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SHORT RESEARCH ARTICLE

Physio-biochemical trait characterization using generation mean analysis in chickpea (*Cicer arietinum* L.) under timely and late sown conditions

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Abstract

Limited information is available regarding the interaction effects, particularly for physio-biochemical traits under heat stress conditions in chickpeas, which are critical for identifying heat-tolerant genotypes. To address this gap, a field experiment was conducted to study gene effects for various physio-biochemical traits of four specific crosses, namely, RSG-973 × HC-5, RSG-963 × RSG-973, CSJD-884 × Avrodhi and RSG-974 × CSJ-515 during the *rabi* seasons of 2019-20 to 2021-20 under two sowing environments. Results revealed duplicate epistasis for specific traits observed in different cross-environment combinations, such as membrane stability index in RSG-973 × HC-5 under E2 and in CSJD-884 × Avrodhi under both E1 and E2, total chlorophyll content in RSG-973 × HC-5 under E2, carotenoid content in RSG-974 × CSJ-515 under E2, proline content in RSG-974 × CSJ-515 under E1, protein content in RSG-973 × HC-5 under E1, and seed yield per plant in CSJD-884 × Avrodhi under E2. The predominance of additive (d) and/or additive × additive 'i' gene effects, along with significant contributions of non-additive gene effects (h and/or j and/or l), for protein content in RSG-973 × HC-5 under E2 condition. Overall, non-additive gene effects (h, j, and l) were predominant for most traits across the studied crosses under both timely and late-sown conditions.

Keywords: Chickpea, gene interaction, duplicate epistasis, complementary epistasis

Introduction

Among abiotic stresses, high temperature is a major constraint limiting chickpea growth and yield across diverse agro-climatic conditions (Rani et al. 2020). Chickpeas are a cool-season legume that is essential for their nutritional content, but during their reproductive and seed-filling stages, they are sensitive to high temperatures (>32/20°C maximum/minimum) (Devi et al. 2023). Delayed harvesting of preceding crops like maize, sugarcane, rice and sesame often leads to late sowing of chickpeas in India. This exposes the crop to elevated summer temperatures during the grain-filling stage, resulting in reduced grain yields. High temperatures negatively influence critical physiological processes, including photosynthesis, respiration, membrane stability, fertilization, seed maturation, and nutrient uptake (Moore et al., 2021). A clear understanding of gene action, its magnitude, and the genetic variance components is crucial for plant breeders to design effective breeding programs. While diallel and line × tester analyses provide insight into additive and dominant genetic components, they fail to account for non-allelic interactions (Muthoni and Shimelis 2020). Hence, assessing epistatic components alongside

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additive and dominance effects is essential. The knowledge of physiological and biochemical traits, along with their inheritance patterns, is vital for developing heat-tolerant varieties (Ullah et al. 2021). Unfortunately, such information is scarce, particularly for heat-stress conditions.

The experiment was conducted at RARI, Durgapura, Rajasthan, over three consecutive *rabi* seasons of 2019-2020, 2020-2021, and 2021-2022. During the 2019-2020 *rabi* season, four specific crosses-RSG-973 × HC-5, RSG-963 × RSG-973, CSJD-884 × Avrodhi, and RSG-974 × CSJ-515-were made. The seven parents (RSG-973, HC-5, RSG-963, CSJD-884, Avrodhi, RSG-974 and CSJ-515) involved in the crosses were selected on the basis broad range of genetic variability for major yield components. In the subsequent 2020-2021 season, these F1 plants backcrossed with the parents to obtain B1 and B2 generations. By the 2021-2022 season, six generations, namely P1, P2, F1, F2, B1, and B2, from the four crosses were evaluated under a compact family block design (CFBD) across three replications. Two environments-timely sown (E1) and late sown (E2)-were created by sowing on two different dates: 1st-November (E1) and 1st-December (E2) of 2021, respectively. Each block was comprised of 20 rows consisting of two row each of P1, P2 and F1; six rows of F2 and four rows each of B1 and B2 generations. The row length was 3.0 m with plant-to-plant and row-to-row spacing of 15 x 30 cm, respectively. The observations were recorded on five competitive and randomly selected plants from P1, P2 and F1, 10 plants from B1 and B2 and 20 plants from F2 generations in each cross in each replication in both the environments. Data were recorded for various traits, including pollen viability (%), assessed using the acetocarmine stainability test; relative water content (RWC), measured following Slavik's method (1974); membrane stability index (MSI), determined by Sairam et al. (1997); total chlorophyll and carotenoid content, measured by Talebi et al. (2013); proline content (μmol/g), calculated based on Bates et al. (1973); and seed protein content, estimated using Lowry's method (1951). Statistical analysis involved the joint scaling test (Cavalli, 1952) to confirm the additive-dominance model. The three-parameter model of Jinks and Jones (1958) was used when the chi-square test was non-significant, while the six-parameter model by Hayman (1958) was applied.

Generation mean analysis

The results of generation mean analysis indicated that the magnitude and direction of different components (d), (h), (i), (j) and (l) of gene effects were influenced by the environments and also by the parents involved in the crosses. It was observed that the adequacy and inadequacy of the additive-dominance model varied from cross to cross and environment to environment within character. The significant value of the 'm' component of gene effect was observed for all the characters understudied in all the crosses, suggesting that different generations of a respective cross statistically differed. Duplicate epistasis was observed for the membrane stability index in RSG-973 × HC-5 under E2 and CSJD-884 × Avrodhi under both E1 and E2, total chlorophyll content in RSG-973 × HC-5 (E2), carotenoid content in RSG-974 × CSJ-515 (E2), proline content in RSG-974 × CSJ-515 (E1), protein content in RSG-973 × HC-5 (E1), (Supplementary Table S1-S3). However, seed yield per plant in CS-JD-884 x Avrodhi showed duplicate epistatis in E2 (Table 1) in CSJD-884 × Avrodhi under E2. Duplicate epistasis can hinder the early selection process, as it slows genetic progress and complicates the fixation of desirable genotypes. Additive (d) and additive × additive (i) gene effects were predominant for relative water content in CSJD-884 × Avrodhi (E1), membrane stability index in RSG-963 × RSG-973 (E1), total chlorophyll content in RSG-974 × CSJ-515 (E1 and E2), proline content in RSG-963 × RSG-973 (E2), protein content in RSG-963 × RSG-973 (E1), and seed yield per plant in RSG-974 × Avrodhi (E2). Choudhary et al. (2023) also reported comparable observations on the prevalence of additive and additive × additive gene effects on physio-biochemical traits in chickpeas.

Both additive and non-additive gene effects (h, j, l) were observed for protein content in RSG-973 × HC-5 (E2). Selection for such traits should be delayed until advanced generations to allow dominance effects to diminish, as suggested by earlier studies (Samad et al. 2016, Choudhary et al. 2024). A predominance of non-additive gene effects (h, j, l) combined with additive effects (d, i) was observed in most crosses. Specific examples include pollen viability in RSG-974 × CSJ-515, RSG-963 × RSG-973, and CSJD-884 × Avrodhi (E2); relative water content in RSG-973 × HC-5 and RSG-974 × CSJ-515 (E1 and E2); membrane stability index in RSG-973 × HC-5 (E2) and CSJD-884 × Avrodhi (E1 and E2); total chlorophyll content in RSG-973 × HC-5 (E1 and E2); carotenoid content in RSG-963 × RSG-973 and RSG-974 × CSJ-515 (E2); proline content in RSG-974 × CSJ-515, RSG-973 × HC-5, and CSJD-884 × Avrodhi (E2); protein content in RSG-973 × HC-5 (E1) and CSJD-884 × Avrodhi (E2); and seed yield per plant in several crosses under both E1 and E2 (Supplementary Tables 1-3). The dominance (h), additive × dominance (j), and dominance × dominance (l) effects, alongside additive components, limit the potential for improvement through early-generation selection. To achieve higher yields, maintaining heterozygosity through intercrossing selected genotypes in early segregating generations or recurrent selection methods is advised (Parlevliet and Van Ommeren 1988). This approach increases the probability of favorable recombinants, which can ultimately lead to the fixation of desirable genes in homozygous lines with improved seed yield. Recurrent selection followed by pedigree breeding has been proposed as an effective strategy for chickpea improvement. Promising heat-tolerant transgressive

Table 1. Estimates of joint scaling test and gene effects for carotenoid content and proline content under E1 and E2 conditions

	RSG-973 × HC-5		RSG-963 × RSG-973		CSJD-884 × Avrodhi		RSG-974 × CSJ-515	
	E1	E2	E1	E2	E1	E2	E1	E2
Carotenoid content								
χ2	8.06	17.28**	9.07*	27.82**	28.89**	9.09**	5.76	20.78**
Gene components (Three or six parameter) model and epistasis type								
m	5.98** ± 0.15	4.62** ± 0.12	6.24** ± 0.14	5.38** ± 0.12	5.43** ± 0.13	4.74** ± 0.12	5.14** ± 0.13	5.03** ± 0.08
d	0.55 ± 0.27	0.16 ± 0.15	0.56 ± 0.30	1.24** ± 0.23	-0.80** ± 0.29	-0.30 ± 0.27	0.53 ± 0.30	0.26 ± 0.21
h	1.74* ± 0.86	-0.97 ± 0.62	0.53 ± 0.89	-0.34 ± 0.71	-0.15 ± 0.81	1.17 ± 0.75	-0.32 ± 0.88	-1.77** ± 0.58
i	0.68 ± 0.81	-0.77 ± 0.58	0.04 ± 0.83	-0.66 ± 0.66	0.30 ± 0.77	1.35 ± 0.71	-0.38 ± 0.81	-2.20** ± 0.54
j	0.09 ± 0.33	-0.18 ± 0.20	0.46 ± 0.35	0.99** ± 0.27	-0.71* ± 0.34	-0.29 ± 0.32	0.66 ± 0.35	0.22 ± 0.25
l	0.81 ± 1.38	2.76** ± 0.89	1.83 ± 1.47	3.63** ± 1.16	2.43 ± 1.36	-0.78 ± 1.26	2.05 ± 1.5	4.89** ± 1.02
	--	--	--	--	--	--	--	Duplicate
Proline content								
χ2	15.39**	39.95**	11.91**	6.56	2.99	34.69**	48.23**	12.96**
Gene components (Three or six parameter) model and epistasis type								
m	5.94** ± 0.15	6.40** ± 0.15	5.54** ± 0.13	6.06** ± 0.71	6.11** ± 0.81	6.94** ± 0.14	4.99** ± 0.09	5.96** ± 0.15
d	0.26 ± 0.21	0.14 ± 0.23	0.06 ± 0.23	-0.50** ± 0.14	-0.18 ± 0.13	0.44 ± 0.27	0.79** ± 0.16	-0.13 ± 0.27
h	-1.01 ± 0.76	3.80** ± 0.78	-0.74 ± 0.75	0.27 ± 1.90	1.14 ± 1.98	3.39** ± 0.83	3.03** ± 0.57	2.06* ± 0.87
i	-1.28 ± 0.73	2.95** ± 0.76	-1.19 ± 0.68	-	-	2.76** ± 0.78	3.01** ± 0.49	1.58 ± 0.81
j	0.31 ± 0.24	0.25 ± 0.26	0.04 ± 0.28	-	-	0.75* ± 0.31	0.47* ± 0.22	-0.22 ± 0.33
l	3.54** ± 1.13	-1.12 ± 1.17	3.68** ± 1.21	-	-	-1.46 ± 1.33	-2.33* ± 0.94	-0.16 ± 1.37
	--	--	--	--	--	--	Duplicate	--

*, ** - Significant at 5% and 1% levels of probability, respectively.

segregants, once evaluated in subsequent generations, may either be released as improved heat-tolerant varieties or utilized as parental lines in future breeding programs.

Supplementary material

Supplementary Tables S1 to S3 are provided, which can be accessed at www.isgpb.org

Author's contribution

Conceptualization of research (SKJ, MPO); Designing of the experiments (SKJ, MPO); Contribution of experimental material (SKJ); Execution of field and lab experiments and data collection (SKJ, MPO, RC, SSP); Analysis of data and interpretation (SKJ, MPO, RC, SSP, CB); Preparation of manuscript (MPO, SKJ, SSP, CB).

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Supplementary Table S1. Estimates of joint scaling test and gene effects for protein content and seed yield per plant under E1 and E2 conditions

	RSG-973 × HC-5		RSG-963 × RSG-973		CSJD-884 × Avrodhi		RSG-974 × CSJ-515	
	E1	E2	E1	E2	E1	E2	E1	E2
Protein content								
χ2	10.69*	27.47**	6.61	0.91	25.65**	90.69**	3.74	4.45
Gene components (Three or six parameter) model and epistasis type								
m	24.71** ± 0.18	22.15** ± 0.17	22.89** ± 2.6	20.72** ± 1.44	24.16** ± 0.13	21.49** ± 0.14	26.37** ± 2.80	23.98** ± 1.41
d	-0.69 ± 0.38	-1.32** ± 0.43	-0.60* ± 0.22	-0.39 ± 0.23	0.13 ± 0.32	0.35 ± 0.30	-0.43 ± 0.24	-0.48 ± 0.28
h	3.01* ± 1.16	4.63** ± 1.19	3.22 ± 6.44	2.83 ± 3.97	-1.21 ± 1.06	1.67 ± 0.97	-2.73 ± 6.08	-3.73 ± 3.61
i	3.09** ± 1.07	4.19** ± 1.11	-	-	-0.91 ± 0.85	1.98* ± 0.84	-	-
j	0.21 ± 0.48	-0.54 ± 0.52	-	-	-0.96* ± 0.42	-0.93* ± 0.4	-	-
l	-4.72* ± 1.94	-2.92 ± 2.05	-	-	7.21** ± 1.89	5.99** ± 1.66	-	-
	Duplicate	--	--	--	--	--	--	--
Seed yield per plant								
χ2	8.04*	21.90**	19.65**	36.85**	73.33**	24.54**	89.49**	102.32**
Gene components (Three or six parameter) model and epistasis type								
m	7.94** ± 0.16	7.4** ± 0.14	7.17** ± 0.16	6.41** ± 0.15	7.15** ± 0.16	6.78** ± 0.13	7.52** ± 0.13	6.91** ± 0.12
d	0.14 ± 0.28	0.87** ± 0.26	0.42 ± 0.39	0.89** ± 0.32	-0.35 ± 0.34	0.35 ± 0.39	-0.57 ± 0.38	0.14 ± 0.34
h	2.68** ± 0.91	-0.97 ± 0.80	0.82 ± 1.10	-0.20 ± 0.97	-1.93 ± 1.02	-3.37** ± 0.99	5.05** ± 0.98	4.70** ± 0.87
i	2.05* ± 0.87	-1.45 ± 0.77	0.69 ± 1.03	-0.67 ± 0.90	-2.63** ± 0.95	-3.93** ± 0.94	4.04** ± 0.94	3.21** ± 0.84
j	0.21 ± 0.35	1.22** ± 0.31	0.58 ± 0.47	0.59 ± 0.38	-0.83* ± 0.39	0.06 ± 0.43	-0.83 ± 0.43	-0.72 ± 0.37
l	-2.07 ± 1.43	3.27* ± 1.27	2.43 ± 1.87	5.81** ± 1.61	10.28** ± 1.68	8.42** ± 1.75	-1.05 ± 1.72	-0.25 ± 1.53
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*, ** - Significant at 5% and 1% levels of probability, respectively.

Supplementary Table S2. Estimates of joint scaling test and gene effects for pollen viability and relative water content under E1 and E2 conditions

	RSG-973 × HC-5		RSG-963 × RSG-973		CSJD-884 × Avrodhi		RSG-974 × CSJ-515	
	E1	E2	E1	E2	E1	E2	E1	E2
Pollen viability								
χ2	13.92**	5.03	10.12*	17.00**	28.41**	33.43**	27.72**	61.74**
Gene components (Three or six parameter) model and epistasis type								
m	91.66** ± 0.60	77.60** ± 6.12	87.71** ± 0.69	82.35** ± 0.93	88.66** ± 0.72	85.36** ± 0.67	84.83** ± 0.93	80.40** ± 0.74
d	-3.16 ± 1.71	0.40 ± 1.25	-1.46 ± 1.40	-5.70** ± 1.62	1.63 ± 1.28	4.23** ± 1.39	-4.70* ± 2.03	-2.89 ± 1.79
h	-6.13 ± 4.41	15.4 ± 15.73	8.10 ± 4.32	14.86** ± 5.27	7.53 ± 3.98	4.49 ± 4.09	-1.36 ± 5.69	-5.16 ± 4.83
i	-7.40 ± 4.21	-	7.4 ± 3.95	11.60* ± 4.94	6.86 ± 3.86	0.59 ± 3.88	-1.53 ± 5.53	-7.39 ± 4.65
j	-2.70 ±1.87	-	0.7 ± 1.82	-4.36* ± 1.85	2.50 ± 1.46	6.46** ± 1.71	-2.46 ± 2.16	-2.13 ± 1.98
l	21.86** ± 7.76	-	-2.00 ± 7.19	-7.93 ± 8.33	2.79 ± 6.19	9.53 ± 6.71	21.26* ± 9.36	36.46** ± 8.17
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Relative water content								
χ2	9.83*	18.24**	4.28	10.34**	2.29	2.19	21.52**	22.39**
Gene components (Three or six parameter) model and epistasis type								
m	76.21** ± 0.98	68.90** ±0.93	69.98** ±4.68	68.99** ± 0.75	86.13** ±7.37	59.82** ± 6.10	74.43** ± 0.32	71.48** ± 0.45
d	-2.83 ± 2.38	-4.64* ± 2.04	1.13 ± 1.21	0.89 ± 1.49	-4.91** ±1.60	-2.96 ± 1.63	4.30** ± 1.37	1.81 ± 1.73
h	-1.87 ± 6.44	7.03 ± 5.67	15.72 ± 12.10	-0.71 ± 4.65	-28.70±19.79	13.16 ± 16.39	-5.88 ± 3.93	-8.50* ± 4.07
i	-3.99 ± 6.18	4.49 ± 5.54	-	1.54 ± 4.24	-	-	-9.80** ± 3.05	-13.97** ± 3.9
j	-1.88 ± 2.71	-5.55* ± 2.26	-	-0.03 ± 1.99	-	-	8.36** ± 2.18	4.00 ± 2.02
l	19.9 ± 10.94	5.84 ± 9.30	-	11.10 ± 7.69	-	-	22.95** ± 7.53	31.68** ± 7.52
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*, ** - Significant at 5% and 1% levels of probability, respectively.

Supplementary Table S3. Estimates of joint scaling test and gene effects of four crosses for membrane stability index and total chlorophyll content under E1 and E2 conditions

	RSG-973 × HC-5		RSG-963 × RSG-97		CSJD-884 × Avrodhi		RSG-974 × CSJ-515	
	E1	E2	E1	E2	E1	E2	E1	E2
Membrane stability index								
$\chi 2$	26.93**	27.72**	8.68*	24.78**	21.93**	84.32**	11.89**	103.11**
Gene components (Three or six parameter) model and epistasis type								
m	82.34** ± 0.47	78.34** ± 0.52	81.73** ± 1.00	73.44** ± 1.04	86.26** ± 0.71	81.83** ± 0.83	78.44** ± 0.78	70.46** ± 0.45
d	0.10 ± 1.030	-0.12 ± 1.00	-4.19* ± 1.97	-2.09 ± 1.83	-0.47 ± 1.70	8.76** ± 1.58	0.72 ± 1.34	0.30 ± 1.01
h	7.26* ± 3.08	-8.10* ± 3.19	0.24 ± 5.97	9.24 ± 5.81	-20.26** ± 5.08	-35.85** ± 4.88	6.02 ± 4.49	-0.07 ± 2.92
i	5.05 ± 2.80	-10.41** ±2.91	-1.50 ± 5.62	6.89 ± 5.56	-18.88** ±4.45	-35.52** ±4.58	4.04 ± 4.12	-2.31 ± 2.72
j	-0.46 ± 1.31	0.34 ± 1.19	-2.19 ± 2.32	-1.52 ± 2.16	-2.13 ± 2.12	6.04** ± 1.75	2.97 ± 1.69	1.42 ± 1.23
l	5.66 ± 5.21	25.51** ±5.25	13.52 ± 9.73	8.97 ± 9.09	32.03** ±8.87	45.51** ±7.89	4.75 ± 7.17	28.04** ± 4.93
	--	Duplicate	--	--	Duplicate	Duplicate	--	--
Total chlorophyll content								
$\chi 2$	25.84**	25.74**	23.09**	11.10*	2.89	1.41	7.14	2.67
Gene components (Three or six parameter) model and epistasis type								
m	30.74** ± 0.21	29.49** ± 0.36	27.83** ± 0.71	26.22** ± 0.67	37.64** ± 4.32	32.07** ± 2.88	23.79** ± 4.09	26.31** ± 3.4
d	0.35 ± 0.33	-1.01 ± 0.50	-0.78 ± 1.22	-1.34 ± 1.48	-1.08 ± 0.58	-0.43 ± 0.51	2.70** ± 0.74	3.05** ± 0.65
h	2.89* ± 1.20	-3.80* ± 1.86	1.95 ± 3.96	1.65 ± 4.08	-0.68 ± 10.61	5.11 ± 7.26	16.94 ± 9.49	2.44 ± 9.40
i	2.29* ± 1.08	-5.01** ± 1.79	0.72 ± 3.77	3.00 ± 4.02	-	-	-	-
j	0.37 ± 0.49	0.24 ± 0.66	-0.24 ± 1.57	-1.40 ± 1.54	-	-	-	-
l	2.00 ± 1.91	12.15** ± 2.7	13.37* ± 6.17	3.18 ± 6.69	-	-	-	-
	--	Duplicate	--	--	--	--	--	--

*, ** - Significant at 5% and 1% levels of probability, respectively.