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Understanding cowpea yield: A comprehensive analysis of physiological traits' contribution through path analysis

Ankrumah Emmanuel[1]
Ogbonna Peter Ejimofor[2]
Onyia Vincent Nduka[3]
Omoigui Lucky[4]
Kamara Alpha Yahya[5]
Ndifon Elias M'jaika[6]

(✉ *Corresponding Author*)

[1,6]*Department of Crop Science, Alex Ekwueme Federal University Ndufu-Alike, Ebonyi State, Nigeria.*
[1]*Email:* ankrumahemmanuel@gmail.com
[6]*Email:* emndi4nn@yahoo.com
[2,3]*Department of Crop Science, University of Nigeria Nsukka, Enugu State, Nigeria.*
[2]*Email:* ogbonna@unn.edu.ng
[3]*Email:* Onyia@unn.edu.ng
[4,5]*Project-Seed System, International Institute of Tropical Agriculture, Kano Station, Sabo Bakin Zuwo Road Kano, Kano State, Nigeria.*
[4]*Email:* L.Omoigui@cgiar.org
[5]*Email:* A.Kamara@CGIAR.ORG

Abstract

This study investigates the physiological processes affecting the grain yield of cowpea (Vigna unguiculata), a key protein, vitamin, and mineral source in human diets. Gaining an understanding of these mechanisms can be crucial for developing high-yielding cowpea varieties in breeding programs. A field experiment was conducted with 30 treatments, including three sowing dates (Early August, Late August, Early September) and ten cowpea genotypes (UAM09-1051-1, UAM09-1046-6-1, UAM14-126-L33, IT99K-573-1-1, IT89KD-288, UAM14-126-L6, UAM14-122-17-7, UAM14-123-18-3, UAM14-127-20-1-1, and UAM14-130-20-4). These treatments were arranged in a split-plot design within a Randomized Complete Block Design, replicated three times. Key physiological traits like Leaf Area Index (LAI), Intercepted Photosynthetically Active Radiation (IPAR), Stomatal Conductance, Photosynthetic Rate, Transpiration Rate, and Chlorophyll Content were measured. Data collected were analyzed using correlation and path coefficient methods; the results showed significant positive correlations between grain yield and traits like LAI, stomatal conductance, and photosynthetic rate. In contrast, the transpiration rate negatively correlated with yield. Path analysis revealed that the net photosynthetic rate had the most direct impact on grain yield, highlighting its role in photosynthesis and grain filling. The study suggests that cowpea breeding efforts should focus on improving photosynthetic efficiency and optimizing traits like LAI and stomatal conductance to boost cowpea grain yields.

Keywords: Breeding program, Correlation coefficient, Cowpea, Grain yield, Path analysis, Physiological traits, Planting date, Yield partitioning.

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Contents

Contribution of this paper to the literature
This study is original in its use of path coefficient analysis to quantify the direct, indirect, and total contributions of physiological traits, such as LAI, IPAR, chlorophyll content, and gas exchange parameters to cowpea grain yield. It provides new insights into trait interactions, supporting targeted breeding for higher, stress-resilient yields.

1. Introduction

Cowpea (Vigna unguiculata L. Walp) is widely cultivated in the tropical and subtropical regions of Africa, primarily for its edible seeds, green pods, and nutritious leaves, which are consumed as vegetables. It serves as a crucial source of calories and protein for millions of people in developing countries [1, 2]. Additionally, cowpea is an affordable and important source of protein, vitamins, and minerals in the human diet, and it also serves as healthy fodder for livestock feed [3, 4]. Cowpea is grown on 14.13 million hectares globally, yielding 4.51 million metric tons with an average productivity of 387.45 kg/ha [5]. Africa, particularly West Africa, accounts for over 90% of the world's production, with Nigeria being the leading producer and consumer in the region, generating 3.6 million tons in 2021 [6].

Cowpea is an important grain legume that is highly adapted to various agro-ecological environments [7]. Its resilience under marginal environmental conditions and its capacity for symbiotic nitrogen fixation make it a critical food security crop in regions prone to environmental stress [8]. Despite these attributes, improving cowpea yield remains a significant challenge, especially due to climate variability and soil nutrient limitations [3]. Cowpea yield is an intricate trait that is affected by multiple yield-contributing traits controlled by different genes and environmental influences [7].

A correlation study was conducted to examine the relationships between different traits and their respective contributions to yield [9]. Several researchers have explored the connection between these traits to identify key factors for selecting high-yielding varieties [10]. The yield of grain legumes is a complex quantitative trait influenced by the interaction of various growth and physiological processes [11].

Therefore, cowpea yield improvement requires an understanding of the physiological traits that influence yield performance. Furthermore, it was noted that physiological traits, including the Leaf Area Index (LAI), the Intercepted Photosynthetically Active Radiation (IPAR), the concentration of chlorophyll, and the gas exchange parameters (stomatal conductance, photosynthetic rate, and transpiration rate), have a major impact on the accumulation of biomass and the potential yield of grain legumes [12, 13]. However, there is inadequate information on the complex relative contributions of these traits, whether direct or indirect, to grain yield.

The path coefficient analysis is essential for use as a criterion for enhancing yield prediction, management, and selection in the improvement of grain yield in cowpea. This could aid in the strategic selection of desirable traits for breeding. This study could fill this gap and gather information on the contributions of various physiological parameters associated with grain yield and yield-related traits. Therefore, this study on path analysis was carried out to dichotomize the direct, indirect, and total contributions of key physiological traits on cowpea grain yield, which is an essential approach to identify the critical traits driving yield improvement and to provide an understanding of their interconnectedness.

2. Materials and Methods

2.1. Experimental Site

Field studies were conducted during the 2021 and 2022 main cropping seasons at the Teaching and Research Farm of the Department of Crop Breeding and Genetics, Joseph Sarwun Tarka University (JST-UAM) in Makurdi (7°44'N, 8°30'E, 686 m ASL) in the Northern Guinea Savanna. Prior to the establishment of the field trial, soil samples were taken from the location and characterized according to the analytical procedures of the soil laboratory of the Department of Soil Science, University of Nigeria, Nsukka. Weather information was collected from the AccuWeather Stations installed at the trial site.

2.2. Cowpea Varieties, Sowing Date and Experimental Design

Ten (10) cowpea varieties and three sowing dates were evaluated. The experimental design was a randomized complete block in a split-plot arrangement with three replications. The main plot consisted of the sowing dates of early August, late August, and early September. The cowpea varieties were assigned to the subplot. Four medium-maturing and semi-determinate varieties (IT99K-573-1-1, UAM14-126-L33, UAM14-126-L6, and UAM09-1051-1, which mature within 75–80 days), and six indeterminate varieties (IT89KD-288, UAM14-122-17-7, UAM14-123-18-3, UAM14-127-20-1-1, UAM14-130-20-4, UAM09-1046-6-1, which mature within 85–90 days) were used. Eight of these varieties were developed by the JST-UAM, while the other two were developed by the IITA. The subplots were 3 × 4 m and consisted of four ridges with 75 cm spacing between the ridges and 20 cm between plant stands on each ridge.

The field was disc-harrowed and ridged before planting. The trial was planted as per the scheduled sowing dates: on the 5^{th} of August, 19^{th} of August, and 2^{nd} of September, 2021, respectively. In 2022, it was done on the 4^{th} of August, the 18^{th} of August, and the 5^{th} of September, respectively. Seeds of the cowpea varieties were planted at a depth of 3 cm. Four seeds were planted and later thinned to two stands per hill. Thinning was performed 14 days after sowing. At sowing, the recommended fertilizer rate for legumes in the Nigerian savannas of 50 kg of P_2O_5 in the form of SSP was applied. A mixture of pendimethalin (500 g L^{-1}) and Gramoxone (1:1-dimethyl-4,4-bipyridinium dichloride), at a rate of 1 L ha^{-1} each, was applied immediately after sowing using a knapsack sprayer. This was followed by hoe weeding 4 weeks after sowing.

2.3. Data Collection and Evaluation

The two middle ridges were used for data collection. At the vegetative stage, Leaf Area Index (LAI) and intercepted photosynthetically active radiation (IPAR) were measured simultaneously at the full bloom stage using the AccuPAR model LP-80 PAR/LAI Ceptometer, following the procedure reported by Kamara et al. [7]. The net photosynthetic rate, stomatal conductance, and transpiration rate were measured simultaneously at the full flowering and podding stages of cowpea using a portable photosynthesis system, model LI-6400XT (LI-COR Biosciences, USA), after calibration according to the manufacturer's instructions. Relative leaf chlorophyll content was measured at the full bloom and podding stages using the Konica Minolta SPAD 502 chlorophyll meters, where a minimum of five different measurements was conducted on different plants, and average readings were recorded.

At pod maturity, the two middle ridges were used for measuring yield components. Pods from the two middle ridges (net rows) were harvested, threshed, and seed weight per plot was obtained. The moisture content of grain samples from each plot was determined using a V-Tech 3.5 to 40% grain moisture tester, Model SF00000885. Grain yield was extrapolated from the total seed weight in grams per plot and adjusted based on moisture content (12%) to obtain grain yield in kilograms per hectare ($kgha^{-1}$) using the relation below.

$$\text{Grain Yield (kg ha}^{-1}) = \frac{\textit{Seeds weight per plot (g)}}{1000} * \frac{100 - \text{moisture (\%)}}{88\%} * \frac{10000\text{m}^2}{4.5m^2}$$

Simple correlation coefficients between the grain yield (Y) and physiological characters (X) and within the physiological traits themselves were worked out using the following equation after [14].

$$rxY = \frac{n(\sum XY) - (\sum X)((\sum Y)}{\sqrt{[n\sum X^2 - (\sum X)^2][n\sum Y^2 - (\sum Y)^2]}}$$

Where: rxY = Correlation coefficient between variables X and Y, n = Number of observations, ΣXY = Sum of the product of X and Y values, ΣX, ΣY = Sums of X and Y values, respectively, ΣX^2, ΣY^2 = Sums of squared values for X and Y.

The calculated coefficients were further used to develop the following simultaneous equations, from the general path equation using the Poolman Equation, in order to partition the correlations into cause and effect by working out the path coefficients (Pi). For the dependent variable Y (grain yield), the path equation is: $Y = P_{Xi} X_1 + P_{X2}X_2 + P_{X3}X_3 + \cdots + P_{Xn}X_n$ + Residual. Where: P_{Xi} is the path coefficient (direct effect) of variable X_i on Y. X_i is the independent variables, and Residual (P_R) is the unaccountable variance by the model.

$$rY1 = PY1 + PY2 \times r_{12} + PY3 \times r_{13} + PY4 \times r_{14} + PY5 \times r_{15} + PY6 \times r_{16} \quad (1)$$
$$rY2 = PY1 \times r_{21} + PY2 + PY3 \times r_{23} + PY4 \times r_{24} + PY5 \times r_{25} + PY6 \times r_{26} \quad (2)$$
$$rY3 = PY1 \times r_{31} + PY2 \times r_{32} + PY3 + PY4 \times r_{34} + PY5 \times r_{35} + PY6 \times r_{36} \quad (3)$$
$$rY4 = PY1 \times r_{41} + PY2 \times r_{42} + PY3 \times r_{43} + PY4 + PY5 \times r_{45} + PY6 \times r_{46} \quad (4)$$
$$rY5 = PY1 \times r_{51} + PY2 \times r_{52} + PY3 \times r_{53} + PY4 \times r_{54} + PY5 + PY6 \times r_{55} \quad (5)$$
$$rY6 = PY1 \times r_{61} + PY2 \times r_{62} + PY3 \times r_{63} + PY4 \times r_{64} + PY5 \times r_{65} + PY6 \quad (6)$$

From the above Equations PY1, PY2, PY3, PY4, PY5, and PY6 are the path coefficients (Direct effect) representing LAI, IPAR, Chlorophyll content, Stomatal conductance SC, Transpiration rate (TR), and Photosynthetic rate (PR), while $PY2r_{12}$, $PY3r_{13}$, $PY4r_{14}$, $PY5r_{15}$, $PY6r_{16}$, ... $PY4r_{64}$, $PY5r_{65}$ are the indirect effects, while r_{12} ...... r_{65} are the correlation coefficients. The individual percentage contributions are computed using.

$$\textit{Percentage Direct Contribution} = \left(\frac{\text{Pi}}{R^2}\right)^2 X\ 100$$

Where, P_i = Direct path coefficient of the i^{th} independent variable. R^2 = Coefficient of determination (sum of the direct and indirect contributions of all variables). While the percentage combined contribution (%) of any two characters were also computed using the following relation.

$$\textit{Combined Contribution} = \left(\frac{(P_i + I_i)^2}{R^2}\right) X\ 100$$

Dewey and Lu [15] Where: I_i is the sum of the indirect effects of the i^{th} variable on the dependent variable through other variables. $P_i + I_i$ is the total effect (direct + indirect) of the independent variable. The residual effect (R_e) was calculated using the relation: $R_e = \sqrt{1 - R^2}$ R^2 is the coefficient of determination, which measures the proportion of the total variance in the dependent variable that is explained by the independent variables.

3. Results and Discussion

3.1. Correlation Coefficients (r) between Grain Yield and Physiological Traits in Cowpea

The results of the correlation analysis revealed some highly significant ($p < 0.01$) positive associations between the physiological components assessed and the grain yield of cowpea (Table 1). LAI showed a strong positive correlation with stomatal conductance (r = 0.746) and photosynthetic rate (r = 0.720), which indicates that increased leaf area contributes to better gas exchange and photosynthetic efficiency. This is in agreement with the studies by Oluwasemire and Odugbenro [16], who demonstrated that higher LAI enhances the plant's ability to intercept light and perform photosynthesis, leading to improved growth and development. However, the negative correlation with transpiration rate (r = -0.561) suggests that as the leaf area increases, water loss through transpiration decreases, likely due to a more efficient water use system or stomatal regulation. This aligns with the findings of Bouranis et al. [17], who discussed the trade-offs between leaf area expansion and water use efficiency in crops. The positive correlations between chlorophyll content and both stomatal conductance (r = 0.495) and photosynthetic rate (r = 0.353) are expected, as higher chlorophyll content is indicative of better light-harvesting capabilities and enhanced photosynthetic activity [18]. The weak negative correlation with transpiration rate (r = -0.329) might suggest that plants with higher chlorophyll content manage water more efficiently, similar to findings in studies on drought-tolerant varieties of crops [19]. The strong positive association recorded between stomatal conductance and photosynthetic rate (r = 0.838) undoubtedly aligns with the physiological role of stomata in regulating CO_2 uptake for photosynthesis. As stomatal conductance increases, more CO_2 is available for photosynthetic reactions, which has been well-documented in studies on plant gas exchange [13]. The significant negative relationship between stomatal conductance and transpiration rate (r = -0.684) reflects the role of stomata in balancing water loss and carbon uptake, a common feature in plants adapted to water-limited environments [12]. A strong negative correlation between transpiration rate and photosynthetic rate (r = -0.642) revealed the potential for cowpea varieties with lower transpiration rates to maintain higher photosynthetic efficiency. This finding is supported by research into the water-use strategies of leguminous crops, where reduced water loss through transpiration helps sustain photosynthesis under water stress [12, 16]. There were significant correlations between LAI (r = 0.759), chlorophyll content (r = 0.490), stomatal conductance (r = 0.684), photosynthetic rate (r = 0.645), and grain yield, suggesting that traits improving carbon assimilation and water use efficiency directly contribute to yield formation. This agrees with several studies emphasizing the importance of these traits in yield improvement under various stress conditions [16, 19-21].

Conversely, the negative correlation between transpiration rate and grain yield (r = -0.572) further reinforces the idea that efficient water use is critical for optimizing yield in cowpea, a finding supported by studies on the physiological responses of cowpea to drought [21]. However, the lack of a significant relationship between IPAR and grain yield in this study contrasts with some literature that highlights the importance of IPAR in determining crop yield potential [18, 22, 23]. Nevertheless, the weak negative association with chlorophyll content suggests that under certain conditions, higher radiation interception does not always translate to better photosynthetic performance, especially if other limiting factors, such as nutrient or water availability, constrain growth.

Table 1. Matrix of correlation coefficients (r) showing the association between grain yield and some physiological parameters of cowpea.

Parameters	LAI	IPAR	Chlorophyll content	Stomatal conductance	Transpiration rate	Photosynthetic rate	Grain yield
LAI	1						
IPAR	-0.087	1					
Chlorophyll	0.487**	-0.271**	1				
Stomatal conductance	0.746**	-0.057	0.495**	1			
Transpiration rate	-0.561**	0.001	-0.329**	-0.675**	1		
Photosynthetic rate	0.720**	-0.038	0.353**	0.838**	-0.642**	1	
Grain yield	0.759**	-0.060	0.490**	0.684**	-0.572**	0.645**	1

Note: ** Correlation is significant at the 0.01 level. IPAR: Intercepted photosynthetic rate. LAI: Leaf area index

3.2. Direct, Indirect and Total Contributions of Some Physiological Characters to Grain Yield in Cowpea

The results of the path coefficient revealed that Leaf Area Index (LAI) and Intercepted Photosynthetically Active Radiation (IPAR) recorded weak to moderate negative direct effects (-0.187 and -0.330, respectively), but strong positive total contributions to grain yield (0.759 and 0.760, respectively) (Table 2). The negative direct effects suggest that dense canopy architecture and suboptimal light interception can cause yield reduction as a result of mutual shading and resource competition [20]. However, their high indirect contributions through Photosynthetic Rate emphasize the importance of canopy architecture in driving efficient utilization of light intercepted [20]. Even though the negative direct effect (-0.217) of chlorophyll content on grain yield exists, its strong positive total association (0.890) suggests that its contribution is highly effective (0.822) via indirect paths, mainly through improvement in Photosynthetic Rate. This finding is in line with the role of chlorophyll as the primary pigment for light absorption during photosynthesis [24]. This means that increasing chlorophyll content alone may not directly increase the grain yield of cowpea; however, maintaining optimal chlorophyll levels is vital for optimizing light interception and carbon assimilation [19]. The study also revealed that Stomatal Conductance displayed a strong positive direct effect (0.572) on cowpea grain yield (Table 2), indicating its critical role in CO_2 and water vapor exchange regulation between the leaves and the atmosphere [25]. The current study aligns closely with the findings of Chikov and Akhtyamova [19], who reported that efficient stomatal conductance can improve photosynthetic rates by ensuring adequate CO_2 uptake while minimizing water loss, which is crucial in maintaining photosynthesis in varying environmental conditions. The highly strong indirect effect through the net Photosynthetic Rate (0.915) confirmed the independent report by Boukar et al. [8], who stated that the reinforcement in stomatal conductance indirectly impacts crop yield performance by optimizing the photosynthetic machinery. However, under extreme drought conditions, high stomatal conductance may lead to high transpiration rates and a potential negative impact on grain yield, as reported by Bouranis et al. [17].

The transpiration rate had a moderate positive (0.339) direct effect; however, it had a strong negative (-0.572) total contribution to grain yield (Table 2). This conflicting effect highlights the dual responsibility of transpiration in plant physiology. While transpiration is necessary for cooling and nutrient uptake, according to Bouranis et al. [17], a higher transpiration rate can deplete water resources, especially under drought conditions. The highly strong negative (-0.701) indirect contribution through the photosynthetic rate emphasizes that high transpiration may affect stomatal regulatory function by closure, leading to a decline in the influx and uptake of CO_2, thus resulting in a decrease in photosynthesis.

The path analysis showed that the Photosynthetic Rate has the highest (1.092) direct effect on grain yield (Table 2). This finding aligns with the central role of photosynthesis in biomass accumulation and grain filling, as it is the fundamental process converting light energy into chemical energy [26]. Previous studies have shown that enhancing photosynthetic efficiency can significantly increase yield, especially in C3 plants like cowpea, which often suffer from photorespiration losses [10, 22]. Additionally, the strong indirect effects of the Photosynthetic Rate through physiological traits like LAI (0.786) and Stomatal Conductance (0.915) indicate the importance of strengthening photosynthetic capacity while optimizing canopy architecture and efficiency in gaseous exchange to achieve higher cowpea grain yields.

Table 2. Path analysis for direct (Diagonal), indirect (Off diagonal) and total contributions effect of some physiological traits to grain yield of cowpea planted during 2021 to 2022 rainfed seasons.

Parameters	LAI	IPAR	Chlorophyll content	Stomatal conductance	Transpiration rate	Photosynthetic rate	Total corr.
LAI	-0.187	0.029	-0.105	0.426	-0.190	0.786	0.759**
IPAR	0.016	-0.330	0.059	0.318	0.000	0.697	0.760**
Chlorophyll content	-0.091	0.090	-0.217	0.397	-0.112	0.822	0.890**
Stomatal conductance	-0.139	-0.184	-0.150	0.572	-0.229	0.915	0.784**
Transpiration rate	0.105	0.000	0.071	-0.386	0.339	-0.701	-0.572
Photosynthetic rate	-0.134	-0.211	-0.163	0.479	-0.218	1.092	0.845**

Note: LAI = Leaf area index. IPRA = Intercepted photosynthetic active radiation. ** significant probability at 0.01 level.

3.3. Direct and Combined Contributions (%) of Yield Components to Grain Yield in Cowpea

The highest percentage (119.2%) direct contribution of photoassimilate to grain yield of cowpea was exhibited by the net photosynthetic rate (Figure 1). This is expected because the capacity to produce high amounts of photoassimilates and efficient partitioning of carbon compounds towards harvestable organs has shown a major impact on crop yield [18, 20]. An increase in the net photosynthetic rate translates into improved dry matter accumulation, translocation, and efficient partitioning of photoassimilates for optimal grain filling [22, 27]. However, its negative percentage indirect contribution (-24.7%) may indicate competitive allocation of assimilates to vegetative growth and possible potential imbalances in the source-sink dynamics [22].

The percentage contribution of stomatal conductance was significant, with a 32.7% direct impact on grain yield (Figure 1). This explains the efficient regulatory role of stomatal conductance in optimizing the rate of CO_2 entry into the leaf mesophyll membrane and the exit of water vapor, thus influencing photosynthetic efficiency [18, 28]. High stomatal conductance is associated with better gas exchange and higher transpiration rates, which often improve yield in sufficient moisture ecology [22]. The moderate indirect contributions of about 21.2% suggest the interconnectedness of stomatal conductance with other physiological processes in cowpea for the maintenance of metabolic gaseous exchange equilibrium and efficient nutrient uptake.

The contributions of about 11.5% of the transpiration rate (Figure 1) directly into cowpea grain are physiologically linked to its role in relatively maintaining leaf temperature and driving nutrient flow through the plant [10]. However, about -91.1% negative indirect contribution indicates that under extreme transpiration, certain conditions, like drought, especially at critical cowpea developmental phases, can lead to excessive loss of water through the stomata, resulting in poor grain filling and a subsequent negative impact on grain yield.

Even though intercepted photosynthetic active radiation contributed relatively 10.9% modestly directly to grain yield, in contrast to about 109% high indirect contribution. Canopy architectural characteristics have been reported to primarily affect light interception efficiency of plants [16, 18, 20]. The huge indirect contributions recorded imply the magnificent role displayed by IPAR through the synergistic interactions with other physiological traits like leaf area and chlorophyll content, which translate to canopy light-use efficiency [16].

The percentage direct contribution (4.7%) of chlorophyll was significantly low (Figure 1); however, the very high indirect contribution of about 110.7% to the grain yield highlights that chlorophyll concentration alone is not a direct driver of grain yield in cowpea, but rather enhances the photosynthetic capacity jointly with other physiological traits like LAI and IPAR [16, 18, 20]. A high chlorophyll content has been reported to correspond to better quality light absorption by the chlorophyll pigments, which facilitates more efficient carbon assimilation [17].

The result of the current study showed that LAI contributed the lowest percentage (3.5%) of direct contribution to grain yield, but had a strong indirect effect (94.5%) on cowpea grain yield. LAI determines the total leaf area available for light capture and gaseous exchange, thus playing a fundamental role in determining crop growth potential [10]. Its strong indirect effect could be attributed to its interaction with IPAR and photosynthetic traits, which together define the crop's radiation-use efficiency [29].

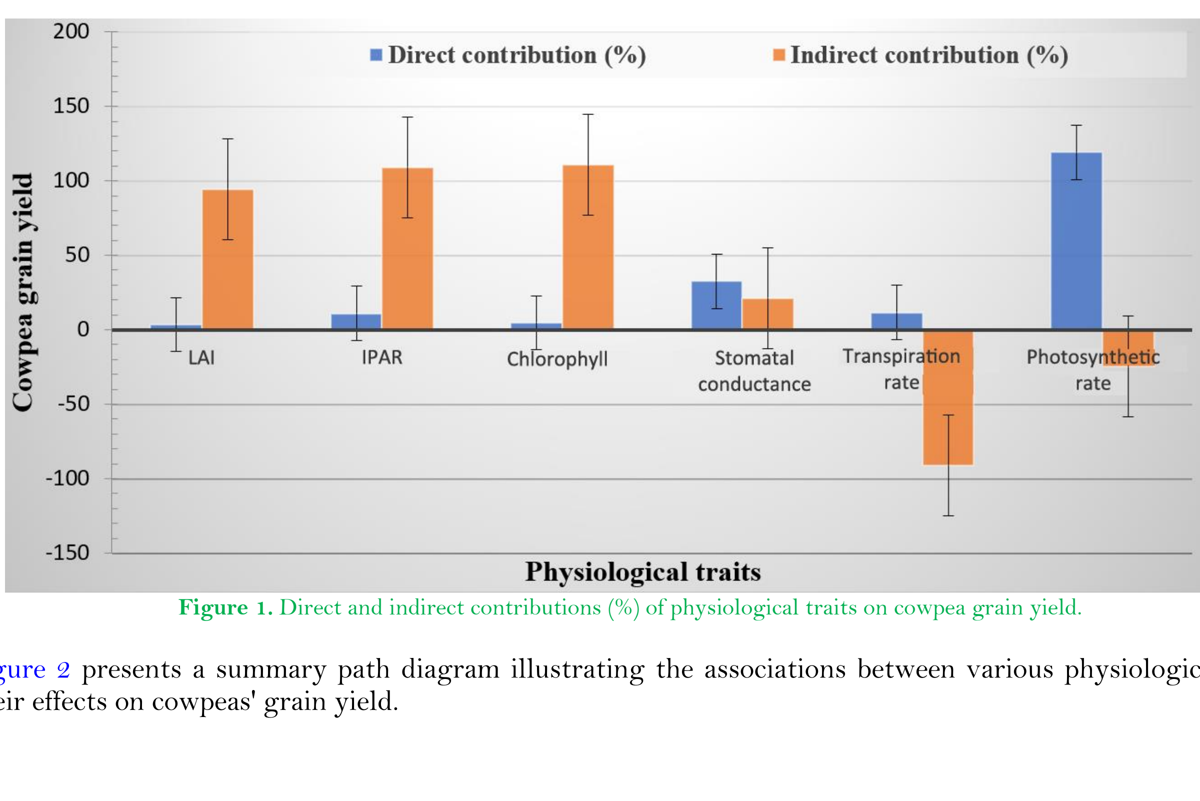

Figure 1. Direct and indirect contributions (%) of physiological traits on cowpea grain yield.

Figure 2 presents a summary path diagram illustrating the associations between various physiological traits and their effects on cowpeas' grain yield.

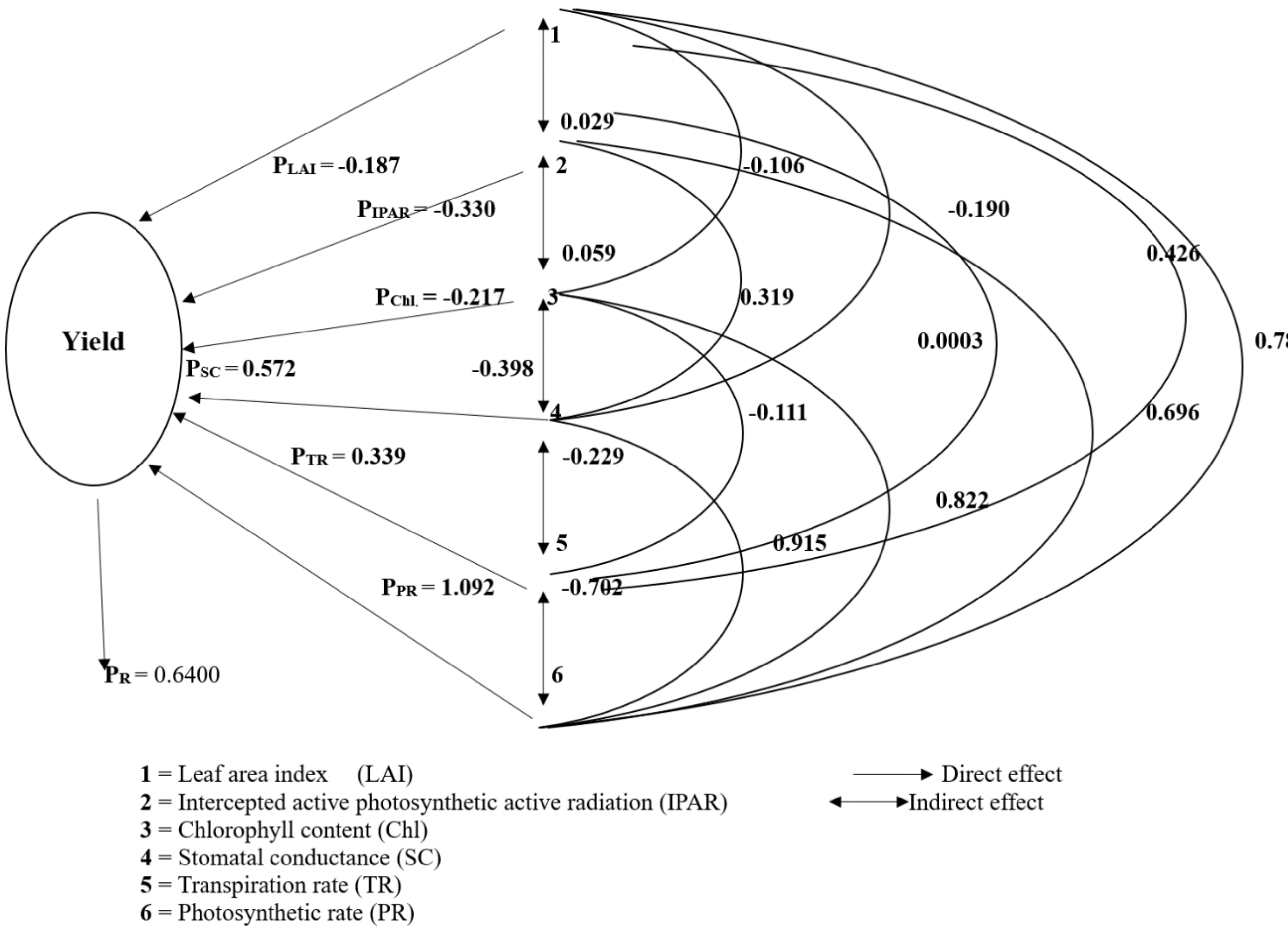

Figure 2. Summary path diagram showing association of some effects of physiological traits to grain yield of cowpea.

4. Conclusion

The simple correlation analysis revealed a highly significant and positive association between and among most of the physiological components assessed and grain yield. The path coefficient analysis explained the contribution of physiological traits to cowpea grain yield through direct and indirect pathways. Photosynthetic rate and stomatal conductance had highly significant direct effects, making them primary targets for breeding programs aimed at enhancing yield. On the other hand, traits like LAI, IPAR, and chlorophyll content contribute mainly through indirect interactions, suggesting that these traits are critical for improving the overall efficiency of the photosynthetic system and canopy structure.

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