RESEARCH ARTICLE

CORRELATION AND PATH ANALYSES FOR SHOOT ARCHITECTURE, PHOTOSYNTHESIS, AND YIELD-RELATED TRAITS IN RECOMBINANT INBRED LINES OF RICE

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SUMMARY

Rice (*Oryza sativa* L.) plant architecture is crucial in rice productivity enhancement, particularly in forecasting agronomic-related traits. The presented research characterized the shoot architecture, photosynthesis, and yield-related traits in the F9 generation of rice recombinant inbred lines (RILs) derived from a cross between cultivar IR64 and local cultivar Hawara Bunar through correlation and path analyses among the various features. Rice RILs and parental cultivars' sowing transpired in the greenhouse and the field. The greenhouse experiment commenced growing the rice seeds of 90 RILs and their parental lines in PVC tubes (20 cm in diameter and 50 cm in height) with sand soil as a medium. The study employed the upland rice cultivation system for the field experiment to cultivate the rice genotypes. The study used a randomized complete block design (RCBD) with three replications. Shoot plant architecture, physiological, and yield traits observation continued at various stages of plant growth. A significant positive correlation to the seed yield per plant appeared in the maturative stage by the total seed weight, transpiration efficiency, intercellular CO_2 concentration, and intercellular CO_2 pressure. A substantial positive indirect effect on grain yield also surfaced from the net transpiration rate and its efficiency, intercellular CO_2 concentration, and CO_2 pressure. Therefore, the shoot architecture significantly affects the photosynthetic rate and grain yield.

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Key findings: Correlation and path analyses revealed a relationship among shoot architecture, photosynthesis rate, and yield-related traits in the 9th generation of rice recombinant inbred lines (RILs) derived from a cross between cv. IR64 × Hawara Bunar.

INTRODUCTION

One of the most severe threats the world could encounter is the incapability to entirely satisfy food needs, particularly rice (*Oryza sativa* L.), a primary source of carbohydrates. Efforts have continued to enhance rice resilience and productivity for abiotic stress tolerance and resistance to pests and diseases (Kato *et al.*, 2006; Fendiyanto *et al.*, 2019a; Miftahudin *et al.*, 2021). However, advancements in plant architecture, particularly in the canopy and photosynthetic abilities, have largely gone unnoticed. Plant architectural engineering is one of the vital approaches for boosting rice productivity (Kato *et al.*, 2006).

Rice plant architecture is imperative in increasing rice yield, primarily determined by plant height, the number of tillers, panicle morphology, and canopy (Kato *et al.*, 2006). New cultivars generally have ideal architecture, such as few productive tillers, sturdy stems, long leaves with a slight stand angle, thick grains, and numerous grains per panicle (Cheng *et al.*, 2023). Improving plant architecture to assemble new cultivars will likely increase the rice yield potential, particularly in optimal environments (Allard and Bradshaw, 1964; Eberhart and Russell, 1966; Tanaka *et al.*, 2023).

As a photosynthetic organ, the plant canopy has a variety of components and arrangements that can manipulate plant productivity (Cheng *et al.*, 2023). The plant height, number of tillers, leaf shape and area, and angle formed by erect leaves affect the plant photosynthesis efficiency (Satrio *et al.*, 2021). Photosynthesis is the primary metabolism influencing plant productivity (Sinclair and Horie, 1989). Shoot architecture is a complex trait made up of several essential traits. However, the impact of these characteristics on photosynthetic rate and efficiency varies according to rice genotypes (Yoshie, 1986; Tominaga *et al.*, 2018; Sharma *et al.*, 2022).

Rice cultivars IR64 and Hawara Bunar have distinct canopy characteristics (Miftahudin *et al.*, 2021). The IR64 is a semidwarf indica rice cultivar with a mature plant height of about 100 cm, relatively short-lived, and a growth period of about 117 days (Fendiyanto *et al.*, 2019a, b). The IR64 has a high yield, especially compared with previously released IRRI cultivars, due to the highest grain-filling percentage and grain weight but with a low spikelet number per m^2 (Peng *et al.*, 1993). Additionally, the cultivar IR64 has a *GS3* gene for grain size and a narrow-leaf gene (*NAL1*) that improves grain yield. Cultivar IR64 is usually a typical high-tillering indica-type cultivar, unlike new plant type (NPT) cultivars with lower tillering but larger tillers and panicle size.

The rice cultivar Hawara Bunar is a landrace with similar leaf, stems, and tiller characteristics to NPT rice. A differential gene expression exists among the rice cultivars IR64 and Hawara Bunar, particularly in abiotic stress-related genes, i.e., *OsGERLP*, *SOD,* and other genes (Satrio *et al.*, 2019; Fendiyanto *et al.*, 2021; Miftahudin *et al.*, 2021). A rice population has materialized from a cross between rice cultivars IR64 and Hawara Bunar, producing the F9 generation recombinant inbred lines (Miftahudin *et al.*, 2021).

The availability of a cross-population derived from parental genotypes with distinct canopy architectural characteristics is an excellent resource for studying how these traits affect grain yield. This study used correlation and path analysis to associate the shoot architecture and photosynthesis-related traits with yield-related features. Characteristics with significant correlation will become materials to develop the high-yielding NPT rice. Therefore, the presented research sought to analyze the phenotypic correlation and path analysis for

direct and indirect effects of rice plant architecture and photosynthesis-related traits on grain yield, particularly in RILs of IR64 × HB.

MATERIALS AND METHODS

Plant materials and the study site

Overall, 90 lines of the 9th generation recombinant inbred lines (RILs) resulting from a cross between cultivars IR64 and Hawara Bunar, referred to as 'IRH,' served as plant material. These rice parental lines have different shoot plant canopy and photosynthesis features. Cultivar IR64 is an elite lowland genotype with a higher grain yield, whereas cultivar Hawara Bunar (HB) is a local upland genotype resembling the wild rice architecture. Under the greenhouse and field conditions, two experiments progressed. Both studies occurred at the Greenhouse and Field Facility, IPB University, Bogor, West Java, Indonesia. The experimental arrangement and the data observations followed the method according to Satrio *et al.* (2021, 2023).

Crop cultivation

The greenhouse experiment comprised growing the seeds of 90 rice RILs and their parental lines in PVC tubes (20 cm in diameter and 50 cm in height) on a sand soil medium (Satrio *et al.*, 2021). Each tube contained up to 10 seeds that germinated directly. For 14 days, watering the rice plants well continued until they had four leaves. The thinning proceeded by pulling the plants and leaving three plants in each tube. Each tube received a slow-release N (15%), P_2O_5 (15%), K_2O (15%), and S (9%) fertilizer to meet their macronutrient needs. The experiments used a randomized, complete nested design with one factor. The rice genotypes served as the determining factor.

Employing the upland system for the field experiment helped cultivate the rice genotypes (Satrio *et al.*, 2021). The study used a randomized complete block design (RCBD) with three replications. Each rice line, grown by direct-seeded planting, had three rows with 3.0 m length and 0.25 m spacing between the rows. During the early vegetative stage, rainfall supplied water to the crop, supplemented with sprinkler irrigation when rainfall was insufficient. Following the standard field management practices occurred for weeding, fertilization, and insect control.

Observations

Shoot plant architecture and agronomical (yield and yield-related) traits underwent scrutiny at various stages of plant growth. Shoot canopy traits assessment commenced at the late vegetative stage by removing the sand-soil media from the roots and photographing the entire plant using a Nikon D3400 camera and a typical 18–55 mm lens. Each photograph had the Image-J software measure leaf area and plant length (Fendiyanto *et al.*, 2019a). The recorded data included the traits, i.e., first leaf area (LA1), second leaf area (LA2), third leaf area (LA3), fourth leaf area (LA4), fifth leaf area (LA5), average leaf area (LAM), total leaf area (TLA), the number of leaves (LN), and shoot length (SL). Data gathering for plant height (PH), tiller number (TN), panicle number (PN), percentage of productive tiller (PPT), seed weight per plant (SWP), and total seed weight (TSW) also continued throughout the maturative stage.

The physiological characteristics observation of the shoot began during the late vegetative (50 days after planting/DAP) and maturation (100 DAP) stages. Using the Li-Cor 6400 Portable Photosynthesis System (Li-Cor, Nebraska, USA), the physiological features of a mature and fully expanded leaf at the late vegetative stage and a flag leaf at the end of the maturity and grain-filling stage underwent measuring. Measurements started at a CO_2 level of 400 mol mol^{-1}, a flow rate of 500 mol s^{-1}, and a PAR of 600 mol m^{-2} s^{-1}. The following physiological characteristics observed included net photosynthetic rate (PR), transpiration rate (TR), transpiration efficiency (TE), total stomatal conductance (CT), intercellular CO_2 pressure (CIP), intercellular CO_2 concentration (CIC), canopy temperature (TS), and the Ball-Berry parameter (BB).

Data analysis

The direct and indirect effects of the shoot architecture, physiological and agronomical attributes, data analysis engaged correlation, and path analyses (Darmadi *et al.*, 2021). The testing of data also used multivariate analysis with the R program (Chang *et al*., 2021), using the gg-plot package (Wickham, 2016; Kassambara, 2017; Wickham and Grolemund, 2017) and factoextra (Kassambara and Mundt, 2020), with the addition of colorbrewer (Wickham, 2010; Neuwirth, 2014). The principal component analysis (PCA) used the R program (Kassambara, 2018).

RESULTS

Performance of observed traits

The results revealed that the performance of rice (*O. sativa* L.) RILs (IR64 × Hawara Bunar) were highly diverse in influencing the morphological and physiological traits and grain yield. The physiological qualities showed normal distribution, indicating a significant difference between the two parental lines (Figures 1 and 2, Table 1). According to agrophysiological attributes, the traits with relevant positive influences on rice grain yield were transpiration efficiency (TE), intercellular CO_2 pressure (CIP), and intercellular CO_2 concentration (CIC) (Table 2).
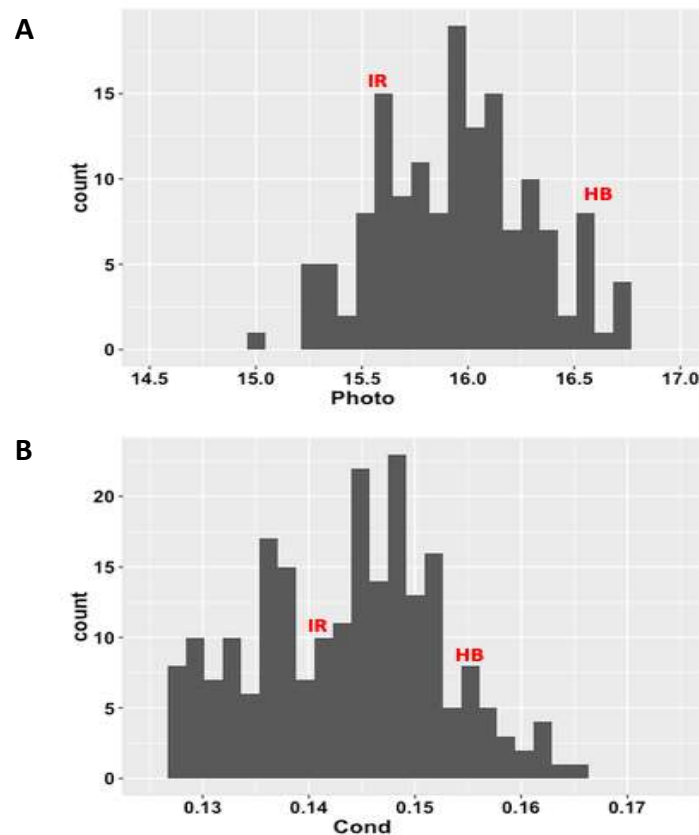
Figure 1. The distribution of photosynthesis rate (A) and stomatal conductance (B) values in the rice Recombinant Inbred Lines (RILs) population (IRH) resulting from a cross between rice cv. IR64 and Hawara Bunar. The photosynthesis rate and stomatal conductance values that represent both parental cultivars IR64 (IR) and Hawara Bunar (HB) appear in red letters. The photosynthesis rate in the IRH population ranges from 14.5 to 16.8 µmol CO_2 m^{-2} s^{-1}, while the stomatal conductance ranges from 0.120 to 0.167 mol H_2O m^{-2} s^{-1}.

Table 1. Descriptive data of the physiological characters in the rice Recombinant Inbred Population derived from a cross between rice cv. IR64 and Hawara Bunar.

Characters	Min	Max	RILs average	HB	IR
Photo (μmol CO_2 m^{-2} s^{-1})	14.510	16.800	15.800	16.700	15.700
Cond (mol H_2O m^{-2} s^{-1})	0.120	0.167	0.146	0.155	0.142
Trmmol (mmol H_2O m^{-2} s^{-1})	2.300	2.500	2.440	2.440	2.340
Ci (μmol CO_2 mol^{-1})	0.000	190.000	100.000	135.000	72.000

Photo: The photosynthesis rate, Cond: stomatal conductance values, Trmmol: Transpiration rate, Ci: intercellular CO_2 concentration
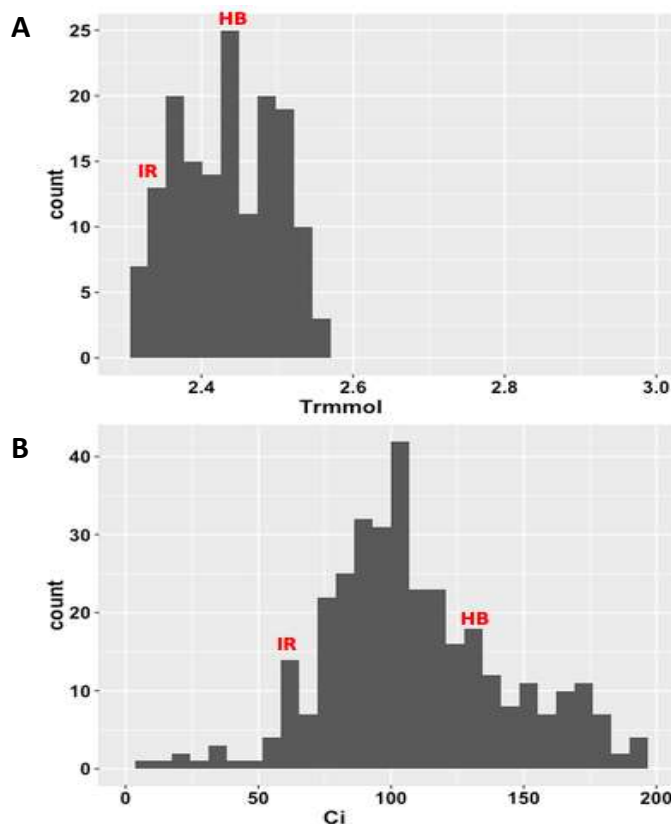

Figure 2. The distribution of transpiration rate (A) and intercellular CO_2 concentration (B) values in the rice Recombinant Inbred Lines (RILs) population (IRH) resulting from a cross between rice cv. IR64 and Hawara Bunar. Transpiration rate (Trmmol) and intercellular CO_2 concentration (Ci) values that represent both parental cultivars IR64 (IR) and Hawara Bunar (HB) appear in red letters. The transpiration rate in the IRH population ranges from 2.3 to 2.5 mmol H_2O m^{-2} s^{-1}, while the intercellular CO_2 concentration ranges from 0 to 190 μmol CO_2 mol^{-1}.

Transpiration efficiency can positively correlate to water use efficiency (WUE) and its further impact on grain yield in temperate crop plants (Yoshie, 1986). High transpiration rates are essential in regulating the water balance in rice, which further affects the grain-filling process in rice (Tominaga *et al.*, 2018). The

CO_2 pressure and concentration are also crucial in influencing the photosynthesis rate and efficiency. The effect of carbon dioxide concentration on the photosynthesis traits is vital in binding the enzyme ribulose 1.5-bisphosphate carboxylase; the higher the carbon dioxide fixation, the higher the glucose

product as photosynthates produced (Polley *et al.*, 2008). Therefore, the CIP and CIC traits greatly influence rice grain yield.

Direct effect

In the vegetative and generative phases, the direct effects on physiological and morphological traits related to photosynthesis are different. In the generative phase, traits with the highest direct outcome on rice productivity correlate to transpiration, photosynthesis, and agronomic features, such as TE, CIC, CIP, and TSW (Tables 2-4). In the rice RILs population (IR64 × Hawara Bunar), the general observation was the potential yield will receive significant influences from TE and seed formation processes when grown under optimal conditions in the generative phase. It is also consistent with the findings of Darmadi *et al.* (2021), who reported that transpiration efficiency is a form of adaptation of rice genotypes to drought closely associated with minimal water use efficiency. The efficient and promising agronomical characteristics can support the TSW characteristic during the generative phase in the seed formation process (Darmadi *et al.*, 2021), indicating the considerable correlation between TSW and productivity. Conversely, the trait that has a direct negative effect on rice productivity in the generative phase is water use efficiency (Table 4).

In the vegetative phase, the characteristic with a direct positive effect on productivity is the total leaf area (TLA). The TLA trait can benefit as a selection biomarker to determine the high productivity in the RILs populations, making it easier to perform selection related to productivity. Satrio *et al.* (2023) also reported the TLA feature in selecting drought-tolerant rice RILs in the vegetative phase in the greenhouse. The presented research also reported a relationship between leaf area and productivity (Tables 2-4). The observations showed similarities with past findings while studying the morpho-physiological traits in rice during the vegetative

stage under drought stress conditions (Satrio *et al.*, 2021; Mu'min *et al.*, 2024).

The correlation values negatively affecting rice productivity were the number of leaves (LN) and the 4th leaf area (LA4) traits. Based on the observed data during the vegetative phase, although the total number of leaves has a positive correlation, the LN and LA4 traits showed an opposite trend. If the number of leaves is high and the 4th leaf area is large, it indicates low productivity after maturity. These LN and LA4 markers are unique, need further verification, and may be limited to the RILs population of IR64 × Hawara Bunar. Based on the morphological traits in rice RILs, a suggestion stated that in the vegetative phase, the number and size of leaves were the main biomarkers related to productivity (Collard *et al.*, 2005). Path analysis showed a significant (p < 0.01) correlation (r = 0.70) between the LN and the LA4 traits. Path analysis also revealed that the TLA characteristic significantly (p < 0.05) influences the correlation (β = 0.50) between the LN and the LA4 traits.

The results indicated a significant correlation between the Ball–Berry at the vegetative stage (BB_V) and the net photosynthesis rate at the vegetative stage (PR_V) traits in the RILs rice population. These findings were also analogous to the previous research in mapping and identification of QTL for agro-physiological traits in *O. sativa* L. under drought-stress conditions (Satrio *et al.*, 2023). Furthermore, the path analysis results showed that the attributes BB_V and PR_V also influenced grain yield. The biplot analysis revealed a strong pattern of association between the transpiration rate characteristic and photosynthesis-related traits. The traits TE_V, BB_V, and PR_V have a positive direction on the X-axis, while the other qualities, i.e., CIC, CIP, TR, and CT, have a positive direction on the Y-axis. Additionally, the PCA analysis showed that the photosynthesis and physiological traits contribute 57.5% to the data variation, while the Y-axis contributes 21.6% (Figure 3, Table 5).

Table 2. The direct and indirect effect of agro-physiological traits at the maturative stage to seed weight per plant in the rice Recombinant Inbred Population derived from a cross between rice cv. IR64 and Hawara Bunar.

Traits	(P)	TSW	CHL	PH	TN	PN	PPT	PR	CIC	TR	WUE	TS	TSD	CT	CIP	TE
TSW	0.902	-	-0.002	0.007	-0.087	0.12	-0.014	0.004	-0.084	0.02	-0.061	0.011	-0.001	-0.022	-0.081	0.207
CHL	0.042	-0.045	-	0.004	0.005	0.007	-0.009	0.003	-0.181	0.061	-0.104	0.014	0.002	-0.068	-0.176	0.414
PH	0.037	0.171	0.005	-	-0.046	0.048	0.004	0.001	0.125	-0.041	0.061	0.025	0.000	0.009	0.122	-0.31
TN	-0.178	0.442	-0.001	0.01	-	0.221	-0.008	0.003	-0.125	0.02	-0.104	0.018	0.001	-0.019	-0.135	0.345
PN	0.240	0.451	0.001	0.007	-0.164	-	-0.034	0.002	-0.07	0.008	-0.069	0.025	0.002	-0.015	-0.068	0.172
PPT	-0.074	0.171	0.005	-0.002	-0.02	0.111	-	-0.001	0.153	-0.045	0.087	0.016	0.000	0.019	0.149	-0.379
PR	0.018	0.198	0.008	0.001	-0.03	0.034	0.003	-	-0.78	0.158	-0.467	-0.028	0.000	-0.084	-0.756	1.896
CIC	1.393	-0.054	-0.005	0.003	0.016	-0.012	-0.008	-0.01	-	-0.37	0.856	0.044	-0.001	0.214	1.351	-3.448
TR	-0.406	-0.045	-0.006	0.004	0.009	-0.005	-0.008	-0.007	1.268	-	0.805	0.012	-0.002	0.26	1.229	-3.137
WUE	-0.865	0.063	0.005	-0.003	-0.021	0.019	0.007	0.009	-1.379	0.378	-	-0.016	0.002	-0.236	-1.337	3.413
TS	-0.178	-0.054	-0.003	-0.005	0.018	-0.034	0.007	0.003	-0.348	0.028	-0.078	-	-0.004	0.124	-0.324	0.758
TSD	0.007	-0.09	0.012	0.001	-0.037	0.058	-0.003	-0.001	-0.181	0.114	-0.199	0.098	-	-0.139	-0.176	0.517
CT	0.31	-0.063	-0.009	0.001	0.011	-0.012	-0.004	-0.005	0.961	-0.341	0.657	-0.071	-0.003	-	0.932	-2.413
CIP	1.351	-0.054	-0.005	0.003	0.018	-0.012	-0.008	-0.01	1.393	-0.37	0.856	0.043	-0.001	0.214	-	-3.448
TE	3.448	0.054	0.005	-0.003	-0.018	0.012	0.008	0.01	-1.393	0.37	-0.856	-0.039	0.001	-0.217	-1.351	-

(P): direct effect, TSW: total seed weight, CHL: chlorophyll content, PH: plant height, TN: tiller number, PN: panicle number, PPT: percentage of productive tiller, PR: net photosynthesis rate, CIC: intercellular CO_2 concentration, TR: transpiration rate, WUE: water use efficiency, TS: canopy temperature, TSD: difference between canopy and air temperature, CT: total stomatal conductance, CIP: intercellular CO_2 pressure, TE: transpiration efficiency.

Table 3. The direct and indirect effect of morphological traits at the vegetative stage to seed weight per plant in the rice Recombinant Inbred Population derived from a cross between rice cv. IR64 and Hawara Bunar.

Traits	(P)	LN	LAM	TLA	LA1	LA2	LA3	LA4	LA5	SL
LN	0.552	-	0.054	-0.616	-0.023	0.049	0.163	0.247	0.031	-0.348
LAM	0.083	0.359	-	-0.81	-0.034	0.088	0.233	0.314	0.035	-0.361
LAT	-0.844	0.403	0.08	-	-0.034	0.081	0.233	0.322	0.038	-0.361
LA1	-0.037	0.337	0.078	-0.777	-	0.075	0.213	0.292	0.032	-0.34
LA2	0.109	0.248	0.068	-0.625	-0.026	-	0.161	0.198	0.024	-0.257
LA3	0.277	0.326	0.07	-0.709	-0.029	0.063	-	0.266	0.033	-0.311
LA4	0.374	0.364	0.07	-0.726	-0.029	0.058	0.197	-	0.033	-0.328
LA5	0.044	0.392	0.067	-0.726	-0.027	0.06	0.205	0.277	-	-0.323
SL	-0.415	0.464	0.073	-0.734	-0.03	0.067	0.208	0.295	0.034	-

(P): direct effect, LN: number of leaves, LAM: average leaf area, TLA: total leaf area, LA1: 1st leaf area, LA2: 2nd leaf area, LA3: 3rd leaf area, LA4: 4th leaf area, LA5: 5th leaf area, SL: shoot length.

Table 4. The direct and indirect effect of physiological traits at the vegetative stage to seed weight per plant in the rice Recombinant Inbred Population derived from a cross between rice cv. IR64 and Hawara Bunar.

Traits	(P)	PR	TR	TE	CT	CIC	CIP	WUE	TS	TSD	BB
PR	1.453	-	-0.156	-0.872	0.182	-0.293	-0.474	0.436	1.213	-0.03	-1.451
TR	-0.648	0.349	-	0.941	1.316	-0.445	-1.129	-0.347	0.696	-0.044	-0.538
TE	-1.743	0.726	0.35	-	-0.840	0.113	0.585	0.717	0.582	0.003	-0.583
CT	1.400	0.189	-0.609	1.046	-	-0.372	-1.129	-0.37	0.388	-0.045	-0.419
CIC	-0.563	0.756	-0.512	0.349	0.924	-	-1.212	-0.081	1.343	-0.054	-0.838
CIP	-1.393	0.494	-0.525	0.732	1.134	-0.49	-	-0.200	0.922	-0.046	-0.568
WUE	0.739	0.857	0.305	-1.691	-0.7	0.062	0.376	-	0.680	-0.005	-0.733
TS	1.618	1.09	-0.279	-0.628	0.336	-0.467	-0.794	0.31	-	-0.044	-1.062
TSD	-0.095	0.45	-0.298	0.052	0.658	-0.321	-0.669	0.037	0.744	-	-0.598
BB	-1.496	1.409	-0.233	-0.68	0.392	-0.315	-0.529	0.362	1.149	-0.038	-

(P): direct effect, PR: net photosynthesis rate, TR: transpiration rate, TE: transpiration efficiency, CT: total stomatal conductance, CIC: intercellular CO_2 concentration, CIP: intercellular CO_2 pressure, WUE: water use efficiency, TS: canopy temperature, TSD: the difference between canopy and air temperature, BB: Ball–Berry parameter.

Table 5. Principal components of the physiological characters at vegetative stage in the rice Recombinant Inbred Population derived from a cross between rice cv. IR64 and Hawara Bunar.

Characters	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9
PR_V	-0.206	0.606	0.189	-0.019	0.091	0.323	-0.544	-0.379	0.044
TR_V	0.392	0.120	0.170	0.594	-0.137	-0.190	-0.431	0.459	0.004
TE_V	-0.415	0.064	-0.155	0.121	0.377	-0.389	-0.043	0.144	0.684
CT_V	0.402	0.190	0.059	0.335	0.235	-0.368	0.324	-0.626	-0.006
CIC_V	0.419	-0.060	0.145	-0.128	-0.332	0.356	0.107	-0.090	0.726
CIP_V	0.387	0.033	0.183	-0.273	0.773	0.233	0.023	0.296	-0.033
TS_V	-0.323	-0.296	0.282	0.611	0.182	0.512	0.240	-0.052	0.004
TSD_V	0.167	0.129	-0.875	0.235	0.091	0.356	-0.011	0.009	0.000
BB_V	-0.112	0.685	0.091	0.031	-0.162	0.060	0.585	0.368	-0.035
Eigenvalue	5.171	1.945	1.008	0.378	0.247	0.232	0.015	0.005	0.000
Variance (%)	57.457	21.609	11.195	4.195	2.744	2.575	0.166	0.057	0.001

PR_V: net photosynthesis rate, TR_V: transpiration rate, TE_V: transpiration efficiency, CT_V: total stomatal conductance, CIC_V: intercellular CO_2 concentration, CIP_V: intercellular CO_2 pressure, TS_V: canopy temperature, TSD_V: the difference between canopy and air temperature, BB_V: Ball–Berry parameter. Dim1 = Principal Component 1 (57.5%), Dim2 = Principal Component 2 (21.6%).
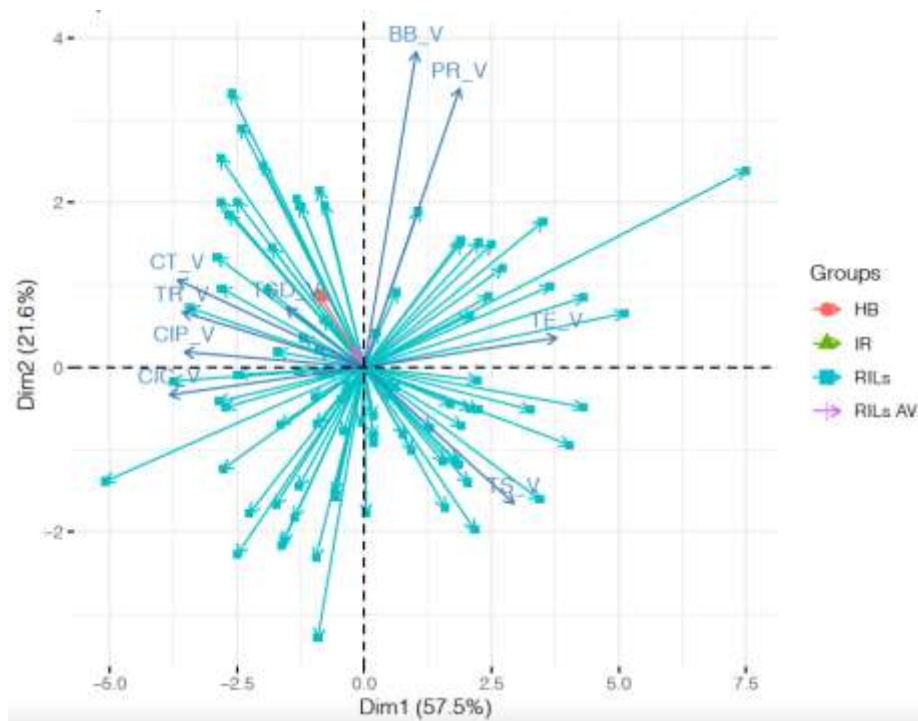
Figure 3. Biplot analysis of physiological trait traits in the rice Recombinant Inbred Population derived from a cross between rice cv. IR64 and Hawara Bunar. IR = IR64, HB = Hawara Bunar, RILs = Recombinant Inbred Lines, RILs AV = the average value of the RIL's traits, PR_V: net photosynthesis rate, TR_V: transpiration rate, TE_V: transpiration efficiency, CT_V: total stomatal conductance, CIC_V: intercellular CO_2 concentration, CIP_V: intercellular CO_2 pressure, TS_V: canopy temperature, TSD_V: the difference between canopy and air temperature, BB_V: Ball–Berry parameter. Dim1 = Principal Component 1 (57.5%), Dim2 = Principal Component 2 (21.6%).

DISCUSSION

Rice is a primary food crop worldwide, especially in Asia. In rice, the canopy architecture is crucial in determining the promising productivity and harvest quality (Jiang *et al.*, 2023). In rice genotypes, the canopy structure correlates with morphological and anatomical characteristics, such as leaves, stems, and panicles, in the upper parts of the plant (Cheng *et al.*, 2023). Well-developed rice canopy architecture can also enhance the efficiency of light and nutrient utilization, increasing rice production and grain quality (Peng *et al.*, 1993). Additionally, rice canopy is vital in determining tolerance to environmental conditions, viz., drought, flooding, pests, and disease attacks (Spindel *et al.*, 2013). Therefore, understanding rice canopy architecture is crucial for the researchers and

farming community to improve productivity by developing superior rice cultivars. In the presented research, we also found that the physiological traits of the rice RIL showed a quantitative trait pattern (Figures 1–2, Tables 1–2).

The relationship between canopy structure and photosynthesis traits appeared considerably high and crucial in rice (Sharma *et al.*, 2022; Tanaka *et al.*, 2023). A well-developed rice canopy design can enhance the light utilization efficiency, thereby increasing photosynthetic rate and rice production (Sinclair and Horie, 1989). Essentially, photosynthesis occurs in rice plants' leaves, and the light distribution within the plant canopy mainly affects the availability of light to the leaves (Murchie *et al.*, 2009; Nagai and Makino, 2009). Therefore, good canopy architecture enables the plant leaves to receive

sufficient light for photosynthesis. The rice cultivar Hawara Bunar has a higher leaf area than IR64, and the RILs population has a broad value of canopy architecture (Table 3). The latest study confirmed that canopy architecture could influence photosynthesis-related traits (Table 4).

Leaf position on the stem and within the canopy is one of the imminent factors influencing the rice canopy architecture (Sakamoto and Matsuoka, 2004). Leaves located higher on the stem and outside the canopy tend to receive more light and exhibit better photosynthetic rates (Tanaka *et al.*, 2023). Additionally, the position of the panicle within the canopy affects the availability of light to the leaves, thereby influencing the photosynthetic rate.

Besides leaf and panicle positions, leaf density within the canopy influences the rice canopy structure (Tanaka *et al.*, 2023). If the leaf density is high, the leaves may overlap and limit light absorption (Kato *et al.*, 2006). Conversely, if the density is too sparse, the leaves cannot cover the entire plant surface, resulting in wasted light (Cheng *et al.*, 2023). Therefore, appropriate leaf density is crucial for achieving the optimal rice canopy architecture.

In addition to affecting the photosynthetic rate, rice canopy architecture is vital in regulating the plant temperature (Tanaka *et al.*, 2023). Leaves protected by other leaves within the canopy tend to experience lower temperatures, receive shield from direct sunlight exposure. Thus, the well-developed canopy structure can help maintain the temperature stability in plants, thereby not disturbing the process of photosynthesis. The existing research also showed a significant positive phenotypic correlation of the seed yield per plant with total seed weight, transpiration efficiency, intercellular CO_2 concentration, and intercellular CO_2 pressure. However, the traits, viz., transpiration rate, transpiration rate and efficiency, intercellular CO_2 concentration, and intercellular CO_2 pressure, provided the maximum positive indirect effects on grain yield (Tables 1-3). Therefore, the selection criteria for high yield in RILs can depend on the transpiration and photosynthetic characteristics.

CONCLUSIONS

The plant canopy architecture significantly affects the rice photosynthetic rate and grain yield. The performance of recombinant inbred lines (RILs) showed alike in the greenhouse and field experiments. The maturity stage exhibited a notable positive phenotypic correlation with seed yield per plant, particularly with the total seed weight, transpiration efficiency, intercellular CO_2 concentration, and intercellular CO_2 pressure. A considerable positive indirect impact of the intercellular CO_2 concentration, intercellular CO_2 pressure, and net transpiration rate and efficiency was evident in seed yield. Consequently, in rice RILs, when selecting for high grain yield, it is advisable to consider the photosynthetic and transpiration characteristics as primary criteria.

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