Indian Journal of Agricultural Sciences **92** (1): 105–9, January 2022/Article
https://doi.org/10.56093/ijas.v92i1.120852

First-second degree statistics-based genetics of powdery mildew and yield attributing traits in blackgram (*Vigna mungo*)

BORAIAH K M[1*], M BYREGOWDA[2], C M KEERTHI[2], S RAMESH[3], CHANDU SINGH[4], RAJIV K SINGH[4] and BASAVARAJ P S[1]

ICAR-National Institute of Abiotic Stress Management, Malegaon (Kh), Baramati, Maharashtra 413 115, India

Received: 07 February 2021; Accepted: 12 July 2021

ABSTRACT

Genetics of yield related traits and powdery mildew disease (PMD) resistance unraveled using the combination of first and second degree of statistics in blackgram [*Vigna mungo* (L.) Hepper]. Eight crosses, their parents, F_2 and F_3 generations were evaluated for six yield attributing traits and PMD during *kharif* 2016 and *rabi* 2016–17 respectively. The first degree statistics suggested the predominance of genes with dominance effects, whereas second degree statistics revealed the additive gene effects in controlling most investigated traits. However, combination of first and second degree statistics revealed significant but lower magnitude of additive genetic effects [d] coupled with large additive genetic variance (σ^2_A) for plant height and seed yield/plant in all six crosses, indicating the dispersion of increasing and decreasing effecting genes between parents. The estimates of σ^2_A were considerably high for percent disease index (PDI) in all three crosses. Conversely, higher estimates of [d] and smaller estimates of σ^2_A indicated small effect additive genes controlling days to 50% flowering, days to maturity and 100 seed weight in all the six crosses. Hence, unraveling the genetics based on both first and second degree statistics provide the comprehensive information on gene action involved in governing PMD resistance and yield attributing traits in blackgram, which helps in deciding efficient selection strategies to be followed for enhancing genetic gain.

Keywords: Additive gene effects, Dominance effects, Epistasis, Inheritance, Powdery mildew disease resistance

Blackgram [*Vigna mungo* (L.) Hepper] is one of the most important grain legumes with easily digestible protein and low flatulence content. Genetic information on the inheritance of yield and its attributing traits is inevitable for any fruitful breeding programme. A considerable research work has been done in the past to know the genetic nature of pulse crops including blackgram. However, the genetic architecture of yield enhancing traits in blackgram is yet to be explored for breaking yield plateau. The genetics of yield traits could be unraveled at first and second degree statistics levels. Unraveling genetics of yield and its component traits at first degree statistics level (Generations mean analysis) by developing and testing the digenic epistasis independent (additive-dominance model) and epistasis inclusive models are most commonly used. Translating covariance of full-sib and half-sibs produced by diallel and line × tester mating designs into components of genotype variance and biometrical genetic analysis of progenies derived from standard triple test cross (TTC) (Kearsey and Jinks 1968) and simplified TTC designs (Jinks *et al.* 1969) are the most commonly used approaches to unravel the genetics of yield traits at second degree statistics. Several studies in the past unraveled the genetics of yield traits based on either first or second degree statistics, and seldom both. Thus, use of both first and second degree statistics provides the most comprehensive mode of action of genes controlling yield and attributing traits in crop plants.

The genetic studies on disease response assist in developing stable resistant cultivars in blackgram. The past studies on genetics of powdery mildew disease (PMD) resistance in blackgram suggested that PMD resistance was controlled by both additive as well as dominant gene actions (Chaitieng *et al*. 2002, Gawande and Patil 2003). Similar to yield traits, these studies are also based on either first or second degree statistics but not the combination of both the statistical approaches. In this context, the present investigation was carried out with an objective to unravel the genetics of yield related traits and PMD resistance using the combination of first and second degree statistics in blackgram.

Present address: [1]ICAR-National Institute of Abiotic Stress Management, Malegaon (Kh), Baramati, Maharashtra; [2]AICRP on Pigeonpea, ZARS, UAS, GKVK, Bengaluru; [3]College of Agriculture, UAS, GKVK, Bengaluru; [4]ICAR–Indian Agricultural Research Institute, Pusa, New Delhi. *Corresponding author e-mail: bors_km@yahoo.co.in.

MATERIALS AND METHODS

Development of experimental materials: Among 40 F_1s developed by following L × T mating design (Kempthorne 1957) during *rabi* 2014, six crosses (C1: VBN 4 × LBG 17; C2: COBG 653 × LBG 17; C3: VBG 10-024 × DBGV 5; C4: DU 1 × TAU 1; C5: LBG 752 × DBGV 5 and C6: T 9 × LBG 685) were selected based on overall general combining ability (GCA) and specific combining ability (SCA) for yield traits. Further, three crosses (C5: LBG 752 × DBGV 5; C7: VBN 6 × LBG 17 and C8: LBG 625 × LBG 17) were based on contrasting responses to PM disease (Boraiah *et al*., 2019). All eight crosses (with C5 common for both yield traits and PMD) were advanced to F_2 & F_3 generation during *rabi* 2015 and *kharif* 2016. The five basic generations (P_1, P_2, F_1, F_2 and F_3) of all the selected crosses were evaluated separately for yield traits and responses to PMD at ZARS, GKVK, UAS, Bengaluru.

Evaluation of experimental materials: The six F_1s (C1, C2, C3, C4, C5 and C6), their parents, F_2 and F_3 progenies were sown in a single row of 2 m length with a spacing of 30 cm ×10 cm in randomized block design with two replications during the *kharif* 2016. A total of 20 parental plants, 20 plants in each F_1, 200 F_2 plants and 60 F_3 progeny of each of the six crosses were maintained. The recommended agronomic packages of practice were followed to raise a healthy crop. Data was recorded on five randomly selected plants in each replication of the P_1, P_2 and F_1, all F_2 plants and 10 randomly selected plants from each F_3 progenies on six yield traits, viz. days to 50% flowering, plant height (cm), days to maturity, pods/plant, seed yield/plant (g) and100 seed weight (g).

The seeds of the five parents, three F_1s (C5, C7 and C8) and their F_2 and F_3 generations were sown during *rabi* 2016 to assess reaction of PMD under natural condition (Table 1). The data on PMD severity was recorded at 55 DAS and time of harvesting using ten randomly selected plants in each replication (Gawande and Patil 2003). The *per cent* disease severity was converted into *Per cent* Disease Index (PDI) (Wheeler 1969):

$$PDF = \frac{\text{Sum of the individual disease ratings}}{\text{Number of Plants observed} \times \text{Maximum disease grade}} \times 100$$

Statistical analysis

Estimation of first degree statistics-based gene effects: First degree statistics-based gene effects were estimated following the perfect-fit solutions based on five parameter models (Hayman 1958). Statistical significance of gene effects were examined using t-test (Mather and Jinks 1982).

Estimation of second degree statistics-based genetics (components of genotypic variation)

Additive genetic variance (σ^2_A): The σ^2_A is estimated using observed and expected mean sum of squares (MSS) from analysis of variance (ANOVA) of F_3 families as suggested by Van Ooijen 1989. The nature of genetic control of six quantitative traits and PMD resistance at first and second degree statistics levels were compared and interpreted.

RESULTS AND DISCUSSION

First degree statistics-based genetics: Additive-Dominance (A-D) model was inadequate to explain the expression of all the traits in all the crosses except for days to maturity in T9 × LBG 685 as indicated by the significance of joint-scaling test (Supplementary Table 1). Non-adequacy of A-D model could be attributed to non-inclusion of parameters specifying di-genic epistasis or genotype × environment interaction. Therefore, in the present study only parameters of di-genic epistasis were included in the model and were estimated and interpreted. The significant, but lower magnitude or non-significant additive gene effects in the inheritance of most traits in all the crosses in present study could be ascribed to the involvement of either genes with smaller additive effects or different degrees of nullifying effects with increasing and decreasing effects in opposite direction (Table 1). Though first degree statistics is valuable for estimation of additive, dominance and epistatic gene effects, it has some limitations. Distribution of increasing and decreasing effects genes between the parents causes serious bias to the estimates of additive and additive × additive gene effects. However, dominance [h] and dominance × dominance [l] gene effects are independent of the degree of gene distribution due to which the combined estimates of [h] and [l] could be considered as the best representative of sign and magnitude of individual h's and l's respectively. Hence, practically [h] and [l] are the only components which can safely be used to determine the type of epistasis that may have influenced the observed performance of generations (Mather and Jinks 1982).

The seed yield/plant in the cross C2 and 100 seed weight in C1 were controlled by dominant increasing effect genes displaying complementary digenic epistasis as indicated by positive estimates of [h] and [l], respectively. Significant [h] and positive [l] suggested possible involvement of dominant decreasing effect genes displaying duplicate digenic epistasis as indicated by negative and positive estimates of [h] and [l], respectively for days to 50% flowering (C1, C2, C5 and C6), days to maturity (C1 and C5), pods/plant (C2 and C5), seed yield/plant (C3, C5 and C4) and100 seed weight and PDI in all the three crosses, viz. C5, C7 and C8. On the other hand, in all the crosses rest of the traits were controlled by dominant increasing effect genes exhibiting duplicate digenic epistasis as indicated by positive and negative estimates of [h] and [l], respectively. Thus, first degree statistics-based components of generation means suggest predominance of genes with dominance and dominance-based effects in the inheritance of most of the traits investigated. These results are in agreement with those reported by Desai *et al.* (2013) in Indian bean. The estimates of [d], [h], [i] and [l] which are based on first degree statistics pose serious limitations on the interpretation due to internal cancellation

Table 1 Estimates of digenic effects of traits for which Additive – Dominance model was inadequate in blackgram

Trait	Cross	[m̂]	[$\hat{h}$]	[$\hat{h}$]	[i]	[$\hat{l}$]	Type of digenic epistasis
Days to 50% flowering	C1	44.02**±0.29	-6.80**±0.16	-12.32**±0.22	2.28**±0.33	11.20**±0.08	DDD
	C2	38.29**±0.27	-8.65**±0.13	-3.58**±1.13	6.16**±0.30	4.09**±1.00	DDD
	C3	36.98**±0.27	-0.70**±0.14	12.00**±1.16	-0.18±0.31	-13.07**±1.00	DDI
	C4	38.06**±0.23	-1.55**±0.15	4.02**±0.98	-0.81**±0.28	-6.67**±0.83	DDI
	C5	41.73**±0.25	2.10**±0.16	-7.40**±1.12	-2.13**±0.29	6.76**±0.02	DDD
	C6	44.13**±0.29	-2.85**±0.17	-10.46**±1.27	-3.28**±0.34	6.63**±1.17	DDD
Plant height (cm)	C1	35.37**±2.18	-19.74**±1.39	83.07**±8.75	39.27**±2.58	-54.96**±7.11	DDI
	C2	24.19**±1.99	-21.67**±1.43	47.72**±0.23	48.53**±2.45	-19.55*±6.97	DDI
	C3	24.07**±2.41	-2.06±1.68	100.59**±9.49	25.54**±2.94	-74.24**±8.93	DDI
	C4	19.24**±2.09	-3.47**±1.03	115.12**±7.85	38.66**±2.33	-88.24**±6.28	DDI
	C5	33.28**±1.95	12.06**±1.44	67.52**±8.05	30.45*±2.42	-39.95**±7.92	DDI
	C6	27.55**±1.70	-20.52**±1.31	94.62**±8.59	45.52**±2.22	-63.65**±8.94	DDI
Days to maturity	C1	83.37**±0.31	-7.15**±0.17	-11.42**±1.51	0.78*±0.35	13.24**±1.31	DDD
	C2	78.37**±0.27	-7.83**±0.15	-1.38±1.91	5.11**±0.31	-0.09±1.0	CDD
	C3	78.67**±0.26	-1.10**±0.18	0.11±1.23	-1.87**±0.32	-2.37*±1.01	DDI
	C4	78.83**±0.23	-1.00**±0.17	-1.92±1.00	-1.13**±0.49	-0.41±1.01	CDD
	C5	81.58**±0.23	1.85**±0.21	-7.73**±1.09	-1.83**±0.39	8.05**±1.05	DDD
Pods/plant	C1	14.76**±2.18	-2.87**±1.03	67.60**±11.01	27.91**±2.41	-27.16**±10.52	DDI
	C2	35.59**±2.72	-5.27**±1.04	-12.17±10.56	4.68±2.92	18.08*±8.82	DDD
	C3	41.19**±2.86	-3.45*±1.46	-33.95**±10.70	-7.94*±3.21	43.36**±9.39	DDD
	C4	26.36**±3.18	-3.35*±1.36	26.82*±11.87	9.69**±3.46	-14.58±9.98	DDI
	C5	34.92**±2.42	1.90**±1.55	-25.29**±9.99	3.68±2.87	36.86**±9.86	DDD
	C6	28.25**±2.59	-6.70**±1.71	43.14**±11.64	12.05±3.10	-29.39**±10.40	DDI
Seed/yield plant (g)	C1	1.71*±0.77	-1.70**±0.49	31.76**±4.21	11.54**±0.92	-12.84**±4.28	DDI
	C2	9.45**±0.84	-2.57**±0.54	1.40±3.66	2.94±1.00	6.31±3.76	CDI
	C3	12.29**±0.85	-1.34*±0.53	-8.40*±3.32	-0.78±1.00	9.89**±3.01	DDD
	C4	11.71**±0.97	-0.82±0.53	-4.69±4.11	-0.56±1.11	10.60**±4.04	DDD
	C5	11.65**±0.85	-0.03±0.68	-8.17*±3.54	1.16±1.08	10.12**±3.37	DDD
	C6	8.77**±0.89	-1.61**±0.49	17.67**±3.96	3.78±1.01	-12.88**±3.30	DDI
100 seed weight (g)	C1	5.23**±0.07	-0.14*±0.07	1.09**±0.23	0.97±0.09	0.10±0.32	CDI
	C2	5.98**±0.07	-0.18**±0.07	-1.46**±0.37	0.19±0.10	1.99**±0.36	DDD
	C3	5.60**±0.07	-0.11±0.08	-0.07±0.34	0.41±0.10	0.59±0.32	DDD
	C4	6.14**±0.08	-0.53**±0.09	-1.91**±0.36	-0.43±0.12	2.33**±0.32	DDD
	C5	5.71**±0.07	-0.07±0.07	-0.49±0.30	0.35±0.09	1.04**±0.29	DDD
	C6	5.63**±0.06	-0.19*±0.08	0.94**±0.29	0.41±0.10	-0.62*±0.30	DDI
PDI	C5	15.48**±3.32	-38.23**±0.81	-37.98**±11.52	36.77±3.42	42.57**±9.10	DDD
	C8	17.89**±4.72	44.08**±0.77	-27.41±16.11	28.51±4.78	23.54±12.03	DDD
	C9	8.83**±2.79	14.03**±1.36	-10.93±10.34	7.53±3.10	10.22±8.40	DDD

*, ** – Significant at 5% & 1% levels, respectively. C1 -VBN 4 × LBG 17; C2 - COBG 653 × LBG 17; C3- VBG 10-024 × DBGV 5; C4 -DU 1 × TAU 1; C5 -LGB 752 × DBGV 5; C6 -T 9 × LBG 685; C7- VBN 6 × LBG 17; C8- LBG 625 × LBG 17. DDD: Duplicate epistasis between dominant decreasing effect genes; DDI: Duplicate epistasis between dominant increasing effect genes; CDD: Complementary epistasis between dominant decreasing effect genes; CDI: Complementary epistasis between dominant increasing effect genes ; PDI: Per cent Disease Index.

of effects of genes in positive and negative direction. Thus, the estimates of genetic components of generation means are most often underestimated. However, the estimates of variances (second degree statistics) arising from additive, dominance and di-genic epistatic effects of genes are not affected by internal cancellation of gene effects in positive and negative direction (Mather and Jinks 1982).

Second degree statistics-based genetics: In the absence of backcross generations, it is not possible to estimate additive genetic variance (σ^2_A) and dominance genetic variation (σ^2_D). However, analysis of variance of F_3 families provides unbiased estimates of σ^2_A. In the present study, analysis of variance of F_3 progenies revealed highly significant mean squares attributable to 'between F_3 progenies' for all the quantitative traits in all the crosses (Supplementary Table 2). The estimates of additive variance (σ^2_A) were higher in cross C4 followed by C5 for the seed yield trait, C6 for days to 50% flowering and in C4 for pods/plantand C3 for plant height (Table 2). The estimates of σ^2_A was comparable across all six crosses for 100 seed weight than other traits. The estimates of σ^2_A was considerably high for PDI in all three crosses. However, σ^2_A was high in C7 compared to other two crosses (Table 2). Das *et al.* (2014), Keerthi *et al.* (2015) and Chandrakant *et al.* (2015) also documented the predominance of additive genetic variance in controlling most of the quantitative traits in *Dolichos* bean. Contrary to first degree statistics, second degree statistics revealed predominance of genes with additive effects. Thus, the inferences on the mode of action of genes controlling quantitative traits solely based either on first or second degree statistics are often ambiguous. The combination of components of means and variances provides complementary and more comprehensive information on the true nature of genetic control of quantitative traits.

Combination of first – and second degree statistic-based genetic parameters: The significant but lower magnitude of additive genetic effects [d] coupled with large σ^2_A for plant height and seed yield/plant in all six crosses indicated dispersion of increasing and decreasing effects of genes between parents (Table 2). Dispersion of increasing and decreasing effects genes reduce the trait means of the genotypes while association increases them. The probability of genes being in the dispersion phase could be minimized by random mating in F_2 genotypes before selecting desired pure-lines (Roy 2000). Hanson (1959) showed that with F_2 inter-mating, the risk of losing desired alleles is less compared to selfing. Higher estimates of both [d] and (σ^2_A) suggests higher frequency of increasing effect genes controlling plant height in all six crosses and PDI in all three crosses (Table 2). On the other hand, higher estimates of [d] and smaller estimates of (σ^2_A) indicate small effect additive genes controlling days to 50% flowering, days to maturity and 100 seed weight in all the six crosses.

Overall, the yield and most of its contributing traits were under the control of additive gene effects with dispersion of increasing and decreasing effects genes between parents indicating possibility of potential promising pure line selection with intermating at early segregating generations preferably at F_2 to be rewarding. Similarly predominance of large additive gene effects [d] coupled with large σ^2_A suggest

Table 2 Estimates of variances, additive gene effects [d] and additive genetic variance (σ^2_A) for yield traits and Per cent powdery mildew Disease Index (PDI)

Trait	Additive gene effects [d] and additive genetic variance (σ^2A) for yield and its attributing traits											
	C1		C2		C3		C4		C5		C6	
	[d]	σ^2_A	[d]	σ^2_A	[d]	σ^2_A	[d]	σ^2_A	[d]	σ^2_A	[d]	σ^2_A
Days to 50% flowering	-6.72**	0.02**	-7.35**	0.65**	-0.32*	0.62**	-2.09**	0.50**	2.28**	0.52**	-2.69**	0.67**
Plant height (cm)	-13.60*	54.98**	-12.53**	36.27**	-5.15*	71.10**	2.06*	52.42**	7.60**	42.34**	-14.66**	30.57**
Days to maturity	-6.84**	0.64**	-6.80**	0.66**	-1.40**	0.46**	-1.12**	0.42**	1.89**	0.37**	-4.45**	0.66**
Pods/plant	-1.56	24.96**	-4.92**	72.32**	3.37*	80.89**	-2.82*	116.88**	1.92	58.54**	-8.23**	56.50**
Seed yield/plant (g)	-0.07	3.02**	-2.33**	6.06**	-1.38*	6.68**	-0.69	8.62**	-0.74	6.72**	-1.47*	6.05**
100 seed weight (g)	0.21*	0.02**	-0.02	0.02**	-0.18*	0.02**	-0.53	0.03**	0.01	0.03**	-0.26*	0.02**

ANOAVA, additive gene effects [d] and additive genetic variance (σ^2A) for PDI

Source of Variation	*df*	*LGB 752 × DBGV 5*	*VBN 6 × LBG 17*	*LBG 625 × LBG 17*
Between F_3 families	59	1538.28**	3122.27**	1044.81**
Within F_3 families	540	58.73	67.19	38.25
Additive variance (σ^2_A)		147.96	305.51	100.66
Additive gene effects [d]		-38.23**	44.08**	14.03**

*, ** – Significant at 5% & 1% levels, respectively. C1 -VBN 4 × LBG 17; C2 - COBG 653 × LBG 17; C3- VBG 10-024 × DBGV 5; C4 -DU 1 × TAU 1; C5 -LGB 752 × DBGV 5; C6 -T 9 × LBG 685; C7- VBN 6 × LBG 17; C8- LBG 625 × LBG 17; PDI: Per cent powdery mildew Disease Index.

higher frequency of increasing effect genes controlling powdery mildew resistance in all three crosses. Therefore, for both yield and PMD the selection may be practiced at an early stage with random intermating among segregating populations. However, the nature (dominance or recessive) and number (monogenic/polygenic) of genes involved in inheritance of PMD may be considered before random intermating of F_2 genotypes for better selection of pure line with PMD resistances coupled with higher yield. Similarly, Showkat *et al*. (2017) dissected the genetic control of yield attributing traits in *dolichos* bean based combination of first and second degree statistics and suggested bi-parental mating in early segregating generations to enrich the frequency of favorable genes.

The inferences based on the magnitudes of only first degree statistics-based additive gene effects are not desirable. Because the distribution of positive and negative gene effects in the parents may result in different degrees of cancellation of effects in the expression of the traits means of generations. For the same reason, the magnitudes of additive gene effects do not necessarily reflect those of σ^2_A. High magnitude of the estimates of σ^2_A indicate long-term genetic gains as they could be exploited through the constellation of desired genes controlling most of the productivity *per se* traits. This is because σ^2_A is fixable by selection and hence it is possible to predict response to selection. Hence, the selection and advancing segregating generations should be based on combination of first and second degree statistics to enhance genetic gain in crop improvement programme.

REFERENCES

Boraiah K M, Byregowda M, Keerthi C M, Vijayakumar H P, Ramesh S and Mary Reena. 2019. Frequency of heterotic hybrids in relation to parental genetic divergence and general combining ability in blackgram (*Vigna mungo* (L.) Hepper). *Legume Research* **42**(5): 595–602.

Chandrakant N, Ramesh S, Vaijayanthi P V, Byregowada M, Mohan Rao A, Keerthi C M and Shivakumar M S. 2015. Impact of bi-parental mating on quantitative traits inter-relationships and frequency of transgressive segregants in dolichos bean (*Lablab purpureus* L.*). Electronic Journal of Plant Breeding* **6**(3): 723–28.

Das I, Seth T, Durwas S V, Dutta S, Chattopadhyay A and Singh B. 2014. Gene action and combining ability for yield and yield component traits in dolichos bean (*Dolichos lablab* var. typicus). *Sabrao Journal of Breeding and Genetics* **46**(2): 293–304.

Desai D T, Patil A B, Patil S A and Ghodke U R. 2013. Diallel analysis for pod yield and its components traits in Vegetable Indian bean (*Lablab purpureus* L.). *African Journal of Agriculture Research* **8**(14): 1229–32.

Gawande V L and Patil J V. 2003. Genetics of powdery mildew (*Erysiphe polygoni* DC.) resistance in mungbean (*Vigna radiat*a (L.) Wilezck). *Crop Protection* **22**: 567–71.

Hanson W D. 1959. The breakup of initial linkage block under selected mating systems. *Genetics* **44**: 857–68.

Hayman B I. 1958. The separation of epistatic from additive and dominance variation in generation means. *Heredity* **12:** 371–90.

Jinks J L, Perkins J M and Breese E L. 1969. A general method of detecting additive, dominance and epistatic variation for metrical traits. II. Application to inbred lines. *Heredity* **24**: 45–57.

Kearsey M J and Jinks J L. 1968. A general method of detecting additive, dominance and epistatic variation for metrical traits I. *Heredity* **23**: 403–09.

Keerthi C M, Ramesh S, Byregowada M, Chandrakant, Vaijayanthi P V, Shivakumar M S and Mohan Rao A. 2015. Epistasis-driven bias in the estimates of additive and dominance genetic variance in dolichos bean (*Lablab purpureus* L.). *Journal of Crop Improvement* **29**: 542–62.

Kempthorne O. 1957. *An Introduction of Genetic Statistics*. pp 468-473. New York, USA: John Willey & Sons Inc.

Mather K and Jinks J L. 1982. *Biometrical Genetics, the Study of Continuous Variation*, 3rd edn. pp. 396-403. London, New York: Chapman and Hall.

Roy D. 2000. *Plant Breeding-Analysis and Exploitation of Genetic Variation*. Narosa Publishing House, New Delhi, India.

Showkath B B M, Jagadeesh B N, Ramesh S, Keerthi C M, Shivakumar M S, Chandrakant N. 2017. First and second degree statistics-based genetics of quantitative traits in dolichos bean (*Lablab purpureus* L.). *Environment and Ecology* **35**(1): 82–86

Van Ooijen J W. 1989. Estimation of additive genotypic variance with the F3 of autogamous crops. *Heredity* **63**: 73–81.

Wheeler B E J. 1969. *An Introduction to Plant Disease*. John Wiley and Sons Ltd., pp.301. London.