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SEEDLING ECOLOGY OF *AUCOUMEA KLAINEANA* PIERRE, THE MOST IMPORTANT TIMBER SPECIES IN CENTRAL AFRICA

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Abstract

Aucoumea klaineana Pierre is the most exploited timber species in Central Africa. In natural forests, its 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 planted among shade houses and 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 (leaves, roots, and stem mass ratios), number of branches, and symptoms of pests 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 lights 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 anastomoses), separated by other species (to limit pest contamination), under light canopy cover (around 9–62 % of relative irradiance, to promote sustained growth rates at the seedling stage). This approach should

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ensure the conservation of *A. klaineana* populations and the long-term viability of Central Africa's timber industry.

1. Introduction

Okoumé, *Aucoumea klaineana* Pierre, is found in four out of the nine Central African countries: Gabon, Equatorial Guinea, southwestern Congo, and southern Cameroon. It covers an estimated area of 24.8 million hectares (12,4 %) (Loubota Panzou et al., 2023), out of the 200 million hectares of Central African tropical moist forest (Vancutsem et al., 2021). Despite this limited distribution, it is the most extensively harvested timber species in the region, with an annual volume exceeding 1.7 million m^3 (FRMi, 2018). It outstands other major commercial species like Sapelli (*Entandrophragma cylindricum* (Sprague) Sprague), Tali (*Erythrophleum* spp.), and Ayous (*Triplochiton scleroxylon* K. Schum) (FRMi, 2018). Collectively, these four species account for almost 70 % of the total production in the Congo Basin (Eba'a Atyi et al., 2022; FRMi, 2018). In Gabon, *A. klaineana* has maintained its market dominance since the early 20th century (Brunck et al., 1990), constituting 60 % of the overall log production (FRMi, 2018). Logs are peeled to produce plywood panels for interior applications, while lower-quality logs are sawn to produce construction timber.

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 m^2) 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 forest: long-lived, light-demanding commercial species (Karsenty and Gourlet-Fleury, 2006) are progressively replaced by poorly 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 ha. 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 ha of plantations were established over 40 years (Biraud and Catinot, 1960; Grison, 1979; Groulez, 1975; Leroy Deval, 1976a). The modalities of these plantations evolved, starting with strip plantations (2–4 m), progressing to broader bands (10–20 m), 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 existing forest management in the 1970s

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(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 anastomoses, a fusion of root steles that enables the interchange of water and carbon between conspecific individuals (Leroy Deval, 1973, 1974), 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 (1993, 1995) 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).

Psyllids (*Pseudophacopteron* sp.) infestation and black canker (*Lasiodiplodia theobromae* (Pat.) Griffon & Maubl.) are two threats to the species (Brunck et al., 1990; Leroy Deval, 1976b). 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

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to establish itself, forming a black sooty film on various plant organs, ultimately leading to growth slowdown and plant death.

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) (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) (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 simulating open gaps and open areas 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. Material and methods

2.1. STUDY SITE

The experiment took place in Bambidie, within the FSC-certified logging concession granted to CEB-Precious Wood, in the Ogooué-Lolo province of Gabon (0°41'65"S–12°59'01"E). According to the Köppen classification, the climate in this region is classified as Aw with average temperatures ranging from 21°C and 28°C and total annual precipitation between 1600 and 1800 mm (Caroff and Rydalesky, 1970). There is a main dry, cloudy season from June to September (**Table 1**), and a shorter dry season between mid-December to mid-January. The forests in the region are evergreen and dominated by *A. klaineana*, *Scyphocephalium mannii* (Benth.) Warb., and *Julbernardia pellegriniana* Troupin (Caballé, 1978; Caballé and Fontes, 1978).

2.2. STUDY SPECIES

Aucoumea klaineana Pierre (*Burseraceae*) is a long-lived dioecious tree that can grow up to 50 m in height and reach a diameter of 2 m, with a cylindrical bole and distinctive pink exuding oleoresin (Meunier et al., 2015). The leaves are compound imparipinnate consisting of 7–13 leaflets along a

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rachis that can reach up to 40 cm. The leaves are initially red and later turning grey-green. The flowers are small and numerous, pollinated by insects, with each flower type bearing the atrophied organ of the opposite sex. The fruits (capsules) open into five valves, releasing winged seeds that are dispersed by wind up to 100 m away (Doucet, 2003). Unlike many pioneer species traits (sensu Swaine and Whitmore, 1998), the seeds are recalcitrant and germinate within three weeks regardless of light conditions (Brunck et al., 1990). Seedlings grow in open environments such as savannah edges, fallow lands, forest gaps, roadsides, and tracks (Delègue et al., 2001; Doucet, 2004). Seedling density varies from 6000 (De Kam et al., 1996) to 35,000 per hectare (Fuhr et al., 1998), with most dying early.

As they grow, *A. klaineana* first forms monospecific to monodominant stands (Dèlegue et al., 2001; Fuhr, 1999; Pangou et al., 2003), then mixed stands with Ozouga (*Sacoglottis gabonensis* (Baill.) Urb.) and Ozigo (*Dacryodes buettneri* H.J.Lam.) in sandy soil areas, and with Alep (*Desbordesia glaucescens* (Engl.) Tiegh.) in the Atlantic rainforest (Saint-Aubin, 1963). As the trees age, their specific density decreases, allowing for the growth of shade-tolerant species, resulting in old mixed stands (White et al., 2000). Growth data are numerous and vary according to forest type (Engone Obiang et al., 2013). In natural forests, Fuhr (1999) reports an average annual growth of 1.9 cm in diameter for trees aged 5–10 years, which can reach up to 3 or 4 cm for larger trees (Brunck et al., 1990). After 50 years, the growth decreases to 0.4–0.8 cm per year (Brunck et al., 1990; Fuhr, 1999). Suppressed trees may exhibit almost no growth but survive due to root anastomoses (Leroy Deval, 1973).

Although it is debatable (Guidosse et al., 2022), *A. klaineana* is considered vulnerable according to the A1 criterion of the International Union for Conservation of Nature (White, 1998). This criterion evaluates the decline in population over three generations, which is difficult to quantify for long-lived tree species. An updated evaluation is needed.

2.3. LIGHT EXPERIMENT

The light response experiment lasted 18 months, from September 2021 to February 2023. Six shade houses (2×3×1.8 m) were constructed with wood slats of increasing spacing to cover the full light intensity gradient. 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 % of relative irradiance, RI). Two others (1 % and 4 %) represented the conditions existing in the forest understory (Kyereh et al., 1999), 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., *Milicia excelsa* (Welw.) C.C.Berg, *Ricinodendron heudelotii* Müll. Arg. or *Terminalia ivorensis* A. Chev.), negative growth rates are expected at 1 % RI (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,

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Ingolstadt, Germany) (**Supplementary Materials 1**). The six plots were arranged in a row, 3 m apart to avoid shading each other, and perpendicular to the path of the sun.

In February 2021, seeds from three healthy *A. klaineana* trees were collected from the forest surrounding the assay site 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-liter buckets containing the same soil mixture to allow for good root development.

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), as well as dry biomass allocation ratios (Dent and Burslem, 2009) and 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):

$$RGR = \frac{\ln(X_2) - \ln(X_1)}{t_2 - t_1}$$

Where X_1 and X_2 represent the height or diameter of a plant at times t_1 and t_2, 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 heteroscedasticity 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). A chi-square test was

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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.

Table 1
Average daily photosynthetic photon flux density (PPFD, mmol.m^{-2}.day^{-1}) and its standard deviation over 7 periods in six shadehouses (A-F) and an unshaded platform (G). Measurements were taken over a seven-day period.

Plot	2021		2022					Mean	SD	% irradiance
	August	November	February	March	May	June	July			
A	4,89	6,22	5,19	5,92	5,67	2,29	4,58	4,97	1,22	1 %
B	19,27	28,52	23,94	24,95	19,86	8,50	8,63	19,09	7,26	4 %
C	49,37		55,50	50,36	55,34	22,97	21,10	42,44	14,62	9 %
D	126,30	144,80	126,22	167,26	140,52	57,85	59,45	117,49	39,34	25 %
E	204,12		245,43	247,73	206,15	83,33	88,69	179,24	68,08	39 %
F	281,52		363,05	372,85	289,18		130,45	287,41	86,83	62 %
G	461,02	683,08	580,88	622,51	489,37	189,48	219,64	463,71	178,29	100 %

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) (**Fig. 1** A). 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, **Fig. 1** A). 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 (**Fig. 1**B), occasionally leading to partial or complete leaf tearing.

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

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 (**Fig. 2**). 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

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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 9–62 % 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 (**Fig. 3**), 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 (25–100 % 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 Materials 2**).

Principal component analysis was conducted to examine the impact of functional traits on growth and biomass (**Fig. 4**). 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 (**Fig. 4**): (i) the 9 % RI treatment displayed superior growth (RGRh, RGRd) and biomass (STB), allocating significant biomass to leaf mass (LMR); (ii) the 25–62 % 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.

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	$\chi^2(6) = 8.0$, $p=0.23$
Symptoms (n=70)	Witches' broom	90	100	100	100	100	70	90	93,0	$\chi^2(6) = 2.51$, $p=0.86$
	Sooty film or protuberances	0	90	10	10	10	10	20	21,4	$\chi^2(6) = 78.61$, $p<0.001$
	Leaves covered with spots	70	90	80	100	90	50	100	82,9	$\chi^2(6) = 6.46$, $p=0.37$

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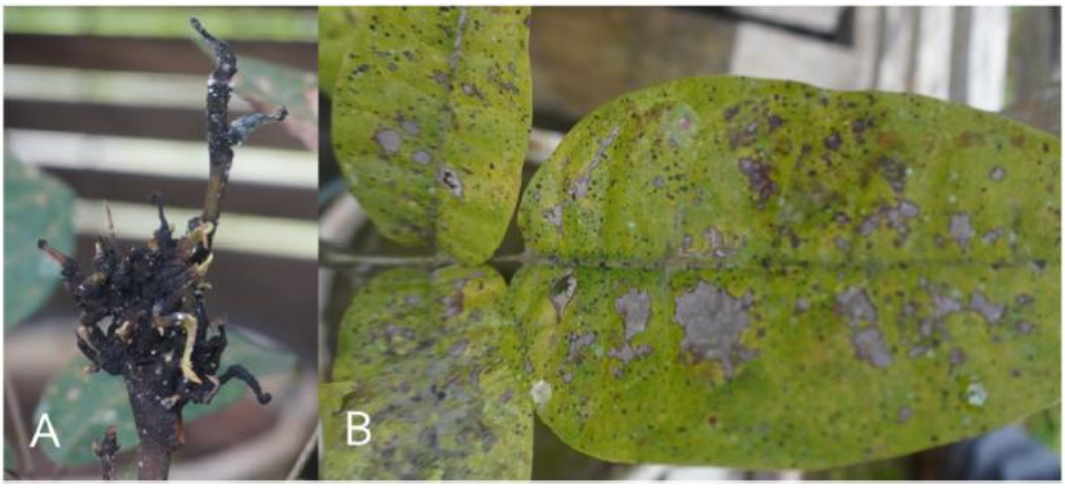

Fig. 1. (A). *A. klaineana* seedling showing dramatic changes following a psyllid attack, with terminal buds deformed into a witch's broom shape and infected by black canker. (B) Grey spots on *A. klaineana* leaf resulting from weakening by psyllids.

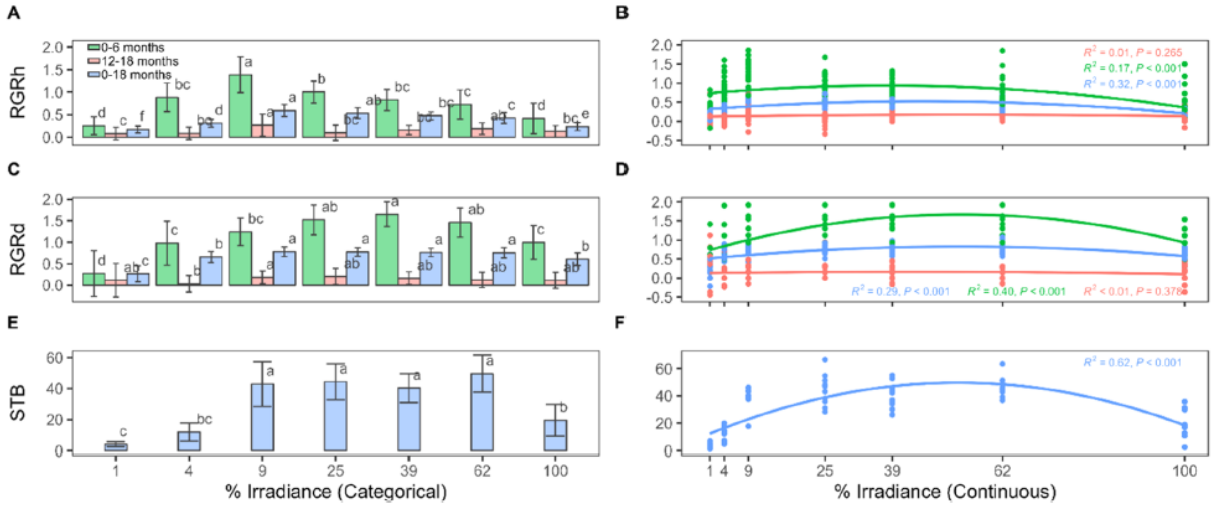

Fig. 2. Relative growth rates (A,B) in height (RGRh in $cm.cm^{-1}$); (C,D) in diameter (RGRd in $mm.mm^{-1}$) and (E,F) final seedling total biomass (STB in g) of *Aucoumea klaineana* seedlings in response to varying light conditions ranging from 1 % to 100 % of relatve irradiance. For irradiance as 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).

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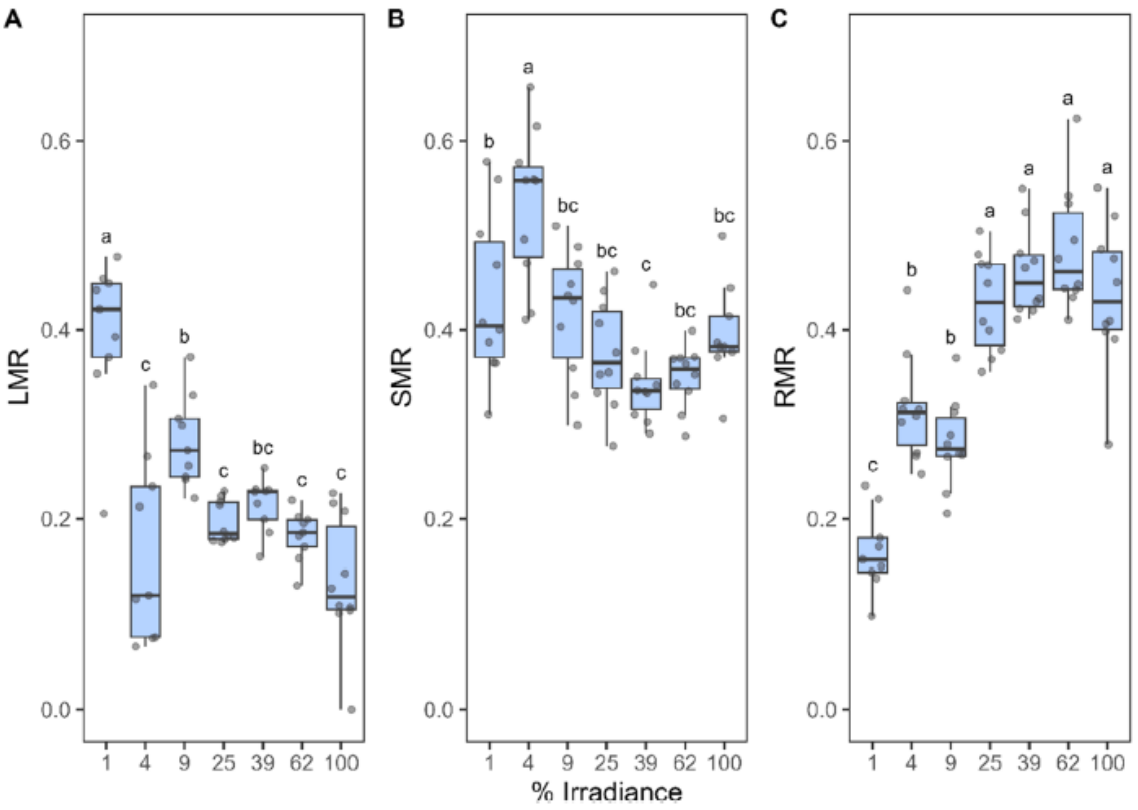

Fig. 3. Biomass allocation of *A. klaineana* seedlings across relative irradiance levels ranging from 1 % to 100 %. LMR: Leaves mass ratio (A); SMR: stem and branches mass ratio (B); RMR: roots mass ratio (C). Letters denote results from ANOVA and Tukey's test, with a common letter indicating no significant differences between groups.

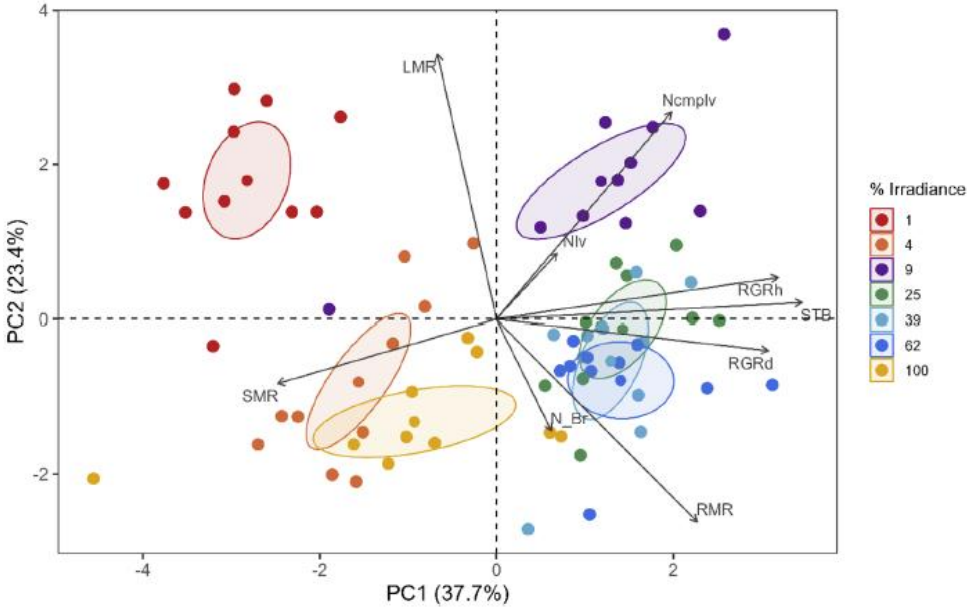

Fig. 4. Principal Component Analysis (PCA) performed on nine different functional traits of *A. klaineana* seedlings subjected to seven light intensities ranging from 1 % to 100 % of relative irradiance. The traits analyzed included included among other the number of leaves (Nlv), the number of compound leaves (Ncmplv), and the number of branches (N_Br) at the end of the experiment.

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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's 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., Brunck et al., 1990; Wagner et al., 1996; Nichols et al., 1998; Bosu et al., 2006). 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 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 inexistant (Brunck et al., 1990; Leroy Deval, 1976b). *M. excelsa*, 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. 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 about 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 and *Piper guineense* Schumach. & Thonn. on seedlings were identified (Ugwu, 2021).

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Despite pest challenges, *A. klaineana* demonstrated a remarkably high survival rate (97.1 %) after 18 months, regardless of the most extreme light conditions (1 % and 100 %) or pest impacts. In comparison, *Guibourtia ehie* (A.Chev.) J. Leonard, 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) *C. gabunensis* and *L. alata* showed a 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, whose seeds are dormant in the soil seed bank and which grow faster than *A. klaineana* (Doucet et al., 2004) can explain 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. heudelottii* (4–66 % RI, higher light conditions not measured) (Agyeman et al., 1999), *Cylicodiscus gabunensis* Harms (10–40 % RI) (Ndonda Makemba, 2023) or *Lophira alata* Banks ex C.F.Gaertn (24–43 % RI) (Biwolé et al., 2015) (**Supplementary Materials 3**). *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 10–44 % RI but *Aucoumea 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 it to etiolation. However, *L. alata* (sharing characteristics of a pioneer and a NPLD species) does not exhibit this etiolation trait around 10 % RI (Biwolé et al., 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

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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 5–9 % 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 et al., 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 trends was also observed in the pioneer species *R. heudelottii* (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 % RI) (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 (**Fig. 2**, B,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., 2019), and particularly regarding the root anastomoses forming interconnected groups of trees (Leroy Deval, 1973).

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Although it is not ideal, seedlings can establish themselves in extreme light conditions. At very low light levels (1 % RI), some seedling perish despite a positive average relative growth rates in 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 9–16 individuals spaced 1 m 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 a better knowledge of the pest biology and 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 advice planting monospecific clusters of 9–16 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 anastomoses.

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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.

CRediT authorship contribution statement

Quentin Guidosse: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ludivine Lassois:** Writing – review & editing, Supervision. **Jean-Louis Doucet:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Conceptualization. **Stevy Nna Ekome:** Writing – review & editing, Investigation. **Caroline De Clerck:** Writing – review & editing, Writing – original draft. **Achille Biwolé:** Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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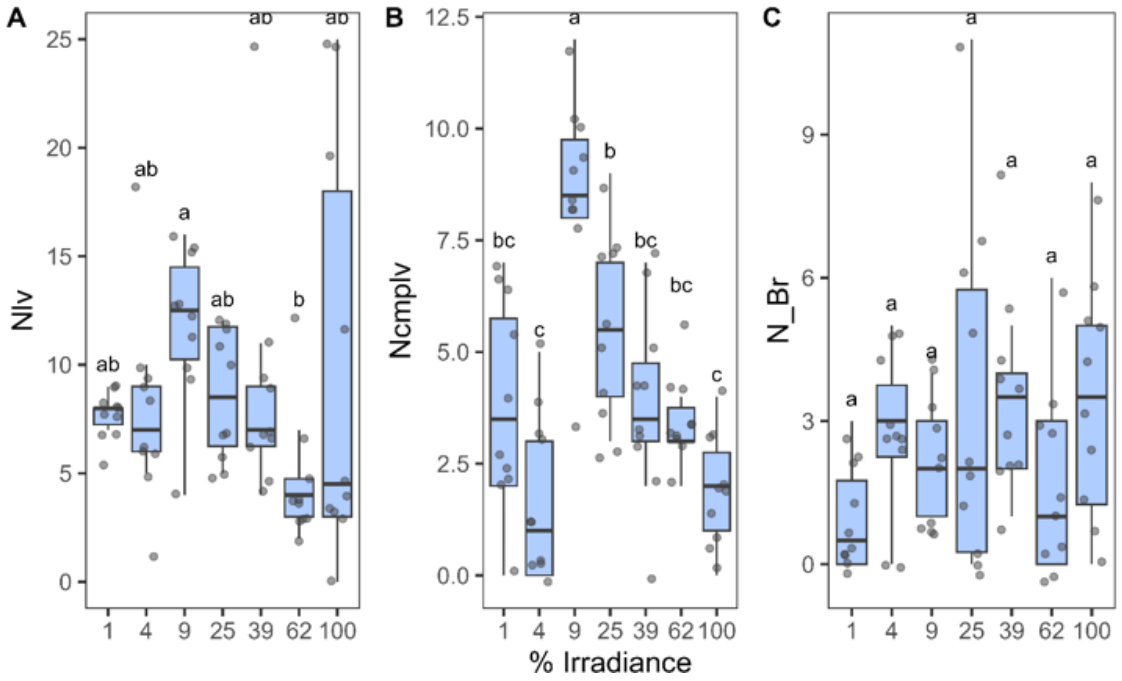
Appendix A. Supporting information

Supplementary Materials 1 : Temperature, Hygrometry and Vapour Pressure Deficit collect with Ebro EBI 20-TH sensors (Xylem Analytics, Ingolstadt, Germany) during the first week of experiment.

% 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 : 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 3 : 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).

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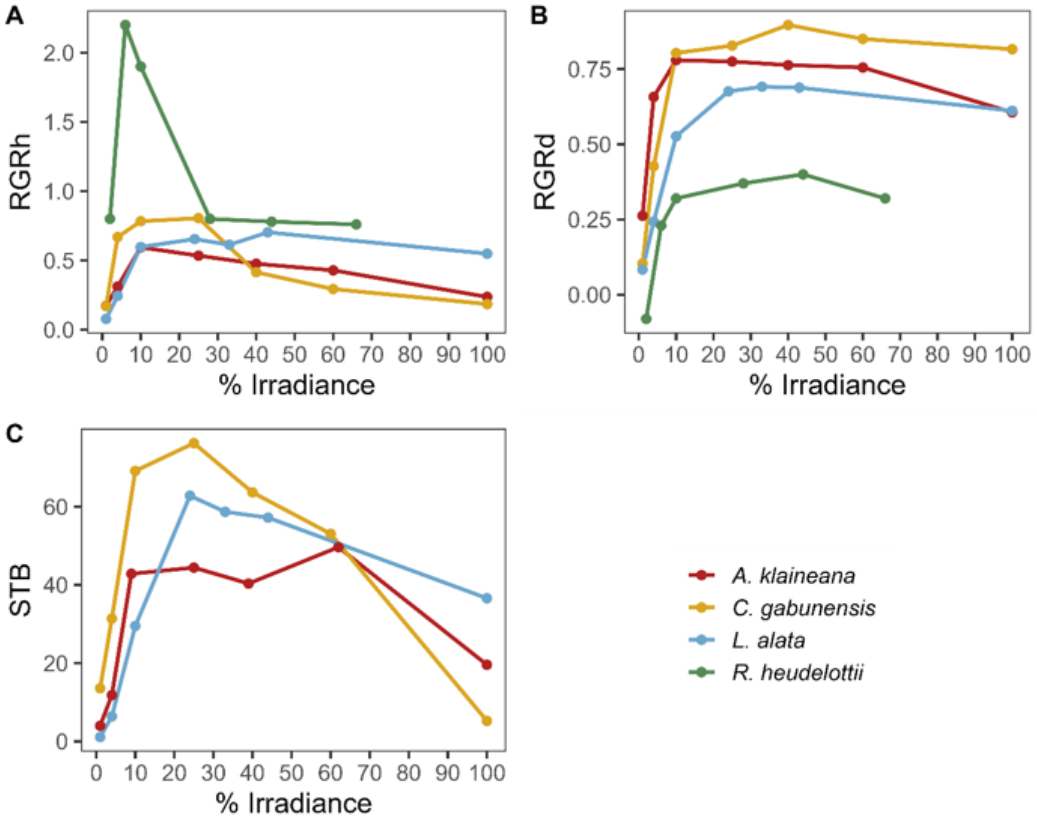

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