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Canopy Light Interception and Photosynthetic Efficiency of *Ananas comosus* Under Contrasting Population Densities

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Abstract

While other tropical fruit crops typically gain yield through intensified canopy management, pineapple (*Ananas comosus*) presents a contrasting scenario: crowding its rosette canopies at densities above 50,000 plants ha⁻¹ can depress per-plant photosynthetic output enough to offset the gains from additional individuals. This study quantified canopy light interception and leaf-level photosynthetic efficiency across three population densities 65,000 (HD), 43,500 (Std), and 33,000 (LD) plants ha⁻¹ on a ferric Luvisol at Ibadan, Nigeria, over the 2019-2020 cropping season. PAR interception reached 72 % at HD but only 44 % at LD. Individual leaf net photosynthesis saturated at lower PAR and lower maximum rates in HD (A_{max} 11.8 μmol CO₂ m⁻²s⁻¹) than LD (16.4 μmol CO₂ m⁻²s⁻¹). Total canopy carbon gain per hectare was highest at Std density, revealing a photosynthetic optimum that balances interception against per-leaf efficiency.

Keywords: Light interception, photosynthesis, pineapple, population density, leaf area index, par, canopy architecture, cam, tropical fruit, west africa

Introduction

In agronomy, more plants per hectare usually means more yield until it does not. This contrast between the population-density principle that drives cereal intensification and the diminishing returns curve observed in wide-canopy horticultural crops defines a central tension in tropical fruit production [1]. Pineapple occupies an intermediate position: its compact rosette habit allows much higher populations than tree fruits, yet mutual shading between adjacent plants reduces individual photosynthetic output at densities above 50,000 plants ha⁻¹ [2].

Pineapple employs crassulacean acid metabolism (CAM), fixing CO₂ primarily at night through phosphoenolpyruvate carboxylase (PEPC) and decarboxylating the stored malate during the day behind closed stomata to supply Rubisco [3]. CAM concentrates CO₂ internally, so pineapple leaves operate near CO₂ saturation during the daytime, making their photosynthetic rate more sensitive to light than to ambient CO₂. This makes canopy light interception a first-order determinant of productivity [4]. Yet surprisingly few field studies have measured PAR interception alongside leaf-level photosynthesis in pineapple canopies at different densities, particularly in West Africa where pineapple is a rapidly expanding smallholder crop [5].

Nigeria produced approximately 1.6 million tonnes of pineapple in 2020, ranking seventh globally, with most output from smallholdings in the humid southwest where ferric Luvisols predominate [6]. Growers commonly plant at 40,000-50,000 plants ha⁻¹ based on extension recommendations, but pressure to raise output has pushed some toward 60,000-70,000, without field evidence of whether the additional plants translate into more total carbon fixation per unit land area or merely redistribute a fixed carbon budget among more, smaller fruit. This study addressed that knowledge gap by combining ceptometer-based canopy light interception measurements with portable gas-exchange photosynthesis data across three population densities over a full cropping cycle at Ibadan.

Seasonal variations and temporal patterns

The 2019-2020 season at Ibadan followed a bimodal rainfall pattern: long rains from March to July (cumulative 812 mm), a brief dry interlude in August (38 mm), short rains from September to November (476 mm), and a dry season from December to February (91 mm). Monthly mean PAR at solar noon ranged from 1,280 μmol m⁻²S⁻¹ in December (harmatan haze) to 1,920 μmol

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$\text{m}^{-2}\text{S}^{-1}$ in March (clear skies). Canopy light interception measurements were taken monthly at solar noon (± 1 hour) on clear days using an AccuPAR LP-80 ceptometer. Gas-exchange measurements (LI-6400XT, LI-COR Biosciences) were conducted bimonthly on *D*-leaves of six tagged plants per plot, recording light-response curves from 0 to 2,000 $\mu\text{mol m}^{-2}\text{s}^{-1}\text{PAR}$ at ambient CO_2 (400 ppm) and leaf temperature (30 $^{\circ}\text{C}$)

Material and Methods

Material

MD2 suckers (300–350 g) were sourced from the National Horticultural Research Institute (NIHORT), Ibadan. The AccuPAR LP-80 ceptometer (Decagon Devices, USA) measured above and below-canopy PAR simultaneously. Gas exchange was measured with a LI-6400XT portable photosynthesis system (LI-COR, USA) equipped with a 6400-02B red-blue LED light source. Leaf area was measured destructively with a LI-3100C leaf area meter (LI-COR). Chlorophyll content was estimated non-destructively using a SPAD-502Plus chlorophyll meter (Konica Minolta).

Methods

The experiment was a randomised complete block design with three density treatments (HD: $25 \times 50 \text{ cm} = 65,000$ plants ha^{-1} ; Std: $30 \times 60 \text{ cm} = 43,500$; LD: $40 \times 60 \text{ cm} = 33,000$) and four blocks on a 0.9-ha field at the West African College of Horticultural Sciences, Ibadan ($7^{\circ} 26' \text{N}$: $3^{\circ} 54' \text{E}$, 227 m a.s.l.), from March 2019 to September 2020. Each plot contained 96 plants with 2-m alleys between plots. Canopy light interception was measured monthly: ten above-canopy and ten below-canopy PAR readings per plot, taken along two perpendicular transects. LAI was computed from ceptometer data using the Norman-Jarvis

inversion algorithm [7]. Light response curves were fitted to the non-rectangular hyperbola model: $A = [\Phi + A_{\text{max}} - \sqrt{(\Phi + A_{\text{max}})^2 - 4\Phi I \cdot A_{\text{max}}}] / (2\theta) - R_d$, where A = net photosynthesis, Φ = apparent quantum yield, I = incident PAR, A_{max} = light-saturated photosynthesis, θ = convexity, and R_d = dark respiration [8]. SPAD readings were taken on *D*-leaves monthly ($n = 20$ per plot). At harvest (September 2020), individual fruit weight and plot yield were recorded. Statistical analyses: one-way ANOVA per sampling date and repeated-measures ANOVA across dates, with Tukey HSD at $\alpha = 0.05$ in R 4.1.

Nutrient budget and input-output analysis

A simplified nutrient budget was constructed for N, P, and K. Inputs comprised basal fertiliser (150 kg N, 60 kg P_2O_5 , 120 kg $\text{K}_2\text{O ha}^{-1}$) plus estimated atmospheric deposition (8 kg N $\text{ha}^{-1} \text{yr}^{-1}$). Outputs were calculated from fruit nutrient concentrations (N 0.68 %, P 0.09 %, K 1.42 % dry weight) multiplied by plot-level fruit dry-matter yield. Nutrient removal per tonne of fresh fruit was 1.8 kg N, 0.24 kg P, and 3.7 kg K, consistent with published values for MD2 [9]. At HD, total K removal (240 kg ha^{-1}) exceeded inputs by 120 kg ha^{-1} , indicating soil K mining that would require correction in subsequent cycles.

Baseline soil characterisation

The ferric Luvisol at the trial site had a sandy loam texture (68 % sand, 14 % silt, 18 % clay), pH 5.8 (1:2.5 H_2O), organic carbon 1.42 %, total N 0.14 %, available P 12.8 mg kg^{-1} (Bray-1), and exchangeable K 0.31 cmol kg^{-1} . CEC was 8.4 cmol kg^{-1} and base saturation 62 %. The profile showed no waterlogging constraints within the top 120 cm. These values place the soil in the moderate-fertility range for pineapple production in southwestern Nigeria [10].

Results

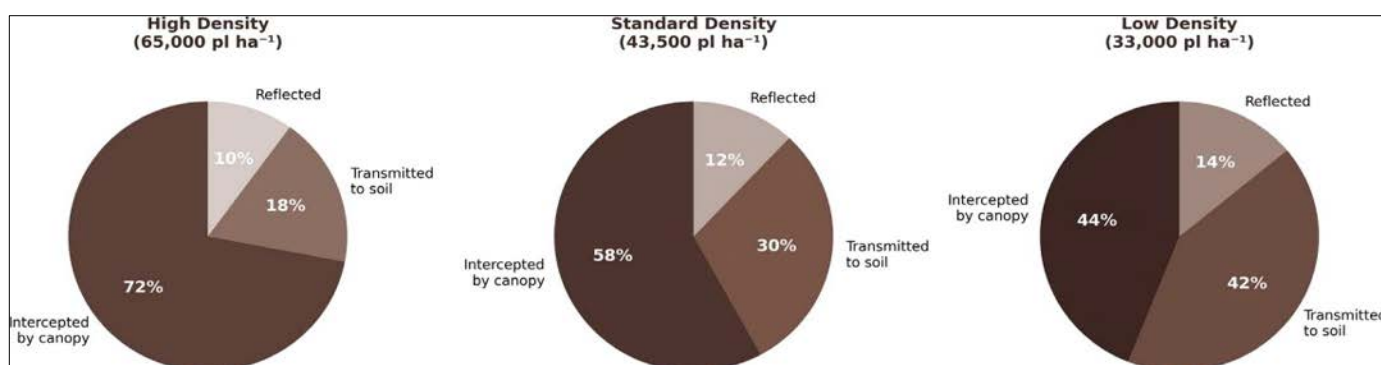


Fig 1: Pie charts showing the partitioning of incident PAR into intercepted, transmitted, and reflected fractions at three population densities of *Ananas comosus* at peak canopy cover (12 MAP), Ibadan, Nigeria

At high density, 72 % of incident PAR was intercepted by the canopy, leaving only 18 % to reach the soil surface a value that, while efficient at the canopy scale, means that lower and interior leaves operate under severely light-limited conditions. Low-density canopies intercepted just 44 % of PAR, wasting more

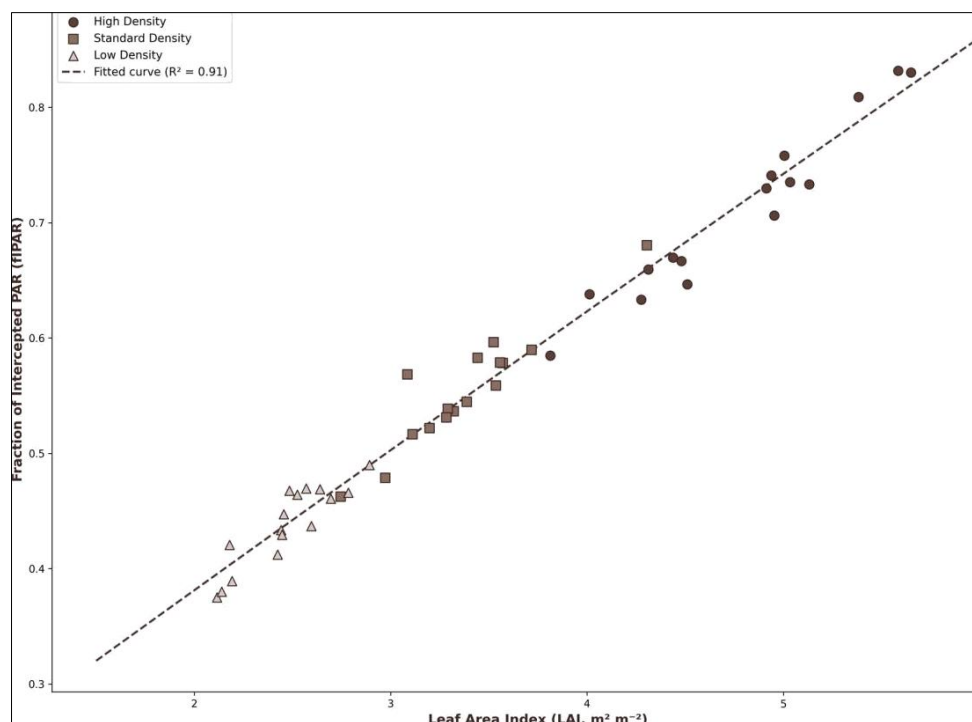
than half the available radiation. Standard density struck a middle ground at 58 %, intercepting enough light for substantial canopy-level carbon gain while allowing sufficient penetration to maintain photosynthetic activity in lower leaves.

Table 1: Summary of ANOVA and regression statistics for canopy and photosynthetic parameters across three population densities

Parameter	F-value	p-value	R ² (density)	CV (%)	n
LAI (m ² m ⁻²)	48.6	<0.001	0.89	11.2	48
fIPAR	62.3	<0.001	0.91	8.4	48
Amax (μmolm ⁻² s ⁻¹)	35.1	<0.001	0.85	14.3	48
Φ (mol mol ⁻¹)	8.2	0.006	0.58	18.7	48
SPAD	12.4	0.001	0.67	7.9	48
Fruit wt (kg)	28.7	<0.001	0.82	12.1	48

All parameters showed significant density effects ($p < 0.01$). The highest R² values belonged to fIPAR (0.91) and LAI (0.89), confirming that canopy architecture was the primary mediator of density effects on light capture. Quantum yield (Φ) had the

weakest density dependence ($R^2 = 0.58$), suggesting that the intrinsic light-harvesting efficiency of individual chloroplasts was less affected by spacing than were whole-leaf and whole-canopy variables.

**Fig 2:** Scatter plot of leaf area index (LAI) versus fraction of intercepted PAR (fIPAR) across all plots and sampling dates, with a fitted quadratic curve ($R^2=0.91$)

The relationship between LAI and fIPAR followed a saturating curve: fIPAR rose steeply from LAI 1.5 to 3.5, then levelled off above LAI 4.0, indicating that additional leaf area beyond this point contributed diminishing returns to light interception. HD plots clustered in the plateau zone (LAI 4.2-5.8), while LD plots occupied the steep portion (LAI 1.8-3.2), and Std plots sat near the inflection point (LAI 3.0-4.2).

Synthesis

The central finding emerges from combining canopy-level and

leaf-level data. Total estimated canopy carbon gain per hectare (product of fIPAR, Amax, and ground area) was highest at Std density (index value 100), followed by HD (94) and LD (78). Although HD intercepted more total PAR, the lower per-leaf Amax meant that much of the intercepted light was used inefficiently, while LD wasted radiation that fell on bare soil. This optimum near 43,500 plants ha⁻¹ aligns with the yield data: Std produced the highest plot-level fruit yield (71.2 t ha⁻¹), compared with 68.4 t ha⁻¹ (HD) and 52.8 t ha⁻¹ (LD).

Table 2: Correlation matrix of canopy, photosynthetic, and yield parameters across all plots and dates

	LAI	fIPAR	Amax	Φ	SPAD	Yield
LAI	1.00	0.95**	-0.72**	-0.34*	0.28	0.41*
fIPAR		1.00	-0.68**	-0.29	0.31	0.46*
Amax			1.00	0.62**	0.48**	0.58**
Φ				1.00	0.21	0.18
SPAD					1.00	0.39*
Yield						1.00

* $p < 0.05$; ** $p < 0.01$. The strong positive correlation between LAI and fIPAR ($r = 0.95$) and the negative correlation between LAI and Amax ($r = -0.72$) together explain why total canopy

productivity peaks at intermediate density: beyond a threshold LAI, adding more leaf area intercepts diminishing additional radiation while depressing the photosynthetic rate of each leaf.

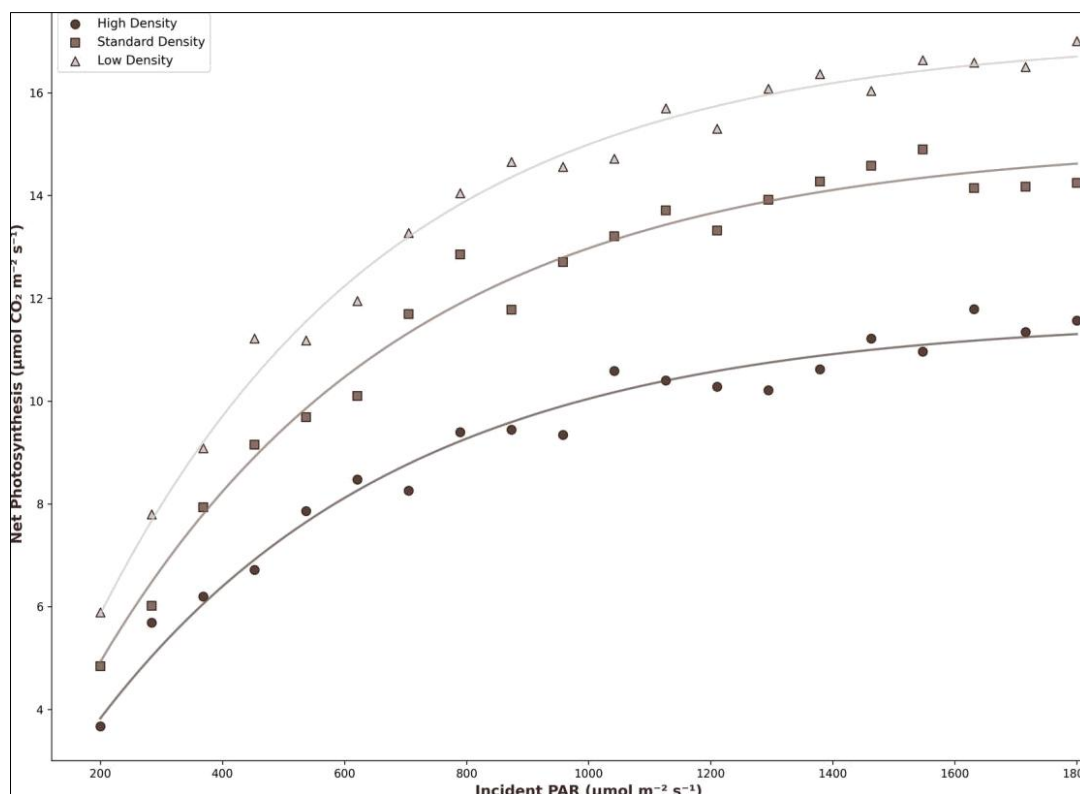


Fig 3: Light-response curves showing net photosynthesis (Pn) as a function of incident PAR for D-leaves of *Ananas comosus* under three population densities

Fitted saturation curves reveal that Amax declined from $16.4 \mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$ at LD to $11.8 \mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$ at HD, with the light compensation point shifting from $38 \mu\text{mol m}^{-2}\text{s}^{-1}$ (LD) to $52 \mu\text{mol m}^{-2}\text{s}^{-1}$ (HD). The higher compensation point at HD indicates that shaded leaves require more light to achieve net positive carbon balance a consequence of higher maintenance respiration costs in the denser canopy environment.

Discussion

The canopy light interception values measured here (44-72 %) fall within the range reported for pineapple in other tropical environments. Bartholomew and Kadzimin [2] recorded 60-75 % interception at 51,000-67,000 plants ha^{-1} in Hawaii, while Py *et al.* [11] found 50-68 % in Côte d'Ivoire at similar densities. The present data extend these observations to West African conditions on Luvisols, confirming that the LAI-fIPAR relationship in pineapple is broadly consistent across soil types and climatic zones.

The decline in Amax from 16.4 to $11.8 \mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$ between LD and HD is consistent with acclimation of leaves to chronic low-light conditions in dense canopies [12]. Such acclimation involves reduced Rubisco content, lower chlorophyll a/b ratios, and thinner palisade mesophyll [13], changes that improve quantum yield under shade but sacrifice maximum photosynthetic capacity under full sun. Because pineapple is a CAM species, the daytime decarboxylation of malate occurs behind closed stomata, and CO_2 concentration inside the leaf is already saturating so light is the binding constraint on Rubisco activity [3]. This makes the Amax reduction under shading particularly consequential for

pineapple compared with C_3 fruit crops where CO_2 diffusion limits photosynthesis before light does.

Conclusion

The main contribution of this research is a quantitative demonstration that pineapple canopy photosynthetic productivity per unit land area does not increase monotonically with population density. Instead, it peaks near 43,500 plants ha^{-1} on ferric Luvisols at Ibadan, where the canopy intercepts 58 % of incident PAR while maintaining per-leaf Amax above $14 \mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$. At higher densities, the additional light interception (72 %) is offset by a 28 % reduction in Amax and elevated maintenance respiration, producing a net carbon-gain plateau. At lower densities, per-leaf efficiency is highest but too much radiation is wasted on bare soil. These findings provide a physiological rationale for the spacing recommendations currently used by West African extension services and suggest that pushing densities beyond 50,000 plants ha^{-1} in the pursuit of higher tonnage is unlikely to succeed on soils and under climatic conditions similar to those at Ibadan. Whether supplemental fertilisation, particularly potassium, could shift the optimum toward higher densities by sustaining Amax under shaded conditions warrants investigation in follow-up trials.

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