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The anatomy of survival — What determines seedling fate after planting in West Africa?

Ibrahim Konaté [a], Evans Ehouman [b], Fatima Wourro [c], Yves Doua-Bi [d], Fabrice Tiéoulé [d], Brahima Coulibaly [e], Jean-Claude Koffi Konan [d], Irie Casimir Zo-Bi [f], Bruno Hérault [g,h,*]

[a] *Ministère des Eaux et Forêts (MINEF), Abidjan, Côte d'Ivoire*
[b] *Cirad Afrique l'Ouest - Forêt et Savane Humide, Abidjan, Côte d'Ivoire*
[c] *Centre WASCAL/CEA-CCBAD, Université Félix Houphouët-Boigny, Abidjan, Côte d'Ivoire*
[d] *SODEFOR, Abidjan, Côte d'Ivoire*
[e] *CNRA, Abidjan, Côte d'Ivoire*
[f] *UMRI SAPT, INPHB, Yamoussoukro, Côte d'Ivoire*
[g] *CIRAD, Forêts et Sociétés, F-34398 Montpellier, France*
[h] *Forêts et Sociétés, Univ Montpellier, CIRAD, Montpellier, France*

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ABSTRACT

Tropical forest restoration is a global priority, yet its success often hinges on seedling survival in degraded landscapes. In West Africa, large-scale restoration is challenged by limited knowledge of how survival drivers interact across diverse native species. This study dissects the "anatomy of survival" by evaluating how planting time, shade, and vegetation competition shape early performance across 21,609 seedlings from 16 native tree species in central Côte d'Ivoire—a region marked by seasonal rainfall and widespread land degradation. A large-scale field experiment tested the effects of delayed planting, shade from intercropped banana, and competition from herbaceous cover, *Panicum* grasses, and the exotic tree *Cedrela odorata*. Seedling survival was monitored over the first growing season under operational planting conditions. Hierarchical Bayesian survival models were used to isolate species-specific responses to each factor while accounting for environmental variability. The analysis revealed a multidimensional structure to seedling survival. Early planting was generally beneficial, especially for slow-growing species. Banana shade consistently improved survival by buffering temperature and preserving soil moisture. *Cedrela* had strong negative effects on most species, underscoring its competitive dominance and incompatibility with native restoration. Herbaceous cover also reduced survival, though effects varied by species. Fromager, Kotibé, Ako, and Asan showed the highest survival probabilities across treatments. This breakdown of survival patterns provides a functional basis for restoration design. We propose species-specific guidelines emphasizing early planting, strategic shading, and targeted weeding. Yet given the complexity and cost of planting, assisted natural regeneration remains the preferred option where viable seed sources persist.

1. Introduction

West Africa has experienced some of the highest deforestation rates in the tropics, particularly across its forest–savanna transition zones (FAO, 2020). The semi-deciduous forest zone, historically rich in endemic tree species and high in floristic diversity (Poorter et al., 2004), has been heavily fragmented (Traoré et al., 2024) and degraded (Dago et al., 2023) due to expanding agriculture, logging, and anthropogenic fires (Elogne et al., 2023). In response, a growing number of reforestation and landscape restoration programs have emerged with the aim of restoring degraded lands and recovering ecosystem services (Houphouët et al., 2025). Notably, the African Forest Landscape Restoration Initiative (AFR100) has mobilized multiple countries, including Côte d'Ivoire, to restore millions of hectares of forest landscapes (AFR100 Secretariat, 2021). These programs also seek to address the growing demand for timber and fuelwood that can no longer be met sustainably by the region's increasingly depleted natural forests (Uzu et al., 2022). These initiatives often promote the planting of native species to support biodiversity conservation and ecological resilience (Chazdon, 2008; Brancalion and Holl, 2020). Yet, despite the scale of these efforts, empirical data on tree survival and plantation

* Correspondence to: Cirad, Univ Montpellier, Campus Baillarguet, Montpellier, France.
E-mail address: bruno.herault@cirad.fr (B. Hérault).

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outcomes in Africa remain surprisingly scarce (Wourro et al., 2026). Many programs operate without robust monitoring, and few studies provide systematic evidence on the conditions that determine early seedling establishment, a critical phase for long-term plantation success and forest recovery (Peroches et al., 2025).

In the semi-deciduous zone, native tree species exhibit substantial variation in first-year survival when planted under field restoration conditions (Blay et al., 2007). These differences are often linked to species-specific life-history traits such as seed size, root-shoot allocation, shade tolerance, drought resistance, and growth rate (Mirabel et al., 2019). For instance, pioneer species with fast growth and high resource demand may suffer more from drought or competition, while late-successional species tend to be more resilient but grow slowly (Paz, 2003; Herault et al., 2010; Hérault et al., 2011). However, beyond inherent functional traits, tree survival is also strongly influenced by plantation shocks—defined as the suite of physiological and environmental stresses seedlings experience during the transition from nursery to field conditions. These include abrupt exposure to full sunlight, root deformation due to prolonged container growth, and transplanting under suboptimal climatic or soil conditions (Grossnickle, 2005). Compared to natural regeneration, which typically occurs in synchrony with the onset of rains, many planting campaigns in West Africa are carried out late in the rainy season due to delays in funding or seedling production. This poor timing often exposes seedlings to dry-season stress shortly after planting, leading to reduced survival and growth rates (Kouassi et al., 2023, 2025). Furthermore, poor nursery conditions — such as inadequate hardening, insufficient light exposure, or irregular watering — can produce physiologically weak seedlings less capable of withstanding post-planting stress (Nyoka et al., 2018; Jacobs et al., 2005).

In addition to abiotic constraints, biotic interactions also play a critical role in shaping seedling fate during the establishment phase. Competitive pressure from aggressive herbaceous species is particularly strong in degraded and open lands typical of reforestation sites. In the West African context, Panicum maximum (guinea grass), a widespread and highly competitive C4 grass, is frequently dominant in early successional fields and can quickly suppress tree seedlings through light interception and root competition (Meli et al., 2017; Lowery et al., 1993). Moreover, the co-occurrence of exotic woody species like Cedrela odorata may further compromise native seedling performance through competition for space and possibly allelopathic effects. A growing body of literature suggests that Cedrela may release chemical compounds that inhibit the germination and growth of neighboring plants, a phenomenon well-documented in tropical systems (Rivas-Torres and Rivas, 2018). Recent field results in Côte d'Ivoire (Van der Meersch et al., 2021), have demonstrated that Cedrela can negatively impact native seedling survival and biomass accumulation of native species in natural forests. Although originally introduced for timber, Cedrela is now naturalizing and regenerating spontaneously in the semi-deciduous zone, which raises new ecological concerns. Its growing presence in disturbed landscapes underscores the importance of understanding its interaction with native species, especially in restoration contexts where its influence may be indirect but persistent.

Conversely, some local planting practices could mitigate these stresses. For example, planting banana plants (Musa spp.) alongside tree seedlings is a common strategy in agroforestry systems (particularly cocoa farms), where they serve as temporary shade providers that buffer seedlings against desiccation and radiation stress by lowering soil temperature, reducing evapotranspiration, and maintaining more favorable microclimatic conditions for newly planted trees (Vanhove et al., 2016). In addition to direct physiological benefits, shade from banana plants may also indirectly reduce competition with fast-growing grasses by limiting light availability at ground level. Additionally, increasing planting diversity through mixed-species plantations has been proposed as a means to reduce competition and pest damage while enhancing facilitative interactions among trees (Depauw et al., 2024; Messier et al., 2022). Mixed plantings may also improve structural complexity and resource use efficiency through niche complementarity, temporal differentiation in resource uptake, and reduced susceptibility to species-specific pests and diseases (Forrester and Bauhus, 2016; Richards et al., 2010). In tropical systems, diverse plantations have shown increased biomass accumulation and greater resilience to climatic stressors, although these effects remain understudied in West African native forest species (Hérault et al., 2020). However, such benefits are context-dependent and remain poorly documented for native species in the West African semi-deciduous forests.

In this study, we focus exclusively on native tree species from the semi-deciduous forest zone of Côte d'Ivoire, aiming to deepen our understanding of the ecological factors that shape early seedling survival following plantation efforts. Our research addresses three key objectives: (i) to compare first-year survival rates among a diverse selection of native species, (ii) to evaluate the effects of various factors — including delays in planting, competition from herbaceous vegetation (especially *Panicum maximum*), pressure from the invasive Cedrela odorata, and the presence of banana nurse plants — on seedling survival, and (iii) to identify the most favorable planting conditions for each species. By exploring how different species respond to their planting environment and biotic interactions, this study seeks to generate actionable insights. Our ultimate goal is to guide more effective reforestation strategies with native species in the complex and often challenging ecological landscape of West Africa's semi-deciduous forests.

2. Materials and methods

2.1. Study area

The data used in this study were collected in an experimental setup in the Téné classified forest (6° 31′14′N, 5° 28′44′W), an area of semi-deciduous forest located in central Côte d'Ivoire. The area has a bimodal climate, characterized by a long rainy season (March–June), a short dry season (July–August), a short rainy season (September–November), and a long dry season (December–March). Average annual rainfall is less than 1200 mm and average daily temperatures are around 27 °C. The soils are ferralitic, with medium to low desaturation. The local landscape is marked by a mosaic of reforestation plots featuring species such as *Tectona grandis*, *Gmelina arborea*, and *Cedrela odorata*.

2.2. ForestInnov experiment

The ForestInnov experiment (https://treedivnet.ugent.be/experiments/ForestInnov.html) was established within a 25-hectare site located at an altitude of 202 m in the Téné Classified Forest, Côte d'Ivoire. The site corresponded to a former Gmelina plantation harvested about ten years before the study. All stumps were dead and largely decomposed, and the area was completely cleared of remaining vegetation before soil preparation. Following this clearing, the soil was manually worked with hoes (houe) in March 2019, following the standard technical itineraries used locally. The site was subdivided into 49 square plots of 0.5 ha each.

Sixteen native species (Table 1) were selected in collaboration with the Téné Classified Forest technical team based on their suitability for plantation establishment, nursery performance, and relevance to ongoing reforestation programs. Seedlings were produced in a nursery for six months before outplanting and were hand-planted in holes 30 cm deep and 20 × 20 cm wide. Between June and September 2019, 441 seedlings were planted per plot, arranged in a 21 × 21 grid with 3.5 m × 3.5 m spacing (70 m × 70 m). Maintenance followed local practice: three manual mowings with machetes were performed during the first year—September 2019, November 2019, and March 2020

Table 1
The 16 studied native tree species from Côte d'Ivoire and their main industrial uses (alphabetical order by vernacular name).

Vernacular name	Scientific name	Family	Main industrial uses
Acajou	*Khaya anthotheca*	Meliaceae	High-value timber for luxury furniture, veneers, joinery, light construction, boats, plywood
Ako	*Antiaris africana*	Moraceae	Lightweight wood for local use
Akatio	*Gambeya africana*	Sapotaceae	Lightweight wood for local use
Amazakoué	*Guibourtia ehie*	Fabaceae	Dense hardwood used as a substitute for rosewood in flooring, carving, turning, musical instruments.
Asan	*Celtis zenkeri*	Cannabaceae	Lightweight wood for local use
Bété	*Mansonia altissima*	Malvaceae	Hardwood for fine carpentry, veneer, instruments
Bi	*Eribroma oblongum*	Malvaceae	Lightweight wood for local use
Dabéma	*Piptadeniastrum africanum*	Fabaceae	Timber used locally for construction and joinery
Eho	*Ricinodendron heudelotii*	Euphorbiaceae	Used for carving, utensils, and as a balsa substitute
Framiré	*Terminalia ivorensis*	Combretaceae	Light-colored wood for light construction, furniture, drums, plywood; bark and leaves used in traditional medicine.
Fromager	*Ceiba pentandra*	Malvaceae	Very light wood for packaging, carving, molding; kapok fiber for stuffing; seeds yield oil; medicinal uses.
Ilomba	*Pycnanthus angolensis*	Myristicaceae	Softwood for boxes, matches; seeds produce oil used in margarine, soap.
Iroko	*Milicia excelsa*	Moraceae	Very durable wood for structural work, stairs, furniture, flooring; termite-resistant; latex and bark used medicinally.
Kotibé	*Nesogordonia papaverifera*	Malvaceae	Hard wood used locally; little documented commercial use.
Samba	*Triplochiton scleroxylon*	Malvaceae	Light wood for plywood, furniture, paneling; not very durable.
Tiama	*Entandrophragma angolense*	Meliaceae	High-quality timber for furniture, interior joinery, veneers, stairs, and boats; bark used in traditional medicine.

Table 2
Operational planting and management recommendations for 16 native species, organized by decreasing survival probability, based on modeled effects of planting delay, shading (banana), and competition (Cedrela, Panicum, herbaceous cover). Successional status for each species was added based on information from the PROTA4U database (https://prota.prota4u.org) and complementary literature (Hammond and Pokornỳ, 2020).

Species	Survival	Early planting	Needs shade	Competition sensitivity	Recommended management strategy	Successional status
Fromager	High	Yes	No	High	Plant early; maintain weed control. Suitable for degraded sites with support	Pioneer
Kotibé	High	No	No	High	Plant in sunlight; Highly sensitive to competition; needs full cover control	Shade Bearer
Asan	High	Yes	Moderate	Moderate	Shade and timely planting help; moderate competitive ability	Non-Pioneer Light-Demanding
Ako	High	No	No	Moderate	Tolerant to sunlight; control surrounding herbs	Non-Pioneer Light-Demanding
Iroko	High	No	No	High	Moderate needs; control surrounding grasses	Pioneer
Framiré	High	Yes	Moderate	Low	Early planting is very important	Pioneer
Bété	High	Yes	Moderate	Low	Early planting and basic cover control	Non-Pioneer Light-Demanding
Eho	Medium	Yes	Yes	Moderate	Requires early planting, benefits from shade conditions and low grass pressure	Pioneer
Amazakoué	Medium	Yes	Yes	High	Very sensitive to competition; plant early with strong weed control	Non-Pioneer Light-Demanding
Akatio	Medium	Yes	Yes	High	Sensitive to competition; plant early with strong grass control	–
Dabéma	Medium	Yes	Yes	Moderate	Moderately competitive; ensure early planting and shade conditions	Shade Bearer
Samba	Medium	No	Moderate	High	Managed cover greatly improves success	Pioneer
Tiama	Medium	Yes	Yes	Low	Tolerates cover if planted early and shaded	Non-Pioneer Light-Demanding
Acajou	Low	Yes	Yes	No	Low vigor; needs full support: early planting and shading	Shade Bearer
Ilomba	Low	No	No	High	Low vigor; Very sensitive to competition; avoid interplanting	Pioneer
Bi	Low	No	No	Moderate	Low vigor; Sensitive to competition; avoid interplanting	Pioneer

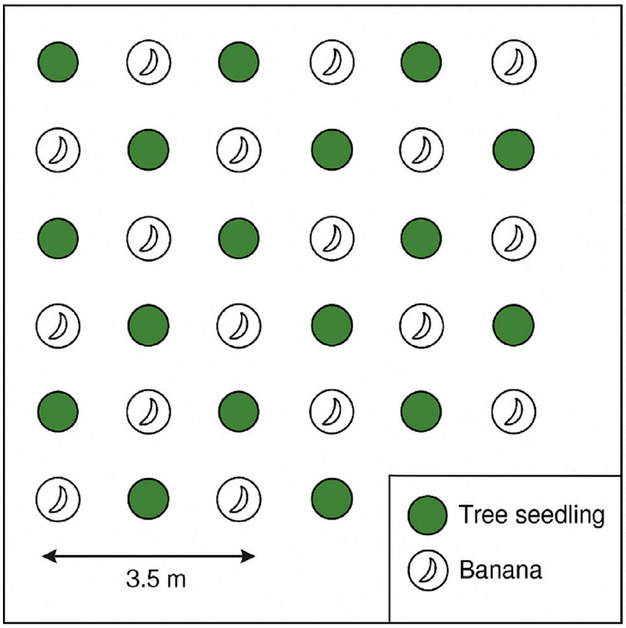

Fig. 1. Schematic representation of the *Tree* × *Banana* intercropping design used in the ForestInnov experiment. Tree seedlings (green circles) and banana trees (white symbols with leaf icons) were planted on a 3.5 m × 3.5 m grid at alternating positions, maintaining equal spacing. The layout represents a subplot (10 5 m × 10 5 m) of the experiment, illustrating the regular alternation of tree and banana planting positions.

(immediately after the dry season). No fertilizers or amendments were applied.

In 22 plots, banana plants (*Musa* sp.) were intercropped at the same 3.5 m × 3.5 m spacing as the tree seedlings, alternating positions within the grid (Fig. 1). Bananas were planted in early April 2019, approximately two months before the optimal tree planting date, ensuring canopy development and partial shading during seedling outplanting. All pre-existing woody vegetation had been cleared prior to soil preparation, leaving banana canopies as the sole source of shade. In contrast, non-intercropped plots were fully exposed to sunlight, with only variable herbaceous cover of low height. This design created a clear contrast between shaded and full-sun conditions across the experimental site.

The experiment was established with plots containing 1, 2, 4, 8, or 16 species. However, because this study focuses solely on first-year seedling survival, the gradient in species richness is not included in the analyses.

2.3. Data collection

Data were collected between April and May 2020, one year after planting. Monitoring covered all 441 seedlings in each of the 49 plots, totaling 21,609 planted individuals in 2019. Given the young age of the seedlings, only their survival status (alive or dead) was recorded. Several explanatory variables potentially influencing survival were recorded:

- The variable *SunLight*, coded as 1 when no banana plants were present in the plot, and 0 otherwise. This variable accounts for the absence of shading effects that could be provided by banana intercropping. Across the 49 plots, 22 plots were shaded (SunLight = 0) and 27 plots were unshaded (SunLight = 1).
- The variable *Delay* was calculated based on the actual planting date of each species in each plot. It represents the number of days between this planting date and June 13, 2019, which was identified by SODEFOR agents as the optimal planting date for the plot in the year considered. This date corresponds to the first 2–3 consecutive days period when the rainy season is typically well established. Values ranged from 0 to 109 days (median 53 days), reflecting usual operational variation in planting schedule.
- The variables *Cedrela*, *Panicum*, and *Cover* describe competitive pressure from surrounding vegetation:
  - For each plot, ten 3.5 m × 3.5 m subplots were randomly selected.
  - The variable *Cover* corresponds to the mean percentage of ground covered by herbaceous vegetation. In each 3.5 m × 3.5 m subplot, a trained observer visually estimated the percentage of ground surface covered by herbs (0 to 100%) using the classic Daubenmire method (Daubenmire, 1959). These subplot-level estimates were then averaged to obtain the plot-level *Cover* value. Herbaceous cover varied widely among plots, ranging from 21% to 100% (median 85%).
  - *Cedrela* and *Panicum* represent the percentage of subplots where the presence of *Cedrela odorata* and *Panicum sp.*, respectively, was recorded (presence = 1, absence = 0). The frequency of *Cedrela* ranged from 0% to 100% (median 20%), while *Panicum* ranged from 10% to 100% (median 60%).

Prior to modeling, we examined pairwise relationships (Fig. 7, Appendix). Correlations among predictors were almost all not significant, indicating limited redundancy between variables such as planting delay, herbaceous cover, and the presence of major competitors. Slight associations between herbaceous cover and *Cedrela* presence were observed but remained weakly significant. Consequently, collinearity among predictors is expected to be minor, and all variables were retained for inclusion in the subsequent hierarchical survival models.

2.4. Data analysis

We analyzed first-year seedling survival using a hierarchical Bayesian logistic regression model. The binary response variable indicated whether each individual seedling was alive (1) or dead (0) at the time of monitoring. The probability of survival was modeled as a function of species identity and five environmental or management covariates. Let i index each observation (seedling) and $s = \texttt{species}[i]$ denote the species identity. Survival probability was modeled using a logistic link:

$$\begin{aligned}\operatorname{logit}(\Pr[\texttt{survival}_i = 1]) = \theta_{0,s} + \\ \theta_{\mathrm{SUN},s} \cdot \texttt{SunLight}_i + \\ \theta_{\mathrm{DEL},s} \cdot \texttt{Delay}_i + \\ \theta_{\mathrm{COV},s} \cdot \texttt{Cover}_i + \\ \theta_{\mathrm{CED},s} \cdot \texttt{Cedrela}_i + \\ \theta_{\mathrm{PAN},s} \cdot \texttt{Panicum}_i\end{aligned} \tag{1}$$

Species-specific intercepts $\theta_{0,s}$ were modeled hierarchically:

$$\theta_{0,s} \sim \mathcal{N}(\mu_0, \sigma_0) \tag{2}$$

and can be interpreted on the probability scale as baseline survival probabilities via the inverse logit:

$$p_{0,s} = \operatorname{logit}^{-1}(\theta_{0,s}), \quad p_{0,s} \in (0, 1). \tag{3}$$

Species-specific effects were modeled as random effects drawn from global (community-level) distributions. For each covariate, we estimate a mean effect across all species (μ) and the among-species standard

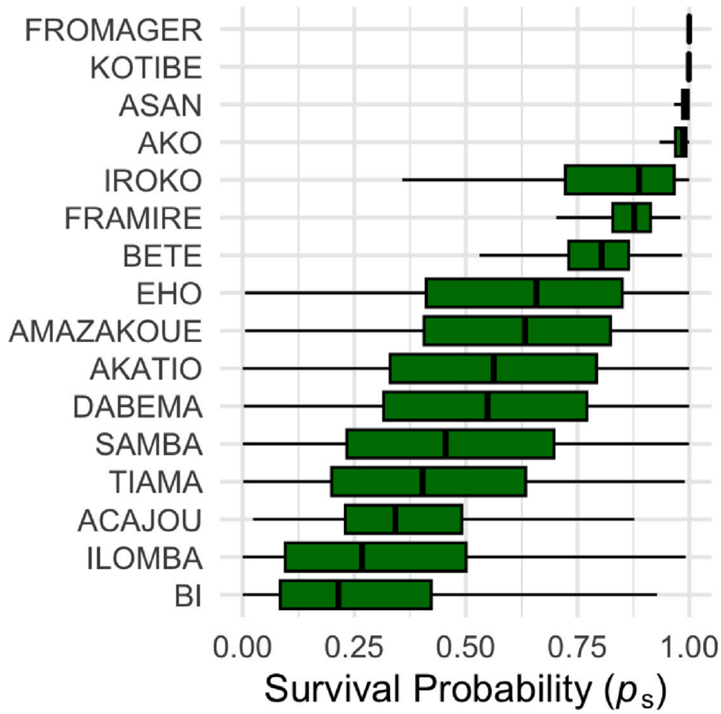

Fig. 2. Posterior distributions of species-specific survival probabilities (p_s) for 16 native tree species one year after planting. Each boxplot summarizes the uncertainty in p_s estimated from a hierarchical Bayesian model fitted to survival data collected in the ForestInnov experiment, Côte d'Ivoire. Survival was monitored across 21,609 seedlings planted in 2019.

deviation (σ). Specifically:

$$\begin{aligned}
&\theta_{\mathrm{SUN},s} \sim \mathcal{N}(\mu_{\mathrm{SUN}}, \sigma_{\mathrm{SUN}}) \\
&\theta_{\mathrm{DEL},s} \sim \mathcal{N}(\mu_{\mathrm{DEL}}, \sigma_{\mathrm{DEL}}) \\
&\theta_{\mathrm{COV},s} \sim \mathcal{N}(\mu_{\mathrm{COV}}, \sigma_{\mathrm{COV}}) \qquad (4) \\
&\theta_{\mathrm{CED},s} \sim \mathcal{N}(\mu_{\mathrm{CED}}, \sigma_{\mathrm{CED}}) \\
&\theta_{\mathrm{PAN},s} \sim \mathcal{N}(\mu_{\mathrm{PAN}}, \sigma_{\mathrm{PAN}})
\end{aligned}$$

The model was implemented in `Stan` using Hamiltonian Monte Carlo (HMC). All continuous covariates were scaled to the [0,1] interval to aid interpretability and sampling efficiency. Posterior distributions of parameters were used to assess both community-level effects (across species) and species-specific responses. We report posterior means and 95% credible intervals for all model parameters. This hierarchical formulation allows us to quantify general drivers of seedling survival as well as idiosyncratic species-level responses.

3. Results

3.1. Species survival

Posterior estimates of first-year survival probability (p_s) varied widely among the 16 native tree species included in the study (Fig. 2). The highest median survival probabilities were observed for *Fromager*, *Kotibé*, *Asan*, and *Ako*, with most posterior samples concentrated above 0.8. In contrast, species such as *Bi*, *Ilomba*, and *Acajou* exhibited lower median survival probabilities, generally below 0.4. Several species, including *Tiama*, *Samba*, *Dabéma*, *Akatio*, and *Amazakoué*, showed intermediate survival performance, with posterior medians between 0.4 and 0.7.

The uncertainty around these estimates, reflected by the width of the posterior distributions, also varied substantially among species. Some species, such as *Fromager*, *Framiré*, and *Ako*, displayed relatively narrow credible intervals, indicating consistent survival outcomes across the dataset. In contrast, wider distributions were observed for species like *Ilomba*, *Eho*, and *Akatio*, suggesting lower data informativeness for those species.

Together, these results highlight strong species-level differences not only in survival performance but also in the confidence with which these estimates can be interpreted.

3.2. Survival determinants

All covariates have negative mean effects on survival (Fig. 3). The effects of *Delay*, *Panicum*, and *SunLight* (absence of banana) are similar in magnitude, with posterior means close to −2. The effect of *Cover* (herbaceous vegetation) is slightly stronger, with a posterior mean around −3.5. The largest negative effect is associated with *Cedrela* presence, with a posterior mean near −4. The width of the credible intervals varies among covariates. *SunLight* has a relatively narrow interval, indicating more precise estimate. *Delay*, *Panicum* and *Cover* have intermediate intervals. In contrast, the interval for *Cedrela* is wider, reflecting lower certainty in the estimated average effects.

3.2.1. Planting delay

Predicted effects of planting delay on seedling survival showed substantial variation among the 16 native tree species analyzed (Fig. 4). For most species, survival probability declined as planting was delayed. In several species, including Framiré, Dabéma, Tiama, and Bété, survival dropped sharply with increasing delay. In contrast, species such as Kotibé, Ako, and Iroko maintained high survival probabilities across the full range of planting delays.

A group of species—including Amazakoué, Eho, Acajou, and Akatio exhibited intermediate responses, with survival decreasing more gradually over time. Fromager and Asan showed little change in predicted survival up to approximately 80 days after the reference date, followed by a marked decline. Three species, Bi, Ilomba and Samba, showed an increasing trend in survival probability with later planting dates.

3.2.2. Effects of sunlight

Species-level effects of sunlight exposure on the log-odds of seedling survival varied markedly among the 16 native tree species analyzed

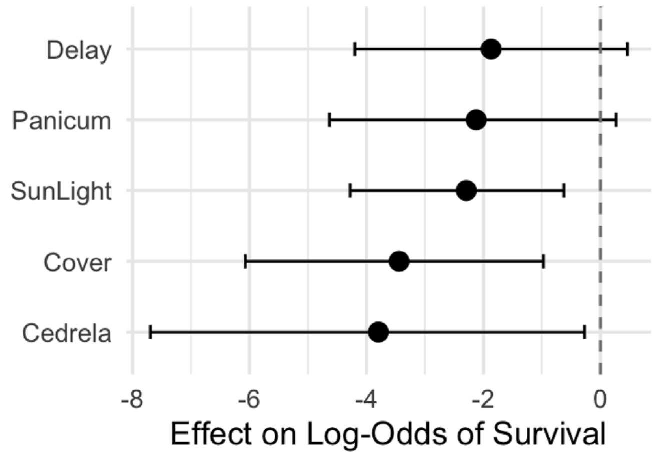

Fig. 3. Posterior means and 95% credible intervals for the average effect of five covariates on the log-odds of first-year seedling survival, estimated across all species. All effects are negative, indicating a detrimental influence of planting delay, *Panicum* presence, absence of banana shading (SunLight), herbaceous cover, and *Cedrela odorata* presence on seedling survival probability.

(Fig. 5). For most species, the posterior distributions of the SunLight effect were negative, indicating a tendency toward reduced survival under full sunlight. The strongest negative effects were observed for Ako, Eho, Acajou, Amazakoué, Akatio, and Dabéma, all of which showed median effects below −4. Intermediate negative effects were observed for Tiama, Asan, Bété, Samba and Framiré with posterior medians ranging from approximately −2 to −4. For several species including Fromager, Iroko, Ilomba, Bi, the estimated effects were close to zero or slightly positive for Kotibé, suggesting minimal impact of sunlight exposure on survival probability.

3.2.3. Competition

Posterior estimates of species-specific effects of biotic competition revealed contrasting responses among the 16 native tree species (Fig. 6). The three competitive factors — Cedrela, Cover, and Panicum — each showed predominantly negative effects on survival, though the magnitude and certainty of these effects varied by species.

The presence of *Cedrela odorata* had the strongest overall impact (Fig. 3), with clearly negative effects for species such as Kotibé, Ilomba, Samba, and Bi. A few species, including Acajou, Bété, and Ako, exhibited weakly positive responses.

Herbaceous cover also reduced survival for most species, though to a lesser extent. Strong negative effects were observed for Amazakoué, Dabéma, Ilomba and Kotibé, while others, like Tiama and Bété, showed little positive response.

The effect of *Panicum sp.* was moderate but similarly variable. Species such as Eho, Bété, and Fromager showed consistent negative responses, whereas Ilomba, and Dabéma appeared more tolerant, with posterior distributions overlapping zero or skewed positive. These findings highlight clear differences in sensitivity to competition among species, with implications for planting strategy and management.

3.3. Optimal planting conditions

The operational synthesis presented in Table 2 highlights clear interspecific variation in optimal planting conditions and management priorities among the 16 native species studied. Species with high survival potential under current conditions include Fromager, Kotibé, Asan, Ako, Iroko, Framiré, and Bété. Among these, early planting was particularly recommended for Framiré, Bété, and Asan, while others like Kotibé, Ako, and Iroko showed greater flexibility in planting period. Shade requirements also varied: Eho, Amazakoué, Akatio, Dabéma, Tiama, Acajou, and Asan benefited from partial or full shading, whereas species like Ako, Iroko, and Kotibé tolerated full sun. Competition sensitivity — aggregating effects from herbaceous cover, *Panicum sp.*, and *Cedrela odorata* — was a major factor for several species. Fromager, Kotibé, Amazakoué, Akatio, Ilomba, Bi, and Iroko were found to be particularly vulnerable to competitive pressure and would require careful vegetation management. In contrast, species such as Tiama, Bété, and Framiré showed lower sensitivity and can be planted under lighter management regimes.

4. Discussion

The overall negative effects of planting delay, sunlight exposure, and vegetation competition on seedling survival (Fig. 3) align with widespread challenges in tropical forest restoration, where early establishment is often limited by harsh microclimatic conditions and intense biotic pressure (Meli et al., 2017). While all covariates showed detrimental effects on survival, species responded with differing intensity, reflecting their ecological strategies and adaptive traits. This variation reinforces a central tenet of restoration ecology: species performance is context-dependent, and effective reforestation requires tailoring planting strategies to species-specific sensitivities (Chazdon et al., 2017).

4.1. Early survival reflects ecological niches

The substantial variation in first-year survival among the 16 native tree species tested highlights the importance of species-level ecological strategies in determining early plantation success. Some species, such as *Ceiba pentandra* (Fromager), *Celtis zenkeri* (Asan), *Antiaris africana* (Ako), and *Nesogordonia papaverifera* (Kotibé), exhibited consistently high survival probabilities, with posterior medians exceeding 0.8 and relatively narrow credible intervals. These generalist species (Swaine, 1996) share traits commonly associated with early-stage resilience, including moderate drought tolerance, light-demanding behavior, and the ability to establish in disturbed or open environments. Although, apart from *Ceiba pentandra*, none of these species are strict pioneers in the classical sense (Swaine and Hall, 1983), their performance under full light suggests ecological strategies that tolerate, or even benefit from, high irradiance and early exposure. This is consistent with previous observations in West African forests, where *Ceiba pentandra* and *Antiaris africana* have been successfully used in degraded lands due to their fast growth and robustness to environmental stress (Appiah et al., 2020; Kumi et al., 2024).

In contrast, species such as *Eribroma oblongum* (Bi), *Pycnanthus angolensis* (Ilomba), and *Khaya anthotheca* (Acajou) showed markedly lower survival probabilities, generally below 0.4. These species are known to be more sensitive to drought (Louppe et al., 2008) and to temporary soil moisture deficits during the early establishment phase, as suggested by previous studies (Hawthorne, 1995; Veenendaal et al., 1996). Their poor performance in open-field plantations thus emphasizes the need for protective silvicultural measures — such as planting in wetter periods or assisted moisture management — if they are to be successfully integrated into reforestation schemes.

Several species, including *Guibourtia ehie* (Amazakoué), *Piptadeniastrum africanum* (Dabéma), *Triplochiton scleroxylon* (Samba), and *Entandrophragma angolense* (Tiama), displayed intermediate survival (posterior medians between 0.4 and 0.7). These are typically light-demanding (Hawthorne, 1995), whose performance likely depends on interactions among planting time, competition, and local site conditions.

Taken together, these findings reinforce that species selection for reforestation must be grounded in ecological understanding (Brancalion and Holl, 2020). Fast-establishing, light-demanding species with robust early survival can serve as structural anchors in early plantation phases,

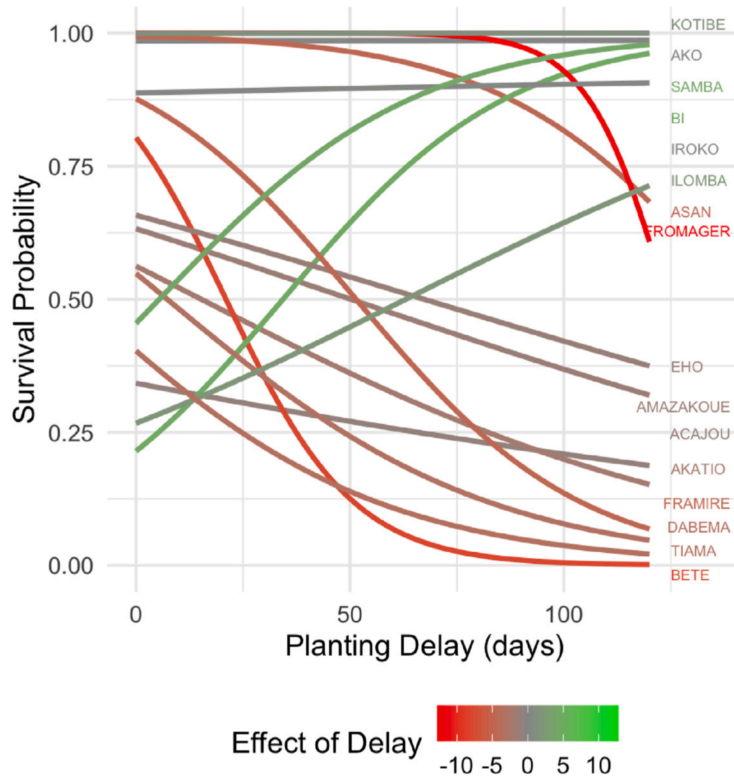

Fig. 4. Predicted survival probability over a range of planting delays for 16 native tree species. Curves represent species-specific posterior median predictions from a hierarchical Bayesian model. Line color reflects the estimated effect of planting delay on the survival probabilities, ranging from strongly negative (red) to positive (green). Because several species exhibit very similar final survival values, species names are positioned and colored identically to their respective curves, following their ranking at the end of the *x*-axis to facilitate matching between labels and trajectories.

particularly in open or degraded areas. However, the observed variation in survival does not correspond neatly to classical successional status (Table 2), as most West African tree species exhibit flexible, light-demanding traits even when classified as mid- or late-successional. This pattern suggests that the ecological niche of each species is broader and shaped by multiple factors beyond the classical pioneer-mature gradient paradigm, other factors such as drought resistance and competition sensitivity. Nonetheless, these differences echo findings from successional consortia and priority-effect frameworks, where the temporal assembly of functionally diverse species enhances establishment success through facilitation and niche complementarity (Rodrigues et al., 2011; Restrepo-Carvajal et al., 2024). Applying such concepts to restoration design could help structure plantations that combine high-surviving facilitators with low-surviving, resource-conservative species, better mimicking species interactions in natural forests.

4.2. Planting time matters

Our results demonstrate a generally negative impact of planting delay on seedling survival, with 10 out of 16 species showing a marked decline in survival probability as the delay increased across most of the 16 studied native tree species (Fig. 4). For many taxa — such as Framiré, Dabéma, Bété and Tiama — survival probabilities drop markedly when planting is delayed beyond the early rainy season, highlighting their sensitivity to initial moisture conditions (Engelbrecht et al., 2006). Early planting allows seedlings to take full advantage of soil water availability at the beginning of the rainy period, facilitating root establishment and reducing exposure to heat and competition stress (Cardoso et al., 2016). Delayed planting, conversely, increases the risk of water deficit during the critical establishment phase and can lead to poor rooting, increased pathogen exposure, and lower resilience (Oliva et al., 2014; Milici et al., 2020).

However, a few species — such as Samba and Bi — display more stable or even positive trends with planting delay, at least in the initial phase. These species may exhibit traits of ecological plasticity that enable them to survive even when planted later. Alternatively, delayed planting may reduce exposure to early pest outbreaks (Welch and Harwood, 2014) or heavy rainfall events that cause seedling washout, especially for species with slow early growth (Palma and Laurance, 2015). It is also possible that late-planting conditions reduce interspecific competition for light if pioneer herbs and grasses have already peaked in biomass and begin senescing (Yin et al., 2023).

In the context of climate change, the effects of planting delay are likely to become more acute in West Africa. Indeed, projections for West Africa indicate increasing rainfall variability and shorter, more erratic rainy seasons in the region (Biasutti, 2019; Le Barbé et al., 2002). These changes may shorten the effective planting window and increase the risk associated with delayed planting, particularly for moisture-sensitive or late-successional species. Moreover, higher temperatures may exacerbate evapotranspiration losses, further penalizing seedlings planted later in the season (Will et al., 2013). As a result, developing flexible planting schedules that reflect species-specific sensitivities to moisture availability and account for increasing climatic unpredictability will be essential to maximizing seedling survival (Ramón Vallejo et al., 2012).

4.3. Banana shade, Better seedlings

Our results indicate a generally negative impact of full sunlight exposure on seedling survival, as demonstrated by the negative posterior means of the sunlight covariate across most species (Fig. 5). These findings are consistent with agroforestry practices — particularly in cocoa and coffee systems — where bananas (*Musa spp.*) are widely used as temporary shade providers during the establishment phase (Olatunde et al., 2014). In our study, most species showed improved survival

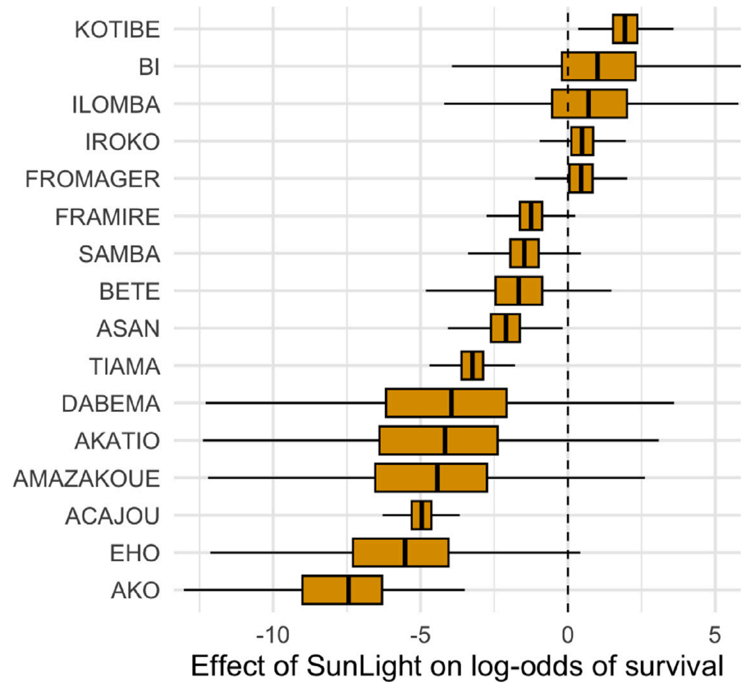

Fig. 5. Posterior distributions of the species-specific effects of sunlight exposure — measured as the absence of banana shading — on the log-odds of seedling survival. Each boxplot summarizes the posterior distribution of the SunLight effect (θ_{SUN}) for a given species, as estimated from the hierarchical Bayesian model.

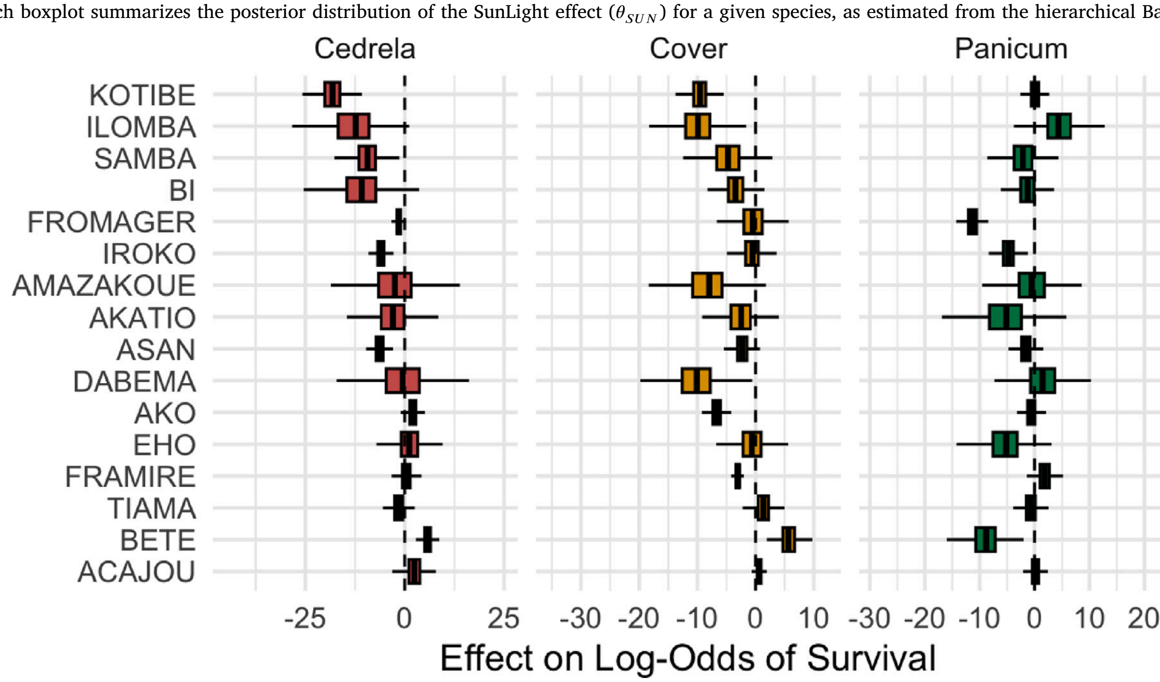

Fig. 6. Posterior distributions of species-specific effects of three biotic competitors — *Cedrela odorata*, general herbaceous cover, and *Panicum maximum* — on the log-odds of seedling survival for 16 native tree species. Each boxplot represents the posterior distribution of the species-specific effect estimate for one covariate, as inferred from a hierarchical Bayesian model. The three panels display the effects of (left) Cedrela presence, (middle) overall herbaceous ground cover, and (right) the presence of Panicum maximum. Species are ranked top to bottom by their average sensitivity across the three sources of competition, with those at the top tending to respond more negatively. Negative values indicate a reduction in survival probability due to competition.

under banana cover, reinforcing the idea that partial shading plays a key role in creating favorable microhabitat conditions for seedlings.

Banana plants contribute to this buffering effect through several mechanisms. Their large leaves intercept direct solar radiation, substantially reducing ground-level temperatures and the intensity of evapotranspiration. They also help maintain higher relative humidity in the understory, a benefit especially important in the early dry spells of the rainy season. Additionally, fallen banana leaves form a thick organic mulch that suppresses weeds, slows evaporation, and enhances soil moisture retention (Niether et al., 2017; Blomme et al., 2022). Farmers frequently report that banana-based systems "keep the ground cooler and moister", a perception supported by empirical measurements in smallholder agroforestry plots (Blomme et al., 2022).

Conversely, species such as Kotibé, Ilomba, and Bi appeared less dependent on shade, suggesting they may possess more plastic or light-tolerant traits. However, even some typically light-demanding species, such as Fromager (*Ceiba pentandra*), experienced modest gains under shaded conditions. This indicates that the benefits of banana

shading may extend beyond simple light attenuation, providing broader microclimatic and edaphic advantages — such as reduced thermal stress, moderated soil moisture fluctuations, and diminished herbaceous
competition — that support seedling establishment across a range of functional strategies.

The facilitative role of banana trees parallels the “nurse-species” effect observed in natural regeneration systems, where fast-growing plants improve soil moisture and temperature regimes for slower species (Gómez-Aparicio, 2009; Bechara et al., 2021). This suggests that agroforestry-based shade mechanisms could be adapted as deliberate facilitation tools in restoration plantings, reducing mortality and accelerating early succession.

4.4. Competition shapes survival

Vegetation cover — woody and herbaceous — strongly shapes seedling survival in tropical reforestation (Morrison et al., 2019). Competition exerts species-specific effects influenced by the traits of both planted seedlings and surrounding vegetation. In our study, the effects of total cover varied widely, suggesting both facilitative and competitive interactions were at play (Dohn et al., 2013). From a forestry perspective, early competition is a key driver of plantation outcomes, influencing both species selection and site preparation strategies (Espinoza, 2004). Fast-growing, shade-tolerant species may thrive under moderate canopy closure, benefiting from reduced evapotranspiration and microclimate buffering. However, their performance often declines when root competition for limited soil resources becomes intense (Herault et al., 2010). Such dynamics highlight the need to match species traits with local conditions and to actively manage competition through spatial arrangement and vegetation control (Onyekwelu et al., 2011).

The strong negative effect of *Cedrela odorata* across species highlights concerns about this exotic. Although valued for timber, *Cedrela* is competitively dominant at early stages, with rapid vertical growth and dense shade (Kilawe et al., 2023). It competes aggressively for light and water and may release allelopathic compounds (Kilawe et al., 2023). Our findings reinforce the need to limit its use in restoration aimed at native biodiversity (Van der Meersch et al., 2021). In contrast, the effect of herbaceous layers like *Panicum* was more variable. Dense grasses can hinder tree regeneration via shading and soil resource competition (Vieira and Scariot, 2006), but they may also buffer soil temperatures and reduce evaporation—benefiting moisture-sensitive species (Holl, 1999). These dual effects suggest that complete weeding may not be optimal. Selective management — partial retention with density control — could support seedling survival.

Total vegetation cover thus exerts a combination of shading, competition, and microclimate regulation. The net impact depends on species strategy: some benefit from moderated conditions, while others suffer from light limitation or root interference. These results support a trait-based and adaptive restoration approach that adjusts vegetation management to species needs.

5. Conclusions

Overall, our results indicate that early survival patterns in mixed-species plantations cannot be explained solely by successional status. While several fast-growing, light-demanding species showed strong establishment, others with comparable pioneer traits displayed lower survival, suggesting that additional factors — such as drought sensitivity or competition — play critical roles. This supports a more nuanced view of species functional diversity in restoration, where both pioneer and slower-growing species contribute complementary functions to ecosystem recovery. Approaches based on successional consortia and staged (scalonated) planting (Rodrigues et al., 2011; Restrepo-Carvajal et al., 2024) recognize that early facilitators can improve conditions for moisture-sensitive or shade-tolerant taxa introduced later, but their effectiveness depends on context-specific interactions among species and environment. Integrating such adaptive strategies with the framework species concept (Elliott et al., 2023) and facilitation-based designs (Gómez-Aparicio, 2009; Bechara et al., 2021) offers a pragmatic path forward—one that balances rapid canopy closure by robust high-surviving species with the long-term persistence and diversity provided by less performing species. In this sense, our findings advocate for mixed, functionally complementary assemblages rather than categorical separation between “pioneer” and “late-successional” species in West African reforestation planning. Practically, our results provide actionable insights for designing and managing native tree plantations in West Africa. The clear message is that no one-size-fits-all strategy exists—species differ in their shade tolerance, sensitivity to competition, and benefit from early planting. Practical guidelines emerge from this work:

- Prioritize early planting for sensitive and slow-growing species such as Acajou, Amazakoué, and Bété. Timely establishment avoids peak dry-season stress and gives seedlings a crucial head start in establishing roots before competition intensifies. These species have low initial vigor and benefit significantly from early moisture availability.
- Implement targeted weed and grass control, especially for high-competition-sensitive species like Kotibé, Ilomba, and Bi. Full removal of herbaceous cover is not always necessary—instead, maintain a balance that limits resource competition while preserving microclimatic benefits such as reduced soil desiccation. Mechanical slashing and timing of weeding relative to rainfall can be effective strategies.
- Promote banana shading as a widely beneficial microclimatic buffer. Most species in this study, regardless of their light preference, showed improved survival under banana shade—likely due to reduced heat, moderated humidity, and soil moisture conservation. Species such as Eho, Ako, and Acajou showed particularly strong responses. Incorporating banana plants early not only helps reduce abiotic stress but also creates a gentler transition from nursery to field conditions
- Avoid and/or remove aggressive companion species such as *Cedrela odorata*, especially in native plantations. While fast-growing and economically valuable, Cedrela can overtop native seedlings quickly and suppress their growth via light and root competition. Unless carefully managed or isolated, its inclusion undermines restoration objectives focused on native diversity and structural heterogeneity.
- For sun-tolerant pioneers like Fromager, open planting is suitable if competition is well controlled. This species is capable of fast establishment in full sun, provided surrounding grasses and herbs are managed early. It is an ideal candidate for degraded sites with high exposure, especially when paired with early interventions to limit competitive pressure. Other robust species such as Kotibé and Iroko also perform well under high light conditions but require strict control of surrounding vegetation due to their high sensitivity to competition. These species combine light tolerance with structural resilience, making them suitable anchors for mixed plantations on exposed sites.

Tree planting provides flexibility and control but remains a complex endeavor that demands context-specific planning. Our results show that early survival varies strongly among species, emphasizing the need for adaptive design rather than uniform prescriptions. In areas where seed sources persist and degradation is moderate, assisted natural regeneration can complement planting as a cost-efficient and ecologically grounded option (Amani et al., 2022; Doua-Bi et al., 2021; Koffi et al., 2025). Effective restoration should integrate enrichment planting, shading management, and competition control to match site history and functional goals. Future work should refine trait-based selection, identify effective nurse species, and track long-term trajectories beyond establishment. Despite challenges from competition and climate variability, our findings demonstrate that diversified, well-planned management can make forest recovery both feasible and resilient. With appropriate strategies, a diverse and durable forest can re-emerge even on the most demanding sites.

CRediT authorship contribution statement

Ibrahim Konaté: Writing – review & editing, Visualization, Methodology, Formal analysis, Data curation. **Evans Ehouman:** Writing – review & editing, Methodology, Investigation. **Fatima Wourro:** Writing – review & editing, Methodology, Investigation. **Yves Doua-Bi:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Fabrice Tiéoulé:** Writing – review & editing, Supervision, Conceptualization. **Brahima Coulibaly:** Writing – review & editing, Funding acquisition, Conceptualization. **Jean-Claude Koffi Konan:** Writing – review & editing, Funding acquisition, Conceptualization. **Irie Casimir Zo-Bi:** Writing – review & editing, Funding acquisition, Conceptualization. **Bruno Hérault:** Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Bruno Herault reports financial support was provided by FIRCA-FCIAD. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix. Scatterplots showing bivariate relationships among the four quantitative predictors recorded at planting

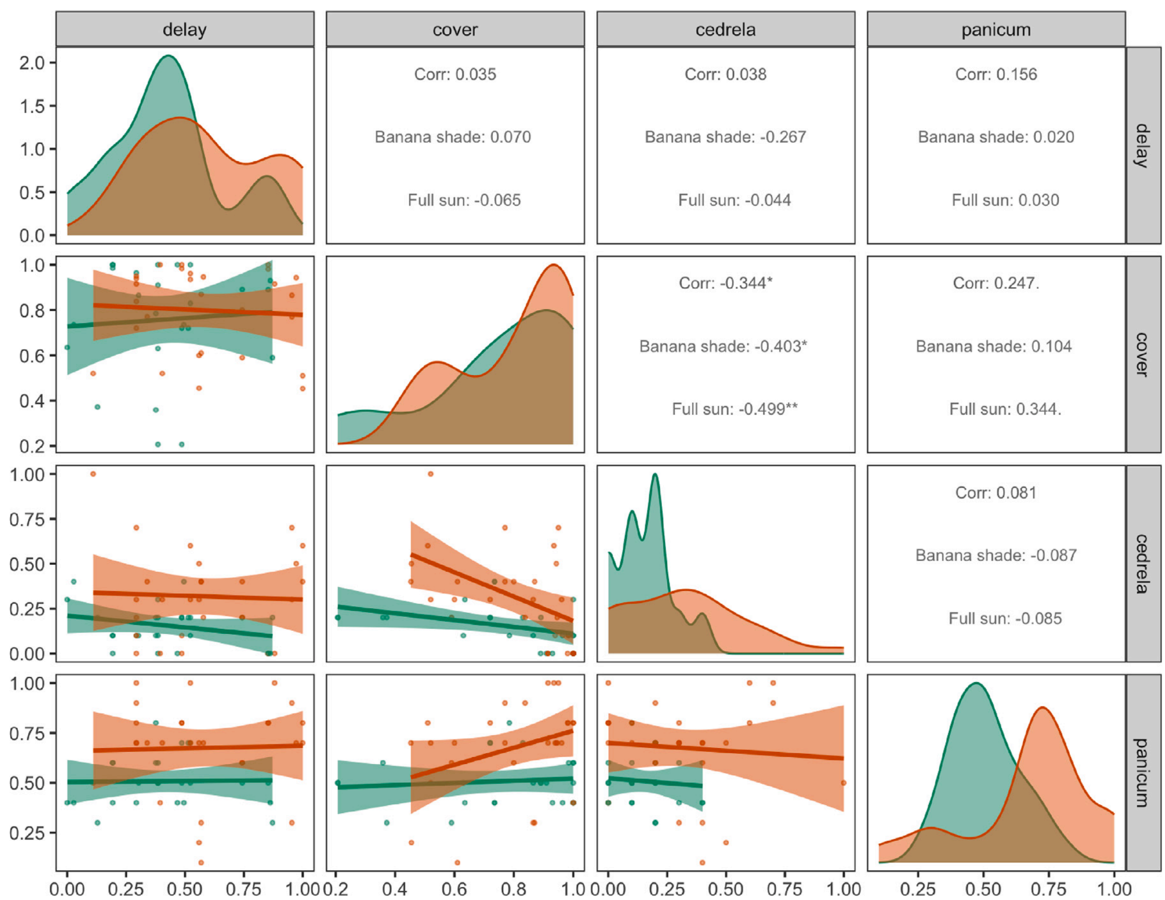

Fig. 7. Scatterplots (lower triangle) show bivariate relationships among the four quantitative predictors recorded: Delay (days after the optimal planting date), Cover (mean herbaceous ground cover, %), Cedrela (presence frequency of Cedrela odorata in sampled subplots, %), and Panicum (presence frequency of Panicum spp., %). Points are colored by the binary light treatment SunLight (green = Banana shade; orange = Full sun), and ordinary least-squares regression lines with 95% confidence bands are overlaid for each treatment level to visualize trends. The diagonal panels display kernel density estimates for each variable, and the upper-triangle panels report Pearson correlation coefficients computed over all observations and for each *Sunlight* level. This single, multi-panel visualization summarizes covariation among competition metrics (Cover, Cedrela, Panicum), planting timing (Delay), and light environment (via color groups), helping diagnose collinearity, reveal potential interaction structure (different slopes by SunLight), and guide model specification and interpretation for survival analyses.

Data availability

Datas are available in Zenodo: https://doi.org/10.5281/zenodo.17045265.

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