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Dynamics of productivity in pigeonpea [*Cajanus cajan* (L.) Millsp.] in subtropical Australia

Sabampillai Mahendraraj¹  | Marisa Collins²  | Yash Chauhan³ | Vincent Mellor⁴ | Rao C. N. Rachaputi¹

¹Queensland Alliance for Agriculture and Food Innovation (QAAFI), The University of Queensland, Gatton, Australia

²(Agronomy) Animal, Plant and Soil Science, The Latrobe University, Melbourne, Australia

³Department of Agriculture and Fisheries, Kingaroy, Queensland, Australia

⁴School of Agriculture and Food Sustainability, The University of Queensland, Gatton, Queensland, Australia

Correspondence

Sabampillai Mahendraraj, Queensland Alliance for Agriculture and Food Innovation (QAAFI), The University of Queensland, 208, Building 8115, Gatton Campus, Australia.
Email: m.sabampillai@uq.edu.au

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Abstract

Pigeonpea productivity can be enhanced by optimally matching the physiology of genotypes to environmental conditions. Information on crop responses to the environment has been lacking for the short-duration pigeonpea genotypes, which are being trialed to develop the Australian pigeonpea industry. The objective of this study was to examine the dynamics of productivity in relation to radiation use efficiency (RUE) and its influence on yield partitioning. Seven field trials, employing three pigeonpea [*Cajanus cajan* (L.) Millsp.] genotypes, were established at the Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons. The study reveals that leaf area development, influenced by growing environment, genotypes, and their interactions, were the key factors for the differences in leaf area duration and RUE. Pigeonpea planted in December had higher seasonal (1.11 g MJ^{-1}) as well as reproductive (0.71 g MJ^{-1}) RUE, resulting in significant differences in total dry matter (TDM) and grain yield (GY). GY was positively associated with seasonal RUE ($R^2 = 0.62$), and the relationship was stronger ($R^2 = 0.83$) for the reproductive phase ($\text{RUE}_{(R)}$). The positive association between GY and $\text{RUE}_{(R)}$ suggested that maintaining optimum leaf area during the grain filling period is crucial to achieve higher productivity. Variations in GY were related to amount and rate of TDM accumulation before flowering ($R^2 = 0.51$ and $R^2 = 0.53$, respectively). Hence, achieving greater TDM before flowering was determinant for achieving higher productivity. The present study provided updated information on dynamics of productivity that will enable more comprehensive modelling of pigeonpea adaptation under subtropical conditions.

1 | INTRODUCTION

Pigeonpea [*Cajanus cajan* (L.) Millsp.] is a grain legume widely grown in tropical and subtropical regions of South and Southeast Asia and Eastern and Southern African countries (Tigga, 2015). It consists an inexpensive plant-based

Abbreviations: CGR, crop growth rate; DAP, days after planting; GY, grain yield; HI, harvest index; LAD, leaf area duration; LAI, leaf area index; PAR, photosynthetically active radiation; RUE, radiation use efficiency; TDM, total dry matter.

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protein, vitamins, and minerals, and it also plays a crucial role for sustainable farming systems (Kumari et al., 2020). There is growing interest in pigeonpea cultivation in some subtropical areas (Chauhan et al., 1999; Mahendraraj et al., 2021) due to its performance in poor soils and ability to withstand low moisture conditions (Reddy et al., 2011). Recent research on pigeonpea in Australia highlights the high production potential in subtropical regions (Rachaputi et al., 2018) as a good long-season summer legume for farmers in Northern Queensland. However, the presence of significant genotype \times environment interactions limits the expansion of the crop to a wider range of latitudes (Chauhan et al., 1999; Yohane et al., 2021).

Traditional pigeonpea genotypes are photoperiod sensitive, long-duration crops and normally grown under rainfed conditions in India (Sheldrake & Narayanan, 1979). Photothermal sensitivity of traditional genotypes is a major drawback for the horizontal expansion to new cropping systems (Kumari et al., 2020). However, the extra-short duration genotypes are relatively less affected by photoperiod and can be grown in different seasons, such as long-day or short-day conditions (Wallace, 1991; Robertson, Silim et al., 2001). Crop growth and reproductive development are mainly driven by temperature and differences in thermal time across planting dates affects crop duration. Crop growth rate (CGR) determines time to flowering and maturity and plays a significant role in productivity.

CGR can be measured using leaf area index (LAI), radiation use efficiency (RUE), and the light extinction coefficient (k) (Chauhan, 1999). A few studies have compared LAI development and interception of photosynthetically active radiation (PAR) in pigeonpea across seasons and maturity groups (Ranganathan et al., 2001). The cumulative intercepted PAR and RUE are the key canopy traits for determining biomass (Pan et al., 2020). The RUE for pigeonpea ranged from 1.40 to 1.76 g MJ⁻¹ (Rachaputi et al., 2018) and 1.61 to 1.82 g MJ⁻¹ (Patel et al., 1999). A study on five forage legumes under reduced light intensity showed that shading reduced TDM by 39% in pigeonpea, followed by Lima bean (43%). However, LAI and light interception were affected depending on genotype and shading up to 50–60 days after planting (DAP) (Angadi et al., 2022). A significantly higher RUE (2.22 g MJ⁻¹) was reported in pigeonpea under 75% shade (Manoj et al., 2021).

Grain yield (GY) can be improved by increasing the efficiency of dry matter production per unit of intercepted radiation and/or by increasing the fraction of total dry matter (TDM) partitioned to grains. The total dry matter (DM) growth rate is determined by the amount of photosynthetic assimilates in the source (leaves) and the fraction of TDM partitioned into the sink (grain) (Jaradat, 2009). With the onset of flowering, the growth rate of leaves starts to decline and approaches zero. The decrease in leaf TDM occurs as

Core Ideas

- Productivity in pigeonpea genotypes is positively correlated with leaf area duration and radiation use efficiency.
- Larger pigeonpea canopies and longer leaf area duration ($^{\circ}\text{Cd}$) resulted in greater radiation use efficiency.
- The rate of dry matter production before flowering is instrumental for achieving higher productivity.
- Variations in grain yield were related to amount of dry matter produced before flowering.
- Differences in extinction coefficient indicate pigeonpea has an adaptive mechanism to changing environmental conditions.

the result of the shifting of carbon resources from growing leaves into developing grain (Charles Edwards & Lawn, 1984). Understanding the trade-off between source and sink to maximize partitioning to reproductive structures is important for optimizing higher harvest index (HI).

While there are a few studies on radiation interception dynamics of TDM growth and partitioning in pigeonpea, these tend to be in tropical environments using the genotypes developed for those environments (Chauhan et al., 1999). Limited studies were conducted in sub-tropical environments, where the length of the crop production period is often limited by low temperatures (Bell et al., 2008). Understanding the dynamics of productivity in these environments using new and improved genotypes is of considerable interest. Therefore, the objective of this study was to examine the dynamics of productivity in relation to radiation use efficiency and its influence on canopy development and yield partitioning in pigeonpea genotypes.

2 | MATERIALS AND METHODS

Field experiments were conducted at the horticulture research farm, Gatton campus of The University of Queensland (27°56' S, 152°33' E, 94 MSL), during 2017/2018 and 2018/2019 summer seasons.

2.1 | Experimental design

The experiments were laid out as a split-plot design with seven planting dates across seasons as main plots and three genotypes as subplots, replicated four times. Genotypes were assigned to sub-plots in a randomized manner (Table 1).

TABLE 1 Details of pigeonpea genotypes corresponding to each planting date in the field experiments conducted at Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons.

Season	Planting date	Genotypes
2017/2018 (S1)	P1–December 6, 2017	Quest—Determinate
	P2–January 9, 2018	QPL1001—
	P3–February 16, 2018	Determinate
	P4–March 13, 2018	ICP14425—
2018/2019 (S2)	P5–October 10, 2018	Indeterminate
	P6–November 15, 2018	
	P7–December 20, 2018	

Note: S1: Season 1; S2: Season 2.

Abbreviations: ICP, ICRISAT pigeonpea germplasm; QPL, Queensland pigeonpea line.

2.2 | Crop management

Fields were left fallow for a season after a maize (*Zea mays*) crop, followed by an oat cover crop. Land was prepared using conventional tillage practices with two passes using a chisel plough and rotary hoe to a depth of 15 cm. The plot size was 1.5 m (width) × 8 m (length) and consisted of four 0.5 m rows. Plant-to-plant distance within a row was 15 cm. Pre-sowing soil testing was conducted (Table 2), and 200 kg ha⁻¹ of CK-88 (15.1N, 11.5 P, and 13.6 K) (Incitec Pivot Fertilisers) was applied 30 days before planting using fertilizer spreader.

Pigeonpea seeds obtained from Australian Grains Gene Bank, Horsham, Victoria (AGGB) were treated with a fungicide (Tetramethylthiuram Disulfide 42%, BAYER Crop Science) before planting. Plots were inoculated with Nodule-N⁷ (Group J—*Mesobacterium sp.* (new edge microbial) immediately after planting by applying inoculum + water suspension (10 g/5 L water). After planting, a pre-emergent herbicide (pendimethalin 440 EC) (Genfarm) was applied at the rate of 1.5 L ha⁻¹ within 48 h of planting, followed by mechanical weeding when necessary. A drip irrigation system was set up in 2017/2018 using “T” tapes (340 LPH/100 m at 0.55 BAR, Rivulis). The pigeonpea crop was irrigated weekly until March and then was irrigated fortnightly until June.

2.3 | Measurements

2.3.1 | Dry matter sampling

In all experiments, above-ground biomass was harvested from 30 DAP until the final harvest (120–160 DAP). Plants from a 1.0 m² area in the middle two rows of each subplot were harvested at monthly intervals for growth analysis. Plants were cut at ground level and separated into stem, leaves, flowers,

immature (green), and mature (brown) pods. Pod counts were recorded before drying. The plant samples were placed in a paper bag and then dried in a fan-forced oven at 70°C for 1 week. Dry weights of stem, leaves, and immature and mature pods were recorded. The final harvest date for each genotype was when at least 80% of the pods had turned brown. For the final harvest, plants from a 2.0 m² area within each subplot were harvested at ground level and separated into their components (stems, leaves, immature, and mature pods). Number of pods, pod length, and seeds per pod were measured. Dried pods were threshed using a mechanical thresher, LD 350 (Wintersteiger Seedmech), and the seed weight was recorded to calculate the GY. HI was calculated as the ratio of seed yield (t ha⁻¹) to TDM (t ha⁻¹). For seed size calculation, 500 seeds were counted using a seed counter (Contador Electric Seed Counter, Hoffman Manufacturing), weight, and converted into 100-seed weights.

2.3.2 | Leaf area measurements

The LAI was measured using a planimeter (LI-3100 C leaf area meter, LICOR Biosciences). The LAI is the ratio of total leaf area divided by the land area from which the plants were harvested (green leaf area/unit ground area).

Beta growth function was used to fit LAI to analyze the leaf area development (Pan et al., 2020).

$$LAI = LAI_{\max} \left[1 + \frac{t_e - t}{t_e} - t_m \right] \times (t/t_e)^{\left[t_e / (t_e - t_m) \right]} \quad (1)$$

where “*t*” is the thermal time (°Cd), *t_e* represents the time (°Cd) when the growth of leaf area ceases and *t_m* (°Cd) at which maximum LAI was achieved.

2.3.3 | Radiation interception

In 2017/2018 (S1), the fractional radiation intercepted was measured at hourly intervals using tube-solarimeters (type TSL, Delta-T Devices Ltd.). A tube solarimeter 90 cm in length was positioned perpendicular to each crop row at 10 cm above the ground. The tubes were flushed with N₂ gas when necessary to remove any moisture condensation in the tube. The tubes were occasionally adjusted to be below the last green leaf of the pigeonpea crop and leveled so that radiation interception by the canopy only was measured. Two reference tube solarimeters were placed 2 m above the plant canopy, and the measurements taken below the canopy were expressed as the proportion of incoming radiation intercepted by the canopy. Data from the tubes were captured using Campbell Scientific data logger CR 1000x at 30-min interval and averaged hourly.

TABLE 2 Summary of soil physical and chemical properties for testing pigeonpea growth at Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons.

Season	Sampling depth (cm)	EC at 25°C (mS/cm)	pH	Moisture (mm)		Available nitrogen (%)	Organic carbon (%)	Bulk density (kg/m ²)
				Sowing	Harvesting			
2017/2018 (S1)	0–30	1.48	7.7	35.7	21.7	0.16	2.24	1.55
	30–60	2.51	7.5	35.0	24.3	0.10	1.53	1.52
2018/2019 (S2)	0–30	1.77	7.6	36.1	25.1	0.14	1.89	1.57
	30–60	3.33	7.5	33.7	23.0	0.11	1.49	1.53

In 2018/2019 (S.5, S.6, and S.7), total incident PAR and the fraction of PAR transmitted through the canopy on clear days were measured using an AccuPAR PAR/LAI ceptometer (Model LP-80). The ceptometer was calibrated to an external PAR sensor. In each replicate, measurement was made in eight sampling positions opposite to each other, and hence, individual PAR readings consisted of an average of eight readings. Measurements were recorded mid-day between 11:00 a.m. and 1:00 p.m.

The fractional intercepted radiation was calculated as the amount of light penetrating the bottom of the canopy (Manoj et al., 2021).

$$f = 1 - \frac{I_0}{I_t} \times 100 \quad (2)$$

f is the fractional radiation intercepted; I_0 is the PAR measured below the canopy, and I_t PAR is measured above the canopy.

2.3.4 | Canopy extinction coefficient (k)

The canopy extinction coefficient was estimated from the LAI and the fraction of intercepted PAR by fitting the logistic function using Equation (3), as the slope of the regression line between $\log(1 - f)$ and LAI (Rezig et al., 2013).

$$k = -\log(1 - f) \quad (3)$$

where k is the light extinction coefficient, f is the fraction of intercepted PAR, and LAI is the LAI. The canopy extinction coefficient quantifies the effects of plant architecture such as leaf angle, optical properties of the leaf surface, and adaptive mechanisms in response to environmental conditions.

2.3.5 | Radiation use efficiency

RUE is defined as the ratio of biomass produced and intercepted PAR expressed as g MJ⁻¹ m⁻². RUE was computed as the slope of the linear regression line between accumulated biomass and cumulative intercepted PAR (Tesfaye et al.,

2006).

Radiation use efficiency (RUE)

$$= \frac{\text{Total above ground biomass}}{\text{Total intercepted PAR}} \quad (4)$$

Daily incident PAR (MJ⁻¹ m⁻²) was calculated as 50% of daily incident total solar radiation (Monteith, 1981). Cumulative PAR intercepted (MJ⁻¹ m⁻²) was calculated as the sum of the product of f and incident PAR from emergence up to the time of each sampling.

2.3.6 | Crop growth rate, pod growth rate, and partitioning

CGR and pod growth rate (PGR) were calculated from the slope of the relationship between TDM and pod dry matter (PDM) with cumulative degree days, respectively. Partitioning was computed as a ratio of PGR and CGR during the reproductive phase.

2.3.7 | Statistical analysis

Differences in time of planting amongst genotypes and TDM, stem DM, leaf DM, grain yield, and HI were analyzed by performing analysis of variance for a split-plot design using R Studio, version 4.0.3. Treatment factors were time of planting, genotypes, and interactions between them (time of planting × genotype), while replicates were treated as random factors at $p < 0.05$.

Dynamic changes in LAI, k , and RUE were analyzed by performing analysis of covariance using R Studio (Packages: Agricol, nls. List) at $p < 0.05$. Differences between treatment means were compared using Tukey's LSD (Least significant difference) at $p < 0.05$.

Growth data were further analyzed for dynamic changes in crop and pod DM growth (CGR) using the partial least square (PLR) linear regression for the linear phase of the growth before and after flowering. DM partitioning was calculated by dividing pod growth rate by CGR after flowering.

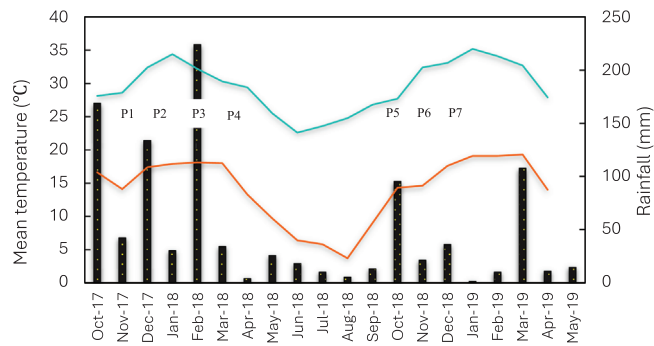


FIGURE 1 Mean maximum and minimum temperatures and in-season rainfall (mm) across the season.1 (2017/2018) and season.2 (2018/2019) at Gatton Campus, the University of Queensland, Australia. P1–P2 represents planting dates (P1–December 6, 2017, P2–January 9, 2018, P3–February 16, 2018, P4–March 13, 2018, P5–October 10, 2018, P6–November 15, 2018 and P7–December 20, 2018).

Slopes of the pre- and post-flowering CGR for the time of planting and genotypes were compared using lsmeans in package “emmeans” and Tukey’s HSD with the significance level at $p < 0.05$. Pearson’s correlation coefficient was conducted to analyze the correlations between yield and growth parameters using package “ggplot.2”.

3 | RESULTS

3.1 | Growing environment

The two field experiments were conducted in 2017/2018 (S1) and 2018/2019 (S2) summer seasons. Both seasons (S1 and S2) experienced different weather patterns of ambient temperature, in-season rainfall, and solar radiation (Figure 1). The mean ambient temperature was consistently higher in S2 versus S1 with a maximum temperature $\geq 40^\circ\text{C}$. The highest mean pre-flowering maximum temperature was recorded at P7 (34.5°C), whereas the post-flowering maximum temperature was high at P6 (33.3°C). The accumulated growing degree days (GDD) during pre- and post-flowering phases and the whole season varied across the season and time of planting. Pigeonpea crop in P6 and P7 accumulated higher GDD (2052°Cd , 2107°Cd , respectively), whereas P3 (1413°Cd) accumulated the lowest GDD. Crops planted in S1 accumulated higher total incident PAR compared to similar planting dates in S2 due to excessive cloud cover, dust, and sandstorms. The highest PAR of 1499 MJ m^{-2} was recorded in P1, followed by P2 (1439 MJ m^{-2}). S1 received the highest in-season rainfall of 843 mm compared to S2 (576 mm). An in-season rainfall during the pre-flowering phase of 247 and 227 mm was recorded in P2 and P3, respectively. The crop was irri-

gated using a combination of T—tape to maintain the soil moisture to avoid significant water stress.

3.2 | Leaf area development

Leaf area development was studied only for plantings P1, P5, P6, and P7. Genotypes had a similar pattern of leaf area development across planting dates, but the maximum (LAI_(max)) and accumulated growing degree day requirement to reach LAI_(max) showed seasonal and genotypic differences ($p < 0.001$) (Table 3). Leaf area development declined once LAI_(max) was attained, and the rate of reduction of LAI varied among genotypes and planting season. The leaf area duration (LAD) was higher in P1 (December 6, 2017) and P7 (December 20, 2018) for all the genotypes (on average 1591°Cd), resulting in $>20\%$ of the average LAD (1219°Cd) across the season (Table 3). Irrespective of genotypes, the crop was sown on November 15, 2018 (P6) and achieved the LAI_(max) faster than other seasons (1088°Cd).

3.3 | Fractional PAR intercepted (f) and canopy extinction coefficient (k)

The dynamic changes in fractional intercepted PAR were measured in four planting dates (P1, P5, P6, and P7). Canopy extinction coefficient (k) was estimated by fitting the relationship between the LAI and fractional PAR intercepted (f). The regression lines were forced through the zero since $f = 0$ when LAI = 0.

The mean k value for the genotypes across sowing dates was 0.72 ± 0.12 and significantly differed among genotypes and between planting dates. Growing environment and genotype accounted for 44% and 53% of mean sums of the square, respectively, for variability in k . Mean canopy k values were generally higher for QPL 1001 (0.79) than Quest (0.65) and ICP 14425 (0.70) (Table 4).

3.4 | Radiation use efficiency (RUE)

Seasonal RUE_(s) was derived as the slope of the linear regression of cumulative TDM at harvest (t ha^{-1}) on cumulative intercepted PAR (MJ m^{-2}) fitted for each genotype. The average RUE_(s) across planting dates was estimated to be 1.12 g MJ^{-1} . Crops planted in December in both seasons were efficient in converting radiation into DM. Hence, sowing date December 20, 2018 had larger RUE ($1.44\text{--}1.63 \text{ g MJ}^{-1}$) than other planting dates. RUE_(R) during the post-flowering phase varied across sowing dates ($0.19\text{--}0.71 \text{ g MJ}^{-1}$). There was a significant drop in RUE_(R) for P6 (November 15, 2018).

TABLE 3 Cumulative thermal time to reach maximum leaf area index ($LAI_{(max)}$, °Cd), maximum leaf area duration ($LAD_{(max)}$) and LAI at pigeonpea harvest computed by β -growth function in P1, P5, P6, and P7 planting dates in pigeonpea at Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons.

Season	Sowing No.	Genotype	$LAD_{(max)}$ (Σ °Cd)	$LAI_{(max)}$	$LAI_{(harvest)}$
S1	P1	Quest	1762***	4.6ns (0.54)	2.93 (0.20)
S2	P5		1273***	2.9** (0.36)	1.77 (0.06)
S2	P6		1094***	4.3*** (0.37)	2.17 (0.08)
S2	P7		1528***	4.6*** (0.38)	3.65 (0.28)
S1	P1	QPL 1001	1616*	2.6ns (0.51)	1.60 (0.11)
S2	P5		1314***	2.8* (0.37)	1.43 (0.20)
S2	P6		1081***	3.8** (0.37)	1.83 (0.19)
S2	P7		1507***	3.9*** (0.38)	2.40 (0.15)
S1	P1	ICP 14425	1674*	3.5ns (0.55)	2.07 (0.15)
S2	P5		1463***	4.1** (0.44)	2.38 (0.13)
S2	P6		1090***	4.2** (0.39)	2.33 (0.24)
S2	P7		1456***	3.8** (0.38)	2.40 (0.15)

Note: Sowing numbers P2, P3, and P4 are excluded from the leaf area analysis. Values in the parenthesis contain a standard error of the mean (\pm).

Abbreviations: ICP, ICRISAT pigeonpea; QPL, Queensland pigeonpea line.

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. ns, not significant.

TABLE 4 Genotypic differences in pigeonpea canopy extinction coefficient across planting dates at Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons.

Season	Sowing No	Extinction coefficient (k)		
		Quest	QPL 1001	ICP 14425
S1	P1	0.54***	0.74***	0.59**
S2	P5	0.74**	0.81**	0.67**
S2	P6	0.60**	0.72**	0.73**
S2	P7	0.71**	0.90**	0.80**
Mean	0.65		0.79	0.79
Sowing date (E)	44%***			
Genotype (G)	53%***			
G \times E	2%ns			

Note: S1, season 1; S2, season 2. Sowing numbers P2, P3, and P4 are excluded from the leaf area and radiation interception analysis.

Abbreviations: ICP, ICRISAT pigeonpea; QPL, Queensland pigeonpea line.

** $p < 0.01$. *** $p < 0.001$. ns, not significant.

3.5 | Crop growth rate, pod growth rate and partitioning

Planting dates had a significant effect on (CGR—TDM per unit of accumulated GDD) and pod growth rate (PGR—pod DM per unit of accumulated GDD) ($p < 0.001$), resulting in differences in TDM, yield, and HI.

In this study, DM partitioning varied significantly across the environment, particularly low yield partitioning that occurred in P6 (November 15, 2018) (Figure 2). There were significant differences among genotypes in rate of reproductive DM growth over sampling dates, resulting in variability in partitioning and in final yield across sowing dates.

The dynamics of DM accumulation and partitioning between stem, leaves, and pods during the post-flowering phase, as a function of cumulative thermal time (°Cd) by partial least square model, revealed differences among genotypes across sowing dates (Table 5).

The slope of the partial least square regression model (β_1) represents the post-flowering growth rates ($g^\circ Cd^{-1}$) of CGR, stem growth rate, leaf growth rate, and PGR. The higher PGR ($>0.6 g m^{-2} ^\circ C^{-1}$) was recorded in P1, P2, and P7, and the lowest was in P6 ($0.33 g m^{-2} ^\circ C^{-1}$). Developing pods significantly contributed to the post-flowering CGR ($0.6 g m^{-2} ^\circ C^{-1}$) followed by the stem ($0.41 g m^{-2} ^\circ C^{-1}$).

3.6 | Total dry matter and grain yield

Analysis of variance showed that total above-ground TDM differed significantly across planting dates ($p < 0.001$). In P1, P5, P6, and P7, planted in the warmer season, produced TDM of $>10 t ha^{-1}$ (Table 6). The mean TDM produced in P1 and P7 plantings that is, $13.3 t ha^{-1}$ and $12.9 t ha^{-1}$, respectively, were higher versus $9.8 t ha^{-1}$ in P2, $10.4 t ha^{-1}$ in P5 and $10.6 t ha^{-1}$ in P6 plantings. A reduction of TDM was observed in P5 and P6 plantings for all the genotypes. A lower TDM ($1.2 t ha^{-1}$) response was observed in P4 sowing which was $<10\%$ of the highest TDM. GY and HI were also significant between sowing dates ($p < 0.001$). The highest yield of $4.1 t ha^{-1}$ was recorded in P1, followed by $3.7 t ha^{-1}$ in P2. Genotype Quest and ICP 14425 achieved a 20% higher GY than QPL 1001. Harvest indices were consistent among genotypes with an average of 26%. The highest HI of 38% was recorded in P2 (Table 6).

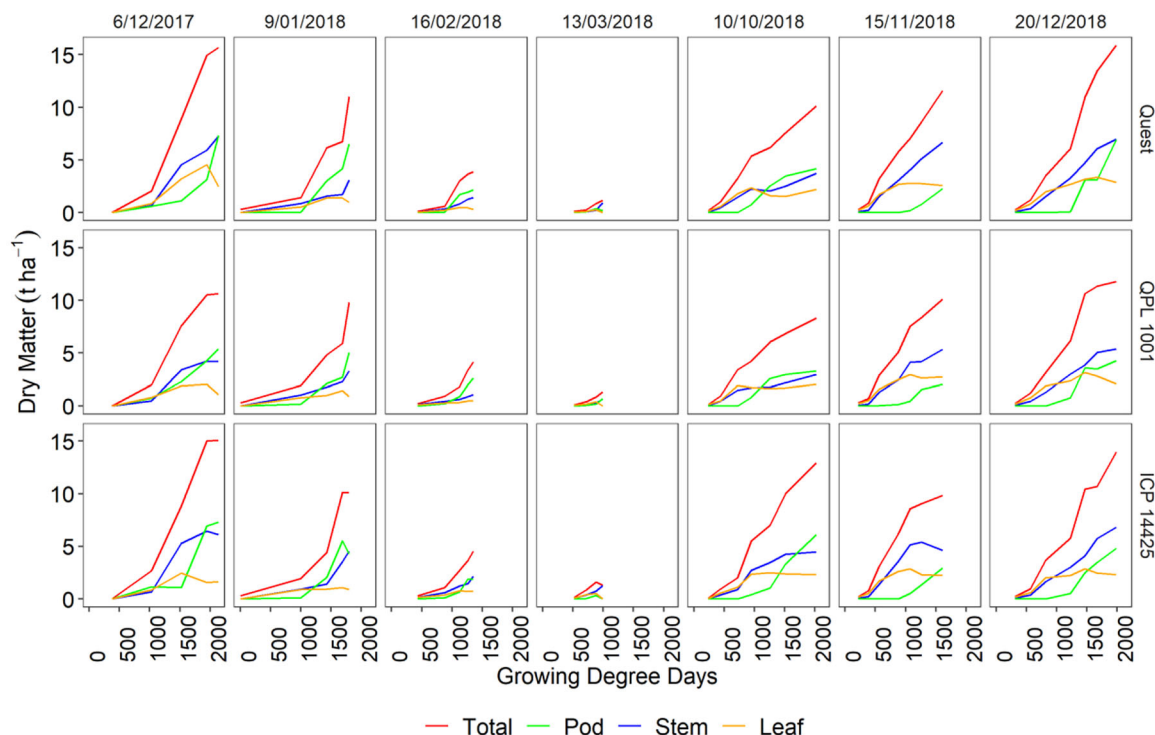


FIGURE 2 Post-flowering total dry matter (TDM), pod, stem and lead dry matter accumulation in three pigeonpea genotypes at seven planting dates at Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons.

3.7 | Yield components

Mean values of yield components (mature pods per plant, pod length, seeds per plant, 100-seed weight and shelling %) across planting dates (environments) were 155 per plant, 5.8 mm, 4.6, 11.1 g and 73%, respectively. Yield components of mature pods per plant, pod length, 100-seed weight and shelling % ratio were significant for the growing environment. No differences were apparent in the number of seeds/pods across planting dates, although seeds/pods varied among genotypes ($p < 0.001$). Similarly, there were no significant genotypic differences in the number of mature pods per plant. The differences in pod length, 100-seed weight and shelling % were significant for genotype, environment, and $G \times E$ interactions (Table 7).

3.8 | Relationship between yield and yield components

Given the coefficients shown in Table 8, a positive association existed between GY and mature pod number, seeds per pod, and 100 seeds weight. However, pod length was negatively correlated with yield (-0.14). The number of pods per plant among all traits had a strong positive correlation (0.72^{***}) with GY, followed by seeds/pods (0.31^{**}) and contributed to the yield performance of genotypes ($p < 0.001$). No relation-

ship was evident between shelling % and other components (Table 8).

3.9 | Relationship between grain yield, leaf area duration, and radiation use efficiency

The $LAD_{(max)}$ ($^{\circ}Cd$) of pigeonpea genotypes was positively correlated with seasonal $RUE_{(S)}$ ($g MJ^{-1} m^{-2}$) ($R^2 = 0.44$), and the relationship was stronger for post-flowering (reproductive) $RUE_{(R)}$ ($R^2 = 0.76$) (Table 9). Our study confirmed the yield of pigeonpea genotypes was positively and significantly correlated with $LAD_{(max)}$ ($R^2 = 0.81$) and reproductive $RUE_{(R)}$ ($R^2 = 0.83$) (Figure 3).

3.10 | Relationship between grain yield, pre- and post-flowering CGR

Results showed that the growth rate of pod DM varied significantly across planting dates ($p < 0.05$). In particular, the low growth rate that occurred in P6. There were significant differences among genotypes in the partitioning of DM to GY, resulting in variation in final yield across planting dates ($p < 0.001$). GY positively and significantly correlated with pre-flowering CGR and TDM at harvest ($R^2 = 0.51$ and 0.53) (Figure 4).

TABLE 5 Partial least square regression model describing post-flowering total dry matter (CGR) partitioned into stem, leaf and pod as a function of dry matter (g m^{-2}) and accumulated growing degree days ($^{\circ}\text{Cd}^{-1}$) for three pigeonpea genotypes and seven planting dates in at Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons.

Plantings	Genotype	Crop growth rate		Stem growth rate		Leaf growth rate		Pod growth rate	
		β_1	R^2	β_1	R^2	β_1	R^2	β_1	R^2
P1	Quest	1.27a	0.98	0.53a	0.84	0.48a	0.96	0.53a	0.72
	QPL 1001	0.79b	0.92	0.34b	0.86	0.22b	0.75	0.41b	0.94
	ICP 14425	1.18c	0.96	0.50a	0.83	0.33c	0.98	0.63c	0.80
	Mean	1.08		0.46		0.34		0.63	
P2	Quest	1.05a	0.86	0.21a	0.63	0.21a	0.95	0.74a	0.94
	QPL 1001	0.85b	0.84	0.26a	0.88	0.05b	0.68	0.53b	0.85
	ICP 14425	1.08a	0.87	0.45b	0.82	0.01c	0.90	0.62c	0.81
	Mean	0.99		0.31		0.09		0.63	
P3	Quest	0.71a	0.87	0.24a	0.91	0.06a	0.85	0.45a	0.77
	QPL 1001	0.69a	0.88	0.14b	0.90	0.03b	0.91	0.51b	0.86
	ICP 14425	0.72a	0.89	0.29a	0.86	0.09c	0.85	0.41a	0.66
	Mean	0.71		0.22		0.06		0.46	
P4	Quest	0.31a	0.70	0.30a	0.77	0.06a	0.94	NA	NA
	QPL 1001	0.34a	0.49	0.17b	0.63	0.09b	0.86	NA	NA
	ICP 14425	0.18b	0.39	0.32a	0.90	0.12b	0.93	NA	NA
	Mean	0.28		0.26		0.09			
P5	Quest	0.46a	0.87	0.15a	0.72	0.18a	0.58	0.30a	0.82
	QPL 1001	0.37b	0.87	0.12a	0.83	0.16a	0.64	0.21b	0.96
	ICP 14425	0.71c	0.93	0.16a	0.75	0.25b	0.91	0.55c	0.94
	Mean	0.51		0.14		0.20		0.35	
P6	Quest	0.80a	0.87	0.49a	0.83	0.32a	0.93	0.32a	0.87
	QPL 1001	0.65b	0.83	0.36b	0.77	0.34a	0.96	0.27b	0.79
	ICP 14425	0.45c	0.64	0.41c	0.52	0.34a	0.93	0.40c	0.91
	Mean	0.63		0.32		0.33		0.33	
P7	Quest	1.26a	0.92	0.39a	0.60	0.26a	0.95	0.83a	0.92
	QPL 1001	0.68b	0.66	0.33b	0.87	0.25a	0.95	0.41b	0.67
	ICP 14425	0.99c	0.87	0.52c	0.83	0.23a	0.75	0.55c	0.92
	Mean	0.98		0.41		0.25		0.60	

Note: P1–P7 represents time of sowing; β_1 is the slope of the regression equation, which represents the growth rate ($\text{g m}^{-2}\text{Cd}^{-1}$). Means with the same letter are not significantly different ($p < 0.05$).

Abbreviations: ICP, ICRISAT pigeonpea; QPL, Queensland pigeonpea line.

4 | DISCUSSION

Crop performance depends on its ability to capture solar radiation and convert it into biomass and GY (Angadi et al., 2022; Ayaz et al., 2004). The leaf area development, interception of PAR, the RUE in the conversion of that radiation to biomass, and the partitioning of biomass to economic yield can be related to the GY differences in crops under an unrestricted environment (Monteith, 1981). The growing environment plays an important role in determining crop yield. The interaction between genotype and growing environment is critical in optimizing planting windows and, hence, maximizing GY. This study aimed to understand the dynamics of productivity

in relation to vegetative growth and reproductive development in pigeonpea genotypes under different planting seasons.

4.1 | Dynamics of leaf area development, radiation interception, and radiation use efficiency on above-ground total dry matter growth and grain yield development across planting dates

The major constraint in commercialization and widespread production in pigeonpea is low GY potential. The growing environment greatly influences crop growth, leading to

TABLE 6 Analysis of variance (ANOVA) of total dry matter (TDM), grain yield and harvest index (HI) across different times of sowings and their significance of three pigeonpea genotypes at Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons.

Season	Plantings	TDM (t ha ⁻¹)	Grain yield (t ha ⁻¹)	Harvest index
S1 (2017/2018)	P1	13.3a	4.1a	0.32a
	P2	9.8c	3.7b	0.38b
	P3	4.2d	1.2e	0.28c
	P4	1.2e	NA	NA
S2 (2018/2019)	P5	10.4bc	2.8c	0.27c
	P6	10.6b	1.7d	0.17d
	P7	12.9a	2.8c	0.22e
Mean		8.9	2.7	0.26
Genotype				
Quest		10.2a	3.0a	0.27a
QPL 1001		8.3b	2.5b	0.26a
ICP 14425		9.9a	2.8a	0.26a
Mean		9.4	2.8	0.26
Percentage of variation (MSS %)				
Sowing date (E)		87%***	88%***	95%**
Genotype (G)		10%**	7%**	1% ^{NS}
G × E		3%**	2%**	4%**
<i>E_a</i> (%)		6.9	7.2	6.9
<i>E_b</i> (%)		6.1	10.2	9.4
<i>n</i>		72	63	63

Note: Values followed by different letters differ significantly from one another ($p < 0.01$). Treatment variabilities were explained by the percentage of mean sums of the square. *E_a* and *E_b* were main-plot and sub-plot errors.

Abbreviations: ICP, ICRISAT pigeonpea; QPL, Queensland pigeonpea line.

*** $p < 0.001$; ** $p < 0.01$.

TABLE 7 Mean values of pigeonpea yield components such as number of pods per plant, pod length (mm), number of seeds per pod, 100-seed weight and shelling % from field experiments conducted at Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons.

Plantings	Pods per plant	Pod length (mm)	Seeds per pod	100-Seed weight (g)	Shelling %
P1	240a	5.1d	4.7ab	12.6a	0.76a
P2	189b	6.3a	5.0a	11.2b	0.76a
P3	52d	6.1ab	4.5b	11.7b	0.80b
P5	163b	5.6c	4.6b	10.1c	0.70c
P6	106c	5.9b	4.6b	10.9b	0.73d
P7	185b	6.1ab	4.6b	11.7b	0.66e
Mean	155	5.8	4.6	11.1	0.73
N	63	63	63	63	63
Date of planting (E)	87%**	37%**	10% ^{ns}	12%**	36%**
Genotype (G)	5% ^{ns}	54%**	82%**	85%**	28%**
G × E	8%**	9% ^{ns}	8% ^{ns}	3%**	36%**
<i>E_a</i> %	18.2	4.8	6.3	5.4	0.8
<i>E_b</i> %	19.2	9.5	8.2	5.5	2.0

Note: Values followed by different letters differ significantly from one another ($p < 0.05$). Treatment variabilities were explained by the percentage of mean sums of the square. *E_a* and *E_b* were main-plot and sub-plot errors.

*** $p < 0.001$; ** $p < 0.01$. ns, not significant.

TABLE 8 Pearson's correlation coefficients among yield components with grain yield of pigeonpea field experiments conducted at Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons.

Components	Number of pods/plant	Pod length (mm)	Number of seeds/pods	100-seed weight (g)	Shelling %	Grain yield (t ha ⁻¹)
Number of pods/plant	1.00	-0.36**	0.13ns	-0.10ns	-0.11ns	0.72***
Pod length (mm)		1.00	0.48***	0.20 ^{NS}	-0.13ns	-0.14ns
Number of seeds/pod			1.00	0.20 ^{NS}	-0.06ns	0.31**
100-Seed weight (g)				1.00	-0.04ns	0.17*
Shelling %					1.00	0.13*
Grain yield (t ha ⁻¹)						1.00

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. ns, not significant.

TABLE 9 Summary of partial least-square regression analysis of leaf area duration ($LAD_{(max)}$, °Cd), seasonal radiation-use efficiency ($RUE_{(s)}$, g MJ⁻¹), radiation-use efficiency during reproductive phase ($RUE_{(R)}$, g MJ⁻¹) and (k) extinction coefficient of pigeonpea field experiments conducted at Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons.

Relationship	Regression equation	Coefficient of determination (R^2)
$LAD_{(max)}$ and $RUE_{(s)}$	$RUE_{(s)} = 0.001 LAD_{(max)} - 0.02$	0.44*
$LAD_{(max)}$ and $RUE_{(R)}$	$RUE_{(R)} = 0.001 LAD_{(max)} - 0.42$	0.76**
$LAD_{(max)}$ and yield	$Yield = 0.004 LAD_{(max)} - 2.37$	0.81**

** $p < 0.01$; * $p < 0.05$.

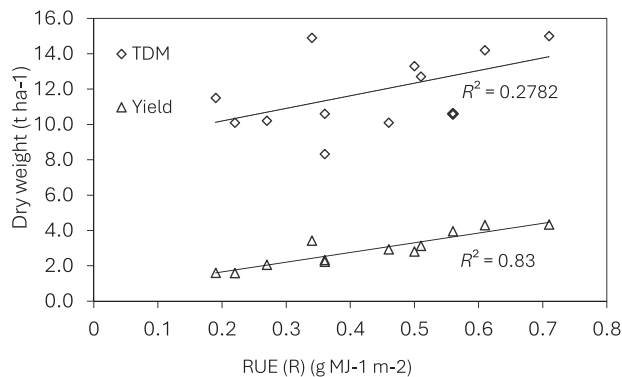


FIGURE 3 Relationship between grain yield (t ha⁻¹), total dry matter (t ha⁻¹) and radiation use efficiency (reproductive) ($RUE_{(R)}$ —g MJ⁻¹ m⁻²) for three pigeonpea genotypes grown at Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons. TDM, total dry matter.

substantial variations in GY. Manipulation of the growing environment can influence leaf area development and consequently impact interception of PAR, DM production, and GY and quality (Chauhan et al., 1998). Previous studies using traditional pigeonpea genotypes in Australia reported a significant effect of the growing environment on leaf area development in terms of LAI and LAD (canopy closure) (Akinola & Whiteman, 1974). This was consistent with studies

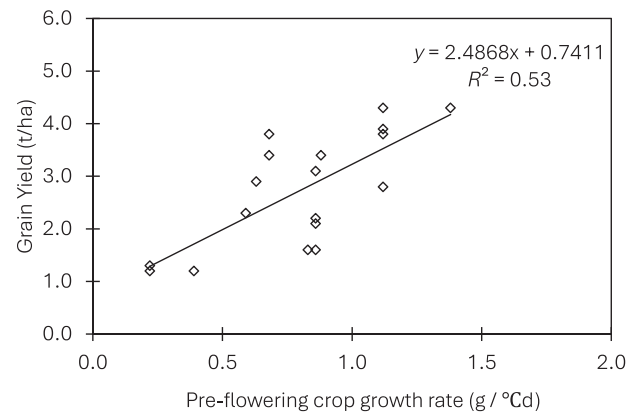


FIGURE 4 The relation of grain yield with pre-flowering crop growth rate in metric tons per degree day (°Cd) across six sowing dates and three pigeonpea genotypes at Gatton Campus, the University of Queensland, Australia, in 2017/2018 and 2018/2019 summer seasons.

on different legumes such as cowpea (*Vigna unguiculata*) and peanut (*Arachis hypogea*). Bell et al. (2008) found that differences in PAR interception accounted for most of the variation in canopy development. Differences in DM production among genotypes and growing environments could be accounted for by the effects of variability in LAI, fraction intercepted radiation, and RUE. Manipulating planting dates can influence the early attainment of the maximum LAI, which leads to

early canopy closure. The crop planted in warmer seasons (P1, P5, P6, and P7) often develop larger canopies associated with longer LAD ($^{\circ}\text{Cd}$), resulting in greater radiation interception and RUE. Results showed that the maximum LAI of pigeonpea ranged from 3.2 to 4.7. These values were consistent with the values reported by Lopez et al. (1997) and Robertson, Carberry, et al. (2001).

Radiation interception also depends on canopy architecture, optical properties of leaves, and plant mechanisms to combat drought conditions measured by extinction coefficient (k). A significant difference in k across seasons indicates pigeonpea has an adaptive mechanism to adjust to changing environmental conditions (Zhang et al., 2014). It was noticed that leaves of pigeonpea were positioned upright to reduce the exposure to excessive radiation during middays and leave more radiation to penetrate the ground. The amount of radiation intercepted depends on the distribution of leaf area in time and space in response to solar radiation and temperature (Sivakumar & Virmani, 1984; Tesfaye et al., 2006). The observed k values for beans, chickpea and cowpea were 0.84, 1.02, and 0.86 under non-stressed conditions, and these values reduced substantially under stressed conditions (Tefaye et al., 2006). The reported value of extinction coefficient (k) 0.69 for traditional pigeonpea genotypes (Sivakumar & Virmani, 1984), was within the range of k value reported in this study (0.54–0.94) with a significant genotypic difference ($p < 0.001$). The genotype with lower LAI and smaller canopy (QPL 1001) had the highest k value. It was reported that GY was negatively associated with k (Chauhan et al., 1998). It is evident that genotypes with a smaller canopy reduced RUE and showed low yield performance (2.5 t ha^{-1}). The higher k value reflected open vertical canopy with smaller leaves and fewer branches is generally associated with decreased radiation interception. Presence of genotypic differences in k values confirmed that differences in radiation interception often depend on LAI. Canopy architecture and RUE can be improved through breeding by developing genotypes with higher LAI and closed canopy.

4.2 | Genotypic differences in leaf area development, radiation interception, and radiation use efficiency on aboveground total dry matter growth and grain yield development

RUE is defined as the quantity of DM produced per unit of intercepted radiation (Geethika et al., 2022). Higher radiation interception and RUE often led to higher DM production in warmer seasons and are advantageous during the post-flowering phase to mobilize the developing pods. Reported values of RUE for soybean (*Glycine max*), mung bean (*Vigna radiata*), and cowpea (*Vigna unguiculata*) were 0.88, 0.94 and 1.05 g MJ^{-1} , respectively (Geethika et al., 2022; Muchow,

1985). Computed RUE for pigeonpea in this study ranged from 0.87 to $1.53 \text{ g MJ}^{-1} \text{ M}^{-2}$, which was influenced by planting dates. The average RUE remained higher during vegetative growth (pre-flowering) and declined near the pod-filling phase. This result confirms the finding in chickpeas that RUE dropped from $1.3 \text{ g MJ}^{-1} \text{ M}^{-2}$ before flowering to $0.96 \text{ g MJ}^{-1} \text{ M}^{-2}$ (Lake & Sadras, 2017). The reduction in RUE during pod filling could be associated with mobilization of leaf assimilates to the reproductive structures and with the loss of biomass due to leaf senescence (Grover & Sinha, 2006). Our study confirmed that yield of pigeonpea genotypes was positively correlated with LAD and $\text{RUE}_{(\text{S})}$. The relationship was stronger for $\text{RUE}_{(\text{R})}$ (post-flowering), which implies maintaining a larger canopy is advantageous, especially during the grain-filling period.

4.3 | Association between grain yield and crop growth rate, pod growth rate, and partitioning across planting dates

The slopes of partial regression analysis (PLS) give rise to crop and pod growth rates as an indicator of GY. Conversely, CGR ($\text{g } ^{\circ}\text{C}^{-1}$) can be defined as the ratio of intercepted radiation and accumulated GDD (Rachaputi et al., 2018). The slopes of the regression relating to stem DM, leaf DM, and pod DM represent the rate at which the DM is partitioned into each component. The ratio between PDG (vegetative) and CGR (reproductive) was defined as partitioning (Reynolds et al., 2012). It was apparent that stem and leaf DM were equal during the pre-flowering phase (63 g m^{-2} and $58\text{--}0.34 \text{ g m}^{-2}$, respectively). However, the stem continued to accumulate DM at a higher rate ($0.14\text{--}0.52 \text{ g } ^{\circ}\text{C}^{-1}$) during the post-flowering phase and hence, the stem became a competitive sink for developing pods. Reduced leaf growth was observed in P2, P3, and P4 most likely because of shorter day length and lower temperature. The highest growth rates of these plant components were observed in December sowings in both seasons. This ontogenetic effect was most prominent in warmer seasons (Reynolds et al., 2012).

It was expected that the growth of the vegetative sink (leaves and stem) would decline during reproductive development to allow rapid growth of the reproductive sink (pods). However, slopes of the partial regression line were positive for all genotypes across sowing dates, indicating that the existence of competition between vegetative and reproductive sinks in DM partitioning. Yet, the lower reproductive sink strength ($0.33 \text{ g } ^{\circ}\text{C}^{-1}$) was observed in sowing date P6, most likely the effect of higher temperature on anthesis (Figure 2).

It was apparent that genotypes differed in DM partitioning or allocation of photosynthetic assimilates into developing pods. Greater partitioning was observed in the determinant genotype (QPL 1001 and Quest) than indeterminate

(ICP 14425). High GY can be achieved by establishing a larger canopy before flowering. In this case, developing pods use available assimilates, leading to the cessation of stem and leaf development (Hearn, 1972). Indeterminate growth habits continued vegetative growth, providing new nodes and each node produced flowers. In this growth habit, reproductive growth competes with the initiation of new nodes for assimilation (Williams & Saxena, 1991). However, increased vegetative growth results in prolonged source activity to produce photosynthetic assimilates and current assimilates can be partitioned into the vegetative and reproductive sink. Determinant growth habits could be useful in environments where extensive vegetative growth occurs, where post-flowering vegetative growth is restricted (Anbessa et al., 2006).

In our study, the growing environment had a significant impact on crop and pod growth rates ($p < 0.001$), leading to differences in TDM, GY, and HI at harvest. The average gain yield was 2.7 t ha^{-1} , higher than previously reported values ($1.3\text{--}1.7 \text{ t ha}^{-1}$) (Chauhan et al., 1999). In contrast, the HI reported here (0.26) was low compared to mungbean (0.3) and soybean (0.5) (Chauhan & Williams, 2018). In addition, we found no genotypic differences in HI suggesting the dynamics of yield development maintain a balance between biomass and yield, which is controlled by genetic factors.

4.4 | Relationship between yield and yield components

In addition, we found no genotypic differences in pods per plant. Further, genotypes contributed the highest percentage of variability for seeds per pod and 100-seed weight, suggesting these traits are inheritable and relatively stable across environments (Table 7). A positive association existed between GY and pods per plant, seeds per pod, and 100-seed weight. Substantial variability in pods per plant across planting dates was evident for yield instability due to the growing environment (Chand et al., 2014). These results were consistent with earlier studies on pigeonpea (Chauhan & Williams, 2018; Egbe et al., 2013). The results of this study reflect that differences in yield were attributed to the growing environment and genetic make up of the accessions and genotype \times environment interaction effect. This information will be helpful in selection of high-yielding genotypes adapted to different environments.

4.5 | Implications for improving agronomic practices and potential yield

Updated information provided in this study on the physiology of yield development and its implications on potential growth and yield, the quantified effect of growing envi-

ronment is useful to widen pigeonpea into new production environments. Reddy et al. (2011) reported pigeonpea is an inherently drought-resistant crop extensively grown in arid and semi-arid regions.

Recent research on pigeonpea in Australia also identified its high production potential ($>4 \text{ t ha}^{-1}$) in subtropical regions (Rachaputi et al., 2018) as a good long-season summer legume for farmers in Queensland. The mean yield potential of pigeonpea genotypes in this study ranged between 1.2 and 4.1 t ha^{-1} depending on planting date. Higher yield potential occurred with early summer planting (October–December).

Quantitative knowledge of the subtle effect of environment and genotype is therefore required to optimize the genotypic selection and time of planting to achieve high productivity. For example, plantings made in late summer (P2 and P3) showed slower growth and reproductive development due to cooler night temperatures (April–June). However, other factors like photoperiod and probable water limitations for dryland crops and detrimental effects of high temperature and subsequent heatwaves during flowering and pod development might affect pollination and GY. The effect of high temperature on pod set was reported in cowpea (Porch & Hall, 2013) and mungbean. In this study, reduced CGR was observed in P2 ($0.09 \text{ g } ^\circ\text{Cd}^{-1}$) and P3 ($0.06 \text{ g } ^\circ\text{Cd}^{-1}$), most likely because of shorter daylength and lower temperature.

Furthermore, this study underscores key physiological parameters that can be modified by manipulating planting windows to achieve high productivity in pigeonpea. Hence, it is likely that crops planted in early summer are at their higher potential to produce maximum LAI, longer LAD, and greater RUE (Table 3). Our study confirmed that yield potential of pigeonpea genotypes was highly correlated with post-flowering RUE ($R^2 = 0.83$). The study suggests that maintaining an optimum canopy during the reproductive stage is instrumental for yield development.

The canopy extinction coefficient (k) is another factor that can be manipulated to improve RUE and productivity through a systematic selection of genotypes, which suit the environment. A higher k value indicates most of the radiation penetrated through the canopy. The genotype with lower LAI and smaller canopy (QPL 1001) had the highest k value. GY was negatively associated with k . It is evident that genotypes with a smaller canopy reduced RUE and showed low yield performance (Hughes & Keatinge, 1983; Sivakumar & Virmani, 1984; Tesfaye et al., 2006). Comparing growth rates and assimilate partitioning among plant organs (stem, leaf, and pods) indicated a significant effect of the growing environment. The highest pre-flowering CGR and longer vegetative period occurred in planting in early December 2017 (P1), resulting in high TDM and GY. Conversely, for the crop planted in late December 2018, these values were found to be different; presumably, the flowering ontogeny coincided with high temperature ($>35^\circ\text{C}$).

5 | CONCLUSION

Results provided updated information on physiological determinants of crop productivity in pigeonpea under subtropical conditions. Pigeonpea genotypes were efficient in conversion of PAR into grains in warmer seasons. GY was positively and significantly related with the quantity and rate of DM accumulation during pre-flowering. Higher RUE during reproductive phase contributed significantly to improving reproductive development in pigeonpea genotypes. Therefore, achieving larger canopy before flowering and maintaining it during reproductive phase are instrumental for higher productivity. Understanding the dynamics of productivity will help optimize agronomic practices which improve the performance of pigeonpea in subtropical regions where crop production is often influenced by cooler weather.

AUTHOR CONTRIBUTIONS

Sabampillai Mahendraraj: Conceptualization; data curation; investigation; methodology; project administration; software; visualization; writing—original draft; writing—review and editing. **Marisa Collins:** Conceptualization; methodology; supervision; validation; writing—review and editing. **Yash Chauhan:** Conceptualization; methodology; supervision; writing—review and editing. **Vincent Mellor:** Data curation; formal analysis; software. **Rao C. N. Rachaputi:** Conceptualization; funding acquisition; methodology; resources; supervision; validation; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data will be available on request.

ORCID

Sabampillai Mahendraraj  <https://orcid.org/0000-0002-5308-8558>

Marisa Collins  <https://orcid.org/0000-0002-5571-9114>

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