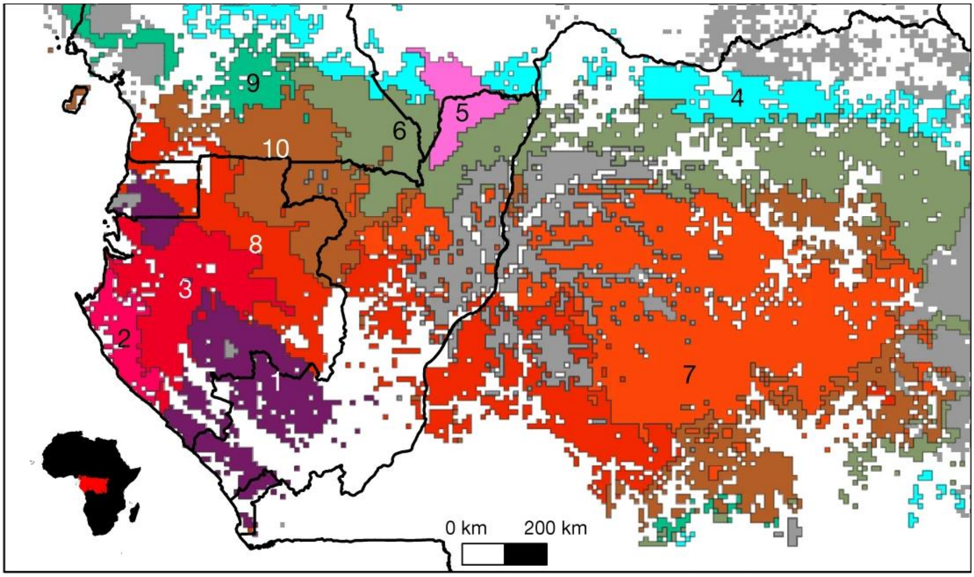


Figure 1 : Réjou-Méchain et al.'s (2021) Central African forest types based on hierarchical clustering of predicted floristic gradients.

the ecological variability of Central African forests and helps to assess their relative sensitivity to climate change and increasing human pressure.

Human activities have shaped these rainforests for more than 650,000 years (Braucher et al., 2022). The advent of agriculture around 10,000 years ago marked a major turning point, locally transforming forest dynamics (Tauger, 2020). Shifting cultivation practices created canopy openings that favored the establishment of light-demanding tree species. Over time, however, the progressive sedentarization of human populations, particularly during the colonial period in the 19th century, led to a decline in such disturbances. This reduction, together with the natural aging of forest stands, limited opportunities for regeneration of many commercially valuable tree species, most of which are light-demanding (Catinot and Bossanyi, 1965; Doucet, 2003; Karsenty and Gourlet-Fleury, 2006; Morin-Rivat et al., 2017; Van Gemerden et al., 2003).

Although this situation does not imply a risk of extinction, it reflects a regeneration shortfall that increasingly favors shade-tolerant competitors (Morin-Rivat et al., 2017;Van Gemerden et al., 2003). Overall, the natural dynamics of Central African forests appear insufficient to ensure the future availability of these commercially important taxa under current conditions in managed forest concessions, (Catinot and Bossanyi, 1965) where selective logging is the main form of intervention and where disturbances remain relatively limited compared to historical or agricultural clearing regimes. This does not overlook broader large-scale pressures such as agricultural expansion, fuelwood collection, and illegal logging, but highlights a specific challenge within production forests, where low-intensity management may not fully meet the ecological requirements of light-demanding species threatening both their economic viability and long-term sustainability.

2 Forest exploitation in Central Africa

2.1 *Forest management*

In Central Africa, approximately 14.9% of the forest are designated as protected areas (Eba'a Atyi et al., 2022; Vancutsem et al., 2021). These protected areas cover slightly less than 30 million hectares, while about 27% (54 million hectares) are classified as production forests. The rest, more than 100 million hectares, remains unallocated and is exploited by local populations (agriculture, artisanal logging, non-forest product harvest) (Bayol et al., 2022).

Production forests are predominantly managed through a forest concession system, under which the State retains ownership of natural forests. The government grants logging rights to private operators within a defined area known as a Forest Management Unit (FMU) for a period typically ranging between 20 and 35 years, corresponding to a forest rotation or cutting cycle (Eba'a Atyi et al., 2022). The aim is to ensure the profitability for both public and private stakeholders while preserving the goods and services provided by these forests (biodiversity, carbon storage, habitat, livelihoods, etc). During this period, forest concessions are required to comply with the management standards set by national authorities, which include the development and implementation of a forest management plan (Nasi et al., 2012). In 2018, 60% of the area allocated to forest operators was covered by management plans (FRMi, 2018).

The management plan serves as the central tool for ensuring sustainable forest use. It defines distinct land-use units, known as “management series”, each with specific objectives and rules. The production series is based on a preliminary forest inventory and aims to ensure a sustained production of timber that is compatible with the long-term availability of the resource and the preservation of the forest's ecological and social functions. This forest inventory combines botanical and dendrological assessments to characterize species populations, diversity, abundance, and spatial distribution. These data inform management decisions, support resource estimation, and assess stock recovery potential.

Among others, the management plan defines minimum cutting diameters (MCD) based on the growth dynamics of harvested taxa and cutting cycles to support the stock recovery. However, the typical 25-30 year cutting cycles are often too short to maintain the same volume of timber species in the long term (Karsenty, 2018). Furthermore, recovery rates are often estimated using parameters that fail to reflect the species dynamics, due to substantial variation in growth, mortality, and recruitment rates across both taxa and habitats. Inaccurate projections in management plans have been widespread, largely due to a lack of reliable data (Sépulchre et al., 2014). Empirical evidence now suggests that actual timber stocks may be declining faster than anticipated, underscoring the need for more robust forest management (Groenendijk et al., 2014).

Over the past two decades, in an effort to address these shortcomings, a network of permanent forest plots has been established in several forest concessions (Doucet et al., 2004; Karsenty and Gourlet-Fleury, 2006; Picart and Gourlet-Fleury, 2008). These plots allow the study of forest dynamics over time, measuring tree growth, monitoring natural regeneration, estimating mortality rates, and even evaluating forest responses to logging and climate change. These data should make it possible to reliably estimate management parameters, including recovery rates.

2.2 *The challenge of light-demanding timber species*

To date, only six taxa account for about 87% of the region’s total timber output (FRMi, 2018) (Figure 2). These include Okoumé (*Aucoumea klaineana* Pierre, 36%), Sapelli (*Entandrophragma cylindricum* (Sprague) Sprague, 19%), Ayous (*Triplochiton scleroxylon* K. Schum., 14%), Tali (*Erythrophleum ivorense* L., 8%), Azobé (*Lophira alata* Banks ex Gaertn., 5%), and Okan (*Cylicodiscus gabunensis* Harms, 5%). Okoumé is the only species in this group primarily dedicated to plywood production, owing to its low density and excellent peeling properties. In contrast, Sapelli and Ayous are mainly used for joinery, furniture, and light construction, although they also exhibit good peeling capacity. Tali, Azobé, and Okan are chiefly employed in heavy-duty applications such as construction, hydraulic works, and infrastructure, due to their high density and durability (Gérard et al., 2016).

Together, these six species represent less than 0.1% of the tree diversity of continental tropical Africa assuming a maximum of approximately 6,000 species (Slik et al., 2015). Yet, around 150 species could each provide more than 15,000 m³ of logs per year each at the regional scale (FRMi, 2018). Notably, five of these six taxa are light-demanding species, requiring high light availability for successful regeneration (Doucet, 2003; Van Gemerden et al., 2003; Karsenty et al., 2006).

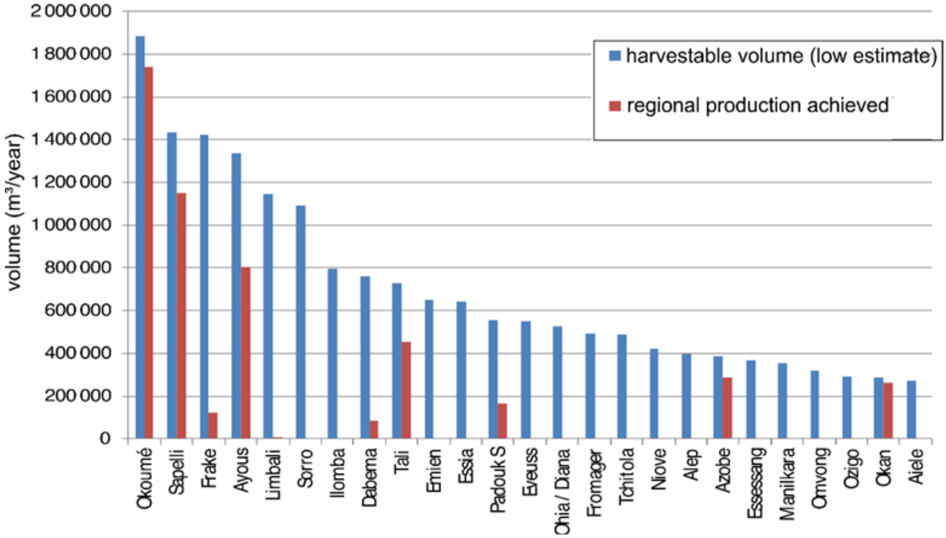


Figure 2 : Comparison of current mobilization rates by species in Central Africa, considering potential production in blue (based on minimum estimates from the year 2018) and actual timber yields in red, for the 25 most abundant tree species, expressed in gross wood volume per year (in m³) (adapted from FRMi, 2018). For scientific names, see Appendix 1 in FRMi (2018, pp. 211-225).

In reduced-impact logging (RIL) systems, harvesting intensity is typically limited to 0.5 to 2 trees per hectare (Desclée et al., 2014). The canopy openings created by selective harvesting are then generally too small and sparse to promote adequate regeneration of these light-demanding species (Biraud, 1959; Doucet, 2003).

However, the fact that these species are light-demanding does not mean they all require the same long-term management strategies. For instance, in addition to being light-demanding, Okoumé and Ayous share several ecological traits: both are long-lived, wind-dispersed, gregarious and characterized by relatively high growth rates (Figure 3). Yet, they differ markedly in their regeneration behavior. Okoumé fruits regularly and can easily colonize open or degraded areas, including savannas. This ability to continuously produce seedlings and rapidly establish in canopy gaps supports a constant recruitment model, which assumes a steady and sufficient inflow of young individuals that adjusts to maintain the first-class population. It also tends to maintain a relatively high density of small-diameter adult trees within stands, even under shaded conditions, thereby contributing to stable population numbers.

Ayous, in contrast, has episodic fruiting and needs fertile soils for a successful regeneration. Its recruitment thus occurs intermittently, only when specific conditions align. Such regeneration dynamics are better represented by a fixed recruitment model independent of current population, which assumes a lower and more variable rate of seedling establishment, often approximating the species' natural mortality rate. Consequently, species like Ayous may require longer cutting cycles to maintain stable timber volumes over the long term (Karsenty, 2018).

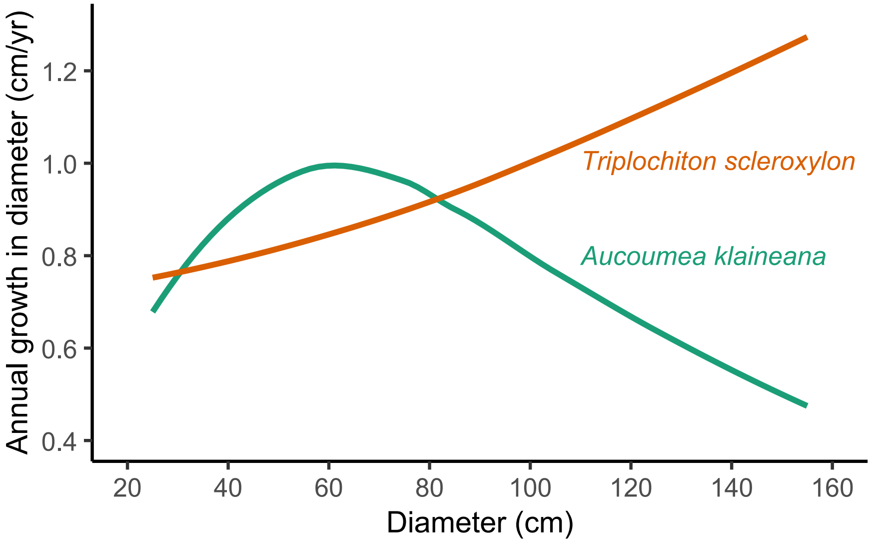


Figure 3: Smoothed growth curves of *Aucoumea klaineana* (Okoumé) and *Triplochiton scleroxylon* (Ayous) (adapted from Nkenne Tikeng, 2025).

Understanding these contrasting dynamics is essential for setting realistic and species-specific management parameters. Improving our knowledge of the ecological functioning of commercial taxa is crucial for reconciling forest ecosystem sustainability with economic imperatives (Zimmerman and Kormos, 2012). In-depth insight into the biotic and abiotic factors that influence their regeneration, growth, and survival will support the development of more effective and sustainable forest management strategies, ultimately ensuring the recovery of timber stocks over successive cutting cycles.

3 Okoumé : Gabon’s green gold

Although its natural distribution is confined to Gabon, Equatorial Guinea, the Republic of Congo, and the southernmost part of Cameroon, Okoumé remains by far the most intensively harvested timber species in Central Africa, earning it the nickname “Gabon’s green gold.” Renowned for its lightweight, defect-free wood, Okoumé is especially prized in plywood production, making it a cornerstone of the region’s timber economy.

Owing to its dual ecological importance and economic dominance, Okoumé represents an ideal model species for exploring the ecological functioning of commercial species. Its ecology and population dynamics are discussed in detail in Chapter 2, but a brief overview is presented here.

Okoumé is an anemochorous, light-demanding, and gregarious pioneer species, characterized by its capacity to colonize open habitats and disturbed sites such as savannas, post-agricultural fallows, former logging yards, and roadsides (Biraud, 1959; Doucet, 2003). Individuals often occur in dense, even-aged patches, where root grafts (vascular fusions between root systems) are thought to facilitate exchanges of water, nutrients, and carbon among neighboring trees. This led Leroy Deval (1973) to describe it as a “social” species. Through such mechanisms, Okoumé efficiently occupies disturbed environments, forming monospecific colonizing forests that later evolve into monodominant stands accounting for 80-95% of the canopy for the most part of its life (Delègue et al., 2001; Pangou et al., 2003) before gradually giving way to mixed and mature forests as more shade-tolerant species establish (Fuhr et al., 1998; Fuhr, 1999a; White et al., 2000).

Okoumé logs were first exported to Germany in 1889 (Brunck et al., 1990). Despite over a century of exploitation, knowledge of its ecology and silviculture remains fragmentary. Prominent works include those by Jean Leroy Deval in the 1970s (1974, 1976a, 1976b) and François Brunck et al. (1990). While they laid a solid foundation, for a sustainable management of Okoumé populations, some knowledge remains empirical and key aspects of the species’ biology such the role of root grafts (Leroy Deval, 1973, 1974) remain unknown. Moreover, Okoumé’s classification as “Vulnerable” by the International Union for Conservation of Nature (IUCN) (White, 1998) is based on outdated assessments, underscoring the need for renewed ecological and conservation studies (Chapter 2).

4 Monodominance in Okoumé forests

4.1 *Hypotheses explaining monodominance*

Tropical forests generally host a high diversity of tree species (Day et al., 2014; Sylvie Gourlet-Fleury et al., 2013). However, in some cases, a single species can represent over 60% of the canopy, forming what are known as monodominant stands (Peh et al., 2011a; Peh, 2024). This is particularly true in parts of Gabon, where Okoumé forms in some places nearly homogeneous stands (Caballé, 1978; Fuhr, 1999a; Fuhr et al., 2001; Mapaga et al., 2002; Saint-Aubin, 1963).

Although the monodominant stands of Okoumé are well documented (e.g., Brunck et al., 1990; Doucet, 2003; Fuhr, 1999a; Leroy Deval, 1976a; Pangou et al., 2003), the ecological processes sustaining their persistence remain unclear. Unlike other light-demanding pioneers such as Ayous, Okoumé can maintain dominance for extended periods, with suppressed trees surviving under deep shade. Unraveling the mechanisms behind this unusual persistence is essential to improve the ecological understanding and sustainable management of this key commercial species.

Peh et al. (2011a; 2024) expanded on Torti et al. (2001) hypotheses to explain tropical monodominance, introducing the concept of interdependent mechanisms and positive feedback loops. Processes differ from one species to another, meaning that each hypothesis has exceptions, no single mechanism is sufficient to fully explain the phenomenon. The key mechanisms are outlined below, with brief reflections on their relevance for Okoumé.

1) **Low frequency of exogenous disturbances**. A reduced frequency of external disturbances limits gap formation, thereby restricting the establishment of competitive light-demanding species. Species living in undisturbed monodominant forest often have a slow growth and a limited seed dispersal (Tovar et al., 2019).

   This hypothesis does not appear to apply to Okoumé since this species requires disturbances for regeneration and has rather high growth rates (Doucet, 2003).

2) **Shade tolerance and seedling survival under closed canopy.** Even though shade tolerance in juvenile trees is not a prerequisite for monodominance, several studies have highlighted a link between seedling persistence in low-light conditions and monodominance (Hall et al., 2020; Marimon et al., 2012). For instance, *Gilbertiodendron dewevrei* (De Wild.) J.Léonard can germinate and grow under dense canopy despite limited light input (Hall et al., 2020).

   In the case of Okoumé, although described as a light-demanding pioneer, the precise light requirements of seedlings have never been quantified. Assessing how Okoumé seedlings respond to varying light levels is therefore essential to determine whether low-light persistence contributes to its local dominance and the formation of monodominant stands.

3) **Slow litter decomposition and low nutrient availability**. A reduced litter decomposition rate affects soil nutrient cycling and may favor monodominant species. In forests dominated by *G. dewevrei*, litter breakdown occurs two to three times more slowly than in adjacent mixed forests, slowing nutrient release and potentially hindering the survival of other species (Peh et al., 2012; Torti et al., 2001). However, several studies report no significant differences in soil properties between monodominant and mixed stands (Peh, et al., 2011a; Van Der Velden et al., 2014; Hall et al., 2020).

   Okoumé also produces abundant and persistent leaf litter (Midoko Iponga et al., 2020), leading Leroy Deval (1974) to suggest that it "*creates its own soil*", enabling growth across diverse edaphic conditions. Investigating litter decomposition and nutrient dynamics in Okoumé monodominant stands compared to mature mixed forests would therefore be crucial to assess whether slow nutrient turnover contributes to its monodominance.

4) **Large seeds to overcome deep litter layers**. Slowly decomposing leaves lead to substantial litter accumulation in monodominant forests, creating a physical barrier that limits the germination of other species by reducing light penetration, altering soil conditions, and potentially releasing allelopathic compounds. Some authors suggest that large-seeded species are better suited to overcome these constraints (Kazmierczak et al., 2016), thereby promoting monodominance.

   This hypothesis does not apply to okoumé because of the small size (3 to 4 cm, wing included) (Aubréville, 1962) and low weight of its seed (0.01 g) (Maisels, 2004).

5) **Association with ectomycorrhizal (EcM) fungi**. Some monodominant species form EcM associations, which may confer a competitive advantage through enhanced nutrient acquisition either via improved soil exploration or direct litter decomposition (e.g., Diedhiou et al., 2014; Ebenye et al., 2017; Fukami et al., 2017; Liang et al., 2020). These mycorrhizal networks could promote seedling survival near conspecific adults.

   Although Okoumé's family members (Burseraceae) generally do not form ectomycorrhizal associations (Bâ et al., 2011), some researchers have suggested that Okoumé might be an exception (Leroy Deval, 1974; Louppe et al., 2000; Peh et al., 2011a). To date, this possibility remains unexplored and clearly warrants further investigation.

6) **Mast fruiting and predator satiation**. Some monodominant species exhibit supra-annual, synchronized flowering and fruiting which may be key to their success (Henkel et al., 2005; Henkel and Mayor, 2019). Such events may increase seedling survival by overwhelming seed predators and suppressing the build-up of specialist populations.

   Even though Okoumé undergoes abundant fruiting events roughly every three years (Hecketsweiler, 1992; Leroy Deval, 1976a) ,this seems unlikely related to predator satiation in this case. Indeed, Okoumé seeds are rarely consumed by predators due to their small size, low nutrient reserves, winged, wind-dispersed woody structure, which limits their attractiveness and accessibility to seed predators.

7) **Limited seed dispersal and gregarious growth.** Restricted dispersal can lead to dense seedling recruitment beneath parent trees, facilitating the formation of monodominant stands (Kazmierczak et al., 2016). This strategy enables gradual expansion through replacement of trees in adjacent mixed forests.

   This mechanism is unlikely to apply for Okoumé as species produces light weighted, wind-dispersed seeds, and its seedlings generally establish in open or disturbed environments rather than in the shaded understory conditions in the vicinity of older conspecifics.

8) **Escape from herbivory**. Low foliar damage may enhance individual survival and promote monodominance. Such resistance to herbivores and pathogens could be attributed to significant investment in leaf defenses. According to Janzen (1974), low species diversity in monodominant forests should exert strong selective pressure on dominant species to evolve robust defenses against specialist herbivores.

   A study conducted in Gabon reported severe defoliation of Okoumé by a lepidopteran species (Maisels, 2004), suggesting that leaf defense is unlikely to be a determining factor in its dominance.

In conclusion, among the previous hypotheses, the mechanisms most likely explaining the monodominance of Okoumé forests include: the temporary shade tolerance of the seedlings (**2**), the slow decomposition of the litter (**3**) and the potential association with ectomycorrhizal fungi (**5**) which is closely linked to soil microbiota whose communities remain poorly understood, particularly in tropical forests (Díaz-Vallejo et al., 2021).

4.2 *Relevant hypotheses to Okoumé monodominant stands*

4.2.1 Shade tolerance

Light is among the most limiting factors for the establishment and growth of tropical tree species (Baker et al., 2003). In old-growth mixed tropical forests, the vertical vegetation structure allows only about 2% of sunlight to reach the ground (Chazdon, 1988; Kyereh et al., 1999). Canopy openings created by natural disturbances, or anthropogenic activities, like selective logging or roads, strongly influence light availability and thus the recruitment and growth of pioneer species.

Okoumé needs sufficiently large gaps with a clear soil for a good regeneration but the size of the opening or the relative irradiance needed by the seedlings have never been quantified (Biraud, 1959; Doucet, 2003; Doucet et al., 2004). The persistence of suppressed seedlings in the understory, waiting for an opening during an unknown period, could also play a key role. The ability to exploit intermittent high-light patches likely could interact with disturbance regimes to shape the species' local dominance. Quantifying these dynamics is therefore essential to better understand how Okoumé maintains its abundance and forms monodominant stands.

4.2.2 Root-associated fungi

Fungal communities and their structural dynamics remain poorly understood in many ecosystems (Anderson et al., 2018; Tedersoo et al., 2014), and a large portion of global fungal diversity is still undocumented (Taylor et al., 2014). Fungi play essential roles in ecosystems as saprotrophs, pathogens, or mutualists, the latter forming complex interactions with plants depending on host identity and developmental stage.

Among these, mycorrhizal fungi form beneficial associations with plant roots (Smith and Read, 2008), enhancing nutrient uptake, disease resistance, and the exchange of essential compounds between individual plants. In tropical tree species as well, they aid in the assimilation of mineral resources found in the upper soil layers (Janos, 1983; Leroy Deval, 1976a). Two main functional groups are generally distinguished: ectomycorrhiza (EcM), dominant in temperate and boreal forests, and arbuscular mycorrhizal fungi (AM fungi), more common in herbaceous plants but also found in many tropical trees (Bâ et al., 2012; McGuire, 2007). AM fungi penetrate root cells, forming arbuscules that facilitate nutrient exchange (Smith et Read, 2008), while EcM envelop the roots and extend a hyphal network between root cells (Courty et al., 2010; Dickie et al., 2015; Smith and Read, 2008).

The mycorrhizal status of Okoumé has never been clearly defined. A single brief study (Onguene et al., 2002) mentioned an association with AM fungi based on root staining, without illustrations or specification of the sampling period. Conducted outside the species' natural range, this study reported an increase in mycorrhizal colonization up to 15 years of age, followed by a non-significant decline, with higher arbuscule frequency observed in naturally regenerating juveniles compared to plantation-grown individuals.

Fungal interactions also influence forest stand structure (Phillips et al., 2013; Soudzilovskaia et al., 2015). Species that form exclusive EcM relationships are often less susceptible to pathogenic infections and may inhibit the establishment of other fungal taxa (Gonthier et al., 2019; Zampieri et al., 2017), promoting dominance of certain plant species (Fukami et al., 2017; Henkel, 2003; Liang et al., 2020). Furthermore, EcM fungi compete for nutrients with saprotrophs through the so-called "Gadgil effect", leaving less available for decomposers, though reducing organic matter decomposition and increasing carbon storage in forest soils (Gadgil and Gadgil, 1971, 1975). However, the generalization of this effect remains uncertain and requires further investigation (Fernandez and Kennedy, 2016).

Broadly characterizing the mycobiome associated with Okoumé roots is therefore essential to better identify the role of fungal interactions in shaping these forest stands. A more comprehensive understanding of this fungal diversity will improve our grasp of ecosystem dynamics and refine conservation and management strategies for the species.

4.2.3 Root grafts

Among the mechanisms proposed above, Peh et al. (2011a, 2024) omit one major hypothesis, underscoring the persistent gaps in our understanding of monodominance in forest stands.

Indeed, Okoumé is known for forming root anastomosis (root grafts), natural root connections, first documented by Catinot (1962). This phenomenon, also called root grafting, allows for the exchange of resources such as water, sugars, minerals, and even microorganisms between individuals, primarily within the same species. These root grafts were discovered serendipitously during forestry operations in Gabon. While surveying old plantations, foresters observed the presence of scarred stumps (Figure 4) that remained alive for up to 40 years after being felled (Catinot, 1962; DIARF et al., 2000; Leroy Deval, 1974). This prolonged survival suggests the transfer of resources from canopy-dominant trees to shaded individuals, likely in exchange for an expansion of the root system.

Root anastomosis or root graft?

Etymologically, *anastomosis* refers to a general physical connection, whereas *graft* implies a more integrated union. Thus, “root anastomose” may describe any root connection, while “root graft” denotes a structurally, and often functionally, integrated union. Although the term “root anastomosis” used by Leroy Deval (1973) to describe root connections in *A. klaineana* is appropriate, the term “root graft” is used throughout this manuscript, following common usage in the scientific literature. Clarifications will be provided when necessary to distinguish whether connections are purely mechanical (physical contact) or involve functional integration between individuals.

Figure 4: Example of a healed Okoumé stump (presence of a callus at the cut site) resulting from root grafting with a neighboring tree reaching the canopy. © J-L Doucet

Leroy Deval explored this process in greater depth, dedicating his doctoral thesis (1974) to the ontogenetic and morphological development of the root system in Okoumé. His work then extended into a forest dynamics perspective, leading him to characterize the species as gregarious, or even social, based on the interactions and exchanges facilitated by these root grafts. By excavating root systems in plantations of various ages and densities (Figure 5), he demonstrated that the first grafts appear between four and six years of age, and exclusively between trees of differing social status (Leroy Deval, 1973). However, the actual functional role of these root grafts, whether they significantly influence water, nutrient, or carbon transfer, or contribute to tree growth or survival, has never been demonstrated.

Such root fusions are actually widespread among woody species (Graham and Bormann, 1966; La Rue, 1952; Mudge et al., 2009). Nevertheless, their ecological role remains poorly understood (Bader and Leuzinger, 2019). Numerous reviews have addressed the causes of these connections and their implications for forest management (Eis, 1972; Graham and Bormann, 1966; Lev-Yadun, 2011; Loehle and Jones, 1998). Several factors appear to influence their formation, including geographic proximity and genetic relatedness (Boys et al., 2005; Jelínková et al., 2009; Loehle and Jones, 1998; Tarroux et al., 2014). However, progress in this field has been limited by the difficulty of directly observing and experimentally manipulating these underground connections. Commonly used methods, such as colored (O’Neal and Davis, 2015) or radioactive tracers (Kuntz and Riker, 1956) remain costly and inappropriate for large-scale studies.

Figure 5: Excavated root systems of an Okoumé stand showing root grafts (Leroy Deval, 1973).

Lev-Yadun (2011) proposed that intraspecific root grafting may confer several evolutionary advantages. These include an expanded rhizosphere, privileged access to resources via the roots of suppressed or crownless individuals (Schenk, 2006), the transmission of mutualistic microorganisms, and reinforced collective chemical defenses. In Okoumé, grafts tend to occur preferentially between individuals of different social status (Leroy Deval, 1973), suggesting mechanisms of kin selection and a strategy comparable to the "dear enemy phenomenon" observed in the animal kingdom (Temeles, 1994), describing how animals are less aggressive toward familiar neighbors because they are predictable and less threatening. Here it suggests that maintaining stable nearby individuals reduces competition, supporting coexistence over replacement by more competitive individuals.

Far from being anecdotal, such belowground interactions could significantly contribute to the cohesion and resilience of Okoumé stands, enhancing their competitive advantage over other species. Investigating this mechanism may reveal an underestimated ecological driver behind its monodominance.

5 Relevance, objectives, and structure of the thesis

Okoumé is the most commercially exploited timber species throughout the Congo Basin. Silvicultural trials have been carried out on this species for over a hundred years with contrasted results. Despite this, its ecology remains poorly understood. Understanding its population ecology is essential not only for optimizing artificial regeneration and productive stand management but also for informing strategies to support forest restoration, particularly in open environments such as savannas and degraded forests.

Okoumé shares many ecological traits with Ayous, including light-demanding behavior, anemochorous seed dispersal, and gregarious growth. However, unlike Ayous, Okoumé exhibits a more balanced population structure which may result from its capacity to form monodominant stands and maintain the survival of small-diameter stems over time. This unique feature raises fundamental questions about the ecological mechanisms that underlie its local dominance.

This thesis aims to investigate the origin and maintenance of Okoumé monodominant stands by testing three hypotheses related to population dynamics: the effect of disturbance-mediated light availability on seedling survival, the influence of root-associated fungi, and the function of root grafts in resource sharing.

Specifically, the study seeks to answer the following questions:

Q1) Under which light conditions do Okoumé seedlings establish and maintain dominance?

Q2) Do specific root-associated fungal communities exist and influence nutrient acquisition, potentially contributing to the establishment and persistence of monodominance?

Q3) What role do root grafts play in resource sharing, stand cohesion, and reinforcement of monodominance?

Finally, we will discuss how these abiotic and biotic mechanisms interact to explain the formation and the long-term stability of Okoumé monodominant forests.

This introduction makes up the **Chapter 1** of this work. **It** defines the most general ideas and describes the fundamental concepts necessary for interpreting the context of this manuscript. **Chapter 2** provides an overview of the current state of knowledge about Okoumé. It revisits the monographs of Jean Leroy Deval (1974, 1976a, 1976b) and François Brunck et al. (1990) which compile the empirical silvicultural learnings of the 20th century. From there, this section traces the state of knowledge over the past thirty years to highlight the gaps that hinder a full understanding of the species, which contribute to its "Vulnerable" status according to the IUCN. This chapter has been published in the journal *Biotechnology, Agronomy, Society and Environment*:

Guidosse, Q., du Jardin, P., White, L.J.T., Lassois, L., Doucet, J.-L., 2022. Gabon's green gold: a bibliographical review of thirty years of research on okoumé (*Aucoumea klaineana* Pierre). *Biotechnology Agrononmy. Society, Environment* **26**(1), 30–42. DOI :10.25518/1780-4507.19458

The **next chapters** address the ecological factors that are crucial for the establishment and good growth of Okoumé monodominant stands. **Chapter 3** aims to answer **Q1** by focusing on a key abiotic factor: light and its impact on the development of Okoumé seedlings under controlled conditions. This chapter quantifies the optimal amount of light required for these seedlings, which are thought to be light-demanding, and provides a precise and nuanced definition of their light requirements, while also considering the risks in terms of pest vulnerability. This chapter has been published in the *Forest Ecology and Management* journal*:*

Guidosse, Q., Biwolé, A., De Clerck, C., Ekome, S.N., Lassois, L., Doucet, J.-L., 2024a. Seedling ecology of *Aucoumea klaineana* Pierre, the most important timber species in Central Africa. *Forest Ecology and Management* **569**, 10. DOI :10.1016/j.foreco.2024.122221

Root-associated fungi are known to play a major role in the mineral nutrition of forest species and in facilitating exchanges between individuals**.** To address **Q2, Chapters 4** focus on these interactions.

First, it integrates an experimental protocol for the extraction and amplification of DNA from fine Okoumé roots, adapted to address the challenges presented by this species since it shows highly pigmented rootlets rich in inhibitory compounds that interfere with classical molecular methods. This protocol was published in the *Journal of Microbiological Methods*:

Guidosse, Q., Roy, M., Lassois, L., Doucet, J.-L., 2024b. Adapted molecular methods to unravel the recalcitrant mycorrhizal associations of *Aucoumea klaineana* Pierre. *Journal of Microbiological Methods* **224**, 4. DOI: 10.1016/j.mimet.2024.107000

Building on this methodology, it investigates the fungal communities associated with the roots of Okoumé, from monodominant stands, old-growth mixed forests, and plantations. The goal is to examine whether there is a relationship between the fungi present on Okoumé roots and the structure of the populations (monodominant vs. old-growth mixed forests, dominant vs. suppressed trees). To do so, various ecological indicators must be measured, such as species richness (α) and diversity (β) per stand type and tree social status, and the identification of a potential core mycobiota. This study has been published in *Mycorrhiza*:

Guidosse, Q., Roy, M., Massart, S., Doucet, J.-L., Lassois, L., De Clerck, C., 2025. High diversity and variability of root-associated fungi in *Aucoumea klaineana*, a monodominant Central African timber species. *Mycorrhiza* **35**(65), 20. DOI: 10.1007/s00572-025-01239-y

Chapter 5 focuses on another aspect of the rhizosphere by addressing **Q3** on root grafts. These root grafts could allow exchanges between trees in a stand, primarily in terms of water and sugars. Using dendrochronology, the objective of this chapter is to study tree rings, and root grafts in monospecific Okoumé stands. This will help determine, on the one hand, the impact of these grafts on the growth of dominant trees, and on the other hand, understand their role in the survival of suppressed trees and stumps.

Finally, **Chapter 6** synthesizes the main results and discusses the silvicultural perspectives that can be implemented to take advantage of these findings and improve the sustainable management of Okoumé populations within their distribution area.

Figure 6 visually summarizes the conceptual framework of this thesis manuscript.

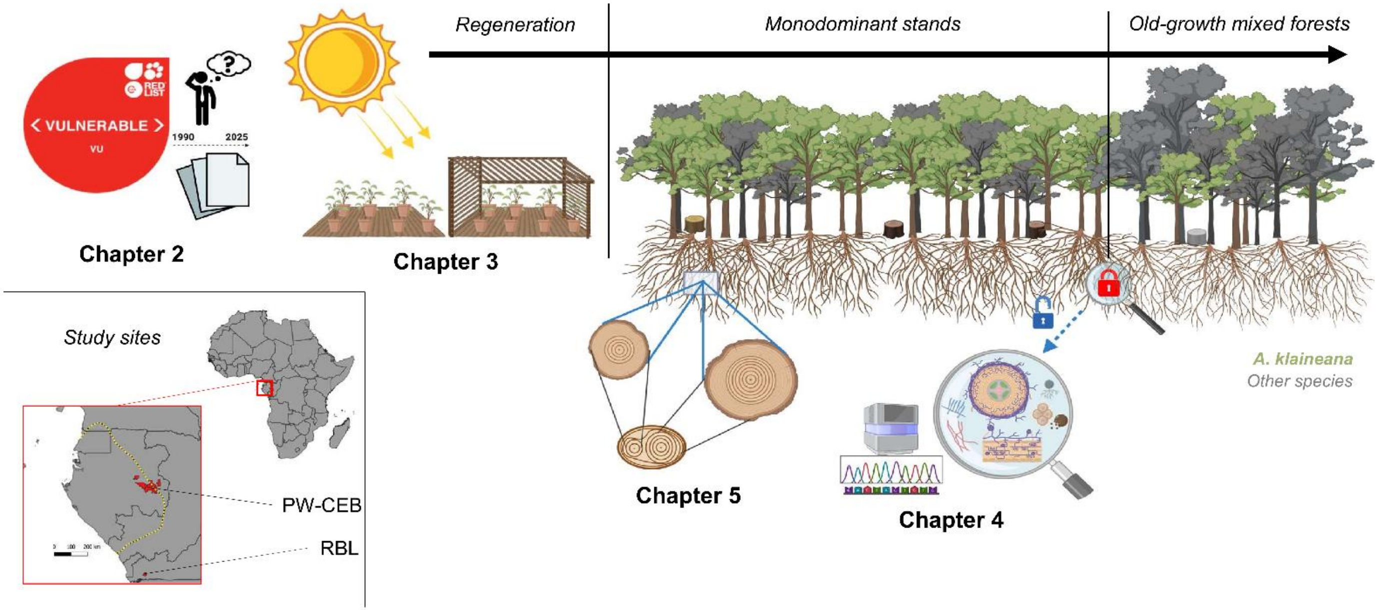


Figure 6 : Conceptual framework of the thesis. Study sites are the Precious Woods -Concession Equatoriale des Bois - (PW-CEB, Gabon) and the Luki Biosphere Reserve (RBL, Democratic Republic of Congo).

6 Study sites

6.1 *Precious Woods Gabon - Compagnie Équatoriale des Bois*

Most of the fieldwork was conducted within the sustainably managed forest concession (CFAD) granted to *Precious Woods Gabon - Compagnie Équatoriale des Bois* (PW-CEB). This concession is representative of the main forest types, climatic conditions, and soil characteristics within the natural distribution range of *A. klaineana*. PW-CEB headquarters are located in Bambidie, approximately 35 km east of Lastoursville, in the Ogooué-Lolo Province of Gabon (0°41’65”S-12°59’01”E). The site has been the focus of long-term collaboration between Gembloux Agro-Bio Tech and PW-CEB since 2003. The company manages a forest concession of 596,800 ha, harvesting around 240,000 m³ of logs annually, and was the first forestry company in Gabon to adopt sustainable forest management principles. It also developed the first comprehensive forest management plan in Central Africa. PW-CEB obtained the Forest Stewardship Council (FSC) certification in 2008, guaranteeing responsible forest operations. Since 2017, the company has also held the Pan African Forest Certification (PAFC), recognized by the Programme for the Endorsement of Forest Certification (PEFC).

Situated in the intertropical zone, the concession experiences a humid equatorial climate (Aw) according to the Köppen-Geiger classification. The region follows a four-seasonal cycle characterized by two rainy seasons alternating with two drier periods (June-August and December-January). Annual rainfall ranges from 1,500 to 1,700 mm, while mean annual temperatures vary between 21°C and 28°C. During the main dry season (July-August), precipitation can drop to less than 1 mm per day. Gabon is also recognized as the cloudiest country in Central Africa, with an average of only 109 sunny days per year, and fewer than 80 sunny days between June and September, typical of the “SW Gabon” climatic zone (Philippon et al., 2019, 2018).

The study area lies on Upper Precambrian (Proterozoic) formations of the Franceville Basin, which extends over about 35,000 km² between Lastoursville and Franceville. Within the PW-CEB concession, two main soil types dominate: Cambisols and Ferralsols. Cambisols are young, clay-rich soils with weak horizon development, while Ferralsols are highly leached soils rich in aluminum and iron oxides and kaolinite, giving them their typical reddish-yellow color (Jones et al., 2015). The terrain is rugged, consisting of plateaus and hills cut by several rivers, with elevations ranging from 230 to 670 m above sea level.

According to Caballé (1978), the logging concession belongs to the central zone evergreen forest type, characterized by a dominance of *A. klaineana*, *Julbernardia pellegriniana* Troupin (Awoura), *Scyphocephalum mannii* (Benth.) Warb. (Sorro), *Pycnanthus angolensis* (Welw.) Warb. (Ilomba), and *Pentaclethra eetveldeana* De Wild. & T.Durand (Mubala). In the southeastern part of the concession, forest–savanna mosaics cover approximately 80,000 ha.

Within the PW-CEB concession, four main forest types have been identified and based on the occurrence and developmental stage of *A. klaineana* (Figure 7):

- Old mixed forest with Okoumé (198.000 ha): Characterized by an abundance of *S. mannii* and *A. klaineana*, this forest type exhibits high species diversity and contains a large proportion of mature, large-diameter trees.
- Old mixed forest without Okoumé (52.400 ha): Structurally like Type 1 but lacking *A. klaineana*, these stands represent advanced successional stages where *A. klaineana* has been replaced by other late-successional species.
- Young Okoumé forest (131.000 ha): Dominated by *A. klaineana* in smaller diameter classes, reflecting recent natural regeneration following past disturbances.
- Very young Okoumé forest (89.800 ha): Found mainly within forest–savanna mosaics, these areas consist of dense stands of young *A. klaineana* stems, representing the earliest stages of forest colonization.

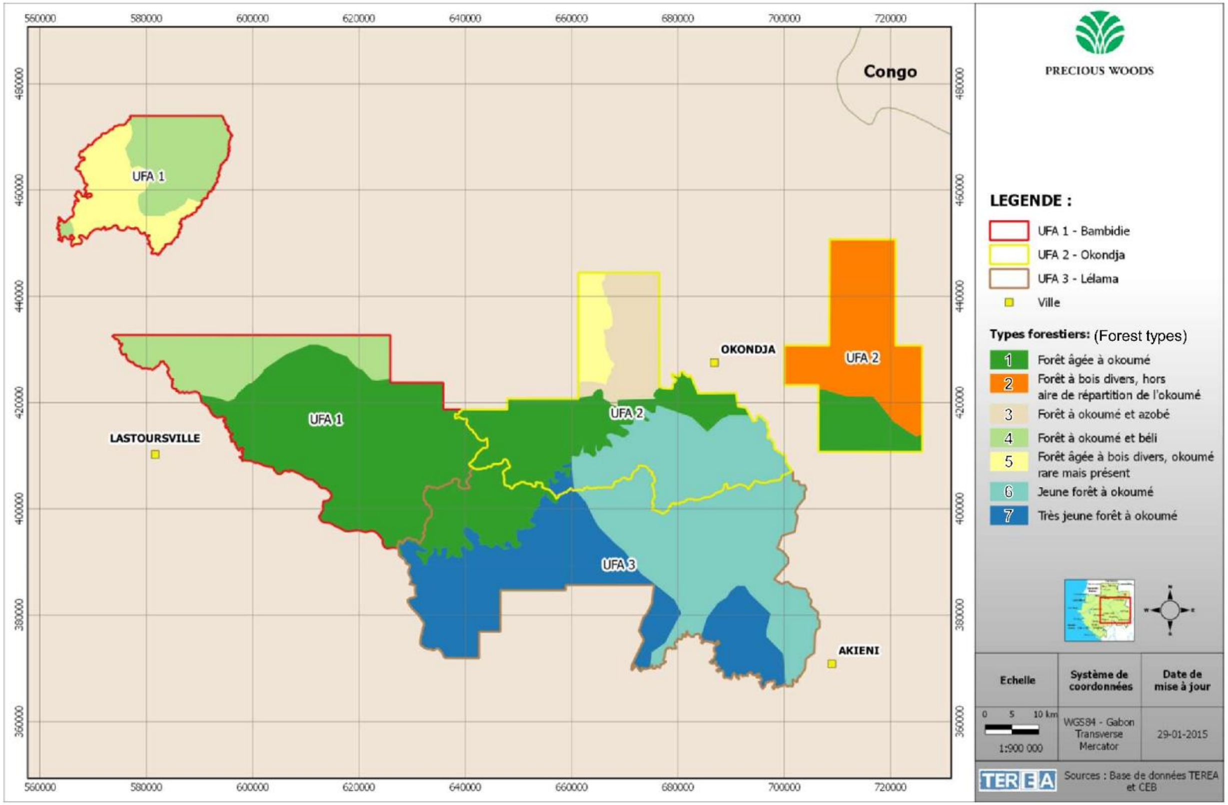


Figure 7: Forest stratification of the PW-CEB sustainably managed forest concession (CFAD) together with its subdivision into Forest Management Units (UFAs). The CFAD was partitioned into homogeneous forest strata based on vegetation composition and stand structure, including (1) old mixed forest with Okoumé, (2) old mixed forest without Okoumé located outside the species' distribution range, (3) forest with Okoumé and Azobé (*Lophira alata*) (4) forest with Okoumé and Béli (*Julbernardia pellegriniana*), (5) old mixed forest where Okoumé is rare but present, (6) young Okoumé forest, and (7) very young Okoumé forest.

6.2 *Luki Biosphere Reserve*

The secondary study site, used exclusively for fine root collection in *A. klaineana* plantations (Chapters 4), was in the Democratic Republic of Congo, in the Luki Biosphere Reserve (33,000 ha), designated under UNESCO’s “Man and the Biosphere” Programme. It is a semi-deciduous rainforest situated within the Mayombe forest region, approximately 120 km from the Atlantic coast (5°36’53”S-13°05’55”E). The area has an Aw type tropical climate, with a mean annual rainfall of 1,300 mm and an average temperature of 25°C (ranging from 19.5°C to 27.9°C) (https://power.larc.nasa.gov/data-access-viewer/). The dry season, defined by monthly rainfall below 50 mm, typically extends from June to September. Luki’s hilly terrain, rising between 150 and 500 m in elevation, contributes to a microclimate marked by high humidity even during the dry season. The soils are heterogeneous but predominantly ferrallitic. The Luki forest is classified as a mesophilous semi-deciduous forest. The most abundant canopy trees are *Prioria balsamifera* (Verm.) Breteler (Agba) and *Terminalia superba* Engl. & Diels (Limba) (Couralet, 2010).

Okoumé is not naturally present in the DRC. The stands in Luki originate from historical introduction trials, with seeds imported from Gabon and planted in the 1940s and 1970s by the National Institute for Agronomic Studies and Research (INERA) (Makaya, 1978). These plantations represent the few surviving Okoumé populations in the reserve today.

Chapter 2

Current state of knowledge on Okoumé and conservation status

Permanent monitoring plot in an Okoumé stand

This chapter is an amended version of **Article 1** presenting a bibliographic synthesis of thirty years of research on *Aucoumea klaineana*, aiming to provide an updated overview of current knowledge and identify major research gaps leading to its current conservation status.

Article 1: Guidosse, Q., du Jardin, P., White, L.J.T., Lassois, L., Doucet, J.-L., 2022. Gabon's green gold: a bibliographical review of thirty years of research on okoumé (*Aucoumea klaineana* Pierre). *Biotechnology Agrononmy. Society, Environment* **26**(1), 30–42. DOI :10.25518/1780-4507.19458

Abstract

Introduction. *Aucoumea klaineana* Pierre is the most harvested timber species in Central Africa and plays a key role in the economy of Gabon. This tree is considered “Vulnerable” for more than three decades by the IUCN because its population is assumed to have been reduced by at least 50% as a result of logging. The objective of this review is to synthesize recent and relevant knowledge in order to update this status. It focuses more specifically on ecology, population dynamics, silviculture and impacts of logging.

Literature. Its natural range mainly covers Gabon. It is a light-demanding and gregarious species that forms root grafts. It principally establishes itself in abandoned fields and savannas. In mature forest its regeneration is rare and limited to large gaps. Selective logging only allows significant regeneration along roads. However, at the scale of Gabon, the species is abundant and its renewal is ensured. Legal logging does not threaten the species. However, after decades of logging focusing on the best-shaped trees**,** the production of lower-quality timber is expected**.** The implementation of appropriate silviculture could be a solution.

Conclusion. *Aucoumea klaineana* is not vulnerable under IUCN A1 criterion and its current status should therefore be revised. However, the maintenance of a high-quality production over the long term calls for the implementation of silviculture based on a thorough knowledge of the factors affecting stand dynamics, especially the role of the rhizosphere. Although long described, the functioning of root grafts has never been studied in depth.

1 Introduction

Aucoumea klaineana Pierre is the most harvested tree in Central Africa (FRMi, 2018) and has played a key role in the economy of Gabon for more than a century (Meunier et al., 2015). Its commercial name is “okoumé” in French and “gaboon” in English (ATIBT, 2016). Its wood is mainly used for plywood manufacturing and interior joinery. It has several qualities that favor its use, including its straight grain, large log size, low and uniform density (Engozogho Anris et al., 2019).

This tree is present at the top of the coat of arms of the Gabonese Republic and contributes to the daily life of rural populations. They use it to build their houses, make their dug-out canoes, make torches and treat various illnesses. It produces an aromatic, flammable oleoresin, with antioxidant and antiseptic properties (Aboughe Angone et al., 2015; DeCarlo et al., 2019; Engozogho Anris et al., 2020; Obame et al., 2014).

Aucoumea klaineana is considered “Vulnerable” since 1998 by the IUCN because its population is assumed to have been reduced by at least 50% as a result of logging (criterion A1). The global assessment report is provided in Supplementary Material 1.However, this statement is only based on five broad-based references while detailed monographs (Brunck et al., 1990; Leroy Deval, 1976a, 1976b, 1974) and more recent publications have been omitted.

Given the economic importance of *A. klaineana*, it is essential to reassess its conservation status based on the most recent work. Consequently, the objective of this review is to synthesize the knowledge that can influence the population dynamics of the species. It focuses more specifically on its ecology, silviculture and logging. It also highlights issues that need to be better studied in order to ensure sustainable management of *A. klaineana* populations. It was carried out using the keywords "okoumé" and "aucoumea" in the following search engines: Orbi (ULiège), Libnet (ULiège), Scopus, Google Scholar, the archives of the FORAFRI project (CIRAD) and the archives of the Gembloux Agro-Bio Tech tropical forestry laboratory.

2 Taxonomy and botanical description

Of the pantropical family *Burseraceae*, *A. klaineana* is the only representative of the genus. *Aucoumea klaineana* can reach 50-60 m in height, 2 m in diameter and live up to 300 years. The bole is cylindrical with a base either widened or with buttresses which can reach up to 3 m in height (Figure 8a) (Meunier et al., 2015). The slice is pink and exudes a characteristic oleoresin (Figure 8b). Its foliage is diffuse. The leaves are hairless, compound and imparipinnate (Figure 8c). The rachis is up to 40 cm long, inserted on a hollow grooved petiole. The veins are joined in an arch near the margin of the leaf. The petiole is 3 to 4 cm long, swollen at the end. Leaflets, 7 to 13 in number, are ovate to oblong, opposite and rounded at the base. The young leaves are red, and turn grey-green after a week.

The tree is dioecious. Inflorescences can carry a few hundred flowers (female) or more than a thousand flowers (male) (Figure 8d). From the outside, flowers are composed by a calyx with five sepals which are tomentose and brownish, triangular in shape and about 5 mm long. The five petals of about 7 mm are also tomentose and brownish. Inside, five orange bilobed nectaries form a crown in the center. In male flowers, the ten stamen filaments are thicker and the gynoecium is attenuated. In the female flowers, the anthers are empty and the pistil is more voluminous. A detailed description of flowers of both types can be found in Aubréville (1962) and Grison (1978).

The fruit is a dehiscent capsule with five valves (Figure 8e). On opening, it releases spoon-shaped woody structures containing five seeds of 3 to 4 cm each, enclosed in the winged endocarp (Figure 8f) (Aubréville, 1962). The germination is phanerocotylar and epigeal. Cotyledons are foliaceous, rapidly turning green (Figure 8g). The cotyledons persist up to 4 months after sowing (Mapaga et al., 2002).

The development of *A. klaineana* roots is complex (Leroy Deval, 1974). Lateral roots appear from 10 to 12 weeks. After 10 years and when the typical litter of *A. klaineana* stands has developed, the taproot atrophies and secondary roots move up towards the shallow soil horizons, between 0 to 25 cm and spread up to 20 meters around the trees. In mature stands, the secondary roots thicken to form buttresses. Fine roots build up a dense network in the litter. Tertiary roots can form directly at the base of the buttresses, where litter accumulates heavily. Roots of *A. klaineana* are coarse and shallow, with few branches, but with fine, long and short pear-shaped elements. The root systems form mechanical and functional root fusions called root grafts.

Figure 8: *Aucoumea klaineana* Pierre. **a** : Cylindrical bole and base with buttresses ; **b** : oleoresin ; **c** : compound leaf ; **d** : inflorescence and flowers ; **e** : fruits ; **f** : seeds ; **g** : young seedling with both cotyledons and the first true leaf. © J.L. Doucet (**a,b,e,f,g**) ; Q. Meunier (**c,d**)

3 Biogeography of populations

3.1 *Distribution*

Aucoumea klaineana is found in all of Gabon other than the north eastern third, limited from a line passing through Okondja in the east and between Mitzic and Oyem in the north (Brunck et al., 1990), at all altitudes from sea level to near the summit of Mount Iboundji, one of the highest points in the country (980 m). It is also found in Equatorial Guinea, in south-western Republic of Congo and in the extreme south-west of Cameroon (Figure 9).

This current distribution of natural populations of *A. klaineana* (Figure 9) corresponds remarkably with the so-called "Gabonese" region (Philippon et al., 2018). This is characterised by **(i)** on average, only 109 W.m^{-2} of incident solar irradiation, a large quantity of dark mornings and dark days with a minimum from June to September (80 W.m^{-2}), i.e. the great dry season; **(ii)** rainfall of less than 1 mm day^{-1} in July and August; **(iii)** generally colder temperatures and **(iv)** higher relative humidity in the dry seasons than the rest of Central Africa.

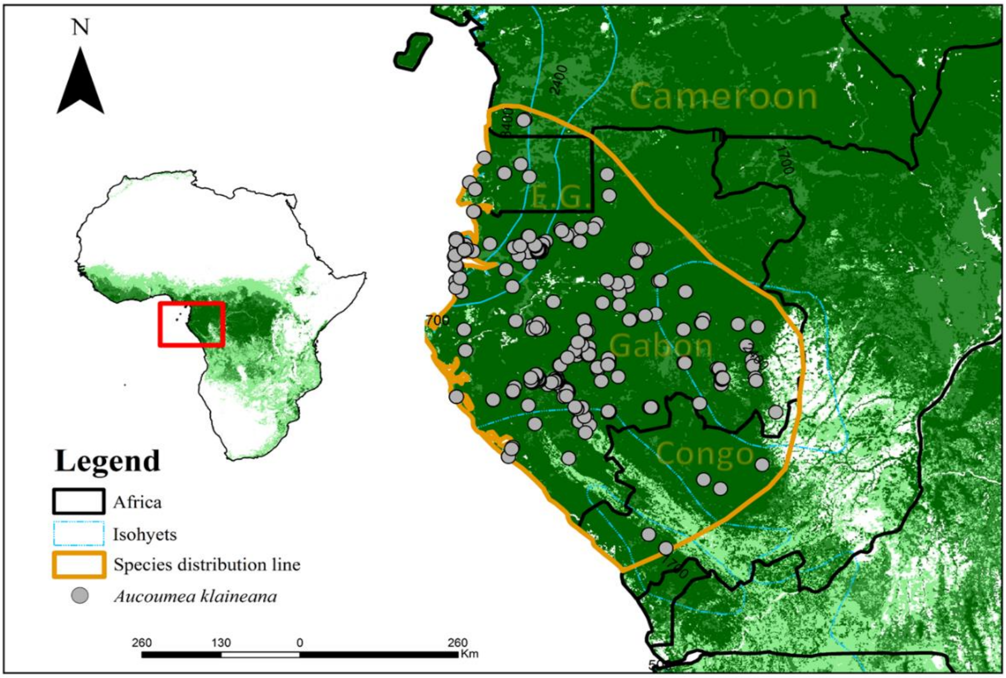


Figure 9: Map of geographical distribution of *A. klaineana*. The points of occurrence in gray are taken from the databases of the Global Biodiversity Information Facility (GBIF, 2020) and the RAINBIO database (Dauby,2016). The yellow line depicts the current range of the species.

Artificially planted, *A. klaineana* is found in its native range but also in other regions of Cameroon, Côte d'Ivoire, DRC, Ghana, Madagascar, Indonesia, Malaysia, Suriname and French Guiana. However, the poor performance of *A. klaineana* plantations outside its natural range seems to confirm that climate is a determining factor for the health of its populations (Brunck et al., 1990).

3.2 *Genetic distribution of populations*

A study of the chloroplast DNA of *A. klaineana* revealed a geographical structuring which suggested a historic separation into two populations: one in the north, confined to the Cristal Mountains, and the other in the south, on the Chaillu massif. This structuring is thought to be linked to the presence of forest refuges in these areas during glacial periods (Muloko-Ntoutoume et al., 1999) which caused dry climate in this region, and is also shown for some mammals populations such as *Mandrillus sphinx* L. (Telfer et al., 2003) and *Gorilla gorilla gorilla* Savage (Anthony et al., 2007).

Born et al. (2006) isolated and used ten polymorphic microsatellites from the nuclear DNA of *A. klaineana* to undertake a finer analysis, revealing two other distinct genetic units that appear to correspond to two additional refuge areas: the "Doudou" and "Mayombe" massifs (Born et al., 2011) (Figure 10).

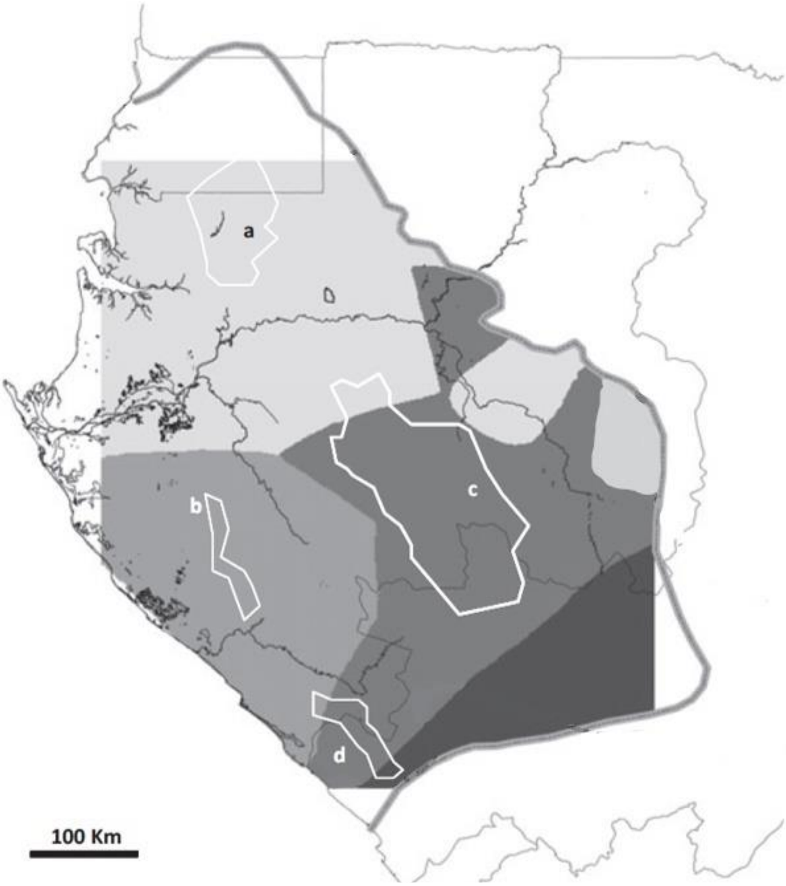


Figure 10: Distribution model of four genetically distinct populations of *A. klaineana* described by Muloko-Ntoutoume et al. (1999) and Born et al. (2011). The grey line shows the current distribution range of the species. White polygons represent elevated areas: **(a)** Cristal Mountains, (**b**) Doudou Mountains, (**c**) Chaillu Massif and **(d)** Mayombe massif. They could correspond to refuge areas during the Last Glacial Maximum and they would have led to these four genetically distinct populations depicted by grey shades (limited by the square area covered by the model). (From Born et al., 2011. Modified. With permission).

4 Ecology

4.1 *Temperament*

Aucoumea klaineana has a pioneer and strictly light-demanding temperament. It colonises open environments of natural (e.g., savanna or forest openings) or anthropic origin (e.g., fallow lands), often in dense patches. As such, *A. klaineana* is generally considered to be a gregarious species.

Leroy Deval (1973) demonstrated that individuals in a population are not simply in close proximity to each other but also establish root fusions. In an even-aged stand, stratification takes place from an early age and it appears that the dominant tree in the population retains higher radial growth than the other trees. Thanks to root grafts, it benefits from an extension of its rhizosphere and in exchange, it provides water, nutrients and minerals to suppressed trees and stumps.

4.2 *Population dynamics and structure*

Aucoumea klaineana can form almost monospecific stands. Its populations are said to follow man, because they regenerate in the post-cultivation fallow (Hymas, 2015). It was nicknamed “the son of cassava” by Aubréville (1948). It is also a coloniser of savannas, with wind dispersed seeds that will carry over 100 m. Delègue et al. (2001) recorded an annual rate of encroachment into savanna of 1 m.yr^{-1} by analysing carbon 13 and 14 isotopes in soils. Favier et al. (2004) proposed an empirical model to study the *A. klaineana* rate of progression at the edge of savannas by linking the age and diameter of the individuals.

Aucoumea klaineana also colonises roadsides, and is sometimes found in large light gaps, but does not regenerate in the forest understory. As the stand increases in age, *A. klaineana* is gradually replaced by more shade tolerant species, leaving only scattered individuals in mature forests. The abundance of young individuals is therefore inversely proportional to the age of the forest (Doucet et al., 2004).

Fuhr et al. (1998, 2001) distinguish three stages of floristic composition following the colonization of the coastal savannas in Gabon. From settlement to 15-20 years, *A. klaineana* accounts for 45-70% stems. From 15-20 years to 30-40 years, it dominates other colonising species reaching 80% dominance. From the third stage of colonization (> 40 years), most of the other colonising species have disappeared and *A. klaineana* reaches a peak of between 90 and 95% of the dominant stratum.

In central Gabon, *Marantaceae* play a fundamental role in the stand dynamics. Present in the undergrowth of the *A. klaineana* monodominant forests, they take advantage of the slightest windfall to develop exuberantly. In doing so, they prevent or delay the regeneration of other woody species (Fuhr et al., 2001; White and Abernethy, 1996).

Monodominant stands of 30 years or more in coastal savanna can have between 300 and 500 stems.ha^{-1} (dbh, diameter at breast height ≥ 10 cm) (Mapaga et al., 2002). In the Lopé Reserve (central Gabon), floristic surveys describe a number of 175 trees.ha^{-1} in monodominant forest, compared to only 8 trees (dbh ≥ 10 cm) in old growth *Marantaceae* forests (called mixed *Marantaceae* forests) (White et al., 2000).

At the country scale, the average density of *A. klaineana* is 6.90 stems.ha^{-1} (dbh ≥ 20 cm) and the distribution of individuals by diameter class is globally balanced with a greater abundance of small diameter trees (Doucet et al., 2021). However, locally in the oldest forests, the distribution follows a Gaussian curve (Figure 11). Biraud (1959) linked it to the translocation of human populations who once lived in the forest. Indeed, from the 1930's onwards the Colonial administration forced villages to resettle along roads and major waterways, resulting in a reduction in the spatial influence of slash-and-burn agriculture (Engone Obiang et al., 2014; Pourtier, 1989) and a reduction in sites favourable to the regeneration of *A. klaineana* and other pioneer long-lived light-demanding species (Morin-Rivat et al., 2017).

4.3 *Phenology*

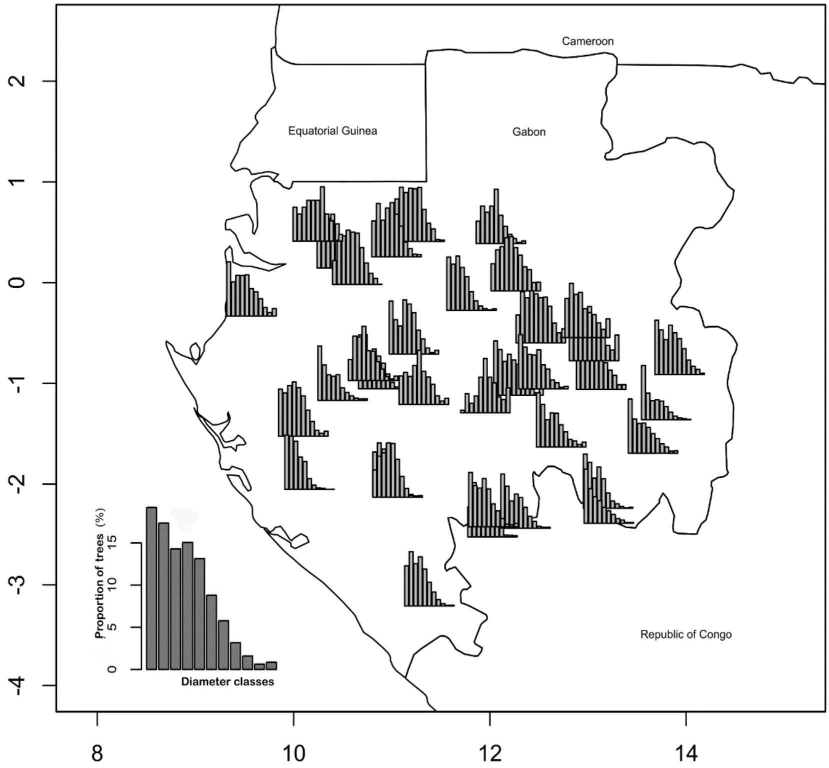


Figure 11: Diametric distribution of *A. klaineana* in 35 logging concessions in Gabon, covering 7,3 million of hectares. The graph on the bottom left shows the average diametric structure at the country scale. Diameter classes start from 20 cm, have a 10 cm range and are incremented of 10 cm per class.

Aucoumea klaineana is not deciduous. However, it renews its leaves simultaneously (Meunier et al., 2015). In some years and across extensive areas leafing occurs following large scale defoliation by a moth (*Sylepta balteata* Fab.) (Leroy Deval, 1976b; Mapaga et al., 2002; van Valkenburg, 2008; White and Abernethy, 1996)

In Gabon, *A. klaineana* flowers at the beginning of the long rainy season, in October (Doucet, 2003). Although it can be fertile from 23 cm diameter, full flowering is observed from 55 cm diameter (Doucet, 2003). It is pollinated by social (*Apidae*: *Apinae, Meliponinae*) and solitary bees (*Xylocopidae*) and by flies (*Diptera*: *Calliphoridae*, *Syrphidae*) (Brunck et al., 1990). According to Gautier-Hion (1997) *Apis mellifera* bees can carry out the pollination of two individuals separated by a maximum of 1.5 km.

Fruiting is episodic and supra-annual (Hecketsweiler, 1992). On average, there is only one year of abundant fruiting every three years (Leroy Deval, 1976a).

In Gabon, female trees of *A. klaineana* start to bear fruit at the end of December, during the short dry season. A “good seed carrier” gives an average of 10 to 30 litres of seeds (there are 800 to 850 seeds per litre). Production depends on the diameter and height of the tree; some dominant trees could produce up to 100 litres (Leroy Deval, 1976a).

Dispersal is by wind. The seeds of a tree of 50 to 60 cm in diameter, with a well-developed crown can be dispersed up to 100 m (Doucet, 2003). Dominant winds thus play a decisive role in the spatial distribution of seeds.

4.4 *Natural regeneration*

In contrast to the rest of the life cycle of *A. klaineana*, germination can take place in the shade and usually 5 to 6 days after sowing. The germination rate drops sharply after 2 to 3 weeks in natural conditions. Germination depends on temperature (at least 15°C), and soil moisture (at least 2%).

Figure 12 *Aucoumea klaineana* regeneration in a savanna. © J.L. Doucet.

A number of factors determine good regeneration (Biraud, 1959) **(i)** a sufficient number of seed trees (4 to 8 per hectare); **(ii)** abundant fruiting and sowing; **(iii)** a large gap (minimum a quarter hectare); **(iv)** perfectly clear soil at the time of sowing. These conditions can be met in savannas or in cassava and banana field fallows, as harvesting can match the fruiting periods of *A. klaineana* (Figure 12). Monospecific stands established naturally can have a density ranging from 6,000 (De Kam et al., 1996) to 35,000 seedlings per hectare (Fuhr et al., 1998). At 6 years, Mapaga et al. (2002) cite a natural stand of 2,650 stems per hectare. By contrast, seedlings and saplings are rare in mature forest stands. They can only be observed in some large openings caused by storms or landslides.

In production forests, logging, which results in an average removal of one to two stems per hectare, does not create sufficient disturbances to allow a significant regeneration of the species. Doucet (2003) surveyed an average of 110 seedlings of *A. klaineana* per hectare in old-growth secondary forests logged four years earlier. On average, the density of young trees of more than two meters in height does not exceed three individuals per hectare of logging gap (Doucet, 2003). Abundant regeneration is only observed along the main roads and in old log yards (Biraud, 1959; Doucet, 2003). This is said to be due to the elimination of competing species from the soil seed bank (Doucet, 2003; Doucet et al., 2004). Doucet (2003) observed average densities of 11 stems (dbh ≥ 10 cm) of *A. klaineana* per hectare along 20-year-old logging roads.

4.5 *Vegetative propagation*

Aucoumea klaineana is generally considered a species that does not sprout from stump. However, Leroy Deval (1975) observed that some young stems cut during thinning operations were able to produce shoots, with coppicing occurring in about 2-5% of stumps (Leroy Deval, 1973), particularly in well-lit stands, occasionally leading to coppice or even coppice-with-standards structures.

Layering and grafting techniques have been reported for the species, although their practical implementation requires further experimental validation (Grison, 1978b; Koumba Zaou, 1989). Propagation by cuttings appears more challenging but has nonetheless been successfully achieved (Grison and Hamel, 1977).

4.6 *Pests and diseases*

The health constraints affecting *A. klaineana* have been extensively documented, notably by Leroy Deval, who devoted an entire volume of his monograph to the species' diseases and defects (1976b) as well as by Brunck et al. (1990). Among these, psyllids (*Pseudophacopteron* sp.) and black canker (*Lasiodiplodia theobromae* (Pat.) Griffon & Maubl.) infestation are two major threats that stand out.

These diseases result from cortical lesions inflicted by piercing insects like cochineals (e.g., *Pseudaonidia trilobitiformis* Green) or ants (*Wassmannia auropunctata* Roy). Psyllids lay their eggs in these lesions, as well as in the leaf petiole grooves, leading to the drying out of terminal buds and the development of adventitious buds. These buds are subsequently attacked, resulting in the formation of terminal axes resembling witch's brooms. While psyllosis usually does not cause plant death, it results in a bushy appearance and slow growth. The fungus responsible for black canker also exploits these entry points to establish itself, forming a black sooty film on various plant organs, ultimately leading to growth slowdown.

Other pests and diseases occur throughout the life cycle but are generally less critical or more context-dependent. In nurseries, damping-off is rare, although occasional rust infections and attacks by leaf-rolling caterpillars may occur, sometimes requiring treatment. In plantations, other defoliating and piercing insects can also affect young trees, particularly during certain seasonal periods. Larger fauna such as rodents and elephants may also cause localized damage. Defoliation by caterpillars (e.g. *Sylepta balteata*) are also reported (Mapaga et al., 2002).

4.7 *Soil and rhizosphere*

4.7.1 **Soil and litter**

Aucoumea klaineana grows on all types of soil. From the sandy, poorly drained soils of the estuary of Gabon to the drier, more clay-rich continental soils. Soil type has a minor influence on the establishment of *A. klaineana* populations compared to climatic and biotic factors (Leroy Deval, 1974).

In the tropics, mineral elements come directly from the litter and not from deep in the soil (Midoko Iponga et al., 2020). *Aucoumea klaineana* “creates” its own soil, drawing most of its resources from the litter formed by its own fallen fragments (Midoko Iponga et al., 2020), which can be up to 25 cm thick (Leroy Deval, 1974). Different categories of microorganisms, including mycorrhizal fungi, contribute to rapid nutrient renewal in the litter.

During savanna colonization, the soil is dry and poor in litter and the roots of *A. klaineana* go deep into the soil. During the cycle until the formation of an old forest, there is a simultaneous evolution of the plant cover, the moisture content of the soil, the accumulation of litter on the surface, fostered by the presence of other species in the understory, and an upward movement of the rhizosphere of *A. klaineana* towards the more superficial horizons (Leroy Deval, 1974).

Floristic composition therefore plays an important role in the prosperity of *A. klaineana*. Commensal species improve litter quality (Leroy Deval, 1974). Reduced leaf turnover in well-formed tree crowns and the removal of secondary species under continuous canopy cover could therefore favor the decline of stands in old-growth forests (Leroy Deval, 1974).

4.7.2 **Root grafts**

Root grafts are common in woody species (Graham and Bormann, 1966; Mudge et al., 2009). Root grafts refer to the merging of root steles allowing an exchange of water, carbon, minerals and/or microorganisms between individuals. However, the physiological mechanisms involved and their importance are poorly understood (Bader and Leuzinger, 2019) even though they are often debated (Eis, 1972; Graham and Bormann, 1966; Lev-Yadun, 2011)

In *A. klaineana*, root merging was first described by Catinot (1962) and detailed by Leroy Deval (1973). Stump healing was observed in 5-15% of cases in natural forests and in 30% of cases in the plantations studied (Leroy Deval, 1973). The survival of these individuals over a long period after felling (up to 42 years (DIARF et al., 2000)) suggests the transfer of photoassimilates from their neighbours reaching the canopy through root grafts or by mycorrhizal associations.

In plantations (5 to 15 years), root merging begins to be observable from densities of 400-500 trees ha^{-1} in 0 to 5% of cases. When the plantation density reaches 1,500 trees.ha-1 or more, the rate of stumps kept alive reaches 30% (Leroy Deval, 1973).

According to Leroy Deval (1973), soil type has no influence on root merging. However, given that the root system of a tree extends wider in sand compared to clay (Kozlowski and Pallardy, 1997), soil texture may have an influence on the establishment of fusions between trees at different distances.

The establishment of merging occurs from the age of 4 to 6 years, when there is a differentiation between the dominant and dominated strata and grafts only form between individuals of different social classes. The growth of the dominant stratum is not affected by variations in the density of the dominated stratum (Leroy Deval, 1973).

4.7.3 Mycorrhizal symbioses

Knowledge of the mycorrhizal status of *A. klaineana* is very limited for now. Only one paper on the topic was found (Onguene et al., 2002). According to the authors, who observed symbiosis in plantations and in natural regeneration in southern Cameroon (outside the species range), all the trees are related to different species of *Glomales* (arbuscular mycorrhizal fungi, AM fungi). Up to the age of 15 years mycorrhizal colonization rate increases but then decreases in a non-significant manner. However, the quantities of septate hyphae and arbuscles are low. The highest rates of arbuscles are found in young individuals undergoing natural regeneration. In *Burseraceae*, Bechem et al. (2018) also found AM fungi on *Dacryodes edulis* (G.Don) H.J.Lam. (Safoutier).

Although the ectomycorrhizal families of tropical Africa do not include the *Burseraceae* (Bâ et al., 2011, 2012), it should be noted that the particular morphology of the fine roots of *A. klaineana* is very similar to pear- or club-shaped structures induced by ectomycorrhizal fungi (Figure 13).

Figure 13: Typical fine root of *A. klaineana*. The thinnest elements are pear- or club-shaped, suggesting ectomycorrhizal structures. © Q. Guidosse

5 Growth dynamics and determinism

5.1 *Measuring techniques and average growth rates in diameter*

Thousands of increment measurements have been carried out on *A. klaineana* since the 1950s (Brunck et al., 1990; DIARF et al., 2000; FAO, 1981; Fuhr, 1999b; Rocek, 1981). Mean values are generally reported in the literature, but measurement techniques (permanent plots and ring analysis) may give different results (Détienne et al., 1998)

Engone Obiang et al. (2013) compiled the average growth rate for *A. klaineana* since 1961 in permanent plots established in natural stands. Average annual increases in diameter per individual ranged from 0.1 to 2.33 cm.yr^{-1}. This compilation shows that the information is not always comparable between sites, because the diameter classes considered are different (from 0 to >100 cm) and the number of observations is sometimes insufficient. This results in very high standard errors.

Ring counts were tested on *A. klaineana* in the early 1960s by Mariaux and Catinot (Mariaux, 1967). Gabonese (and Congolese) climate generally has four seasons: a long and a short rainy season and a long and a short dry season. In theory, this alternation makes it possible to observe biennial rings in *A. klaineana* under optimal conditions and thus to trace its growth dynamics (Détienne et al., 1998). However, measurements are reported to be easy or difficult depending on the growth rate of the tree, due to missing or false rings (Détienne et al., 1998; Rivière, 1992). Ring analyses gave the following average annual diameter increments: 9.4 mm (Sindara, Gabon), 7 to 15 mm (Oyane, Gabon) and 5 to 6 mm (interior of Gabon).

By synthesizing all available data (plots and ring analyses) on *A. klaineana* growth, Picard and Gourlet-Fleury (2011) obtained an average annual increase of 8 mm in unlogged forests. But, according to some authors, *A. klaineana* grows faster in coastal areas than in the interior of Gabon (Brunck et al., 1990; Durrieu de Madron et al., 2000). According to Mapaga et al. (2002), dominant and co-dominant individuals in the coastal zone grow an average of 10 mm.yr^{-1} in diameter compared to 6 mm.yr^{-1} in the continental zone. The growth rate is said to reach a maximum at 10 years. According to other authors, there are no differences between coastal and continental areas (Croisé and Fabbri, 1991).

Local factors such as stand structure (density, age, species composition, etc.) and disturbances (logging, fire, competition, etc.) are sources of significant variations in the growth of *A. klaineana* (Engone Obiang et al., 2013). Durrieu de Madron et al. (2000) report that *A. klaineana* in mixed stands grows more rapidly below 30 cm (dbh) and that this rate decreases from 40 cm (dbh) onwards. But, according to Nasi (1997), the rate of growth increases constantly for even-aged stands.

5.2 *Growth models for Aucoumea klaineana*

The first model for *A. klaineana* was constructed from data from Oyan (Gabon, coastal zone) (Louppe et al., 2000; Mapaga et al., 2002)

Engone Obiang et al. (2013) developed a lognormal growth rate model for stands from six sites. The model estimates the growth rate (A, in cm yr^{-1}) including the diameter of the studied tree (D, in cm), the stand density (N, per hectare) and the basal area of the stand (B, in m².ha^{-1}). The last two parameters concern all species in the vicinity of the tree studied, which gives information on its biotic environment:

$$A = 2.26 \exp\left(-\left[\frac{1}{1.26}\ln\left(\frac{21.0}{D}\right)\right]^2 \right.$$
$$\left. - (0.121B - 6.038 \times 10^{-4}N)\exp(-3.350 \times 10^{-2}D)\right)$$

By using the average values of basal area and density calculated from the Gabonese national inventory data (25 m².ha^{-1} and 410 stems.ha^{-1} ; Poulsen et al., 2020), the diameter growth of *A. klaineana* peaks between 40 and 70 cm and then decreases (Figure 14).

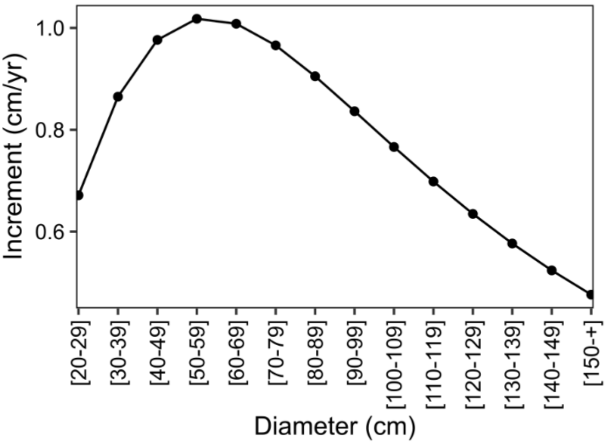


Figure 14: Illustration of the growth model used. This is the model proposed by Engone Obiang et al. (2013) with a basal area of 25 m².ha^{-1} and a density of 410 stems.ha^{-1}.

6 Silviculture

6.1 *Artificial regeneration*

The history of *A. klaineana* silviculture in Gabon is detailed by Brunck et al. (1990). The main results are summarized hereafter.

6.1.1 Monospecific plantations

Density. A density of between 625 and 950 stems ha^{-1} seems optimal until a first thinning at 4 years, which reduces the density of the plantation to 350 stems ha^{-1}. This range makes it easy to find a good compromise between bole quality and plantation cost price (Leroy Deval, 1976a). A lower density may be associated with reduced opportunities for root grafts due to increased spacing between individuals, theoretically leading to higher mortality and to a greater competition with various species depending on the region of the plantation (Louppe et al., 2000). However, the consequences of this potential reduction in root grafts remain unclear and should be further investigated.

Considering this assumption, Louppe et al. (2000) propose to plant the species in plots with a density of 9 to 16 plants spaced 1 meter apart to promote the formation of root grafts. Spacing these plots 12 x 12 m or 10 x 15 m apart should yield 70 stems per hectare.

Thinning. Fuhr et al. (2001) assume that thinning should not take place too late because, after 10 years, the growth gain did not compensate for the loss in basal area. Other authors also advocate thinning out at around 10 years (Leroy Deval, 1974; Bibani, 1987, cited by Onguene, 2002). However, Onguene (2002) suggests undertaking only a single thinning around 15 years. Thinning before this age would damage a possible mycorrhizal network and thus the carbon assimilation.

Leroy Deval (1973) recommends two thinnings, between 8 and 15 years of age, in order to promote the good health of the plantation while maintaining good bole conformation.

Costs. Louppe et al. (2000) compare clear-cutting and monospecific natural or artificial regeneration to selective harvesting every 30 years above 60 or 70 cm in diameter. They conclude that neither method is clearly superior. In the case of clearcutting, harvesting allows natural or artificial regeneration of *A. klaineana* immediately afterwards. However, the operation releases a large amount of carbon and the market for *A. klaineana* wood is not suitable for small-diameter stems.

In the case of selective logging, they specify that after the third cutting cycle, an enrichment or a new plantation is essential because the trees exploited will not have formed openings large enough for the species to regenerate by itself.

In terms of costs, exploitation by clear-cutting would cost 1,641,200 FCFA.ha^{-1} (2502 €.ha^{-1}) against 295,500 FCFA.ha^{-1} (450 €.ha^{-1}) for enrichment after selective cutting (conversion based on 2020 values).

6.1.2 Multi-species plantations

Multi-species plantation tests on thirteen species were carried out at the Ekouk experimental site between 1988 and 1994 (Koumba Zaou et al., 1998b). Planting was carried out either after clearcutting and clearing of the soil, or using the undergrowth method, by clearing the shrub and herbaceous layers and ringing trees of little interest.

The study showed that *A. klaineana* grows faster in diameter in clearcutting (about 2.3 cm.yr^{-1} compared to 2 cm.yr^{-1} in undergrowth), while the undergrowth method favors better tree form and at a lower cost (about half that of clearcutting). In both cases, it grows in height by about 2.4 m.yr^{-1} . Basal area, reached 9.2 m².ha^{-1} in clearcutting after six years, compared to 6.9 m².ha^{-1} in undergrowth. Koumba Zaou and al. (1998) cite costs of about 800,000 FCFA.ha^{-1} (1219 €) for clearcutting and 316,000 FCFA.ha^{-1} (481 €) for the undergrowth method.

6.2 *Assisted natural regeneration*

Doucet et al. (2004) tested an assisted natural regeneration technique in ten plots ranging from 0.3 to 1.6 ha. These plots were centred on well-formed, *A. klaineana* stems with healthy fruit crops just before the seeds were released. The undergrowth was removed with a machete. Then, trees and shrubs of non-commercial species were felled.

The results obtained were encouraging. After six months, the density of *A. klaineana* seedlings was 0.38 m^{-2}. The average annual growth in height of the seedlings was 86 cm, reaching 196 cm for the dominant ones. In 2003, the costs were estimated at 233,000 FCFA.ha^{-1} (356 €), excluding subsequent depressing or clearing operations.

7 Forest management

In Central Africa, logging is subject to legislation aimed at ensuring the sustainable management of forest resources. Trees must reach a minimum cutting diameter (MCD) before they can be exploited. In Gabon and Republic of Congo, the MCD of *A. klaineana* is set at 70 cm (Decree No. 1993-11285, Law 1-82 [Gabon]; Decree n˚2002-437 [Republic of Congo]), while it is 80 cm in Cameroon (ONADEF, 1992).

This MCD may need to be revised upwards in order to meet national standards in terms of recovery rates. For *A. klaineana*, this rate must be at least 75% in Gabon and 50% in Cameroon. In Republic of Congo, the rates are calculated by species group and not individually. These rates are calculated for a cutting cycle. This time is a minimum of 20 years in Gabon (law n°016/01), 25 to 30 years in Republic of Congo (Karsenty et al., 2016) and 30 years in Cameroon (ONADEF, 1992).

8 Wood market

8.1 *Use*

The characteristics of *A. klaineana* wood are described in Gérard et al. (2016). It is one of the best timbers for veneer and plywood production. The exploitation of *A. klaineana* was once very selective. It was limited to the best trees for peeling, i.e. 30 to 40% of the trees having reached the minimum cutting diameter (MCD). Today, the species is also used to produce sawn timber and this proportion can locally reach 65 to 75% (FRMi, 2018). The physico-mechanical characteristics of plantation woods are very close to those of natural forests (Medzegue et al., 2007; Ngavoura, 1998).

8.2 *Market*

In Gabon, in 2007, *A. klaineana* accounted for 930,000 m³ of wood entering factories, 82% of Gabon's total production (de Wasseige et al., 2009). In 2010, the Gabonese government banned the export of logs. This strongly encouraged local wood processing (Yoan et al., 2018) and the export of veneers to the European market which reached 142,000 m³ in 2017 (ITTO, 2019). On the other hand, other producing countries (Republic of Congo and Equatorial Guinea) have taken advantage of this ban to export more logs to China. For example, the Republic of Congo increased its exports of *A. klaineana* logs by 20% between 2016 and 2017 to reach 940,000 m³ (ITTO, 2019). Since July 2020, the Republic of Congo has also banned the export of logs except "*logs of heavy and hardwood species whose processing requires specific technology*" (art. 97, Law No. 33-2020). In 2018, sawn timber was mainly directed to China (61%), Vietnam (15%) and Belgium (6%) (ITTO, 2019).

According to recent modelling (FRMi, 2018), the net volume that could be mobilised would be between 1.88 and 2.71 million $m^3.y^{-1}$, whereas the volumes harvested reach 1.70 million $m^3.y^{-1}$.

As approximations given only for information purposes, *A. klaineana* logs sold between 2015 and 2020 to China ranged 160-250 € m^{-3}. For sawn timber, 270-460 € m^{-3} (pers. com. in line with the latest ITTO tropical timber market report https://www.itto.int/market_information_service/). Veneer sheets for the European FSC market can be sold for around 800-860 € m^{-3} for face and back and 450 € m^{-3} for cores (pers. com.). According to FRMi (2016), Asian buyers were spending 280-380 € m^{-3} for Gabonese plywood compared to 660-850 € m^{-3} towards the European FSC market. It should also be noted that current prices are high due to the SARS-COV2 pandemic.

9 Conclusion and study perspectives

Aucoumea klaineana is classified by the IUCN as "Vulnerable" under criterion A1. This criterion considers the past reduction of the species' population over a period of three generations. Given their long lifespan, this criterion is difficult to objectivise for tree species. Like populations of other light-demanding colonising taxa, it is even likely that *A. klaineana* populations have increased over the past few centuries as explained in this review. Furthermore, with an average of 6,9 trees (dbh ≥ 20 cm) per hectare, the species is not rare and its regeneration is not problematic at the level of its distribution range. Finally, in logging concession, the exploitation leaves enough seed trees because the legal cutting diameter is well above the fruiting diameter. Therefore, we do not believe that *A. klaineana* is vulnerable under criterion A1.

While logging is not a concern for the survival of the species, the reduction in the quality of the logs due to decades of exploitation focused on the best shaped trees, could have unfortunate consequences on the quality of the production.

Optimising *A. klaineana* silviculture and thus maintaining its trade is essential for the economic future of Gabon and bordering regions. This species remains the leader in a niche market which is the production of veneer sheets by peeling.

It has been shown that the wood quality of *A. klaineana* in plantations is comparable to that of natural forest wood (Medzegue et al., 2007). The success of plantations should make it possible to keep a low pressure on the natural resource by concentrating production on small areas. Furthermore, the light-demanding temperament as well as the rapid growth of the species should ensure that *A. klaineana* is a prime choice for regenerating degraded forests and recreating a habitat suitable for restarting the forest dynamics.

To improve stand management and ensure sufficient regeneration of the species, it is important to understand the determinants of its growth. This synthesis has revealed a high variability in the growth and productivity of natural and artificial stands of *A. klaineana*. It also highlighted the lack of knowledge about the role of the rhizosphere in the dynamics of the species populations. To be effective, silviculture of *A. klaineana* should take theses aspects into account to a greater extent (Leroy Deval, 1976a).

Mycorrhizal symbiosis in *A. klaineana* roots has never been observed in its area of origin. However, it could explain the mixed productivity of the species, in comparison with other light-demanding species in plantations.

The phenomenon of root grafts could also be a determining factor in the dynamics of *A. klaineana* populations by promoting strata differentiation in stands and extending the rhizosphere of dominant trees while providing photoassimilates to the dominated. This phenomenon could be complementary with mycorrhizae. It is therefore necessary to improve our knowledge of the rhizosphere of populations of the most exploited woody species in Central Africa.

Chapter 3

Regeneration dynamics under light and pest constraints

Seedlings grown at 25% relative irradiance for 5 months

In the previous chapter, it was emphasized that Okoumé is a light-demanding species, however, its shade tolerance and the relative irradiance required for survival and optimal growth have not yet been quantified. Through an 18-month experiment, the initial objective of this chapter (based on **Article 2**) was to determine under which light conditions Okoumé seedlings establish and initiate stand dominance. However, the experimental focus shifted following the occurrence of significant pest attacks, which revealed the need to explicitly account for biotic stress.

Article 2 : Guidosse, Q., Biwolé, A., De Clerck, C., Ekome, S.N., Lassois, L., Doucet, J.-L., 2024a. Seedling ecology of *Aucoumea klaineana* Pierre, the most important timber species in Central Africa. *Forest Ecology and Management* **569**, 10. DOI :10.1016/j.foreco.2024.122221

Abstract

In natural forests, *A. klaineana*'s regeneration is hindered by various factors, including limited light availability and pest attacks. To address these challenges and develop effective forest management practices, a comprehensive understanding of *A. klaineana* seedling ecology is necessary. This study investigated the light requirements and pest resistance of *A. klaineana* seedlings under different light conditions through an 18-month experiment conducted in Gabon. Six shade houses with varying light intensities were constructed, ranging from 1% to 62% of full irradiance, along with an unshaded platform representing 100% light. Six-month-old seedlings were placed in the shade houses and on the platform and monitored monthly for growth parameters (relative growth rate in height and diameter), morphological parameters (number of leaves, both total and compound), and mortality. Productivity (total seedling biomass), biomass allocation traits (leaf, root, and stem mass ratios), number of branches, and symptoms of pest attacks were assessed after 18 months.

Results reveal that light conditions influence seedling performance, with optimal levels for biomass and relative growth rate in diameter and height identified between 9% and 62% of relative irradiance. However, pest infestation, particularly by psyllids and black canker, poses substantial threats to seedling growth, health, and form, regardless of light conditions. Pest attacks had a significant impact on growth but not on survival, which remained high (97.1%) even under extreme light conditions (1% and 100% of relative irradiance). The findings underscore the importance of integrating pest management strategies and adapting silvicultural practices to meet the species' ecological requirements. We suggest planting *A. klaineana* in small groups (to allow root grafts), separated by other species (to limit pest transmission), under light canopy cover (around 9-62% of relative irradiance, to promote sustained growth rates at the seedling stage). This approach should ensure the conservation of *A. klaineana* populations and the long-term viability of Central Africa's timber industry.

1 Introduction

Aucoumea klaineana is considered to have a pioneer and light-demanding behavior, colonizing open areas. Nowadays, its natural regeneration is constrained for two main reasons: (i) Shifting agriculture historically provided fallow lands suitable for seedling establishment. Since the 1950s, sedentarization has reduced these practices, leading to fewer abandoned open spaces (Biraud and Catinot, 1960; Morin-Rivat et al., 2017) ; (ii) Logging companies must comply with forest management plans, selectively logging one to two trees per hectare every 20-30 years (Durrieu de Madron et al., 1998; Nasi et al., 2012; Van Gemerden et al., 2003). Reduced-impact logging (Durrieu de Madron et al., 1998; Ezzine De Blas and Ruiz Pérez, 2008) limits forest cover loss to 10% (Ruiz Pérez et al., 2005), creating gaps that are too sparse (Blaser et al., 2021) and small (ca. 300 m²) for good regeneration of light-demanding timber species (Biraud, 1959; Doucet, 2003; Fredericksen and Putz, 2003; Hall et al., 2003). As a consequence, there is a shift in the canopy of logged forests: long-lived, light-demanding commercial species (Karsenty and Gourlet-Fleury, 2006) are progressively replaced by less-harvested shade-tolerant species (Morin-Rivat et al., 2017; Van Gemerden et al., 2003).

In Gabon, foresters addressed early the challenges of intensive exploitation of *A. klaineana* by attempting to replenish the stocks (Bouet, 1980; Brunck et al., 1990; Leroy Deval, 1976a; Waag and Duplaquet, 1936). Efforts began in the 1930s with the establishment of management areas covering 75,000 hectares. Young stands were protected to promote elite tree growth through thinning and seedling clearance. However, this approach proved insufficient in severely impacted areas. Subsequently, 26,000 hectares of plantations were established over 40 years (Brunck et al., 1990; Grison, 1979; Groulez, 1975; Leroy Deval, 1976a). The modalities of these plantations evolved, starting with strip plantations (2-4m), progressing to broader bands (10-20m), and eventually exploring full-planting conversion methods to improve sapling access to light (Brunck et al., 1990). Productivity was modest in places, averaging no more than 2 $m^3.ha^{-1}.yr^{-1}$ (Marien and Mallet, 2004). High maintenance costs and limited success of these techniques led to a shift back to preexisting forest management in the 1970s (Brunck et al., 1990).

In the late 20th century, other investigations including multispecies plantations and comparisons between clear-cut and undergrowth methods, were carried out (Koumba Zaou et al., 1998b). These plantations were based on trial-and-error methods, focusing on planting densities, thinning, and maintenance practices. The goal was to strike a balance between the species' light requirements and the need for straight conformation while addressing the issue of parasitism, all at a lower cost. However, due to limited quantitative information on the biology of *A. klaineana*, these trials yielded variable and non-reproducible outcomes.

The future development of local species plantations, including *A. klaineana*, requires focused research on silvicultural practices aligned with the species' ecological characteristics, aiming to produce high-quality seedlings (Marien and Mallet, 2004). However, there are no current guidelines for the regeneration of commercial species. A thorough understanding of the growing conditions, establishment, and management of plantations is needed but unfortunately lacking for most exploited species (Dos Santos and Ferreira, 2020). This lack of focus on the species' biology is evident for *A. klaineana*. For example, the dioecious nature of the species (Grison, 1976) and the presence of root grafts, a fusion of root steles that enables the interchange of water and carbon between conspecific individuals (Leroy Deval, 1974, 1973), were only discovered 40 years after the beginning of the reforestation operations. This last characteristic has allowed the innovation of a promising planting approach using tree densities promoting small groups as a single biological unit, serving the dominant target tree (Louppe et al., 2000).

To focus on the ecological characteristics of *A. klaineana*, it is crucial to revisit the challenges posed by limited open habitats and selective logging, both of which impact the plant’s light regime. Light is a crucial environmental factor that significantly affects the establishment, growth, and survival of plants in tropical forests, leading to notable changes in their morphological, physiological traits (Agyeman et al., 1999; Hawthorne, 1995; Poorter, 1999; Swaine and Whitmore, 1998) and sensitivity to pests (Bosu et al., 2006; Leroy Deval, 1976b). Trees species are usually classified into regeneration guilds, using systems such as Hawthorne's Pioneer (P) - Non-Pioneer Light-Demanding (NPLD) - Non-Pioneer Shade Bearer (NPSB) species (1995, 1993) or indices relying on the relationship between tree size and crown exposure to light (Loubota Panzou et al., 2018; Sheil et al., 2006).

While *A. klaineana* is typically described as a pioneer species that thrives in well-lit environments, excessive light can alter its structure, producing offshoots, that result in a bushy appearance rather than vertical and diameter growth (Brunck et al., 1990). As the tree ages, the stem exhibits impressive flexibility to reach for light, compromising the necessary straightness for log peeling. Excessive light also increases its susceptibility to parasitism, negatively impacting plant populations (Brunck et al., 1990; Leroy Deval, 1976a).

Further information on pests and diseases affecting *A. klaineana* is provided in Chapter 2, Section 4.6, as well as in Leroy-Deval (1976b) and Brunck et al. (1990).

A quantitative investigation of *A. klaineana* growth and adaptive strategies under various light conditions could yield valuable insights into its biology. As a pioneering, light-demanding species, the seedlings are expected to perform better under intermediate to high irradiance conditions, which mimic large canopy gaps and open areas such as savannahs. However, increased light exposure is likely to increase their vulnerability to pest attacks by providing more or higher-quality food for herbivores, as described by the Plant Vigour Hypothesis (PVH), which predicts that herbivores preferentially attack fast-growing, vigorous plants (Price, 1991). Additionally, local resources that are scarce for plants, such as light in the understory, can affect the impact of herbivory by influencing a plant's ability to regenerate lost tissues and survive, as explained by the Limiting Resource Model (LRM), which states that plant tolerance to herbivory depends on the most limiting resource (Wise and Abrahamson, 2007, 2005).

Consequently, we hypothesize that (**i**) seedlings of *A. klaineana* will develop optimally under intermediate light conditions, where attacks are reduced but growth remains adequate; (**ii**) leaves and buds will sustain greater damage under higher light conditions due to the simulation of open gaps than under lower light conditions simulating the forest understory (PVH); and (**iii**) seedling survival will be worse in low light conditions because they will be less able to replace infested tissues due to limited light resources (LRM).

Our study aims to provide, for the first time, a comprehensive understanding of seedling light requirements, responses, and survival of this major timber species from Central Africa, based on an experiment conducted in Gabon under semi-controlled conditions. This will lead to practical recommendations for integrated pest management in plantations and sustainable management of forest stands.

2 Materials and Methods

2.1 *Study species*

Unlike many traits of pioneer species (sensu Swaine and Whitmore, 1998), *A. klaineana*'s seeds are recalcitrant and germinate within three weeks regardless of light conditions (Brunck et al., 1990). Seedlings grow in open environments such as savanna edges, fallow lands, forest gaps, roadsides, and tracks (Delègue et al., 2001; Doucet et al., 2004). Their density varies from 6,000 (De Kam et al., 1996) to 35,000 per hectare (Fuhr et al., 1998), with most seedlings dying early.

2.2 *Seedlings preparation*

In February 2021, seeds from three healthy *A. klaineana* trees were collected from the forest surrounding the study site in PW-CEB (Bambidie, Ogooué-Lolo, Gabon) and randomly planted in a nursery receiving 30% of Relative Irradiance (RI). They were sown in polystyrene bags (35 cm high x 15 cm diameter) containing a mixture of 4/5 forest topsoil and 1/5 river sand. By August 2021, 210 healthy seedlings ready for planting (mean height = 25.8 ± 3.4 cm; mean diameter at collar = 3.2 ± 0.5 mm) were randomly distributed among the shade houses (30 per treatment). The plants were watered daily, and weeds were regularly removed. In November 2021, the seedlings were repotted into 15-L buckets containing the same soil mixture to allow for good root development.

2.3 *Light experiment*

The light response experiment lasted 18 months, from September 2021 to February 2023. Six shade houses (2 x 3 x 1.8 m) were constructed with wood slats of increasing spacing to cover the full light intensity gradient (Figure 15). Four levels were chosen following Agyeman et al. (1999) to simulate the light conditions prevailing in small to very large canopy gaps (9%, 25%, 39%, and 62% RI). Two others (1% and 4%) represented the conditions existing in tropical forest understory (Kyereh et al., 1999), considered as shaded environment, where greater variation is expected attributed to the seedlings light compensation point (Agyeman et al., 2010, 1999). Finally, an unshaded platform (100% RI) corresponded to the conditions encountered in deforested or grassland areas. If *A. klaineana* has the same behavior than other well-known pioneer species (*Ceiba pentandra* (L.) Gaertn. (Fromager), *Milicia excelsa* (Welw.) C.C.Berg (Iroko), *Ricinodendron heudelotii* Müll. Arg. (Ndjanssang) or *Terminalia ivorensis* A. Chev.) (Framiré), negative growth rates due to physiological stress are expected at 1% RI (Agyeman et al., 1999).

Figure 15 : Experimental setup including six shade houses receiving, from front to back, 4%, 1%, 10%, 25%, 40%, and 60% of Relative Irradiance (RI), and a platform (left) receiving 100% RI. The structures were built in 2019 for a similar experiment on *Cylicodiscus gabunensis* (Okan) (Ndonda Makemba, 2023), and were inspired by the protocol of Agyeman et al. (1999).

Photosynthetic photon flux density (PPFD, $mmol.m^{-2}.day^{-1}$) was measured using photosynthetically active radiation (PAR) sensors (Solems PAR/CBE 80, Palaiseau, France) during seven periods to maintain relative irradiance (RI) constant (Table 1). Each calibration campaign lasted seven days. During the first week, temperature and hygrometry were also measured with Ebro EBI 20-TH sensors (Xylem Analytics, Ingolstadt, Germany) (Supplementary Material 2). The six plots were arranged in a row, 3 meters apart to avoid shading each other, and perpendicular to the path of the sun.

Table 1: Average daily photosynthetic photon flux density (PPFD, mmol.m^{-2}.day^{-1}) and its standard deviation over seven periods in six shade houses (**A-F**) and an unshaded platform (**G**). Measurements were taken over a seven-day period.

2021		**2022**					**Mean**	**SD**	**% Irradiance**
August	November	February	March	May	June	July			
	6.22	5.19	5.92	5.67	2.29	4.58	4.97	1.22	1%
19.27	28.52	23.94	24.95	19.86	8.50	8.63	19.09	7.26	4%
49.37		55.50	50.36	55.34	22.97	21.10	42.44	14.62	9%
126.30	144.80	126.22	167.26	140.52	57.85	59.45	117.49	39.34	25%
204.12		245.43	247.73	206.15	83.33	88.69	179.24	68.08	39%
281.52		363.05	372.85	289.18		130.45	287.41	86.83	62%
461.02	683.08	580.88	622.51	489.37	189.48	219.64	463.71	178.29	100%

Every month from September 2021 to January 2023, the following parameters were recorded: height (vertical distance from root collar to apical meristem), stem collar diameter, number of simple leaves (Nlv), number of compound leaves (Ncmplv), and mortality. The number of branches (N_Br) was also counted after 18 months (February 2023).

In February 2023, ten seedlings per light treatment were randomly collected, removed from their buckets, and had their roots washed. After oven drying for 72 hours at 70 °C, leaves (including petioles and rachis), stems (including branches) and roots (including taproot and finer roots) were separately weighted to compute leaf mass ratio (LMR), stem mass ratio (SMR) and root mass ratio (RMR) (i.e., the proportion of leaf, stem, and root dry mass relative to the seedling total biomass), (Dent and Burslem, 2009) as well as seedling total biomass (STB).

Among these 70 individuals, symptoms of pests that might affect plant growth and architecture were recorded and divided into three categories: (i) psyllids damage - terminal shoots shaped like a witch's broom; (ii) black canker - sooty black film on at least one organ and/or cankerous protuberances on at least one woody organ; (iii) necrosis spots on leaves, sometimes leading to wilting.

2.4 *Data analysis*

All statistical analyses were performed in the open R environment (version 4.1.2). For all seedlings, the relative growth rate in height (RGRh) and diameter (RGRd) were computed as in Poorter (1999):

$$RGR_{\mathrm{X}} = \frac{\ln(X_2) - \ln(X_1)}{t_2 - t_1}$$

Where X1 and X2 represent the height (h) or diameter (d) of a plant at times t1 and t2, respectively. Due to pest events, the analysis of plant growth was carried out in three periods: before pest spread (0-6 months), after pest spread (12-18 months) and over the entire experiment (0-18 months). Subsequently, a principal component analysis (PCA) was performed to highlight the impact of functional traits on growth parameters. To compare our data, we used one-way ANOVA followed by a Tukey test from the ‘stats’ package (R Core Team, 2021). The Tukey test assigns a letter to each group, with groups sharing the same letter indicating no significant difference. To respect homoscedasticity and equality of variances, RGR values were square root transformed, except for RGR calculations during the first six months (no transformations) and RGRd during the entire experiment (squared transformation). A chi-square test was carried out to analyze the proportion of plants affected by pest symptoms across the different shading modalities. Additionally, quadratic regression models were fitted using the ‘ggpmisc’ R package (Aphalo et al., 2024), considering the irradiance as a continuous factor.

3 Results

3.1 *Pests and mortality*

After 18 months, all 70 collected individuals exhibited at least one symptom (Table 2). Ninety-three percent were infested by psyllids (*Pseudophacopteron* sp.). Initial attacks rapidly spread during the 8th month (March 2022) in the 4% and 9% RI shade houses, and then appeared in the 25% RI plots after 10 months. By 12 months, all light treatments were affected. Plants showed atrophy of terminal buds, resulting in a "witch’s broom" appearance (Brunck et al., 1990; Leroy Deval, 1976b) (Figure 16A). In the months following psyllid damage, fungal lesions identified as black canker (*L. theobromae*) were observed on 21.4% of the plants, affecting stems (cankerous protrusions), leaves (petioles and/or rachis covered with a black sooty film), and/or terminal and adventitious buds (sooty film, Figure 16A). Buds were particularly affected in the 4% RI plot, with 90% of plants infected. Concurrently, 82.9% of the seedlings displayed unidentified black, gray, brown, or white spots on the leaves by the end of the experiment (Figure 16B), occasionally leading to partial or complete leaf tearing.

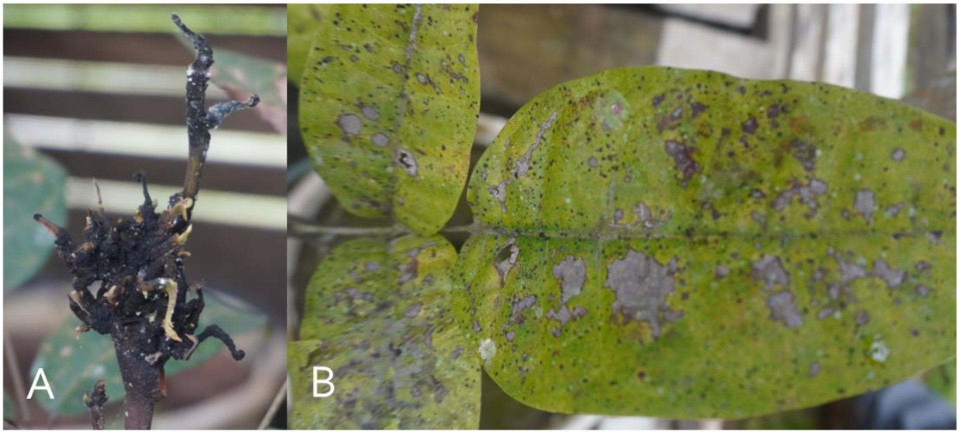


Figure 16: (**A**). *A. klaineana* seedling showing dramatic changes following a psyllid attack, with terminal buds deformed into a witch's broom shape and infected by black canker. (**B**) Gray spots on *A. klaineana* leaves resulting from damage caused by psyllids. © Q. Guidosse

Table 2: Percentage (%) of dead (out of 210; 30 per plot) and diseased (out of 70; 10 per plot) *A. klaineana* seedlings at the end of the experiment (18 months). Symptoms are described in the text.

Plot (% RI)		1	4	9	25	39	62	100	**Total**	Chi square tests
Mortality (n=210)		3	0	0	0	3	3	10	**2,9**	χ^2 (6) = 8.0, p=0.23
Symptoms (n=70)	**Witches' broom**	90	100	100	100	100	70	90	**93,0**	χ^2 (6) = 2.51, p=0.86
	Sooty film or protuberances	0	90	10	10	10	10	20	**21,4**	χ^2 (6) = 78.61, $p<0.001$
	Leaves covered with spots	70	90	80	100	90	50	100	**82,9**	χ^2 (6) = 6.46, p=0.37

Despite these pest issues, mortality rates were very low, with only 2.9% of seedlings dead by the end of the experiment across all treatments. Only one seedling (3%) died under 1% RI, similar to the 39% and 62% RI treatments (Table 2). The modality with full light exposure (100% RI) had the highest mortality rate, with three dead seedlings (10%). Among these, one seedling died after only 2 months, while the other two perished after 13 and 15 months, with no clear association with the observed pests.

3.2 *Growth response*

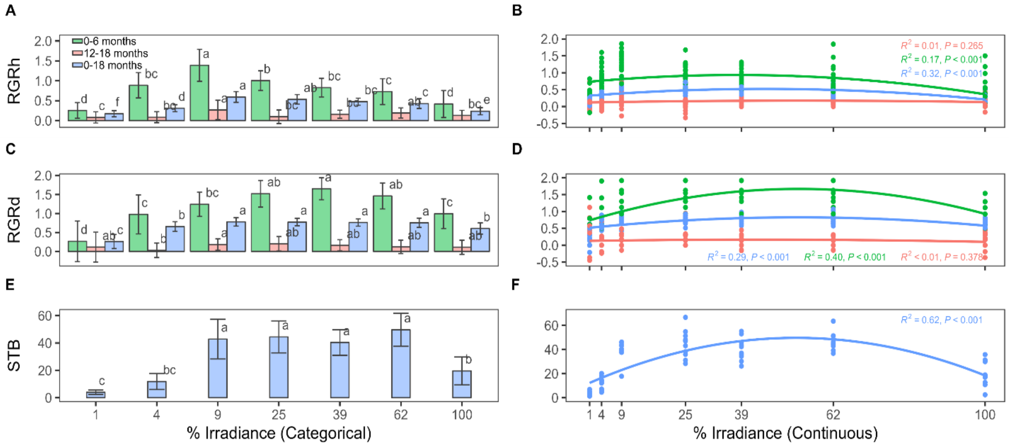


Figure 17 : Relative growth rates (**A**,**B**) in height (RGRh in cm.cm^{-1}); (**C**,**D**) in diameter (RGRd in mm.mm^{-1}) and (**E**,**F**) final seedling total biomass (STB in g) of *Aucoumea klaineana* seedlings in response to varying light conditions ranging from 1 % to 100 % RI. For irradiance as a categorical factor (**A**,**C**,**E**), standard deviations are indicated by error bars. Significant differences ($p < 0.05$) between groups are denoted by different lowercase letters according to Tukey's post-hoc test. Quadratic regressions were fitted when considering irradiance as a continuous factor (**B**,**D**,**F**).

Before pest attack (during the first six months), optimal diameter growth (RGRd) occurred between 25% and 62% relative irradiance (RI), whereas optimal height growth (RGRh) was observed at 9% RI (Figure 17). Throughout the entire experiment, including the period affected by pests, there were no longer significant differences in performance between RGRd and seedling total biomass (STB), with both showing optimal values between 9% and 62% RI. The advantage in RGRh observed under low light conditions was negated by pest emergence, resulting in a plateau extending from 9% to 62% RI. Plant growth during the first six months was generally higher (RGRh: $F(2, 18) = 12.92$, $p< 0.001$) compared to the rest of the experiment. Overall, in terms of relative growth rate in diameter, plants exhibited the best growth during the first six months and the poorest growth during the final six months of the experiment (RGRd: $F(2, 18) = 21.38$, $p < 0.001$).

Quadratic regressions were also performed. Over the entire experiment, the R^2 values were 0.29 for RGRd, 0.32 for RGRh and increased to 0.62 for STB, with a peak between 39% and 62% RI. Optimal performance ranges in terms of RGRh, RGRd, and STB were identified ($p < 0.001$) except during the last 6 months (RGRh: $p=0.265$; RGRd: $p = 0.376$).

3.3 *Biomass allocation and functional traits*

When focusing on biomass allocation ratios (Figure 18), LMR was notably higher at low irradiance, particularly at 1% RI, and decreased as light intensity increased. In the 4% RI plot, LMR was particularly low and variable. This plot was also the first to show multiple pest symptoms. The proportion of biomass allocated to the stem was higher in the 4% RI plot and lower in the 39% RI plot. Conversely, RMR was significantly higher in brighter light conditions (25% to 100% RI) and decreased progressively with reduced light. The number of simple or compound leaves, as well as the number of branches, did not exhibit clear correlations with the amount of available light (Supplementary Material 3).

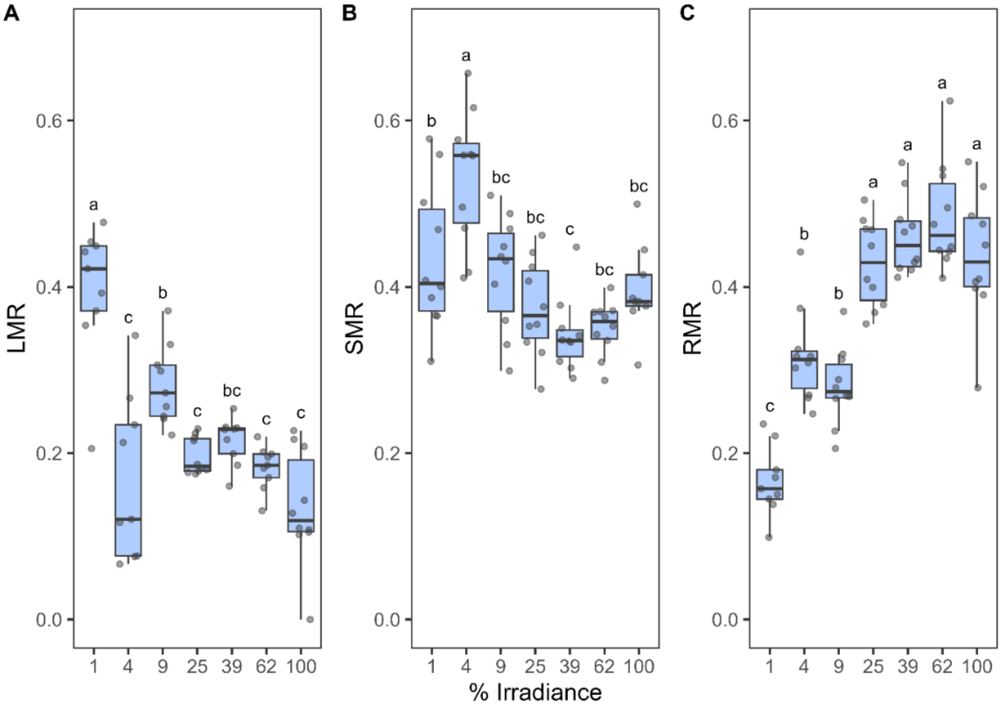


Figure 18 : Biomass allocation of *A. klaineana* seedlings across relative irradiance levels ranging from 1% to 100%. LMR: leaf mass ratio (**A**); SMR: stem and branch mass ratio (**B**); RMR: root mass ratio (**C**). Letters denote results from ANOVA and Tukey's test, with a common letter indicating no significant differences between groups.

Principal component analysis was conducted to examine the impact of functional traits on growth and biomass (Figure 19). The first two PCA dimensions accounted for 61.1% of the total variation. The first axis (37.7%) reflects overall plant growth (RGRd, RGRh) and biomass (STB), showing a positive correlation with root mass ratio (RMR) and an inverse relationship with aboveground woody biomass (SMR). The second axis (23.4%) contrasts seedling development strategies opposing foliar functional traits (LMR and number of compound leaves) with root system biomass (RMR). Four distinct groups emerged from the PCA (Figure 19): (**i**) the 9% RI treatment displayed superior growth (RGRh, RGRd) and biomass (STB), allocating significant biomass to leaf mass (LMR); (**ii**) the 25% to 62% RI range indicated substantial growth and biomass but with less pronounced foliar traits; (**iii**) the 1% RI plot shows prominent foliar traits but limited growth and biomass; (**iv**) the 4% and 100% RI categories generally manifested weaker outcomes in terms of growth, biomass, and development of both roots and leaves.

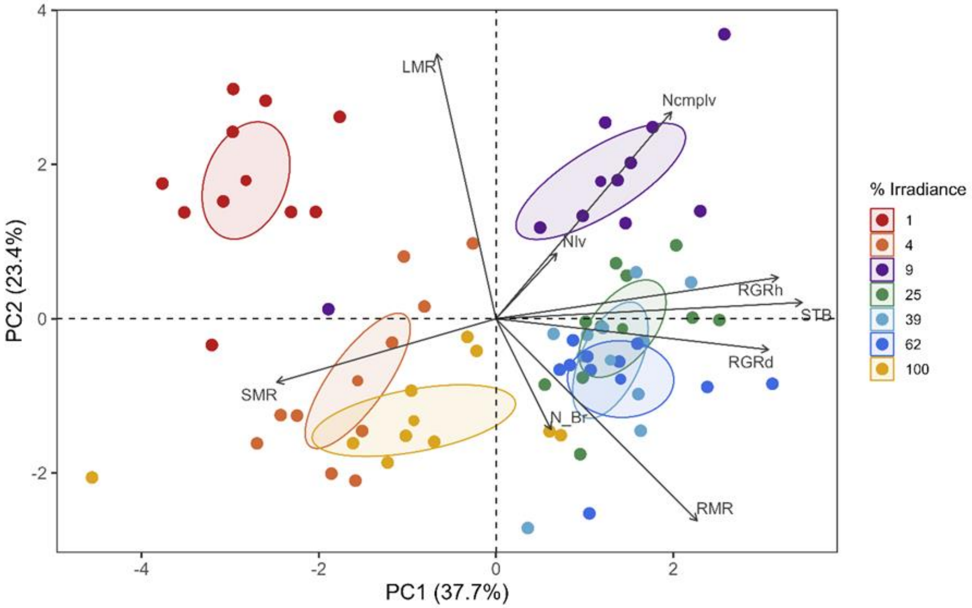


Figure 19 : Principal Component Analysis (PCA) performed on nine different functional traits of *A. klaineana* seedlings subjected to seven light intensities ranging from 1 % to 100 % of relative irradiance. The traits analyzed included, included among other, the number of leaves (Nlv), the number of compound leaves (Ncmplv), and the number of branches (N_Br) at the end of the experiment.

4 Discussion

4.1 *Pests and mortality*

This experiment, carried out in Gabon under semi-controlled conditions, aimed to explore how light affects the growth and survival of *A. klaineana* seedlings, a major timber species from Central Africa. Given the substantial impact of parasitism observed, it is crucial to first address its influence on growth parameters. Previous research by Brunck et al. (1990) highlighted that damage from psyllids or cankers on *A. klaineana* was more prevalent in highly illuminated environments. They advised against planting this species in open areas near villages that attract *W. auropunctata* ants and noted that depleted or hydromorphic soils are high-risk zones, particularly in densely packed stands where tree crowns are underdeveloped, resulting in less vigorous plants.

To mitigate infestation risks, a common recommendation for tropical timber species is to plant them in shaded conditions (e.g., Bosu et al., 2006; Brunck et al., 1990; Nichols et al., 1998; Wagner et al., 1996). However, our results did not demonstrate a reduction in symptoms with decreasing relative irradiance. In contrast, pest attacks began at 4% and 9% RI. This lack of effect might be attributed to the proximity of shade houses, facilitating the rapid spread of pests from higher to lower light conditions. In a natural forest setting, seedlings in shadier conditions would likely benefit from greater species diversity, which could serve as a barrier against pest proliferation.

Healthy seedling production is essential for the artificial regeneration of *A. klaineana*. Current pest control measures for major pests (e.g., *Pseudophacopteron* sp. and *L. theobromae*) are nonexistant (Brunck et al., 1990; Leroy Deval, 1976b). *Milicia Excelsa* (Welw.) C.C.Berg (Iroko), another economically important timber species in Central and West Africa, has accumulated extensive knowledge and experience in dealing with similar challenges. It is also a light-demanding species and other psyllids, the Iroko gall flies (*Phytolyma lata* Walker (Scott) and *Phytolyma fusca* Alibert) present severe issues for its regeneration.

Research over the past 70 years (e.g., Bosu et al., 2006; Nichols et al., 1998; Ugwu, 2021; White, 1964) on these pests can serve as a valuable reference for improving the health management of *A. klaineana*. When focusing on silviculture, research indicates that *M. excelsa* exhibited fewer galls in mixed-species plantations comprising 50% *M. excelsa* and 50% *Terminalia superba* Engl. & Diels. (Limba). This combination provided shade and hindered pest spread (Bosu et al., 2006; Nichols et al., 1999).

For pest management, detailed biological data on *Phytolyma* spp. were provided, including pre-oviposition and oviposition periods, fecundity, egg incubation viability, nymph instar stages and growth rates, sex ratio, and the longevity of reproductive and non-reproductive males, forming a foundation for sustainable pest management (Ugwu and Omoloye, 2014a). It was recommended to use 16 mm mesh mosquito nets with carbofuran and dimethoate to prevent insects from laying eggs on seedlings (Ugwu and Omoloye, 2014b). To promote integrated pest management, awareness was raised among stakeholders and training on these control measures was encouraged (Ugwu and Omoloye, 2015). More recently, the protective effect of ethanol extracts of *Azadirachta indica* A. Juss (Neem tree) and *Piper guineense* Schumach. & Thonn. (Ashanti pepper) on seedlings was identified (Ugwu, 2021).

In addition, part of the leaf damage observed after eight months may reflect early senescence processes rather than solely pest activity. However, while adult *A. klaineana* trees exhibit relatively synchronous leaf renewal, seedlings show a more continuous and plastic leaf turnover, with less pronounced and less synchronized shedding. This suggests that natural leaf turnover alone is unlikely to account for the extent of the observed damage.

Despite pest challenges, *A. klaineana* demonstrated a remarkably high survival rate (97.1%) after 18 months, regardless of extreme light conditions (1% and 100%) or pest impacts. In comparison, *Guibourtia ehie* (A.Chev.) J. Leonard (Ovengkol), a non-pioneer light demanding species, exhibited a lower survival rate (20%) in full sunlight (100% RI) after 15 months (Tosso, 2018). Under the lowest light conditions (1% RI) *Cylicodiscus gabunensis* Harms (Okan) and *Lophira alata* Banks ex C.F.Gaertn (Azobé) showed survival rate of 63% and 87%, respectively (Biwolé et al., 2015; Ndonda Makemba, 2023).

Although *A. klaineana*, assumed to be a pioneer species, was expected to have higher mortality rates in the lowest light conditions (Agyeman et al., 2010), it survived well, likely due to its leaf allocation strategy. However, in enriched logging gaps located in the same logging company as our experiment, Maus (2018) observed high mortality rates for planted *A. klaineana* seedlings, aligning with the deficit in natural regeneration of light-demanding species in forest openings (Goodale et al., 2012) even after post-logging thinning (Ouédraogo et al., 2011).

Competition from short-lived such as *Macaranga* spp. and *Musanga cecropioides* R. Br. ex Tedlie (Umbrella tree), whose seeds are dormant in the soil seed bank and which grow faster than *A. klaineana* (Doucet et al., 2004) can explain the observed high mortality rates.

4.2 *Light requirements for seedling growth*

The primary goal of this study was to quantify the light requirements of *A. klaineana* seedlings to optimize planting techniques. Among the plants that survived, pest impacts significantly affected overall growth, diminishing differences in productivity and performance across light conditions.

During the first six months, the optimal PPFD for RGRd ranged from 115 to 290 $mmol.m^{-2}.d^{-1}$ (25-60% RI). Other Central African pioneer species grow best in relatively bright environments such as R. heudelotti (4-66% RI, higher light conditions not measured) (Agyeman et al., 1999), *C. gabunensis* (10-40% RI) (Ndonda Makemba, 2023) or *L. alata* (24-43% RI) (Biwolé et al., 2015) (Supplementary Material 4). *Aucoumea klaineana* thus shows optimal development in the upper range of these conditions.

In comparison, two timber species of *Guibourtia* (NPLD) showed the best performances at 25% RI (Tosso, 2018). Over the entire experiment (18 months), the advantage of *A. klaineana* in RGRd at higher light intensities was less pronounced, with an optimum range from 9% to 62% RI, also corresponding to the highest seedling total biomass (STB) after 18 months. Agyeman et al. (1999) suggested an ideal growth range of 10% to 44% RI but *A. klaineana* demonstrated greater versatility, thriving from 9% to 62% RI, both before and despite pest issues.

In our experiment, the optimum RGRh peaked at 9% RI, similar to *C. gabunensis* (Ndonda Makemba, 2023). Agyeman et al. (1999) observed similar results for *R. heudelotii* (pioneer) seedlings, attributing this to etiolation. However, *L. alata* (sharing characteristics of a pioneer and a NPLD species) does not exhibit this etiolation trait around 10% RI (Biwolé, 2015), distinguishing it from *A. klaineana*, *C. gabunensis* (Ndonda Makemba, 2023), and *R. heudelotii* (Agyeman et al., 1999).

For light-demanding timber species like *A. klaineana*, rapid height growth is crucial for maximizing photosynthesis and competing with *Marantaceae* (White et al., 2000), short-lived pioneers such as *Macaranga monandra* Müll. Arg. (Doucet et al., 2004) and other long-lived light-demanding species (Brunck et al., 1990; Gilbert, 1984; Leroy Deval, 1976a). Typically, there is a trade-off between rapid canopy growth and survival in the understory while awaiting canopy openings (Baraloto et al., 2005; Brienen and Zuidema, 2006; Poorter and Bongers, 2006; Poorter and Kitajima, 2007).

Aucoumea klaineana thrives in high light (9-62% RI) to reach the canopy but also survives in very low light conditions (1% RI), similar to *L. atala* (Biwolé et al., 2015) for at least the first two years. It performs better in low light than *C. gabunensis* which shows less than 65% survival in shade (1% RI) (Ndonda Makemba, 2023). This good performance has also been observed in an *A. klaineana* plantation in Nigeria after 6.5 weeks (Wadsworth and Lawton, 1968). In contrast, Koumba Zaou et al. (1998a)'s *A. klaineana* provenance trials found no seedling growth in height under 5% to 9% RI, depending on the provenance.

4.3 *Phenotypical adaptation to light conditions*

In high light conditions (25-100% RI), *A. klaineana*, like *L. alata* (Biwolé, 2015), adapts by allocating a larger proportion of biomass to roots (RMR). This adaptation improves nutrient and water uptake efficiency, enhancing growth and survival in soils with limited resources (Poorter, 2001). In older plantations, highly exposed *A. klaineana* typically assumes a ball-shaped form that limits its height growth and promotes strong branching (Brunck et al., 1990). However, in our 18-month study, light levels did not affect SMR or the number of branches (N_Br), possibly due to the seedlings' young age.

In low light conditions, plants allocate most biomass to leaves (LMR) to optimize light capture (Poorter, 2001; Veneklaas and Poorter, 1998). This trend was also observed in the pioneer species *R. heudelotti* (Agyeman et al., 1999). Additionally, we noted a darker leaf coloration with decreasing light, which may indicate a higher chlorophyll concentration, enhancing photosynthetic efficiency and survival in low light (Agyeman et al., 2010). This adaptation could explain *A. klaineana* survival in dark conditions.

Typical pioneer species exhibit a negative relative growth rate (RGR) at low irradiance levels (<2%) (Agyeman et al., 1999; Kyereh et al., 1999), which corresponds to the light reaching the understory in a mixed old rainforest (Kyereh et al., 1999). Such negative values indicate that plants are withering. However, in our study, the average RGRh and RGRd did not show negative values, even after pest occurrence. This demonstrates the strong adaptability and resilience of *A. klaineana* under the tested conditions, without competition or intraspecific interactions.

Despite this, pests negatively impacted several individuals, particularly from the 12th month onward, with some exhibiting negative RGRd and RGRh across all light intensities (Figure 17B, D). Notably, even after infestation, all seedlings at 39% and 62% RI maintained zero or positive RGRd. This suggests that A. *klaineana* can tolerate full light intensity (100% RI), maintaining a neutral to positive RGRd and RGRh when healthy. However, in very low light conditions (1% RI), some individuals withered regardless of the experimental period and their health status.

4.4 *Species management*

Considering the susceptibility of *A. klaineana* to pests, we recommend prioritizing heterogeneous forests and avoiding monoculture plantings to encourage light filtration and the establishment of diverse species. This is supported by results obtained with *M. excelsa* which grows better in logging gaps with competition, than in free-to-grow plantations (Fayolle et al., 2015) primarily due to reduced pest attacks in mixed-species environments. Nonetheless, the proximity among *A. klaineana* trees observed in nature suggest the interactions through mycorrhizal associations (Onguene et al., 2002), the renewal of their own litter (Midoko Iponga et al., 2020), and particularly regarding the root grafts forming interconnected groups of trees (Leroy Deval, 1973).

Although suboptimal, seedlings can establish themselves in extreme light conditions. At very low light levels (1% RI), some seedlings perish despite positive average relative growth ratesin height (RGRh) and diameter (RGRd) and their survival is jeopardized if disturbances do not quickly increase the irradiance level. At 100% RI, seedlings continued to grow slowly before eventually dying. Advances in pest control could potentially enable seedlings to thrive in full light conditions, even though this environment is not optimal due to other stress factors such as drought, UV radiation, and conformation constrains.

Given these points, we recommend testing a planting technique inspired by both the method of degraded forest enrichment proposed by Doucet et al. (2016) (particularly proven for *T. scleroxylon*, presenting a similar ecology to *A. klaineana* (light-demanding, wing dispersed seeds, monospecific stands)) and the spaced blocks method suggested by Louppe et al. (2000) to promote intraspecific interactions.

Specifically, we advise planting monospecific blocks of 9 to 16 individuals spaced 1 meter apart in areas with 9-62% RI at ground level. Such a level of irradiance could be encountered in degraded forest areas, after clearing the undergrowth and leaving a few spaced large trees. To ensure the proper development of the young plants, it is necessary not to plant directly under these trees. Subsequently, clearing and thinning will be necessary to allow the better-performing trees to develop properly.

This method should promote optimal growth and shape of *A. klaineana* seedlings, facilitate self-resilient mechanisms against interspecies competition, enable belowground exchanges between individuals, and prevent pest propagation between groups, ultimately ensuring a healthy and sustained growth.

5 Conclusion

The development of *A. klaineana* seedlings under semi-controlled conditions was optimal across a surprisingly broad range of light intensities (9-62% RI), for diameter, height, and biomass. However, the health and architecture of these seedlings were severely impacted by psyllids and black canker. Despite these challenges, *A. klaineana* showed remarkable resilience, with high survivability even under extreme light conditions (1% and 100% RI).

Our study underscores the importance of effective pest management and tailored silvicultural practices that align with the species' ecological requirements. Emphasis should be placed on better knowledge of pest biology and on implementing integrated pest management strategies, drawing on synthetic, physical (Ugwu and Omoloye, 2014b), and biological control methods (Ugwu, 2021), as suggested by prior research on *M. excelsa*.

To optimize *A. klaineana* regeneration and growth, we recommend planting techniques that leverage heterogeneous forest structures and conspecific interactions. Specifically, we advise planting monospecific clusters of 9 to 16 individuals, with 1-meter spacing, in shaded zones (9-62% RI), and placing these clusters among groups of different species. This can enhance growth and intraspecific interactions while reducing competition pressure and pest propagation. This approach aligns with practices proven effective for similar species and promotes a healthy, sustained growth of *A. klaineana*.

Future research should focus on planting techniques in forest conditions to better understand inter- and intraspecific interactions, especially concerning mycorrhizal associations and root grafts. Additionally, studies should explore the long-term effects of pest management strategies and the resilience of *A. klaineana* in various ecological settings. Implementing and monitoring our proposed planting techniques in diverse forest environments will further validate their efficacy and contribute to the sustainable management of the most harvested species of Central Africa.

Chapter 4

Root-associated fungal communities of *Aucoumea klaineana*

Prospecting for Okoumé fine roots in an old-growth mixed forest

The slow decomposition of *A. klaineana* litter and its potential associations with ectomycorrhizal fungi suggest that soil mycobiota may also contribute to its monodominance. Building on adapted molecular methods (**Article 3**) this chapter is a modified version of **Article 4** and investigates the root-associated fungal communities of *A. klaineana* to better understand their potential role in monodominance and the persistence of suppressed trees survival by using high-throughput DNA sequencing.

Article 3 : Guidosse, Q., Roy, M., Lassois, L., Doucet, J.-L., 2024b. Adapted molecular methods to unravel the recalcitrant mycorrhizal associations of *Aucoumea klaineana* Pierre. *Journal of Microbiological Methods* **224**, 4. DOI: 10.1016/j.mimet.2024.107000

Article 4 : Guidosse, Q., Roy, M., Massart, S., Doucet, J.-L., Lassois, L., De Clerck, C., 2025. High diversity and variability of root-associated fungi in *Aucoumea klaineana*, a monodominant Central African timber species. *Mycorrhiza* **35**(65), 20. DOI: 10.1007/s00572-025-01239-y

Abstract

While soil fungi are crucial for plant growth, their role in promoting monodominance or supporting suppressed, light-demanding trees remains underexplored. This study is the first to analyze the root mycobiota of *A. klaineana*, investigating fungal communities in monodominant stands and old-growth mixed forests in Gabon, and plantations in the DRC, sampling both canopy-reaching and suppressed individuals, using ITS2 rDNA and 18S rDNA high-throughput sequencing.

An optimized DNA extraction and amplification protocol, incorporating activated charcoal and bovine serum albumin, was developed to mitigate inhibitors in *A. klaineana* roots, enabling reliable analysis of the root mycobiota.

High fungal diversity was observed across all sites, but no "core mycobiota" was detected across stand types or tree social status (canopy-reaching vs suppressed). Fungal communities varied significantly between stand types, highlighting their context-dependent nature. Moreover, no distinct fungal communities characterized suppressed trees. These findings indicate that fungal associations, including mycorrhizal ones, are unlikely to drive monodominance in *A. klaineana***.**

These results highlight the need to consider alternative processes, not related to fungal interactions, such as root grafting, in explaining the persistence of suppressed trees and the dynamics of monodominant stands of *A. klaineana*. Finally, this study illustrates the highly variable and diverse belowground communities associated with *A. klaineana*, whose functions and interactions could contribute to the sustainable management of this major timber tree species.

1 Introduction

African tropical forests are highly diverse ecosystems, harboring between 4,600 and 6,000 tree species (Slik et al., 2015). In Central Africa, one hectare of forest can host between 50 and 150 tree species (diameter at breast height > 10 cm) (Day et al., 2014; S. Gourlet-Fleury et al., 2013). However, locally, a single tree species, such as *Gilbertiodendron dewevrei* (De Wild.) J. Léonard or *Julbernardia seretii* (De Wild.) Troupin (Peh et al., 2011a) can cover more than 60% of the canopy, forming so-called monodominant stands (Connell and Lowman, 1989; Hart et al., 1989; Peh et al., 2014; Torti et al., 2001). While the processes by which a single tree species becomes monodominant have been extensively studied, a complete understanding remains elusive. Connell and Lowman (1989) suggested that species monodominance could arise through rapid recruitment in frequently disturbed environments, or competitive exclusion in stable ones. Building on this, Peh et al. (2011a) compared eight hypotheses to explain this phenomenon.

Although no single factor can solely explain persistent monodominance, they emphasized the importance of ectomycorrhizal (EcM) associations and slow decomposition rates, both linked to soil microbiota, as key processes that may generate positive feedbacks contributing to species dominance. For instance, in the well-studied *G. dewevrei* forests, monodominance is associated with positive feedback between EcM associations and slow leaf litter decomposition, as well as other life-history traits such as shade tolerance and large seed production (Peh et al., 2011a; 2011b; Torti et al., 2001).

As monodominant stands age, stratification among conspecifics occurs. Surprisingly, some tree individuals survive despite limited light availability, even in stands dominated by light-demanding pioneer species (Connell and Lowman, 1989), then referred to as suppressed trees. While this phenomenon has received limited attention, increasing evidence suggests that plant responses to abiotic factors are mediated by soil microorganisms (Friesen et al., 2011; Xi et al., 2019). Although few studies have examined soil feedback under varying light conditions (Mccarthy-Neumann and Kober, 2010), Xi et al. (2019) demonstrated that, at least at the seedling stage, soil microorganisms can influence plant light responses through traits related to carbon gain and nutrient availability. Soil microorganisms might also help understory trees survive in low light via common mycorrhizal networks (Balandier et al., 2022; McGuire, 2007; Sen, 2000; Simard et al., 1997), allowing them to benefit from resources acquired by neighboring canopy-reaching trees. However, how these belowground processes mediate interactions between understory and overstory trees remains unclear (Deng et al., 2023).

Aucoumea klaineana forms dense, monospecific stands, eventually becoming monodominant (e.g., Delègue et al., 2001; Fuhr, 1999; Pangou et al., 2003; White et al., 2000), similar to the process described for *G. dewevrei* by Leroy Deval (1974). However, the mechanisms driving this monodominance have never been elucidated for this major commercial species. While Burseraceae species typically do not form ectomycorrhizal associations (Bâ et al., 2011), some researchers have hypothesized that *A. klaineana* might be an exception (Leroy Deval, 1974; Peh et al., 2011a).

However, studies on its root-associated fungi are scarce, likely due to methodological barriers. Tropical tree roots, rhizoplane, rhizosphere and surrounding soil often contain various secondary metabolites such as alkaloids, flavonoids, phenols, terpenoids, lignans, etc. (Becerra, 2015; Richards et al., 2015) that inhibit DNA extractions and PCR reactions. This is particularly true for trees belonging to the Burseraceae family, which secrete substances that contain many inhibiting molecules (De Nicolai and Rodrigues, 2022). In this context and considering the frequent lack of fungal amplification on tropical roots, adapted molecular protocols are needed.

Existing records include a single *Endogone* sp. observation (Leroy Deval, 1976a) and a brief mention of arbuscular mycorrhizal (AM) fungi based on root staining (Onguene et al., 2002). Considering the coarse and shallow morphology of the tree rootlets (Guidosse et al., 2022), similar to structures formed by EcM fungi (Smith and Read, 2008), this assumption requires further investigation.

In logging concessions, the natural regeneration of *A. klaineana* is constrained by the sedentarization of human populations, leading to a decrease in open fallow lands (Biraud and Catinot, 1960; Morin-Rivat et al., 2017). Additionally, sustainable logging practices create gaps that are too small and sparse (Blaser et al., 2021; Ezzine De Blas and Ruiz Pérez, 2008; Nasi et al., 2012; Van Gemerden et al., 2003) for new populations to establish. This lack of disturbance causes the natural aging of the forest and the closure of its canopy with the consequence that long-lived, light-demanding commercial species are progressively replaced by poorly harvested, shade-tolerant species (Morin-Rivat et al., 2017; Van Gemerden et al., 2003). In Gabon, forest managers addressed this challenge early on with extensive plantation campaigns (Brunck et al., 1990; Guidosse et al., 2022). However, in some cases, the results have been inconclusive probably due to a lack of understanding of the species’ ecology, a challenge common to many tropical timber species (Dos Santos and Ferreira, 2020).

Unraveling the root-associated fungi of *A. klaineana* could contribute to improving the species' management and performance, especially in plantations. Root-associated fungi, which are key components of the soil microbiota, may explain the poor performance of *A. klaineana* in some artificial stands (Van Der Heijden and Horton, 2009). Based on findings from other timber trees (Sawada et al., 2021), natural mixed forests may host a higher taxonomic and functional diversity of soil and root associated microbes as compared with monospecific stands of *A. klaineana* in plantations. Additionally, suppressed trees may also host distinct microbial communities, associated with their lower photosynthetic activity in low-light conditions (Alsanius et al., 2019; Balandier et al., 2022; Konvalinková and Jansa, 2016), compared with local canopy-reaching individuals. Understanding the variations in these fungal communities is thus essential for sustainable forest management in *A. klaineana*-dominated forests, including the understanding of the roles and functions of root mycobiota.

Among fungal trophic guilds, AM fungi are ideal candidates for such investigations. They are essential for tropical forest resilience and play a pivotal role in these ecosystems (Martinez-Garcia et al., 2017; Sousa et al., 2022). They form symbiotic associations that support plant-soil feedbacks and nutrient exchange (Van Der Heijden et al., 2015) with approximately 70% of terrestrial plant species (Brundrett and Tedersoo, 2018) including a wide range of tree species, particularly in Central Africa (Bâ et al., 2012). AM fungal communities are shaped primarily by niche-based processes, such as environmental filtering driven by soil pH, precipitation, and temperature, though they can also be influenced by neutral processes (i.e. by stochastic processes and spore dispersal limitation)(Dumbrell et al., 2010; Horn et al., 2014; Roy et al., 2017). Their specialization makes them valuable bioindicators of soil properties and forest health (De Assis et al., 2016; Weber et al., 2021), with their adaptability underscoring their ecological significance and relevance in forest management. The advent of high-throughput sequencing (HTS) technologies in ecology over the past few years (Hu et al., 2021) offers an excellent opportunity to explore the fungal assemblages (Miyauchi et al., 2020) associated with *A. klaineana* roots using molecular methods.

The objectives of this study are to: (**i**) explore the diversity and identity of fungal communities associated with *A. klaineana* roots through its distribution across different contexts: in plantations, monodominant natural forests, and old-growth mixed forests, while considering tree social status (canopy-reaching versus suppressed trees) ; (**ii**) evaluate whether these communities are shaped by neutral (stochastic) or niche-based processes, and assess the effects of stand type and tree social status on community diversity, composition and structure ; and (**iii**) identify any specific fungal taxa or functional groups that are more closely associated with dominant tree individuals, shaping a core microbiota potentially contributing to the maintenance of high-density populations of *A. klaineana,* or supporting the survival of suppressed trees in natural and artificial forest stands.

2 Materials and Methods

2.1 *Study sites and sampling design*

Two sampling campaigns were carried out in two different regions (Figure 20), both on ferralsols (Jones et al., 2015) and within the so-called “SW Gabon” climatic region (Philippon et al., 2019, 2018). The first one took place in February 2021 (rainy season), in two plantations (Minkuku, Ntozi) within the Luki Biosphere Reserve, Mayombe, west of the Democratic Republic of Congo (DRC). The Minkuku plantation was established on savanna along a roadside, with trees planted at regular 3 × 2.5 m spacing. It is reportedly still managed despite substantial undergrowth clearing during sampling. In contrast, the unmanaged Ntozi plantation, located at the bottom of a valley near the Ntozi River, features irregularly spaced trees, including some codominant *Terminalia superba* Engl. & Diels (Limba). The second collection period extended from July to August 2021 (dry season). Sampling sites were located in the FSC-certified logging company *Precious Woods - Concession Equatoriale des Bois* (PW-CEB) in Bambidie, Ogooué-Lolo, Gabon. Samples were collected in young monodominant *A. klaineana* forests, with plots ranging from 0.25 to 1 ha, where *A. klaineana* dominates the canopy, whilethe understory hosts more shade-tolerant species. Old-growth mixed forests were sampled over larger areas (6.25 ha per plot) to obtain sufficient samples, as *A. klaineana* has largely been replaced by other species and is now mostly found as isolated individuals.

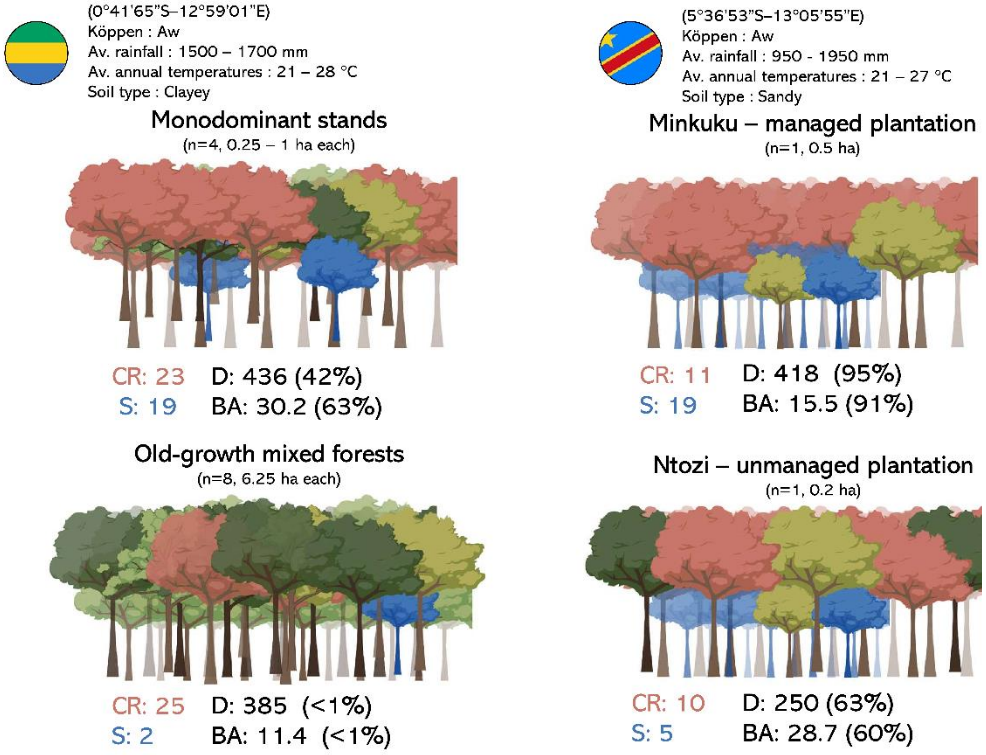


Figure 20: Characteristics of the study sites and stands. Distribution of tree types: canopy-reaching *A. klaineana* (red, CR), suppressed *A. klaineana* (blue, S), and other species (green). The number of collected samples is represented by the corresponding colors for each stand type. Tree density (D, N/ha) and basal area (BA, m²/ha) are reported with the proportion of *A. klaineana* in parentheses. **Note**: the 42% proportion of *A. klaineana* in monodominant stands includes all trees, not only the canopy-reaching ones.

2.2 *Sampling protocols*

For each randomly chosen tree, from the trunk in three different directions, roots were tracked and excavated to the finest rootlets (< 2 mm diameter). Rootlets were collected, gently washed with sterile water and passed through a 500 µm mesh sieve to remove soil and debris without damaging the tissue, and pooled into a ca. 20 g sample.

During the first collection campaign (the DRC), rootlets were put in a porous paper bag then in a sealable bag filled with silica beads for desiccation. Initial DNA extraction attempts from this material resulted in low yields, poor DNA quality, and PCR inhibition (Guidosse et al., 2024b). Consequently, the storage protocol was modified during the second sampling campaign. During this second one in Gabon, rootlets were directly poured in 2 mL tubes containing 1 mL of 2% Cetyltrimethylammonium bromide (CTAB) for future DNA extraction.

In total, 113 samples were collected: 68 in natural stands from Gabon and 45 from the DRC plantations. Samples from the first sampling campaign in the DRC were used for molecular protocol optimization prior to downstream analyses.

2.3 *PCR protocols*

Due to initial difficulties in recovering high-quality DNA from *A. klaineana* rootlets, a preliminary optimization phase was conducted prior to large-scale molecular analyses. This phase, based on samples collected in the DRC, aimed at improving DNA extraction and PCR amplification in recalcitrant *A. klaineana* roots. The validated protocol was subsequently applied to a broader dataset including samples from both the DRC and Gabon for fungal community characterization.

2.3.1 **Adapted molecular methods**

Rootlets (including rhizoplane) from the DRC, kept dry by silica beads, were shredded using liquid nitrogen, mortar and pestle.

To improve the quality of the DNA extract, the DNeasy® Plant Mini Kit by Qiagen (Hilden, Germany) for DNA extraction was first chosen, as commonly used in temperate regions for root-associated fungi research, and by Born et al. (2006) on *A. klaineana* fresh leaves. It was compared to the CTAB method (Doyle and Doyle, 1987) and briefly tested other "classic" methods such as sodium dodecyl sulfate + polyvinylpyrrolidone (SDS + PVP) (Demeke and Jenkins, 2010) and phenol-chloroform protocols. However, none yielded satisfactory results, consistently producing low yields and poor-quality DNA (see below).

Second, the Qiagen DNeasy® Plant Mini Kit extraction protocol was optimized and improved by testing the effect of polyvinylpolypyrrolidone (PVPP), a common choice for removing polyphenolic compounds, and of activated charcoal (AC), known to be less expensive and less toxic. Details of the tested extraction protocols are provided in Supplementary Material 5. Protocols to remove the remaining inhibitors were tested using bovine serum albumin (BSA) for the amplification step. During the PCR thermal cycles, the BSA could help stabilize the already degraded DNA. Detailed information on the reagents used is available in Supplementary Material 6.

The best DNA extractions consisted of a modified Qiagen DNeasy® Plant Mini Kit protocol, including AC, as recommended by Vroh Bi et al. (1996). Root powder (15-20 mg) was poured in a 2 mL tube with 15-20 mg of AC before adding SDS (AP1 buffer).

Other protocol modifications were: (**i**) a period of incubation of 30 min. instead of 10 min. after adding SDS (AP1 buffer), **(ii)** incubation period on ice of 15 min. instead of 5 min. after adding acetic acid (P3 buffer) and (**iii**) pre-heating the AE buffer to 65 °C before the elution step. Final incubation was also extended to 15 min. Then, DNA quantity and quality were assessed with a Quantus™ Fluorometer (Promega, Madison, WI, USA) and a NanoDrop™ 2000 (Thermofisher, Waltham, MA, USA).

The addition of AC and modification of the kit protocol not only increased the quantity of DNA extracted compared to other methods (Figure 21A; Kruskal-Wallis test (1952), $\chi^2 = 27.283$, $p=1.2*10^{-6}$), but also significantly improved its purity (Figure 21B-C) according to the 260/280 nm ratio (Kruskal-Wallis test, $\chi^2 = 9.846$, $p=0.0073$) and to the 260/230 ratio (Kruskal-Wallis test, $\chi^2 = 11.900$, $p=0.0026$).

When improving the kit protocol, the addition of AC versus PVPP was also compared. AC is slightly more efficient than the PVPP regarding the 260/280 nm ratio (Wilcoxon test (1945), $p=0.044$), but not regarding 260/230 nm purity. Finally, the 260/230 nm ratio shows no significant improvement when adding PVPP only compared to the standard kit protocol.

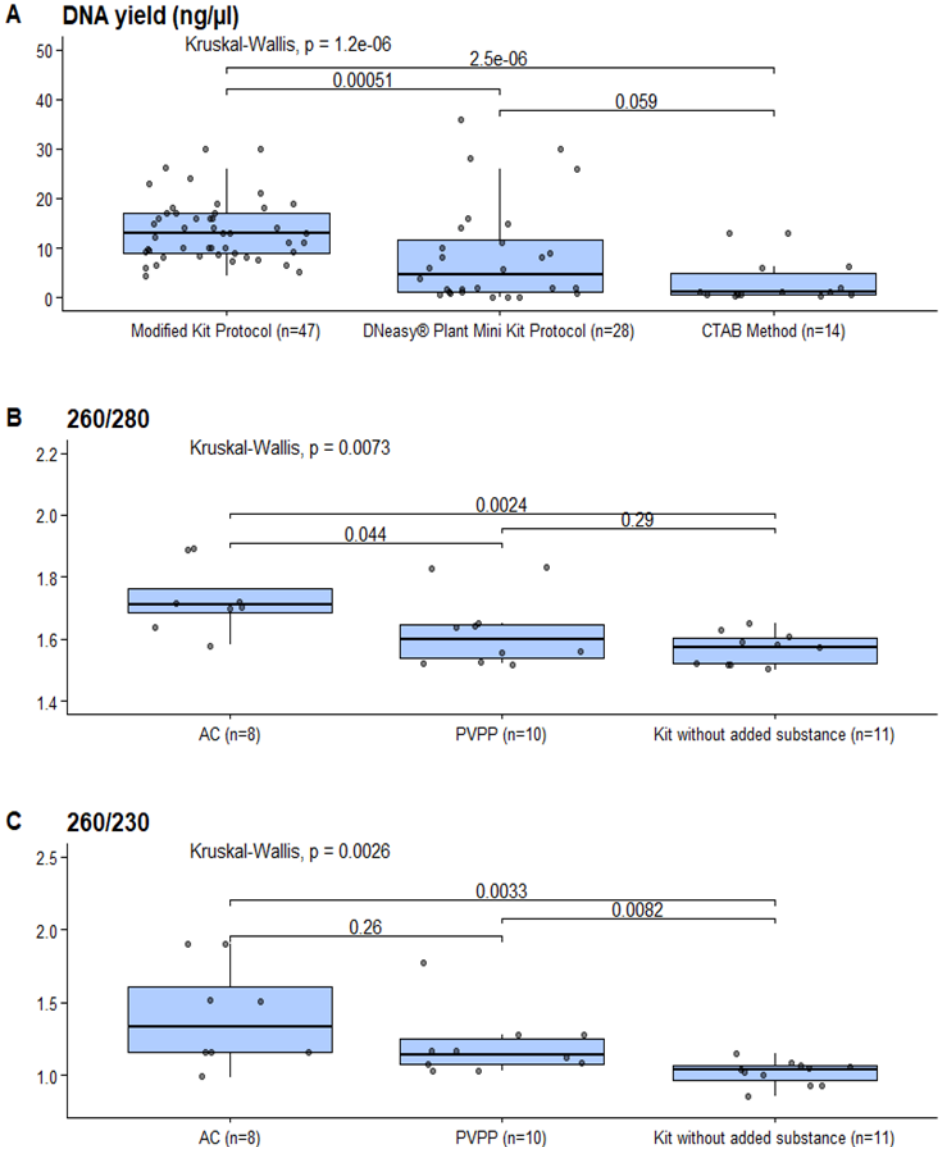


Figure 21 : Comparison of DNA extraction protocols. (**A**) DNA yield (ng/µl) according to extraction protocols. (**B**) Average 260/280 nm purity ratios obtained by Nanodrop per treatment reflecting protein, phenol, and other organic compound contaminations. DNA extracts are considered pure between c.a. 1.8 to 2.0. (**C**) Average 260/230 nm purity ratios obtained by Nanodrop per treatment indicating contamination from salts, phenols, and other organic compounds. AC: Activated Charcoal; PVPP: polyvinylpolypyrrolidone. DNA purification Kit: DNeasy® Plant Mini Kit (Cat. No. 69106) (Qiagen, Hilden, Germany) without additional reagent. Significant differences are tested using the non-parametric Kruskal-Wallis test (1952) and Wilcoxon test (1945) for pairwise comparisons.

To test the amplification of fungal DNA, the entire ITS rDNA region was first targeted by the popular primers pair ITS1 and ITS4 (Gardes and Bruns, 1993; Porter and Golding, 2011; White et al., 1990). Once inhibition was no longer apparent due to the addition of 2% (w/v) BSA (Figure 22A), the protocol was repeated to test its efficacy on a larger number of samples and on short fragments dedicated to MiSeq sequencing (Hu et al., 2021), using more specific primer pair, ITS86F and ITS4 (Vancov and Keen, 2009; Waud et al., 2014) targeting only the ITS2 region (Figure 22B). This excludes the ITS1 region but also the 5.8S rRNA gene that can cause chimera formation (Haas et al., 2011).

PCR amplifications were performed on a Bio-Rad T100 thermal cycler (Hercules, CA, USA) by mixing 1 µl of DNA template, 0.5 µl of 10 µM forward primer, 0.5 µl of 10 µM reverse primer, 2 µl of BSA 2% (w/v), 12.5 µl of Q5 High-Fidelity 2X Master Mix (NEB, Ipswitch, MA, USA) and completed with 8.5 µl PCR-grade water to reach a 25 µl volume. The following amplification program was used: denaturation step 5 min. at 95 °C, 35 cycles of 30 s at 95 °C, 30 s at 55 °C, 20 s at 72 °C and a final extension phase of 10 min. at 72 °C. As controls, PCR-grade water (Supplementary Material 6) free of nucleases and of nucleic acid contamination, was used as a negative control and a DNA strain of *Aspergillus* sp. was also extracted using the same protocol as for the samples, then amplified under the same conditions to serve as a positive control.

Inhibitors were present in the DNA extracts, as adding a root sample DNA mixed with positive control (C+, *Aspergillus* sp.) hindered the amplification of the positive control, regardless of the proportions of the mixture (3/2 µl or 2/3 µl) (Figure 22A). When 2% (w/v) BSA was added to the various DNA extracts from *A. klaineana* roots, all samples were amplified, indicating the presence of root-associated fungi (Figure 22B)

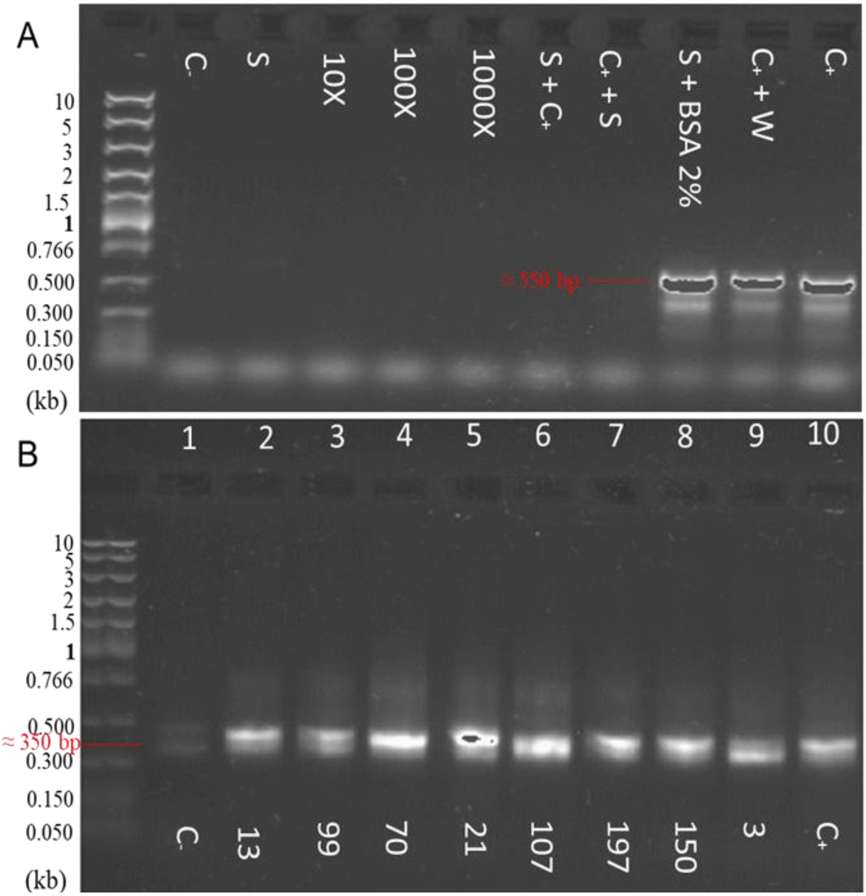


Figure 22 : Agarose gel electrophoresis (1.5% w/v agarose) of PCR amplified products performed for 50 minutes at 15 V/cm on 6 cm. DNA Fast Ladder (NEB, Ipswitch MA, USA) was used as the molecular marker. (**A**) inhibition of amplification of the entire ITS region (ITS1-ITS4) due to secondary metabolites present in the DNA sample (S), even after dilutions (10-1000X). The inhibitors also affected the amplification of the positive control (S + C+; C+ + S). When BSA 2% (w/v) was added to the DNA sample (S + BSA 2% w/v), the inhibition was not apparent. For two substances in a single well (marked with a "+"), the first substance is in 3 µl and the second in 2 µl. W is PCR-grade water (Supplementary Material 5) free of nucleases and free of nucleic acid contamination. (**B**) shows amplification of the ITS2 region (ITS86F-ITS4) for multiple samples to which 2 µl of BSA 2% (w/v) was added. Samples IDs and controls are indicated vertically at the bottom of the gel. Lanes are numbered from 1 to 10. Images were acquired with a Bio-Rad Gel Doc XR+ Imaging System and Image Lab v6.0.0 software (Hercules, CA, USA).

2.3.2 Experimental application

The validated extraction and amplification protocol described above was applied to all samples: rootlets from DRC plantations, dried in silica beads, and from Gabonese natural forests, stored in 2% CTAB.

For tissue disruption, rootlets from Gabon were ground in a FastPrep-24™ bead beater (MP Biomedicals, France) for 4 cycles of 30 seconds at 4.5 $M \cdot s^{-1}$ after adding 3 ceramic beads (Ø 2 mm) and 10 mg of Carborundum coarse powder (Prolabo, France). In contrast, rootlets from the DRC were processed as described in Section 2.3.1 using liquid nitrogen, mortar and pestle.

DNA extracts were amplified targeting both the ITS2 rDNA region and the nuclear 18S rDNA gene. The ITS2 region was amplified using the fungal-specific primer pair ITS86F-ITS4 (Vancov and Keen, 2009; Waud et al., 2014), while AM fungi were targeted through the NS31-AML2 primer pair (Morgan and Egerton-Warburton, 2017), specific to Glomeromycotina. Primers were adapted for Illumina MiSeq sequencing by addition of 5′ overhangs to enable dual-indexed paired-end sequencing (Kozich et al., 2013).

PCR reactions for the ITS2 region followed the conditions detailed in Section 2.3.1.

For the 18S rDNA region (NS31-AML2), PCR reactions mix (25µL) were similar. Thermal cycling for this primer pair consisted of an initial denaturation at 94 °C for 15 min., followed by 35 cycles of 94 °C for 55 s, 58 °C for 40 s, and 72 °C for 30 s, with a final extension at 72 °C for 5 min.

Amplicons were handed over to the GIGA-Genomics platform at the University of Liège (Belgium) for outsourced sequencing according to the Illumina 16S metagenomic workflow protocol. The workflow included the following steps: purification of PCR products from the first amplification using AMPure XP beads (Beckman Coulter, USA), addition of Illumina adapter overhangs and dual-index barcodes through a second limited-cycle PCR, and a second purification step using AMPure XP beads. During the second PCR step, Illumina adapter overhang sequences were appended to the locus-specific primers. The forward overhang sequence was 5′ TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG-[locus-specific sequence], while the reverse overhang sequence was 5′ GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG-[locus-specific sequence]. The dual-index barcodes enabled multiplexing libraries by appending unique 8-base sequences to each sample for demultiplexing during downstream bioinformatics analyses.

The concentration of the final library was normalized to 7 $ng \cdot \mu L^{-1}$ using the Quant-iT™ PicoGreen™ dsDNA Assay Kit (ThermoFisher, USA), and quality control was performed on the QIAxcel Advanced System (Qiagen, Germany). Before proceeding to high-throughput sequencing, the concentration of the final pool was quantified by qPCR using KAPA SYBR® FAST qPCR Kits (Sopachem, Netherlands) and Illumina Library Quantification DNA Standards (Roche, Switzerland). Sequencing was carried out on an Illumina MiSeq system (version 3) with a v3 reagent kit (2 × 300 cycles), using a final denatured library pool concentration of 8.5 pM.

2.4 *Quality control, clustering and taxonomic assignation*

Initial control of raw sequencing data was performed using FastQC to assess reads quality. Using DADA2 (Callahan et al., 2016) from the QIIME2 pipeline (Bolyen et al., 2019), demultiplexed reads of sequencing were merged for the ITS2 rDNA region and chimeric sequences were identified and removed. Regarding the 18S rDNA region, sequences quality did not allow for a paired-end approach after sequencing. Downstream analyses were then performed using only the forward reads (ca. 240 bp). Four samples presenting ≥ 60% of chimeric sequences or <300 reads were removed. The resulting high-quality reads were clustered into Operational Taxonomic Units (OTUs) at a 97% similarity threshold. Taxonomic assignment of the OTUs was performed against the UNITE database v10.0 (Abarenkov et al., 2024) for fungal ITS2 sequences and against the MaarjAM database v2021 (Öpik et al., 2010) for 18S rDNA glomeromycotinan sequences. OTUs obtained from the ITS2 rDNA region were assigned to functional guilds using the FUNGuild database (Nguyen et al., 2016) when classifications were deemed "Probable" to "Highly Probable”. FUNGuild was preferred over FungalTraits (Põlme et al., 2020) due to its cautious assignment of pathogens, reflecting the context-dependent nature of fungi. Samples were classified by trophic guild, separating saprotrophs and pathotrophs, while symbiotrophs were divided into ectomycorrhizal (EcM) fungi, arbuscular mycorrhizal (AM) fungi, and others through the ITS2 rDNA region. Every relevant raw sequence read were deposited in GenBank Bioproject accession No. PRJNA1214243.

2.5 *Diversity analyses*

Downstream analyses were performed in R (R Core Team, 2021). The initial data in QIIME2 format (.qza, .tsv) were converted to R-compatible objects using the ‘qiime2R’ package (Bisanz, 2018) and subsequently formatted into phylogenetic data using the ‘phyloseq’ package (McMurdie and Holmes, 2013) for data manipulation and visualization.

Rarefaction curves were generated using the ‘vegan’ R package (Oksanen et al., 2025), which determined optimal sampling depths of 10,000 sequences for ITS2 rDNA and 3,000 sequences for 18S rDNA. Due to the clear differences in sample processing between the two sampling campaigns (e.g., storage and grounding methods, country, stand types, seasonality, and soil), data analyses were conducted separately: for the natural stands in Gabon, and the plantations in the DRC. Extremely rare fungal OTUs, representing < 0.001% of the total sequences, were removed. Subsequently, the impact of stand type on the mycobiota was examined by comparing two plantations in the DRC and young monodominant stands with old-growth mixed forests in Gabon. Additionally, the interaction between fungal communities and the social status of the trees was explored by comparing canopy-reaching trees (dominant, codominant) with those surviving in the shade (suppressed) for all sites.

Diversity analyses were performed using the ‘MicrobiotaProcess’ R package (Xu et al., 2023). Alpha diversity was assessed using the OTU richness, the Shannon index, and the Pielou evenness index. Kruskal-Wallis non-parametric tests were applied to check for significant differences for these indexes. Fungal community comparisons (beta diversity) were conducted by constructing Bray-Curtis dissimilarity and Jaccard distance matrices from abundance tables. Principal Coordinates Analysis (PCoA) was used to visualize the Bray-Curtis dissimilarity matrices. To test for significant differences among fungal communities, permutational multivariate analysis of variance (PERMANOVA) was performed with 9,999 permutations using the ‘vegan’ R package (Oksanen et al., 2025), applying Bray-Curtis and Jaccard matrices. To assess the nestedness of fungal communities, the weighted nestedness metric based on overlap and decreasing fill (WNODF) (Almeida-Neto and Ulrich, 2011) was calculated, ranging from 1 (no nestedness) to 100 (maximum nestedness).

To provide insights into any stable and functionally important fungal taxa associated with the studied trees and stands, the core mycobiota was investigated by identifying OTUs that were consistently present in 10–100% of the samples, both in general and for each factor separately, specifically stand types and tree social status.

Independently of the core mycobiota analysis, an indicator species analyses (Dufrêne and Legendre, 1997) was performed on size-equalized groups using the ‘indicspecies’ R package (De Cáceres et al., 2010; De Cáceres and Legendre, 2009). This analysis was performed to test whether particular fungal taxa were consistently associated with the monodominance of *A. klaineana* or with the persistence of suppressed trees under low-light conditions. Indicator taxa were identified as described by Bakker (2008):

$$A_{ij} = {}^{\overline{x}_{ij}}\!\Big/_{\sum_j \, x_{i\cdot}}$$

$$B_{ij} = {}^{n_{ij}}\!/_{n_{\cdot j}}$$

$$Indval_{ij} = \sqrt{A_{ij} \times B_{ij}}$$

with A defined as specificity or relative abundance, i.e. the mean cover of taxa i in each stand types or tree social status modality (j) as a proportion of its mean cover in all groups; and B defined as fidelity or relative frequency, i.e. the proportion of trees in modality j on which taxa i occurs. The indicator value (Indval) ranges from 0 to 1. Indicator taxa were identified using Monte Carlo randomization tests based on 9,999 permutations. Following this, indicative taxa across studied factors and guilds were visualized on heatmaps using the ‘pheatmap’ R package (Kolde, 2018).

3 Results

3.1 *Fungal composition*

A total of 3,549,465 high quality reads assigned to 4,119 fungal OTUs were obtained from sequencing the ITS2 rDNA region across samples from Gabon. After removing the rarest (< 0.001% of reads), 1,694 fungal OTUs were retained (41%, 3,522,826 sequences). Among the seven identified phyla, the five most represented were Ascomycota (60.8% sequences, 961 OTUs), Basidiomycota (37.6% sequences, 547 OTUs), Glomeromycota (1.3% sequences, 166 OTUs), Mucoromycota (0.1% sequences, 28 OTUs), and Mortierellomycota (0.03% sequences, 9 OTUs). The rest of the phyla (Chytridiomycota, Entomophtoramycota) were represented by less than 120 sequences and one OTU each, or were unidentified (0.2% sequences, 15 OTUs). Functional guilds were assigned to 861.801 sequences (24.5%) represented by 719 (42.4%) fungal OTUs (Figure 23), with unsure trophic mode (Mixed, 55.6% sequences, 258 OTUs) and saprotrophic fungi were dominant (28.9% sequences, 222 OTUs). Symbiotrophic OTUs accounted for only a tenth of representative reads (10.1% sequences, 203 OTUs) and a low abundance of pathogenic fungi was observed (5.7% sequences, 36 OTUs).

Among the symbiotrophic fungal OTUs, half of the sequences (49.4%, 165 OTUs) were represented by AM fungi and a small part by lichenized OTUs (11 OTUs, 0.007% symbiotic sequences) and epiphytic OTUs (4 OTUs, 0.003% symbiotic sequences).

Another large proportion of symbiotrophic sequences (46.1%) was assigned to EcM fungi. They comprised 23 OTUs distributed across four taxa: *Russula* spp. (Russulaceae, 61.1% of EcM sequences), *Lactifluus* spp. (Russulaceae, 31.8% of EcM sequences), *Lactarius* spp. (Russulaceae, 0.06% of EcM sequences), and *Laccaria* spp. (Hydnangiaceae, 0.009% of EcM sequences).

In the DRC, 2,016,514 reads from 45 samples passed the quality filtering and were assigned to 4,502 fungal OTUs. After removing the rarest (< 0.001% of reads), 2,003 fungal OTUs were retained (44%, 1,997,950 sequences). Among the seven identified phyla, the five most represented were Ascomycota (63.4% sequences, 1,129 OTUs), Basidiomycota (32.9% sequences, 604 OTUs), Mucoromycota (2.6%, 44 OTUs), Glomeromycota (1.0% sequences, 189 OTUs), and Mortierellomycota (0.04% sequences, 9 OTUs). The rest of the phyla (Rozellomycota, Chytridiomycota) were represented by less than 488 and 65 sequences respectively and two OTU each, or were unidentified (0.12% sequences, 24 OTUs). Functional guilds were assigned to 945,709 sequences (47.3%) represented by 1,015 (50.7%) fungal OTUs **(**Figure 23**)**. Saprotrophic fungi (48.4% sequences, 440 OTUs) and mixed trophic modes (43.67% sequences, 348 OTUs) were dominant. Symbiotrophic OTUs had only a few representative reads (3.4% sequences, 196 OTUs) and a low pathogenic charge was observed (4.5% sequences, 31 OTUs).

Among the symbiotrophic fungal OTUs, 59.6% of the sequences and 96.4% the OTUs were represented by AM fungi. Another large proportion (40.1% of the sequences) was represented by epiphytic fungi, but clustered into 6 OTUs only. The 115 other sequences were assigned to lichenized OTUs. No EcM OTUs were found in the DRC.

Regardless of the region, the most abundant families (Supplementary Material 7-8) included Glomeraceae, as well as Chaetosphaeriaceae, and Herpotrichiellaceae, which contain numerous endophytic fungi. Genera within these families, such as *Cladophialophora*, *Cyphellophora*, and *Knufia*, were frequently detected in root samples. Other detected genera, including *Hyaloscypha, Oidiodendron*, *Glutinomyces*, *Scytalidium*, and *Xylogone*, belonging to these families, are largely composed of saprotrophs and potential pathogens that were also abundant across samples (Cannon and Kirk, 2007; Newsham, 2011; Vandepol et al., 2020).

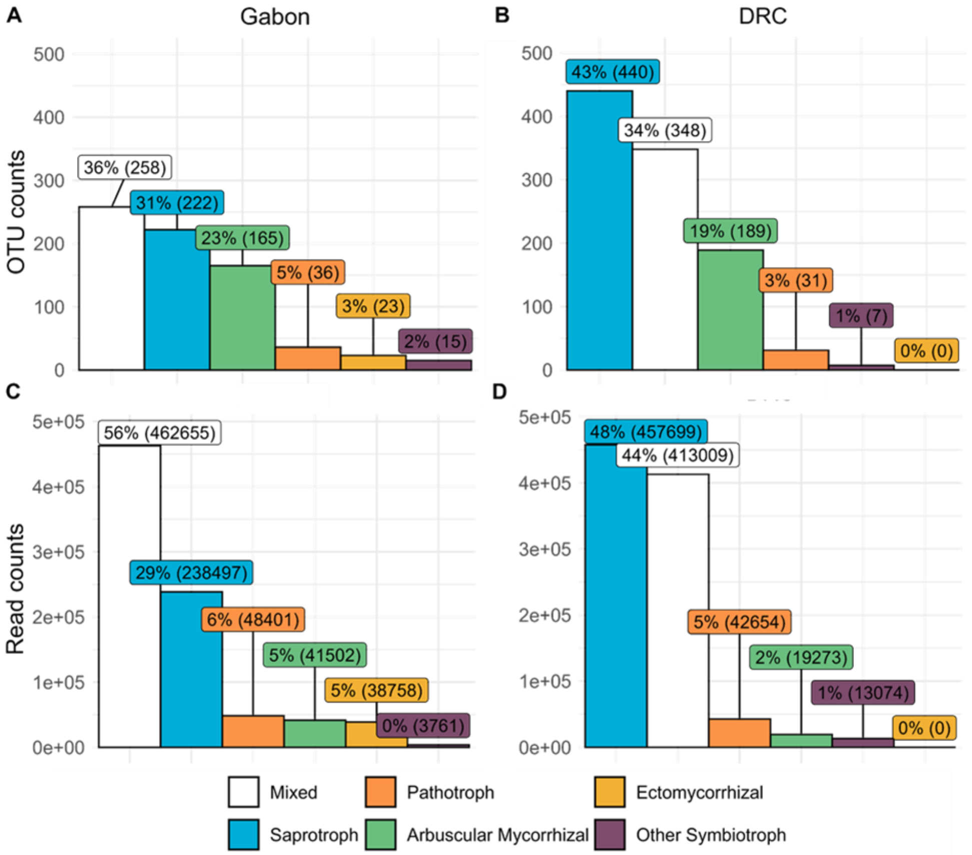


Figure 23: Trophic guild distribution based on the number of OTUs (**A,B**) and sequence reads (**C,D**) obtained from Gabon (**A,C**) and the DRC (**B,D**) after sequencing the ITS2 rDNA region. Fungal OTUs with uncertain trophic associations are categorized as "Mixed". The “Other Symbiotroph” group includes lichenized and epiphytic OTUs.

Regarding the 18S rDNA gene for samples from Gabon (Figure 24), 1,187,360 reads from 49 samples passed the quality filtering and were assigned to 625 glomeromycotinan OTUs. After removing the rarest (< 0.001% of reads), 526 fungal OTUs remained (84%, 1,186,767 sequences). Three classes have been identified: Glomeromycetes (95.7% sequences, 440 OTUs), Paraglomeromycetes (3.9% sequences, 74 OTUs), and Archaeosporomycetes (0.4% sequences, 9 OTUs), the rest was unidentified (0.03% sequences, 3 OTUs). At the genus level, a large majority were represented by *Glomus* spp. (93.4% sequences, 362 OTUs). The rest was shared by *Paraglomus* spp. (3.9% sequences, 74 OTUs), *Acaulospora* spp. (1.3% sequences, 61 OTUs), *Scutellospora* spp. (0.9% sequences, 16 OTUs), and *Archaeospora* spp. (0.4% sequences, 5 OTUs). 0.04% of the sequences (8 OTUs) were unassigned.

In the DRC, 1,331,094 reads from 39 samples passed the quality filtering and were assigned to 1,037 glomeromycotinan OTUs (Figure 24). After removing the rarest (< 0.001% of reads), 951 fungal OTUs remained (91.7%, 1,330,094 sequences). Three classes have been identified: Glomeromycetes (98.7% sequences, 850 OTUs), Paraglomeromycetes (1.0% sequences, 85 OTUs), and Archaeosporomycetes (0.2% sequences, 8 OTUs), the rest was unidentified (0.1% sequences, 8 OTUs). At the genus level, the majority was represented by *Glomus* spp. (73.6% sequences, 523 OTUs). Almost a quarter of the sequence was also represented by *Acaulospora* spp. (23.7% sequences, 286 OTUs). The rest was shared by *Scutellospora* spp. (1.4% sequences, 39 OTUs), *Paraglomus* spp. (1.0% sequences, 85 OTUs), *Archaeospora* spp. (0.07% sequences, 5 OTUs), and *Diversispora* spp. (0.01% sequences, 2 OTUs). 0.24% of the sequences (11 OTUs) were unassigned.

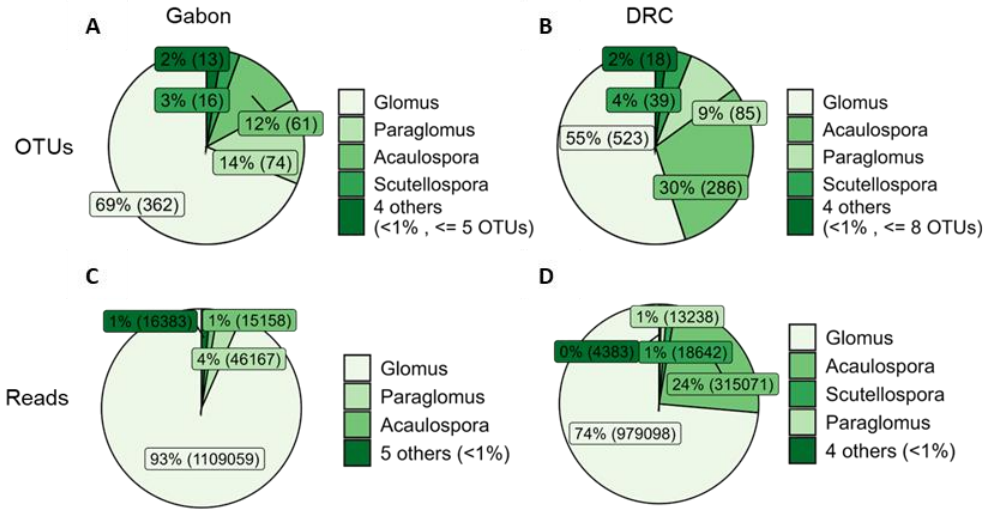


Figure 24: Distribution of arbuscular mycorrhizal (AM) fungal taxa at the genus level in terms of OTUs counts (**A,B**) and sequence reads (**C,D**) obtained from Gabon (**A,C**) and the DRC (**B,D**) using glomeromycotinan-specific 18S rDNA primers.

3.2 *Alpha diversity analyses*

To assess within-sample fungal diversity, OTU richness, Shannon diversity index, and Pielou’s evenness for all fungi, by trophic guild, were calculated. For EcM-associated OTUs, only their richness was calculated, but could not be compared across all samples, as their presence was largely restricted (with the exception of one OTU) to canopy-reaching trees in old-growth mixed forests in Gabon. Alpha diversity metrics for other trophic guilds and for all fungi showed no consistent variation across stand types and tree social status, regardless of the country or the primer pair (Supplementary Material 9-11).

In natural stands (Gabon), canopy-reaching trees exhibited higher specific diversity of saprotrophic OTUs (Shannon index: mean = 1.33, SD = 0.09; Kruskal-Wallis test, p = 0.043) compared with suppressed trees. However, this slight variation was not observed in plantation samples from the DRC. In these artificial stands, Pielou evenness (mean = 0.94, SD = 0.007; Kruskal-Wallis test, p = 0.043) was higher at the Minkuku site compared with Ntozi, indicating a more balanced saprotrophic community at Minkuku.

3.3 *Community composition*

The PERMANOVA analysis on Bray-Curtis dissimilarity and Jaccard distance matrices revealed a strong and significant differentiation in fungal community composition between monodominant stands and old-growth mixed forests in Gabon, regardless of trophic guild (all p-values < 0.001).

A similar differentiation was observed between plantations in the DRC, with significant differences for saprotrophs (Bray-Curtis p-value = 0.043), pathotrophs (Bray-Curtis p-value = 0.005), symbiotrophs (ITS2, Bray-Curtis p-value = 0.021), and AM fungi (18S, Bray-Curtis p-value = 0.002). However, no significant difference was found when considering all fungal OTUs (Bray-Curtis p-value = 0.426) (Supplementary Material 13).

In natural stands, tree social status significantly influenced saprotrophic (Bray-Curtis p-value = 0.003) and AM fungal communities (18S, Bray-Curtis p-value = 0.004), as well as symbiotrophs (ITS2, Bray-Curtis p-value = 0.008). In contrast, no significant differences were found for pathogenic fungi in natural stands (Bray-Curtis p-value = 0.192) or across social status in DRC plantations for any fungal trophic guild.

These differences were visualized in a PCoA plot for trophic guilds of interest (Figure 25) and for every obtained fungal OTUs (Supplementary Material 13-14) where samples from different stand type and tree social status formed separate clusters. Symbiotrophic OTUs obtained from the ITS2 rDNA region are presented only in Supplementary Material 14, as EcM fungi were found solely in canopy-reaching trees from old-growth mixed forests, and the resolution for AM fungi was better with the 18S rDNA region. Interestingly, the stand type showed a higher impact than tree social status on every fungal assemblage.

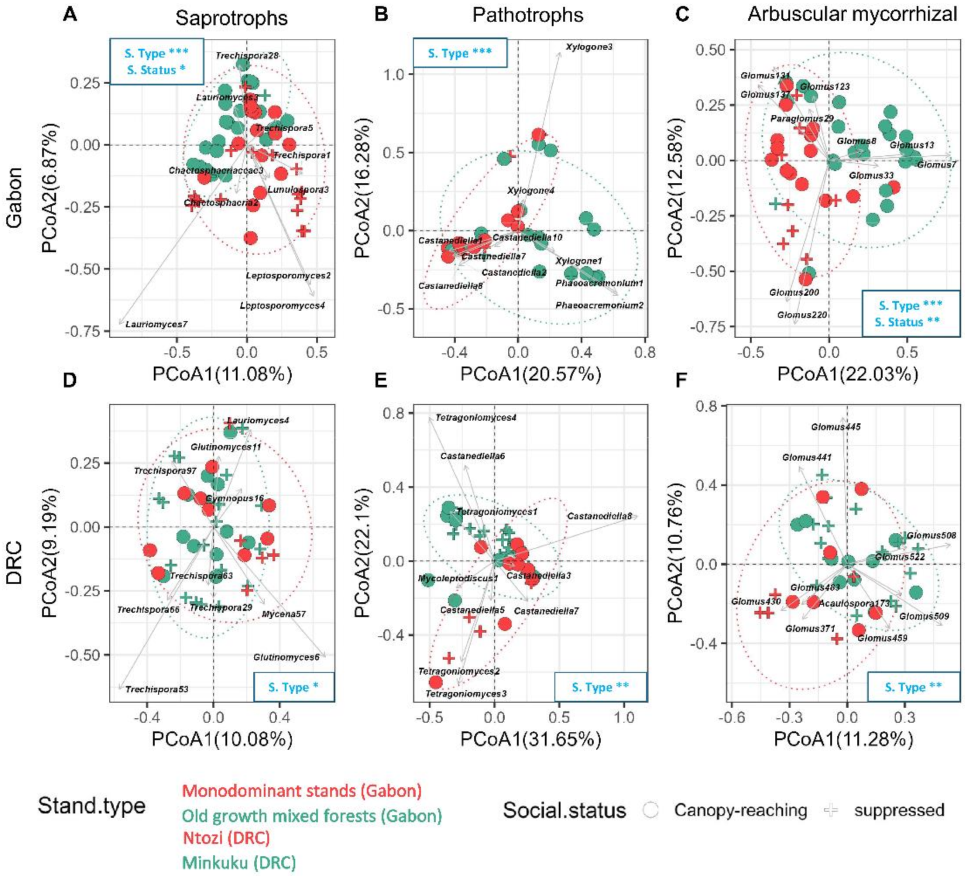


Figure 25 : PCoA plots based on Bray-Curtis dissimilarity matrices on OTUs obtained from Gabon (**A,B,C**) and the DRC (**D,E,F**) assigned to saprotrophic (**A,D**), pathotrophic (**B,E**) through the ITS2 rDNA region, and arbuscular mycorrhizal (**C,F**) through the 18S rDNA. Significant differences between modalities were assessed using permutational multivariate analyses of variance (PERMANOVA) with 9,999 permutations. Blue labels indicate significant differences, with p-values categorized as: $p \leq 0.05$ (significant), $p \leq 0.01$ (highly significant), and $p \leq 0.001$ (very highly significant). Variables "S.type" = stand type and "S.status" = social status. The 10 taxa that have the highest contributions to the ordinations are labelled in each plot.

3.4 *Community structure*

To assess the nestedness of fungal communities, the weighted nestedness metric based on overlap and decreasing fill (WNODF) was calculated (Table 3). Overall, fungal communities at the genus level exhibited a low nestedness, showing a high turnover, with a WNODF score ranging between 0.70 and 19.75 (mean = 7.48, SD = 5.46), no matter the trophic guild. This pattern suggested for instance that the fungal communities in monodominant stands are not subsets of the more diverse community associated with, old-growth mixed forests and even at the individual level this turnover occurred locally between trees. However, symbiotrophic fungi in DRC plantations displayed a more structured pattern (overall WNODF = 19.75; genus-level = 40.07), suggesting that trees with fewer symbiotrophic taxa hosted subsets of richer communities. The low matrix fill (41%) indicates caution, as sparse data can constrain the detection of nestedness. Similarly, for AM fungi, although per-genus values reached relatively high levels (62.40 in the DRC), these results are difficult to interpret given the very limited genus pool (only *Glomus*, *Acaulospora*, *Scutellospora*, *Paraglomus*, and *Archaeospora).*

Table 3: Weighted Nestedness (WNODF, scaled 1-100) calculated for fungal communities at the genus level in Gabon and the DRC, for all fungi and per trophic guild, with values presented overall, per sample, per genus, and as matrix fill (density of non-zero values in abundance matrix).

WNODF [1-100]		Overall	Per sample	Per genus	Fill (%)
Gabon	All (ITS2)	4.75	5.80	3.74	53
	Saprotrophs (ITS2)	7.80	7.56	8.63	9
	Pathotrophs (ITS2)	3.11	2.83	10.44	21
	Symbiotrophs (ITS2)	8.44	8.37	13.35	18
	AM fungi (18S)	0.70	0.46	28.33	29
DRC	All (ITS2)	4.01	4.80	3.66	8
	Saprotrophs (ITS2)	12.56	12.89	12.10	14
	Pathotrophs (ITS2)	8.45	7.57	30.64	21
	Symbiotrophs (ITS2)	19.75	19.42	40.07	41
	AM fungi (18S)	5.25	4.79	62.40	50

3.5 *Core and specific indicator mycobiota*

3.5.1 Core mycobiota

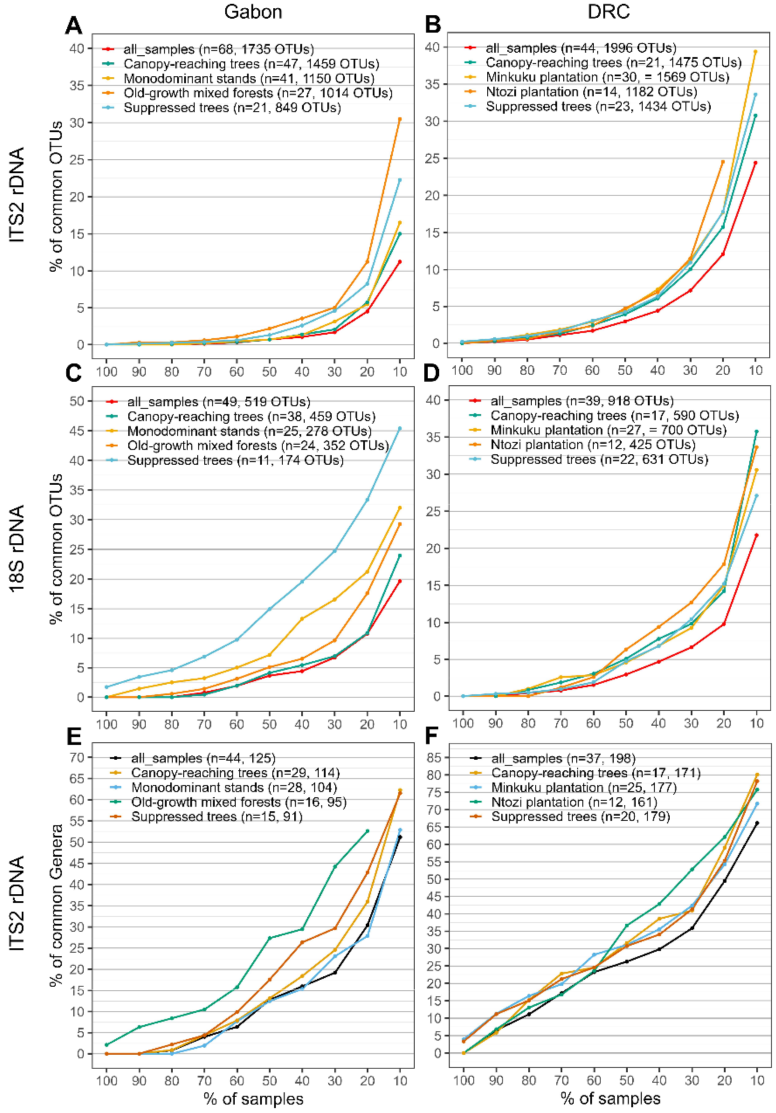


Figure 26 : Proportions of shared OTUs between samples from natural stands in Gabon (**A,C,E**) and plantations in the DRC (**B,D,F**), based on the ITS2 rDNA (fungi-specific, **A,B**) and 18S rDNA (glomeromycotinan-specific, **C,D**) regions. Shared proportions at the genus level are also shown for Gabon (**E**) and the DRC (**F**) using ITS2 rDNA.

A very low proportion of shared OTUs, or even genera, was observed between samples, irrespective of the country, stand type, or tree social status, which hindered any identification of core mycobiota (Figure 26). The only exception is for the suppressed trees in Gabon, where, when studying the 18S rDNA (Figure 26C), three *Glomus* OTUs were common across all samples (n=11).

For the ITS2 rDNA region, in natural stands (Gabon), 0.69% of OTUs (25.0% of sequences) were present in at least 50% of the samples, while only 0.11% of OTUs (13.0% of sequences) were found in 70% or more. In plantations (the DRC), the proportions were higher, with 2.96% of OTUs (40.11% of sequences) present in at least 50% of the samples and 1.10% of OTUs (26.93% of sequences) found in 70% or more. When considering each factor separately, the proportion did not exceed 4.74% of OTUs (5.78% of sequences) for 50% of the samples and 1.84% of OTUs (1.56% of sequences) for 70% or more. The higher proportions observed in the DRC are primarily due to the smaller number of samples. For the 18S rDNA concerning AM fungi, in natural stands (Gabon), 3.66% of OTUs (58.92% of sequences) were present in at least 50% of the samples, while only 0.77% of OTUs (21.82% of sequences) were found in 70% or more. In plantations (the DRC), 2.94% of OTUs (48.78% of sequences) were present in at least 50% of the samples, and 0.76% of OTUs (20.55% of sequences) were found in 70% or more.

Repeating the analysis at the genus level confirmed the absence of genera consistently shared across all ITS2 rDNA samples (Figure 26E, F). This excludes the existence of a universal core mycobiota for *A. klaineana* in general, and even within monodominant stands, where only two genera were shared across 70% of samples (n = 28). The only genus detected in ≥80% of all samples was *Cladophialophora spp.* (Herpotrichiellaceae, Chaetothyriales; Supplementary Material 15), a dark septate endophyte known to influence plant growth (Diez-Hermano et al., 2024). In contrast, in the DRC 21 genera were shared among ≥80% of samples, occurring broadly across stand types and tree social statuses, without specificity to a given plantation or tree social status (Supplementary Material 15).

3.5.2 Indicator taxa

Among the considered trophic guilds, 161 fungal OTUs were identified as potential indicator taxa associated with stand types and tree social status (Figure 27). Canopy-reaching trees harbored the fewest indicator taxa in both the DRC and Gabon, with the exception that all EcM-associated OTUs were obtained from samples collected from dominant trees in the old-growth mixed forests of Gabon. In the DRC plantations, only four OTUs were identified as indicators of canopy-reaching trees. They belonged to four genera: *Umbelopsis* sp. (saprotroph), one *Castanediella* sp. (pathotroph), as well as *Glomus* sp. and *Scutellospora* sp. as AM fungi. In natural stands, only one *Glomus* sp. was identified as indicator.

The indicator OTUs of canopy-reaching trees displayed markedly different trends between Gabon and the DRC. In Gabon, they were characterized by a high diversity of

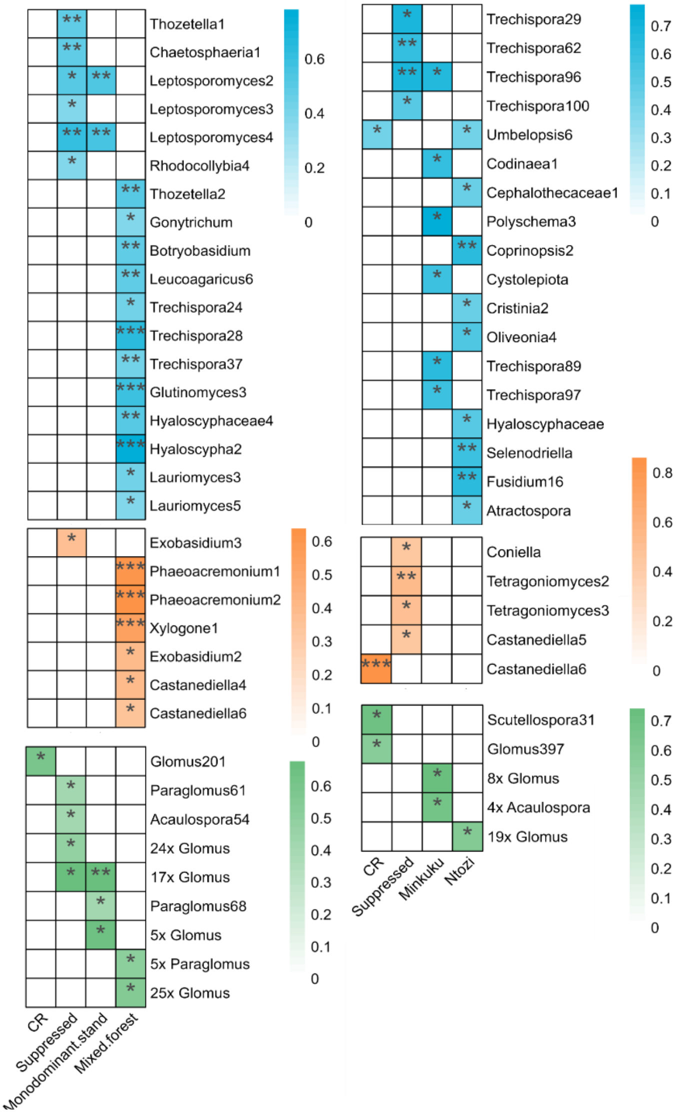


Figure 27 : Heatmaps of significant taxa from Gabon (**left**) and the DRC (**right**) identified through indicator species analyses and Monte Carlo randomization tests. The color scale indicates indicator values (Indval). Asterisks represent p-values:* ≤ 0.05 significant, ** ≤ 0.01 highly significant, and *** ≤ 0.001 very highly significant. Heatmap colors correspond to trophic guilds: blue = saprotrophs, orange = pathotrophs, green = arbuscular mycorrhizal (AM) fungi. Ectomycorrhizal (EcM) fungi are excluded, as they were only found in canopy-reaching trees (CR) of old-growth mixed forests (Mixed.forests) in Gabon. For AM fungi (based on 18S rDNA), the abundance of distinct OTUs within the same genus is grouped on a single line, with indicator values and p-values representing the mean of all OTUs.

AM fungi and four genera of saprotrophs, with *Exobasidium* sp. serving as the only indicator pathogen. In contrast, the suppressed trees in the DRC were characterized by four pathogenic OTUs (*Coniella* sp., two *Tetragoniomyces* spp., and another *Castanediella* sp.) and four OTUs associated with *Trechispora* spp.(saprotrophic). The plantations in the DRC exhibited distinctly different indicator taxa. Among them, four *Acaulospora* sp. (AM fungi) were identified at Minkuku. Finally, the old-growth mixed forests housed the most specific taxa, comprising 12 saprotrophs, six pathotrophs, and 30 AM fungi.

4 Discussion

Our study based on the high-throughput sequencing of ITS2 rDNA and 18S rDNA regions provided for the first time a detailed overview of root-associated fungi of *Aucoumea klaineana*, Central Africa's most harvested timber species. The analyses were enabled by an improved DNA extraction and amplification protocol using activated charcoal (AC) and bovine serum albumin (BSA), which overcame inhibitors and produced high-quality DNA for recalcitrant *A. klaineana* roots.

Fungal communities were investigated both in monodominant stands and old-growth mixed forests from Gabon and in plantations from the DRC, as well as through a comparison of two different tree social status, illustrating the wide ecological range of *A. klaineana*.

Our results showed a highly diverse community, extremely variable between stand types and tree social status, at a regional and local scale. Our results did not reveal any “core mycobiota” (Figure 26**)** but instead complex and diverse fungal assemblages, of symbiotic as well as saprotrophic and pathogenic fungi.

Root-associated fungi appeared to have minimal impact on the survival of suppressed *A. klaineana*, as these trees did not host any distinct fungal communities (Figure 25). In natural forests, only slight differences in saprotrophic and AM fungal guild composition were observed (Figure 25). Despite minor richness differences, suppressed trees hosted more AM fungal indicator taxa (43 OTUs) compared with just one in canopy trees. This trend was absent in plantations, maybe due to an insufficient stand age for clear stratification. This also contrasts with Neuenkemp et al. (2021), who suggested that favorable light conditions reduce selectivity for specific AM fungi and promote compatibility with a broader range of taxa.

Overall, our findings indicated that the root-associated fungal communities in *A. klaineana* forests were shaped more by processes linked to stand-type context rather than tree social status (Figure 25). This pattern may align with stochastic processes of fungal assemblage (Dumbrell et al., 2010) (Table 3) or reflect the influence of soil physicochemical differences between monodominant versus old-growth mixed forests in Gabon (Bonito et al., 2014; Fern et al., 2011). However, no differences in terms of fungal communities emerged across the factors studied, highlighting the complexity of these interactions.

Considering the variability of root-associated fungal communities of *A. klaineana* characterized for the first time, the ITS2 fungal diversity observed across both countries was substantial, with 1,694 OTUs identified across 68 samples in Gabon (3,522,826 sequences) and 2,003 OTUs across 45 samples in the DRC (1,997,950 sequences), following quality filtering and removal of rare taxa. This richness is similar to what is known for temperate forest soils, studies reporting between 600 and over 5,000 fungal OTUs (e.g., Bahnmann et al., 2018; Buée et al., 2016; Kujawska et al., 2021; Lynikienė et al., 2020), whereas roots generally exhibit lower fungal richness than soils (e.g., Boeraeve et al., 2019; Olanipon et al., 2024; Větrovský et al., 2023). By comparison, studies focusing on root-associated fungi report approximately 2,200 OTUs in Serbian riparian forests (Marjanović et al., 2020) and around 1,000 OTUs in neotropical forests in Mexico (Schroeder et al., 2018) after data curation, but from multi-specific rootlets samples. Tropical forests are underrepresented in fungal diversity studies (Powell and Rillig, 2018), leading to a sampling bias toward temperate regions (Větrovský et al., 2023). A notable data gap in Central Africa (Bahram et al., 2018; Cameron et al., 2019; Díaz-Vallejo et al., 2021) could have limited the taxonomic classification of OTUs, with 42.3% assigned to at least a "mixed" trophic guild in Gabon and 50.7% in the DRC. Nevertheless, the overall functional guild composition was consistent across both sampling campaigns, suggesting that these patterns are recurrent.

In both Gabon and the DRC, the dominant fungal phyla were Ascomycota and Basidiomycota, reaching together more than 95% of sequences for both countries. Saprotrophic fungi were the most represented in our study no matter the phylum, while EcM fungal OTUs were rare in Gabon and absent in the DRC.

A consistent pathogenic prevalence was also observed across sampling campaigns and sites: 5% of OTUs in Gabon (6% of sequences), 3% in the DRC (5% of sequences) (Figure 23). This is higher than those found in soils from Scots pine forests (Kujawska et al., 2021) or beech forests (Raimbault et al., 2024). Pathogenic fungal OTUs presented a higher read abundance than symbiotrophic ones in both countries. Among them, *Xylogone* and *Phaeocremonium* were indicators in old-growth mixed forests, benefiting from the variety of wood substrates and root structures that enhance decay. However, no symptoms of tree decline were observed and only generalist taxa have been identified as indicators (Figure 27).

Regarding the ITS2 rDNA region, symbiotrophic fungi were diverse in both regions, accounting for 28% of OTUs and 10% of reads in Gabon, and 20% of OTUs and 3% of reads in the DRC. Most of these fungi were AM fungi, reflecting the dominance of AM fungi-associated tree species across Central Africa (Bâ et al., 2012). For this guild, the ITS2 rDNA dataset showed many AM fungi OTUs but at low abundance. Glomeromycota harbored the largest part of symbiotrophic OTUs, consistently present among samples but comprising only 1.0% of reads in Gabon and 1.2% in the DRC. This low proportion was also reported in temperate (Schröter et al., 2019), boreal (Nagati et al., 2018), and subtropical (Li et al., 2021) regions. This may be due to lower primer affinity and the high proportion of non-glomeromycotan sequences, as in comparison, AM fungi were detected in all samples using the 18S rDNA barcode.

Supporting this, Onguene et al. (2002) found AM fungi in every stained *A. klaineana* rootlets samples from plantations, however, only a few arbuscules were observed, indicating low nutrient exchange activity (Smith and Read, 2008). A similar pattern was noted by Onguene and Kuyper (2001) in Anacardiaceae and Sapindaceae (other Sapindales) tree species from Cameroon, as well as in *Protium sagotinium* March. (Burseraceae) in French Guiana (Béreau et al., 1997). Like *A. klaineana*, these species possess large rootlets with few root hairs, with large cortical area and root diameter to facilitate colonization by mycorrhizal partners (Brundrett and Tedersoo, 2018; Kong et al., 2014), consistent with the typical ‘outsourcing’ strategy of allocating carbon to symbionts. (Bergmann et al., 2020; Hogan et al., 2023; McCormack and Iversen, 2019). Instead, it seems that *A. klaineana*’s rootlets primarily obtain nutrients independently, with limited use of fungal symbioses, which is characteristic of saprotrophic fungi dominance.

Sequencing the 18S rDNA region with glomeromycotinan-specific primers enhanced resolution for AM fungi identification (Öpik et al., 2010, 2014), despite shorter reads resulting from the single-end approach. *Glomus* was systematically the dominant taxon, consistent with prior research on AM fungal composition in forest communities (e.g., Boeraeve et al., 2019; da Silva et al., 2005; Olanipon et al., 2024; Tchiechoua et al., 2023). While other taxa were less abundant, they were more diverse, indicating high turnover rates and niche partitioning among taxa. In the DRC plantations, *Acaulospora* was the second most abundant genus, representing 24% of reads and 30% of OTUs. This is often the second most abundant AM genus in perturbed (Suárez et al., 2023) and natural forests (Kebede et al., 2023; Wang and Jiang, 2015), and it can exceed *Glomus* in some cases (Belay et al., 2020). However, it can also be poorly represented (Tchiechoua et al., 2023), as in Gabonese natural forests in our study (1% of reads and 12% of OTUs). The rapid nuclear multiplication of *Glomus* and *Acaulospora*, particularly during spore formation, contributes to their dominance in plant roots, enhancing their resilience to soil disturbances and ecosystem changes (Hart and Reader, 2002; Lindhal et al., 2013; Muleta et al., 2008; Sanders and Croll, 2010; Wang and Jiang, 2015).

Comparatively, EcM fungi were notably absent in *A. klaineana* monodominant stands (except for one OTU) and plantations, declining previous hypothesis by Leroy Deval (1974) and Peh et al. (2011a) that suggested that EcM fungi may support *A. klaineana* monodominance as shown for many species in tropical ecosystems (e.g., Diedhiou et al., 2014; Ebenye et al., 2017; Fukami et al., 2017; Henkel, 2003; Liang et al., 2020). In contrast their presence and mostly their high read counts (5% of sequences, equal to AM fungi, Figure 23) in old-growth mixed forests might come from potential contact with fungi associated with neighboring tree without functional relevance to *A. klaineana* (Amend et al., 2010; Smith and Read, 2008). Indeed, more than 90% of the reads associated with EcM fungi (43% of every symbiotrophic sequences from Gabon, Figure 23) belonged to the *Russula-Lactarius* lineage, which is the most represented in the Afrotropical region (Corrales et al., 2022), and could associate with *Anthonotha fragrans* (Baker f.) Exell & Hillc and *Julbernardia pellegriniana* Troupin two EcM-associated trees species (Bâ et al., 2012; Bakarr and Janos, 1996) observed at less than 10 m from our sampled *A. klaineana* trees from old-growth mixed forests (Supplementary Material 16).

Despite the low proportion of mycorrhizal sequences in *A. klaineana* compared with other trophic guilds, root-associated fungal communities were nevertheless diverse. Instead, across both regions, the Chaetosphaeriaceae, and Herpotrichiellaceae families dominated the root mycobiota (Supplementary Material 7-8). Notably, *Cladophialophora* and *Knufia*, both dark septate endophytes (DSE) or closely related taxa, were particularly abundant and may play important roles in the persistence of *A. klaineana* monodominant stands by enhancing nutrient acquisition and stress tolerance of roots even though the role of these fungi are still unclear (Newsham, 2011).

In our study, saprotrophic fungi represented the largest share of assigned OTUs richness (31% in Gabon and 43% in the DRC, Figure 23) and counts (29% in Gabon and 48% in the DRC, Figure 23). These fungi play essential roles in carbon and nutrient cycling, and soil organic matter turnover (Talbot et al., 2015), aligning with the slow litter decomposition rate observed in *A. klaineana* stands (Leroy Deval, 1974), even after logging activities (Midoko Iponga et al., 2020). Indicator saprotrophs in old-growth mixed forests, showed greater diversity due to the variety of decomposable materials. *Trechispora* and *Botrybasidium* decompose lignin-rich wood, while *Thozetella*, *Gynotrichum*, *Lauriomyces*, and *Hyaloscyphaceae* break down finer debris like leaves, releasing nutrients into the soil (Cannon and Kirk, 2007; Põlme et al., 2020; Tedersoo et al., 2014)**.** In contrast, fungal communities in plantations in the DRC showed less differentiation overall, especially among saprotrophs, likely due to the small surface of study sites (0.5 ha in Minkuku, 0.2 ha in Ntozi), and to lower tree diversity.

Overall, our study did not detect clear fungal compositional distinctions across tree social status or stand type. Interestingly, the concept of "core mycobiota" was not observed in our data, and the level of nestedness was very low, whether considering stand type or tree social status. This suggests that fungal communities are highly variable and context-dependent rather than forming stable, core associations with *A. klaineana*. One possible explanation for this variability is root grafting, a resource-sharing adaptation that could facilitate nutrient transfer among trees and commonly observed for *A. klaineana* (Leroy Deval, 1974, 1973). As for *Dacryodes excelsa* Vahl, another Burseraceae but shade-tolerant and late-successional (Basnet et al., 1993), root grafting in *A. klaineana* could help suppressed trees survive and explain how *A. klaineana* maintains its dominance by enabling direct transfer of water and nutrients among conspecifics, as a potential alternative to the role attributed to consistent fungal community patterns and limited reliance on abundant mycorrhizal partnerships.

Future research should also explore other factors, such as root exudates and allelopathic compounds, which can influence microbial community structure and dynamics ((Balandier et al., 2022; Gris et al., 2019)). These hypotheses highlight the need for a deeper understanding of *A. klaineana*’s belowground strategies, its interactions with microbial species, and the potential genetic traits that enable it to thrive in shaded, nutrient-limited conditions while sustaining monodominance.

5 Conclusion

This study provides the first comprehensive analysis of root-associated fungal communities in *Aucoumea klaineana*, Central Africa's most harvested timber species, using ITS2 rDNA and 18S rDNA high-throughput sequencing. This was made possible by optimizing molecular methods using activated charcoal (AC) and bovine serum albumin (BSA) that enabled the extraction and amplification of high-quality DNA from root-associated fungi, overcoming inhibitors and providing a cost-effective, low-toxicity solution suitable for other recalcitrant tropical roots.

No consistent “core mycobiota” associated with *A. klaineana* was found. Instead, fungal assemblages were highly variable and diverse across stand type, tree social status, and regions. This suggested a context-dependent, stochastic assemblage driven more by other ecological factors than by stable host associations.

These results indicated that fungal associations were not a primary driver of monodominance in *A. klaineana* nor individual tree social status. This was also supported by the lack of distinct core fungal communities related to monodominant stands and to the status of suppressed trees. Arbuscular mycorrhizal (AM) fungi were consistently present, confirming the AM status of *A. klaineana*, and rejecting the hypothesis of an EcM-related monodominance. Other mechanisms, such as the root grafting processes frequent in these stands, could enhance nutrient-sharing and shape stand monodominance. Further research should examine *A. klaineana*’s reliance on belowground strategies including root grafting, root exudate processing, and litter dynamics in interactions with root-associated fungi, to better understand the mechanisms of persistent monodominance and the resilience of suppressed trees, laying the foundation for the sustainable management of this key timber species.

Chapter 5

Root grafting and monodominant stand structure

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Excavated root systems revealing root grafts in an Okoumé monodominant stand

The previous chapter showed that fungal associations were not a primary driver of monodominance in *A. klaineana* stands.

This chapter investigates the occurrence and ecological role of root grafts in monodominant *A. klaineana* stands. Hydraulic excavation of root systems, combined with dendrochronological analysis and radiocarbon dating, was used to examine how root grafts form and influence growth dynamics and stand structure.

Abstract

Root grafting forms direct physiological connections between tree roots and enables resource sharing, stability, and stress buffering among connected individuals. Its potential role in shaping monodominant stands of *Aucoumea klaineana,* a key timber species in Central Africa, remains poorly understood. Here we examine whether root grafting contributes to growth dynamics and the persistence of *A. klaineana* monodominance.

Hydraulic excavation of root systems was performed in three monodominant stands, combined with dendrochronological analysis and radiocarbon dating to investigate root graft formation and its relationship with growth patterns and stand structure. A total of 54 trees exceeding 5 cm in diameter were excavated across 245 m².

We identified 31 confirmed grafts involving 29 trees, with the proportion of grafted individuals ranging from 30.8% at one site to 100% at another. Grafted trees were significantly larger in both diameter and height (Wilcoxon test, $p < 0.001$ and $= 0.001$, respectively). All dominant and codominant trees were grafted except one, while suppressed grafted individuals showed significantly greater diameter than non-grafted suppressed trees ($p < 0.001$) but no significant height difference. Spatial analysis revealed 7 clusters of 2-7 interconnected individuals, generally centered on dominant trees.

Shared growth rings observed in graft cross-sections confirmed cambial continuity and are consistent with potential functional integration between connected roots. Radiocarbon dating in 8 samples, however, revealed numerous false and missing rings, hampering precise age estimates and growth rate estimation. Nevertheless, overlapping radiocarbon-derived age ranges among trees of different sizes were observed both within grafted clusters and among isolated individuals, suggesting partially synchronous establishment patterns.

These results show that root grafting is frequent and associated with tree size in *A. klaineana,* contributing to the structural cohesion of stands and potentially influencing resource sharing among conspecifics. Yet, its influence in monodominance likely operates alongside other facilitative processes, such as litter accumulation and microsite advantages, rather than acting as a single causal mechanism.

1 Introduction

Tree-tree interactions have traditionally been viewed through the lens of competition (Keddy, 2017; Pommerening and Sánchez Meador, 2018). Yet, processes such as facilitation and mutualism also play important roles in forest dynamics (Gross, 2008; McIntire and Fajardo, 2014). These interactions occur through both aboveground and belowground pathways, including the release of volatile organic compounds (VOCs), root exudates, and the formation of common mycorrhizal networks (CMNs) (Barto et al., 2011; Boyno and Demir, 2022; Rahman et al., 2019;

Rasheed et al., 2023). CMNs have received increasing attention for their role in transferring nutrients between plants and for supporting the widely discussed idea that trees « communicate » (Allen, 2007; He et al., 2009; Sen, 2000; Simard et al., 1997). However, the extent to which these networks facilitate cooperative interactions such as resource sharing or kin support remains highly debated. Experimental findings vary across systems, and many observed patterns can be interpreted through alternative ecological or physiological explanations (Henriksson et al., 2023; Karst et al., 2023; Robinson et al., 2024). In contrast, root grafts create direct anatomical connections between root systems, establishing xylem and phloem continuity that enables the exchange of water, carbohydrates, minerals, and signaling molecules between trees (e.g., Bader and Leuzinger, 2019; Fraser et al., 2006; Graham, 1960; Klein et al., 2016; Kuntz and Riker, 1956; O’Neal and Davis, 2015; Wimmler et al., 2022). These connections can also transmit pathogens between individuals, with important implications for stand health (e.g., Baric et al., 2008; Epstein, 1978; Jones and Bretz, 1958; O’Neal, 2014).

Root grafts were first identified through observations of tree stumps surviving for extended periods when physiologically connected to neighboring trees (e.g., Bader and Leuzinger, 2019; Dutrochet, 1833; Fraser et al., 2007; Lanner, 1961; Leroy Deval, 1973; Schultz, 1963). Nearly 200 tree species have been reported to form such connections (Graham and Bormann, 1966; La Rue, 1952) and several hypotheses have been proposed to explain their occurrence, including resource sharing during stress, hydraulic redistribution, and increased mechanical stability within stands (Bormann, 1966; Lev-Yadun, 2011; Loehle and Jones, 1998). However, the functional significance of root grafting remains uncertain and may vary across species and ecological contexts.

Investigating the impact of root grafts on stand dynamics is challenging, as most research relies on labor-intensive excavation of root systems (e.g., Adonsou et al., 2016; DesRochers and Lieffers, 2001; Fraser et al., 2005; Gaspard and DesRochers, 2020; Leroy Deval, 1973; Quer et al., 2022; Tarroux and DesRochers, 2011). As a result, its ecological purpose and silvicultural implications remain largely unresolved (Eis, 1972; Graham and Bormann, 1966; Lev-Yadun, 2011; Loehle and Jones, 1998).

Dendrochronology is a key tool for investigating the importance of root grafting after root system excavation (Adonsou et al., 2016; Alcalá-Pajares et al., 2025; DesRochers and Lieffers, 2001; Fraser et al., 2005; Gaspard and DesRochers, 2020a; Quer et al., 2022; Tarroux and DesRochers, 2011). Growth rings analysis allows determination of graft formation timing, detection of growth synchrony among connected trees, and assessment of the potential of root grafting to enhance tree resilience and support stand dominance.

Central African rainforests rank among the most diverse ecosystems, with up to 150 tree species per hectare (Day et al., 2014; Sylvie Gourlet-Fleury et al., 2013). However, in some areas, a single species can dominate over 60% of the canopy, forming extensive monodominant stands (Fuhr et al., 1998; Maisels, 2004; Peh, 2024). Monodominance can result from the combination of different features, including shade tolerance, large seeds, ectomycorrhizal associations, masting, and low disturbance, which create positive feedbacks maintaining conspecific recruitment and long-term dominance (Peh et al., 2011; Peh, 2024). Root grafting may represent an additional or complementary mechanism supporting these dynamics, although its prevalence and ecological significance in tropical monodominant forests remain poorly understood.

Aucoumea klaineana usually does not sprout from stumps (Leroy Deval, 1975), and propagation by cuttings is not easy (Grison and Hamel, 1977). However, it has been reported to form root grafts as early as four to six years of age, often linking individuals of different social status (Catinot, 1962; Leroy Deval, 1973). This combination of traits makes *A. klaineana* an exceptional model for exploring belowground mechanisms of monodominance, as root grafting, though long recognized as a potentially important ecological process, remains poorly documented (Guidosse et al., 2022; Leroy Deval, 1974; Louppe et al., 2000).

Here, we investigate the occurrence, spatial organization, and potential ecological function of root grafting in natural monodominant *A. klaineana* stands. We combine field-based root system excavations with dendrochronology and radiocarbon dating to examine how root grafts may influence tree growth and stand structure. By integrating spatial mapping with wood anatomical observations and radiocarbon data, this study provides new insights into belowground connectivity in *A. klaineana* and its potential contribution to conspecific dominance and ecological resilience.

2 Materials and Methods

2.1 *Study sites*

This study was carried out in the Ogooué-Lolo province of Gabon, within the logging concession granted to PW-CEB. Three sampling sites were located near Baposso village (1°0’1.043”S, 12°29’42.9”E), within a few hundred meters of each other.

The sites covered areas of 100 m² (site 1), 120 m² (site 2), and 25 m² (site 3) and were established in evergreen forests dominated by *A. klaineana*. Sites were selected based on the presence of monodominant stands of *A. klaineana* trees with densities ranging from 2,600 to 4,800 trees per ha, and size sizes varied according to the extent of pure *A. klaineana* patches, which were limited by the presence of other species. To accommodate experimental constraints, including hydraulic excavation with fire truck, sites were positioned along roadsides, and within 3 km of a river.

2.2 *Sample collection*

In August 2023, three sites were cleared by removing dead branches, shrubs, lianas, and litter. The sites contained pure *A. klaineana* stands, except for two suppressed

Barteria sp. individuals in site 1 and one suppressed *Musanga cecropioides* in site 2. Vegetation under 1.3 m was cleared to facilitate measurements and sampling.

A total of 87 trees and saplings were mapped using a 50-meter tape and a compass: 52 in site 1, 28 in site 2, and 7 in site 3. Diameter at breast height (DBH, 130 cm) and height were measured for all individuals, starting from 0.5 cm DBH saplings and 1.3 m height, in order to assess whether regeneration could potentially form grafts. Dawkins index (1958) and health status were also recorded (1 = healthy crown and stem, 2 = visible damage or decline).

After cutting every tree, stem cross-sectional disks of at least 2 cm in diameter and 2 cm thick were collected as close to the ground as possible for further analysis.

As *A. klaineana*'s root systems are very shallow extending only 0-25 cm in depth (Leroy Deval, 1974), around 20 to 40 cm of soil was removed using two methods: (**i**) hydraulic excavation was performed using a fire truck with a 2.500 liters tank and a high-pressure fire hose; (**ii**) while refilling the tank and due to heavy clayey soil, mechanical excavation was sequentially processed using pickaxes and shovels while paying attention to preserve the roots. Next, root systems were manually mapped based on previously digitized stand maps, and every excavated root graft were collected.

2.3 *Sample preparation*

After two months of air drying, root grafts were cut along their appropriate anatomical planes to maximize the visibility of potential fusion zones between roots. Given the low wood density of *A. klaineana* wood (Gérard et al., 2016) and its high susceptibility to surface scratches during sanding, a collaborative robotic arm was used to achieve a consistent and high-quality sanding following Van den Bulcke et al.'s (2025) protocol. Samples were sanded progressively with increasing grit up to 2000. Sanded samples were scanned using an Epson Expression 12000XL (Epson, Japan) flatbed scanner at 1600 dpi using Epson's Scan 2 software application. Images were then processed in FIJI (Schindelin et al., 2012), where the longest radius were traced from pith to bark and cropped accordingly.

Based on observations in mature dominant trees, Mariaux (1967, 1973) first described a distinctive ring pattern in *A. klaineana*, comprising a broad light zone, a progressively darkening band, a thin pale layer, and a narrow dark line. This structure reflects the four-seasonal cycle of the "SW Gabon" climatic zone, which overlaps with the species' distribution (Philippon et al., 2019). Later studies on *A. klaineana* dendrochronology adopted simplified ring-counting methods to estimate growth, either by counting only broad dark bands as annual rings (Medzegue et al., 2007), or halving the total number of dark features regardless of width (Détienne et al., 1998).

These methods, however, require caution due to *A. klaineana*'s high growth plasticity. In slow-growing non-dominant individuals, ring boundaries may merge, producing irregular patterns (Détienne et al., 1998; Mariaux, 1973, 1967; Rivière, 1992). Bomb-peak radiocarbon dating offers an alternative by measuring ^{14}C decay in wood (Libby et al., 1949), independent of ring clarity. Recent high-resolution techniques enable near-annual precision (Capano et al., 2020; Groenendijk et al., 2014), with the potential to validate or refine ring counts in species with indistinct boundaries. This may improve the accuracy of dendrochronological analyses, particularly for dating root grafting events.

Ring-width analysis was carried out using freely available custom tree-ring software (De Mil et al., 2016; De Mil and Van den Bulcke, 2023; Van den Bulcke et al., 2019, 2014; Verschuren et al., 2025), running in Matlab v2022 computer compiler environment. The analytical workflow included: (**i**) conversion from dpi to micrometers using the CoreProcessor; (**ii**) digitization of ring boundaries with RingIndicator; and (**iii**) cross-dating and ring-width file export using CoreComparison software.

2.4 *Radiocarbon dating*

Despite high-quality sanding and image processing, the annual resolution of growth rings in *A. klaineana* remains challenging to discern due to minimal variation in fiber and vessel density or size, with ring formation resulting from only minor changes in fiber lumina and wall thickness (Détienne et al., 1998; Mariaux, 1973, 1967; Medzegue et al., 2007).

To validate the accuracy of ring counts, a subsample of 10 tree-rings (Supplementary Material 17) was selected for radiocarbon dating (^{14}C). As the pith itself generally yields unreliable results, samples were taken from the earliest growth rings wide enough to allow cellulose extraction from a single ring.

Cellulose was extracted using an adaptation of the BABAB method (Němec et al., 2010) commonly used for radiocarbon sample preparation. Approximately 50 µg of wood, cut into thin chips, was placed in labeled 10 mL glass tubes. Samples were first treated with 1 M NaOH (5 mL) and incubated overnight at 70°C to remove humic substances and other alkali-soluble components, followed by two rinses with MilliQ water. Subsequently, samples were treated with 1 M HCl (5 mL) for 30 minutes at 70 °C to remove carbonates and then rinsed twice with MilliQ water. A second alkaline treatment with 1 M NaOH (5 mL) was applied for 1.5-2 hours at 70 °C, followed by a short acid rinse (1 M HCl, 5 mL, 15 min). Delignification was achieved by adding 5 mL of 5% $NaClO_2$ and 200 µL of 1 M HCl, incubating at 70 °C for 2 hours once the solution turned yellow; if delignification was incomplete, incubation was extended overnight. Samples were then rinsed twice with MilliQ water, and dried overnight at 70°C.

After that, radiocarbon dating was done at the the Royal Institute for Cultural Heritage (KIK-IRPA) in Brussels (Belgium). The samples were graphitized on the Automated Graphitization Equipment (AGE) (Boudin et al., 2019; Němec et al., 2010; Wacker et al., 2010) which is linked to the Elementar Vario Isotope Select and measured by AMS (Boudin et al., 2015).

2.5 *Microtomography Scan*

To further illustrate internal structural continuity in grafted roots prior to cutting, X-ray imaging computed microtomography (XµCT) scanning was performed on one graft to visualize the fusion pattern between the root partners. The XµCT scanner used is a TESCAN CoreTOM (TESCAN, Ghent, Belgium), which is a versatile, general-purpose system. It features a 30–180 kV / 300 W X-ray tube and a large flat panel detector with a resolution of 2,856 × 2,856 pixels and a pixel pitch of 0.15 mm. A smooth scan was performed with an exposure time of 1s per projection at 40W tube power. In total, 4,282 projections were taken, after reconstruction with the accompanying PantheraTM software resulting in an image stack with an approximate voxel pitch of 30µm. 2D visualization was performed with the open-source software Fiji (Schindelin et al., 2012) and 3D renderings were performed using VGStudioMAX (Volume Graphics, Germany).

2.6 *Data analysis*

Given the methodological challenges associated with accurately estimating the exact age of the counted rings, especially due to a lack if distinct ring boundaries, data analysis was conducted in two distinct phases to account for uncertainty.

First, a binary classification was applied to distinguish grafted trees from isolated individuals within the population. This allowed for a general description of root grafting and an assessment of its potential structural and ecological impact on the stand. In addition, linear regressions were performed to explore potential relationships between tree size (DBH and height) and the number of roots and grafts per tree. Spatial analysis of root systems and graft networks was conducted using the *igraph* R package (version 2.1.4) (Csardi and Neputsz, 2006; Csardi et al., 2025), enabling the characterization of network topology and spatial connectivity among individuals.

In a second step, the results of radiocarbon (^{14}C) dating were used to validate our tree-ring counts and ensure chronological accuracy. Once validated, age estimates of trees, roots, and root grafts were included in the analysis to provide insights into the development dynamics of root grafts in relation to tree growth and stand history.

3 Results

3.1 *Characteristics of stands*

A total of 87 trees were sampled across the three monospecific stands, covering a combined area of 245 m² (Table 4). Among them, 54 individuals had a diameter at breast height (DBH) greater than 5 cm.

The three sites exhibited a clear regeneration gradient. At site 1, 50% of individuals had a diameter at breast height (DBH) below 5 cm, compared to 25% at site 2 and none at site 3. Conversely the largest individuals in both height and diameter found at site 3. The gradient also corresponded to the proportion of grafted trees: 30.8

(0.08/m^2), 66.7 (0.12/m²), and 100.0 % (0.28/m²) of trees at sites 1 to 3, respectively. Root abundance, defined as the number of roots starting from the stump and measuring ≥ 2 cm in diameter, followed the same trend, with an average of 1.65 roots per tree at site 1 (86 roots from 52 excavated trees), 3.39 at site 2 (95 roots from 28 trees), and 6.43 at site 3 (45 roots from 7 trees).

Despite these variations, and differences in site surface, the number of confirmed grafts, identified by shared growth rings in sanded cross-sections, remained remarkably consistent across sites, with 10 grafts (0.10/m²) at site 1, 11 grafts (0.09/m²) at site 2 and 10 grafts (0.40/m²) at site 3. One tree was linked to up to six different root grafts.

Table 4: Characteristics of stands

	Site 1	Site 2	Site 3	**Total**
Excavated surface (m²)	100	120	25	**245**
Number of excavated trees	52	28	7	**87**
Number of excavated trees ≥ 5 cm DBH	26	21	7	**54**
Number of confirmed grafts	10	11	10	**31**
Number of grafted trees ≥ 5 cm DBH	8	14	7	**29**
Proportion of grafted trees ≥ 5 cm DBH (%)	30.8	66.7	100.0	**53.7**
Density (stems ha^{-1})	5,200	2,333	2,800	
Density of trees ≥ 5 cm DBH (stems ha^{-1})	2,600	1,750	2,800	
Mean DBH of trees ≥ 5 cm DBH (cm)	7.1	11.9	23.1	
Mean height of trees ≥ 5 cm DBH (m)	8.3	14.8	18.2	
Mean distance between grafted trees (m)	0.8	2.8	1.0	
Maximum distance between grafted trees (m)	1.3	6.1	1.5	

When examining the spatial distribution of trees (Figure 28), two distinct root-connected clusters were identified at each site. Additionally, a third cluster was observed at site 1 between tree 51 and a dead individual (no evidence of callus formation). Grafts were more numerous when associated with dominant trees, which might be linked to more extensive root systems. Despite the similarity in the number of clusters and confirmed grafts across sites, the structure of the networks differed notably.

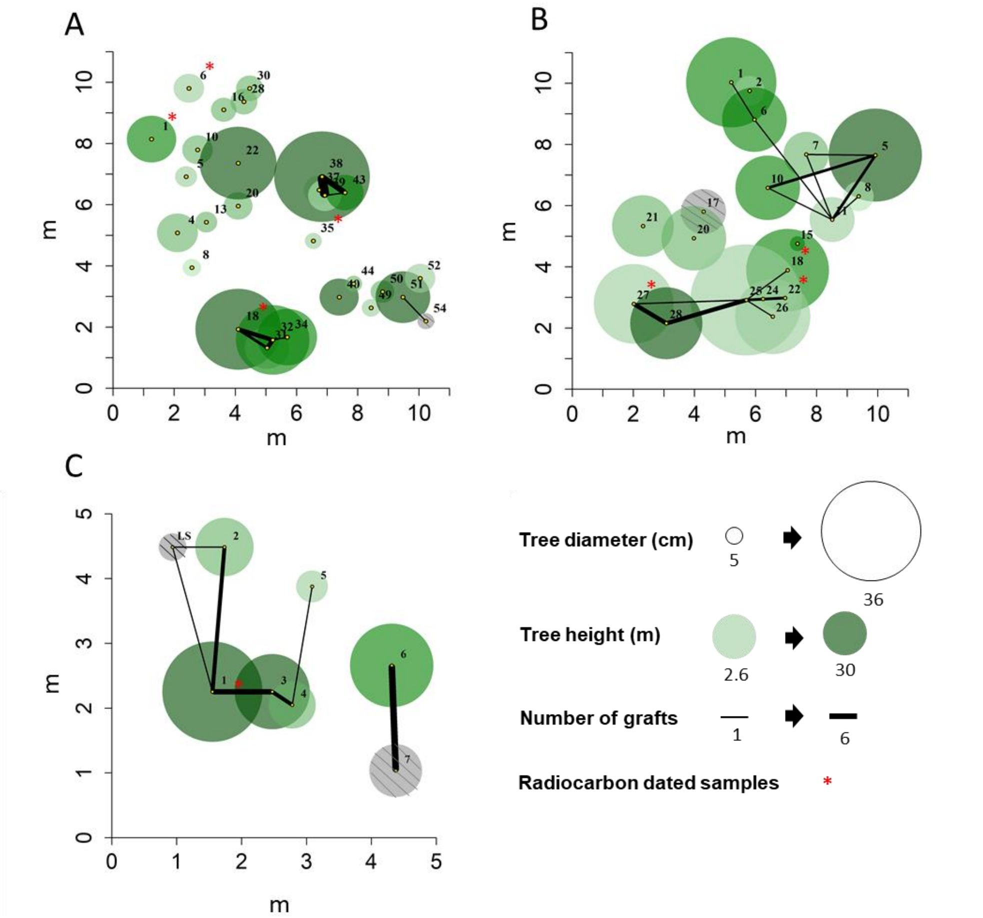

Figure 28 : Tree network maps (**A-C** = sites 1-3). Nodes represent trees, with diameter proportional to tree diameter at breast height (≥5 cm) and green shading indicating tree height. Recently dead or broken individuals are shown in hatched grey shading, and "LS" denotes living stumps. Black lines represent grafted connections, with line width proportional to the number of grafts between individuals. Self-grafts are not shown here. Red asterisks indicate trees sampled for radiocarbon dating.

On average, grafted trees shared 2.0 ± 0.5 fusions with other trees. All trees exceeding 21 meters in height or 23 cm in DBH were grafted, whereas none below 8 cm in DBH showed evidence of grafting (Supplementary Material 18), with the exception of tree 22 in site 1. Individuals within intermediate size ranges exhibited variable grafting status.

The number of roots per tree showed no strong correlation with tree size. Linear regressions testing the number of roots yielded low coefficients of determination, with $R^2 = 0.15$ and 0.24 for DBH and height in grafted trees, and $R^2=0.46$ and 0.34 for non-grafted trees, respectively (Supplementary Material 18).

At site 1, the two clusters (groups of trees connected to each other) were organized around the two largest and tallest dominant trees, each associated with one, and two subordinate individuals, forming groups of three and four trees. The number of grafts per pair was proportional to the dominance of the central tree. Site 1 also exhibited the highest number of isolated individuals, characterized by lower mean DBH and height compared to the other sites.

At site 2, isolated trees were less frequent and generally larger in both DBH and height. All dominant trees were integrated into clusters, which were more complex, each involving seven individuals connected through sequential grafts. Grafted trees were also more widely spaced in site 2, with an average inter-tree distance of 2.8 meters (compared to 0.8 m and 1.0 m at sites 1 and 3, respectively), and a maximum of 6.1 meters between trees 6 and 11.

Site 3, being smaller and composed of older trees, contained no isolated individuals. Instead, it featured two closely spaced and highly connected clusters: one comprising five trees and a living stump, and the other consisting of six grafts between two trees, one of which died likely one year prior to sampling.

3.2 *Root graft formation*

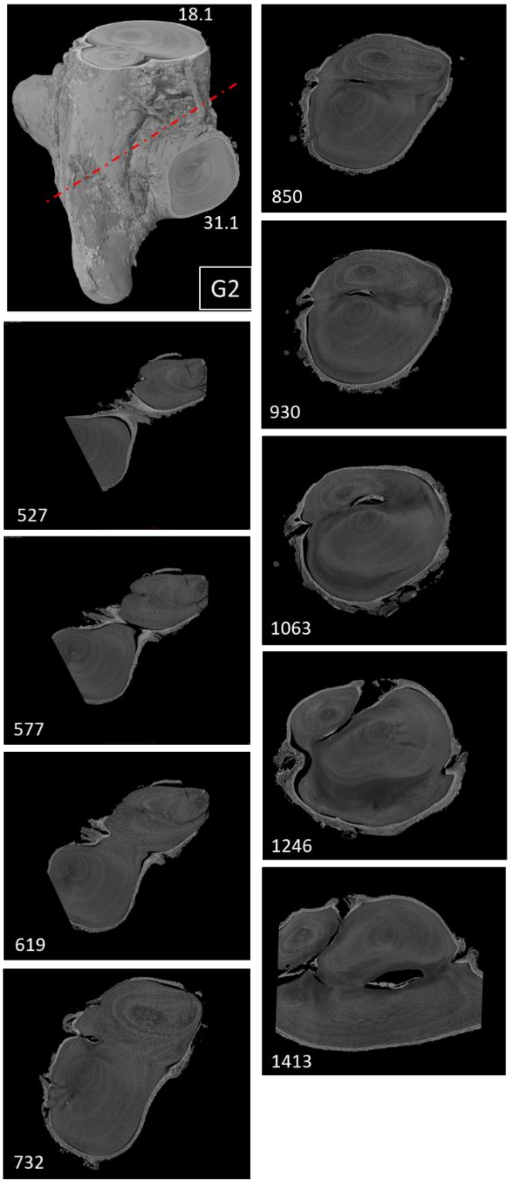

Figure 29 : X-ray micro-computed tomography (XµCT) scan of root graft G2. The first panel shows an external view of graft G2 from Site 1, formed between root 1 of tree 18 and root 1 of tree 31. Other panels are sequential 2D slices through the graft following the red dashed line in first panel, illustrating internal fusion of vascular tissues between roots. These images highlight structural continuity and vascular integration within the graft prior to sectioning.

To determine whether the grafts described above are purely mechanical or if the fusions allow functional integration through cambial continuity, resulting in a shared xylem and phloem, a micro-computed X-ray tomography scan was performed. The scan of graft G2 between trees 18 and 31 at site 1 revealed fusion of root tissues and formation of wood facilitating sap exchange (Figure 29). Depending on the observation angle, up to seven shared growth rings were observed.

Another graft (G8), between tree 31 root 1 and tree 32 root 1, is shown in Figure 30. The image clearly reveals two individual roots coming into contact and forming a callus, after which cambial continuity is established, leading to the development of several common but indistinct growth rings. This represents the clearest case observed, whereas other cross-sections may reveal three or more distinct piths.

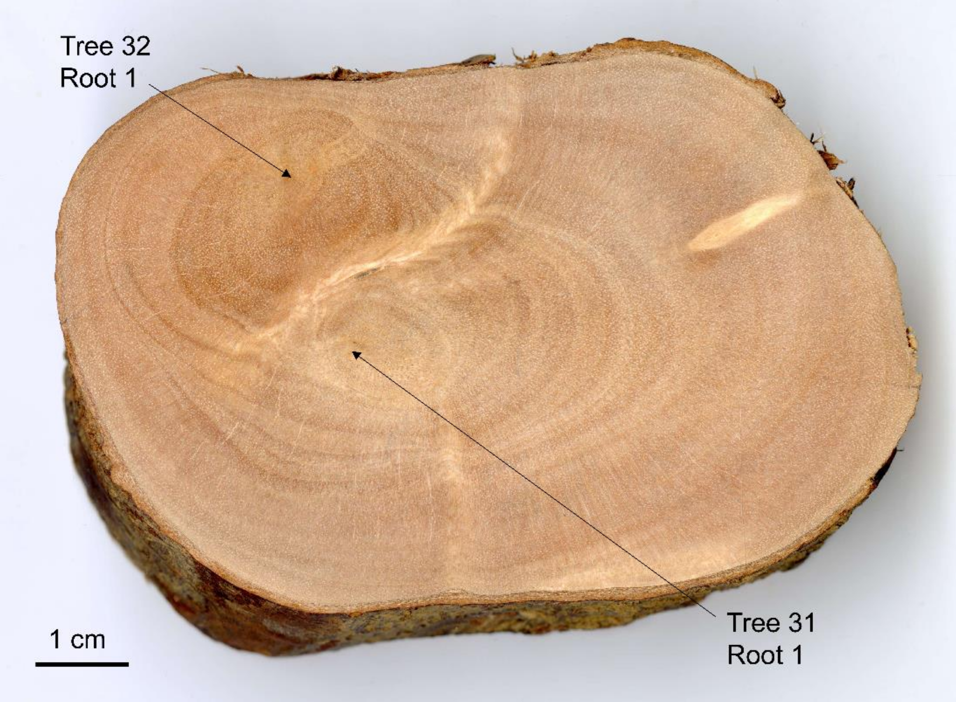

Figure 30 : Cross-section of root graft G8 from Site 1, connecting tree 31 root 1 and tree 32 root 1. Samples were sanded with 2000-grit paper using a collaborative robot (Van den Bulcke et al., 2025) and scanned at 1600 dpi. **Note:** the continuity of xylem and phloem layers at the graft interface, as well as the central area exhibiting callus formation, indicating tissue fusion.

3.3 *Root grafts and stand growth dynamics*

To assess the relationship between grafting and tree structural traits, DBH and height were compared between grafted and non-grafted individuals, without considering graft age due to challenges in identifying annual growth rings in *A. klaineana*.

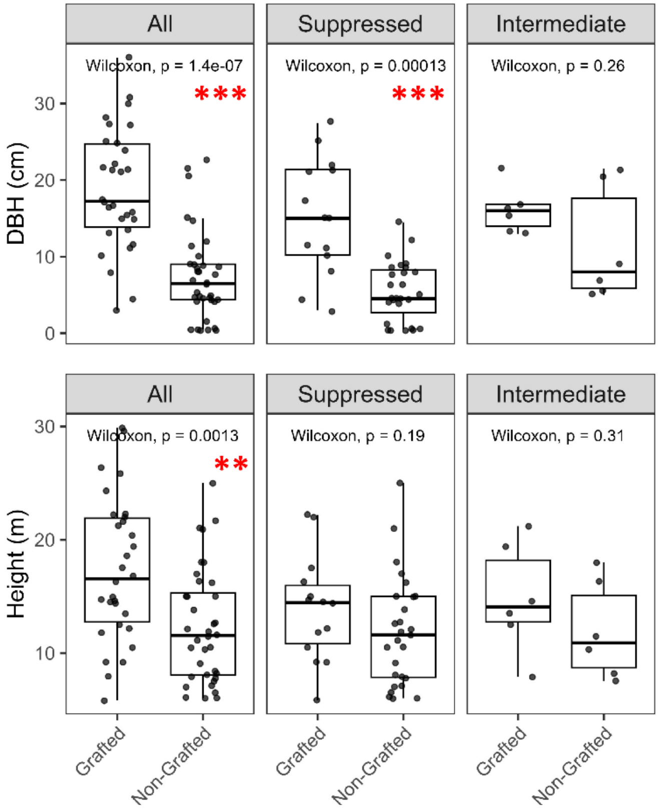

Figure 31 : Tree size variation by grafting status across canopy dominance classes (Dawkins social status from 1 to 5). Boxplots show DBH in cm and height in meters for grafted (yellow) and non-grafted (blue) trees across all canopy positions ("All") and within Dawkins status groups ("1–2" = Suppressed, "3" = Intermediate). Status 4 and 5 are not shown as they are all grafted except for tree 22 from site 1. P-values <0.05 indicate significant differences.

Grafted trees exhibit greater DBH and height when considering all individuals (Figure 31, Wilcoxon test, p<0.001 and =0.001, respectively). When classified by Dawkins social status, no significant height differences were found between grafted and non-grafted trees in suppressed (Status 1-2; Wilcoxon test, p=0.19) or intermediate trees (Status 3; Wilcoxon test, p=0.31).

However, among suppressed individuals (Status 1-2), grafted trees showed significantly greater DBH (Wilcoxon test, $p<0.001$). This difference was no longer apparent in intermediate trees, which are more likely to receive only vertical light (Status 3; Wilcoxon test, $p=0.36$). In the dominant class (Status 4-5), all trees were grafted except one. The differences in DBH are therefore more pronounced than in height among individuals, especially at the extremes of the social status gradient.

3.4 *Tree ages*

To clarify whether root grafts influence tree growth or are instead a consequence of it, identifying consistent annual growth ring patterns is necessary. Growth ring identification in *A. klaineana* is challenging (Mariaux, 1973) due to its diffuse-porous wood anatomy and frequent production of false rings. As shown in Figure 32, ring visibility varies with the scale of observation: macroscopic views (Figure 32A) display distinct wide dark bands, commonly interpreted as annual rings. However, closer examination along the radius (Figure 32BC) reveals additional, finer lines that likely correspond to intra-annual density fluctuations rather than true annual boundaries. At the microscopic level (Figure 32D), no consistent anatomical transitions are observed between ring boundaries.

Bomb-peak ^{14}C radiocarbon-dated ring highlighted in red aligns with the 2005-2009 period macroscopically counted in Figure 32A but not with higher magnification in Figure 32B, supporting the hypothesis that only broad dark bands represent true annual increments. This suggests that macroscopic inspection yields the most reliable ring count for age estimation in *A. klaineana*, while higher-resolution methods typically used in dendrochronology tend to overestimate age due to the presence of false rings.

To further validate this method, nine additional growth ring samples were Bomb-peak ^{14}C radiocarbon-dated following a preliminary macroscopic age estimation. Samples were selected to maximize representation across Dawkins social status (1, 2, 3, 5), tree DBH (5-36 cm) and the three sites, including for two trees (site 1, tree 18; site 2, tree 18) one sample near the pith and one at mid-radius to capture intra-tree variability.

Figure 33 and Supplementary Material 17 shows the radiocarbon dates results for the ten growth ring samples. Despite targeting only macroscopic rings boundaries (broad dark bands as detailed above), five out of six samples from intermediate (status 3) to dominant (status 5) trees were overestimated in terms of number of rings, suggesting that numerous false rings were mistakenly included. Among four samples from suppressed trees (status 1-2), only half yielded accurate counts. The other half were underestimated, suggesting missing rings and underscoring the difficulty of obtaining precise age estimates in suppressed individuals.

Finally, we could not identify any consistent tree-ring morphological features that reliably indicate annual growth increments. Annual ring appearance varied from one sample to another, but also from one year to another within the same sample. This variability appears to depend on multiple factors as growth rate, tree age, social status, and morphological traits (e.g., grooves), as noted by Mariaux (1973) and illustrated in Supplementary Material 19.

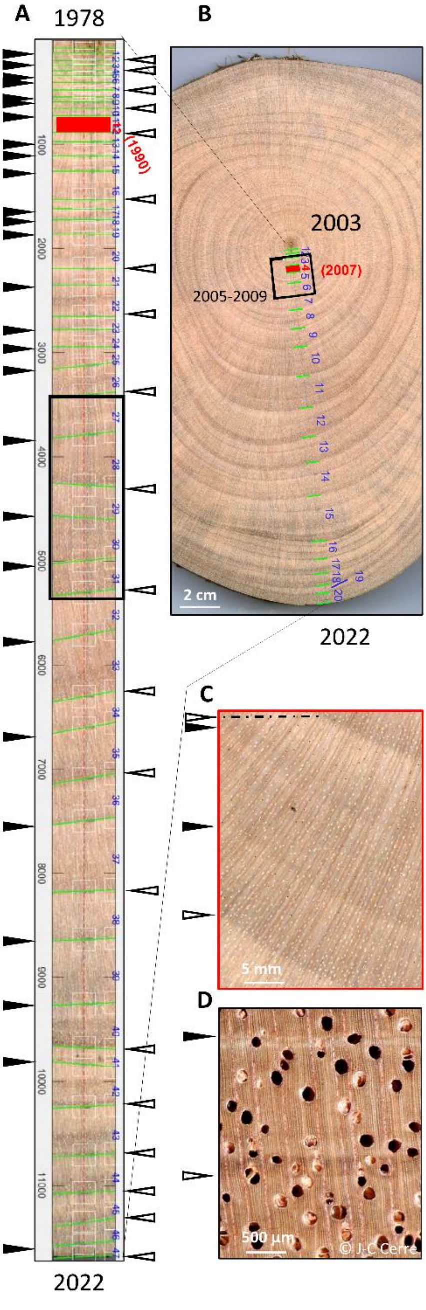

Figure 32 : Growth ring identification in *Aucoumea klaineana* varies with the scale of observation. Red square: sample with assigned counted ring date. Black box: date interval based on ^{14}C bomb-peak radiocarbon analysis. At the macroscopic level **(A)**, examination along the longest radius reveals multiple anatomical features caused by short-term environmental fluctuations within a single year, some of which are false rings (black arrows). White arrows indicate true annual ring boundaries. A trunk cross-section **(B)** shows apparently distinct growth rings visible to the naked eye. At higher magnification **(C)**, anatomical features distinguishing true rings are not clearly visible. (**D**) *A. klaineana* wood anatomy (InsideWood, 2026; Wheeler, 2011; Wheeler et al., 2020; © JC Cerre). Radiocarbon dating confirms that the ring marked in red corresponds to the 2005-2009 period

As a result, further analyses were conducted but remained inconclusive to consistently define the boundaries of true annual rings in this species using a visual approach only and for those age classes. Microscopic inspection revealed approximately twice as many ring-like structures, but these did not correspond to a consistent doubling of true annual rings. Instead, the degree of over- or underestimation varied strongly with tree status and DBH. Under current conditions, any attempt to test for relationships between root graft age and growth variation in grafted trees was therefore not feasible.

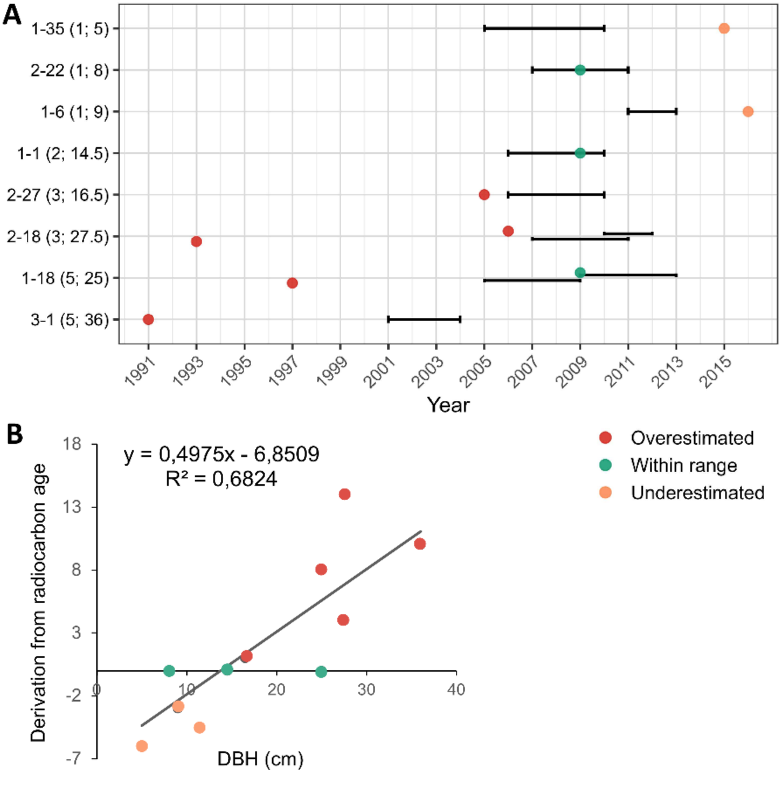

Figure 33 : Comparison of manual tree-ring counts with radiocarbon (^{14}C)-derived age intervals. (**A**) Black horizontal lines represent calibrated age ranges obtained from radiocarbon dating, while points show ages estimated from manual ring counts. Sample labels include site-tree ID, Dawkins status, and DBH (cm). When two black bars appear for the same tree ID, they represent independent samples extracted from different positions along the same wood core. Tree are ordered first by Dawkins status, then by tree DBH. (**B**) Tree age estimates based on linear regression between radiocarbon-calibrated ages and ring counts.

Radiocarbon analyses were performed on the earliest growth rings wide enough for cellulose extraction. Consequently, each sample (and, when applicable, the first of the two subsamples taken from the same core) reflects an age close to the tree's origin. Notably, these age ranges obtained by radiocarbon dating largely overlap for most samples from sites 1 and 2, despite significant differences in DBH (Figure 33), suggesting that they have a similar age.

4 Discussion

This study is the first to investigate the role of root grafting in shaping growth dynamics and stand structure in a tropical rainforest. Despite technical limitations, including the absence of clear growth dormancy and the difficulty of identifying annual ring boundaries in the wood of *A. klaineana* (Détienne et al., 1998; Mariaux, 1973; Medzegue et al., 2007) root grafts were consistently observed through shared tree-ring patterns across connected individuals.

4.1 *Root grafting and stand structure*

Dominant trees were grafted in nearly all cases, with only a single exception, and were frequently part of clusters, indicating the presence of belowground integration in monodominant *A. klaineana* stands. The complexity of these graft networks varied, ranging from simple pairwise fusions to clusters involving up to seven individuals. This contrasts with patterns observed by Leroy Deval (1973), where connections were limited to individuals of different social status, and no stratification appeared before age of four to six, when the first grafts occurred.

As supported by earlier works (Alcalá-Pajares et al., 2025; Fraser et al., 2005; Gaspard and DesRochers, 2020; Leroy Deval, 1973; Tarroux and DesRochers, 2010), the observed relationship between graft occurrence and tree proximity suggests that grafting in *A. klaineana* may be a general response to high stem density or intense competition , likely driven by mechanical root contact and potential selective advantages (Lev-Yadun, 2011). In this study, grafted trees were also consistently larger in both diameter and height than isolated individuals, as also observed in boreal forests for *Populus* spp. (Gaspard and DesRochers, 2020) and *Abies balsamea* (L.) Mill. (Balsam fir) (Quer et al., 2022). This was also true for DBH among suppressed social classes but not among the intermediates (status 3). This pattern aligns with the hypothesis that root grafts allow resource redistribution and may support the survival of weaker individuals (Bader and Leuzinger, 2019; Fraser et al., 2006; Tarroux and DesRochers, 2011).

In the context of *A. klaineana* ecology, root grafting may support the maintenance of monodominant stands by facilitating intraspecific cooperation and limiting the establishment of other tree species. This would occurs through the expansion of the effective rooting zone, which would enhance stand-level access to soil resources and may ultimately increase tree growth rates (Basnet et al., 1993; Bormann, 1966; Loehle and Jones, 1998; Tarroux and DesRochers, 2011). However, this hypothesis requires further verification, as the transfer of resources toward suppressed individuals could also operate at the expense of dominant trees, potentially constraining their growth. Such mechanisms may also occur in *A. klaineana* stand development, particularly in disturbed habitats where fast-growing pioneers such as *Macaranga* spp. and *Musanga cecropioides* R. Br. (Umbrella tree) can temporarily outcompete regenerating individuals (Doucet et al., 2004). However, both taxa have also been reported to form root grafts (Dosso et al., 1981; pers. com.), albeit possibly to a different extent or frequency. In our study, one strong root connexion was also observed between a large *A. klaineana* and a dominant *M. cecropioides* individual outside the excavated area; however, this connection appeared to be mechanical only, with no anatomical fusion.

4.2 *Dendrochronological constraints and insights*

Although macroscopic tree rings were visible, radiocarbon analysis revealed frequent false rings in dominant and intermediate individuals, and numerous missing rings in suppressed trees. In the absence of clear criteria for identifying annual growth rings, accurately determining the age of *A. klaineana* trees and the timing of root graft formation remains challenging. Nevertheless, the combined use of dendrochronological observations and radiocarbon dating provided valuable insights into the structure and variability of growth patterns in this species. This highlight important limitations in using ring width as a consistent proxy for growth variation, thereby preventing a clear assessment of the relationship between grafting and growth patterns, including dominant tree growth promotion as previously suggested (Leroy Deval, 1973), or instead reflecting a consequence of pre-existing vigour in dominant *A. klaineana* individuals.

Such limitations were highlighted in earlier anatomical studies on *A. klaineana* (Détienne et al., 1998; Mariaux, 1973; Medzegue et al., 2007). The present study builds on these findings by demonstrating that even fast-growing, dominant individuals previously used as reference models exhibit irregular ring patterns. This reinforces the relevance of the methodological approach used here and emphasizes the challenges of applying dendrochronological methods to this species.

4.3 *Potential drivers of root grafting in monodominant* A. klaineana *stands*

Radiocarbon dating suggests that despite large differences in diameter and social status, *A. klaineana* individuals within monodominant stands may be of similar age. At site 2, confidence intervals on radiocarbon year for both dominant and suppressed trees overlap around 2009, indicating synchronous establishment of individuals with contrasting sizes.

A similar pattern was also observed at site 1, where sampled trees were mostly isolated. In this case, alternative explanations apart from root grafting may include the combination of *A. klaineana* seedlings' tolerance to a wide range of light conditions, even in deep shade (Guidosse et al., 2024a), and the benefit gained from thick litter layers produced by neighboring conspecifics, which may support persistence despite limited growth.

As a pioneer species, *A. klaineana* is known to "*create its own soil*" (Brunck et al., 1990). It produces thick, slowly decomposing litter layers (Midoko Iponga et al., 2020) which is uncommon in many African rainforests where litter rarely accumulates. This slow decomposition may contribute to soil modification and resource retention as suggested for *Dacryodes excelsa* Vahl (Tabonuco), another Burseraceae (Basnet et al., 1993). For that species, many individuals were growing on slopes, where root grafting between neighbouring trees appeared to create terrace-like structures, stabilizing accumulated litter and sediments later colonized by dense mats of fine roots.

Root grafting has also been proposed to contribute to contribute to mechanical anchorage of vulnerable stands (Alcalá-Pajares et al., 2025; Basnet et al., 1993; Loehle and Jones, 1998; Stokes et al., 2005). This function may apply to *A. klaineana* as well, as it is characterized by a shallow root system and early taproot atrophy (Leroy Deval, 1974), which may reduce its mechanical stability. Moreover, its marked heliotropic growth characterized by flexuous stems leaning toward even small light openings can lead to strongly tilted forms. These traits suggest that large individuals may rely on root grafts with smaller neighbours to maintain structural stability and avoid mechanical failure.

4.4 *Future perspectives*

Future research should prioritize approaches that overcome current methodological constraints. In particular, dendrochronology remains challenging in *A. klaineana* due to irregular growth rings patterns. Permanent plots with at least annual measurements, as already implemented in monodominant stands within the logging concession that hosted this study, could offer a more robust framework for tracking the long-term dynamics of graft formation, tree persistence, and growth outcomes. However, obtaining accurate long-term data on growth dynamics would still remain challenging and require patience, given the lifespan of these trees.

In *A. klaineana*, it remains unclear whether root grafts arise preferentially among genetically related individuals as proposed in some conifers (Tarroux and DesRochers, 2010; Henriksson et al., 2023) or are only related to spatial proximity and root architecture. As in boreal forests, grafting in *A. klaineana* tends to occur between larger and spatially proximate individuals (Gaspard and DesRochers, 2020; Quer et al., 2022). Lev-Yadun (2011) proposed several hypotheses linking root grafting to kin selection, three of which may be particularly relevant to *A. klaineana*: (**i**) as it is wind-dispersed, seeds are transported in the same direction and establish in clusters, potentially allowing grafting between siblings and thus reflecting kin selection *sensu stricto*; (**ii**) grafting may promote reproductive success by sustaining a nearby conspecific mate. This is an interesting hypothesis given the species' dioecy, warranting investigation into whether grafted clusters consistently include both sexes and whether dominance patterns correlate with gender; and (**iii**) it may expand the chemical defense repertoire via shared root-derived secondary metabolites, enhancing resistance to herbivores and pathogens (Erb et al., 2009). This possibility is particularly intriguing considering the species' distinctive litter production (Midoko Iponga et al., 2020), particular fine-root morphology (Guidosse et al., 2022; Onguene et al., 2002), and the high secondary metabolite diversity typical of Burseraceae (De Nicolai and Rodrigues, 2022; DeCarlo et al., 2019).

Previous studies, including this one, often reduce root grafting to a binary state: grafted or not. This oversimplifies a complex phenomenon that likely functions along a continuum (Vovides et al., 2021; Wimmler and Berger, 2024). In our study, grafts rarely occurred as isolated pairs; instead, clusters typically involved multiple connections, with up to six grafts connecting just two trees. Variability in graft number, age, and size likely affects the intensity and direction of resource exchange, emphasizing the need for a more nuanced approach to studying graft functionality.

Moreover, self-grafts, where roots fuse with other roots of the same tree, and grafts of more than two roots, were frequently observed in the studied stands, further highlighting the complexity of those root systems. Interestingly, some roots also formed connections with certain neighboring tree roots while others, even of similar diameter from the same individual, remained independent despite close proximity. While some of this variability may be due to microsite conditions or random chance, it nonetheless adds an additional layer of complexity.

Applying quantitative biology methods to well-designed field experiments could elucidate sap flows within interconnected *A. klaineana* tree populations and resource redistribution across individuals, offering critical insight into the functional and selective value of grafting in ecosystems and populations (Kragler and Bock, 2025), as well as its influence on stand-level growth dynamics.

5 Conclusion

This study provides a spatial exploration combined with dendrochronological analysis and radiocarbon dating of root grafting in monodominant *A. klaineana* stands, revealing complex belowground networks primarily involving dominant individuals. Grafts were frequent, often connecting multiple trees, and were associated with patterns of spatial clustering and tree size variation. Despite limitations in age estimation due to irregular growth rings, radiocarbon dating suggests synchronous establishment of trees with contrasting social status highlighting the coexistence of multiple processes that may contribute to stand structure, including root grafting, litter dynamics, and shade tolerance. These processes must be further investigated using modern quantitative biological methods to better understand their functional role in stand development, species dominance, and forest resilience. Overall, these findings document the prevalence of root grafting in *A. klaineana* monodominant stands and provide a basis for future studies on its ecological implications to support the sustainable management of the most harvested timber species in Central Africa.

Chapter 6

General Discussion


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A dominant Okoumé in an old-growth mixed forest

The primary objective of this thesis was to clarify the ecological mechanisms underlying the functioning of *Aucoumea klaineana* populations, with the applied aim of supporting their sustainable management and improving silvicultural practices. Despite *A. klaineana*'s central economic role in the forestry sectors of Gabon, Republic of Congo, and Equatorial Guinea and the focus on silvicultural trials for over a century, its population ecology remains poorly understood. This work focused on identifying the environmental conditions that favor its establishment, exploring how belowground interactions such as root grafting and fungal root associations influence stand dynamics, and examining how these ecological insights can guide more effective regeneration strategies. To address these questions, a multidisciplinary approach was implemented across seven chapters.

1 Key findings summary

Chapter 2 offered a comprehensive bibliographical synthesis of more than thirty years of research on *A. klaineana*. This review revealed that, although the species is currently classified as "Vulnerable" under IUCN criterion A1, this status may no longer reflect its actual demographic situation. The species is neither rare nor threatened across its natural range as it averages nearly seven adult trees per hectare (dbh ≥ 20 cm) in Gabon, regenerates effectively in disturbed environments, and benefits from legal logging practices that preserve sufficient seed trees. However, the chapter highlighted two key concerns for the future: (**1**) the potential decline in wood quality due to decades of selective harvesting of superior trees, and (**2**) the lack of detailed ecological understanding of the species' ecology, especially the role of the rhizosphere. The roles of mycorrhizal symbioses and root grafts were identified as critical, yet poorly understood, in shaping *A. klaineana* population dynamics and stand structure. These gaps laid the foundation for the ecological investigations presented in the following sections.

In **Chapter 3**, the effects of both light availability and pest pressure on *A. klaineana* seedlings were investigated through an 18-month experiment under semi-controlled conditions. It was found that seedlings grow best in a wide range of intermediate light levels (between 9% and 62% of relative irradiance) with high productivity in terms of diameter and biomass. However, their health was significantly affected by pest pressure, particularly psyllids and black canker, regardless of light conditions. Interestingly, survival remained high (97.1%) even under extreme light (1% and 100% RI), highlighting the species' resilience.

These findings directly address the first objective of this thesis (**Q1**), showing that while light influences growth performance, it is not a limiting factor for seedling survival, thereby supporting the hypothesis that persistence under low-light conditions may contribute to monodominance. These results suggest that, for successful regeneration, the priority should shift from optimizing light conditions to developing effective pest management strategies. The study also recommends planting seedlings in small monospecific groups, ideally under moderate canopy cover, to encourage growth and root grafts while limiting pest transmission through spatial species diversification.

To investigate fungal belowground processes in *A. klaineana* **(Chapter 4)**, the protocol of a widely used DNA extraction kit was modified to suit the challenges of recalcitrant tropical tree roots mycobiota. It was improved by incorporating activated charcoal, and PCR amplification was enhanced by adding bovine serum albumin to overcome inhibitory secondary metabolites. This low-toxicity method enabled the first high-throughput sequencing of *A. klaineana*'s root mycobiota across tree social status, forest types and regions. Results revealed that *A. klaineana*'s root-associated fungal communities were highly diverse and variable, with no consistent "core" mycobiota. Notably, ectomycorrhizal (EcM) fungi, proposed in our hypotheses to support nutrient acquisition and monodominance, were absent from monodominant stands, wheres arbuscular mycorrhizal fungi were consistently present but remained scarce across all forest types and tree social status. In contrast, saprotrophic fungi were highly abundant and dominant regardless of the sampled individual.

These findings address the second objective of the thesis (**Q2**), indicating that specific root-associated fungal communities do not strongly influence suppressed tree survival or contribute to monodominance. Based on root-associated fungal assemblages, it remains unclear whether litter decomposition and nutrient dynamics play a major role in *A. klaineana*'s monodominance, highlighting the need to explore other belowground ecological mechanisms that are more likely to underlie *A. klaineana*'s monodominance and resilience in Central African forests.

Building on this, **Chapter 5** highlights the occurrence of root grafting as an alternative belowground mechanism. Excavations in monodominant stands revealed frequent root grafts mainly among larger, dominant trees, forming interconnected complex clusters that likely promote resource sharing and stand cohesion. Radiocarbon dating suggested synchronous establishment of trees, which may reflect shared establishment dynamics, potentially linked to graft networks but also by the effects of canopy gaps and effects of conspecific litter accumulation. Taken together, these observations provide important insights into belowground structure and potential functions of root grafts, even though their actual role in resource sharing, stand cohesion, and reinforcement of monodominance (**Q3**) remains to be further explored, as addressed in the next chapter.

Despite the challenges associated with accurately estimating tree age and growth rates due to indistinct annual rings, the combination of excavation, dendrochronological observations, and radiocarbon dating provides complementary insights into belowground structure and stand development. These limitations highlight the value of the approach while identifying key areas where further methodological refinement and quantitative studies are needed to better understand the functional role of root grafting in stand dynamics and species resilience.

This **final Chapter** brings together the main findings of the manuscript, comparing the results across chapters and evaluating their originality in relation to other species. It discusses the broader significance of these findings, particularly in terms of sustainable silvicultural practices for *A. klaineana*, and reflects on their possible implications for the species' conservation status under IUCN and the CITES. The chapter concludes by proposing future research directions, acknowledging that while the study offers important insights despite inherent uncertainties, it provides a solid foundation and multiple avenues for further investigation.

2 Ecological interpretation

2.1 *Biotic interactions and establishment strategy*

The seedling establishment phase of *A. klaineana* appears to be more strongly constrained by biotic pressures than by abiotic conditions. At the stand scale, it tolerates a wide range of soil types (Leroy Deval, 1974) but also grows in a wide range of light conditions, as it survives both in deep shade and full sun (Chapter 3), suggesting greater ecological flexibility than previously assumed for a supposed strictly light-demanding tropical species. This shade tolerance of *A. klaineana* young seedlings may contribute to the maintenance of monodominant stands while growth remains limited under closed canopies. Survival strategies including leaf allocation in low light environment likely interact with disturbance regimes and competition from faster-growing species. However, pest pressure, particularly from psyllids and black canker, emerged as a major limitation across light levels, underscoring the need to prioritize biotic stress management over light optimization.

Classic pest management strategies for tropical species include promoting partial shade (e.g., Bosu et al., 2006; Brunck et al., 1990; Nichols et al., 1998; Wagner et al., 1996) or diversifying species composition in stands to disrupt pest cycles (Bosu et al., 2006; Nichols et al., 1999). However, interspecific competition is the second most limiting factor for *A. klaineana*, which naturally establishes in monospecific to monodominant stands and struggles to compete in mixed-species environments (Doucet et al., 2004).

Further research on plant-insect-microbe interactions is essential for species-specific management. For instance, the role of volatile organic compounds (VOCs) in *A. klaineana* defence also deserves attention. As a Burseraceae, a pantropical family rich in terpene-based metabolites (De Nicolai and Rodrigues, 2022; DeCarlo et al., 2019), *A. klaineana* also produces VOCs such as α-pinene and d-limonene (DeCarlo et al., 2019), known in neotropical genera such as *Bursera* (Becerra et al., 2001) and *Protium* (Da Silva Menezes et al., 2025) to deter herbivores and attract natural enemies. This is also linked to physical barriers through resin exudation.

These mechanisms are poorly documented in Central African species, but VOCs may similarly protect *A. klaineana* against insects. However, persistent outbreaks suggest that some pests such as psyllids may have evolved counter-adaptations, as seen in *Blepharida* beetles on *Bursera* (Becerra et al., 2001). Then, investigating VOC-mediated interactions in *A. klaineana* could help clarify their ecological role in natural conditions. Interspecific competition appears to be a key factor driving natural or artificial regeneration success. In open, species-poor environments (e.g., fallows, savanna, log yards, roadsides), *A. klaineana* establishes readily and can maintain dominance. In contrast, where short-lived faster-growing species (e.g., *Musanga* spp., *Macaranga* spp., …) are already present in the soil seed bank (e.g., canopy gaps), its regeneration is limited, regardless of light availability.

Biotic interactions also include important belowground relationships, particularly with root-associated fungi on which we focused on (Chapter 4) due to their importance in tropical tree nutrition and health (Van Der Heijden and Horton, 2009). Root-associated fungal communities, analyzed in adult trees, showed high diversity and variability but no consistent patterns linked to forest type or tree social status, suggesting a limited role for mycorrhizal facilitation or any other fungal effects[1]. In our study, AM fungi were consistently detected, but their relative abundance remained low. Unlike many tropical species (Onguene and Kuyper, 2001), *A. klaineana* does not seem to rely on strong specific early mycorrhization. This is surprising, given that AM fungi typically play a central role in phosphorus acquisition (Smith and Read, 2008), a nutrient not measured in this study but which is often limiting in Central African forest soils (Vitousek et al., 2010). This is particularly true for fast-growing species colonizing savannahs, such as *A. klaineana*, having substantially greater nutrient demand than mature forests species (Pellegrini, 2016).

In some other species, AM fungi enhance seedling growth and drought tolerance in tropical forests (Birhane et al., 2023; Pereira et al., 2021). The relative scarcity of AM fungi in *A. klaineana* roots is even more surprising given its restricted distribution to the “SW Gabon” climate sector which is characterized by the longest and driest dry season at the regional scale (Philippon et al., 2019).

On the other hand, other authors have suggested that mycorrhizal colonization may be down-regulated under drought conditions because maintaining this symbiosis becomes too costly for the host plant (Yaffar et al., 2024). Instead, the species’ regeneration strategy may rely more on stress tolerance, which may be helped by dark septate endophyte taxa such as *Cladophialophora* (Diez-Hermano et al., 2024; Santos et al., 2021) and possibly beneficial microsite conditions shaped by conspecific’s litter (Brunck et al., 1990) or root exudates.

2.2 *Belowground dynamics and stand structure*

In contrast to the even-aged uniform canopies typical of plantation species such as *Eucalyptus spp.* and *Picea spp.*, monodominant stands of *A. klaineana* often comprise both dominant and markedly suppressed individuals (Louppe et al., 2000), even over the long-term. Once the stand is well established, belowground processes, including root grafting, may contribute to sustain the long-term dominance of *A. klaineana* and

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[1] Although these patterns were observed in adult trees, they likely extend to earlier life stages as well, as very small side analysis on seedlings (n=4) revealed similarly variable fungal assemblages among each other and compared to adult trees.

to ensure the survival of suppressed trees, although their relative importance remains to be clarified (Chapter 5).

In our study, this stand structuration did not correspond to any detectable assemblages in root-associated fungal communities (Chapter 4). The frequent occurrence of root grafts among larger individuals suggests the existence of cohesive conspecific networks, a phenomenon well documented in other tree species, that may facilitate resource redistribution and enhance stand stability. Such interconnected systems could enable suppressed individuals to persist until canopy openings provide an opportunity for growth.

Radiocarbon dating analysis further supports that *A. klaineana* populations are largely even-aged, raising the possibility that trees within the same cohort form grafted clusters that help them survive under competition. However, whether these connections contribute to persistence under competition cannot be determined from the present data. Even among non-grafted, suppressed trees of similar age, some individuals remained healthy, suggesting that persistence may also be explained by factors independent of root grafting. This is probably due to a certain level of shade tolerance and potentially benefiting from the favorable microenvironment created by conspecific litter and root activity. However, it is important to note that this last hypothesis is based on a very limited sample size (n=3 for isolated suppressed individuals), and its validity over the longer term remains uncertain. Isolated suppressed individuals may eventually die, whereas grafted trees could maintain vitality for much longer as observed by Catinot (1969) in natural forests where clusters of three or four vigorous *A. klaineana* individuals, each 60-70 cm in diameter and only 5-6 m apart was common, likely through root connections between them.

Fungal communities are not a driver of monodominance. Despite the high fungal diversity, the consistent but sparse presence of AM fungi and absence of EcM point to a limited role of mycorrhizal root-associated fungi in structuring dominance or facilitating regeneration. Instead, other beneficial endophytic fungi, including dark septate endophytes, may provide benefits to individual trees, for example by enhancing nutrient uptake or stress resilience. Moreover, the dominance of saprotrophs instead aligns with a system driven more by decomposer activity and nutrient recycling through litter dynamics.

Based on our results, only two of the eight interdependent mechanisms proposed in the introduction of this manuscript (Chapter 1) to explain tropical monodominance persist and could be relevant for *A. klaineana*: a higher tolerance to shade than expected (at least at the seedling stage) and a slow decomposition rate of litter and low nutrient availability. A slower rate of litter decomposition can alter nutrient cycling in the soil, creating conditions that benefit certain monodominant species. In *G. dewevrei* forests, for instance, litter decays two to three times more slowly than in nearby mixed forests, delaying nutrient availability and potentially reducing the survival of other tree species (Torti et al., 2001; Peh et al., 2012). About *A. klaineana*, litter decomposition was not directly assessed in this study. However, previous research has reported unusually thick litter layers in *A. klaineana* stands, with average monthly litter thickness varying from 7 to 10 cm (Midoko Iponga et al., 2020) and depths that can reach up to 25 cm (Leroy Deval, 1974). Decay rates are slow, with more than 25% of the litter mass still present after one year (Midoko Iponga et al., 2020).

Although leaf secondary metabolites were not quantified in this study, the high tannin content and molecular recalcitrance observed in fine roots point to strong chemical defenses likely extending throughout the plant. Moreover, *A. klaineana* resin exhibits proven antifungal and antibacterial properties largely due to monoterpenoids and phenolic compounds (Aghoutane et al., 2020; Ambindei et al., 2014; DeCarlo et al., 2019; Obame et al., 2014). The bark is also rich in polyphenols such as tannins and flavonoids (Engozogho Anris et al., 2020). Such traits, combined with the pronounced dry season characteristic of the species' range (Philippon et al., 2019), may jointly limit microbial activity and slow organic matter turnover.

In tropical forests, variation in litter chemistry, driven by factors such as micronutrients (Kaspari et al., 2008), lignin:phosphorus ratios (Wieder et al., 2009), and carbon quality (Hättenschwiler and Jørgensen, 2010) are known to exert strong control over litter decay rates (Waring, 2012). Yet, the relative influence on *A. klaineana* litter decomposition has never been tested, representing a key avenue for future research into the mechanisms underpinning its litter persistence. Such persistence may improve soil fertility, maintain moist microhabitats, and chemically suppress the regeneration of heterospecific plants, thereby indirectly promoting conspecific recruitment and competitive exclusion. In this context, *A. klaineana* may progressively improve its edaphic environment (Brunck et al., 1990) through the accumulation and gradual mineralization of its litter, with decomposer fungi contributing to fast nutrient renewal. This litter-driven process could represent one component of a broader positive feedback loop reinforcing monodominance (Peh et al., 2011a), acting jointly with other factors such as root grafting and the survival of *A. klaineana* seedlings under very shaded conditions.

3 Silvicultural implications

It must be acknowledged that earlier researchers already possessed substantial knowledge of *A. klaineana* biology. Several authors proposed innovative silvicultural techniques for this species (e.g., Brunck et al., 1990; Doucet, 2003; Doucet et al., 2004; Fuhr, 1999; Fuhr et al., 1998; Leroy Deval, 1976; Louppe et al., 2000). Our findings largely corroborate these earlier observations, demonstrating that the species shows tolerance to a broader range of light than previously expected, does not appear to depend on specific root-associated fungal communities to thrive, and exhibits functional root grafts. However, the overall functional impact of these grafts is still unquantified. Although litter and soil chemistry were not investigated in this study, our observations suggest that they may play an important role. Taken together, these results reinforce existing knowledge while providing additional insights to guide sustainable management of *A. klaineana*.

The following section addresses the main recommendations of earlier researchers, with which our results generally concur. The most recent is the "*Guide pratique des plantations d'arbres des forêts denses humides d'Afrique*" (Daïnou et al., 2021), which states[2] that:

- "*The species tolerates acidic or nutrient-poor soils*".
    - In fact, *A. klaineana* can adapt to a wide range of soil types (Brunck et al., 1990; Leroy Deval, 1973). This adaptability makes it a strong candidate for reforestation on degraded lands or for afforestation plans, as it gradually re-establishes the edaphic conditions most favorable to its growth (Leroy Deval, 1974) thanks to its own litter as well as that of associated species. Although this process is not yet fully understood, it is advisable to implement reduced-impact logging in established *A. klaineana* stands, in order to preserve the litter layer, which serves as the species' main nutrient reservoir, potentially supported by saprotrophic root-associated fungi.

- *"In plantations, a slight shading during the first five years promotes growth"*.
    - This recommendation is consistent with the results presented in the Chapter 3 of this dissertation, at least for the first year and a half in our case. While some authors suggest planting *A. klaineana* in full sunlight, our findings demonstrate that this is not optimal in terms of growth, health, or stem conformation. As described earlier, excessive light promotes bushy growth at the expense of vertical development and diameter, reduces stem straightness needed for quality timber (Brunck et al., 1990), and increases vulnerability to pests (Brunck et al., 1990; Leroy Deval, 1976b).

- "*Gaps in the forest canopy do not appear suitable for A. klaineana planting, and areas with high elephant abundance should be avoided*".
    - Although the impact of macrofauna was not assessed in this study, elephants are frequently reported as major drivers of damage to young *A. klaineana* plantations (Biraud and Catinot, 1960; Fuhr, 1999b; Grison, 1979; Maus, 2018). Rivière (1992) observed substantial declines in stem density in 3 to 10 year-old plantations due to elephant activity, with *A. klaineana* trampled, uprooted, or broken. He also noted a preferential impact on this species compared to others, possibly linked to its turpentine-like odor. Yet, they are not consumed, perhaps for the same reason. Moreover, as noted in Section 2.1 of this chapter, competition is intense in these gaps because the soil seed bank is rich in short-lived, fast-growing species that outcompete *A. klaineana* (Doucet et al., 2004). In areas dominated by *Marantaceae*, dense herbaceous cover can also further prevent *A. klaineana* establishment (White et al., 2000).

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[2] Author's translation from French to English

Instead, open habitats with disturbed soils such as roadsides, log yards, and fallows are preferable sites for planting.

- "*A possible thinning regime consists of reducing stand density from approximately 350 stems per hectare at 5 years to around 200 stems per hectare between 9 and 12 years, depending on growth rates*".
  - ➢ This topic has been one of the most debated in *A. klaineana* silviculture for decades. This recommended range offers a practical balance between bole quality and plantation costs (Leroy Deval, 1976a). Regarding the initial planting density, Leroy Deval (1974) argues that trees in the dominant layer grow uniformly, no matter the distances. In terms of timing, Fuhr et al. (2001) agree and argue that thinning should not be delayed beyond 10 years, since growth gains after this age do not compensate for basal area loss. Conversely, Onguene et al. (2002) suggest a single thinning at about 15 years, warning that earlier thinning could damage mycorrhizal networks. However, in our work (Chapter 4), root-associated fungal assemblages were inconsistent across trees, indicating that these communities are likely opportunistic and could recover after thinning without major impact. Leroy Deval (1973) proposes two thinnings between 8 and 15 years to maintain plantation health and promote good bole form while waiting for the first root grafts.

    Given the highlighted occurrence of root grafting processes and the potential litter-specific dynamics in *A. klaineana* stands, we advise avoiding any thinning operations, in line with Louppe et al. (2000). Thinning does not appear to be essential or even desirable, except for removing poorly formed trees with limited technological value from the dominant layer. Following such removal, co-dominant trees typically accelerate their growth to fill canopy gaps. Selective harvesting of mature trees serves as effective thinning. Low-impact techniques are essential to protect remaining trees and allow for three to four successive harvests every 15-20 years. Louppe et al. (2000) also suggest that root grafting may explain how some stands sustain this frequency of harvests in less than a century, which is much faster than other species that require about 50 years to regenerate. However, *A. klaineana* regenerates poorly under these regimes, leading to a gradual shift toward mixed-species forests after multiple harvests.

    If root grafting enables rapid successive harvests of mature trees already present in the stand stock, this would imply that before harvesting the dominant tree, hydraulic coupling through the grafts primarily occurs from the dominant tree to the codominant/suppressed one. After harvesting, the stump of the dominant tree would be sustained by the codominant/suppressed, now the new dominant, which in turn would supply photoassimilates to the living stump and benefits from the expansion of the root system. Since maintaining such an extensive root system is energetically costly and may slow the growth of standing trees, especially for a non-dominant tree (Bormann, 1966; Loehle and Jones, 1998; Quer et al., 2020), this hypothesis requires verification. In *Populus tremuloides* Michx. (Trembling aspen), interconnected trees can respond collectively to environmental stress. Defoliation of a dominant sucker induced compensatory photosynthesis, especially in suppressed individuals, likely through increased surface leaf area under dry conditions (Baret and DesRochers, 2011). However, if most trees in the connected system experience severe stress, the remaining trees may be unable to compensate, potentially leading to stand-wide decline (DesRochers and Lieffers, 2001).

To investigate this, we propose expanding on a preliminary experiment we conducted (Figure 34). To verify vascular tissue continuity between grafted trees, we used a dye translocation method inspired by O'Neal et al. (2015) and Graham (1960). We identified a pair of *A. klaineana* trees, a dominant and a nearby suppressed individual, assuming that closer proximity increases the likelihood of root grafting (Chapter 5). The suppressed tree was fallen and a tank was built on the stump with 0.15% fuchsin acid dye solution, sealing and covering it to prevent evaporation. After three weeks, fuchsin acid was detected in the stem of the remaining dominant tree, demonstrating vascular connection, at least for xylem sap. Repeating this experiment across multiple pairs, using either the suppressed or dominant tree as the donor stump, should help clarify the direction and extent of hydraulic coupling among these trees, and address a key question: does this process involve mutual exchange between individuals, including the translocation of phloem sap to the living stump/suppressed tree, or a one-way redistribution of carbon surplus from one dominant tree to subordinate individuals?

Figure 34 : Dye translocation experiment on a pair of *Aucoumea klaineana* trees showing (**A**) preparation of the donor stump, (**B**) filling with 0.15% fuchsin acid dye solution, and (**C**) a slice of the receptor tree after three weeks, demonstrating effective dye translocation.

Apart from the planting recommendations made by Daïnou et al. (2021), here are two other key points to consider for managing *A. klaineana* regeneration, either natural or artificial.

- As briefly discussed in Chapter 2, the future of *A. klaineana* is threatened by genetic erosion through preferential harvesting of the best-shaped trees. Decades of logging focused on straight, high-quality stems have likely diminished the genetic pool for desirable traits, with potential long-term impacts on production quality. Grison (1979) already warned of the need for genetic selection in *A. klaineana,* yet little progress has been made. This concern is amplified by the species' heliotropic and flexible stem habit, which naturally hinders straightness. Efforts in conserving genetic resources for specific traits such as fast growth and straightness could for instance involve collecting seeds. In this context, seed sourcing should prioritize seed orchards of selected trees, followed by natural forests rich in ideotypes such as outstanding individuals in protected areas, while plantations of unknown origin should only be used as a last resort (Daïnou et al., 2021). . Even though this is challenging given their winged seeds that disperse up to 150 m (Doucet, 2003), they can be used to set new plantations. This approach would help maintain desirable traits, especially since plantation timber can match the quality of natural forest wood (Medzegue et al., 2007).

- As a reminder, plant-insect-microbe interactions are another major topic to work on (Chapter 3). Black canker can cause extensive damage to stands within a few months, leading to bark loss, epicormic shoot production, and windthrow. Several authors (Leroy Deval, 1974; Louppe et al., 2000) have suggested that the disease could be transmitted through root grafts, as in many other tree species (Baric et al., 2008; Epstein, 1978; Meunier et al., 2019; O'Neal, 2014). We consider this unlikely for *A. klaineana*. In our excavations (Chapter 5), root system contamination was never observed. Moreover, Leroy Deval (1976b) reported no symptom development on *A. klaineana* trees inoculated with four different pathogenic fungi, including black canker. Evidence suggests that fungal infection occurs only via scar tissue created by psyllid attacks, particularly on resin secretions produced in response to these wounds. Conversely, it has been hypothesized that root grafts between different genotypes could expand the defensive chemical arsenal of the connected trees and enhance resistance to herbivores and pathogens (Erb et al., 2009; Lev-Yadun, 2011). This is also unlikely in *A. klaineana*, as grafts appear to occur mainly among individuals established simultaneously in dense seedling patches originating mostly from the same parent tree or relatives. Directly tracing fungal spores and mycelia, as done with stable isotopes in *Quercus* sp. and grasses (Kuntz and Riker, 1956; Robinson and Lucas, 1963), could clarify whether fungal pathogens move through root grafts or other belowground pathways in *A. klaineana*.

> Although the diseases result from a chain reaction involving different organisms, controlling psyllid infestations should be the top priority. This would not only reduce “witches’ broom” formation on terminal buds but also lower the incidence of secondary fungal attacks. Leroy Deval (1976b) and Brunck et al. (1990) recommended avoiding disturbed soils, such as fallows or old log yards. We disagree, as our results show that light availability does not affect infestation levels (Chapter 3). Avoiding these soils would also miss out on *A. klaineana*’s strong potential to reforest and regenerate degraded sites. As noted earlier, seedlings perform best on these soils with a reduced soil seed bank, minimizing interspecific competition. Therefore, it is essential to follow the recommendations from Chapter 3: focus on a better understanding of pest biology and implement integrated pest management strategies using a combination of chemical, physical, and biological controls that remain to be studied.

Considering the points discussed above, the relevance of the planting strategy based on Louppe et al. (2000) and Doucet et al. (2016) as proposed in Chapter 3 remains the most promising. Specifically, we recommend establishing monospecific blocks of 9-16 individuals spaced 1 m apart in areas with 9-62% RI at ground level, leaving a few spaced large trees as seed bearers. In contrast, we no longer advise thinning, in order to preserve optimal conditions for root grafting. Although the ecological benefits of root grafts remain unclear and their direct impact on tree productivity is uncertain, it is safer to maintain natural stand dynamics. Other potential positive drivers may outweigh any drawbacks of preserving root connections, including preserving optimal conditions for litter dynamics and its companion species, improved mechanical anchorage, and hypothetical kin-selection effects (see Sections 4.3 and 4.4 in Chapter 5).

These companion species cited by Leroy Deval (1974), such as *Pycnanthus angolensis* (Welw.) Exell (Ilomba), *Enantia* sp., *Tetrorchidium didymostemon* (Baill.) Pax & K.Hoffm. (Ossié), and *Xylopia* sp., can be used as block separators, partly to prevent pest proliferation. Their litter, derived from minerals drawn from deeper soil horizons, may enhance growth and nutrient cycling for *A. klaineana*. In colonizing *A. klaineana* forests of central Gabon, Doucet (2003) also reports additional associated species including *Chaetocarpus africanus* Pax., *Klainedoxa gabonensis* Pierre (African walnut), *Psychotria* sp., *Funtumia* sp., *Maprounea membranacea* Pax & K.Hoffm., *Barteria* sp., and *Xylopia aethiopica* (Dunal) A.Rich. (Guinea pepper), among others. However, the full range of companion species associated with *A. klaineana* still deserves more precise characterization. Although the details of this process require further study, implementing these guidelines in degraded or partially cleared forest areas offers a practical pathway to sustainable, high-quality timber production while maintaining ecosystem functions.

4 Conservation and policy perspectives

While the IUCN Red List provides a scientific assessment of extinction risk, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) listings are legally binding for signatory countries and focus on trade regulation. In practice, IUCN assessments often inform CITES proposals. At the CITES CoP20 held in Samarkand from November 24th to December 5th 2025, the EU has proposed adding *A. klaineana* to Appendix II. However, even though this has finally been postponed to CoP21 in 2028, this would require, if adopted, export permits proving legal, sustainable harvest, adding administrative burdens with potential economic impacts for Gabon and other producing countries.

As discussed in Chapter 2, *A. klaineana* has been listed as “Vulnerable” by the IUCN since 1998 under criterion A1cd (Supplementary Material 1), based on criteria that are no more applicable (White, 1998). The outdated classification, which considers reductions over three generations or ten years (whichever is longer), is difficult to apply to long-lived tree species and may not accurately reflect the species’ current abundance or regeneration capacity in managed forests (Doucet et al., 2021).

Numerous initiatives to maintain *A. klaineana*’s populations over the long-term are already in place such as sustainable forest management plans in logging concessions, promotion of reduced impact logging by certification schemes, log export ban, and thematic studies on *A. klaineana’*s population ecology into which this manuscript seeks to contribute with new insights and refined management recommendations. However, Appendix II listing would impose complex import/export permit requirements, potentially disrupting Gabon’s forest economy, where *A. klaineana* remains the primary commercial timber species. Given the limited diversification of commercial species (Doucet, 2024), such restrictions could inadvertently encourage conversion of forests to more profitable but biodiversity-harmful agribusiness, contrary to CITES conservation goals.

The main threat cited in the IUCN assessment report (White, 1998) is : “*It continues to be Gabon's most important commercial timber. Repeated felling has led to the deterioration of the gene pool in certain areas. There is some concern as to the long-term status of the species”*. While this aspect is not factored into the IUCN threat criteria, and then should not be considered, we fully agree on its importance, as discussed in the previous section of this manuscript.

5 Constraints and further research opportunities

Our results show that the belowground ecology of *A. klaineana* monodominant stands still contains important unknowns, but several key processes have been discussed ands could guide management strategies to sustain dominance and resilience. We found that dominance is not driven by root-associated fungi. Instead, it appears linked to a certain level of shade tolerance and probably to root grafting and litter-mediated facilitation. The functioning of root grafts is still poorly quantified, especially with regard to carbon and water transfers between connected trees. If dendrochronology is unsuitable for assessing growth in grafted stands, other methods should be developed using alternative physiological approaches. Root-associated fungi seem to form stochastic associations, but the role of other microorganisms, including bacteria and archaea as well as plant-facilitating endophytic fungi such as dark septate endophytes and relatives, remains to be explored. The composition and effects of *A. klaineana* root exudates are also underexplored. These aspects may hold key insights into the mechanisms of belowground interactions in monodominant stands.

5.1 *Root grafting dynamics*

A central silvicultural question in root graft research concerns their impact on tree growth dynamics. Studies from Canada and the USA focusing on conifer plantations report mixed outcomes: in some cases, grafts appear to enhance the growth of dominant trees (Bormann, 1966; Tarroux and DesRochers, 2011), while in others, growth slows down (Eis, 1972; Quer et al., 2022). These studies typically rely on dendrochronology to compare tree-ring widths before and after graft formation, which is unsuitable for *A. klaineana* due to its irregular wood anatomy (Chapter 5).

In Central Africa, *A. klaineana* is famous for its impressive root grafting behavior, notably featured in Hallé's documentary "*Une vie en forêt*" (Santantonio et al., 2019), with living stumps in Gabon, and observed since Catinot (1962) during thinning operations. In fact, root grafts are widespread, reported in over 150 woody species (Graham & Bormann, 1966; La Rue, 1952; Mudge et al., 2009), though often overlooked because functional grafts require living stumps or root excavation to detect. This number is likely an underestimate, and this phenomenon may be the norm rather than the exception. Trees of the same species possess similar cambial anatomy, meaning that they could theoretically all form intraspecific grafts, with frequency shaped by ecological opportunities.

Aucumea klaineana is therefore an ideal model for studying root grafting. Despite challenges related to dendrochronology, its dense monodominant stands and shallow root system allow for frequent root grafts, and relatively easy excavation, sometimes simply by removing the surface litter. Its clear seasonal variation between dry and rainy periods creates strong hydrological contrasts, highlighting potential effects on resource sharing. Its rapid growth may enable the observation of growth dynamics in permanent plots over relatively short periods compared to slower-growing species. Finally, its abundance and ability to grow along roadsides make monodominant stands easily accessible for field studies. Together, these features provide unique opportunities to investigate the ecological, physiological, and functional significance of root grafting in tropical forests.

5.1.1 Growth monitoring

The only alternative, though challenging due to the trees' longevity, would be to use permanent monitoring plots, as already implemented in monodominant stands within the logging concession hosting this study. Annual increments measured manually, or with automatic dendrometers, could provide long-term growth monitoring over several decades. Eventually, these stands could be excavated to identify and collect root grafts. The age of graft formation (i.e., the age of the first shared ring) could then be determined via radiocarbon dating analysis, as done for a small subset of stem samples in Chapter 5. However, this method is currently not feasible because the permanent monitoring plots in the concession have only been measured for around 24 years, and the radiocarbon dating uncertainty remains high for the youngest samples as it lacks precision for recent wood due to minimal year-to-year variation in atmospheric ^{14}C.

Based on mean diameters and ^{14}C-dated subsamples, the stands in our study appear to be under 25 years old. Root grafts in *A. klaineana* stands seem to form only after 5 to 7 years of age (Leroy Deval, 1973), and establishing functional graft networks is an energetically demanding process (Bormann, 1966; Loehle and Jones, 1998). It has been reported to take 5 to 10 years after root graft formation to the boreal stand growth dynamics to find a new balance (Tarroux et al., 2011), and an average of 14 years in another case (Quer et al., 2020). These observations suggest that the graft networks in our study sites may still be in the process of developing their functional potential and reach an equilibrium.

5.1.2 Sap flow

Investigating the consequences of root grafting on the growth of *A. klaineana* stands remains very complex. However, improving the understanding of these mechanisms is possible, but perhaps expensive, through quantification of sap flow transfers. Bader and Leuzinger (2019) applied such measurements to an adult *Agathis australis* (D.Don) Steud. (Kauri) and a grafted neighboring living stump. Using heat ratio method sensors, they detected inverted daily sap flow patterns in the stump compared with the intact tree. When the standing tree evapotranspired, it benefited from water from the stump's extended root system, whereas in the absence of transpiration, water and nutrients circulated in a closed loop within the stump.

Their results further show that living, leafless stumps can sustain vertical and horizontal sap flow and maintain stem water potential through osmotically driven movements, largely independent of transpiration. Such root pressure and hydraulic connectivity may similarly enable *A. klaineana* stumps to survive after tree harvesting or natural damage, by allowing continued water and nutrient transport, and metabolic activity. Quantifying sap flow and root pressure in *A. klaineana* would therefore provide valuable insights into the physiological mechanisms underlying stump survival and regeneration.

To quantify both magnitude and direction of sap flow between dominant and suppressed trees in monodominant *A. klaineana* stands would also provide valuable information on graft dynamics for this species. Based on discussions with tree physiologists Katty Steppe (Ghent University) and Jose Gutierrez Lopez (Swedish University of Agricultural Sciences), they both suggest using a similar heat-pulse approach (Burgess et al., 2001; Lopez et al., 2021; Vandegehuchte and Steppe, 2013). The very shallow root system of *A. klaineana* (Leroy Deval, 1974) should further allow direct sensor placement on roots without major degradation to the stand to identify preferential transfer pathways. Such measurements could (**i**) assess network effects on suppressed tree survival and stand resilience; (**ii**) monitor post-harvest dynamics, such as stump maintenance by neighboring trees and associated growth costs for donors; and (**iii**) characterize transfer directionality and asymmetry, including seasonal shifts or reversals following disturbance.

Additionally, considering the seasonal cycle in *A. klaineana* range (SW Gabon), root grafts may mediate dynamic allocation of water and nutrients among interconnected trees. During the main dry season, dominant trees could preferentially access scarce water while still redistributing just enough to suppressed neighbors or living stumps, helping maintain their metabolic activity and survival. Conversely, in the rainy season, excess water and nutrients may flow more freely through the graft network, supporting radial growth and recovery of stressed individuals. This could partly explain why in our experiment, grafted suppressed trees were thinner than dominant trees but still larger than non-grafted conspecifics as they would have sufficient access to water during part of the year. This seasonal redistribution may thus buffer environmental fluctuations, enhance stand cohesion, and contribute to the persistence of monodominant *A. klaineana* stands.

Stable isotope tracing could also help determine the direction of carbon or nutrient flow between grafted *A. klaineana* trees (Klein et al., 2016; Simard et al., 1997), but it cannot quantify the magnitude of transfer. Moreover, such fluxes may occur via other belowground pathways such as rhizosphere microbes, not solely through root grafts. Combining sap flow measurements with isotopic approaches would thus provide a more complete picture of belowground resource sharing.

5.1.3 Apical dominance

Apical dominance and hormonal signaling may also contribute to the structuring of *A. klaineana* monodominant stands. Auxin, produced in apical meristems, is known to regulate vertical growth and inhibit lateral development (Barbier et al., 2017; Kebrom, 2017), and may potentially be translocated between conspecifics through root grafts. According to that, grafted dominant *Abies balsamea* (L.) Mill. (Balsam fir) have been hypothesized to influence the growth of suppressed conspecific neighbors through hormonal signals, thereby contributing to stand structuration and self-thinning (Quer et al., 2022).

This could align with young *A. klaineana* trees that usually harbor a triangular and heliotropic crown architecture suggesting a marked apical control, whereas dominant individuals tend to develop more laterally expanded crowns. However, it contrasts with the studied stands, in which grafted suppressed trees exhibited larger diameters compared to non-grafted individuals, without significant differences in height, suggesting no clear inhibitory effect on vertical growth.

Alternatively, the absence of strong negative effects may reflect the likely recent formation of root grafts in the studied stands, as stand-level integration may require several years to stabilize. Moreover, despite being considered light-demanding, *A. klaineana* shows unexpected persistence in deep shade, at least at the seedling stage. This degree of shade tolerance could be extended to suppressed adult trees. This seems to differ from the hypothesis of *A. balsamea* hormonally driven self-thinning (Quer et al., 2022) and instead supports the idea that root grafting may contribute to the maintenance, rather than elimination, of suppressed trees in *A. klaineana* monodominant stands. However, direct evidence for hormonal transfer and its functional effects in grafting trees is still lacking.

5.2 *Other rhizosphere-mediated processes*

5.2.1 **Litter dynamics**

Litter is a key driver of nutrient cycling across forests at different developmental stages (Paudel et al., 2015). Among the belowground mechanisms proposed to explain *A. klaineana* monodominance (Peh et al., 2011, 2024; Chapter 1), only slow litter decomposition and low nutrient availability remain relevant. Despite the high diversity and dominance of saprotrophic root-associated fungi (Chapter 4), *A. klaineana* litter decomposes slowly, but released nutrient recycling occurs so rapidly that most elements are retained in a closed-loop between litter and roots, with negligible export to the soil or to other species (Leroy Deval, 1974). Litter layers in degraded stands average 7-10 cm, unusually thick compared to most African rainforests where decomposition is rapid, with less than half lost in 200 days (Midoko Iponga et al., 2020). Even accounting for potential overestimation from trap placement in Midoko Iponga et al.’s experiment, litter production in *A. klaineana* exceeds that of *Scorodophloeus zenkeri* Harms (Olombo) mixed forests and *G. dewevrei* monodominant stands in the DRC (Cassart et al., 2017). Unlike the evergreen *G. dewevrei*, *A. klaineana* is a semi-deciduous species shedding and replacing its leaves annually, potentially explaining why its litter is composed of more than 80% of leaves. In some cases, it contributes over 60% of total litter in *A. klaineana* monodominant stands (Loumeto, 2002). Litter is thicker and decomposes more slowly in recently disturbed sites than in older logged areas, highlighting the species’ ability to thrive in degraded environments (Midoko Iponga et al., 2020).

Our observations of fine root growth in the root-associated fungi experiment (Chapter 4) confirmed patterns described by Leroy Deval (1974): roots proliferate toward areas with thicker, partially decomposed litter. In artificial plantations, fine roots extend toward interband areas where debris accumulates, while in natural vegetation clusters, roots grow outward toward litter formed by mixed-species debris, including *A. klaineana*. This aligns with Basnet et al. (1993), who observed in *D. excelsa* (Burseraceae) that root grafting stabilizes litter and sediments, which are later colonized by dense mats of fine roots. Accordingly, in *A. klaineana* stands, fine roots can also emerge directly from buttresses bases without gradual tapering, forming dense mats attached to accumulated debris (pers. obs.; Leroy Deval, 1974). Collectively, these observations suggest that maintaining or enhancing litter in plantations could help replicate natural facilitation processes, improving soil fertility, and supporting root network development.

5.2.2 Extending litter biota research to other microorganisms

Exploring the microbial partners of *A. klaineana* litter dynamics is also essential. Originally, this study aimed to investigate both root grafting and nutrient exchanges through mycorrhizal networks. However, microscopic observations revealed that mycorrhizal structures were extremely rare across samples, regardless of origin or collection timing. This prompted a shift toward DNA sequencing to characterize the full fungal microbiome (Chapter 4), aiming to identify organisms that could both facilitate *A. klaineana* monodominance and potentially improve plantation growth through targeted inoculations. Given the scarcity of microbiota studies on *A. klaineana*, focusing on fungi was logical, as fungal communities are well documented in other tropical species, making comparisons possible between tree species. In contrast, plant bacteria in tropical forestry are a more recently studied group with high but still underexplored potential in forestry (Hijri and Bâ, 2018). As potential application, in the neotropics, Cely et al. (2016) demonstrated that inoculation of *Schizolobium parahyba* (Vell.) S.F.Blake (Serebo) with native AM fungi, *Rhizobium* strains, and non-native *Burkholderia* plant-growth promoting rhizobacteria increased wood yield by 20% compared to fertilizer alone under field conditions.

Since fungi appear to play a limited role in *A. klaineana* litter dynamics, exploring other microorganisms offers a promising avenue to better understand monodominance mechanisms. Interestingly, every monodominant species in Central Africa cited in Peh et al. (2011, 2024) belong to the Caesalpinioideae except for *A. klaineana*. They may share functional traits or belowground strategies promoting monodominance in nutrient-poor environments, which remains to be investigated.

5.2.3 Root exudates

Root exudates are chemical compounds released by fine roots including sugars, amino acids, organic acids, phenolic compounds, and enzymes, that can shape soil microbial communities, mobilize nutrients, and influence plant–plant or plant-microbe interactions (Freschet et al., 2021; Reichert et al., 2022). Studying root exudates in *A. klaineana* could offer an opportunity to understand how chemical inputs from fine roots contribute to litter decomposition and shape rhizosphere microbial communities. Linking exudate chemistry to zones of thick litter accumulation and dense fine-root networks, for instance around buttresses, may clarify how *A. klaineana* sustains nutrient capture, and complements structural mechanisms such as root grafting and litter retention.

Root exudates could also reinforce conspecific dominance through the production of allelochemicals as it is the case of the worldwide invasive species *Lantana camara*

L. (Common lantana) (Kato-Noguchi and Kurniadie, 2021). In monodominant stands, recruitment limitation may arise not only from direct competition for resources but also from the release of allelopathic substances (Peguero et al., 2012; Ridenour and Callaway, 2001). For instance, allelopathy is a well-known effect in *Eucalyptus* sp. monocultures (Fang et al., 2009) and has been shown to play a greater role than resource competition in such stands (Qin et al., 2018). Although their role has never been studied in *A. klaineana*, root exudates are likely highly active, as suggested by the distinct color and odor of fine roots (Chapter 2), the presence of inhibitory compounds that interfere with classical molecular protocols (Chapter 4), and the high diversity of secondary metabolites typical of Burseraceae (De Nicolai & Rodrigues, 2022; DeCarlo et al., 2019).

Furthermore, root exudates may influence the formation of root grafts in *A. klaineana* stands, either through hormonal signaling that would guide preferential connections between compatible trees or via enzymatic modification of cell walls, analogous to mechanisms observed in fungi to make root grafting easier. Such chemical cues may also help explain why some roots form grafts while others remain independent, even between the two same neighboring trees, possibly reflecting differences in local chemical compatibility, or microsite conditions. While chance or mechanical constraints may play a role, it remains striking to commonly observe a root merely “resting” on another or superficially connected to it, yet forming a functional graft with a root of similar diameter just a few centimeters away, even from the same tree. This raises the possibility that exudates play a direct role in connecting root systems, reinforcing nutrient sharing, and selectively promoting or inhibiting fusion between neighboring tree roots, thereby contributing to the structured integration within monodominant stands.

Conclusion

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Field team posing beside a fire truck used for root excavation in monodominant stands

This dissertation aims to clarify the ecological mechanisms underlying the functioning of *Aucoumea klaineana* populations, with the goal of informing silvicultural practices and supporting the sustainable management of this emblematic timber species of Central Africa. Despite its century-long history of silvicultural trials and its central role in the forestry economies of Gabon, the Republic of Congo, and Equatorial Guinea, major aspects regarding the ecological processes that sustain its dominance remain under investigation.

The findings of this research highlight several key insights. First, *A. klaineana* displays a broader tolerance to light than previously assumed, suggesting greater ecological plasticity in establishment than reported by earlier studies. Second, pest infestations, particularly by psyllids and black canker, emerge as a major constraint on regeneration, reducing seedling growth and form despite high survival across various light environments. Third, the species does not appear to depend on specific fungal symbionts to thrive, pointing instead to stochastic associations with root-associated fungi. Finally, the presence of functional root grafts suggests an overlooked mechanism of stand cohesion and demographic stability, although their physiological impact remains to be quantified.

Collectively, these results support the idea that monodominance in *A. klaineana* is not the product of a single process, but rather the outcome of multiple interacting mechanisms, particularly root grafting, and litter-mediated processes potentially including soil chemistry, root exudates, and complex microbial interactions that remain promising avenues for future study. Similarly, the wood anatomy of *A. klaineana* presents challenges for dendrochronological reconstruction, but alternative approaches, such as sap-flow measurements, offer promising pathways to assess growth dynamics and belowground connectivity. Root-associated fungi appear mostly as neutral stochastic assemblages, yet this pioneering work opens avenues to explore specific functional groups, such as dark septate endophytes, as potential contributors to stand dynamics. Overall, these observations highlight root grafting and litter dynamics as central mechanisms supporting stand cohesion and resilience, and help refine the hypotheses that future research should prioritize.

The frequent occurrence of root grafts has been documented morphologically, and while their direct contribution to water or carbon transfers remains under exploration, these networks suggest a capacity for integrated stand functioning. Similarly, the wood anatomy of *A. klaineana* presents challenges for dendrochronological approaches, but alternative approaches, such as sap-flow measurements, offer promising pathways to assess growth dynamics and belowground connectivity. The study of root-associated fungal communities, approached here for the first time, necessarily remained general. It revealed mostly stochastic assemblage processes with few or no consistently recurring taxa, suggesting that fungi are not decisive for *A. klaineana* monodominance. Nonetheless, this pioneering work opens the way for more focused research on the potential role specific fungal groups such as dark septate endophytes as potential contributors to stand dynamics, even though no species emerged clearly from our results. Taken together, these constraints mean that the present work rules out fungal dependence as a central factor, underscores root grafting and litter dynamics as promising mechanisms, and thereby narrows the field of hypotheses that future research should prioritize.

From a silvicultural perspective, the findings of this thesis refine rather than overturn earlier knowledge. First, regeneration efforts should be organized around the establishment of small, monospecific groups rather than isolated seedlings, as this configuration favors natural cohesion processes, and reduces the intensity of interspecific competition during early development. Second, although not investigated directly in this thesis, the conservation of the litter layer appears as a logical priority, given its likely role in seedling establishment and the long-term stability of stands. Third, thinning practices should be approached with caution, as maintaining natural stand structure preserves belowground connections that may contribute to overall stand integrity. Finally, seedling mortality linked to pest pressure remains a critical obstacle, highlighting the importance of integrating pest management into regeneration strategies. By linking ecological processes to stand-level practices, this study provides a mechanistic framework that point to a management approach building on natural facilitation processes to secure the persistence and productivity of *A. klaineana* stands.

Future research should prioritize quantitative and physiological methods to assess the functional role of grafts, as well as the influence of soil and microbial communities on population dynamics. Such advances will not only deepen ecological understanding but also generate actionable knowledge for sustainable forest management. In the current context, where international trade regulations such as potential CITES listing could profoundly reshape the economic landscape of Gabonese forestry, developing robust silvicultural strategies for *A. klaineana* is both an ecological and socioeconomic priority.

Ultimately, this thesis underscores that the resilience of *A. klaineana* monodominant forests rests on ecological processes that are only beginning to be understood. By bringing belowground dynamics to the forefront, it offers a framework for rethinking silvicultural interventions and for safeguarding a species that will likely remain a cornerstone of Central African forestry in the decades to come.

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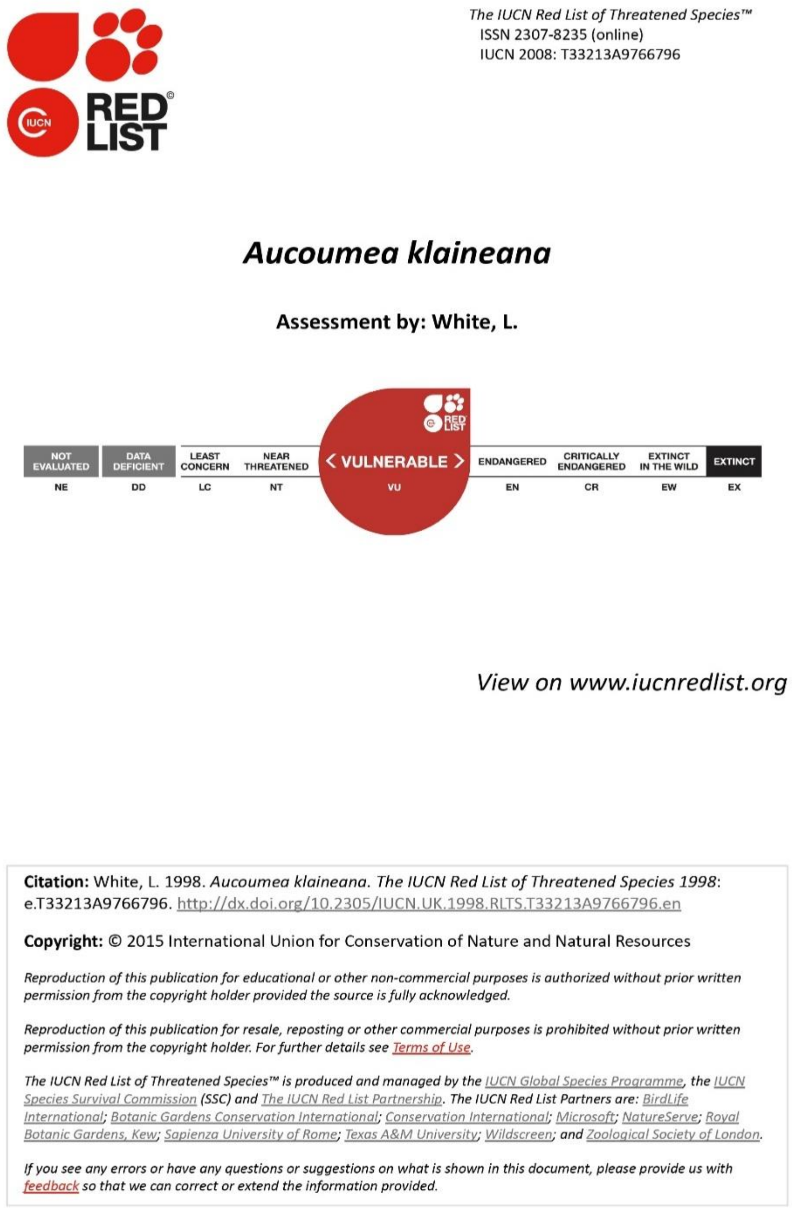
Supplementary Materials



The IUCN Red List of Threatened Species™
ISSN 2307-8235 (online)
IUCN 2008: T33213A9766796

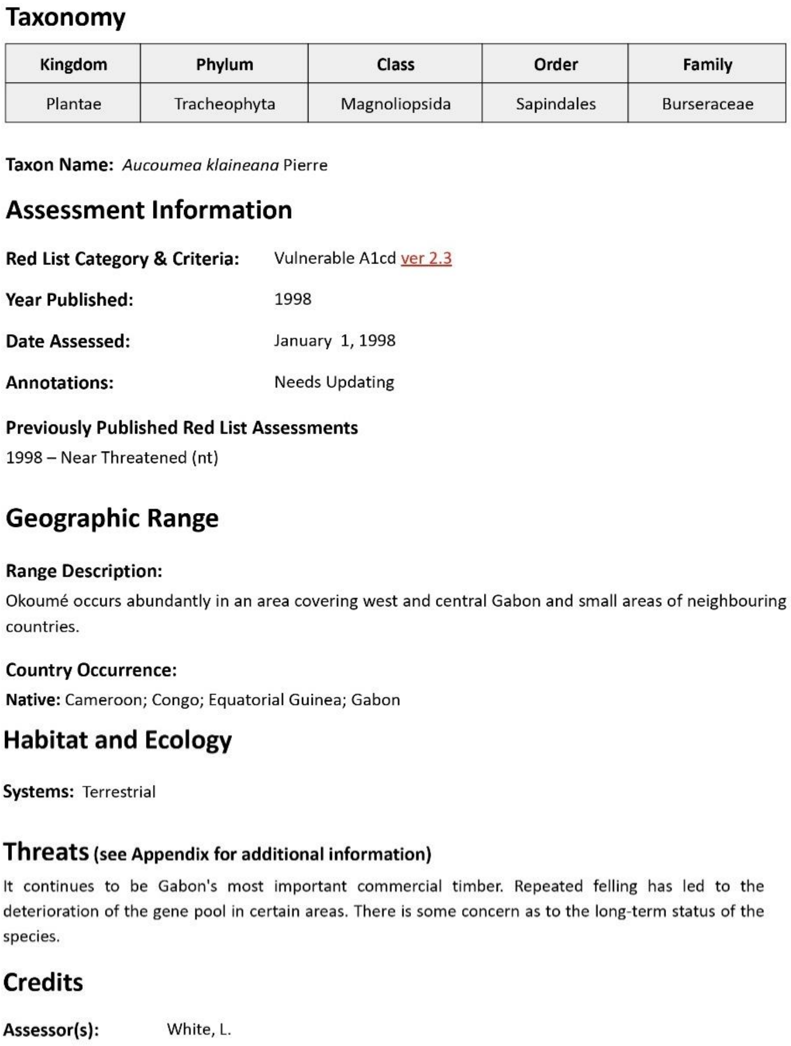
Aucoumea klaineana

Assessment by: White, L.

View on www.iucnredlist.org

Citation: White, L. 1998. *Aucoumea klaineana. The IUCN Red List of Threatened Species 1998*: e.T33213A9766796. http://dx.doi.org/10.2305/IUCN.UK.1998.RLTS.T33213A9766796.en

Supplementary Material 1 : Global assessment report: conservation status of Aucoumea klaineana (Okoumé), IUCN Red List.



Taxonomy

Kingdom	Phylum	Class	Order	Family
Plantae	Tracheophyta	Magnoliopsida	Sapindales	Burseraceae

Taxon Name: *Aucoumea klaineana* Pierre

Assessment Information

Red List Category & Criteria: Vulnerable A1cd ver 2.3

Year Published: 1998

Date Assessed: January 1, 1998

Annotations: Needs Updating

Previously Published Red List Assessments

1998 – Near Threatened (nt)

Geographic Range

Range Description:

Okoumé occurs abundantly in an area covering west and central Gabon and small areas of neighbouring countries.

Country Occurrence:

Native: Cameroon; Congo; Equatorial Guinea; Gabon

Habitat and Ecology

Systems: Terrestrial

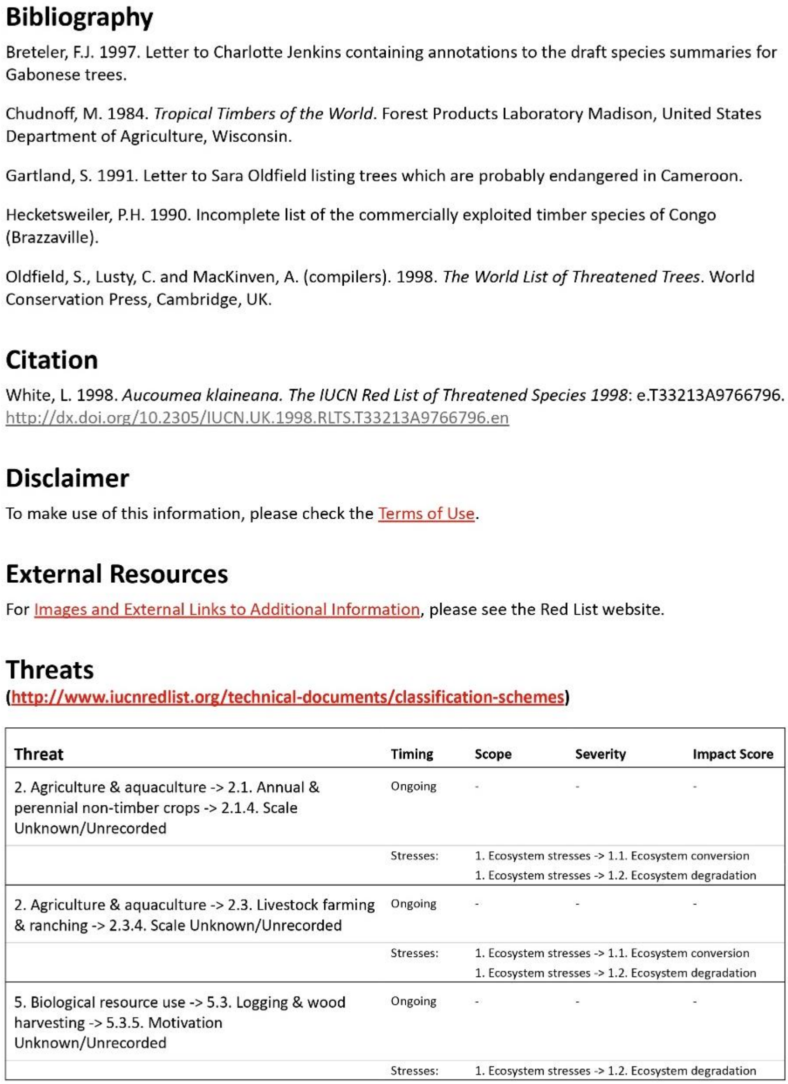
Threats (see Appendix for additional information)

It continues to be Gabon's most important commercial timber. Repeated felling has led to the deterioration of the gene pool in certain areas. There is some concern as to the long-term status of the species.

Credits

Assessor(s): White, L.

Supplementary Material 1 (continued)



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Citation

White, L. 1998. *Aucoumea klaineana. The IUCN Red List of Threatened Species 1998*: e.T33213A9766796. http://dx.doi.org/10.2305/IUCN.UK.1998.RLTS.T33213A9766796.en

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External Resources

For Images and External Links to Additional Information, please see the Red List website.

Threats

(http://www.iucnredlist.org/technical-documents/classification-schemes)

Threat	Timing	Scope	Severity	Impact Score
2. Agriculture & aquaculture -> 2.1. Annual & perennial non-timber crops -> 2.1.4. Scale Unknown/Unrecorded	Ongoing	-	-	-
	Stresses:	1. Ecosystem stresses -> 1.1. Ecosystem conversion 1. Ecosystem stresses -> 1.2. Ecosystem degradation		
2. Agriculture & aquaculture -> 2.3. Livestock farming & ranching -> 2.3.4. Scale Unknown/Unrecorded	Ongoing	-	-	-
	Stresses:	1. Ecosystem stresses -> 1.1. Ecosystem conversion 1. Ecosystem stresses -> 1.2. Ecosystem degradation		
5. Biological resource use -> 5.3. Logging & wood harvesting -> 5.3.5. Motivation Unknown/Unrecorded	Ongoing	-	-	-
	Stresses:	1. Ecosystem stresses -> 1.2. Ecosystem degradation		

Supplementary Material 1 (continued)

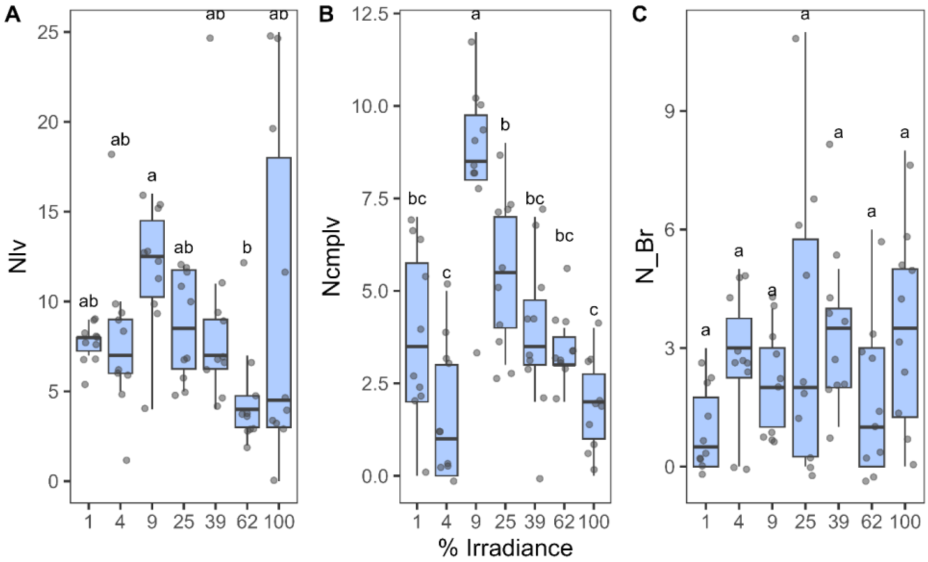
The IUCN Red List Partnership

The IUCN Red List of Threatened Species™ is produced and managed by the IUCN Global Species Programme, the IUCN Species Survival Commission (SSC) and The IUCN Red List Partnership. The IUCN Red List Partners are: BirdLife International; Botanic Gardens Conservation International; Conservation International; Microsoft; NatureServe; Royal Botanic Gardens, Kew; Sapienza University of Rome; Texas A&M University; Wildscreen; and Zoological Society of London.

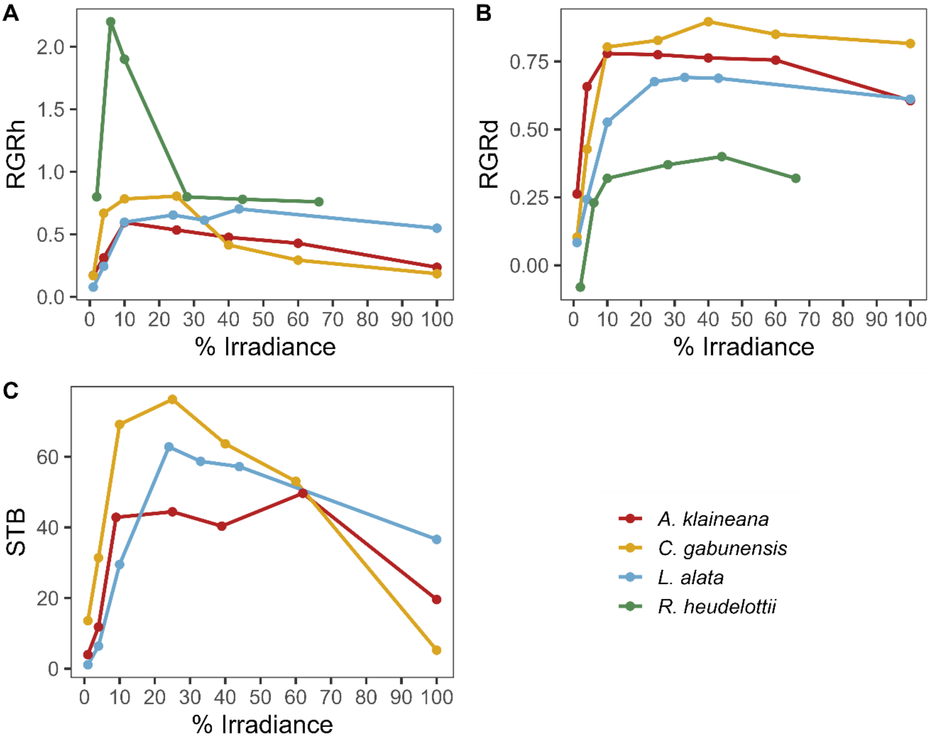
Supplementary Material 1 (continued)

% Irradiance	Relative Humidity (%)			Temperature (°C)			Vapour Pressure Deficit (kPa)		
	Min	**Max**	**Mean**	**Min**	**Max**	**Mean**	**Min**	**Max**	**Mean**
1	43.0	98.6	79.5	19.2	32.0	24.6	0.04	2.04	0.68
4	46.9	98.3	81.1	19.1	31.3	24.1	0.04	1.86	0.60
9	44.6	99.7	81.9	18.9	31.2	24.1	0.01	2.02	0.59
25	47.9	100.0	80.5	18.7	33.1	24.5	0.00	2.31	0.66
39	43.4	100.0	80.6	18.6	33.9	24.6	0.00	2.56	0.69
62	41.6	100.0	80.3	18.5	33.9	24.7	0.00	2.57	0.71
100	35.7	100.0	78.6	17.7	40.7	25.3	0.00	4.94	0.89

Supplementary Material 2 : Temperature, Hygrometry and Vapour Pressure Deficit collect with Ebro EBI 20-TH sensors (Xylem Analytics, Ingolstadt, Germany) during the first week of experiment.



Supplementary Material 3 : Morphological functional traits of *A. klaineana* seedlings across relative irradiance levels ranging from 1% to 100%. Nlv : Number of leaves (**A**) ; Ncmplv : Number of compounds leaves (**B**) ; N_Br Number of branches (**C**). Letters results from ANOVA and Tukey groups, a common letter means no significant differences between groups.



Supplementary Material 4 : Comparison of the performance of four considered pioneer species in terms of Relative growth rates (**A**) in height (RGRh in cm.cm^{-1}); (**B**) in diameter (RGRd in mm.mm^{-1}), and (**C**) final seedling total biomass (STB in g) in response to varying light conditions ranging from 1% to 100%. Data for *C. gabunensis* were retrieved from Ndonda Makemba et al. (2023), those for *L. alata* from Biwolé et al. (2015) and those for *R. heudelottii* from Agyeman et al. (1999).

Step	CTAB Method (Doyle & Doyle, 1987)	DNeasy® Plant Mini Kit Quick-Start Protocol (Qiagen, Hilden, Germany)	Modified Qiagen Protocol
Sample Preparation:	Grind the plant tissue in liquid nitrogen using a mortar and pestle to create a fine powder.	idem	idem
Sample Lysis:	Preheat CTAB Buffer at 65 °C.		
	Prepare CTAB Buffer and add 2-mercaptoethanol to a final concentration of 2%.		
	Add the powdered plant tissue (15-20 mg) to a 2 ml microcentrifuge tube.	idem	Add the powdered plant tissue (15-20 mg), and **15-20 mg of activated charcoal** (AC) to a 2 ml microcentrifuge tube.
	Add an appropriate volume of CTAB Buffer (about 2-3 times the volume of the tissue).	Add 400 µl Buffer AP1 and 4 µl RNase A.	idem
	Mix well and incubate at 65°C for 60 minutes, shaking occasionally.	Vortex and incubate for 10 min at 65°C. Invert the tube 2–3 times during incubation.	Vortex and incubate for **30 min** at 65°C. Invert the tube 2–3 times during incubation.
		Add 130 µl Buffer P3. Mix and incubate for 5 min on ice.	Add 130 µl Buffer P3. Mix and incubate for **15 min** on ice.
	Centrifuge the lysate for 5 min at 14,000 rpm.	Centrifuge the lysate for 5 min at 14,000 rpm.	idem
Extraction:	Transfer the upper aqueous phase to a new tube. Add an equal volume of chloroform:isoamyl alcohol (24:1) to the tube.	Pipet the lysate into a QIAshredder spin column placed in a 2 ml collection tube.	idem
	Mix thoroughly for 5 minutes.		

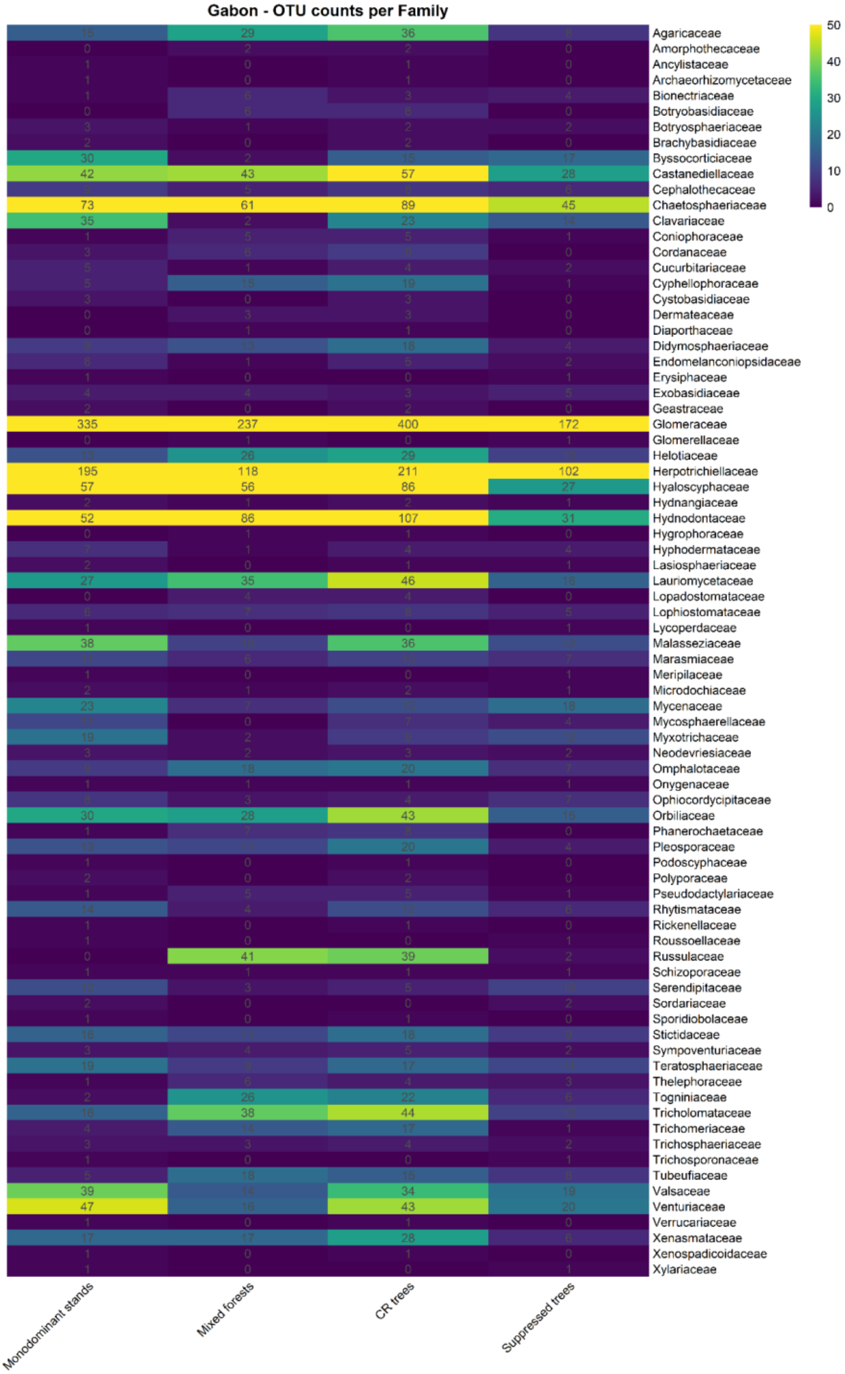
	Centrifuge at 14,000 rpm for 10 minutes.	Centrifuge for 2 min at 14,000 rpm.	idem
Precipitation:	Transfer the upper aqueous phase to a new tube.	Transfer the flow-through into a new tube without disturbing the pellet if present.	idem
	Add 0.7 volumes of isopropanol to the aqueous phase.	Add 1.5 volumes of Buffer AW1, and mix by pipetting.	idem
	Mix well and incubate at -20°C for at least 1 hour or overnight.		
	Centrifuge at 14,000 rpm for 30 minutes at 4°C.		
DNA Pellet Collection:	Carefully decant the supernatant without disturbing the pellet.	Transfer 650 µl of the mixture into a DNeasy Mini spin column placed in a 2 ml collection tube.	idem
	Wash the pellet with ethanol 80%	Centrifuge for 1 min at 14,000 rpm.	idem
	Centrifuge at 8,000 rpm for 10 minutes at 4°C.	Discard the flowthrough. Repeat this step with the remaining sample.	idem
		Place the spin column into a new 2 ml collection tube. Add 500 µl Buffer AW2, and centrifuge for 1 min at 14,000 rpm. Discard the flow-through.	idem
		Add another 500 µl Buffer AW2. Centrifuge for 2 min at 14,000 rpm.	idem
		Transfer the spin column to a new 1.5 ml or 2 ml microcentrifuge tube	idem

DNA Resuspension:	Air-dry the pellet briefly and then resuspend it in TE Buffer or distilled water.	Add 100 µl Buffer AE for elution. Incubate for 5 min at room temperature (15–25°C). Centrifuge for 1 min at 14,000 rpm. Repeat.	**Pre-heat the AE buffer to 65°C, then** add 100 µl Buffer AE for elution. Incubate for **15 min** at room temperature (15–25°C). Centrifuge for 1 min at 14,000 rpm.
Optional RNase Treatment:	Add RNase to the resuspended DNA and incubate at 37°C for 30 minutes if RNA contamination is a concern.		

Supplementary Material 5 : Comparison of Tested DNA Extraction Protocols. The Modified Qiagen Protocol (Column 3) is a modified version of the DNeasy® Plant Mini Kit Quick-Start Protocol (Qiagen, Hilden, Germany) (Column 2) with the addition of activated charcoal (AC). Each protocol may exhibit slight variations from the original papers.

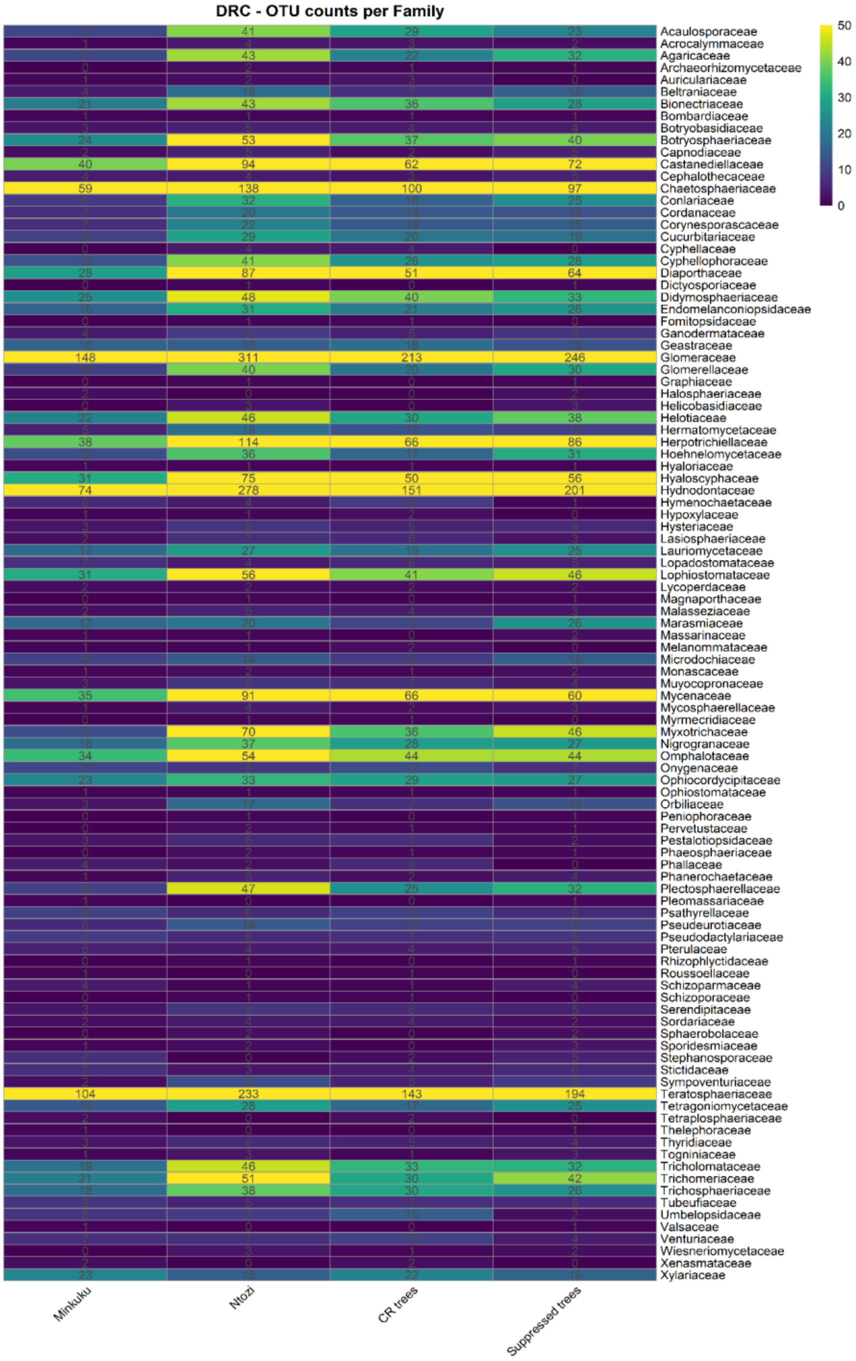
Reagent	Vendor/Source	Concentration (w/v)	pH	Link
Cetyltrimethylammonium bromide (CTAB)	PanReac AppliChem - ITW Reagents (Monza,Italy)	2%	8	Link
Polyvinylpyrrolidone (PVP) (K30)	Sigma-aldrich, Merck KGaA (Darmstadt, Germany)	-	-	Link
Polyvinylpolypyrrolidone (PVPP)	Supelco, Sigma-aldrich, Merck KGaA (Darmstadt, Germany)	-	-	Link
Sodium Dodecyl Sulfate (SDS)	VWR (Radnor, Pennsylvania, USA)	2%	8	Link
Activated charcoal (AC)	Supelco, Sigma-aldrich, Merck KGaA (Darmstadt, Germany)	-	-	Link
Bovine Serum Albumin (BSA)	Sigma-aldrich, Merck KGaA (Darmstadt, Germany)	-	5-5.6	Link
RT-PCR grade water	Thermo Fisher Scientific (Waltham, MA, USA)	-	6-8	Link
Qiagen DNeasy® Plant Mini Kit Cat. No. 69106 (Hilden, Germany)				
Buffer AE		-	9	Link
Acetic acid (Buffer P3)		10-20% w/w	5.5	
Sodium Dodecyl Sulphate (Buffer AP1)		1-10% w/w	5.5	
Guanidine Hydrochloride (Buffer AW1)		50-70% w/w	4.5	
Buffer AW2		-	7.5-9	
Ribonuclease (Rnase A)		1-10% w/w	-	

Supplementary Material 6 : Detailed information about each reagent used in the experiment. It includes the brand/source, concentration (when available/applicable), pH (when available), and a link to the product for further reference



	Monodominant stands	Mixed forests	CR trees	Suppressed trees
Agaricaceae	15	29	36	8
Amorphothecaceae	0	2	2	0
Ancylistaceae	1	0	1	0
Archaeorhizomycetaceae	1	0	1	0
Bionectriaceae	1	6	3	4
Botryobasidiaceae	0	6	6	0
Botryosphaeriaceae	3	1	2	2
Brachybasidiaceae	2	0	2	0
Byssocorticiaceae	30	2	15	17
Castanediellaceae	42	43	57	28
Cephalothecaceae	9	5	8	6
Chaetosphaeriaceae	73	61	89	45
Clavariaceae	35	2	23	14
Coniophoraceae	1	5	5	1
Cordanaceae	3	6	9	0
Cucurbitariaceae	5	1	4	2
Cyphellophoraceae	5	15	19	1
Cystobasidiaceae	3	0	3	0
Dermateaceae	0	3	3	0
Diaporthaceae	0	1	1	0
Didymosphaeriaceae	9	13	18	4
Endomelanconiopsidaceae	6	1	5	2
Erysiphaceae	1	0	0	1
Exobasidiaceae	4	4	3	5
Geastraceae	2	0	2	0
Glomeraceae	335	237	400	172
Glomerellaceae	0	1	0	1
Helotiaceae	13	26	29	10
Herpotrichiellaceae	195	118	211	102
Hyaloscyphaceae	57	56	86	27
Hydnangiaceae	2	1	2	1
Hydnodontaceae	52	86	107	31
Hygrophoraceae	0	1	1	0
Hyphodermataceae	7	1	4	4
Lasiosphaeriaceae	2	0	1	1
Lauriomycetaceae	27	35	46	16
Lopadostomataceae	0	4	4	0
Lophiostomataceae	6	7	8	5
Lycoperdaceae	1	0	0	1
Malasseziaceae	38	10	36	12
Marasmiaceae	11	6	10	7
Meripilaceae	1	0	0	1
Microdochiaceae	2	1	2	1
Mycenaceae	23	7	12	18
Mycosphaerellaceae	11	0	7	4
Myxotrichaceae	19	2	9	12
Neodevriesiaceae	3	2	3	2
Omphalotaceae	9	18	20	7
Onygenaceae	1	1	1	1
Ophiocordycipitaceae	8	3	4	7
Orbiliaceae	30	28	43	15
Phanerochaetaceae	1	7	8	0
Pleosporaceae	13	11	20	4
Podoscyphaceae	1	0	1	0
Polyporaceae	2	0	2	0
Pseudodactylariaceae	1	5	5	1
Rhytismataceae	14	4	12	6
Rickenellaceae	1	0	1	0
Roussoellaceae	1	0	0	1
Russulaceae	0	41	39	2
Schizoporaceae	1	1	1	1
Serendipitaceae	12	3	5	10
Sordariaceae	2	0	0	2
Sporidiobolaceae	1	0	1	0
Stictidaceae	16	11	18	9
Sympoventuriaceae	3	4	5	2
Teratosphaeriaceae	19	9	17	11
Thelephoraceae	1	6	4	3
Togniniaceae	2	26	22	6
Tricholomataceae	16	38	44	10
Trichomeriaceae	4	14	17	1
Trichosphaeriaceae	3	3	4	2
Trichosporonaceae	1	0	0	1
Tubeufiaceae	5	18	15	8
Valsaceae	39	14	34	19
Venturiaceae	47	16	43	20
Verrucariaceae	1	0	1	0
Xenasmataceae	17	17	28	6
Xenospadicoidaceae	1	0	1	0
Xylariaceae	1	0	0	1

Supplementary Material 7: Heatmap of OTU counts per fungal family in Gabon (ITS2), shown across the studied factors. Color intensity represents the amount of different OTUs for each family.

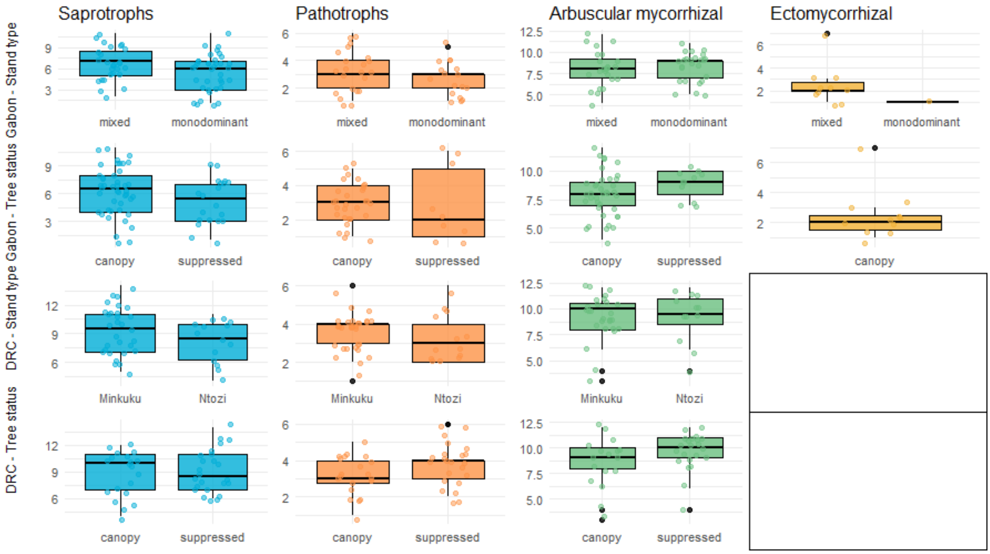


Supplementary Material 8 : Heatmap of OTU counts per fungal family in DRC (ITS2), shown across the studied factors. Color intensity represents the amount of different OTUs for each family.

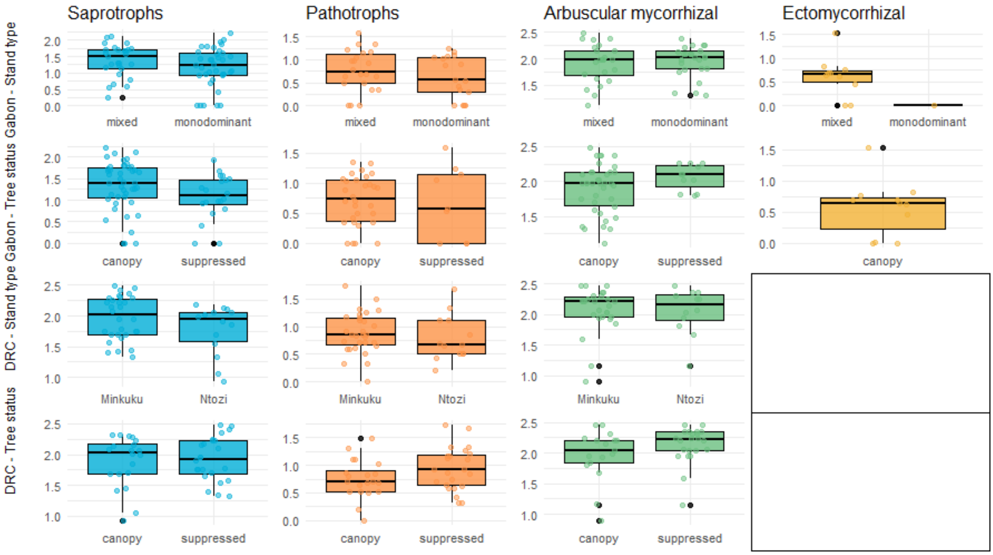
Alpha diversity

GABON		OTU richness	Pielou index	Shannon index
Stand type	**All (ITS2)**	0.106	0.238	0.369
	Saprotrophs (ITS2)	0.113	0.648	0.159
	Pathotrophs (ITS2)	0.169	0.833	0.348
	Symbiotrophs (ITS2)	0.139	0.087	0.107
	AM fungi (18S)	0.598	0.968	0.681
Tree social status	**All (ITS2)**	0.829	0.938	0.990
	Saprotrophs (ITS2)	0.100	0.061	**0.043* (CR)**
	Pathotrophs (ITS2)	0.695	0.412	0.947
	Symbiotrophs (ITS2)	0.625	0.095	0.437
	AM fungi (18S)	0.123	0.296	0.139
DRC		**OTU richness**	**Pielou index**	**Shannon index**
Stand type	**All (ITS2)**	0.133	**0.043* (Minkuku)**	0.101
	Saprotrophs (ITS2)	0.137	0.060	0.115
	Pathotrophs (ITS2)	0.184	0.903	0.266
	Symbiotrophs (ITS2)	0.852	0.817	0.905
	AM fungi (18S)	0.975	0.855	0.927
Tree social status	**All (ITS2)**	0.536	0.260	0.487
	Saprotrophs (ITS2)	0.877	0.517	0.869
	Pathotrophs (ITS2)	0.077	0.752	0.119
	Symbiotrophs (ITS2)	0.961	0.724	0.990
	AM fungi (18S)	0.155	0.238	0.108

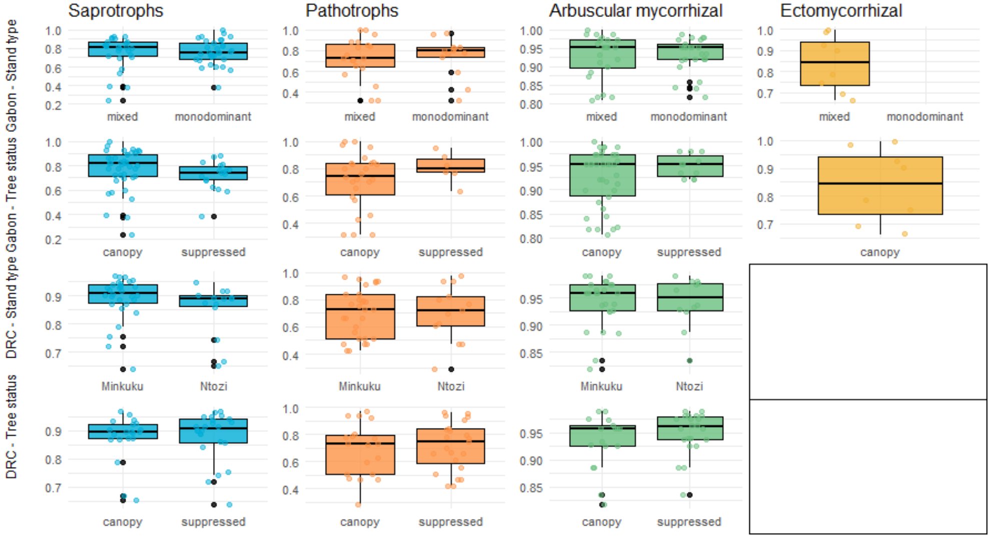
Supplementary Material 9 : p-values from Kruskal-Wallis non-parametric tests applied to determine significant differences across Alpha diversity assessed using OTU richness, Shannon diversity index, and Pielou's evenness index for each trophic guild



Supplementary Material 10 : Boxplots of **OTU richness** for each trophic guild in Gabon and DRC, comparing canopy-reaching trees (canopy) and suppressed trees (suppressed) across different forest types: old-growth mixed forests (mixed), monodominant stands (monodominant), and plantations (Minkuku and Ntozi) in the DRC. Every trophic guilds are tested according to the ITS2 rDNA region except for Arbuscular mycorrhizal that are tested through the 18S rDNA.



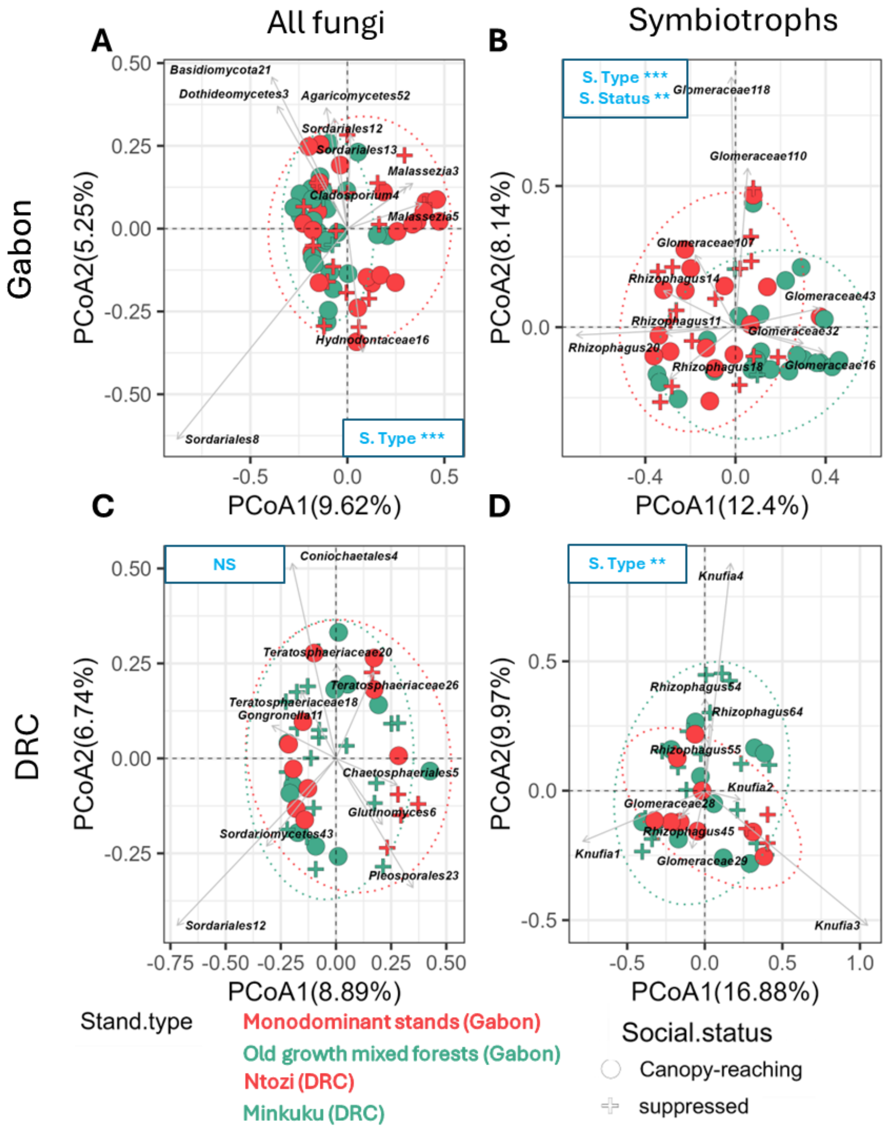
Supplementary Material 11 : Boxplots of **Shannon diversity index** for each trophic guild in Gabon and DRC, comparing canopy-reaching trees (canopy) and suppressed trees (suppressed) across different forest types: old-growth mixed forests (mixed), monodominant stands (monodominant), and plantations (Minkuku and Ntozi) in the DRC. Every trophic guilds are tested according to the ITS2 rDNA region except for Arbuscular mycorrhizal that are tested through the 18S rDNA.



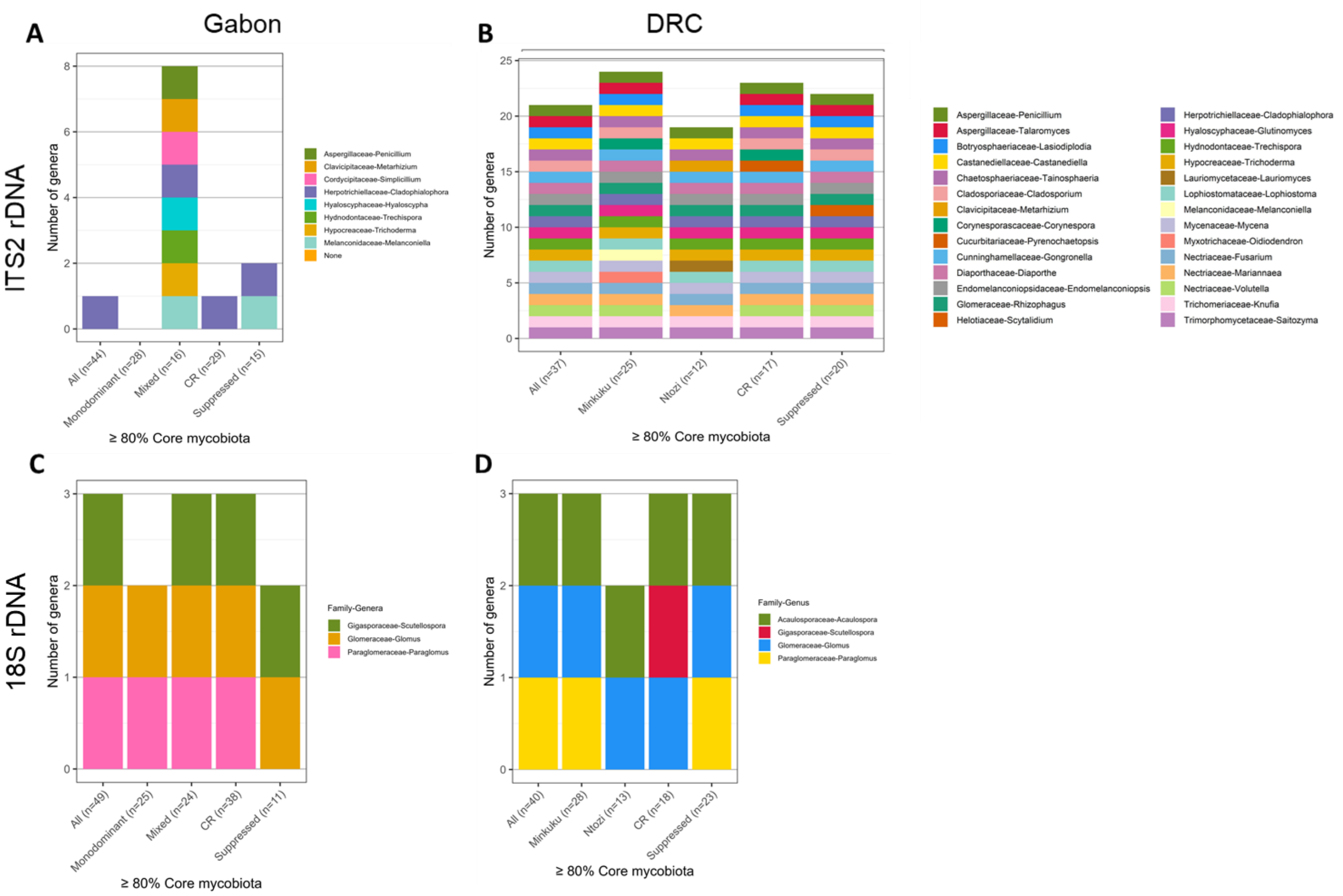
Supplementary Material 12 : Boxplots of **Pielou evenness index** for each trophic guild in Gabon and DRC, comparing canopy-reaching trees (canopy) and suppressed trees (suppressed) across different forest types: old-growth mixed forests (mixed), monodominant stands (monodominant), and plantations (Minkuku and Ntozi) in the DRC. Every trophic guilds are tested according to the ITS2 rDNA region except for Arbuscular mycorrhizal that are tested through the 18S rDNA.

		Beta diversity	
GABON		**Bray-Curtis**	**Jaccard**
Stand type	**All** (ITS2)	**<0.001*****	**<0.001*****
	Saprotrophs (ITS2)	**<0.001*****	**<0.001*****
	Pathotrophs (ITS2)	**<0.001*****	**<0.001*****
	Symbiotrophs (ITS2)	**<0.001*****	**<0.001*****
	AM fungi (18S)	**<0.001*****	**<0.001*****
Tree social status	**All** (ITS2)	0.426	0.382
	Saprotrophs (ITS2)	**0.003****	**0.001****
	Pathotrophs (ITS2)	0.192	0.226
	Symbiotrophs (ITS2)	**0.008****	**0.008****
	AM fungi (18S)	**0.004****	**0.004****
DRC		**Bray-Curtis**	**Jaccard**
Stand type	**All** (ITS2)	0.475	0.454
	Saprotrophs (ITS2)	**0.043***	**0.033***
	Pathotrophs (ITS2)	**0.005****	**0.043***
	Symbiotrophs (ITS2)	**0.021***	**0.031***
	AM fungi (18S)	**0.002****	**0.003****
Tree social status	**All** (ITS2)	0.097	0.101
	Saprotrophs (ITS2)	0.467	0.475
	Pathotrophs (ITS2)	0.737	0.538
	Symbiotrophs (ITS2)	0.668	0.793
	AM fungi (18S)	0.629	0.618

Supplementary Material 13 : Results from permutational multivariate analyses of variance (PERMANOVA) with 9,999 permutations performed and Bray-Curtis and Jaccard distance matrices. P-values were categorized as follows: $p \leq 0.05$ (significant), $p \leq 0.01$ (highly significant), and $p \leq 0.001$ (very highly significant).



Supplementary Material 14 : PCoA plots based on Bray-Curtis dissimilarity matrices on OTUs obtained from Gabon (**A,B**) and the DRC (**C,D**) assigned to every fungal OTUs (**A,C**), and symbiotrophic (**B,C**) trophic guild obtained from te ITS2 rDNA region. Significant differences between modalities were assessed using permutational multivariate analyses of variance (PERMANOVA) with 9,999 permutations. Blue labels indicate significant differences, with p-values categorized as follows: p ≤ 0.05 (significant), p ≤ 0.01 (highly significant), and p ≤ 0.001 (very highly significant). The variables "S.type" stands for stand type and "S.status" for social status. The 10 taxa that have the highest contributions to the ordinations are labelled in each plot.



Supplementary Material 15 : Stacked barplots showing fungal community composition at the genus level common to ≥80% of the samples across studied factors in Gabon (**A, C**) and the DRC (**B, D**), based on ITS2 rDNA (**A, B**) and 18S rDNA (**C, D**).

Species	**Family**	**Mycorrhizal status**	**References**
Anthonotha fragrans	Fabaceae	EcM + AM	Bakkar & Janos (1996) ; Diédhou et al., 2010 ; Onguene & Kuyper, 2001
Anthonotha pynaertii	Fabaceae	NA	
Blighia welwitschii	Sapindaceae	AM	Onguene & Kuyper, 2001
Centroplacus glaucinus	Centroplacaceae	NA	
Coelocaryon preussii	Myristicaceae	AM	Bechem et al., 2014
Coula edulis	Olacaceae	AM	Onguene & Kuyper, 2001
Dacryodes letestui	Burseraceae	NA	
Dialium bipindense	Fabaceae	NA	
Dialium guineense	Fabaceae	AM	Bakkar & Janos (1996) ; Onguene & Kuyper, 2001
Dialium pachyphyllum	Fabaceae	AM	Bechem et al., 2014
Dichostemma glaucescens	Apocynaceae	NA	
Diospyros gabunensis	Ebenaceae	NA	
Diospyros hoyleana	Ebenaceae	NA	
Diospyros iturensis	Ebenaceae	NA	
Diospyros piscatoria	Ebenaceae	NA	
Diospyros zenkeri	Ebenaceae	NA	
Drypetes spinosodentata	Putrangivaceae	NA	
Drypetes spp.	Putrangivaceae	AM	Bechem et al., 2014
Eriocoelum macrocarpum	Euphorbiaceae	NA	
Garcinia ovalifolia	Clusiaceae	NA	
Garcinia punctata	Clusiaceae	NA	
Gilletiodendron pierreanum	Olacaceae	NA	
Greenwayodendron suaveolens	Olacaceae	NA	
Heisteria parvifolia	Olacaceae	NA	
Hymenostegia pellegrinii	Caesalpiniaceae	NA	
Julbernardia pellegriniana	Caesalpiniaceae	ECM	Bâ et al., 2012
Klaineanthus gaboniae	Caesalpiniaceae	NA	
Lasiodiscus marmoratus	Caesalpiniaceae	NA	
Neochevalierodendron stephanii	Olacaceae	NA	
Oncoba mannii	Salvadoraceae	NA	
Ongokea gore	Olacaceae	AM	Onguene & Kuyper, 2001
Pausinystalia johimbe	Apocynaceae	AM	Onguene & Kuyper, 2001
Pentaclethra eetveldeana	Fabaceae	NA	
Petersianthus macrocarpus	Olacaceae	NA	
Plagiostyles africana	Olacaceae	NA	

Pseudospondias microcarpa	Anacardiaceae	AM	Bechem et al., 2018 ; Olanipon et al., 2024
Pterocarpus soyauxii	Fabaceae	AM	Onguene et al., 2019 ; Onguene & Kuyper, 2001
Rhabdophyllum calophyllum	Apocynaceae	NA	
Santiria trimera	Burseraceae	AM	Davison et al., 2015 cited by Gorzelak et al., 2017
Scorodophloeus zenkeri	Olacaceae	AM	Onguene & Kuyper, 2001
Scyphocephalium mannii	Olacaceae	NA	
Staudtia kamerunensis	Myristicaceae	NA	
Trichoscypha oddonii	Annonaceae	NA	
Vangueriella soyauxii	Rubiaceae	NA	

Supplementary Material 16 : Tree species recorded within a 10 m radius of sampled A. klaineana individuals in old-growth mixed forest; mycorrhizal status from the literature (ECM = ectomycorrhizal; AM = arbuscular mycorrhizal; NA = no data)

Bâ, A.M., Duponnois, R., Moyersoen, B., Diédhiou, A.G., 2012. Ectomycorrhizal symbiosis of tropical African trees. Mycorrhiza 22, 1–29. https://doi.org/10.1007/s00572-011-0415-x

Bakker, M.R., Brunner, I., Ashwood, F., Bjarnadottir, B., Bolger, T., Børja, I., Carnol, M., Cudlin, P., Dalsgaard, L., Erktan, A., Godbold, D., Kraigher, H., Meier, I.C., Merino-Martín, L., Motiejūnaitė, J., Mrak, T., Oddsdóttir, E.S., Ostonen, I., Pennanen, T.L., Püttsepp, Ü., Suz, L.M., Vanguelova, E.I., Vesterdal, L., Soudzilovskaia, N.A., 2019. Belowground Biodiversity Relates Positively to Ecosystem Services of European Forests. Front. For. Glob. Change 2, 6. https://doi.org/10.3389/ffgc.2019.00006

Bechem, E., Njoh, N., Egbe, A., 2018. Mycorrhizal status of some indigenous tree species in the Takamanda rainforest, South West Region, Cameroon. J. Ecol. Nat. Environ. 10, 41–52. https://doi.org/10.5897/JENE2018.0684

Bechem, E.E.T., Chuyong, G.B., Fon, B.T., 2014. A Survey of Mycorrhizal Colonization in the 50-ha Korup Forest Dynamic Plot in Cameroon. AJPS 05, 1403–1415. https://doi.org/10.4236/ajps.2014.510155

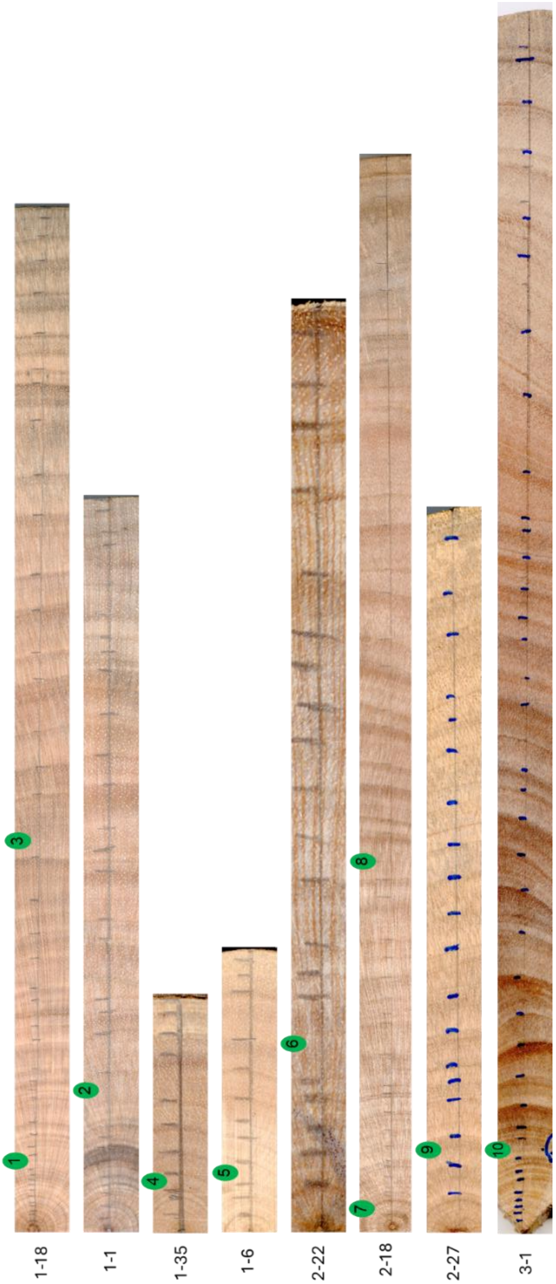
Davison, J., Moora, M., Öpik, M., Adholeya, A., Ainsaar, L., Bâ, A., Burla, S., Diedhiou, A.G., Hiiesalu, I., Jairus, T., Johnson, N.C., Kane, A., Koorem, K., Kochar, M., Ndiaye, C., Pärtel, M., Reier, Ü., Saks, Ü., Singh, R., Vasar, M., Zobel, M., 2015. Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism. Science 349, 970–973. https://doi.org/10.1126/science.aab1161

Diédhiou, A.G., Selosse, M.-A., Galiana, A., Diabaté, M., Dreyfus, B., Bâ, A.M., de Faria, S.M., Béna, G., 2010. Multi-host ectomycorrhizal fungi are predominant in a Guinean tropical rainforest and shared between canopy trees and seedlings. Environmental Microbiology. https://doi.org/10.1111/j.1462-2920.2010.02183.x

Gorzelak, M.A., Ellert, B.H., Tedersoo, L., 2020. Mycorrhizas transfer carbon in a mature mixed forest. Mol Ecol 29, 2315–2317. https://doi.org/10.1111/mec.15520

Olanipon, D., Boeraeve, M., Jacquemyn, H., 2024. Arbuscular mycorrhizal fungal diversity and association networks in African tropical rainforest trees (preprint). Ecology. https://doi.org/10.1101/2024.02.06.578868

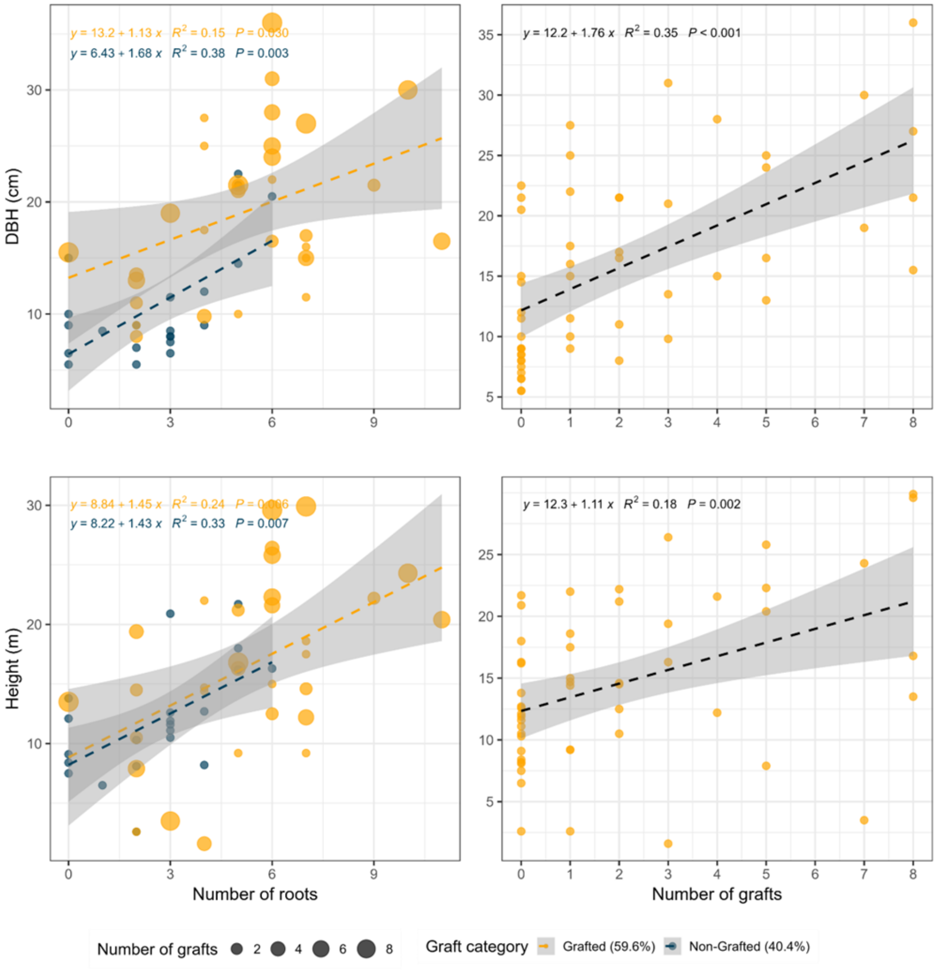
Onguene, N.A., Kuyper, T.W., 2001. Mycorrhizal associations in the rain forest of South Cameroon. Forest Ecology and Management 140, 277–287. https://doi.org/10.1016/S0378-1127(00)00322



ID	Site-Tree	Sample length (cm)	RICH-number	Percent modern carbon (uncalibrated)	Age (AD, calibrated)
1	1-18	18.6	37025	106,56+/-0,31	2005-2009
2	1-1	10.0	37026	106,13+/-0,30	2006-2010
3	1-18	18.6	37392	104,93+/-0,30	2009-2013
4	1-35	2.5	37393	106,39+/-0,32	2005-2010
5	1-6	3.1	37394	104,68+/-0,33	2011-2013
6	2-22	4.6	37395	105,83+/-0,31	2007-2011
7	2-18	29.8	37396	105,77+/-0,30	2007-2011
8	2-18	29.8	37397	104,88+/-0,26	2010-2012
9	2-27	10.3	37398	106,33+/-0,31	2006-2010
10	3-1	29.3	37399	108,59+/-0,30	2001-2004

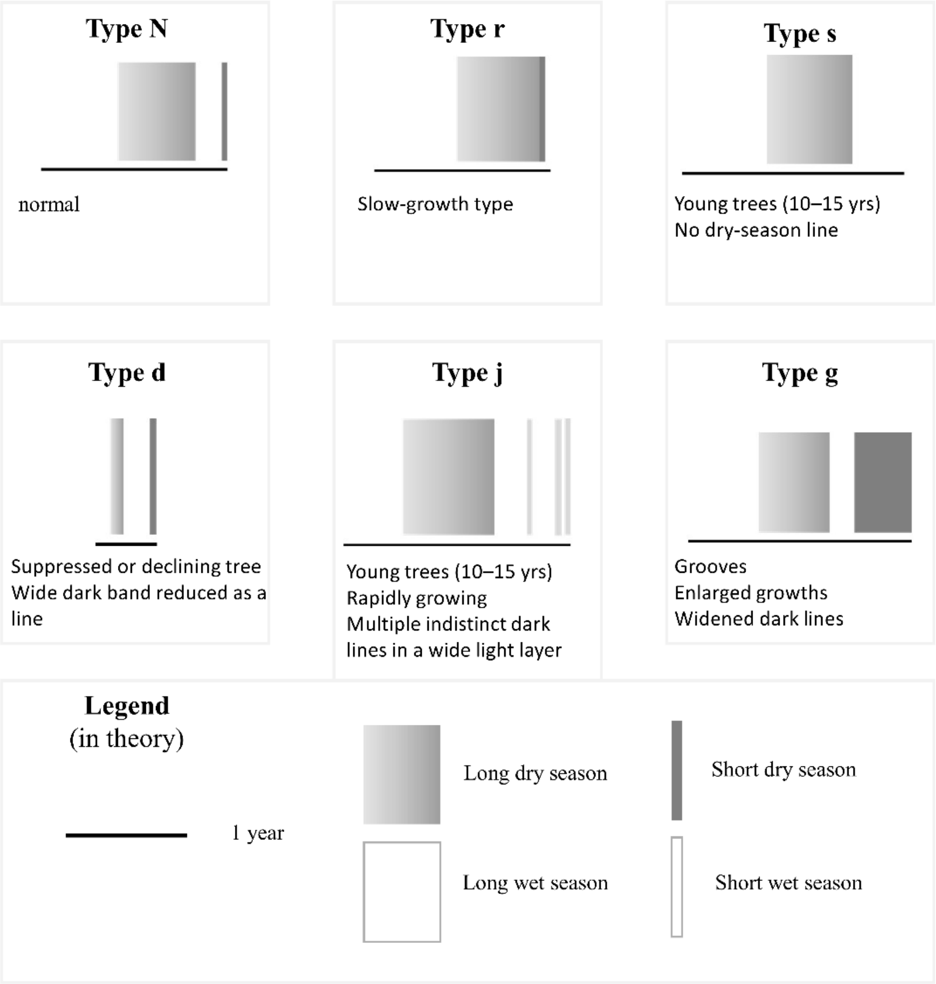
Supplementary Material 17 : Scan of each wood core along the longest radius of the sampled tree cross sections. The grey/blue marks correspond to growth rings boundaries delimited manually. The numbered green markings indicate the locations of radiocarbon-dated growth ring samples. Th table presents the ID samples with the radius length, RICH

(Radiocarbon Inventories of Switzerland) identification number, percent modern carbon remaining, and calibrated age of the samples.



Supplementary Material 18 : Relationships between tree structural attributes and belowground connectivity. Linear regressions examine how tree size relates to the number of roots (**A, C**) and number of grafts (**B, D**). DBH (cm) is shown on the x-axis in (**A, B**) and height (m) in (**C, D**). Blue points represent non-grafted trees; yellow points indicate grafted individuals, with point size proportional to the number of grafts. Dashed lines show linear regression fits with 95% confidence intervals.

Classification of annual growth ring types in *Aucoumea klaineana* Pierre
after Mariaux, 1973



Supplementary Material 19 : Classification of annual growth ring types in *Aucoumea klaineana* Pierre after Mariaux (1973)