Genotypic Variation Studies in Biomass Partitioning Patterns during Post-flowering Stages under the Late Sown Conditions of Chickpea (*Cicer arietinum* L.) Germplasm

R. G. Vyshnavi [a++*], R. K. Samaiya [a#], R. Shiv Ramakrishnan [b†], Anita Babbar [c‡], Karishma Behera [c], Anubha Upadhyay [a] and Preeti Sagar Nayak [a]

[a] Department of Crop Physiology, Jawaharlal Nehru Krishi Vishwa Vidyalaya, Jabalpur, Madhya Pradesh, 482004, India.
[b] Seed Technology Research, Jawaharlal Nehru Krishi Vishwa Vidyalaya, Jabalpur, Madhya Pradesh, 482004, India.
[c] Department of Plant Breeding and Genetics, Jawaharlal Nehru Krishi Vishwa Vidyalaya, Jabalpur, Madhya Pradesh, 482004, India.

Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

Original Research Article

[++] *Ph.D. Research Scholar;*
[#] *Professor and Head;*
[†] *Scientist;*
[‡] *Principal Scientist;*
Corresponding author: E-mail: gnanavaishnavi@gmail.com;

ABSTRACT

This study conducted during the 2021-2022 year under field conditions investigates the genotypic variation in biomass partitioning among different chickpea genotypes during post-flowering stages, with a specific emphasis on late sown conditions. The main aim of the study was to elucidate the efficiency of resource allocation toward pod production, measured by the pod harvest index. This research enhances understanding of chickpea performance under delayed sowing conditions by examining genotypic variations in key parameters during critical post-flowering stages, specifically pod filling and seed filling. Biomass partitioning in branches and pods varied considerably during both growth stages, with branches playing a crucial role in pod development during pod filling. The transition from pod filling to seed filling stage resulted in increased biomass partitioning in pods, highlighting their importance as storage organs for seed development. Seed yield exhibited significant variability among genotypes, with some surpassing 2000 kg/ha, while pod harvest index ranged from 35.62% to 70.48%, indicating differences in resource allocation efficiency. Regression analysis showed varying degrees of association between biomass partitioning and pod harvest index, with seed yield and pod harvest index, biomass partitioning in pods exhibiting the highest explanatory power during seed filling. By studying the adaptation of plants towards biphasic and allometric allocation patterns during unfavorable conditions can result in developing the resource use efficient climate resilient varieties. These findings contribute to our understanding of crop productivity under varying environmental conditions and inform strategies for optimizing chickpea yield and resilience.

1. INTRODUCTION

Climate change amplifies the occurrence and effect of the abiotic stresses on plant, posing a significant threat to crop production. Among these stresses, heat stress stands out as a limiting factor for plant development leading to yield penalty. Heat stress is characterized by an increase in temperature that surpasses a specific threshold over a period, resulting in irreversible damage to plant growth [1,2]. The impact of heat stress results in protein denaturation, membrane damage, reduction in pollen viability and anther structure anomalies, degradation and reduction of photosynthesis. These detrimental effects primarily stem from the negative repercussions of heat stress on photosynthetic activity. Crop development exhibits a positive linear relationship with the net photosynthetic rate [3] influencing dry-matter accumulation [4] and allocation (biomass partitioning) [5,6]. The carbohydrate partitioning through photosynthesis results to constitute 60% of the total dry matter of the plant [7]. Dry matter accumulation refers to the dynamic process of photosynthesis by which plants accumulate photosynthates in their tissues [8]. Dry matter allocation refers to the process where partitioning of the accumulated dry matter takes place to the different plant organs or tissues. The allocation patterns can vary based upon the different stages of plant growth and in response to environmental conditions such as light, temperature, and water availability [9,10], plant genetics, and nutrient availability [11]. The allocation is not uniform throughout the plant which includes different patterns such as biphasic pattern and allometric. In the biphasic pattern, resources are allocated in two distinct phases or stages of plant growth or development. During the initial phase, often referred to as the "vegetative phase," resources are primarily allocated to support vegetative growth, including the development of leaves, stems, and roots. This phase is characterized by rapid biomass accumulation and expansion of vegetative structures as the plant establishes itself and prepares for reproductive growth. In the second phase, known as the "reproductive phase," resources are redirected towards reproductive structures and functions, such as flowers, fruits, and seeds. This phase typically occurs after the plant has reached a certain level of maturity and environmental conditions are favorable for reproduction. Resources previously allocated to vegetative growth are now reallocated to support reproductive processes, including flower formation, pollination, seed development, and fruit maturation. The biphasic allocation pattern reflects the dynamic resource allocation strategies employed by plants to optimize their growth, reproduction, and survival in response to changing environmental conditions and life cycle stages. The transport of photosynthates from leaves (considered sources)

to the harvestable target organs (referred to as sinks) has a direct impact on the accumulation of dry matter in these organs. This process supports the expansive growth of sink tissues, contributing significantly to both crop yield and quality. Another allocation pattern observed in plants is the "allometric allocation pattern." In this pattern, the allocation of resources is proportional to the size or biomass of the plant or its individual organs. [12]. For example, in allometric allocation, larger plants or plant organs receive a greater proportion of resources compared to smaller ones. The allometric allocation pattern involves root shoot allocation, reproductive allocation, leaf allocation, and storage allocation. Overall, the allometric allocation pattern highlights the scaling relationships between plant size, resource allocation, and physiological processes. The efficient resource allocation and high rates of photosynthesis is needed for more pod setting and retention to pods. In situations where high temperatures reduce the photosynthetic rate, the strategic distribution of assimilated photosynthetic products to different plant organs becomes crucial, significantly influencing pod yield. In late-sown chickpea crops, there may be shifts in biomass partitioning to various organs. The availability of conclusive quantitative data on dry matter accumulation and allocation in chickpea (*Cicer arietinum* L.) currently is inadequate. According to the research conducted by [13] the biphasic distribution of biomass was found to be around 48–51% of the generated biomass was directed towards leaves before flowering stage, while the remaining portion was allocated to stems. However, the study did not provide quantification of biomass partitioning after flowering. Biomass partitioning during vegetative growth in various crops has been reported with the consistent pattern of around 50:50 percent distribution between leaves and stems across various crops, including chickpea [13], faba bean [14], pigeon pea [15], Wheat [4], as well as soybean, mung bean, and cowpea [16]. Achieving high pod setting and retention not only necessitates elevated rates of photosynthesis but also efficient resource allocation to pods. Crop productivity hinges not solely on the accrual of dry matter but also on its efficient distribution to plant components [17]. Despite the importance of this process in heat tolerance, there has been no effort to investigate the impact of varying temperatures on the allocation of photo-assimilates. Such an examination could contribute to a better understanding of the mechanisms underlying heat tolerance. Hence, the study has been conducted to examine the genotypic variation and the effect of environment on the biomass partitioning patterns in chickpea germplasm under late-sown conditions.

2. MATERIALS AND METHODS

The field experiment was conducted during rabi season in the year 2021–22, from December to April, at the experimental farm of the breeder seed production unit which is situated at 22°49' and 20°80' North latitude and 78°21' and 80°58' East longitude, with an elevation of 411.78 meters above mean sea level at Jawaharlal Nehru Krishivishwa Vidhyalay (JNKVV), Jabalpur, Madhya Pradesh. The 40 chickpea genotypes (32 germplasm lines and 8 prominent genotypes) were sown in the randomized block design at late-sown (15–December) conditions. The experiment consisted of three replications, and each plot had a net size of 1.80 m2. The mean temperature during vegetative stage is recorded 25.27°C with minimum 4.8°C while the maximum temperature during reproductive and post reproductive stage was noted to be 30.3°C and 36.8°C under late-sown conditions. Weekly mean values of significant weather parameters throughout the crop season were documented at the Meteorological Observatory of JNKVV, Jabalpur. The observations to be recorded included as dry weight (g) of leaves, stem and pods at post reproductive stages i.e, pod filling (70 days from sowing) and seed filling stages (90 days from sowing). For dry matter production, three consecutive plants were selected randomly from the field and segmented into leaves, main stem, primary branches, and pods. These segments were then placed in an electric oven at 80°C for 48 hours. The dry weight of each plant part, as well as the total dry weight, was recorded individually for estimating dry Biomass portioning. Biomass partitioning is defined as the proportion or percentage of the dry matter allocated in the individual plant part to the total plant part [18]. The collected data was analyzed by using the formulas

$$\text{Biomass partitioning of leaves (\%)} = \frac{\text{Dry weight of leaves}}{\text{Total above ground biomass}} \times 100$$

$$\text{Biomass partitioning of main stem (\%)} = \frac{\text{Dry weight of main stem}}{\text{Total above ground biomass}} \times 100$$

$$\text{Biomass partitioning of branches (\%)} = \frac{\text{Dry weight of branches}}{\text{Total above ground biomass}} \times 100$$

Biomass partitioning of pods (%)

$$= \frac{\text{Dry weight of pods}}{\text{Total above ground biomass}} \times 100$$

$$\text{Pod Harvest Index (\%)} = \frac{\text{Biomass of harvested pods}}{\text{Total above ground biomass}} \times 100$$

3. RESULTS AND DISCUSSION

3.1 Biomass Partitioning in Leaves and Stem during Pod Filling and Seed Filling Stages

Analysis of Variance (ANOVA) results (Table 1) indicates the significant differences among genotypes in biomass partitioning. The biomass partitioning of leaves during the pod filling stage under late sown conditions ranges from 18.62 to 27.20, indicating a considerable span of variability among the genotypes. At the pod filling, the dry matter accumulation was more in leaves due to efficient biomass partitioning around 24.99% where as it was reduced to 10.68 % during the seed filling stage. The observed shifts in biomass partitioning between the pod filling and seed filling stages suggest a biphasic pattern of allocation in chickpea plants in the studied germplasm, as plants transition from vegetative to reproductive growth. The decrement percentage in biomass partitioning between the pod filling stage and the seed filling stage is approximately 57.25%. The decreasing trend of the accumulation is attributed due to the restricted leaf area expansion, and limited function of leaves as active sinks during pod filling stage. The observed mean biomass partitioning of leaves is consistent with the findings reported by [5,19]. Genotype G33 exhibited high biomass partitioning of leaves (27.20%), suggesting its distinct physiological characteristic of higher biomass partitioning due to the adaptive response under late sown conditions. During the pod filling stage under late sown conditions, biomass partitioning in stems ranged from 38.00% (G12) to 45.29% (G13), showcasing considerable variability among genotypes. However, during the seed filling stage, this range narrowed, with values ranging from 15.92 % to 22.34 %. This decrease in biomass partitioning suggests a substantial reduction in dry matter accumulation in stems as the plant progresses from the pod filling to the seed filling stage. The decrement percentage in biomass partitioning between these two stages is approximately 59.74%, which parallels the trend observed in leaf biomass partitioning suggesting a shift in resource allocation towards seed development. The observed variability in stem biomass partitioning underscores the diverse physiological responses of chickpea genotypes to late sown conditions. While all the genotypes exhibited a half fold decrease in biomass production in stems during the seed-filling stage the genotype G2 exhibited lowest (15.92%) accumulation of dry matter during seed filling stage in stem. Results are in similar with the findings reported by [20, 21].

3.2 Biomass Partitioning in Branches and Pods during Pod Filling and Seed Filling Stages

Significant differences in biomass partitioning among genotypes were observed during both the pod filling and seed filling stages in chickpea plants. The potential for stem storage as a sink is determined by factors such as stem length and stem weight density. The decline in dry matter accumulation primarily stems results in decreased production and accumulation of photosynthate in seed [22]. During the pod filling stage, the highest biomass partitioning in branches was recorded at 53.42%, with genotype G33 closely following at 53.00%. In contrast, during the seed filling period, biomass partitioning decreased to 16.09%. This decrement of 69.81% underscores the dynamic nature of biomass allocation during chickpea growth stages. Studies have shown that during the pod filling stage, biomass partitioning in branches tends to be relatively high compared to other plant parts such as stems and leaves [19]. Similar to the findings for leaves and stems, biomass partitioning in branches and pods also exhibits a biphasic pattern during the pod filling and seed filling stages. During the pod filling stage, branches serve as active sinks for resource allocation, supporting pod development through the provision of energy and nutrients. However, during the seed filling stage, there is a decrease in biomass partitioning in branches, indicating a shift towards remobilization of stored reserves to support seed development and maturation. This shift in biomass allocation reflects the plant's priority to maximize seed yield by directing resources towards seed filling. The observed variability in biomass partitioning among genotypes suggests potential allometric relationships between branch length, branch weight density, and biomass allocation in branches and pods. Genotypes exhibiting higher biomass partitioning in branches during the pod filling stage may also demonstrate proportional increases in pod biomass, reflecting allometric patterns of resource allocation.

Table 1. The rate of modification in the biomass partitioning of leaves, main stem, branches, pods of the post reproductive stages under late-sown conditions along with the seed yield and pod harvest index

Germplasm	Biomass partitioning in leaves		Biomass partitioning in main stem		Biomass partitioning in branches		Biomass partitioning in Pods		Seed Yield (Kg/ha⁻¹)	Pod Harvest Index (%)
	PF	SF	PF	SF	PF	SF	PF	SF		
G1: IC 83686	19.09	4.35	38.99	16.42	39.61	16.09	34.61	66.59	448.55	66.59
G2: IC 95100	18.78	4.22	39.33	15.92	37.19	17.09	32.05	66.19	373.2667	66.19
G3: IC 83958	19.38	5.74	38.47	17.15	39.71	21.35	34.87	69.76	770.0833	69.76
G4: IC 27238	19.39	5.47	39.20	17.20	39.28	20.31	35.10	70.41	600.2333	70.41
G5: IC 83346	20.37	5.58	39.00	17.93	39.15	22.25	36.43	69.57	840.7167	69.57
G6: IC83720	19.71	5.96	38.47	17.46	39.35	21.035	35.00	70.88	465.25	70.88
G7: IC 487371	21.17	5.87	39.11	17.85	39.49	22.97	36.16	71.62	777.8	71.62
G8: IC 83374	20.57	5.00	39.12	17.47	40.01	21.16	40.19	68.48	534.4667	68.48
G9: IC 83383	17.41	5.20	39.08	16.43	38.09	17.73	36.58	69.315	510.1167	69.315
G10: IC 486759	20.75	5.10	39.11	17.64	38.23	20.77	36.06	71.395	620.7167	71.395
G11: IC326761	21.20	5.85	39.25	18.68	39.84	21.44	37.99	71.01	696.6667	71.01
G12: IC83448	16.77	4.53	38.00	17.67	38.98	21.16	39.15	66.73	343.9	66.73
G13: IC 83767	24.99	10.68	45.29	20.29	48.81	27.135	48.48	74.73	2058.333	74.73
G14: IC 83474	21.95	6.19	40.63	16.73	42.21	23.86	43.34	74.4	1302.167	74.4
G15: IC 83448	20.85	5.90	39.69	17.55	41.58	23.71	40.47	71.03	892.25	71.03
G16: IC 83537	20.80	5.76	38.97	17.09	39.94	21.47	40.36	72.12	821.95	72.12
G17: IC 83653	21.95	6.02	39.62	18.73	41.88	24.48	42.49	72.48	982.0633	72.48
G18: IC 83677	21.33	5.86	41.43	18.84	42.99	22.68	42.09	72.46	972.745	72.46
G19: IC 83843	21.03	6.00	40.29	16.77	42.23	22.71	42.44	72.49	1054.178	72.49
G20: IC 83892	22.05	5.93	41.40	19.62	44.03	20.68	41.84	72.16	1136.233	72.16
G21: IC 84011	20.42	6.02	40.17	18.01	39.59	24.22	40.51	72.35	843.65	72.35
G22: IC 3171	20.45	6.68	40.73	19.78	41.62	23.65	42.25	72.5	1119.033	72.5
G23: IC 83449	20.23	6.04	41.83	18.24	42.52	21.12	43.48	71.16	821.0833	71.16
G24: IC 83983	18.62	5.98	38.88	17.89	38.99	22.17	37.20	71.26	882.2833	71.26
G25: IC 83811	22.55	5.80	39.01	18.08	43.15	22.13	40.00	72.79	1291	72.79
G26: IC 84049	25.56	10.68	42.10	21.78	47.77	27.42	50.42	75.05	1983.175	75.05
G27: P 554	26.41	10.97	43.76	20.67	52.01	30.64	49.32	76.42	2082.248	76.42
G28: ICC 7855	24.61	10.64	42.47	21.28	45.53	28.06	52.50	75.68	2279.725	75.68
G29: P 558	22.39	6.52	40.53	17.39	42.56	24.66	45.11	72.93	1483.115	72.93
G30: P 556	24.03	5.64	40.49	17.11	41.93	24.11	42.08	70.31	923.56	70.31
G31: IC 251855	22.69	5.56	41.13	17.36	44.35	22.34	44.67	70.16	899.3167	70.16
G32: ICC 4425	21.93	7.59	42.09	19.37	47.14	24.79	44.59	73.42	1905.615	73.42
G33: IC 83985	27.20	10.51	44.32	22.34	53.00	31.63	49.90	74.77	2078.948	74.77

Germplasm	Biomass partitioning in leaves		Biomass partitioning in main stem		Biomass partitioning in branches		Biomass partitioning in Pods		Seed Yield (Kg/ha^{-1})	Pod Harvest Index (%)
	PF	SF	PF	SF	PF	SF	PF	SF		
G34: JG 14	23.22	7.96	41.12	20.07	43.20	25.73	48.37	73.12	1620.4	73.12
G35: JG 36	23.93	7.76	40.57	19.84	44.81	24.9	43.45	73.35	1626.505	73.35
G36: JG 24	24.29	8.91	42.38	19.58	46.08	26.26	43.08	73.38	1887.967	73.38
G37: JG12	23.27	8.76	40.95	19.69	44.47	23.45	43.99	74.51	1721.275	74.51
G38: JAKI 9812	23.24	8.09	41.68	21.38	44.64	24.29	44.89	73.96	1714.005	73.96
G39: JG 315	24.68	8.58	42.84	19.69	45.43	26.06	44.85	74.28	1771.37	74.28
G40: JG 11	23.13	8.88	42.08	20.07	44.95	24.48	51.09	74.12	1714.167	74.12
SEm±	**0.39**	**0.47**	**0.19**	**0.45**	**0.76**	**1.04**	**1.16**	**1.20**	**53.08**	**1.20**
CD	**1.117**	**1.334**	**0.550**	**1.293**	**2.178**	**2.979**	**3.320**	**3.440**	**151.811**	**3.440**

(PF- Pod filling stage, SF- Seed filling stage)
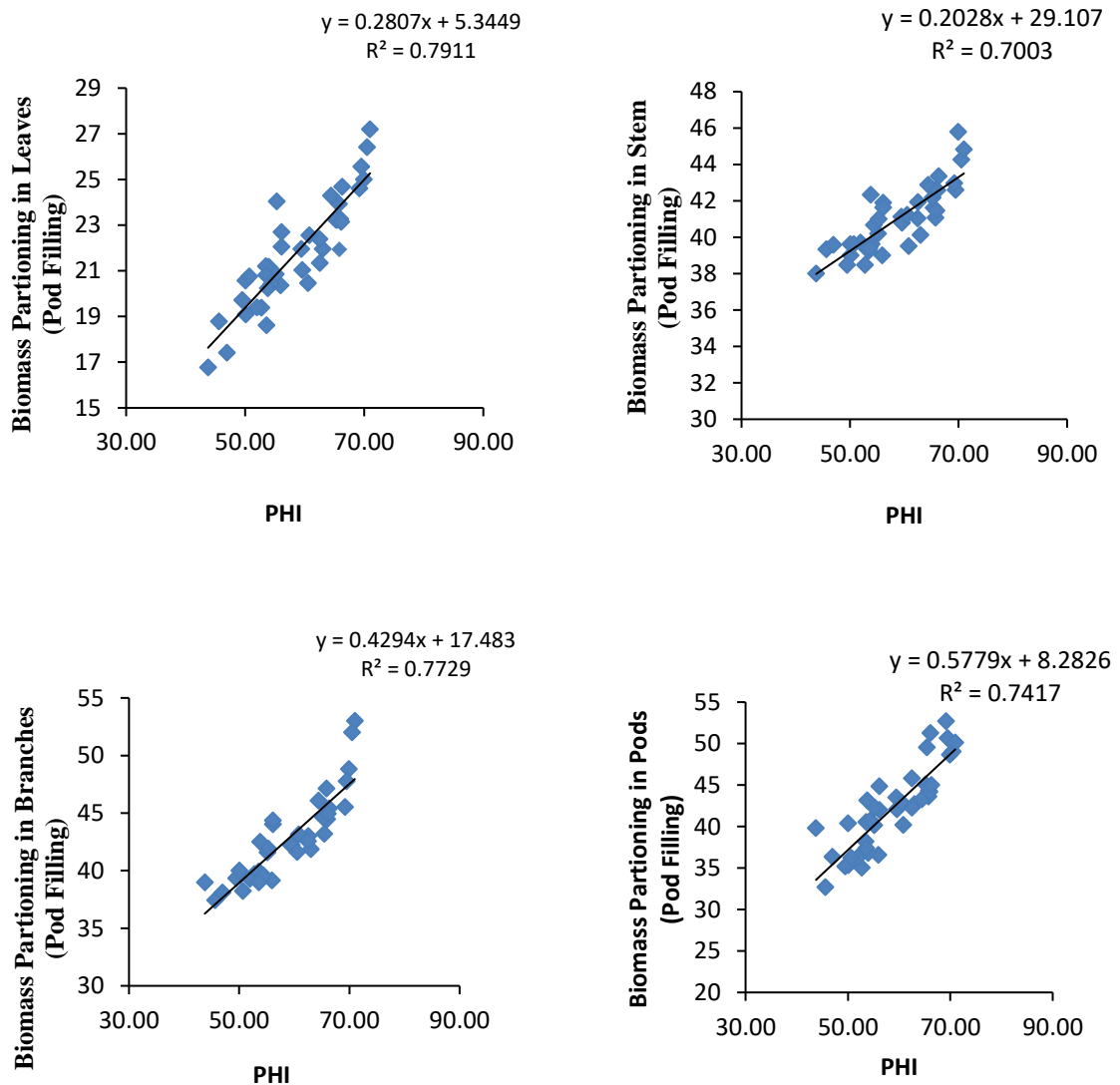
Fig. 1. The relationship between the biomass partitioning in leaves, stem, branches and pods with the pod harvest index (PHI) during the pod filling stage

During the pod filling stage, the biomass partitioning in pods ranged from approximately 32.00% to 52.50%, indicating variability among the samples. The observed variability among genotypes in biomass partitioning in pods emphasizes the genetic diversity and potential for selection of high-yielding varieties with enhanced pod development and seed filling characteristics. The average biomass partitioning during the pod filling stage was approximately 43.55%. During the seed filling stage, the biomass partitioning in pods ranged from approximately 66.19% to 76.42%, with slightly higher values compared to the pod filling stage. The average biomass partitioning during the seed filling stage was approximately 72.90%.

The results are in accordance with [23] the transition from pod filling to seed filling stage resulted in an increase in biomass partitioning in pods by approximately 29.35%. The results are in accordance with [24] the pod wall demonstrates a characteristic growth pattern wherein it undergoes initial development and reaches its final weight before the seeds commence rapid growth.

This phenomenon highlights the sequential nature of pod and seed development in chickpea plants. Specifically, during the early stages of reproductive growth, resources are predominantly allocated towards pod formation and maturation. Once the pod wall has achieved

its full size and weight, resources are subsequently redirected towards seed development, facilitating the accumulation of biomass necessary for seed enlargement and maturation. This sequential growth pattern ensures optimal utilization of resources and contributes to the overall reproductive success and yield potential of chickpea.

3.3 Pod Harvest Index and Seed yield

Seed yield varied considerably among the genotypes, ranging from 373 to 2279.26 kg/ha. These findings underscore the genetic diversity among chickpea genotypes in their ability to produce seeds and allocate resources to pod

development Notably, genotypes such as G28, G27 and G13 followed by G33 exhibited high seed yield, surpassing 2000 kg/ha.

For instance, genotypes with seed yields exceeding 2000 kg/ha include 2084.61 and 2281.26, while genotypes with high pod harvest index values above 65% include 2084.61 and 2281.01. Conversely, some genotypes like G2, G12 and G1 displayed relatively lower seed yield, indicating differences in their productivity under the conditions studied. Pod harvest index, representing the proportion of pod weight to total above-ground biomass, ranged from 35.62% to 70.48%.
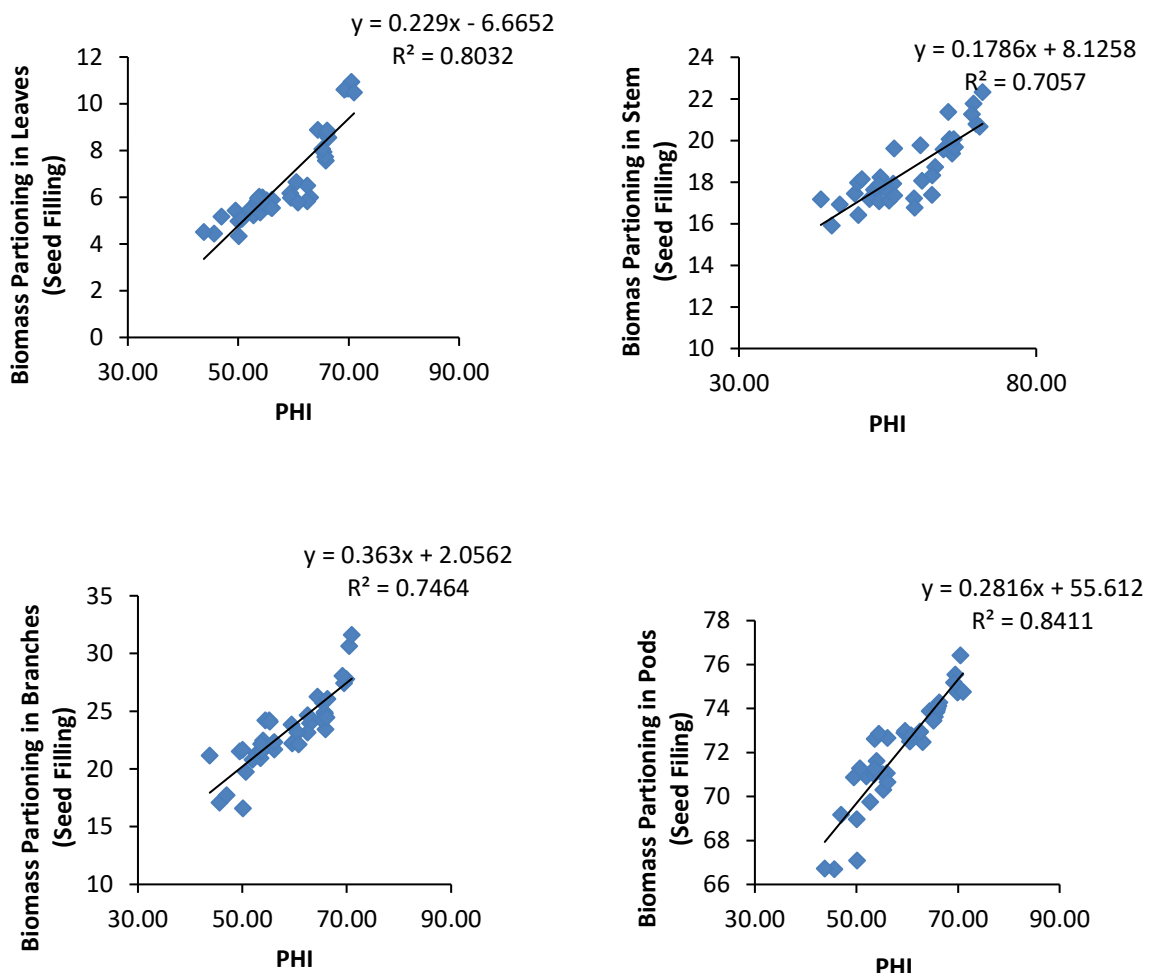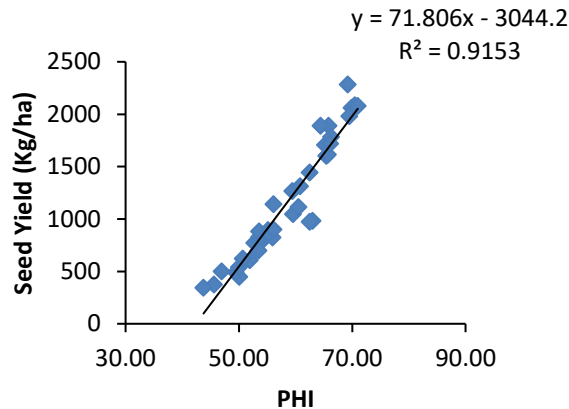

Fig. 2. The relationship between the biomass portioning in leaves, stem, branches and pods with the pod harvest index (PHI) during the Seed filling stage

$$y = 71.806x - 3044.2$$
$$R^2 = 0.9153$$

Fig. 3. The relationship between seed yield with the pod harvest index (PHI)

Genotypes like G27 and G26 demonstrated high pod harvest index values, indicating efficient utilization of resources for pod formation. Conversely, G2 exhibited lower pod harvest index values, suggesting suboptimal pod development relative to total biomass production. The concomitant link exists between pod dry weight and the seed development. Divergent growth rates led to analogous variances in pod dry weight and harvest index, both of which displayed sensitivity to temperature fluctuations. The observed biphasic patterns of biomass allocation during the pod filling and seed filling stages are closely associated with changes in pod harvest index and seed yield. During the pod filling stage, when biomass partitioning in branches and pods is high, there is a corresponding increase in pod harvest index, reflecting the efficient utilization of resources for pod development. As the plants progress to the seed filling stage and biomass allocation shifts towards seed development, there is a subsequent increase in seed yield, indicating successful conversion of biomass into viable seeds. Allometric pattern of biomass allocation may also influence pod harvest index and seed yield, particularly through their effects on pod and seed development. Genotypes exhibiting higher biomass partitioning in branches and pods may also demonstrate proportional increases in pod harvest index and seed yield, reflecting the efficient allocation of resources towards reproductive structures. Conversely, genotypes with lower biomass partitioning in branches and pods may exhibit lower pod harvest index and seed yield, suggesting suboptimal utilization of resources for reproductive purposes.

3.4 Association between Biomass Partitioning in Leaves, Stem, Branches, Pods and Pod Harvest Index during Pod and Seed Filling Stage with Pod Harvest Index

The regression analysis (Fig. 1 and Fig. 2) assesses the relationship between biomass partitioning and pod harvest index during the seed filling stage yielded varying degrees of explanatory power, as indicated by the R^2 values. The R^2 values ranged from 0.700 to 0.791, indicating relatively strong associations between biomass partitioning in different plant parts and pod harvest index during this stage. Notably, biomass partitioning in leaves showed a slightly stronger relationship with pod harvest index ($R^2 = 0.791$) compared to other plant parts followed by branches (0.772), pods (0.741), and stem (0.700). In contrast, the regression analysis conducted during the seed filling stage yielded more stronger associations between biomass partitioning and pod harvest index. The R^2 values ranged from 0.705 to 0.841, with biomass partitioning in pods exhibiting the highest explanatory power ($R^2 = 0.841$). Additionally, the relationship between yield and pod harvest index during this stage showed a relatively higher R^2 value of 0.951 (Fig. 3), suggesting a stronger association between these variables. It's important to consider the complex nature of plant growth and development, as well as other factors that may influence pod harvest index. Overall, the regression analyses provide valuable insights into the relationships between biomass partitioning and pod harvest index during different stages of chickpea growth.

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4. CONCLUSION

The study highlights the dynamic nature of biomass partitioning in different plant parts during pod filling and seed filling stages in chickpea. These findings highlight the complex interplay between plant growth, resource allocation, and reproductive success in chickpea plants. Understanding the biphasic and allometric patterns of biomass allocation can help designing breeding strategies aimed at enhancing seed yield and productivity under optimal and sub-optimal environmental conditions. The observed variability in biomass partitioning traits among genotypes helps designing the breeding strategies for development of chickpea ideotype with enhance biomass partitioning towards leaves and pods at pod filling and seed filling stage, respectively with optimum resource allocation for seed production. Superior genotypes such as G13, G27, G28 and G33 with high biomass partitioning towards leaves at pod filling stage and pods (seed filling stage) which can be utilized for yield enhancement projects in chickpea improvement under optimal and sub-optimal environment.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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