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RECEIVED 25 December 2025
REVISED 10 March 2026
ACCEPTED 11 March 2026
PUBLISHED 14 April 2026

CITATION
Ntamwira J, Ocimati W, Kearsley E,
Mirindi TC, Shabani G and Blomme G
(2026) Screenhouse-based shade-
tolerance assessments of coffee and
bean varieties, and cover crops, to
optimize multi-strata intercropping in
African smallholder systems.
Front. Agron. 8:1775355.
doi: 10.3389/fagro.2026.1775355

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Screenhouse-based shade-tolerance assessments of coffee and bean varieties, and cover crops, to optimize multi-strata intercropping in African smallholder systems

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Introduction: Intercropping annuals with perennials such as banana, coffee and trees is widespread in East and Central Africa, where farms are typically small and fragmented. Within such multi-strata production systems, shade is a critical constraint affecting crop productivity. This study aimed to identify crop species and varieties tolerant to varying shade levels.

Methods: Twenty common bush and climbing bean (*Phaseolus vulgaris*) varieties each, eight Arabica coffee (*Coffea arabica*) varieties, and three cover crops (velvet bean (*Mucuna pruriens*), rattle pod (*Crotalaria grahamiana*), and elephant grass (*Pennisetum purpureum*)) were screened under four screenhouses transmitting photosynthetically active radiation (PAR) levels of 70%, 50%, 35% and 10% compared to open field light levels.

Results: Eight bush and four climbing bean varieties maintained grain yields comparable to open-field conditions at low (70% light transmission) shade conditions. High tolerance persisted for many beans at 50% and 35% transmission, though only two bush beans (HM21-7, CODMLB 499) remained unaffected at the deepest shade (10% light transmission). Bush beans consistently elongated under shade, whereas climbing beans showed mixed height responses. Arabica coffee seedlings exhibited stable height and stem diameter across all shade levels, with only a few varieties showing modest reductions. Cover crops showed no shade tolerance, with > 84% above-ground biomass loss across all shade levels for elephant grass. Meanwhile velvet bean and rattle-pod suffered 48–58% biomass losses even at 70% light transmission, though velvet bean retained a high root mass until the deepest shade.

Discussion: These findings suggest a high diversity in shade tolerance within existing bean and coffee varieties. They demonstrate that selecting shade-tolerant bean cultivars and stable coffee varieties can substantially improve productivity in

multi-strata systems, while many common cover crops are unsuitable beneath canopy shade. Rapid phenotypic screening could offer a low-cost strategy for optimizing crop mixtures and guiding breeding efforts toward greater shade resilience in smallholder multi-strata agro-ecosystems.

KEYWORDS

banana, coffee, intercropping, light intensity, perennial, greenhouse

Introduction

Intercropping annual crops among perennial species such as banana, coffee, and various trees is widespread throughout East and Central Africa (ECA) and provides substantial value to smallholder farmers (Ouma, 2009; Blomme et al., 2023). These diversified systems deliver multiple ecosystem services and livelihood benefits, including improved food and nutrition security, fuel provision, income diversification, soil conservation, pest and disease suppression, and greater climate resilience (Jha et al., 2011; Lithourgidis et al., 2011; van Asten et al., 2011; Bongers et al., 2015; Gebru, 2015; Duguma et al., 2019; Blomme et al., 2023; Gambart et al., 2020; Kishaija et al., 2025). Beyond these advantages, intercropping is often practiced out of necessity. Farmlands in the ECA region are typically small (< 2 ha) and highly fragmented (Tinzaara et al., 2018; Marinus et al., 2022), thus, intercropping enables farmers to maximize the productivity of limited plots (Ouma, 2009; Titttonell and Giller, 2013; Nassary et al., 2020; Ocimati et al., 2019, 2021). Moreover, other cultural practices, such as crop rotation, afforestation, shifting cultivation, and fallowing, previously crucial for maintaining or restoring the productivity and health of agroecosystems are increasingly unfeasible given the shrinking and fragmented nature of farms (Bogaert et al., 2008; Kristjanson et al., 2012; Bishaw et al., 2013). Consequently, intercropping has become a critical strategy for maintaining agricultural productivity and resilience in the region.

Common multi-layered systems in smallholder settings in ECA include coffee- or banana-based production systems, their combination into coffee–banana systems, and coffee or banana agroforestry systems (van Asten et al., 2011; Duguma et al., 2019; Blomme et al., 2023). Here, farmers often integrate diverse companion understory crops such as annual legumes, cover crops, cereals, vegetables, and forages (van Asten et al., 2011; Harelimana et al., 2018; Siles et al., 2022). In such multi-strata systems, the ability of a crop to tolerate shade is a critical factor. Shade tolerance is the ability of a plant to survive, grow, and reproduce in environments with low light availability, such as below the canopy of other vegetation (Valladares and Niinemets, 2008; Avalos, 2019). Some crops such as coffee (*Coffea arabica*) are relatively shade-tolerant and may even benefit in terms of bean quality and reduced pest pressure under moderate shade (Vaast et al., 2006; Haggard et al., 2021). The modification of microclimate through shading helps buffer against extreme heat and drought, potentially mitigating coffee suitable area losses (Merle et al., 2022; Getachew et al., 2023). Several legumes such as lablab (*Lablab purpureus*), cowpea (*Vigna unguiculata*), and pigeon pea (*Cajanus*

cajan) have also been reported to exhibit a good level of tolerance to shade (Manoj et al., 2019; Umesh et al., 2023).

In contrast, for other crops, shade can be a key biophysical constraint, limiting photosynthesis, reducing yields, and altering plant morphology and pest dynamics (Hadi et al., 2006; Umesh et al., 2023). For example, common crops such as some bush and climbing bean (*Phaseolus vulgaris*), chickpea (*Cicer arietinum*), cassava (*Manihot esculenta*) and soybean (*Glycine max*) varieties exhibit strong yield declines under shade (Blomme et al., 2020, 2022). For beans specifically, Akyeampong et al. (1999) reported a 27% decline in yield due to a 42% decline in total Photosynthetic Active Radiation relative to the control. Wortmann and Sengooba (1993) also reported a 50% decline in the yield of 16 bush bean genotypes under banana, due to competition, including for light. Thus, the success of the understory crop species or varieties largely depends on their ability to maintain growth and yield under light-limited conditions.

Despite shade being a major agronomic constraint that limits yields in perennial production systems, the shade-tolerance of common intercrops used by smallholders in ECA remains poorly quantified. Key ECA studies have explored shade responses of individual crops or crop varieties within coffee and banana plantations in field conditions (e.g., Ntamwira et al., 2021; Blomme et al., 2020, 2022). However, without standardized shading gradients, these results provide only limited insight into the true shade-tolerance of the intercrops and lack systematic comparisons across species and varieties. Screening species and varietal combinations for inherent shade-tolerance within the existing diversity, matched to different shading levels, offers a practical solution towards improving productivity and system resilience without requiring major structural modifications to cropping systems. Such standardized shade-tolerance assessments are also key for crop selection towards improved breeding. Crop selection for future breeding programs rarely incorporates shade tolerance as a screening criterion, even though this trait is essential for most smallholders in the region. Most breeding initiatives have prioritized attributes such as drought tolerance, water-use efficiency, high yields, and resistance or tolerance to pests and diseases (Tester and Langridge, 2010; Mukankusi et al., 2019; Assefa et al., 2019; Parker et al., 2022; Ngure and Watanabe, 2024). Aligning shade tolerance with existing production systems, however, could markedly boost farm productivity. As an initial step, systematically screening this extensive genetic pool could identify specific species and varieties that possess shade-tolerance, providing valuable targets for use on farm and subsequent breeding work.

Accordingly, this study evaluated the shade tolerance of 20 common bean (*Phaseolus vulgaris*) varieties and eight Arabica coffee varieties grown under screenhouses providing 90%, 65%, 50%, and 30% shade levels, as well as in open field controls. Two leguminous cover crops, velvet bean (*Mucuna pruriens*) and rattle pod (*Crotalaria grahamiana*), and a fast-growing forage grass (*Pennisetum purpureum*) were also assessed. These insights aim to guide more effective crop selection and intercrop design for multi-strata systems in the ECA region, contributing to the development of more productive, diverse, and resilient smallholder agroecosystems.

Materials and methods

Screenhouse experiments were conducted at the Institut National pour l'Etude et la Recherche Agronomiques (INERA) Mulungu research station (02°19'22"S, 028°51'29"E, 1711 masl) in South Kivu province, eastern Democratic Republic of Congo (DR Congo). To establish four shade levels, four screenhouses (from the brand 'Balton Tanzania'), each having a different density of mesh netting to regulate light transmission were established with a North-South orientation to maximize sunlight exposure. The screenhouses, which measured 9 m x 5 m x 2.5 m height, allow light levels corresponding to 70%, 50%, 35% and 10% of full sunlight ([Supplementary Figure S1](#)). Exposure to full sunlight, i.e. open field conditions, served as a control. Shade tolerance of 20 common bean (*Phaseolus vulgaris*) varieties (including 10 bush and 10 climbing types) and 8 Arabica coffee varieties (*Coffea arabica*) was evaluated by assessing changes in crop growth and yield. Two leguminous cover crops (velvet bean (*Mucuna pruriens*) and bushy rattlerpod (*Crotalaria grahamiana*)), and a fast-growing forage grass (elephant grass (*Pennisetum purpureum*)) were also assessed. Shade-tolerance measurements were based on yield and/or biomass stability, and not the full physiological shade-tolerance attributes. A randomized complete block design was used within the different light scenarios.

Pots of different sizes according to the size of the different plant species were used for their establishment. Pots with a circumference of 50 cm and a height of 18 cm, spaced 20 cm apart, were used for the bean varieties and for the velvet beans. Due to their extensive root systems, elephant grass cuttings and bushy rattlerpod seeds were planted in larger pots measuring 86 cm in circumference and 27 cm in height and spaced 30 cm apart. Coffee seedlings were transplanted into pots measuring 70 cm in circumference and 30 cm in height, positioned 30 cm apart. A mixture of fertile forest soil [obtained from an INERA field] and river sand [bought in Bukavu], at a ratio of 67/33%, was used as a planting substrate for all plant species, with fresh soil substrates used for each new cropping cycle. Watering was carried out as needed, with less frequent watering occurring in rainy season months.

Limited temporal sampling and measurement of light intensity (i.e., photosynthetically active radiation, PAR values) within each screenhouse and in an open field adjacent to the screenhouses (control site) was conducted using a handheld digital light meter

(brand 'Photobio Phatom'), on a sunny day (between 11.00 am. and 3.00 pm., on August 30, 2023). Similarly, the ambient temperature was measured inside each screenhouse, at the center, and outside the screenhouses at 9 am and 12 pm on August 17, 2023. The diverse bean varieties evaluated, included CIAT hybrid lines, and bean varieties/hybrids sourced from the INERA legume research program. A summary of the characteristics of the various bean varieties/hybrids (market suitability, yield, growth, pest and disease reaction) are provided in [Supplementary Table S1](#). The experimental design was a RCBD in which each experimental unit consisted of one pot containing five plants for climbing beans and seven plants for bush beans. Pots were arranged in rows oriented in a north-south direction, and each block contained one pot per variety. For each bean variety, three pots were assessed at each shade-level, repeated during three cropping cycles. Bean plantlets were consecutively planted and harvested from September-December 2023, May-June 2024, and September 2024 - January 2025. To control aphid infestation, the beans were occasionally sprayed with a chemical pesticide [Dudu Ethoate 40%], especially in the dry season months. At each harvest event, plant height, number of bean pods per plant, total bean pod weight per plant (air dried weight) and total bean grain weight (air dried weight) per plant was assessed.

Eight Arabica coffee varieties were assessed. Two coffee cultivars 'Mulungu', and 'BM71' were obtained from the INERA-Mulungu nursery, while six other varieties (BM79, BM139, Jackson, Catuai, Burundi and BJ76) were sourced from the Virunga coffee cooperative nursery located in Kabare territory, South Kivu Province. For each variety, 8 plantlets (9-month-old coffee seedlings), with each seedling planted in a separate pot, were assessed at each shade-level for a period of one year between December 2023, and May 2025. The coffee plants were arranged in 8 rows, each row acting as a block (North-South orientation), with each cultivar appearing once and placed randomly per block. At the end of this trial, tree height and stem diameter at soil level were assessed. Coffee trees had not yet started flowering at trial end.

Single varieties of velvet bean (*Mucuna pruriens*) and bushy rattlerpod (*Crotalaria grahamiana*) were used. For each leguminous cover crop, 5 pots containing 3 plants each were assessed at each shade-level, repeated during two cropping cycles. The pots were placed randomly in a single row in the north-south direction to ensure uniform access to light. Velvet bean seeds and rattlerpod seeds were consecutively planted and harvested from January-June 2024, and June 2024 - January or March 2025 (for velvet beans and rattlerpod, respectively). At each harvest event, plant height, aboveground biomass (AGB; FW), root biomass (FW) and longest root length was assessed. Root biomass and length were assessed at pot level (i.e. not plant level), as roots were difficult to separate per plant within a pot.

The fast-growing elephant grass (*Pennisetum purpureum*) was similarly assessed, with 5 pots containing 3 cuttings (of 20 cm height) each at each shade-level, again during two cropping cycles. The pots were placed in a row as for the velvet beans and rattler pods. Cuttings were consecutively planted and harvested from January-August 2024, and July 2024 - March 2025. At harvest, plant height,

aboveground biomass (FW), root biomass (FW) and longest root length were assessed, in addition to the circumference of the grass mat at soil level, and the number of new lateral branches developed.

Growth and yield parameters were compared between varieties, for bush beans, climbing beans, and coffee across the different shade-levels and across shade levels for the cover crops and elephant grass. As yields varied between varieties and seasons, yield changes (loss or increase) as related to shade-levels were compared to average yields per plant of each variety in open field conditions. For analysis, measurements from plants within a pot were averaged, and the pot mean was used as the unit of analysis. Because yields differed between plants or varieties and between seasons, yield responses to shade were expressed relative to the average yield per plant of each variety under open-field conditions. Changes in plant growth and yield across shade levels were analyzed using an analysis of variance (ANOVA) based on the RCBD structure, after assumptions of normality and homoscedasticity (were evaluated using the Shapiro–Wilk and Bartlett’s tests, respectively. When assumptions were satisfied, treatment means were separated using Tukey’s HSD test at the 5% significance level. When ANOVA assumptions were not met, the non-parametric Kruskal–Wallis test was applied, followed by pairwise comparisons using the Mann–Whitney U (Wilcoxon rank-sum) test at $\alpha = 0.05$, with continuity correction (Benjamini and Hochberg, 1995). All statistical analyses were conducted in R statistical software version 4.5.1 (R Core Team, 2025), using the packages stats version 4.5.2 (R Core Team, 2025) and agricolae version 1.3.7 (de Mendiburu, 2023).

Shade tolerance at each shade level was assessed based on bean grain yield for all bean varieties, and on aboveground biomass for the cover crops, as these are the critical products for these crops. The percentage of yield change as compared to open field conditions was investigated. When bean grain yield in a shaded condition was not significantly different from open field, the bean variety was classified as having high tolerance. If yield loss was significantly different from open field, a threshold of average yield loss was used, with yield loss <50% classified as medium tolerance, and of >50% as low tolerance.

Results

Mean photosynthetically active radiation (PAR; $\mu\text{mol m}^{-2} \text{s}^{-1}$) inside the four screenhouses, expressed relative to the open-field control, confirmed the intended shade gradient. PAR in the screenhouses allowing 70%, 50%, 35%, and 10% nominal light transmission averaged 1340 ± 119 , 932 ± 93 , 653 ± 44 , and $216 \pm 50 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, compared with $2150 \pm 108 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the open field. These values corresponded to mean measured light transmissions of 65.6% (± 6.1), 44.7% (± 4.1), 30.8% (± 1.9), and 9.6% (± 2.3), closely aligning with the manufacturers’ specifications of 70%, 50%, 35%, and 10% light transmission. For clarity, and due to observed rapid changes in PAR with light intensity e.g. due to cloud cover resulting in the possible deviation between the measured and nominal transmission, the nominal values, were used. Air temperature did not differ between the open field and the screenhouses at 9:00,

but at 12:00 decreased significantly ($p < 0.001$) with increasing shade from $35.5 \pm 1.0^\circ\text{C}$ in the open field to $32.5 \pm 1.0^\circ\text{C}$ under 10% light transmission (Table 1).

Eight bush bean cultivars and four climbing bean varieties demonstrated a high tolerance to low shade (70% light transmission; Supplementary Figure S1; Table 2; Supplementary Table S2). Under these conditions their bean grain yields were statistically indistinguishable from those obtained in open-field conditions. Three climbing bean varieties already exhibited a low tolerance at the same shade level, namely NABE12C, MAC44 and COD59/1-2, with bean grain yields significantly reduced by 53–73% on average. The remaining bean varieties also showed significant yield reductions relative to open-field conditions, though the losses were more moderate, ranging from 25% to 50%, which we classify as medium shade tolerance.

Most bean varieties with high tolerance to low shade maintained high yields at 50% light (Supplementary Figure A2; Table 2; Supplementary Table S2), except for climbing bean variety RWV1129 reducing to medium shade tolerance. On the other hand, bush bean variety CODMB 514 showed a high tolerance to 50% light, even though a reduced tolerance was observed at 70% light transmission.

At deeper shade levels of 35% light transmission, six bush bean cultivars and four climbing bean varieties maintained a high tolerance (Supplementary Figure S2; Table 2), i.e. with yield losses indistinguishable from open field conditions. Finally at the deepest shade level of 10% light transmission, only two bush bean varieties maintained high shade tolerance, namely HM21-7 and CODMLB 499, showing no significant yield reduction compared with open-field conditions (Supplementary Figure S2; Table 2). Five bush bean varieties and nine climbing bean varieties showed low tolerance under deep shade (10% light transmission), each with > 50% average yield losses. Remaining varieties fell into the medium-tolerance category, experiencing smaller (but significant) average yield declines.

Overall, bush bean varieties outperformed climbing beans in shade tolerance (Supplementary Figure S2; Table 2). Nevertheless, even the most tolerant lines showed seasonal fluctuations, with yield losses generally higher during the third investigated cropping cycle (season 3; Supplementary Figure S2). For example, the highly tolerant HM21-7 and CODMLB 499 presented reduced yields across all shade levels during this season.

TABLE 1 Average temperatures in the screenhouses and the open field control in the morning and at noon.

% light transmission	Temperature at 9am	Temperature at 12pm
100	12.1 ± 0.6	35.5 ± 1.0 a
70	12.6 ± 0.4	34.5 ± 0.9 ab
50	12.4 ± 0.3	33.7 ± 0.5 b
35	12.4 ± 0.2	33.7 ± 0.3 b
10	12.2 ± 0.6	32.5 ± 1.0 c
p	ns	< 0.001

Mean temperature values followed by the same letter are not significantly different at 5% Tukey’s HSD test level.

TABLE 2 Mean bean yield (as weight of bean grains) for each bush bean (BB) and climbing bean (CB) variety at low to deep shade expressed as a percentage of the average plant-level bean yield at 100% light.

Bean varieties	% bean yield change at 70% light	Tolerance to 70% light	% bean yield change at 50% light	Tolerance to 50% light	% bean yield change at 35% light	Tolerance to 35% light	% bean yield change at 10% light	Tolerance to 10% light	diff to open field
BB: HM21-7	98.8 ± 190.5 AB	high	96.5 ± 203.9 AB	high	58.2 ± 119.2 B	high	6.1 ± 107.3 AB	High	p < 0.05
BB: CODMLB 499	63.9 ± 190.7	high	52 ± 168.3	high	11.7 ± 95.5	high	-16.1 ± 113.6	High	ns
BB: KKREOBEAN13	58.2 ± 176.8 A	high	26.5 ± 188.6 A	high	11.4 ± 87.2 A	high	-58.3 ± 61.5 B	Low	p < 0.001
BB: RWR 2154	4.8 ± 73.1 A	high	-9.6 ± 74.4 AB	high	-35.4 ± 45.3 B	medium	-59.4 ± 36.1 C	Low	p < 0.001
BB: MLB 122-9	18.3 ± 121.5 A	high	16.8 ± 69.4 A	high	-2.3 ± 47.5 A	high	-49.8 ± 49.2 B	medium	p < 0.001
BB: CODMLB104	16.9 ± 126.9 AB	high	-14.3 ± 83.1 AB	high	-16.6 ± 73.1 AB	high	-30.1 ± 67.9 B	medium	p < 0.05
BB: MARUNGI	-13.4 ± 59.4 A	high	-6.1 ± 72.9 A	high	-32.4 ± 39.7 A	high	-54.6 ± 29 B	Low	p < 0.001
BB: M'Sole	-13.9 ± 31.7 A	high	-11.2 ± 49.8 A	high	-35.6 ± 30 B	medium	-80.6 ± 32.8 C	Low	p < 0.001
CB: VCB81013	-2.3 ± 61.1 A	high	-12.4 ± 52.8 A	high	-16.1 ± 51.1 A	high	-50.4 ± 38.8 B	Low	p < 0.001
CB: RWV1129	-22.6 ± 58.2 AB	high	-42.1 ± 36.6 B	medium	-37.3 ± 42 B	medium	-57.1 ± 47.6 C	Low	p < 0.001
BB: CODMB 514	-25.8 ± 81.1 B	medium	-3.2 ± 53 A	high	-34.6 ± 50.6 B	medium	-45.5 ± 36.1 B	medium	p < 0.001
CB: NUV15-1	-32.2 ± 53.1 AB	high	-44.1 ± 35.6 AB	high	-28.2 ± 56.9 A	high	-51.3 ± 37.3 B	Low	p < 0.001
CB: CODMLV096	-37 ± 49.8 AB	high	-27.3 ± 60.1 AB	high	-18.3 ± 62.6 AB	high	-48.2 ± 50.3 B	medium	p < 0.05
BB: NABE20	-40.3 ± 53.5 B	medium	-56.1 ± 39.8 BC	low	-50.6 ± 54.6 BC	low	-70.6 ± 19.7 C	Low	p < 0.001
CB: NUV131-1	-40.7 ± 36.6 B	medium	-46.6 ± 36 BC	medium	-58.9 ± 24.1 C	low	-72.6 ± 16.6 D	low	p < 0.001
CB: NAMULENGA	-41.6 ± 42.6 B	medium	-36.1 ± 45.1 B	medium	-25.8 ± 37.9 AB	high	-71.4 ± 19.3 C	low	p < 0.001
CB: KINURE	-48.6 ± 41.1 BC	medium	-40.8 ± 43.6 BC	medium	-40.1 ± 38.2 B	medium	-59.5 ± 36.6 C	low	p < 0.001
CB: NABE12C	-52.5 ± 42 B	low	-48.1 ± 35.5 B	medium	-55.1 ± 36 B	low	-59.6 ± 24.1 B	low	p < 0.001
CB: MAC44	-59 ± 37.5 BC	low	-59.1 ± 29.5 BC	low	-45.5 ± 38.2 B	medium	-70.5 ± 18.5 C	low	p < 0.001
CB: COD59/1-2	-72.6 ± 23.4 BC	low	-70.9 ± 19.5 B	low	-72.9 ± 22.2 B	low	-81.1 ± 19.9 C	low	p < 0.001

For each variety, average % yield change at all shade levels is compared to open field conditions, with yield changes with the same letter in a row not significantly different (Kruskal-Wallis and Wilcoxon rank sum; letter comparisons along rows, not columns). Positive values indicate increased yields compared to open field conditions, while negative values indicate yield losses compared to open field conditions. Tolerance to specific shade levels is classified as high if not significantly different to open field conditions. Further distinctions are made using the thresholds: (i) medium tolerance with average yield loss <50%; and (ii) low tolerance with average yield loss >50%. Bean varieties are sorted according to tolerance to low shade levels.

All bush bean varieties showed significantly increased plant height compared to open field, even at low shade levels (70% light transmission), with further increases with increased shade (Figure 1; Supplementary Tables S2, S3). Climbing beans either maintained plant height at low shade (70% light transmission) or showed a decrease in plant height (varieties KINURE and MAC44). With increasing shade levels, climbing beans either maintained

plant height, or showed increased plant height (e.g. RWV1129, NUV15-1, VCB81013).

Most coffee varieties showed no significant change in plant height or diameter in low to deep shade compared to open field (Figures 2, 3; Supplementary Tables S4–S6). The coffee variety BJ76 showed a 19% reduction in plant height compared to open field conditions in low shade (70% light transmission) and a 24%

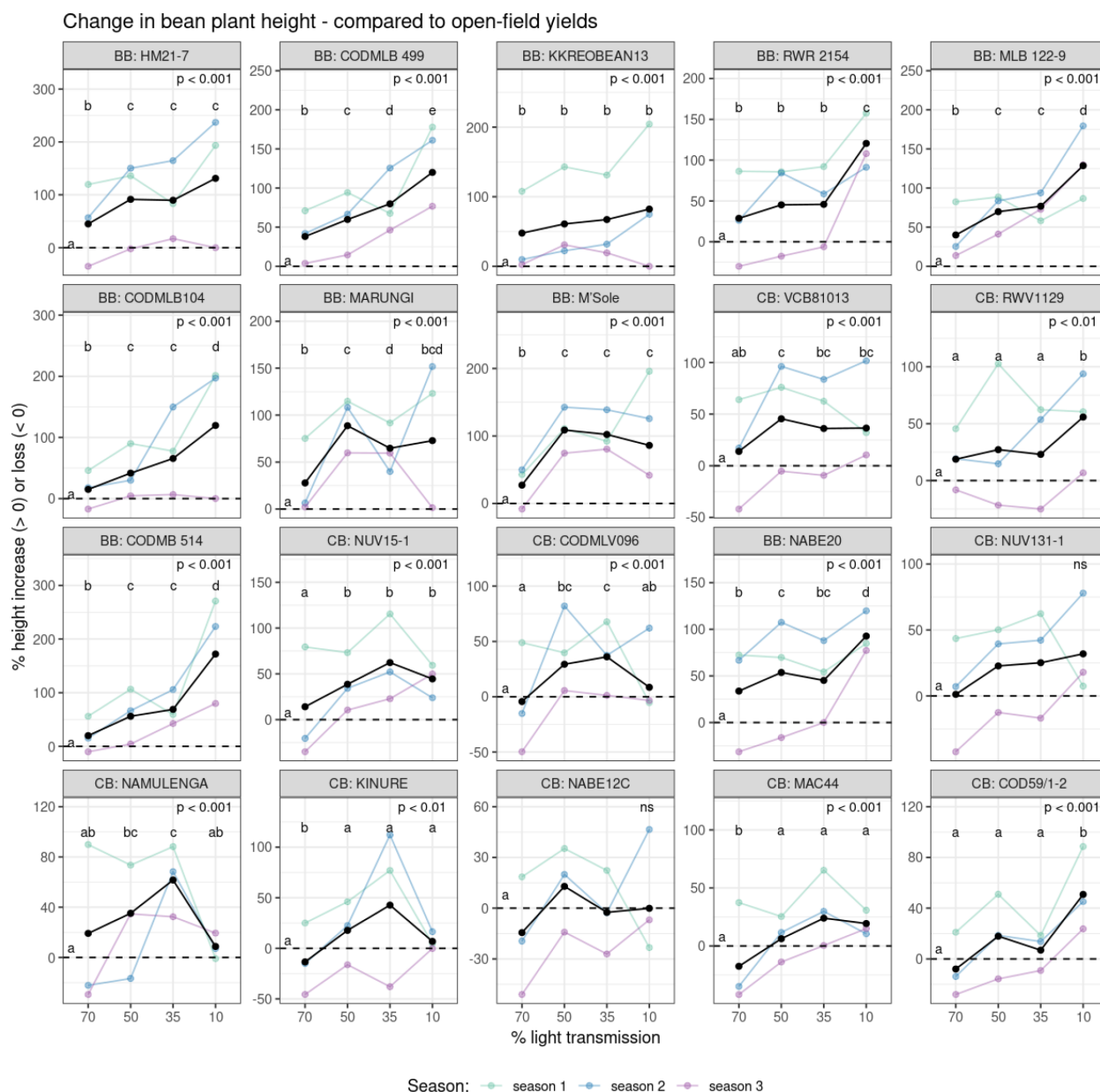


FIGURE 1

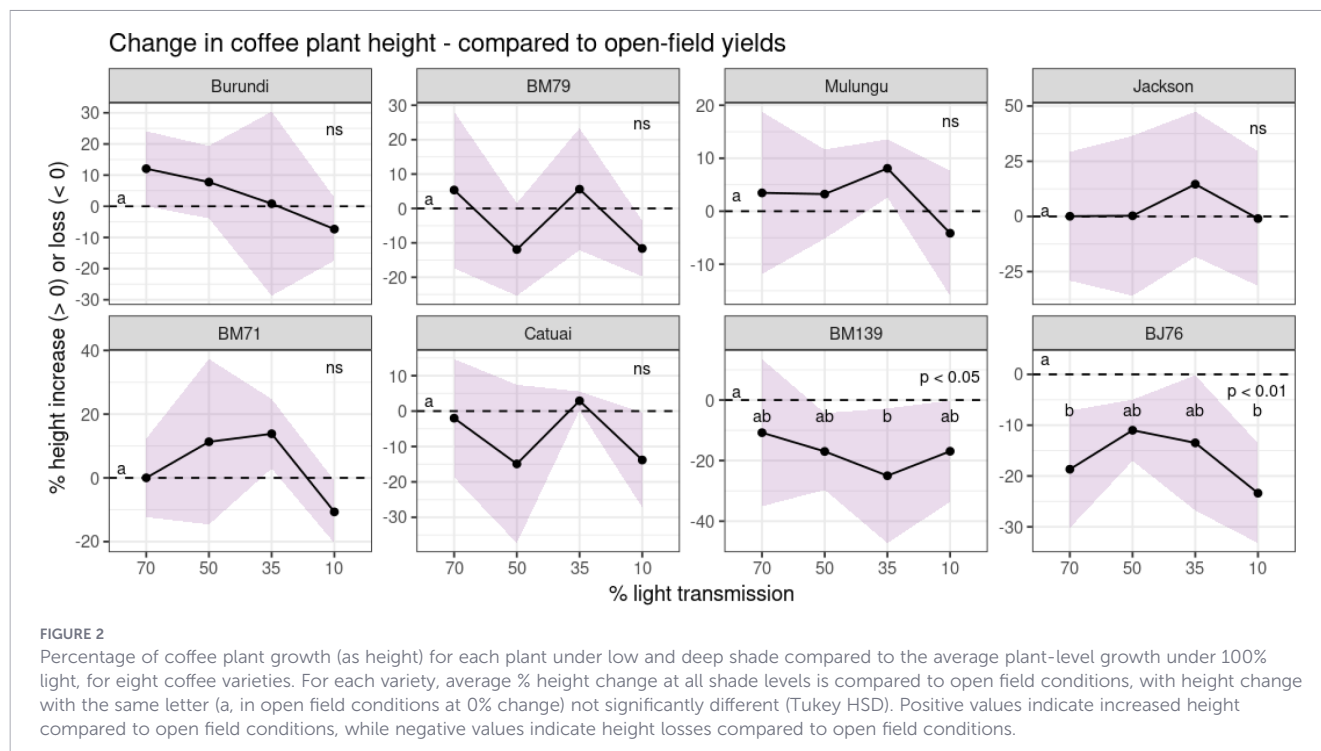
Percentage of plant height under low to deep shade compared to the average plant height at 100% light, for bush bean (BB) and climbing bean (CB) varieties. For each variety, average % height change under all shade levels is compared to open field conditions, with height changes with the same letter (a, in open field conditions at 0% change) not significantly different (Kruskal-Wallis and Wilcoxon rank sum). In black the average yield change across all three seasons, with distinction between seasons displayed by colours. No change (0%) is indicated by a dotted line. Positive values indicate increased yields compared to open field conditions, while negative values indicate yield losses compared to open field conditions.

reduction in deep shade (10% light transmission); while BM139 showed a 25% reduced height at 35% light transmission. The variety Mulungu showed a 17% reduced diameter size in deep shade (10% light transmission; Figure 3).

Elephant grass exhibited a low tolerance to all shade levels, with AGB and root biomass showing significant ($p < 0.05$) reductions of 84–87% and 61–73%, respectively, in low to deep shade (Figure 4; Supplementary Tables S7, S8). The diameter of the elephant grass mat significantly reduced under heavy shade, namely with 26 to 37% at 35% light and 10% light, respectively. The number of

branches also significantly reduced at all shade levels, ranging between 54%–58%, fewer branches in 70–35% light, and a maximum reduction of 85% at 10% light transmission. Elephant grass plant height was lowest at 35% light transmission.

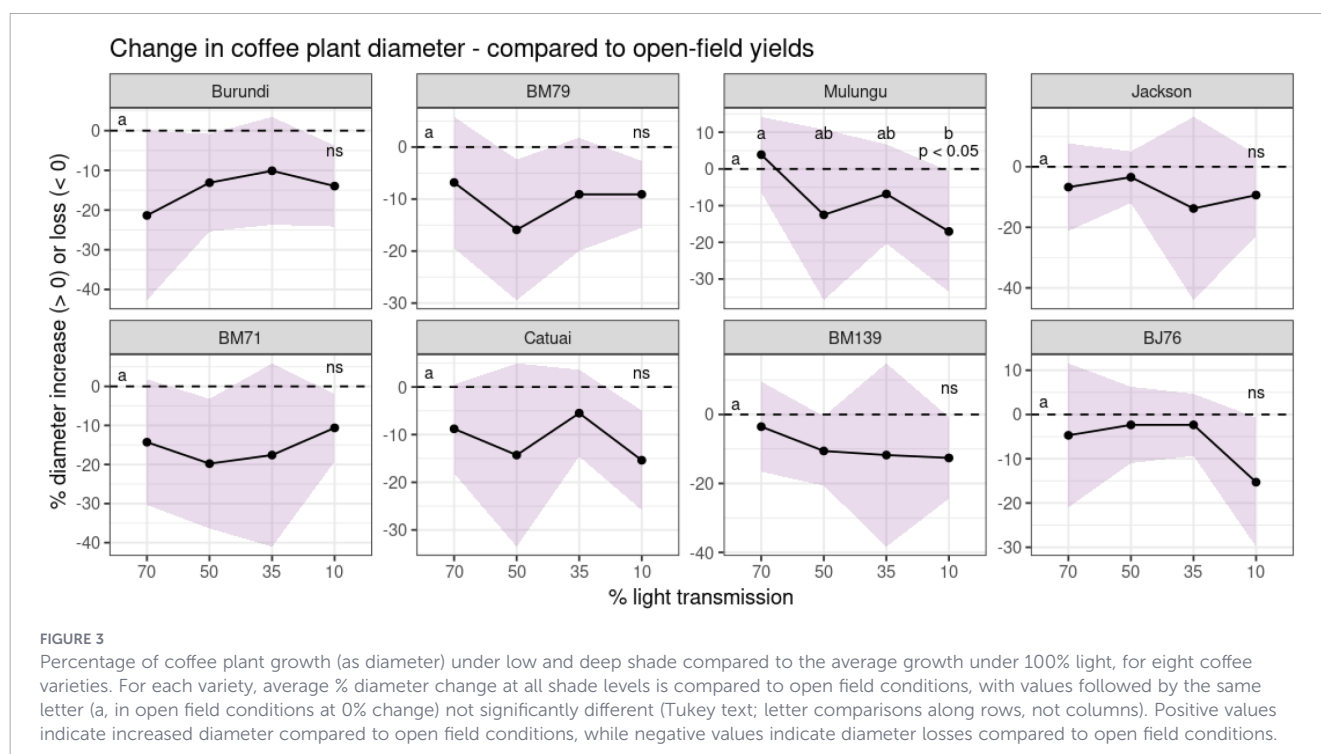
The leguminous cover crops, bushy rattlepod and velvet beans showed significant AGB losses at minimal shade (70% light transmission), classified as low tolerance for rattlepod (58% loss) and medium tolerance for velvet bean (48% loss; Figure 4; Supplementary Tables S7, S8). Both crops showed significant drops in AGB at 10% light transmission, with average losses of



85–91%. Notably, velvet beans, maintained root biomass levels similar to open field conditions between 70% and 35% light transmission (Figure 4; Supplementary Tables S7, S9). A significant drop in velvet bean root biomass (40%) only occurred at the deepest shade level (i.e., 10% available light). No difference in plant height of either leguminous cover crops was observed related to shade-level.

Discussion

This study demonstrates substantial variation in shade tolerance among common bean and Arabica coffee varieties, and cover crops, with important implications for the design and management of multi-strata intercropping systems in ECA. By applying standardized shade gradients under controlled greenhouse conditions, the study provides



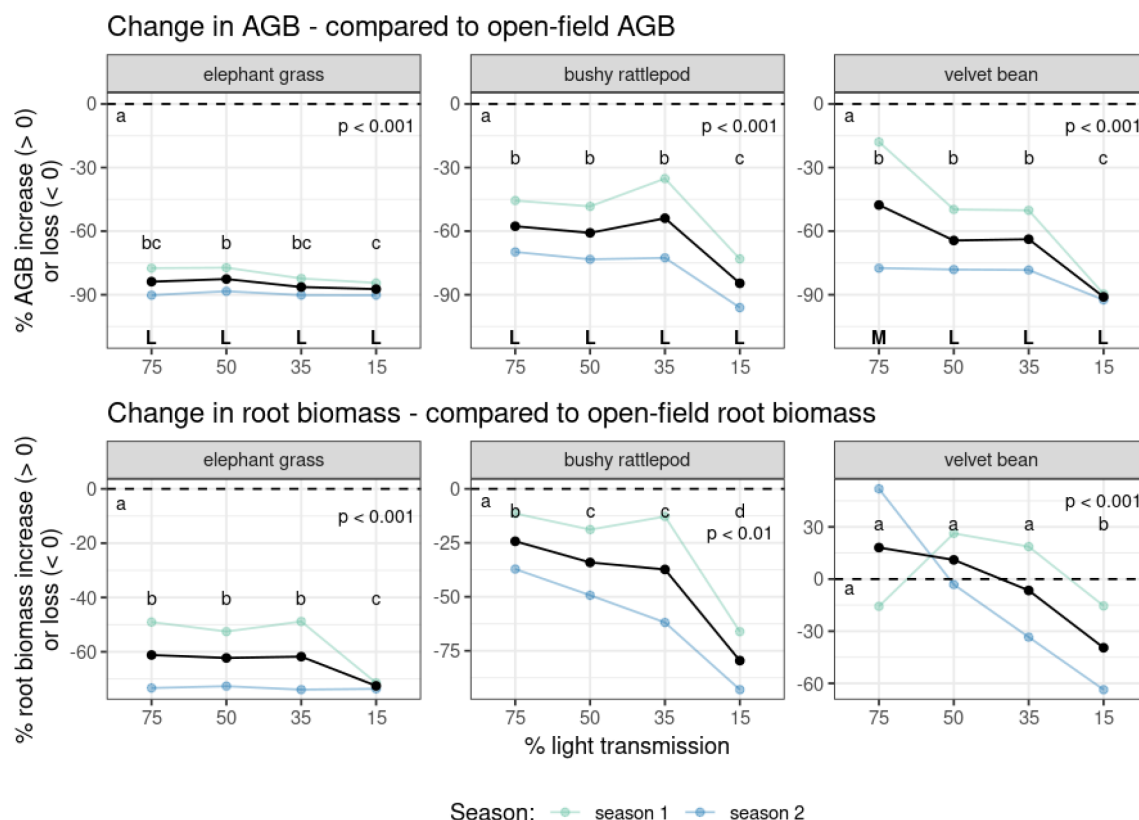


FIGURE 4

Percentage of cover crop plant growth as fresh aboveground biomass (AGB) (top row) and root biomass (bottom row) for each plant at low to deep shade compared to the average plant growth at 100% light. For each CC, average % biomass change at all shade levels is compared to open field conditions, with biomass change with the same letter (a, in open field conditions at 0% change) not significantly different (Kruskal-Wallis and Wilcoxon rank sum). In black the average yield change across all three seasons, with distinction between seasons displayed by colours. The line for no change (0%) is indicated by the dotted line. Positive values indicate increased biomass compared to open field conditions, while negative values indicate biomass losses compared to open field conditions. Tolerance to specific shade levels is classified as high (H, in bold) if AGB is not significantly different to open field conditions. Further distinctions are made using the thresholds: (i) medium tolerance (M, in bold) with average AGB loss <50%; and (ii) low tolerance (L, in bold) with average AGB loss >50%.

an assessment of varietal performance under low-light environments to a good extent mimicking agroforestry, and mixed perennial systems. The results highlight clear opportunities for screening, selecting and deploying shade-tolerant germplasm already available at breeding centres, national research centres, and farmer's fields.

Responses of common bean varieties to shade gradients

Common beans exhibited substantial variability in both yield and morphological responses across the shade gradient. Bush bean varieties HM21-7 and CODMLB 499 maintained grain yields statistically indistinguishable from open field controls even under deep shade (10% light transmission), highlighting their strong inherent shade tolerance (cf. Table 2; Supplementary Figure S2). Four additional bush bean varieties (KKREOBEAN13, MLB 122-9, CODMLB104, and MARUNGI) and four climbing bean varieties (VCB81013, NUV15-1, CODMLV096, and NAMULENGA) also performed well under deeper shade (35% light; cf. Table 2), indicating their potential suitability for mid-shade understories typical of young to mid-age coffee–banana systems or moderately spaced perennial crop canopies.

Evidence from other studies reinforces the presence of such varietal differences (Komariah et al., 2007; Ronner et al., 2021; Li et al., 2025). For example, Ronner et al. (2021) compared shade responses of widely adopted climbing bean varieties (NABE 10C and NABE 8C) with a newer hybrid (NABE 12C) and found that the widely adopted genotypes relatively performed better in intercrop situations, with all varieties yielding highest in the least shaded sections of banana fields. Investigations of soybean cultivars have revealed that physiological, morphological, and molecular responses to shading vary among genotypes, reflecting differential expression of genes linked to shade tolerance or avoidance (Li et al., 2025; Zhang et al., 2025). Together, such findings underscore substantial inherent differences in shade tolerance among bean varieties, differences that can be strategically leveraged to enhance productivity and resilience in smallholder farming systems. These results however, contrast with earlier field observations documenting yield collapses of HM21-7 and NAMULENGA under heavily shaded banana canopies (14–30% PAR) in South Kivu (Ntamwira et al., 2021). This discrepancy likely reflects complex field interactions including competition for water and nutrients, root interference, and microclimatic heterogeneity, factors absent in potted controlled studies. For example, in the

third year of an intercrop of *Grevillea robusta* trees, bananas and beans, Akyeampong et al. (1999) reported below ground competition between beans on the one hand, and bananas or bananas and *G. robusta* on the other to be more important than competition for light. These studies underline the importance of follow-up field validation and suggest that shade-tolerance of some bean genotypes might be weakened by field competition.

Notably, many of the bush bean cultivars displayed a marked increase in plant height under shade (cf. Figure 1), a response that mirrors the height elongation reported for green beans (Komariah et al., 2007) and for certain soybean genotypes that extend their stems to capture more light (Gong et al., 2015). While this height increase could be interpreted as a shade-avoidance strategy, the fact that grain yield remained stable for specific bean varieties (up to various shade levels) suggests that the elongation possibly serves a compensatory function rather than reflecting a true avoidance phenotype. Such compensatory mechanisms can include expanding leaf area and prolonging grain-filling, thereby preserving grain weight even when plant height increases (Hadi et al., 2006; Nasrullahzadeh et al., 2007). Other investigations have documented parallel leaf-trait adjustments under shade, such as higher leaf-area index, specific leaf area, and leaf-area ratio (Hadi et al., 2006; Umesh et al., 2023), as well as increased chlorophyll content and altered chlorophyll a/b ratios (Gong et al., 2015), all of which support a shade-tolerance suite of traits. Across all bean varieties examined, however, grain yield exhibited considerable variability, underscoring the heterogeneous nature of shade responses. Consequently, a more detailed examination of shade effects on additional plant attributes, such as branching architecture and physiological efficiency, would refine the assessment of shade tolerance among these bean genotypes. Such assessments could further refine varietal shade-tolerance screening, informing breeding programs and accelerating the development of improved, shade-adapted cultivars.

Response of Arabica coffee seedlings to shade gradients

Arabica coffee seedlings displayed generally stable morphological performance across all tested shade levels. Most varieties showed no significant differences in tree height or stem diameter between shaded and full sun conditions (cf. Figures 2, 3; Supplementary Tables S4–S6), indicating a high degree of shade tolerance typical of *Coffea arabica* (DaMatta, 2004; Matos et al., 2009). The modest reductions observed in BJ76 and BM139 at specific shade levels fall within the range documented for shade-acclimatizing genotypes in agroforestry systems (Baliza et al., 2012; Rodríguez-López et al., 2014). This relative stability in the 8 coffee varieties suggests a tendency towards shade tolerance, rather than the shade avoidance reported in some coffee studies (Ayalew, 2018). This corroborates findings of shade being beneficial to coffee yield, especially under sub-optimal conditions (Pinard et al., 2014; Rahn et al., 2018).

These findings differ from studies reporting stronger shade-induced elongation, decrease in plant height or shifts in slenderness

indices under intermediate to deep shade (Ayalew, 2018; Bote et al., 2018; Baliza et al., 2012; Rodríguez-López et al., 2014). This could reflect the young age of seedlings, genetic differences among local cultivars, or the stable light environment provided by screenhouses, in contrast with dynamic sun-fleck-influenced field conditions. While early vegetative stability is promising, long-term monitoring is needed to determine whether low-light responses translate into improved or diminished productivity as plants reach bearing age. Monitoring for shade tolerance in coffee should also factor in other morphological and physiological traits such as leaf size, chlorophyll levels and contents, to better define tolerance or avoidance strategies. It is also crucial to assess how these varieties perform within heterogeneous light environments found in complex intercropping systems in the field. For example, coffee trees have been reported to be slow-growing and sensitive to interference from intercrops, leading to losses when competition for resources is strong (Van Kanten, 2003; Ronchi and Silva, 2006; Jassogne et al., 2013).

Shade responses of cover crops

Diverse responses were observed from three investigated cover crops, with elephant grass and bushy rattlepod showing low tolerance to shade under even mild shade while velvet beans being moderately tolerant (cf. Figure 4; Supplementary Table S7, S8). These patterns are consistent with previous findings on light-demanding forage legumes and grasses in agroforestry contexts (Angadi et al., 2022; Yemataw et al., 2018). The poor performance of elephant grass and bushy rattlepod under mild shade contrasts reports that have shown elephant grass and bushy rattlepod to be moderately tolerant under field conditions (Muhtarudin et al., 2020; Botanikks, 2024a). This observed discrepancy could potentially be attributed to limitations from the confined root zones in the pots and other interactions that occur under field conditions. Velvet bean modestly maintained root biomass under 35–70% light transmission (cf. Figure 4; Supplementary Tables S7, S9) despite exhibiting major aboveground growth suppression. The root biomass patterns from velvet beans suggest that velvet beans can potentially benefit moderately shaded systems for root biomass and soil cover. This is supported by earlier studies that have reported velvet beans to tolerate moderate levels of shade (Blomme et al., 2020, 2022), with prolonged exposure to shade resulting in stunted growth and fewer flowers (Botanikks, 2024b). The strong shade sensitivity observed here suggests that many commonly used soil-covering species may function well only in the early years of perennial crop establishment when canopy cover is minimal (DaMatta et al., 2007; Ntamwira et al., 2021). Beyond this window, more shade-tolerant alternatives should be prioritized where available. These could include legume species such as perennial horse gram (*Macrotyloma axillare*), centro or butterfly pea (*Centrosema pubescens*), tropical kudzu (*Pueraria phaseoloides*), lablab, wynn cassia (*Chamaecrista rotundifolia*), hairy vetch (*Vicia villosa*), and cowpea, all of which have been reported to produce moderate to high amounts of above-ground biomass when intercropped with perennials or grown under heavy shading (Yemataw et al., 2018; Angadi et al., 2022).

Light-demanding cover crops could however still be employed in more lit places as hedges along field margins, or open spaces within fields (Siles et al., 2022). Ntamwira et al. (2024) documented a significant negative impact of elephant grass hedges on coffee productivity in highly degraded soils, underscoring the need to assess both shade and resource competition when selecting cover-crop strategies. Where suitable shade-tolerant legumes are unavailable, options such as mulching between cropping cycles should be evaluated to maintain and protect soil health while minimizing competitive pressures on the primary crops.

Study limitations and implications for perennial, multi-strata cropping system design

Study limitations: The controlled screenhouse conditions using potted plants grown in a homogeneous forest soil–sand substrate relative to farmers' fields, reduced environmental heterogeneity, largely removing below- and above-ground competition with perennials, other crops and weeds under field conditions. As a result, only response to reduced light is captured, rather than the combined effects of shade, water, and nutrient competition typical of banana–coffee and other agroforestry systems. In addition, the shade environment was relatively static and spatially uniform, not fully capturing the highly dynamic light regimes (e.g. sunflecks) observed beneath tree canopies. Other potentially important variables, like relative humidity and vapor pressure deficit with potential influence on photosynthesis, evapotranspiration and disease pressure were not measured despite being modified by the screenhouses. More still, the confined root volume and soil substrate could have also modulated the response of the crop species and varieties especially the cover crops and coffee varieties to shade. These limitations highlight the necessity of field evaluations as a crucial additional step prior to promotion.

For Arabica coffee, only vegetative traits of seedlings were assessed, without evaluation of reproductive performance or physiological parameters, so conclusions regarding shade tolerance in the productive phase remain preliminary. Although multiple seasons and cycles were assessed for beans and cover crops, seasonal effects and genotype $\times$ environment interactions were not explored. Finally, the categorical thresholds used to define shade tolerance classes were based on pragmatic but somewhat arbitrary yield-loss cut-offs.

Implications for practices: Despite these limitations, the standardized shade gradients and multi-species screening approach provide a practical first step for identifying crop species and varieties including bean and coffee germplasm with superior performance under low light, and for excluding highly shade-sensitive cover crops from dense perennial systems.

The shade-tolerance gradient identified here can also help farmers sequence crops as the perennial canopy grows and closes. At perennial crop establishment when shade levels are still low (years 1 to 2), low shade-tolerant under story crop and crop varieties can be intercropped (DaMatta et al., 2007; Ndiritu et al., 2022; Ntamwira et al., 2021; de Carvalho et al., 2024). As the perennials establish (years ≥ 2 to fully established fields), moderately

and highly shade tolerant crop species and varieties can be integrated. Thus, the strong biomass reductions observed in elephant grass, velvet bean, and bushy rattlepod under even moderate shade suggest that these cover crops are best suited to early plantation stages or more open canopy zones or should be replaced by more shade-tolerant species where year-round ground cover is needed. In perennial banana–coffee and -tree systems with mid- to high-shade strata (Ntamwira et al., 2021; Koutouleas et al., 2022), high-performing bush bean varieties such as HM21-7 and CODMLB 499, as well as climbing beans that maintained yields at 35% light, emerge as promising candidates for deployment, provided their field performance is validated under realistic competition for water and nutrients. Even for the shade tolerant species like coffee, matching varieties to shade levels is crucial as yields of less shade-tolerant varieties begin to decline under dense shade systems (beyond 50% canopy cover) (DaMatta, 2004; Bosselmann et al., 2009; Durand-Bessart et al., 2020).

These insights can also inform adaptive canopy management. Strategic pruning of perennial crops and trees (Pinard et al., 2014; Buyinza et al., 2024) can maintain acceptable understory light regimes while reducing excessive competition, extending the productive window for annual intercrops and understory plant species (Ndiritu et al., 2022). This could involve regular pruning for coffee shrubs (Pinard et al., 2014) and shade trees (Buyinza et al., 2024) or the de-suckering or partial de-leafing of banana mats (Ntamwira et al., 2013; 2014; Ocimati et al., 2019, 2021). Optimal shade levels and tree configurations could also be site-specific, while interactions with pests such as the coffee berry borer (Jaramillo et al., 2011) could inform intercropping recommendations. Thus, by integrating shade-tolerance gradients with assessments of resource competition and employing adaptive pruning regimes, agroforestry designs can become informed, dynamic, and better suited to long-term sustainability.

For breeding programs, the results highlight the value of integrating standardized shade screening (e.g., at 35% and 10% light transmission) into selection pipelines, with a focus on yield stability across shade levels combined with adaptive morphological traits. These top-performing genotypes should then be validated in on-farm trials across contrasting multi-strata configurations.

Conclusion

This study provides a comparative evaluation of crop and varietal responses to shade across a gradient relevant to multi-strata perennial cropping systems in ECA. The strong performance of several bush and climbing bean varieties, the stability of Arabica coffee plants and the poor performance of commonly used cover crops under deep shade suggest a high diversity in response of crops and crop varieties to shade. This applied approach of shade-tolerance assessments could act as a first step to simultaneously evaluate shade tolerance of hundreds of crop species and varieties prior to evaluations under complex on farm conditions. This approach could also help in identifying genes responsible for shade tolerance to feed into potential breeding efforts.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#). Further inquiries can be directed to the corresponding author.

Author contributions

JN: Visualization, Writing – original draft, Supervision, Investigation, Writing – review & editing, Validation, Methodology. WO: Supervision, Validation, Conceptualization, Writing – review & editing, Methodology, Funding acquisition, Resources, Project administration, Data curation, Writing – original draft. EK: Data curation, Writing – review & editing, Validation, Software, Visualization, Writing – original draft, Formal analysis. TM: Writing – original draft, Investigation. GS: Investigation, Writing – original draft. GB: Methodology, Project administration, Conceptualization, Validation, Writing – review & editing, Supervision, Writing – original draft, Funding acquisition, Resources.

Funding

The author(s) declared that financial support was received for this work and/or its publication. This work was undertaken through funds from the CGIAR Trust Fund: www.cgiar.org/funders/ (accessed on 20 July 2025) to Bioversity International through the CGIAR Initiative on West and Central Africa Food Transformation System, and the Scaling for Impact Program. A financial contribution from the Belgium Development Cooperation through the Consortium for Improving Agriculture-based Livelihoods in Central Africa (CIALCA) was used for establishing the screenhouses for the study.

Acknowledgments

We thank the Belgium Development Cooperation for their support in establishing screenhouses through the Consortium

for Improving Agriculture-based Livelihoods in Central Africa (CIALCA).

Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fagro.2026.1775355/full#supplementary-material>

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