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# 1 Combining modelling and experimental approaches to assess the 2 feasibility of developing rice-oil palm agroforestry system

3

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12 **Keywords:** agroforestry, light intensity, light fluctuation, rice, shading, yield

13

## 14 Abstract

15 Climatic hazards affecting the main rice producing regions of Indonesia increase the risk of annual  
16 production loss and encourage the development of innovative strategies to maintain stable  
17 production. Conversion of oil palm monocultures to rice-based intercropping systems is a strategy to  
18 be considered, but relies on the existence of suitable planting management that optimizes both palm  
19 productivity while providing enough light for undergrowth rice varieties tolerant to shady conditions.  
20 This paper proposes to couple a model of light interception on virtual canopies with indoor  
21 experiments to evaluate the feasibility of developing rice-oil palm agroforestry systems. We first  
22 selected a planting design that optimized the transmitted light available for rice using a functional-  
23 structural plant model (FSPM) of oil palm. Secondly, we reproduced the light regime simulated with  
24 specific changes in the intensity and the daily fluctuation of light in controlled conditions. Three light  
25 treatments were designed to test independently the effect of daily light quantity and the effect of  
26 diurnal fluctuation on contrasted rice subpopulations.

27 Light quantity was the main factor driving changes in plant morphology and architecture, while light  
28 fluctuation only appeared to explain variations in yield components and phenology. This study  
29 highlighted the importance of light fluctuation in the grain filling process and resource reallocation.

30 The conservation of relative change among varieties between treatments suggests that varietal  
31 responses to low light are likely to be heritable, and that varietal screening under full light can provide  
32 clue on varietal behavior under low light. However, the identification of specific traits such as a limited  
33 expansion of leaf area and a conservation of leaf senescence under shade and high light fluctuation  
34 paves the way for selecting varieties dedicated to agroforestry systems. Further investigations  
35 including light quality and larger genotypic population to screen are discussed.

## 36 Introduction

37 The recurrent droughts caused by the 'El Niño' phenomenon have a significant impact on both rice and  
38 oil palm cultivation in Southeast Asia, particularly in Indonesia. These climatic hazards affecting the  
39 main rice-producing regions (Java and Bali), increase the risk of annual production loss (Naylor *et al.*  
40 2007) and encourage the development of innovative strategies to maintain stable production. Oil palm  
41 yields also decrease in regions where more and more drought periods are recorded (South Sumatra),  
42 and thus raise interest in limiting competition for water through adapted planting density.  
43 Subsequently, oil palm/rice intercropping in the rainy season alternating with palms alone at reduced  
44 density in the dry season could be a strategy to extend suitable area for rice while reducing competition  
45 for water between palms during dry spells. The feasibility of such a system depends on a specific  
46 management of the resources depending on the two species and seasons: the water availability for oil  
47 palm during the dry season and the transmitted light for rice during the rainy season. A main concern  
48 is therefore on adjusting the palm density to maintain high yields of both crops, and on screening rice  
49 varieties best adapted to shady conditions.

50 Research on oil palm agroforestry systems is rapidly expanding in the scientific literature  
51 (Bhagwat & Willis 2008; Khasanah *et al.* 2020). The majority of these studies focused on the ecological  
52 impact of these systems compared to conventional monoculture systems (Gérard *et al.* 2017; Ashraf  
53 *et al.* 2018; Zemp *et al.* 2019; Koussihouèdé *et al.* 2020; da Silva Maia *et al.* 2021). Rare studies  
54 highlighted the interest of palm agroforestry systems for their good agronomic performance and  
55 economic profitability on the one hand (Gawankar *et al.* 2018; Ahirwal *et al.* 2021), but also for  
56 buffering extreme climatic events and thus improving the sustainability of these systems (Ashraf *et al.*  
57 2019). However, very few studies proposed intercropping with rainfed rice (Alridiwirah *et al.* 2019), a  
58 crop that is nevertheless predominant in Asia. Oil palm-based intercropping is often considered at  
59 juvenile stage of oil palm, as a transitory option for a couple of years, since less than five percent of  
60 the incident light forages the canopy when oil palms reach maturity at a conventional density of 136  
61 or 143 plants ha<sup>-1</sup>. So far, no study investigated how changes in planting patterns and density of oil  
62 palm could be optimized for intercropping purposes, because i) such study requires years and strong

63 financial support, and ii) suitable planting management that optimizes palm productivity while  
64 providing enough light for undergrowth crop is not straightforward. The recent development of  
65 modelling tools, using 3D models of plants in combination with light modelling (Perez *et al.* 2022) now  
66 opens the way to test how planting design would modulate light availability under oil palm canopy  
67 without involving expensive trials.

68 Despite the growing interest in rice-based agroforestry systems (Wangpakapattanawong *et al.*  
69 2017; Rodenburg *et al.* 2022; Masure *et al.* 2022), the diversity of rice response to fluctuations in  
70 radiation as well as low light remains unexploited. Up to now, varietal improvement programs in rice  
71 have focused on the selection of productive materials in full sun conditions. The existence of genetic  
72 variability in response to photosynthesis induction rate during shade/light alternations (Qu *et al.* 2016;  
73 Acevedo-Siaca *et al.* 2020; Taniyoshi *et al.* 2020), and independently to shade tolerance (Wang *et al.*  
74 2015a; Dutta *et al.* 2018), suggest that it could be possible to select rice material suitable for  
75 agroforestry. Nevertheless, these studies investigated shade tolerance using continuous artificial light  
76 attenuation with shade nets, often starting at the reproductive stage of plant growth, thus preventing  
77 mimicking light conditions in agroforestry, where undercrop can be exposed to full sunlight around  
78 noon. In these systems, the light environment is much more complex than a constant light attenuation,  
79 since both effects of shading and daily light fluctuation can affect plant growth, from germination to  
80 harvesting.

81 This study raises the question of whether rice genotypes selected to be most efficient under  
82 optimal radiation are most efficient when the amount and the dynamics of radiation are altered, as  
83 found in agroforestry systems. Given the nonlinear relationship between light interception and  
84 photosynthesis, not only the reduction in light quantity but also the changes in daily light fluctuation  
85 can affect resource acquisition and subsequently plant growth, development and yield. Using a  
86 functional-structural plant model (FSPM) estimating light transmission through 3D canopy, we first  
87 simulated how palm density and planting design affect the quantity of transmitted light to rice, and  
88 selected a pattern optimizing light foraging for rice and oil palm density. Secondly, we reproduced in  
89 controlled conditions the specific changes in light intensity and fluctuation obtained in the simulation.  
90 Three light treatments differing in either the quantity or the dynamics of radiation were thus set up to  
91 investigate changes in phenological, morphological, physiological, and productive traits including  
92 physicochemical traits on eight contrasted rice varieties.

## 93 Material and Method

### 94 *Modelling light transmission in innovative oil palm-based agroforestry system*

95 We can test how planting design can modulate light availability under oil palm canopy by coupling a  
96 3D structural model of oil palm (Perez *et al.* 2016, 2018) with a light interception model (Dauzat & Eroy  
97 1997). This modelling approach helps to compute the light transmitted over time and space according  
98 to any design and thus allows the exploration of innovative and suitable planting patterns for  
99 agroforestry systems. In this study, we assumed that the architectural plasticity of oil palm had  
100 negligible impact on light capture in comparison to the changes in light interception due to planting  
101 patterns, as concluded in a previous study (Perez *et al.* 2022). A simulation study was performed with  
102 3D mock-ups of oil palm representing plant architecture at the mature stage (8 years after planting),  
103 and displayed in rows defined by two parameters: the distance between rows and the distance  
104 between plants within rows (Fig S1). Eight planting patterns were designed *in silico* to estimate the  
105 light transmitted through the palms in a horizontal plane placed one meter above the ground (Table  
106 1).

107 *Table1: The eight designs tested with the corresponding distance between plants and density. The two parameters*  
108 *to define a design are the distance between rows (dist inter) and within rows (dist intra).*

dist intra (m)	dist inter (m)	density (plants ha <sup>-1</sup> )
8	14	89
7	14	102
8	12	104
7	12	119
8	10	125
8	9	138
7	10	142
7	9	158

109

110 Distances within rows (7 and 8 m) were selected according to the average crown dimensions of mature  
111 oil palm, with the objective to mutual shading. Distance between rows (9, 10, 12, 14m) were selected  
112 to modulate planting density from low (89 plants ha<sup>-1</sup>) to high density (158 plants ha<sup>-1</sup>). Simulations  
113 were done using radiative data collected in South Sumatra on March 20th, 2019 (sunny day), with a

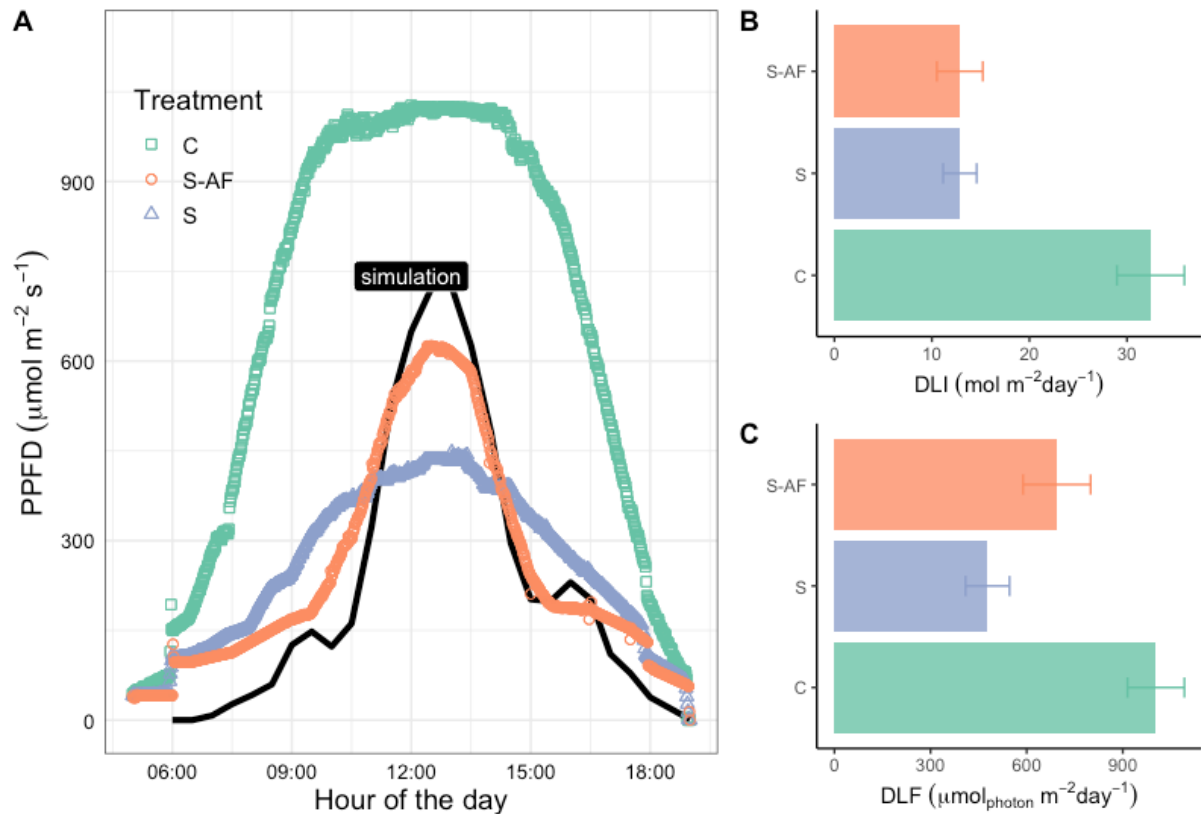
114 global radiation reaching  $28.4 \text{ MJ m}^{-2}$ . The light transmitted under the canopy was integrated over the  
115 day for every element of the horizontal plane (each element is a  $16 \text{ cm} \times 16 \text{ cm}$  square). Considering  
116 the space for growing rice at least  $3 \text{ m}$  distant from oil palm rows, we estimated on average  
117 photosynthetically active radiation (PAR) available in the rice area over a day.

### 118 *Reproducing the simulated agroforestry light conditions in growth chambers*

119 The experiment was carried out in the Abiophen platform of Montpellier in controlled conditions  
120 (Aralab Fitoclima 25000HP Growth chamber) in which light intensity and time course were adjusted  
121 while maintaining equivalent temperature and air humidity (Fig S2). Three light treatments (light  
122 supplied using Philips Master Colour CDM-T Elite MW 315W) were designed to test independently the  
123 effect of daily light quantity and the effect of diurnal fluctuations of light on rice. The three light  
124 treatments were set up in three independent growth chambers, respectively:

- 125 • a control treatment (C) following the dynamic of incident light observed in Sumatra (with a  
126 ceiling radiation value that can be reached *i.e*  $1100 \mu\text{mol}_{\text{photons}} \text{ m}^{-2} \text{ s}^{-1}$ )
- 127 • the agroforestry shading regime corresponding to the planting design selected from the  
128 simulation study (S-AF)
- 129 • a uniform shading treatment (S)

130 The light reduction in the S treatment was performed to obtain the same amount of total daily  
131 radiation than in the S-AF treatment (Fig 1A), and corresponded to a constant shade that could be  
132 obtained with a shading net. We characterized this amount of light by integrating the photosynthetic  
133 photon flux density (PPFD) over a day, hereafter called daily light integral (DLI, Poorter et al. 2019).  
134 The DLI were  $32.4 \text{ mol m}^{-2} \text{ d}^{-1}$ ,  $12.9 \text{ mol m}^{-2} \text{ d}^{-1}$  and  $12.9 \text{ mol m}^{-2} \text{ d}^{-1}$  for C, S-AF and S, respectively, both  
135 shading treatments thus providing equivalently 60% of light attenuation (Fig 1B). Regarding light  
136 fluctuation, we calculated an index of daily light fluctuation (DLF) as the daily difference between the  
137 maximal and the minimal PPFD (*i.e*  $0 \mu\text{mol} \cdot \text{m}^{-2} \text{ s}^{-1}$ ). DLF for S and S-AF were 478 and 694  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ,  
138 thus representing respectively a reduction of 52% and 30% of light fluctuation compare to the control  
139 treatment. Light spectra were also compared in the three growth chambers to ensure similar light  
140 quality among treatments (Fig S3).



141

142 *Figure 1: A) Mean diurnal time course of the photosynthetic photon flux density (PPFD) measured under three*  
 143 *light treatments in the phytotrons during the whole cycle of plant growth (C: control. S-AF: agroforestry-like*  
 144 *shade. S: constant shade). The black line indicates the PPFDF simulated in silico in the 7m x 12m planting design.*  
 145 *B) Daily light integral (mean and inter-days standard deviation) measured for the three treatments. S and S-AF*  
 146 *represent 60% loss of radiations in comparison to C. C) Daily light fluctuation (mean and inter-days standard*  
 147 *deviation) measured for the three treatments. S and S-AF represent respectively 52% and 30% loss of light*  
 148 *intensity in comparison to C.*

149

## 150 *Plants material and phenotypic monitoring*

151 Eight accessions of rice representing diversified subpopulations and geographical regions were  
 152 provided by the seeds and genetic resources laboratory (TBRC) held in Montpellier, France (Table 2).  
 153 Seeds were sown in individual pots of 4.8L (16cm x 16cm x 23cm) and fertilized using 3g L<sup>-1</sup> of NPK  
 154 fertilizer (50% of Basacote 13-5-18 and 50% of Bio 5-3-8; Compo – expert). In each of the three growth  
 155 chambers, accessions were grouped in tables of 28 plants (corresponding to a density of 32 plants m<sup>-2</sup>)  
 156 to prevent any competition for light among varieties within the table. Eight tables were placed in  
 157 each phytotron, and pots were kept flooded to prevent any water stress. Temperature and relative  
 158 humidity followed the average value observed in South Sumatra: temperature varied from 22°C by  
 159 night up to 32°C during the day and relative humidity from 83% down to 65% during the day (Fig S2).  
 160 Temperature and vapour pressure deficit were monitored similarly in the three treatments so that  
 161 phenotypic variations were interpreted as the consequence of light treatment alone.

162  
163  
164

Table 2: Rice accessions monitored during the experiment in controlled conditions. \*accessions with full phenotypic monitoring from sowing to harvesting.

Accession	Ref	Gervex	Subpopulation	Origin
JC1	V1	9 091	Basmati	India
MALAGKIT PIRURUTONG	V6	8 182	Japonica	Philippines
IR64 *	V3	8 531	Indica	Philippines
TREMBESE *	V7	43 675	Japonica	Indonesia
SINNA SITHIRA KALI	V4	51 064	indica	Sri Lanka
IRAT 177 *	V8	7 415	Javanica	Guyane
BRASILEIRO *	V5	809	Japonica	Brasil
CASAMANCE V2	V2	1123	Glaberrima	Sénégal

165

166 Phenotypic monitoring was conducted from sowing to harvesting, with phenological, morphological,  
167 physiological and yield measurements (Table 3). On each table, the 10 inner plants among the 28 plants  
168 constituting the canopy were studied to prevent border effects in the analyses. Phenological  
169 observations (leaf tip appearance on main stem and tillers count) were made once a week. For leaf  
170 appearance a Haun scale was used: the leaf was counted once its tip was visible and the total number  
171 of emerged leaves was expressed on a decimal scale, with partially emerged leaves counted according  
172 to the visible fraction of the full size (Haun 1973; Tivet *et al.* 2001).

173

Table3: Phenotypic variables collected during the experiment

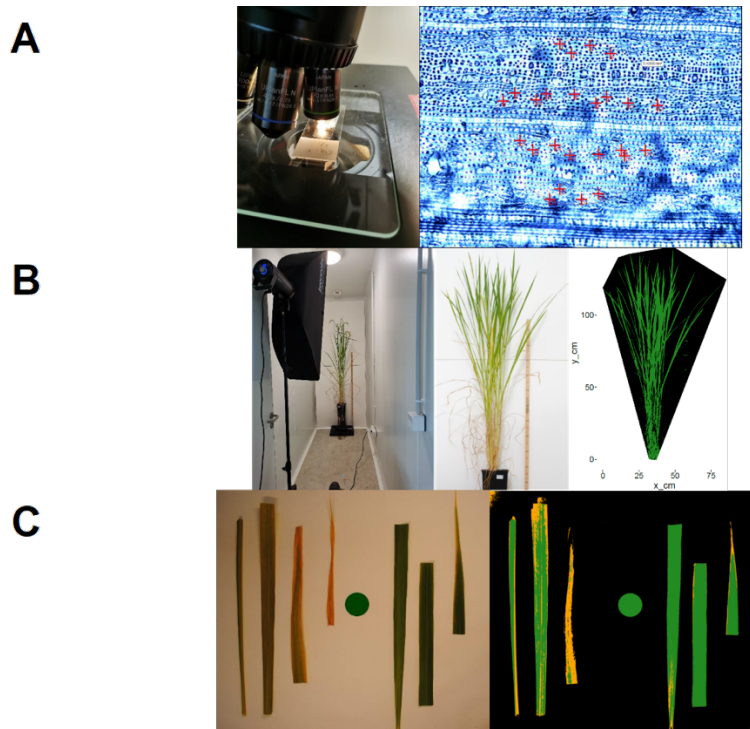
Type	Variable	Unit	Definition	# replicates (per genotype and treatment)	Scale	Method
phenology	DaysFL	days	Number of days from sowing to flag leaf appearance	6	plant	manual
	Phyllochron	days leaf <sup>-1</sup>	Average period between the sequential emergence of leaves on the main stem			
Plant morphology & architecture	#Til		Maximal number of tillers	4	plant	image analysis
	#Lea		Total number of leaves on main stem			
	SGA	cm <sup>2</sup>	Stay green area			
	PH	cm	Plant height (from collar to flag leaf)			
	CPN	-	Plant compactness	4		image analysis
	PLA	cm <sup>2</sup>	Plant leaf area at flowering			
	SLA	cm <sup>2</sup> g <sup>-1</sup>	Specific leaf area of total green leaves at flowering			4
	VDW	g	Total aerial vegetative dry matter at harvesting	4	planimeter, oven and scale	
Leaf	Length	cm	Flag leaf length	10	Flag & leaf	manual

	Width	cm	Flag leaf maximum width	4		
	Area	cm <sup>2</sup>	Flag leaf area			
	Incli	degree	Flag leaf inclination			
	StoDen	m m <sup>-2</sup>	Flag leaf stomatal density			
Ecophysiology	ETRm	μmol <sub>e</sub> m <sup>-2</sup> s <sup>-1</sup>	maximum rate of electron transport	6		planimeter
	alpha	μmol <sub>e</sub> μmol <sub>photons</sub> <sup>-1</sup>	initial slope of the light curve, related to maximum yield of photosynthesis			
	Ik	μmol <sub>photons</sub> m <sup>-2</sup> s <sup>-1</sup>	PAR value of the point of intersection between the horizontal line ETRmax and the extrapolated initial slope			
	Asat	μmol <sub>CO2</sub> m <sup>-2</sup> s <sup>-1</sup>	Saturating assimilation			gas exchange (Licor 6800)
	Aqe	μmol <sub>CO2</sub> μmol <sub>photons</sub> <sup>-1</sup>	apparent quantum efficiency			
	Lcp	μmol <sub>photons</sub> m <sup>-2</sup> s <sup>-1</sup>	Light compensation point			
Production	Yield	g	Plant grains dry matter	6		Plant
	#Pan		Panicles number			
	#Kern		Number of grain per panicle			Panicle
	TKW	g	1000 grains dry weight			Grain
	SF	%	Spikelet fertility rate			
	HI	%	Harvest index			Plant
Post harvest quality	M	cm	kernel major axis (length)	3	grain	image analysis
	m	cm	kernel minor axis (width)	3	grain	image analysis
	Star %	g.100g <sup>-1</sup> db	flour starch content on dry basis	3	grain	enzymatic colorimetry
	Amy %	g.100g <sup>-1</sup> db	starch amylose content on dry basis	3	grain	differential scanning calorimetry
	ε %	%	pore volume to total volume ratio	3	grain	pycnometry and hydrostatic balance

174

175 At flowering, four out of the ten studied plants were collected for image-based analysis and destructive  
176 measurements. Destructive measurements consisted in total plant leaf area (PLA) using a planimeter  
177 and the shoot vegetative dry matter (leaves and stems). The ratio between PLA and the leaves dry  
178 matter gave an estimate of plant specific leaf area (SLA). The stomatal density (StoDen) was observed  
179 on flag leaves, from a footprint taken by a nail polish on the leaf surface and counted with ImageJ on  
180 the images observed on the microscope (Fig 2A). An index of plant compactness (CPN) was derived

181 from plant image, expressed as the ratio of the projected area of leaves over the projection of the  
182 volume defined by the whole aerial part of the plant (Fig 2B).



183

184 *Figure 2: Image-based phenotypic variables. A) Right: Stomatal density observed on microscope slide, left:*  
185 *microscope image with stomata indicated with red crosses within a fixed area of 0.1 mm<sup>2</sup>. B) Whole plant picture*  
186 *to retrieve compactness. Compactness is estimated as the ratio between the number of green pixels over the total*  
187 *pixels defining the convex hull of the areal part of the plant (green and black pixels). C) Estimation of the stay*  
188 *green area (SGA) from a picture of green leaves at harvesting. SGA corresponds to the area in green defined by*  
189 *green pixel. The green coin in the middle is used as a green reference for the segmentation process and scaling*  
190 *the pixel.*

191 At harvesting, the six remaining plants were dissected into vegetative parts and reproductive parts. On  
192 the vegetative part, the total dry mass was weighted (vegetative dry weight: VDW) and pictures of the  
193 green leaves were used to estimate a stay green area (SGA) from pixel segmentation, defined as the  
194 green area left on the main stem (Fig2 C). On the reproductive part, the yield was measured as the  
195 total grains dry matter collected on all the panicle of the plant. The panicle of the main stem was used  
196 to count the number of fertile and unfertile grain per panicle and derive a spikelet fertility rate (SF).  
197 The harvest index (HI) was estimated as the ratio of the yield over the total aerial biomass (vegetative  
198 and panicles structural components).

199 Further analyses were performed on grain morphological and physicochemical feature on a subsample  
200 of the harvested spikelets. Paddy kernels were oven-dried at 45°C in a ventilated oven until constant  
201 weight was reached. Kernels were then dehusked and polished using a Satake model laboratory testing  
202 husker THU35C-T and Tadd mill 4E-230 machines. Digital RGB images (800 dpi) of polished kernels  
203 were acquired using a flatbed scanner (Epson Perfection v700 Photo). The grain major (length  $M$ ) and  
204 minor axis (width  $m$ ) were computed from the projected area of the binarized image of individual

205 kernels fitted from an ellipse, using ImageJ analysis software platform. Fine-ground rice flours were  
206 obtained using cargo kernels a ball mill (Dangoumill 300, Prolabo, France). After fine-group flour  
207 moisture content determination by thermogravimetry at 104°C, total starch content (%db) was  
208 estimated in triplicate by enzymatic colorimetry (515 nm) from the total released glucose after  
209 incubation and hydrolysis of about 300 mg db of flour with thermostable- $\alpha$ -amylase (Novo Nordisk,  
210 Denmark), and later with glucose oxidase and peroxidase (GOD & POD, Sigma, USA), as per Giraldo  
211 Toro et al. (2015). The trace of free glucose was neglected in the native rice flours. The amylose content  
212 was then estimated in duplicate using Differential Scanning Calorimetry DSC 8500 (Perkin Elmer, USA)  
213 as per Pérez et al. (2013) with modifications. The enthalpy change of formation of complexes between  
214 amylose and phospholipids during cooling was estimated from 10-11mg db of flour mixed to 40 $\mu$ l of  
215 lysophospholipid 2% (w/V in water) against a pure amylose standard. The kernel porosity ( $\epsilon = 1 - \text{app } d/d$ )  
216 expressed as percentage was then computed based on the estimation of the true density ( $d$  in  
217  $\text{g.cm}^{-3}$ ) of fine-ground flour by pycnometry using helium carrier and the apparent density (app  $d$  in  $\text{g.cm}^{-3}$ )  
218 using few kernels on a hydrostatic balance with ethanol. and expressed as percentage.

219 Gas exchange measurements were conducted on the flag leaf few days after flag leaf emission on the  
220 six plants monitored until harvesting. Response curves to photosynthetic photon flux density (PPFD)  
221 were performed using a portable photosynthesis system (LI-6800; LiCor Biosciences, Lincoln, NE, USA)  
222 at around 10 a.m. each morning over a week. Assimilation- irradiance ( $A - \text{PPFD}$ ) curve fitting analysis  
223 were then conducted using the Mitscherlich function (Eq 1) (Heschel *et al.* 2004) to estimate the three  
224 photosynthetic parameters: the light saturated assimilation ( $A_{\text{sat}}$ ), apparent quantum yield ( $A_{\text{qe}}$ ) and  
225 the light compensation point ( $L_{\text{CP}}$ ) for each individual.

226

$$227 \quad A = A_{\text{sat}} \left[ 1 - e^{-A_{\text{qe}}(\text{PPFD} - L_{\text{CP}})} \right] \quad (\text{Eq1})$$

228 Electron transport rate - irradiance (ETR-PPFD) curve fitting analysis were also determined using  
229 equation (Eq 2) to extract the maximum electron transport rate ( $\text{ETR}_m$ ), the quantum efficiency of  
230 photosynthesis ( $\alpha$ ) and the minimum saturating irradiance ( $I_k = \text{ETR}_m / \alpha$ ).

231

$$232 \quad \text{ETR} = \text{ETR}_m \tanh(\alpha \text{PPFD} / \text{ETR}_m) \quad (\text{Eq2})$$

233

234 *Assessing the effect of daily light integral (DLI) and daily light fluctuation (DLF) on*  
235 *phenotypic traits*

236 The three treatments considered in this study varied either from the amount of light receive (DLI)  
237 and/or in the intensity of light fluctuation perceived over a day (DLF). Each light treatment was a single  
238 combination of DLI and DLF. To evaluate if the difference in phenotypic variations were due to DLI or  
239 DLF, we conducted statistical analysis based on analysis of covariance models (ANCOVA). For each  
240 phenotypic variable studied, we tested the two following ANCOVA models:

241 *Model 1:*  $Y_{ij} = \mu + V_i + DLI + DLF + V_i DLI + V_i DLF + \varepsilon_{ij}$  (Eq 3)

242 *Model 2:*  $Y_{ij} = \mu + V_i + DLI + V_i DLI + \varepsilon_{ij}$  (Eq 4)

243 Where  $Y_{ij}$  is the phenotypic value of the individual  $j$  of the variety  $i$ ;  $\mu$  is model grand mean;  $V_i$  is the  
244 effect of the variety  $i$ ; DLI and DLF are covariates,  $V_i DLF$  and  $V_i DLI$  are the interaction terms and  $\varepsilon_{ij}$  is  
245 the residual term. Normality of model residuals and homoscedasticity were tested, and response  
246 variables were transformed using square-root or Box-Cox transformation accordingly to ensure  
247 normality. For each phenotypic trait, we conducted model testing by comparing the two models fit  
248 using a likelihood ratio test (LRT):

249 
$$LRT = -2(\log LK_{model1} - \log LK_{model2})$$

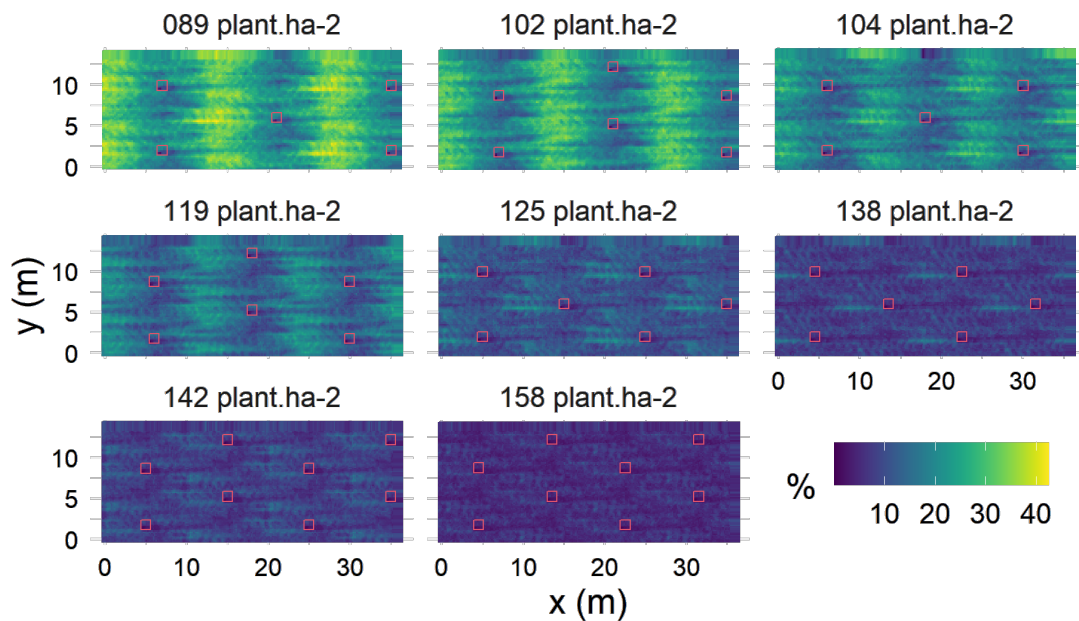
250 Where  $\log LK$  is the model log likelihood. LRT was compared with a Chi-squared distribution to obtain a  
251 p-value. Significant differences between the two nested models (p-value<0.05) meant that DLI alone  
252 did not explained the phenotypic variations observed, and therefore that considering the changes in  
253 light fluctuation (DLF) improved model prediction. Likelihood ratio tests were performed using the  
254 `lrtest` function of the `lmtest` R package (Zeileis & Hothorn 2002).

## 255 Results

### 256 *Defining the light regime available for growing rice under an oil palm-based* 257 *agroforestry system*

258 The simulation of light transmission on the eight planting patterns investigated clearly demonstrated  
259 the significant reduction in the light transmitted with increasing planting density (Fig 3). For the lowest  
260 density, light transmission reached a maximum of 43% in the middle of the inter row, while it only  
261 reached 13% for the highest density. Simulation outputs showed an important decrease in radiation  
262 with increasing palm density, with a maximum irradiance around midday. The daily radiation available

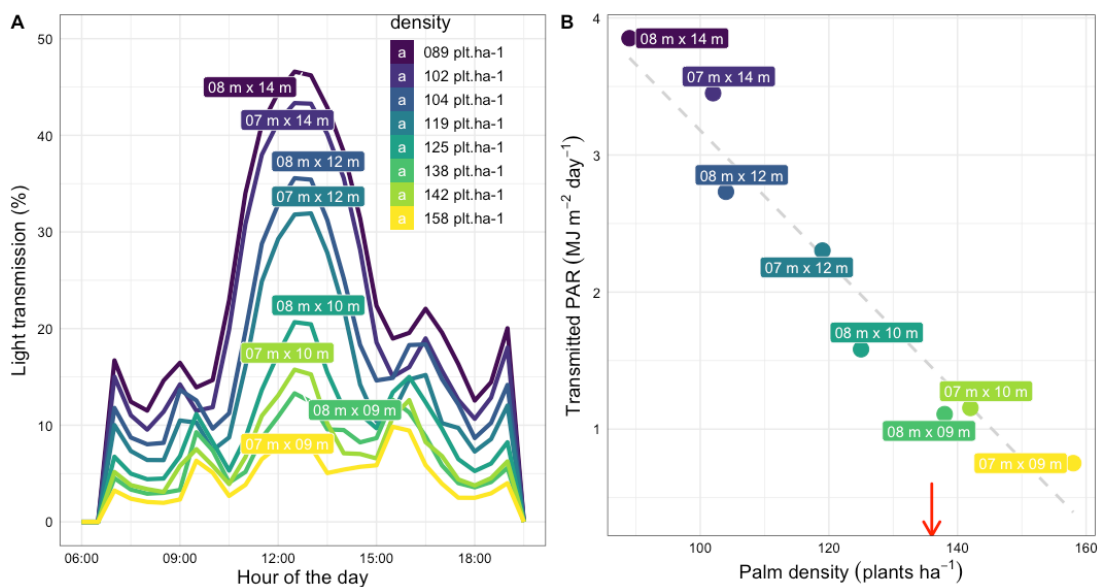
263 for rice decreased with planting density (Fig 4), the selection of an interesting design hence depended  
 264 on the trade-off between oil palm density and daily PAR transmitted for rice.



265

266 *Figure 3: Simulated light transmission under oil palm canopies with various planting designs. Colors indicates*  
 267 *percentage of incident light and red squares the positions of palm trees.*

268



269

270 *Figure 4: A) Average light transmission in the rice area over a day for the height simulated designs. B) Average*  
 271 *daily photosynthetic active radiation available for rice between palm rows. The red arrow represents the*  
 272 *conventional density (136 plants ha<sup>-1</sup>) and the dotted line the average loss of transmitted light with increasing*  
 273 *density.*

274 In one hand, the distance between rows strongly influenced the intensity of light around midday (Fig  
 275 4A), distances lower than 12m sharply limiting the maximum light transmission below 20%. In the other

276 hand, distances over 12m decreased oil palm density below 110 plants ha<sup>-1</sup>. The 7 m x 12 m design  
277 exhibited the best compromise to ensure a sufficient palm density and limiting shading between rows.  
278 Moreover, this density of 119 plant ha<sup>-1</sup> is close to the conventional densities of 136-143 plants ha<sup>-1</sup>.  
279 The 7 m x 12 m design was thus chosen as the reference to mimic in controlled conditions rice-palm  
280 agroforestry light, i.e the 60% of light attenuation over the day (Fig 1).

281

282 *Changes in plant morphology are mainly explained by daily light quantity while*  
283 *plant phenology is also impacted by light fluctuation*

284 Under the shading treatments two varieties showed drastic increased in leaf length and etiolation  
285 symptoms leading to severe lodge, which prevented conducting them up to harvest: varieties V1 and  
286 V2 were thus removed from the three growth chambers 55 days after sowing. This first result pointed  
287 out how morphological responses to shade could introduce additional yield-reducing factor as lodging,  
288 and can be a first criterion to select adapted varieties. The variety V6 did not reach production maturity  
289 within the experimental time window, and the variety V4 was sensitive to the photoperiod chosen for  
290 the experiment, thus preventing plants to flower. Consequently, the following results will focus on the  
291 four other varieties on which phenotypic monitoring was performed from sowing to harvest.

292 Reduction in daily light quantity significantly affected the dynamic of leaf and tiller emission (Table 3  
293 and Fig 5A & B). The phyllochron on the main stem increased under shade, with variations in the total  
294 number of leaves emitted depending on treatments and varieties (Table 4). During the first month  
295 after sowing, the number of leaves on the main stem was higher under the control treatment than  
296 under shade, but at maturity, plants under shade produced more leaves on the main stem for the  
297 *japonica* varieties (Fig 5A). The *indica* variety V3) emitted more leaves on the main stem under the  
298 control treatment than in the S treatment whereas the japonica V5 presented an opposite behavior  
299 with an increased number of leaves both shading treatments (Table 4). A significant effect of light  
300 fluctuation was revealed on phyllochron and the total number of leaves on the main stem, with  
301 important variations among varieties (Table 4). Regarding tiller emission, reduction in DLI induced  
302 significantly less tillers. DLF modulated the total number of tillers emitted, with more tillers in S-AF  
303 than in S, with significant differences for V5 and V8. Leaves length and width on the main stem sharply  
304 increased under both shading treatment (Fig 5C), and these changes in leaf dimensions were attributed  
305 to DLI and not to DLF (Table 3). The flag leaf shape (LW ratio) changed significantly for variety V3 with  
306 a higher length to width ratio under shade, while the other three varieties maintained a comparable  
307 shape and even tended to reduce the ratio by contrast (Table 4).

308

309  
310  
311  
312

*Table 3: Summary of models analysis to assess the effect of variety, daily light integral (DLI), daily light fluctuation (DLF) and their interaction on phenotypic traits. An ANCOVA is performed with variety as factor and DLI and DLF as covariables (ns: non-significant, \*P<0.05; \*\*P<0.01; \*\*\*P<0.001). For variable abbreviations, see Table 2.*

	Rep	var	Variety	DLI	DLF	V x DLI	V x DLF	r2	LRT
Yield components	6	Yield	***	***	ns	ns	*	0.76	***
	6	#Pan	***	***	ns	ns	ns	0.83	ns
	6	#Kern	***	ns	**	ns	*	0.65	***
	6	TKW	***	***	***	**	**	0.90	***
	6	SF	***	*	***	ns	*	0.42	***
	6	HI	***	***	***	**	***	0.92	***
Flag leaf morphology	10	Length	***	***	ns	ns	ns	0.52	ns
	10	Width	***	***	ns	**	ns	0.77	ns
	10	LWratio	***	ns	ns	*	*	0.56	ns
	10	Area	***	***	ns	ns	ns	0.56	ns
	4	Incli	***	***	ns	***	***	0.94	***
	4	StoDen	***	***	ns	ns	ns	0.73	ns
Phenology	10	DaysFL	***	***	*	ns	ns	0.66	ns
	10	Phyllochron	***	***	*	***	*	0.65	**
Plant architecture	10	#Lea	***	*	ns	***	***	0.77	***
	10	#Til	***	***	***	**	ns	0.94	***
	4	PLA	***	***	ns	ns	ns	0.47	ns
	4	CPN	***	***	ns	*	ns	0.84	ns
	4	SLA	***	***	ns	ns	ns	0.64	ns
	6	VDW	***	***	*	ns	**	0.54	***
	6	PH	***	***	ns	ns	ns	0.85	ns
Ecophysiology	6	SGI	***	***	***	***	**	0.90	***
	6	Lcp	***	**	*	*	***	0.61	***
	6	Asat	*	ns	**	ns	***	0.34	***
	6	Aqe	***	ns	ns	ns	***	0.48	***
	6	Rd	*	ns	*	ns	**	0.27	***
	6	ETRm	ns	ns	*	ns	*	0.21	**
	6	alpha	***	*	ns	ns	***	0.49	***
	6	lk	**	ns	**	ns	ns	0.24	*
Grain morphology	3	M	***	ns	ns	ns	ns	0.95	ns
& physicochemical quality	3	m	***	ns	ns	ns	ns	0.48	ns
	3	Star %	*	**	*	ns	ns	0.49	**
	3	Amy %	***	ns	ns	ns	ns	0.97	ns
	3	ε %	***	*	***	***	***	0.92	***

313

314 Interestingly, stomatal density on flag leaf significantly decreased with DLI, but only for the two  
315 varieties V7 and V8, while the two others varieties V3 and V5 kept a comparable stomatal density while  
316 increasing flag leaf area. At the plant level, the decrease in DLI involved taller and less erected plants  
317 (lower CPN), mainly due to longer, wider and thinner leaves as well as longer internodes (Fig S4).

318  
319

Table 4: Phenotypic variations of traits with varieties and treatments. Numbers indicate mean value and letters represent significant difference between treatments for each variety assessed by Tuckey's test ( $P < 0.05$ )

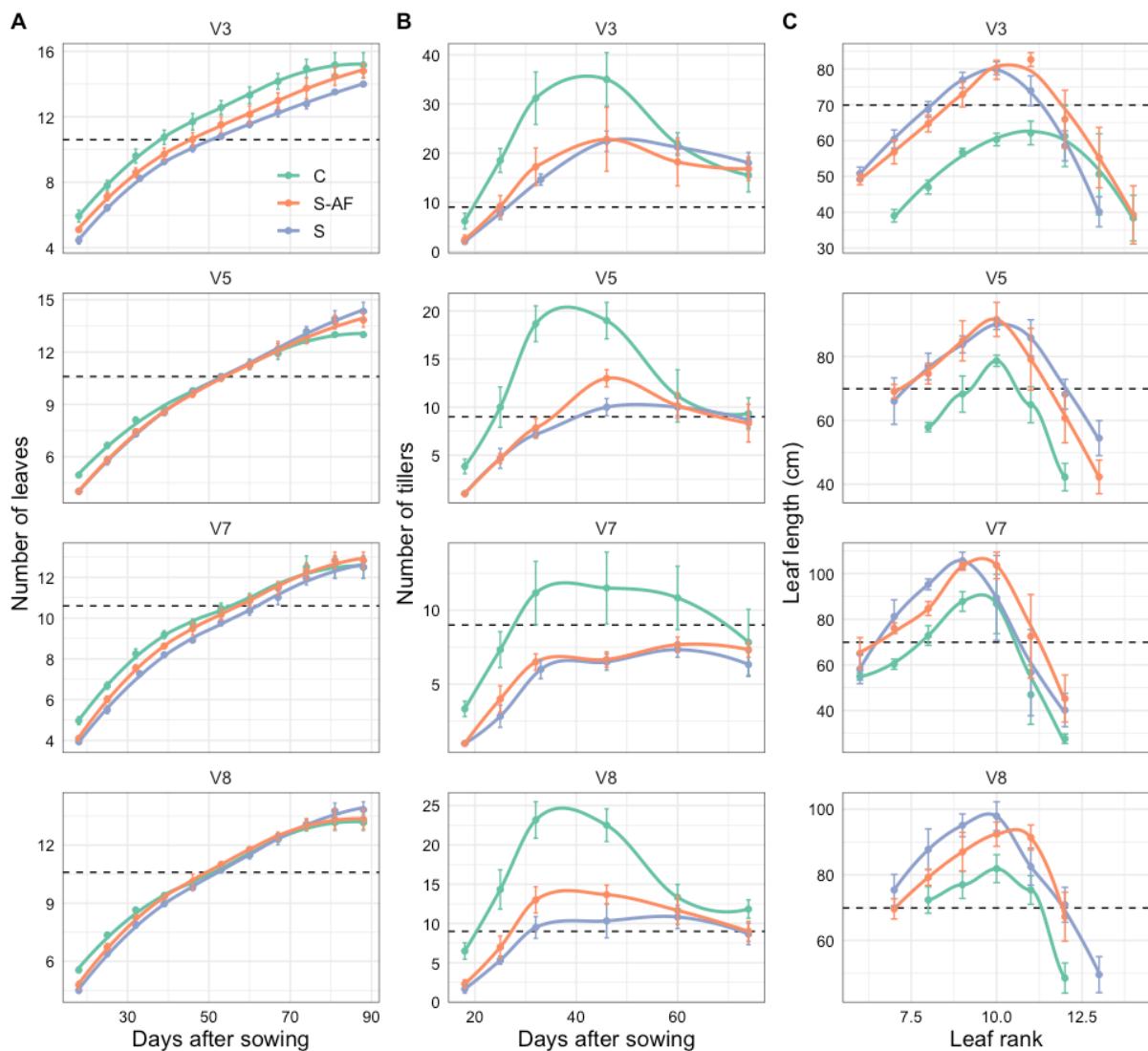
	V3			V5			V7			V8		
	C	S	S-AF	C	S	S-AF	C	S	S-AF	C	S	S-AF
Yield	34.2a	28.7ab	19.9b	38.7a	25.8b	31.2b	18.5a	14.1a	12.9a	33.4a	28.5ab	23b
Nb_Pan	14.8a	13.0a	12.8a	9.33a	7.33a	7.67a	6.5a	5.17a	4.83a	10a	7.67b	8.33ab
Nb_Kern	92.1a	90.9a	68a	143a	138a	143a	115a	116a	111a	97.7b	<b>120a</b>	<b>89.1b</b>
TKW	27.9a	26.6a	28.5a	30.7a	<b>27.2b</b>	<b>30.7a</b>	27.1a	24.4b	26ab	36a	32.8b	32.2b
SF	85.9a	<b>80.4a</b>	<b>59.5b</b>	89.5a	86.4a	85a	85.8ab	<b>94.3a</b>	<b>76.1b</b>	94.2a	92.6a	90.2a
HI	35.2a	<b>37.7a</b>	<b>21.3b</b>	46.3a	<b>41.2c</b>	<b>43.4b</b>	26a	25.3a	23a	35.7b	<b>38.1a</b>	<b>33.8b</b>
DaysFL	77.5b	88a	86.2a	76.3b	85.7a	83.3a	74b	81a	81a	76.3b	82.2a	78.7ab
phylochron	5.11c	<b>6.28a</b>	<b>5.75b</b>	5.87a	5.98a	6.03a	5.93b	6.49a	6.32a	5.8a	5.94a	5.9a
Nb_Lea	15.2a	<b>14b</b>	<b>15a</b>	13b	14.3a	13.8a	12.5a	12.5a	12.8a	13.2a	13.8a	13.3a
Nb_Til	35a	22.6b	25.2b	19.3a	<b>10.5c</b>	<b>13b</b>	11.5a	7.33b	7.67b	23.7a	<b>11c</b>	<b>14.2b</b>
CPN	0.32a	0.23b	0.21b	0.24a	<b>0.12c</b>	<b>0.16b</b>	0.19a	0.14b	0.14b	0.19a	0.14b	0.14b
PH	88.8a	82.3a	97.2a	113c	<b>121b</b>	<b>128a</b>	137a	141a	148a	110b	123a	117ab
VDW	60a	<b>44.8b</b>	<b>68.8a</b>	43a	35.6a	38.9a	51.9a	40.4a	42.3a	58.2a	45.1b	44.3b
PLA	2316b	3279ab	3348a	2173a	2223a	2487a	1615b	2117ab	2515a	2063a	2552a	2630a
SLA	209b	252a	263a	177b	218a	220a	158b	229a	216a	165a	210a	215a
FL Length	31.4b	40.3a	40a	38.1b	47.2a	40.9ab	32.9b	41.6a	43.7a	46.3b	54.6a	56.7a
FL Width	1.33b	1.51a	1.46a	1.39b	1.79a	1.76a	1.69b	2.15a	2.12a	1.54b	1.94a	1.83a
FL LWratio	23.7b	26.7ab	27.2a	27.6a	26.5a	23.3a	19.4a	19.2a	20.6a	29.9a	28a	31a
FL Area	30.4b	45.2a	45.4a	40.5b	60.8a	50.7ab	37.8b	60.4a	59.5a	48b	75.2a	73.4a
FL Incl	168a	165a	166a	164a	161a	162a	93.8ab	<b>107a</b>	<b>63.2b</b>	160a	<b>128b</b>	<b>146a</b>
FL StoDen	748a	698a	671a	641a	623a	649a	594a	531ab	516b	583a	512b	544ab
SGA	70.8b	150a	136a	3.66c	<b>176a</b>	<b>68.9b</b>	68b	344a	305a	16.2c	<b>165a</b>	<b>119b</b>
SPAD	31.9a	34.3a	37.1a	35.4b	<b>43.1a</b>	<b>36.7b</b>	41.6a	41.2a	35.3a	36.2a	36.1a	36.2a
Lcp	55.6a	<b>67.1a</b>	<b>33.1b</b>	34.2a	22.3a	31.2a	39.6a	<b>29a</b>	<b>16.7b</b>	30.8a	32.4a	35.7a
Asat	16.6a	15.6a	20.3a	13.7b	<b>19.7a</b>	<b>11.7b</b>	17.2a	15.1ab	11.6b	18.1a	17.6a	15.4a
Aqe	0.0021b	<b>0.0018b</b>	<b>0.0028a</b>	0.0027ab	<b>0.0033a</b>	<b>0.0023b</b>	0.0029b	<b>0.0028b</b>	<b>0.0042a</b>	0.0031a	0.0029a	0.0027a
Rd	0.50a	0.42a	0.81a	0.57ab	<b>0.67a</b>	<b>0.25b</b>	0.75a	0.64a	0.34a	0.9a	0.85a	0.63a
ETRm	154a	142a	166a	153ab	<b>173a</b>	<b>136b</b>	163a	149ab	121b	168a	159a	152a
alpha	0.29ab	<b>0.27b</b>	<b>0.32a</b>	0.32a	<b>0.33a</b>	<b>0.3b</b>	0.33ab	<b>0.32b</b>	<b>0.34a</b>	0.33a	0.32a	0.31a
lk	522a	547a	516a	476a	526a	458a	491a	<b>469a</b>	<b>356b</b>	505a	500a	490a
M	6.71a	6.67a	6.68a	6.22a	6.55a	6.33a	4.73a	4.99a	4.67a	6.79a	6.57a	6.65a
m	2.35a	2.25a	2.25a	2.43a	2.55a	2.44a	2.70a	2.67a	2.69a	2.60a	2.54a	2.55a
Star %	77.5a	77.2a	78.4a	84.5a	72b	79.2ab	84.6a	77.6a	75.4a	76a	68.6a	77.8a
Amy %	23.5a	25a	23.7a	14.2a	14.5a	14.8a	21a	21.7a	21.6a	12.8a	12.6a	10.6a
ε %	10.3a	9.60a	9.78a	8.45b	<b>10.7a</b>	<b>8.38b</b>	11.7a	<b>9.54c</b>	<b>10.3b</b>	8.66ab	<b>8.82a</b>	<b>8.29b</b>

320

321 The total plant leaf area increased under shading treatments without marked difference between S  
 322 and S-AF. The SLA increased in both shading treatments without marked difference du to DLF,  
 323 traducing the effect of light quantity alone in leaf elongation and widening. The effect of DLF was only  
 324 important for the total vegetative dry matter (VDW) at harvesting, partly because of the contrasted  
 325 behavior of V3 between S and S-AF (Table 4).

326

327 *Figure 5: Dynamic of leaf emission according to varieties and treatments (A), dynamic of tillers emission*  
 328 *according to varieties and treatments, (B) and length of leaves on the main stem (C). Smooth lines and points*  
 329 *represent average va*



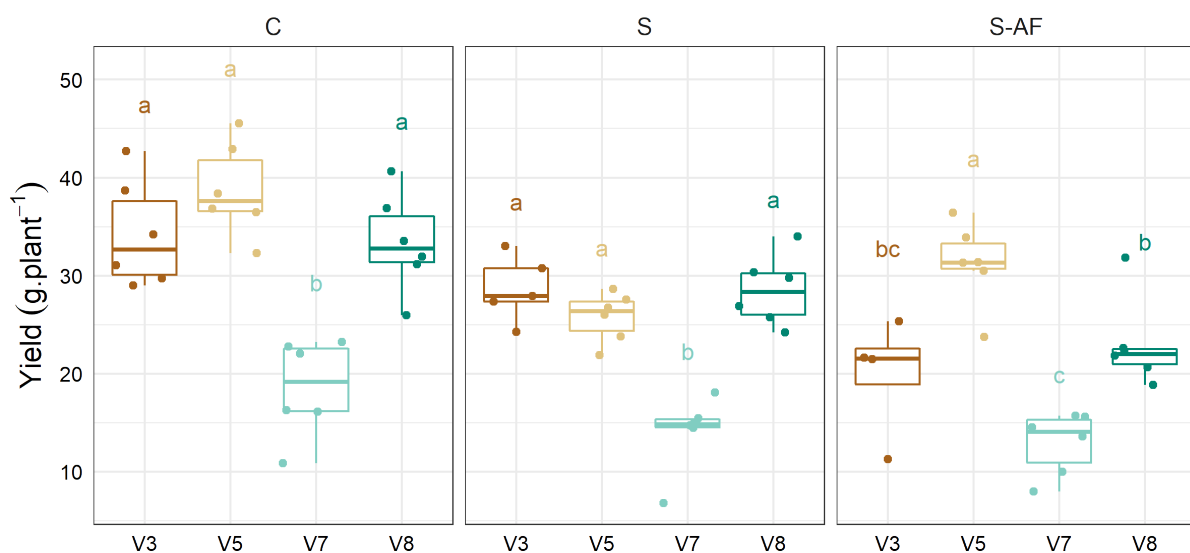
330 *ues and vertical lines standard deviations. Dotted lines indicates the median value (taking all treatments and*  
 331 *varieties together) for better visualize the difference between varieties.*  
 332

333 *Light fluctuation impacted leaf senescence and grain filling, and involved high*  
 334 *variation in photosynthetic capacities among varieties*

335 At the plant scale, the most marked difference between treatments was the stay green area at  
 336 physiological maturity (Table 3 & Table 4). We observe a gradient in leaf senescence with light

337 fluctuation, plants from the control treatment presenting higher senescence than plants under shade  
338 that stayed greener. Increasing DLF significantly increased senescence (low SGA), suggesting that  
339 resource reallocation may depend on irradiance intensity.

340 Plant yield was significantly higher in the control treatment, and no major differences were stressed  
341 between the two shading treatments (Tables 3 & 4). Lower yield under shade was mainly explained by  
342 the reduction in the number of panicles per plant, but the establishment of grain yield varied with DLF.  
343 Indeed, the comparison of production between S and S-AF revealed that under higher light irradiance  
344 (S-AF), spikelet fertility was reduced, thus limiting the number of kernels per panicle. Nevertheless,  
345 yield was maintained under S-AF through higher TKW (bigger grains) (Table 3), suggesting that grain  
346 filling was enhanced with irradiance intensity. The varieties V3, V5 and V8 produced more than the  
347 variety V7 in all the treatments. Interactions between varieties and shade treatments was stressed,  
348 the variety V5 producing significantly more than V3 and V8 under S-AF conditions while no significant  
349 difference was stressed between these three varieties in the two other treatments (Fig 6).



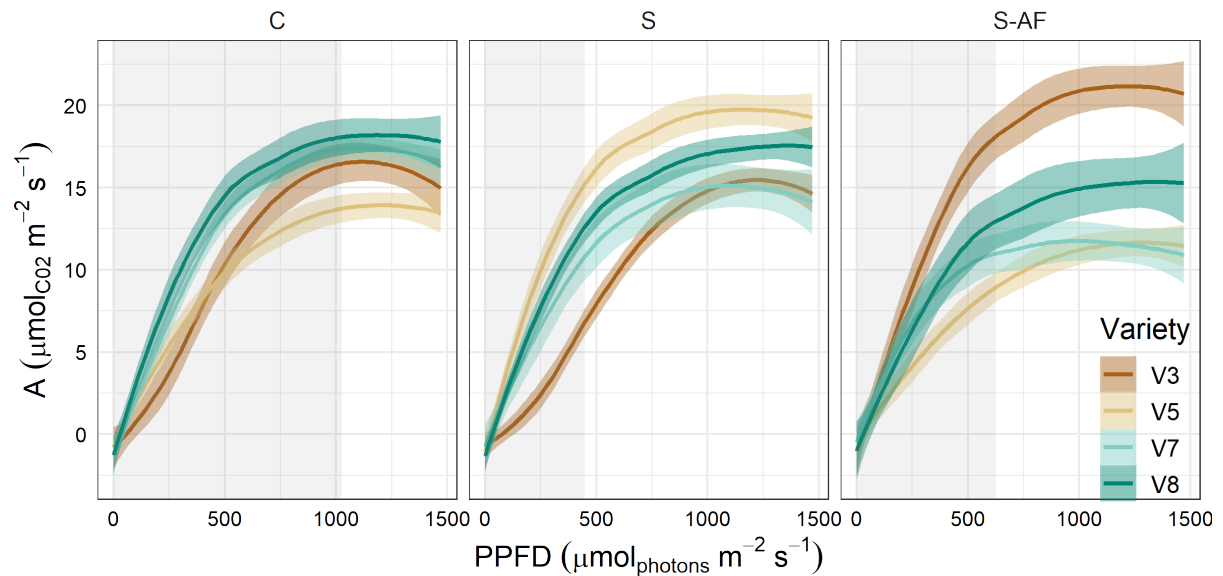
350

351 *Figure 6: Plant yield for the four varieties studied in the three light treatments. Letters indicate significant*  
352 *differences between varieties in each treatment (Tuckey s test P<0.05).*

353

354 The study of flag leaf CO<sup>2</sup> assimilation revealed high interaction effects (V x DLF) for nearly all  
355 photosynthesis parameters (Table 3). Light-responses curves exhibited contrasted behavior of  
356 varieties, with more varietal variability under the S-AF treatment than in the two other treatments (Fig  
357 7). The variety with maximal photosynthesis was different in each treatment, revealing the high  
358 variability in photosynthetic processes with environment and the potential weak heritability of  
359 photosynthetic traits. No clear relationship could be established between photosynthetic capacity and

360 other morphological or yield-related variables, highlighting the complexity and multifactorial  
361 processes involved in plant growth and production. At the grain scale, the morphology of grain (length  
362 and width) was not significantly affected by the light treatments (Table 4). Complementary ANCOVA  
363 confirmed that DLI and DLF has no significant effect on grain morphology (Table 3) contrarily to the  
364 factor variety, suggesting that kernel length and width are heritable traits.



365

366 *Figure 7: Response curves of carbon assimilation with irradiance according to treatments and varieties. Lines*  
367 *indicate smooth curves adjusted per variety and per treatment with 95% confidence interval. Grey areas represent*  
368 *the light fluctuation domain provided in each treatment.*

369

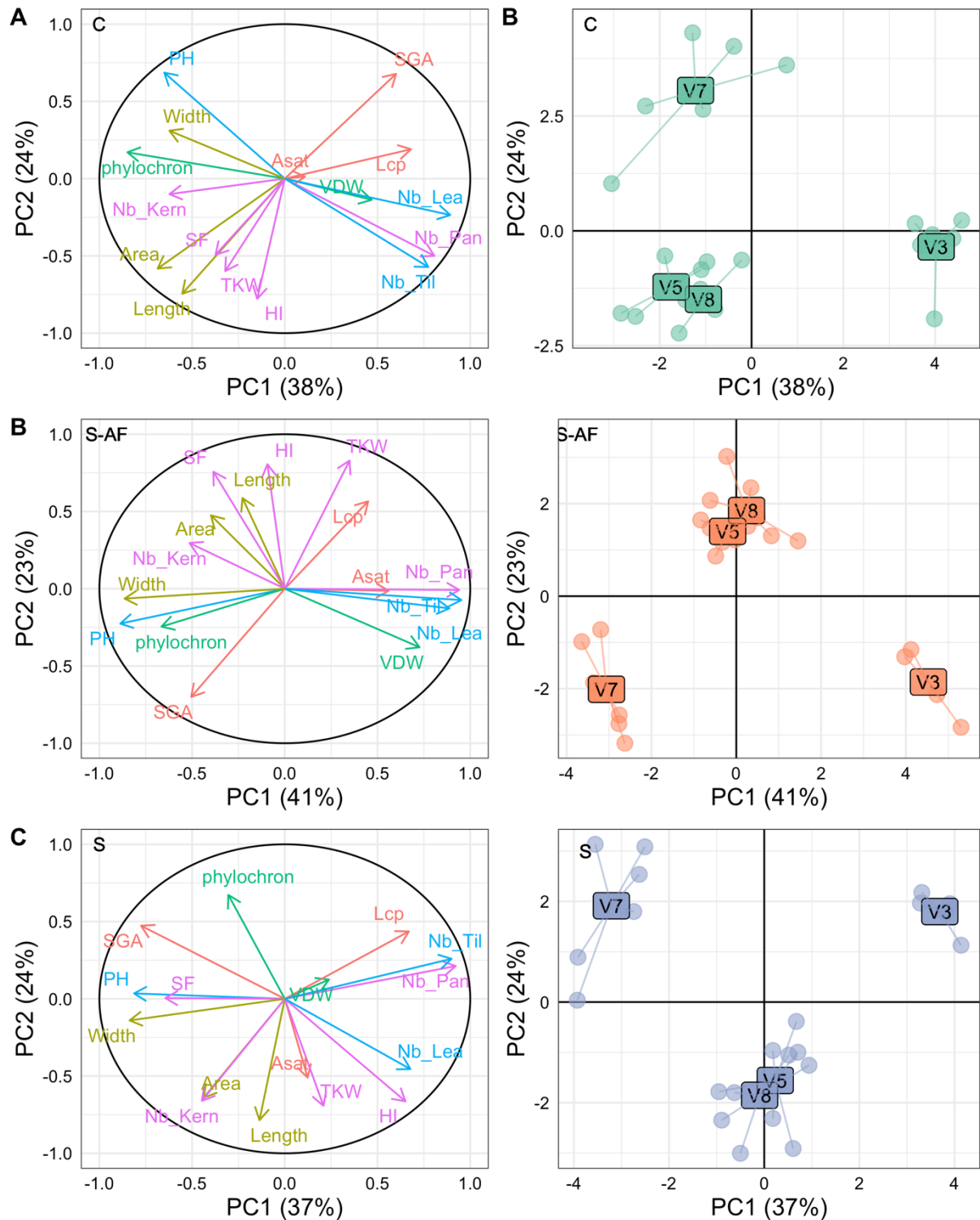
370 Both amylose and starch content were revealed being also significantly affected among varieties. The  
371 variation of the composition of starch was only observed among V5 under low light, where the DLI  
372 treatment induced a significant reduction of the amylose content as compared to the control one.  
373 Varieties V3, V5, V8 exhibited significant variation in their porosity. The kernel porosity was  
374 significantly affected by varieties, by treatments and their interactions (Table 4). Contrary to V5 and  
375 V8 varieties, V7 presented a significantly lower level of air space for the kernel grown under S than  
376 that of S-AF environment.

377

378 *Relative changes among varieties are maintained between the light treatments*

379 Three principal component analysis (PCA) were performed, one for each treatment (Fig 8). For all PCA,  
380 more than 60 % of the phenotypic variance was explained by the two first components (PC1 & PC2),  
381 the contribution of PC3 to total variance being markedly lower than PC2. In the control treatment (Fig

382 8A), vegetative components (number of tillers, number of leaves) were the major contributors to PC1  
 383 while yield components (kernel weight, harvest index) contributed to PC2.



384  
 385 *Fig 8: Principal component analyses performed on the three treatments (A: treatment C, B: treatment S-AF and C:*  
 386 *treatment S). Graphics on the left represent the projection of traits on PCA axes and graphics on the right the*  
 387 *projection on PCA of individuals grouped per varieties*

388

389 Interestingly, flag leaf morphology (length and area) contributed more to PC2 than PC1, suggesting a  
390 closer link between flag leaf geometry and yield components than between the whole plant vegetative  
391 attributes and yield. PCA for S-AF (Fig 8B) resulted in similar interpretations, the vegetative  
392 components contributing to PC1 and yield components to PC2. Additionally, plant height and flag leaf  
393 width contributed markedly to PC1, which revealed the architectural variations triggered by lower light  
394 intensity. Physiological variables such as Lcp, Aqe and SGA were highly correlated to yield components.  
395 Plants with the highest yield presented low SGA (high senescence), low photosynthetic efficiency and  
396 high light compensation point. This result confirmed that under S-AF treatment, yield depended more  
397 on resource remobilization to the panicle rather than enhancement of the photosynthetic capacities  
398 of the flag leaf. The PCA performed on the treatment S (Fig 8C) indicated only small discrepancies with  
399 the PCA for the S-AF. The dichotomy between vegetative/architectural features and yield features was  
400 marked in both shading treatments. Variations in flag leaf width particularly discriminated individuals  
401 in shading treatments, and in contrast to the control treatment, a higher correlation was observed  
402 between flag leaf width and yield than between flag leaf length and yield (Fig S5). Projection of  
403 individuals on the three PCAs clearly split varieties, revealing that the studied phenotypic traits and  
404 their combination were specific to varieties. In the three treatments, projections of V5 and V8 were  
405 superposed, denoting the phenotypic similarities between those two varieties. Architectural features  
406 of V3 and V7 were significantly different since their projections were in opposition in respect to PC1,  
407 notably in the shading treatments. Finally, the similarity between varieties projections from the three  
408 PCAs may suggest that varietal responses to low light are likely to be heritable, and that varietal  
409 screening under full light can provide clue on varietal behavior under low light.

## 410 Discussion

411 *Using functional-structural plant models to design innovative agroforestry*  
412 *systems*

413 The development of agroforestry system often depends on the success of smallholders' initiatives to  
414 test new farming practices. The adoption of oil palm agroforestry systems has been promoted among  
415 smallholders through empirical practices conferring socio-economic and environmental benefits  
416 (Susanti *et al.* 2020). However, it is not straightforward to conduct specific studies to understand and  
417 optimize the agronomic performance of oil palm agroforestry systems, since such studies require years  
418 of investigation and are very costly. Intercropping is generally only associated in the first years after  
419 planting, in systems where the density of oil palm is optimized for growing the palm alone at maturity  
420 (Koussihouèdé *et al.* 2020). In this study, we considered that future food security and environmental

421 concerns would require the development of sustainable oil palm agroforestry systems, with the  
422 possibility of growing food crop in association with mature oil palms.

423 In this context, we proposed a new approach, based on the assessment of light distribution in  
424 a mature oil palm agroforestry system. Using a quantitative trade-off between light resource for rice  
425 cultivation and oil palm density to optimize oil production, the modelling approach proposed in this  
426 paper showed how FSPM could help designing oil palm-based intercropping systems with scientific  
427 background. The proposed methodology could be adapted to many systems that requires time-  
428 consuming and expensive trials. However, it is worthy to note that this approach was particularly  
429 suitable for oil palm-based systems due to the low architectural plasticity of the oil palm, and its low  
430 impact on light interception efficiency at the plot level (Perez *et al.* 2022). The low plasticity of oil palm  
431 reinforces its suitability for association with other crops. In this study we did not consider the effect of  
432 planting density on oil palm architecture and subsequently light interception, but it is likely that the  
433 same approach with perennial plants with complex branching patterns and highly plastic to the  
434 radiative environment would require additional modeling inputs to derive reliable light partitioning  
435 predictions. The number of designs tested in the presented simulation study was limited to a few  
436 numbers, but further simulations could be performed to mathematically optimize light partitioning  
437 and oil palm density, including new patterns different from the row planting proposed here.

438 Studies focusing on the effect of light attenuation are often performed in outdoor conditions using  
439 shading net (Liu *et al.* 2014; Chen *et al.* 2019; Jia *et al.* 2021), and more recently in growth chambers  
440 (Yang *et al.* 2018; Zhang *et al.* 2020). Highly controlled growth chambers are generally used to simulate  
441 future climate conditions (i.e rising CO<sub>2</sub> or temperature), but can now be used to simulate change in  
442 light regime (Violet-Chabrand *et al.* 2017). The originality of our study was to use modeling outputs to  
443 set up light treatments in controlled conditions. Conversely to outdoor conditions where the dynamic  
444 of light cannot be controlled, here we were able to investigate the impact of both light quantity and  
445 the dynamic of light intensity. Such experimental device aimed at mimicking the light regime of an  
446 agroforestry system not yet implemented, taking into account the reduction of light and its variation  
447 over the day. However, the major drawback of our experiment was the inability to modulate light  
448 quality (red/far red ratio) as it would be in the shade of oil palm, which can affect growth and  
449 development of the understorey crops (Chen *et al.* 2019; Zhang *et al.* 2020).

450

451 *Toward the selection of rice varieties adapted to agroforestry light conditions*

452 Three characteristics of light are modulated under agroforestry systems: the quantity of light, the  
453 fluctuation of light, and the quality of light. The inexistence of real conditions to screen the tolerance

454 of rice varieties to the agroforestry system of interest involved setting up a trial in controlled conditions  
455 mimicking these conditions. Our controlled conditions prevented us from modulating light quality, and  
456 more precisely the red to far-red ratio, which is known to be a light signal triggering a suite of  
457 physiological and morphological responses called the shade avoidance syndrome (Franklin 2008;  
458 Ballaré & Pierik 2017). Zhen and Bugbee (Zhen & Bugbee 2020) recently stressed the importance of  
459 far-red photons on plant photosynthesis, suggesting the need to integrate a larger range of wavelength  
460 in studies dedicated to investigate responses to light. Other studies already demonstrated the genetic  
461 inheritance of cereal crops in responses light quality (Wille *et al.* 2017), but only few investigated the  
462 interaction between light quantity and quality (Yang *et al.* 2018). Further dedicated experiments  
463 integrating response to light quality, in combination with light quantity and light fluctuation would  
464 thus be of great interest to complement the result found in the present study and better understand  
465 responses to agroforestry light regime. However, in the intercropping design prospected here, change  
466 in light quality would appear only a few hours during the day. This part time change in light quality  
467 raises new question about how long the light signal must last to trigger the shade avoidance syndrome  
468 (Li *et al.* 2021).

469 In our experiments, we focused on the effect of light integral (DLI) and light fluctuation (DLF) on rice  
470 growth and production. DLI represented an index of resource availability, whereas DLF was considered  
471 as a light signal. Our results confirmed that the reduction in the quantity of light on rice prolonged the  
472 period of growth, increased plant height and leaf area, decreased the number of tillers and total plant  
473 dry mater (Liu *et al.* 2014) and subsequently reduced grain yield (Wang *et al.* 2015b; Chen *et al.* 2019).  
474 Our result clearly showed the changes in resource investment under low light: plants produced fewer  
475 tillers but increase the number and the size of leaves in the main stem. Shading treatments triggered  
476 leaf elongation and widening, conferring a higher leaf area than under high light intensity. In parallel,  
477 leaves were thinner under shade, traducing a lower capacity to accumulate nitrogen (Murchie *et al.*  
478 2005). The adjustment in leaf morphology were consistent with other studies in rice (Liu *et al.* 2014)  
479 or others crops (Arenas-Corraliza *et al.* 2019; Poorter *et al.* 2019), notably the increase of SLA, but  
480 showed some discrepancies with respect to leaf widening. Contrarily to the present study and the  
481 review by Liu (Liu *et al.* 2014), reductions in leaf width under shade were observed for rice (Lafarge *et al.*  
482 *et al.* 2010) and for maize (Lacube *et al.* 2017). These discrepancies could be explained by the duration  
483 and the intensity of shade, and raises question about the existence of light signal thresholds that  
484 trigger morphological adjustments.

485 Light quantity was the main factor driving morphological and architectural changes, while light  
486 fluctuations only appeared to explain variations in yield components and phenology (Table 3). This  
487 study highlighted the importance of light fluctuation in the grain filling process and resource

488 reallocation. The stay green area was particularly affected by the intensity of light experienced by the  
489 plant, revealing that fluctuating light matters to trigger some process linked to resource reallocation  
490 and subsequently plant yield. Here we demonstrated that light fluctuation is part of the light signaling  
491 pathway that regulates leaf senescence (Woo *et al.* 2019), and that stay green can be an informative  
492 trait for the selection of varieties adapted to agroforestry systems. The reaction between light intensity  
493 and reallocation patterns have already been observed in wheat with vegetative dry matter  
494 redistribution into grains (Li *et al.* 2010), and with nitrogen reallocation in the leaves to optimize  
495 photosynthetic performance exposure (Li *et al.* 2021).

496 Among others, it has been established that low light intensity under shading nets could affect the grain  
497 quality traits, including the starch content its and composition (Li *et al.* 2006; Wang *et al.* 2013; Liu *et*  
498 *al.* 2014) and grain appearance. Our results confirmed that light quantity affected starch content in  
499 the grain, without altering the fraction of amylose. Wang *et al.* (2013) earlier reported some significant  
500 differences in total starch content and amylose content of milled rice flour, and concluded to the  
501 contribution of heredity, environment and their interaction for indica hybrid rice varieties under  
502 shading. The decrease in the amount of starch and amylose was also claimed by Li *et al.* (2006) in two  
503 grain varieties indica and japonica under shading treatments with nets (50% transmittance rate). The  
504 presence of chalk, which is a key criterion for visual assessment of grain marketability, can also be  
505 affected by shading environmental-related stress (Liu *et al.* 2014; Patindol *et al.* 2015). High porosity  
506 is usually related to the presence of chalk (Singh *et al.* 2003), and characterized by the presence of  
507 disorganized cellular structure (Lisle *et al.* 2000) leading to a greater cell and granular swelling,  
508 detrimental to grain eating quality. The four studied varieties showed contrasted grain porosity in  
509 responses to light quantity and fluctuation. The indica variety tended to present a lower porosity under  
510 both shading treatments while the three other varieties showed either higher or lower porosity than  
511 the control treatment. In this study, the significant loss in yield under shading treatments did not result  
512 in a significant decrease in milling quality as it observed in previous studies (Liu *et al.* 2014). Further  
513 research would be needed to investigate the qualitative response of rice plants to fluctuating  
514 radiations and shading, whose tolerance might be genotype-dependent. It is likely to favor the  
515 selection of suitable cultivars to meet the expectations of end-users, under constrained agroforestry  
516 growing environment.

517 The photosynthetic capacity measured via light response curve highlighted that light quantity  
518 and fluctuation triggered different responses among the four studied varieties. The high interaction  
519 between varieties and shading treatments was already stressed in previous studies (Wang *et al.*  
520 2015b; Pan *et al.* 2016), revealing the difficulty to select adapted varieties through photosynthetic  
521 measurements. The physiological measurements performed did not help retrieve the difference in

522 production among varieties, suggesting that yield is the consequence of multifactorial processes that  
523 can compensate variations in photosynthetic capacity. These specific responses to light intensity and  
524 fluctuation did not provide substantial benefits in term of production. Nevertheless, the absence of  
525 evolution of the morphological kernel traits under shading stressed that kernel shape is highly  
526 heritable and irresponsive to change in light intensity and fluctuation. It is likely that leaf scale  
527 measurements did not reflect an average value of the whole canopy photosynthesis. Besides,  
528 photosynthesis measurements are time consuming, preventing the efficient screening of varieties for  
529 breeding purpose.

530 Even if marked interactions were observed in physiological traits among varieties and treatments, the  
531 yield ranking between the four varieties was maintained in the three treatments. From an  
532 experimental and phenotyping perspective, this result tends to support that artificial light depletion  
533 using shade net could be sufficient to screen varieties of interest for agroforestry systems not yet  
534 implemented. Our result also confirmed previous findings revealing that productive materials in full  
535 sun conditions are also good producers in low radiation (Bueno & Lafarge 2017). The very specific  
536 behavior and low production (with potential low cooking and eating quality) of V7 together with the  
537 comparable production of the three other varieties made the identification of traits of interest difficult,  
538 without implementing reliable and discriminating descriptors. Indeed, the contrasted traits values  
539 between the two groups of individuals, formed by V7 and the three other varieties, could bias trait  
540 correlations. However, the variety V5 showed a significant higher production than the other varieties  
541 in the S-AF treatment, without exhibiting a chalky endosperm appearance potentially detrimental to  
542 its grain marketability. This variety maintained the highest harvest index among all the varieties and  
543 treatments, with a limited expansion of vegetative biomass in response to shade and a high leaf  
544 senescence under shade. These characteristics are consistent with the shade tolerant responses  
545 optimizing the trade-off between the elongation of vegetative parts and yield (Wille *et al.* 2017), and  
546 pave the way for selecting varieties dedicated to agroforestry systems. Further research would be  
547 needed to enlarge the diversity of the genotypes to screen and clearly identify if specific traits are  
548 better adapted to agroforestry systems. Other perspectives studies would also need to integrate other  
549 factors than the light resource, including a more global analysis with the environmental, social and  
550 economic aspects of the agroforestry system proposed (Rodenburg *et al.* 2022).

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